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**Modellbasierte Analysen zur kosteneffizienten räumlich-
zeitlichen Allokation von Artenschutzmaßnahmen**

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Modellbasierte Analysen zur kosteneffizienten räumlich-zeitlichen Allokation von Artenschutzmaßnahmen

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Zusammenfassung

Der anhaltende Verlust der Biodiversität stellt aktuell eines der größten umweltpolitischen Probleme dar. Die ökonomischen Konsequenzen, die drohen, wenn dieser Verlust nicht gestoppt wird, sind dramatisch, wie die jüngste Studie der Vereinten Nationen „The Economics of Ecosystems and Biodiversity“ aufzeigt. Die Ausweisung großräumiger Schutzgebiete stellt eine wichtige Strategie für den Erhalt der Biodiversität dar, sie ist jedoch nicht ausreichend, da viele Arten in land- und forstwirtschaftlich genutzten Landschaften beheimatet sind, wo sie unter anderem durch die zunehmende Intensivierung der Land- und Forstwirtschaft bedroht sind. Da diese Landschaften häufig in privatem Besitz sind, gewinnen marktwirtschaftliche Naturschutzinstrumente zunehmend an Bedeutung. Zu nennen sind hier vor allem Kompensationszahlungen für biodiversitätserhaltende Landnutzungsmaßnahmen und handelbare Landnutzungsrechte.

Der Erhalt der Biodiversität ist nicht nur mit einem hohen gesellschaftlichen Nutzen verbunden sondern verursacht auch erhebliche Kosten. Die kosteneffiziente Ausgestaltung der Naturschutzinstrumente ist damit von höchster politischer Wichtigkeit. Da ökonomische Kosten und ökologische Wirksamkeit stark von der Art einer Artenschutzmaßnahme sowie dem Ort und dem Zeitpunkt der Maßnahmendurchführung abhängen, müsste idealerweise genau entschieden werden, wann und wo welche Maßnahme durchzuführen ist, so dass bei gegebenen Kosten ein Höchstmaß an Biodiversität erhalten werden kann. Eine solche räumlich und zeitlich zielgenaue Steuerung der Landnutzung ist mit marktwirtschaftlichen Instrumenten jedoch nicht oder nur begrenzt möglich.

Favorisiert wird in der vorliegenden Arbeit daher ein „second best“-Ansatz: die Verwendung marktwirtschaftlicher Instrumente zu Steuerung makroskopischer Landschaftseigenschaften, sogenannter Landschaftsindizes. Zu diesen Landschaftsindizes gehören zunächst die Gesamtfläche an Habitat („Habitatmenge“) für die zu schützenden Art(en), aber auch die räumliche Aggregation („Habitatkonnektivität“) der einzelnen Habitatflächen und deren zeitliche Dauerhaftigkeit („Habitatkontinuität“). In der Arbeit wird argumentiert, dass diese Landschaftsindizes durch eine entsprechende Ausgestaltung marktwirtschaftlicher Naturschutzinstrumente sehr gut steuerbar sind.

Zwischen den genannten Landschaftsindizes bestehen jedoch ökologische und ökonomische Trade-offs in dem Sinne, dass einerseits eine Verschlechterung in einem Landschaftsindex durch eine Verbesserung in einem anderen Landschaftsindex ausgeglichen werden muss, damit ein gegebenes Naturschutzniveau aufrechterhalten werden kann (ökologischer Trade-off), und andererseits bei gegebenem Naturschutzbudget eine Verbesserung in einem Landschaftsindex durch eine Verschlechterung in einem anderen Landschaftsindex erkaufte werden muss (ökonomischer Trade-off). Die Form dieser ökologischen und ökonomischen Trade-offs bestimmt maßgeblich die kosteneffizienten Niveaus der Landschaftsindizes und damit auch die kosteneffiziente Ausgestaltung marktwirtschaftlicher Naturschutzinstrumente.

Während zu den ökologischen Trade-offs einige Forschungsergebnisse vorliegen, sind die ökonomischen Trade-offs unerforscht, und ebenso das Zusammenspiel der ökologischen und ökonomischen Trade-offs, welches die kosteneffizienten Niveaus der Landschaftsindizes bestimmt. Um diese Wissenslücke zu schließen, muss ökologisches und ökonomisches Wissen integriert werden, was in dieser Arbeit über die Methode der ökologisch-ökonomischen Modellierung geschieht.

Betrachtet wird eine Landschaft mit Flächenstücken, die jeweils landwirtschaftlich oder für den Artenschutz genutzt werden können. Die Nutzung für den Natur- und Artenschutz ist mit Kosten (Ertragsausfällen) verbunden, die sich zwischen den Flächenstücken unterscheiden und über die Zeit ändern können. Bei der Modellierung der Landnutzung in Reaktion auf die

durch die marktwirtschaftlichen Instrumente gesetzten ökonomischen Anreize wird angenommen, dass die Landnutzer ihren Gewinn maximieren. Die resultierende Landnutzungsdynamik bestimmt die räumlich-zeitliche Dynamik der Habitate in der Landschaft und schließlich die Überlebensfähigkeit der in der Landschaft lebenden Arten. Letztere wird mit Hilfe ökologischer Modelle ermittelt.

Die vorliegende Arbeit ist eine kumulative Dissertationsschrift und basiert auf sieben Zeitschriftenartikeln, deren Ergebnisse über die ökonomische Produktionstheorie miteinander verknüpft werden. Die Produktionstheorie, zum ökonomischen Standardrepertoire gehörend, beschäftigt sich mit der effizienten Produktion von Gütern aus einer Menge von Produktionsfaktoren. Im Kontext der vorliegenden Arbeit bilden die einzelnen Habitate in der Landschaft Produktionsfaktoren, aus denen „Zwischenprodukte“, die Landschaftsindizes „produziert“ werden, welche schließlich in die Erzeugung des „Endprodukts“, der Überlebensfähigkeit der zu schützenden Art, münden. Die oben erwähnten ökonomischen und ökologischen Trade-offs lassen sich dabei als Grenzzraten der Transformation bzw. Substitution der Zwischenprodukte identifizieren.

Aus der Analyse der Grenzzrate der Substitution folgt unter anderem, dass bei hoher Ausbreitungsfähigkeit der zu schützenden Art die kosteneffizienten Niveaus von Habitatkonnektivität und -kontinuität relativ niedrig, während das kosteneffiziente Niveau der Habitatmenge relativ hoch ist.

Die Analyse der ökonomischen Trade-offs bzw. Grenzzraten der Transformation ergibt unter anderem, dass eine hohe räumliche und zeitliche Variabilität der Naturschutzkosten die kosteneffizienten Niveaus von Habitatkonnektivität und Habitatkontinuität senkt und das kosteneffiziente Niveau der Habitatmenge erhöht. Werden Naturschutzmaßnahmen über räumlich homogene Kompensationszahlungen – das in Europa am weitesten verbreitete marktwirtschaftliche Naturschutzinstrument – induziert, führt eine hohe räumliche Variabilität der Kosten zudem zu hohen Produzentenrenten. Eine geeignet ausgestaltete Agglomerationszahlung, eigentlich zur Steuerung der räumlichen Habitatkonnektivität propagiert, eignet sich jedoch zur Abschöpfung dieser Produzentenrenten. Der Grund hierfür ist, dass die Erzeugung räumlicher Habitatkonnektivität die Kooperation benachbarter Landnutzer erfordert, so dass Landnutzer mit geringen Kosten einen Anreiz haben, über ihre entsprechend hohen Produzentenrenten Artenschutzmaßnahmen auf teureren Flächen zu (ko-) finanzieren.

Die ökonomischen Trade-offs zwischen den Landschaftsindizes können von der Wahl des Naturschutzinstruments und der Rationalität der Landnutzer abhängen. So kann bei begrenzter Rationalität der Landnutzer die Transformationskurve zwischen den Landschaftsindizes unstetig sein, d.h. es können beispielsweise nur bestimmte Niveaus an Habitatkonnektivität induziert werden. Benötigt ferner die Erzeugung von Habitaten Zeit, so kann in einem Markt für handelbare Landnutzungsrechte die Grenzzrate der Transformation zwischen Habitatmenge und -kontinuität negativ sein, d.h. ein Mehr an Habitatkontinuität korreliert mit einem Mehr an Habitatmenge. Grund hierfür sind Fehlentscheidungen der begrenzt rationalen Landnutzer.

Den Analysen, die zu diesen Ergebnissen geführt haben, liegen verschiedene vereinfachende Annahmen zugrunde. Beispielsweise wurden räumliche Korrelationen zwischen den Naturschutzkosten ignoriert, ebenso wie strategisches Verhalten der Landnutzer. Ferner wurde nur der Schutz einer einzelnen Art betrachtet. Nichtsdestotrotz liefern die Ergebnisse einige wertvolle Hinweise für die Ausgestaltung kosteneffizienter Naturschutzinstrumente. Außerdem sollte die Grundidee dieser Arbeit, Trade-offs zwischen Landschaftsindizes mit Hilfe der Produktionstheorie zu untersuchen, auch nach Fallenlassen der genannten Annahmen eine hilfreiche Strategie zur Analyse der Kosteneffizienz marktwirtschaftlicher Naturschutzinstrumente darstellen.

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1 Einleitung

1.1 Allgemeine Motivation der Arbeit

Der Verlust an Arten geschieht zurzeit mit einer Geschwindigkeit, die um Größenordnungen oberhalb des über die Erdgeschichte durchschnittlichen Wertes liegt. Versuche, ihn zu verlangsamen oder gar zu stoppen, sind bisher weitgehend gescheitert (MA 2005). Artenschutzanstrengungen bezogen sich bisher vor allem auf die Ausweisung von Schutzgebieten wie Nationalparks. Es hat sich jedoch herausgestellt, dass diese Schutzgebiete bei Weitem nicht ausreichen, vor allem aus zwei Gründen: Zum einen sind sie oft zu klein, um die Habitatsprüche aller zu schützenden Arten abdecken zu können. Zum anderen sind vor allem in Mitteleuropa viele Arten an die traditionelle land- und forstwirtschaftliche Nutzung angepasst und benötigen für ihr Überleben daher extensiv genutzte land- und forstwirtschaftliche Flächen. Deshalb rücken land- und forstwirtschaftlich genutzte Flächen in Europa aber auch in anderen Teilen der Welt zunehmend in den Fokus von Artenschutzanstrengungen (Polasky & Doremus 1998, Wätzold & Schwerdtner 2005, Engel et al. 2008).

Gegenüber der Ausweisung von Schutzgebieten ist der Artenschutz auf land- und forstwirtschaftlichen Flächen mit zusätzlichen Herausforderungen verbunden. Dies liegt vor allem daran, dass hier das Land nicht von staatlichen sondern überwiegend von privaten Akteuren bewirtschaftet wird. Die Kosten für Artenschutzmaßnahmen fallen damit zunächst auf der Seite dieser privaten Akteure an. Häufig ist ihre genaue Höhe nur den Landnutzern, nicht jedoch den mit dem Artenschutz betrauten Behörden bekannt (Polasky & Doremus 1998, Smith & Shogren 2002). Nicht zuletzt wegen dieser Informationsasymmetrie wird die Durchführung von Artenschutzmaßnahmen auf land- und forstwirtschaftlichen Flächen daher häufig und in zunehmendem Maße über marktwirtschaftliche Instrumente gesteuert (Smith & Shogren 2002, Baylis et al. 2008). Eine flächenscharfe Steuerung der Artenschutzmaßnahmen sehen diese Instrumente im Allgemeinen nicht vor; möglich ist jedoch eine Steuerung der „makroskopischen“ Eigenschaften einer land- oder forstwirtschaftlich genutzten Landschaft, wie etwa der Gesamtfläche, auf der eine bestimmte Landnutzungsmaßnahme durchgeführt wird oder der räumlichen Aggregation von Landnutzungsmaßnahmen (Parkhurst et al. 2002).

Zwischen diesen makroskopischen Landschaftseigenschaften – im Folgenden als *Landschaftsindizes* bezeichnet – bestehen jedoch ökologische und ökonomische Trade-offs in dem Sinne, dass einerseits eine Verschlechterung in einem Landschaftsindex durch eine Verbesserung in einem anderen Landschaftsindex ausgeglichen werden muss, damit ein gegebenes Artenschutzniveau aufrechterhalten werden kann (ökologischer Trade-off), und andererseits bei gegebenem Artenschutzbudget eine Verbesserung in einem Landschaftsindex durch eine Verschlechterung in einem anderen Landschaftsindex erkaufte werden muss (ökonomischer Trade-off).

Die Form dieser ökologischen und ökonomischen Trade-offs bestimmt maßgeblich die kosteneffizienten Niveaus der Landschaftsindizes und damit die Ausgestaltung von marktwirtschaftlichen Instrumenten für eine kosteneffiziente Allokation von Artenschutzmaßnahmen. Während zu den ökologischen Trade-offs zwischen Landschaftsindizes einige Informationen in der Literatur vorliegen (z.B. Drechsler & Wissel 1998), wurden bislang weder die ökonomischen Trade-offs noch deren Zusammenspiel mit den ökologischen Trade-offs systematisch untersucht. Die vorliegende Arbeit will diese Wissenslücke schließen und damit Empfehlungen für die kosteneffiziente Ausgestaltung marktwirtschaftlicher Artenschutzinstrumente geben.

Um dieses Ziel zu erreichen, muss das bestehende ökologische und ökonomische Wissen integriert werden. Dies geschieht mit Hilfe ökologisch-ökonomischer Modellierung, die sich

bereits in vielen Bereichen des Naturressourcen-Managements bewährt hat (Wätzold et al. 2006, Tschirhart 2009, Polasky & Segerson 2009).

Die folgenden Unterkapitel führen in die drei inhaltlichen Kernthemen dieser Arbeit ein. Abschnitt 1.2 befasst sich mit der Effizienz im Naturschutz und zeigt auf, wie diese grundsätzlich durch eine bessere räumliche und zeitliche Allokation von Artenschutzmaßnahmen gesteigert werden kann. Abschnitt 1.3 gibt einen kurzen Überblick über gängige politische Instrumente für den Natur- und Artenschutz und unterscheidet hier zwischen ordnungspolitischen und marktwirtschaftlichen Instrumenten. Dabei wird auch das oben bereits erwähnte Problem näher erläutert, dass eine flächenscharfe Steuerung von Artenschutzmaßnahmen über gängige marktwirtschaftliche Instrumente im Allgemeinen nicht, die Steuerung von Landschaftsindizes dagegen durchaus möglich ist. Abschnitt 1.4 geht schließlich ausführlicher auf die in dieser Arbeit betrachteten Landschaftsindizes ein und erklärt, warum zwischen diesen Landschaftsindizes sowohl in ökologischer als auch ökonomischer Hinsicht Trade-offs zu erwarten sind.

1.2 Effizienz im Natur- und Artenschutz

1.2.1 Zur Bedeutung des Effizienzgedankens im Natur- und Artenschutz

Eine zentrale Herausforderung des menschlichen Daseins ist die Endlichkeit der verfügbaren Ressourcen. Die Notwendigkeit, Entscheidungen im Angesicht begrenzter Ressourcen treffen zu müssen, ist für die meisten Ökonomen das Kernthema der Ökonomik (Robbins 1932). Wesentlich für die Beantwortung der Frage, wie verfügbare Ressourcen einzusetzen sind, ist die Definition des angestrebten Ziels: wofür sollen die Ressourcen eingesetzt werden? Ist das Ziel definiert, so sollten Ressourcen grundsätzlich so eingesetzt werden, dass der Grad der Zielerreichung bei gegebenem Ressourceneinsatz maximiert bzw. ein gesetztes Ziel mit minimalem Ressourceneinsatz erreicht wird. Ein solches Handeln bezeichnet die Ökonomik als effizient (Feess 1997: S. 64, Siebert 2003: S. 21).

Im Natur- und Artenschutz¹ besteht die Ressourcenknappheit vor allem in der begrenzten Landfläche. Arten benötigen zum Überleben Lebensraum („Habitate“), und die Größe dieses Lebensraumes korreliert zumindest bei terrestrischen Arten mit der Landfläche, die der Lebensraum einnimmt. Dies führt zum einen dazu, dass Arten um Platz konkurrieren, zum anderen entsteht ein Konflikt zwischen anthropogener, insbesondere land- und forstwirtschaftlicher Nutzung, und dem Naturschutz. Damit nämlich ein Stück Land für eine Art als Habitat geeignet ist, muss es je nach den Eigenschaften der Art bestimmte Anforderungen erfüllen. Diese Anforderungen schränken die Nutzung des Landes für andere Zwecke, beispielsweise für die Landwirtschaft, häufig ein (Plachter 1991: S. 350 ff., Hampicke 1991: S. 221 ff.).² Eine artenschutzfreundliche Landnutzung führt in diesem Fall zu landwirtschaftlichen Ertragsausfällen (Plachter 1991: S. 350 ff., Hampicke 1991, S. 221 ff.) und damit zu ökonomischen Kosten. Effizienter Naturschutz definiert sich in diesem Kontext

¹ Der Artenschutz, auf den die vorliegende Arbeit fokussiert, ist ein Teilbereich des Naturschutzes, der z. B. auch den Schutz von Böden und des Wasserhaushalts beinhaltet. Der Einfachheit halber werden die beiden Begriffe Naturschutz und Artenschutz in dieser Arbeit jedoch synonym verwendet.

² Dies gilt weniger für die extensive Landwirtschaft, wie sie bis Mitte des letzten Jahrhunderts bestanden hat, als vielmehr für die moderne intensive Landwirtschaft. Bei der Landwirtschaft früherer Jahrhunderte erzwang der Mangel an technologischen Möglichkeiten Landnutzungsformen, die mit den Anforderungen vieler Arten kompatibel waren – was bis ins 18. Jahrhundert hinein den Artenreichtum in Mitteleuropa sogar gefördert hat (Plachter 1991: S. 69). Erst der technologische Fortschritt der letzten Jahrzehnte ermöglichte Landnutzungsformen, die zwar zu immensen landwirtschaftlichen Ertragssteigerungen geführt, die genutzten Flächen aber für die meisten heimischen Arten unbrauchbar gemacht haben.

dadurch, dass für gegebene Kosten ein Maximum an Naturschutz erzielt bzw. ein gegebenes Naturschutz-Niveau zu minimalen Kosten erreicht wird (Wätzold & Schwerdtner 2005).

Häufig werden Landwirte für Ertragsausfälle, die mit Naturschutzmaßnahmen³ auf ihrem Land einhergehen, entschädigt (Hampicke 1991: S. 278 ff., Hanley & Oglethorpe 1991, Wätzold & Schwerdtner 2005). In diesem Fall verlagern sich die Kosten des Naturschutzes auf die Gesellschaft. Für den Zeitraum von 2007-2013 gibt die EU 22 Milliarden Euro für Agrarumweltprogramme aus (EU 2010), wobei die tatsächlichen Ausgaben noch höher sind, da die Programme von den Mitgliedstaaten kofinanziert werden. Der Betrag, der in diesem Zeitraum allein in England für Agrarumweltmaßnahmen ausgegeben wird, beträgt beispielsweise ca. 3,1 Milliarden britische Pfund (Natural England 2009). Unabhängig davon, ob die Landwirte oder die Gesellschaft als ganze diese Kosten zu tragen hat, zeigt diese Zahl, dass ein effizienter Naturschutz dringend geboten ist, da finanzielle Mittel, die für den Naturschutz ausgegeben werden, für andere Belange nicht zur Verfügung stehen. Ineffizientes Wirtschaften im Bereich des Naturschutzes reduziert damit nicht nur die gesellschaftliche Wohlfahrt sondern birgt darüber hinaus die Gefahr, dass der Naturschutz seine Akzeptanz in der Gesellschaft verliert (Wätzold & Schwerdtner 2005). Die im vorangegangenen Abschnitt aufgeworfene Frage, wie Naturschutzinstrumente kosteneffizient auszugestalten sind, ist damit gesellschaftlich höchst relevant.

1.2.2 Die effiziente räumliche und zeitliche Allokation von Naturschutzmaßnahmen

Wie lässt sich nun prinzipiell die Effizienz des Naturschutzes steigern? Grundsätzlich gibt es hierfür zwei Möglichkeiten: Als erstes kann man versuchen, die *Effektivität* bzw. Wirksamkeit des Naturschutzes zu erhöhen, indem man Maßnahmen so auswählt und durchführt, dass sie einen möglichst hohen Beitrag zur Erreichung des gesetzten Naturschutzziels leisten. Hier ergibt sich eine Reihe an Wahlmöglichkeiten: *Welche* Maßnahmen sind *wann* und *wo* durchzuführen?

- Die Frage nach der Art der Maßnahme stellt sich beispielsweise, wenn entschieden werden soll, ob eine Wiesenvogelart besser durch ein angepasstes Wiesenmahdregime oder ein angepasstes Beweidungsregime geschützt werden kann.
- Der Zeitpunkt der Durchführung einer Maßnahme spielt beispielsweise bei der Auswahl eines „angepassten“ Mahdregimes eine Rolle. Im mitteleuropäischen Flachland brüten viele Wiesenvogelarten etwa bis Mitte Juli, so dass Mahdzeitpunkte vor diesem Datum für die entsprechenden Arten äußerst schädlich sind (Mühlenberg & Slowik 1997: Abb. 32). Ebenso hängt das Überleben vieler Schmetterlingsarten von einem angepassten Mahdregime ab. Um beispielsweise die Reproduktion des Wiesenknopf-Ameisenbläulings (*Maculinea teleius*) nicht zu gefährden, sollte in den Wochen vor, während und nach der Flug- und Eiablagezeit nicht gemäht werden (Johst et al. 2006).
- Schließlich hängt die Effektivität einer Maßnahme häufig auch von dem Ort ihrer Durchführung ab. Verständlicherweise ist es im Hinblick auf den Schutz einer bestimmten Art ineffektiv, Maßnahmen an Orten durchzuführen, an denen die Art gar nicht vorkommt, und die von der Art in der nahen Zukunft auch nicht besiedelt werden können. Darüber hinaus sind auch innerhalb des Verbreitungsgebiets einer Art nicht alle Flächen gleichwertig. Manche Flächen stellen Kernhabitate dar, deren Verlust

³ Als Maßnahme wird hier auch die *Nichtdurchführung* einer (landwirtschaftlichen) Maßnahme, wie beispielsweise Pflügen eines Ackers oder das Mähen einer Wiese zu einem bestimmten Zeitpunkt (im letzteren Fall besteht die Naturschutzmaßnahme in der *Verschiebung* der Mahd auf einen anderen Termin).

zum Verlust der gesamten Artenpopulation führen kann, selbst wenn andere, marginale Habitate noch vorhanden sind (Verboom et al. 2001, Ovaskainen & Hanski 2003). Andere Flächen wiederum können die Funktion von Trittsteinen haben, die es Individuen ermöglichen, zwischen verschiedenen Kernhabitaten zu wandern.

Die zweite Möglichkeit zur Erhöhung der Effizienz im Naturschutz ist, (bei gegebener Effektivität) die *Kosten* zu senken. Wie bei der oben betrachteten Effektivität spielen auch hier Art, Zeitpunkt und Ort der Durchführung von Naturschutzmaßnahmen eine wichtige Rolle. So verursachen nicht nur unterschiedliche Maßnahmen unterschiedliche Kosten, auch ein und dieselbe Maßnahme kann an unterschiedlichen Orten und zu unterschiedlichen Zeitpunkten unterschiedlich viel kosten. Der Nährstoffgehalt von Mahdgut und damit seine ökonomische Verwertbarkeit nehmen beispielsweise von dem Zeitpunkt ab, an dem es geschnitten wurde (Opitz von Boberfeld 1994). Eine Verzögerung der ersten Mahd im Jahr auf einen Zeitpunkt nach dem 15. Juli kann daher beträchtliche Ertragsausfälle verursachen. Auch der Ort, an dem eine Maßnahme durchgeführt wird, kann die Kosten einer Maßnahme beeinflussen (Ando et al. 1998, Polasky et al. 2008). Reduziert man die Erträge auf einem ertragsarmen Produktionsstandort um einen bestimmten Prozentsatz, so wiegt dies weniger stark als eine entsprechende Reduktion der Erträge auf einem ertragsreichen Standort.

Will man nun versuchen, ein gegebenes Naturschutzziel effizient, also zu den geringstmöglichen Kosten, zu erreichen, so gilt es, die Orte und Zeitpunkte der Maßnahmendurchführung möglichst so zu wählen, dass die Effektivität der Maßnahmen hoch und ihre Kosten niedrig sind (vgl. Naidoo et al. 2006). Selten jedoch besteht ein solch einfacher Zusammenhang zwischen hohen Kosten und geringer Effektivität bzw. niedrigen Kosten und hoher Effektivität. Stattdessen können Standorte oder Zeitpunkte mit hohen Kosten sowohl eine hohe als auch niedrige Effektivität aufweisen; gleiches gilt für Standorte mit niedrigen Kosten. In diesem Fall ist die Auswahl der Standorte und Zeitpunkte nicht mehr trivial: nicht selten muss gewählt werden zwischen der Kombination „hohe Effektivität bei hohen Kosten“ und der Kombination „geringe Effektivität bei niedrigen Kosten“. In diesen Fällen erfordert die kosteneffiziente Auswahl von Standorten und Zeitpunkten die genaue quantitative Kenntnis sowohl der Kosten als auch der Effektivität der Maßnahmen in Abhängigkeit von Zeit und Ort der Maßnahmendurchführung.

Die Bestimmung der Effektivität ist vor allem Aufgabe der Naturwissenschaften und insbesondere der Ökologie, während die Bestimmung der Kosten eine ökonomische Fragestellung darstellt. Zur Beantwortung der Frage, wie Naturschutzmaßnahmen unter Maßgabe der ökonomischen Effizienz räumlich und zeitlich zu allozieren sind, muss also ökologisches und ökonomisches Wissen integriert werden (vgl. Wätzold et al. 2006). Derartige Untersuchungen sind wissenschaftliches Neuland, und zur kosteneffizienten räumlichen und zeitlichen Allokation von Naturschutzmaßnahmen liegen – jenseits von Fallstudien wie z.B. Ando et al. (1998) und Polasky et al. (2008) – nur wenige allgemeine und übertragbare Erkenntnisse vor. Die vorliegende Arbeit ist die erste, die sich dieser Thematik in systematischer Weise annimmt und mit Hilfe konzeptioneller und angewandter Modelle wissenschaftliche Aussagen zur kosteneffizienten räumlich-zeitlichen Allokation von Naturschutzmaßnahmen entwickelt.

1.2.3 Ziele und Kosten im Naturschutz

Eindeutige, mess- und überprüfbare Ziele für den Naturschutz zu formulieren ist nicht einfach, da man es hier mit einem sehr heterogenen Gut zu tun hat. So besteht ein Ökosystem aus vielen miteinander interagierenden Tier- und Pflanzenarten, jede mit ihrem eigenen Anspruch an die biotischen und abiotischen Lebensbedingungen. Die Ansprüche einzelner Arten stehen häufig im Gegensatz zu denen anderer Arten (Huth & Ditzer 2001, Drechsler et

al. 2007), so dass Naturschutzentscheidungen häufig ein Werturteil für eine Artengruppe und gegen eine andere beinhalten. Werturteile aber sollen weder die Natur- noch die Gesellschaftswissenschaften treffen, dies soll die Gesellschaft selbst. Die Wissenschaften können allerdings bei der Entscheidungsfindung behilflich sein.

Die vorliegende Arbeit fokussiert auf den Schutz einzelner Arten. Welche Arten in Europa gesetzlich geschützt sind, regelt die Flora-Fauna-Habitat- (FFH-) Richtlinie (EU 1992). Naturschutzfachlich zu rechtfertigen ist die Betrachtung einzelner Arten zum einen durch die Annahme, dass es sich bei diesen um besonders gefährdete oder für das Ökosystem besonders wichtige „Schlüsselarten“ handelt, von deren Präsenz viele andere Arten abhängen (Mills et al. 1993). Zum anderen stellt der Artenschutz in der Agrarlandschaft (wohlgemerkt: nicht unbedingt der Landschaft insgesamt) eine eher marginale Landnutzungsform dar, in dem Sinne, dass der Anteil geschützter Flächen eher gering ist. Angesichts knapper Kassen ist beispielsweise nicht zu erwarten, dass ein eventuell neu aufgelegtes Schutzprogramm für den Wiesenknopf-Ameisenbläuling im Kreis Landau, Rheinland-Pfalz, einem der letzten Vorkommensgebiete des Schmetterlings in Europa, Ausmaße annehmen würde, die zum Aussterben anderer Arten in der Region führen würde (vgl. Wätzold et al. 2008). Die Fokussierung auf eine Art ist in diesem Fall also zu rechtfertigen.

Nicht minder komplex als die Ermittlung einer Naturschutzzielfunktion ist die vollständige Berücksichtigung der Kosten. Wätzold & Schwerdtner (2005) (siehe auch Birner & Wittmer 2004) unterscheiden zwischen Produktions-, Implementations- und Entscheidungskosten. Erstere repräsentieren die schon oben erwähnten Gewinneinbußen (Opportunitätskosten), wenn statt der ökonomisch gewinnträchtigsten Landnutzungsform eine andere, artenschutzfreundlichere gewählt wird. Die Implementationskosten umfassen alle Kosten, die bei der Durchsetzung und Kontrolle von Artenschutzmaßnahmen („monitoring and enforcement“) anfallen (Becker 1968, Downing & Watson 1974), da nicht angenommen werden kann, dass sich alle Landnutzer an Umweltgesetze oder geschlossene Verträge halten. Entscheidungskosten fallen an, wenn für das Fällende einer Entscheidung Informationen beschafft werden müssen und der Abwägungsprozess Zeit und Arbeitskraft in Anspruch nimmt. In der Naturschutzökonomie werden meist nur die Produktionskosten betrachtet, da die Implementations- und Entscheidungskosten schwer abzuschätzen, geschweige denn quantitativ zu modellieren sind. Auch die vorliegende Arbeit folgt diesem Ansatz und betrachtet nur die Produktionskosten des Artenschutzes, die im Folgenden kurz als „Kosten“ bezeichnet werden.

1.3 Politische Instrumente zur Umsetzung von Naturschutzmaßnahmen

1.3.1 Ordnungspolitische Ansätze

Ist das Naturschutzziel eindeutig definiert, und ist bekannt, wie die Kosten und die Effektivität aller zur Wahl stehenden Naturschutzmaßnahmen von Ort und Zeit ihrer Durchführung abhängen, so ist die Ermittlung der effizienten räumlich-zeitlichen Allokation der Maßnahmen ein rein mathematisches Optimierungsproblem, für dessen Lösung eine Vielzahl von Methoden und Computerprogrammen existiert. Die Frage ist jedoch, wie man die Landnutzer dazu bringt, die Naturschutzmaßnahmen an genau jenen Orten und zu jenen Zeiten durchzuführen, die die Optimierung als effizient erkannt hat. Am einfachsten ist es anzunehmen, dass Landnutzer durch gesetzliche Vorschriften zu einer naturschutzgerechten Landnutzung angehalten werden. In verschiedenen Bereichen der Umweltpolitik ist ein solcher ordnungspolitischer Ansatz durchaus effektiv, insbesondere wenn die mit der Einhaltung der Vorschrift verbundenen Kosten bekannt sind (Feess 1995: S. 62 ff.). Als

einfache Beispiele seien die Einhaltung gesetzter Abgasnormen bei Kraftfahrzeugen und Verordnungen zur Beschränkung des Düngemittleinsatzes in der Landwirtschaft genannt.

Für die kosteneffiziente Allokation von Artenschutzmaßnahmen ist ein solcher Ansatz jedoch nur eingeschränkt umsetzbar. Ein Grund hierfür ist, dass für eine kosteneffiziente Regulierung die genaue Kenntnis der Kosten der verschiedenen Maßnahmen notwendig wäre. Während nun Informationen über die Kosten von Abgaskatalysatoren recht leicht erhältlich sind, sind die Kosten von Naturschutzmaßnahmen, insbesondere deren Abhängigkeit von Ort und Zeit der Durchführung, nur schwer zu ermitteln. Auch wenn man mithilfe von allgemein weitgehend zugänglichen Datentabellen derartige Kosten abschätzen kann (z.B. Bergmann 2004), so handelt es sich bei den Ergebnissen dieser Abschätzungen nur um Durchschnittswerte. Zwischen verschiedenen Landwirten können diese Kosten trotz gleicher äußerer Bedingungen variieren, und wie hoch die Kosten für den einzelnen Landwirt tatsächlich sind, ist im Allgemeinen nur diesem bekannt.⁴ Die Landwirte beispielsweise nach ihren Kosten zu befragen, wäre hingegen zeitaufwändig und kostspielig, und die Antworten würden aufgrund möglichen strategischen Verhaltens der Befragten mit großer Wahrscheinlichkeit nicht den wahren Kosten entsprechen.

Ein weiterer Nachteil von ordnungspolitischen Ansätzen ist, dass sie die freie Entscheidung der privaten Akteure einschränken und damit die Akzeptanz für das verfolgte Politikziel gefährden. Im Extremfall können ordnungspolitische Ansätze im Naturschutz sogar zu perversen Anreizen führen: Brütet beispielsweise ein seltener Vogel auf einem Feld, so dass der Landwirt befürchten muss gezwungen zu werden, dieses Feld unter Gewinneinbußen im Interesse dieser Art zu bewirtschaften, so könnte der Landwirt sich veranlasst sehen, den Vogel von seinem Feld zu entfernen⁵.

1.3.2 Marktwirtschaftliche Instrumente

Eine Alternative zu ordnungspolitischen Ansätzen, die im Naturschutz zunehmend an Bedeutung gewinnt, sind marktwirtschaftliche Instrumente (Hampicke 1991: S. 285 ff., Sterner 2003: S. 128 ff.). Anstatt jedem Landnutzer explizit vorzuschreiben, wann und wo er welche Umweltmaßnahme durchzuführen hat, werden finanzielle Anreize für die Durchführung der Umweltmaßnahme gesetzt. Die Landnutzer entscheiden nun frei, ob die Durchführung der Umweltmaßnahme unter Berücksichtigung der Anreize für sie „besser“ als die Nichtdurchführung der Maßnahme ist oder nicht. Dieses Entscheidungskalkül wird üblicherweise durch eine Nutzenfunktion beschrieben, wobei angenommen wird, dass ein Akteur stets diejenige Aktion wählt, die diese Nutzenfunktion maximiert. Repräsentiert werden kann eine Nutzenfunktion beispielsweise durch den Gewinn, also die Differenz zwischen der Summe aller finanziellen Erträge und der Summe aller Kosten, oder durch den erwarteten zukünftigen Gewinn (ggf. unter Berücksichtigung zeitlicher Diskontierung), oder auch durch eine Risikonutzenfunktion, welche die Unsicherheiten über zukünftige Erträge und Kosten sowie die persönliche Einstellung des Landnutzers gegenüber Risiko (Risikofreude, -neutralität bzw. -aversität) berücksichtigt.⁶

⁴ Liegen bestimmte Informationen nur einem Teil der Akteure (hier: den Landnutzern aber nicht der Behörde) vor, so spricht man von einer asymmetrischen Informationsverteilung (z.B. Feess 1997: S. 583 ff., Baumol & Blinder 2003: S. 247, Sterner 2003, S. 150 ff.).

⁵ „Shoot, shovel, shut up“: vgl. Innes et al. (1998) zu ungewollten Konsequenzen des US-amerikanischen Endangered Species Act.

⁶ Alternativ zum Modell des „Nutzenmaximierers“ gibt es beispielsweise noch das Modell des „Satisficers“ (March & Simon 1958), den lediglich interessiert, dass der Nutzen einen gewissen Mindestwert überschreitet.

Marktwirtschaftliche Instrumente der Umweltpolitik können einer von zwei Kategorien zugeordnet werden: den preis- und den mengenbasierten Instrumenten (Bonus 1990). In einem preisbasierten Instrument spezifiziert die Behörde den Preis, den sie für die Durchführung einer gewünschten Maßnahme zu zahlen bereit ist bzw. den sie bei Nichtdurchführung der Maßnahme fordert. Durch die Höhe des Preises lässt sich die Zahl der Akteure, die die gewünschte Maßnahme durchführen, steuern. Die genaue Zahl der Akteure, die die gewünschte Maßnahme durchführen, hängt jedoch nicht nur von dem Preis sondern auch von den mit der Maßnahme verbundenen Gewinnen (im Vergleich zu allen anderen verfügbaren Maßnahmen) und den Entscheidungskalkülen der Akteure ab. Sie ist daher unbestimmt. Zu den preisbasierten Instrumenten gehören beispielsweise Steuern und Subventionen. Im Kontext des Natur- und Artenschutzes sind Kompensationszahlungen, bei denen Landnutzer für Gewinneinbußen bei der Durchführung von Naturschutzmaßnahmen entschädigt werden, ein gängiges Instrument. Praktisch in allen Teilen der Welt erfreuen sich diese Instrumente unter der Bezeichnung „payments for environmental services“ (PES) einer steigenden Beliebtheit (Wätzold & Schwerdtner 2005, Engel et al. 2008).

In einem mengenbasierten Instrument spezifiziert eine Behörde die Menge an gewünschten Maßnahmen, die in einem bestimmten Gebiet durchzuführen ist. Dies geschieht meist über die Auflage, dass jeder Akteur eine gewünschte Maßnahme in einem vorgegeben Umfang durchführen muss. Im Gegensatz zu dem oben beschriebenen ordnungspolitischen Ansatz kann sich jeder Akteur von der Durchführung der Maßnahme ganz oder teilweise „freikaufen“. Dies geschieht über den Erwerb von handelbaren Eigentums- oder Nutzungsrechten auf einem Zertifikatemarkt. Anbieter solcher Rechte sind Akteure, die die gewünschte Maßnahme in einem größeren Umfang als vorgeschrieben durchführen und dies durch die Behörde zertifiziert bekommen. Der Preis dieser Zertifikate – und damit der Preis der gewünschten Maßnahme – ergibt sich aus der Interaktion der Teilnehmer des Zertifikatemarkts. Die Handlungen der einzelnen Marktteilnehmer (Kauf bzw. Verkauf von Zertifikaten) hängen von den mit der gewünschten Maßnahme verbundenen Gewinnen (im Vergleich zu den anderen verfügbaren Maßnahmen) und dem Entscheidungskalkül der Akteure ab und sind unbestimmt. Zu den bisher häufigsten Anwendungen solcher Zertifikatemarkte in der Umweltpolitik gehört der Handel mit Emissionsrechten (Hansjürgens 2005, Tietenberg 2006). Auch im Bereich des Natur- und Artenschutzes nimmt die Bedeutung dieses Instruments zu; bezeichnet werden sie hier oft als Märkte für handelbare Landnutzungsrechte („tradable land-use permits“), oder „conservation banking“ (Salzmann & Ruhl 2000, TEEB 2009, eftec IEEP 2010).

Der Vorteil dieser marktbasierenden Instrumente gegenüber den ordnungspolitischen Ansätzen ist, dass eine kosteneffiziente Allokation der gewünschten Maßnahme auch ohne die genaue Kenntnis der mit der Maßnahme verbundenen Kosten möglich ist (Feess 1995: S. 77/78, Siebert 2003: S. 91-93). Diese Aussage basiert auf der Annahme, dass die Akteure stets diejenige Entscheidung treffen, die ihren Gewinn maximiert. Diese Annahme impliziert nämlich, dass Naturschutzmaßnahmen von denjenigen durchgeführt werden, bei denen die Kosten *ceteris paribus* am geringsten sind. Bei Kompensationszahlungen werden sich beispielsweise all diejenigen für die Durchführung der gewünschten Naturschutzmaßnahme entscheiden, deren Kosten (d.h. die mit der Maßnahme verbundene Gewinnverluste) geringer als die angebotene Zahlung sind. In einem Markt für handelbare Landnutzungsrechte werden die Akteure mit den geringsten Kosten ihr Land für Naturschutz nutzen, um die erzeugten Landnutzungsrechte gewinnbringend an diejenigen zu verkaufen, deren Kosten hoch sind,

Erfüllen mehrere Maßnahmen diese Bedingung, so werden für die Auswahl der durchzuführenden Maßnahme weitere Kriterien herangezogen, beispielsweise ob die Maßnahme schon in der Vergangenheit (mit zufrieden stellendem Nutzen) durchgeführt wurde oder ob andere Landnutzer dieselbe Maßnahmen durchführen oder auch nicht durchführen (Jager & Janssen 2002).

und die auf ihrem Land daher keine Naturschutzmaßnahmen durchführen wollen. Der sich einstellende Marktpreis der Landnutzungsrechte separiert gerade die hohen (marginalen) Kosten der Rechte-Nachfrager von den niedrigen (marginalen) Kosten der Rechte-Anbieter.

Ein weiterer Vorteil zumindest von Kompensationszahlungen ist ihr freiwilliger Charakter. Jeder Landnutzer hat die Freiheit, sein Land so zu nutzen wie er möchte: zur Produktion landwirtschaftlicher Güter oder für die Durchführung der gewünschten über die Kompensationszahlung geförderten Naturschutzmaßnahme(n). Dies erhöht die Akzeptanz der Landnutzer für den Naturschutz und vermeidet insbesondere die oben erwähnten „perversen Anreize“ (Smith & Shogren 2002). Dieser Vorteil der Kompensationszahlungen hat natürlich auch einen Preis: zur Aufwendung der Kompensationszahlungen muss die Gesellschaft die erforderlichen Gelder, beispielsweise über Steuern, bereitstellen.

Märkte für handelbare Landnutzungsrechte kann man bezüglich des Grades der Freiwilligkeit zwischen die Kompensationszahlungen und die ordnungspolitischen Ansätze einordnen: einerseits werden den Landnutzern gewisse Auflagen gemacht, denen sie nicht ausweichen können, andererseits können sie selbst entscheiden, ob sie diese Auflagen durch die Durchführung der geforderten Maßnahmen oder den Erwerb der entsprechenden Landnutzungsrechte erfüllen. Die Verteilung der Kosten des Naturschutzes zwischen den Landnutzern einerseits und der Gesellschaft andererseits bestimmt sich bei handelbaren Landnutzungsrechten über die Art und Weise, wie die Landnutzungsrechte bei der Einrichtung des Marktes den Landnutzern zugeteilt werden (Tietenberg 2006: S. 127 ff., Gagelmann 2008, Wissel & Wätzold 2010). Keine zusätzlichen Kosten entstehen den Landnutzern beispielsweise, wenn die Zuteilung der Landnutzungsrechte die aktuelle Landnutzung widerspiegelt („grandfathering“); zusätzliche Kosten entstehen den Landnutzern beispielsweise, wenn diese die Landnutzungsrechte im Rahmen einer Auktion ersteigern müssen.

1.3.3 Räumliche und zeitliche Zielgenauigkeit marktwirtschaftlicher Instrumente

Wie im vorangegangenen Abschnitt erläutert, versprechen marktwirtschaftliche Instrumente ökonomische Effizienz in dem Sinne, dass derselbe Umfang an gewünschten Maßnahmen zu geringeren Kosten erzielt werden kann. Im Naturschutz bedeutet dies, dass Naturschutzmaßnahmen bei gegebenem Budget bzw. gegebenen Gesamtkosten auf mehr und/oder größeren Flächen durchgeführt werden können. Problematisch ist in der Anwendung im Natur- und Artenschutz jedoch die ökologische Effektivität marktwirtschaftlicher Instrumente. Im Abschnitt 1.2.2 wurde erläutert, dass die ökologische Effektivität von Naturschutzmaßnahmen von Art, Ort und Zeit ihrer Durchführung abhängen kann. Die im vorangegangenen Abschnitt genannten Instrumente sind für eine zielgenaue Steuerung von Ort und Zeit in dem Sinne, dass genau festgelegt werden kann, wann und wo welche Maßnahme durchgeführt wird, jedoch nur sehr eingeschränkt in der Lage. Bei Kompensationszahlungen wird beispielsweise die gewünschte Naturschutzmaßnahme durch die Landnutzer genau dort und nur dort durchgeführt, wo die Kompensationszahlung die Kosten überschreitet. Das bedeutet, dass die räumliche Verteilung der Landnutzung im Wesentlichen durch die räumliche Verteilung der Kosten bestimmt ist, die die Behörde nicht beeinflussen kann und oft nicht kennt. Die Behörde kann lediglich die Höhe der Kompensationszahlung bestimmen und damit die Gesamtfläche, auf der die gewünschte Maßnahme durchgeführt wird, steuern.

Um die räumliche Zielgenauigkeit marktwirtschaftlicher Naturschutzinstrumente zu erhöhen, wurden in der Vergangenheit verschiedene Ansätze diskutiert. Der einfachste Ansatz ist die Einrichtung von Zonen, von denen bekannt ist, dass die ökologische Effektivität der Maßnahmen hier besonders hoch ist (Parkhurst & Shogren 2005, Tietenberg: S. 89 ff.).

Kompensationszahlungen würden dann nur für Maßnahmen angeboten, die in einer solchen Zone durchgeführt werden. Kosteneffizient ist dieser Ansatz natürlich nur, wenn die Kosten der Maßnahmen in einer solchen Zone nicht zu hoch sind. Andernfalls könnten Flächen außerhalb der Zone, die bei geringerer ökologischer Effektivität sehr geringe Kosten haben, kosteneffizienter sein. Selbst wenn bekannt ist, dass im Mittel die Kosten innerhalb der Zone sich nicht erheblich von denen außerhalb der Zone unterscheiden, bleibt außerdem immer noch das Problem der kosteneffizienten Allokation innerhalb der Zone. Als Lösungsansätze für diese Steuerung auf regionaler Skala wurden in der Literatur bisher sogenannte Agglomerationszahlungen oder –boni vorgeschlagen (Parkhurst et al. 2002, 2007). Hier erhöht sich die Kompensationszahlung für die Durchführung einer Naturschutzmaßnahme, wenn in der Nähe ebenfalls (dieselben) Naturschutzmaßnahmen durchgeführt werden. Dadurch entsteht für die Landnutzer ein ökonomischer Anreiz, ihre Naturschutzmaßnahmen im Raum zu „agglomerieren“.

Die ökologische Begründung für solche Agglomerationsanreize liegt darin, dass eine Art in einem zusammenhängenden Habitat meist besser überleben kann als in einem Habitat, das in mehrere weit voneinander entfernte Teilhabitate fragmentiert ist (Hanski & Gilpin 1991, Drechsler 1994). Wo die Habitate genau verortet sind, ist in diesem Zusammenhang weniger relevant, entscheidend ist die räumliche Konnektivität der Habitate. Aus dieser ökologischen Flexibilität lassen sich über Agglomerationsanreize nun Effizienzgewinne abgreifen: Kann eine Naturschutzmaßnahme an zwei Orten durchgeführt werden, die zu derselben räumliche Konnektivität des gesamten Habitatsystems führt, und ist die Durchführung der Maßnahme an dem einen der beiden Orte kostengünstiger als an dem anderen, so werden die marktwirtschaftlichen (Inter-) Aktionen der Landnutzer zur Durchführung der Maßnahme an dem kostengünstigeren Ort führen. Das Naturschutzziel wird damit zu geringeren ökonomischen Kosten erreicht.

Bisher wurde angenommen, dass die Kosten der Naturschutzmaßnahmen zeitlich konstant sind. Kosten können sich jedoch im Rahmen ökonomischen oder sozialen Wandels ändern (vgl. Lubowski 2008, Wissel & Wätzold 2010), was Auswirkungen auf die Landnutzung hat und das Allokationsproblem zu einem (raum-) zeitlichen Allokationsproblem erweitert. Wurden beispielsweise auf einem Stück Land Naturschutzmaßnahmen durchgeführt, weil die dafür angebotene Kompensationszahlungen die Kosten überstiegen, und steigen Kosten mit der Zeit so stark an, dass sie die Kompensationszahlung übersteigen, so wird der Landnutzer die Maßnahme nicht mehr durchführen und das Habitat zerstören. Umgekehrt kann auf einem Stück Land, auf dem Naturschutz bisher mit Verlusten verbunden gewesen wäre, die Abnahme der Kosten dazu führen, dass die Durchführung von Naturschutzmaßnahmen für den Landnutzer gewinnbringend wird und ein Habitat erzeugt wird. Steuern lässt sich mit Hilfe marktwirtschaftlicher Instrumente diese Reallokation von Naturschutzmaßnahmen zwar nicht explizit für jedes einzelne Stück Land, jedoch lässt sich die Häufigkeit solcher Reallokationen beeinflussen. Im Rahmen von Kompensationszahlungen könnte dies beispielsweise durch die Laufzeit der Verträge, die zwischen Behörde und Landnutzern geschlossen werden, geschehen, während man bei Märkten für handelbare Landnutzungsrechte die Erzeugung und/oder Zerstörung eines Habitats besteuern oder subventionieren könnte.

In beiden Allokationsproblemen, dem räumlichen und dem zeitlichen, ist eine detaillierte räumlich-zeitliche Allokation der Naturschutzmaßnahmen mit Hilfe der genannten marktwirtschaftlichen Instrumente zwar nicht möglich, gewisse aggregierte Eigenschaften des Landnutzungsmusters lassen sich jedoch steuern.

1.4 Zielstellung: Kosteneffiziente Niveaus von Landschaftsindizes

1.4.1 Landschaftsindizes in der Ökologie

Im vorangegangenen Abschnitt wurde erläutert, dass man mit marktwirtschaftlichen Instrumenten aggregierte Eigenschaften von Landnutzungsmustern steuern kann. In der Ökologie und Naturschutzbiologie werden solche Eigenschaften auch als Landschaftsindizes bezeichnet. Der Verlust von Habitat ist eine der wesentlichen Ursachen für den Verlust von Biodiversität, und damit ist die *Habitatmenge* einer der wichtigsten – wenn nicht der wichtigste – Landschaftsindex, der die Überlebensfähigkeit einer Art bestimmt.

Neben der Habitatmenge ist die räumliche Verteilung der Habitate eine weitere wesentliche Determinante der Überlebensfähigkeit von Arten. Es existiert eine Vielzahl von statistischen Maßen, mit Hilfe derer man die räumliche Verteilung von Objekten beschreiben kann (Moilanen & Hanski 2001, Wiegand & Moloney 2004). Hierzu gehören beispielsweise Korrelationsfunktionen und Variogramme, die messen, mit welcher Wahrscheinlichkeit ein Objekt von Typ y im Abstand von einem Objekt von Typ x beobachtet werden kann, Abstandsverteilungen zwischen Objekten und Klumpungsmaße. Die Landschaftsökologie beschäftigt sich unter anderem mit der Frage, wie ökologische Prozesse und insbesondere die Überlebensfähigkeit von Arten von diesen Landschaftsindizes abhängen. Dass ein Zusammenhang zwischen räumlichen Landschaftsindizes einerseits und der Überlebensfähigkeit von Arten andererseits besteht, erklärt sich vor allem daraus, dass viele ökologische Prozesse, insbesondere die Ausbreitung von Arten distanzabhängig sind: je weiter zwei Habitate voneinander entfernt sind, desto geringer der Austausch von Individuen zwischen den beiden Habitaten. Ein hoher Austausch von Individuen, ermöglicht durch eine hohe räumliche Konnektivität der Habitate („*Habitatkonnektivität*“), wirkt sich im Allgemeinen positiv auf das Überleben von Arten aus (Wiegand et al. 2005).⁷

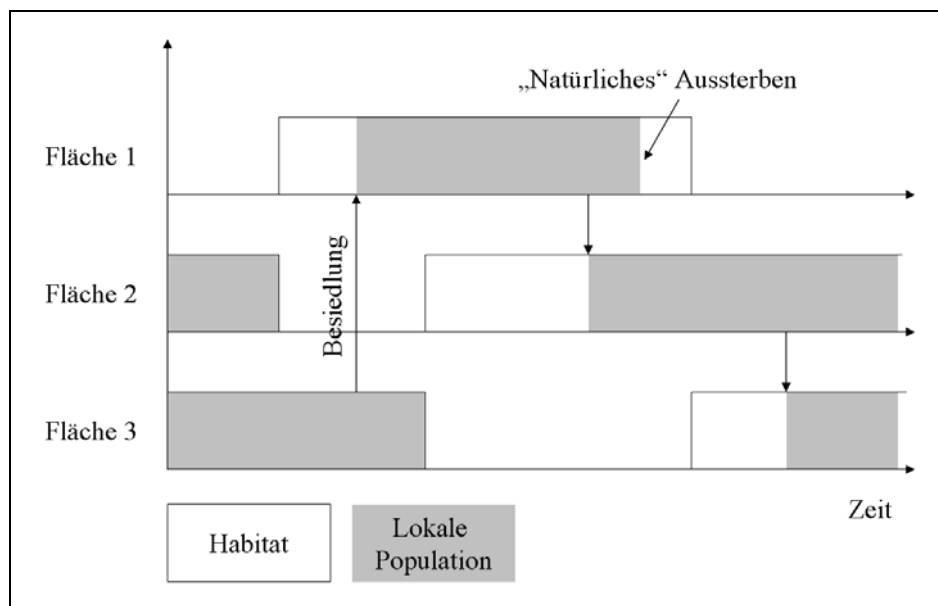
Ambivalenter ist in der Ökologie die Rate, mit der Habitat realloziert werden. Einerseits ist jede Habitatzerstörung mit dem Verlust der dort lebenden Arten verbunden, während ein neu erzeugtes Habitat erst besiedelt werden muss, bevor es zum Überleben der Art in der Region beitragen kann. Abbildung 1 zeigt das Beispiel einer hypothetischen Landschaft, in der Habitate erzeugt und wieder zerstört werden – unter der Restriktion, dass stets genau zwei der drei Flächenstücke in der Landschaft ein Habitat für die Art darstellen. Obwohl also die Habitatmenge konstant ist, wird die Art negativ durch die Landnutzungsdynamik beeinflusst. Wird nämlich ein Habitat zerstört, so wird die darauf befindliche lokale Population ebenfalls zerstört, während das gleichzeitig erzeugte neue Habitat zunächst leer ist. Die Zahl der lokalen Populationen hat sich also durch die Habitat-Reallokation zumindest temporär reduziert, was mit einem erhöhten Aussterberisiko der Art verbunden ist. Von diesem Standpunkt aus gesehen ist jede Reallokation von Habitat bzw. Naturschutzmaßnahmen daher negativ zu sehen (Keymer et al. 2000).

Andererseits sind Störungen eine wesentliche Voraussetzung für Biodiversität (Grime 1973). Würde man beispielsweise die „natürliche“ ökologische Dynamik in Mitteleuropa nicht stören, so wäre ein Großteil der Fläche bald mit Wald bedeckt, zum Nachteil aller Tierarten, die nur im Offenland überleben können. Ebenso können manche Beutearten nur dadurch überleben, dass durch Störungen permanent Fressfeinde getötet und Refugien geschaffen werden, in denen die Beutearten sich vor ihren Fressfeinden verbergen können (Roy et al. 2004). Während die regelmäßige Reallokation von Habitaten also aus ökologischer Sicht sowohl negativ als auch positiv bewertet werden kann, beruhen die in dieser Arbeit

⁷ Im Gegensatz dazu kann eine größere Entfernung zwischen Habitaten beispielsweise dann von Vorteil sein, wenn die Art von einem Krankheitserreger oder durch eine konkurrierende oder räuberische Art bedroht ist, deren Ausbreitung durch größere Abstände verringert werden kann (z.B. Tilman 1994).

verwendeten Modelle ausschließlich auf der ersteren, negativen Sichtweise, während auf die positive Sichtweise in der abschließenden Diskussion der Ergebnisse kurz Bezug genommen wird. Da Menge und räumliche Konnektivität der Habitate positiv mit der Überlebensfähigkeit von Arten korrelieren, wird aus Konsistenzgründen im Folgenden die negativ bewerte Reallokation von Habitaten durch eine positive Größe ersetzt: die *Habitatkontinuität*. Diese misst, wie lange ein geschaffenes Habitat erhalten bleibt, bis es im Rahmen einer Reallokation wieder zerstört wird, und ist umgekehrt proportional zur Reallokationsrate.

*Abbildung 1: Beispiel einer an eine Landnutzungsdynamik gekoppelte Metapopulationsdynamik**



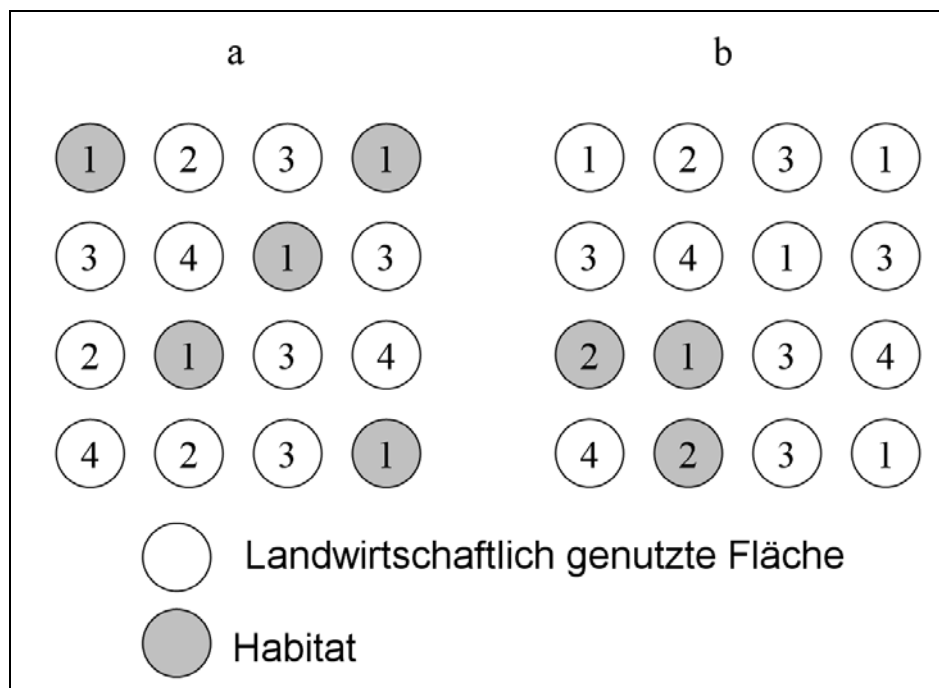
* Dargestellt ist eine hypothetische Landnutzungsdynamik auf drei Flächenstücken über die Zeit. Ein Flächenstück kann für den Naturschutz genutzt werden, also ein Habitat für die Art darstellen (weiße Rechtecke), oder nicht. Ein Habitat kann von der Art besiedelt sein, d.h. eine lokale Population beherbergen (graue Rechtecke), oder nicht. Ein leeres Habitat kann von der Art besiedelt werden, indem Individuen von einem der anderen Habitate in das leere Habitat einwandern (Pfeil „Besiedlung“). Eine lokale Population kann aufgrund natürlicher Prozesse aussterben („natürliches Aussterben“). Darüber hinaus impliziert die Zerstörung eines Habitats den sofortigen Verlust der darin befindlichen lokalen Population. Die gezeigte Landnutzungsdynamik erfolgt unter der Restriktion, dass stets genau zwei der Flächen für den Naturschutz genutzt werden. Die Habitatmenge in der Landschaft ist also zeitlich konstant.

1.4.2 Trade-offs zwischen Landschaftsindizes

Bei gegebenem Naturschutzbudget besteht im Allgemeinen ein Trade-off zwischen der Menge an Habitat, die insgesamt bereitgestellt werden kann, und der räumlichen Konnektivität der einzelnen Habitate. Indem man die Habitate dort bereitstellt, wo die Kosten am geringsten sind, maximiert man einerseits die Habitatmenge, die bei gegebenem Budget bereitgestellt werden kann; sofern die Orte mit den geringsten Kosten aber nicht benachbart sind, wird diese Konfiguration nicht die Habitatkonnektivität maximieren. Umgekehrt wird eine Konfiguration, die die Habitatkonnektivität maximiert, im Allgemeinen nicht alle kostenminimalen Flächen beinhalten und damit die Habitatmenge bei gegebenem Budget nicht maximieren. Damit besteht ein Trade-off zwischen Menge und Konnektivität der Habitate (vgl. Abb. 2), dessen Form von den ökonomischen Randbedingungen wie z.B. der räumlichen Verteilung der Kosten abhängt.

Habitatmenge und -konnektivität sind nicht nur auf der ökonomischen Ebene, sondern auch auf der ökologischen Ebene miteinander verknüpft, da es von den Eigenschaften der Art abhängt, ob und um welchen Faktor die Habitatmenge oder die Habitatkonnektivität für das Überleben der Art wichtiger ist (Drechsler & Wissel 1998, Wiegand et al. 2005). Zu diesen Eigenschaften gehört beispielsweise die Ausbreitungsfähigkeit der Art. Die kosteneffizienten Niveaus von Habitatmenge und -konnektivität, die also das Überleben der Art bei gegebenem Budget maximieren, hängen damit sowohl von den ökonomischen Randbedingungen als auch den biologischen Eigenschaften der zu schützenden Art ab.

Abbildung 2: Zwei hypothetische Landschaften mit Habitaten und landwirtschaftlich genutzten Flächen. Die Zahlen geben den betriebswirtschaftlichen Gewinn bei landwirtschaftlicher Nutzung bzw. die Kosten bei Nutzung der Fläche als Habitat an.*



* Auf der linken Seite werden die kostengünstigsten Flächen als Habitat genutzt, so dass bei einem Budget von fünf Geldeinheiten fünf Habitate finanziert werden können. Die Habitate sind jedoch in der Landschaft verstreut, so dass ihre räumliche Konnektivität gering ist. Auf der rechten Seite werden die Habitate so gewählt, dass sie nebeneinander liegen und ihre räumliche Konnektivität hoch ist. Dadurch ist es jedoch nicht mehr möglich, die kostengünstigsten Flächen als Habitat zu nutzen, so dass bei einem Budget von fünf Geldeinheiten nur drei Habitate finanziert werden können.

Ein ähnlicher Trade-off wie der zwischen Habitatmenge und Habitatkonnektivität besteht zwischen Habitatmenge und zeitlicher Kontinuität. Variieren die Kosten der Bereitstellung von Habitat räumlich und über die Zeit, so maximiert man bei gegebenem Budget die Habitatmenge, indem man die Habitate stets an den Orten mit den geringsten Kosten bereitstellt, was eine permanente Reallokation von Habitaten bedingt. Maximierung der Habitatmenge geht daher mit einem Verlust an Habitatkontinuität einher. Umgekehrt wird die Habitatkontinuität maximiert, indem Habitate nicht realloziert werden, was dazu führt, dass Habitate nicht zu allen Zeitpunkten an den jeweils kostengünstigsten Orten bereitgestellt werden und damit die Habitatmenge bei gegebenem Budget nicht maximiert wird. Die Form des Trade-offs zwischen Habitatmenge und -kontinuität hängt wieder von den ökonomischen Randbedingungen ab. Dazu gehört vor allem die Verteilung und Dynamik der Produktionskosten. Zu berücksichtigen sind hierbei nicht nur Einnahmeverluste

(Opportunitätskosten), die durch den Verzicht auf die betriebswirtschaftlich profitabelste Landnutzungsform entstehen, sondern auch Transformationkosten. Diese entstehen im betrachteten Kontext dadurch, dass die Umwandlung eines Habitats in landwirtschaftliche Produktionsfläche, aber vor allem auch die Umwandlung einer landwirtschaftlichen Fläche in ein Habitat, mit besonderen, über die Produktionskosten hinausgehenden, Kosten verbunden ist.

Wie bei dem Trade-off zwischen Habitatmenge und Habitatkonnektivität gibt es auch eine biologische Verknüpfung zwischen der Habitatmenge und der Habitatkontinuität. Je nach Eigenschaften der Art kann erstere oder letztere Größe für das Überleben der Art wichtiger sein.⁸ Zu diesen Eigenschaften der Art gehören ihre Sensitivität gegenüber Störungen und ihre Fähigkeit, neu erzeugte Habitate zu besiedeln (Hanski 1999).⁹ Darüber hinaus spielt auch die Zeit, die für die Erzeugung eines neuen Habitats benötigt wird, eine wichtige Rolle. Dieser Zeitraum kann je nach Habitattyp Jahrzehnte und mehr betragen (Mühlenberg & Slowik 1997: S. 229). Analog zu dem Trade-off zwischen Habitatmenge und Habitatkonnektivität hängen die kosteneffizienten Niveaus von Habitatmenge und Habitatkontinuität von den ökologischen und ökonomischen Parametern ab.

Wie in den Abschnitten 1.3.2 und 1.3.3 erläutert, können die Landschaftsindizes durch marktwirtschaftliche Instrumente gesteuert werden. Aufgrund verschiedener Faktoren wie z.B. asymmetrischer Informationsverteilung (Landnutzer sind über die Kosten von Naturschutzmaßnahmen oft besser informiert als Naturschutzbehörden) kann man erwarten, dass die Form der ökonomischen Trade-offs zwischen den Landschaftsindizes auch von der Wahl des Instruments abhängt. Deshalb werden im Rahmen dieser Arbeit die Trade-off und die kosteneffizienten Niveaus der Landschaftsindizes für verschiedene Instrumente (Regulation bei perfekter Information, Kompensationszahlungen, handelbare Landnutzungsrechte) untersucht.

2 Methodische Vorbetrachtungen

Dieser Abschnitt enthält einige methodische Vorbetrachtungen, die für das Verständnis der in Abschnitt 3 präsentierten Zeitschriftenartikel und deren Synthese in Abschnitt 4 hilfreich sind. Der folgende Abschnitt 2.1 stellt grundlegende Annahmen und Definitionen vor, auf denen die Analysen der vorliegenden Arbeit beruhen. Für das Verständnis und die Diskussion der Trade-offs zwischen den ökologischen und ökonomischen Landschaftsindizes und die daraus abgeleiteten kosteneffizienten Niveaus der Landschaftsindizes ist die ökonomische Produktionstheorie, die sich mit der effizienten Produktion von Gütern aus einer Menge von Produktionsfaktoren beschäftigt, sehr gut geeignet. Die für die Arbeit relevanten Aspekte dieser Theorie werden in Abschnitt 2.2 rekapituliert und in den Kontext des vorliegenden Problems gestellt.

⁸ Wie oben bemerkt wird im Rahmen dieser Arbeit davon ausgegangen, dass Habitatkontinuität für das Überleben einer Art förderlich; Abweichungen von dieser Annahme werden in der Diskussion der Ergebnisse erörtert.

⁹ In dem Artikel von Hanski (1999) hängt die Überlebensfähigkeit einer Metapopulation vom Produkt aus Habitatmenge und einer Art „räumlich-zeitlicher Konnektivität“ ab. Letztere hat eine zeitliche Komponente, die der hier verwendeten Habitatkontinuität ähnelt und u.a. von der räumlichen Ausbreitungsfähigkeit der Art abhängt.

2.1 Grundsätzliche Annahmen und Definitionen

Betrachtet werden in dieser Arbeit Landschaften mit jeweils N Flächenstücken $i=1, \dots, N$. Alle Flächenstücke haben dieselbe Größe, ihre jeweiligen räumlichen Positionen in der Landschaft sind gegeben durch die Ortsvektoren $\mathbf{r}_i$. Jedes Flächenstück i kann für landwirtschaftliche Produktion (ausgedrückt durch $x_i=0$) oder für den Naturschutz ($x_i=1$) verwendet werden. Die Landnutzung ist damit durch den Vektor $\mathbf{x}=(x_1, \dots, x_N)$ vollständig charakterisiert. Sie kann von der Zeit t abhängen, so dass $\mathbf{x}=\mathbf{x}(t)$. Die Nutzung einer Fläche i für den Naturschutz verursacht Produktionskosten in der Höhe c_i . Diese Kosten können sowohl im Raum als auch in der Zeit variieren, so dass $c_i=c_i(t)$. Um von konkreten Landschaften zu abstrahieren und ein größtmögliches Maß an Allgemeinheit zu erzielen, werden zufällige hypothetische „Kostenlandschaften“ betrachtet. Hierzu werden die c_i aus einer Zufallsverteilung gezogen mit Mittelwert 1 (womit alle c_i in Einheiten des Mittelwerts gemessen werden) und Variabilität (Streuung) σ . Um die Analysen handhabbar zu machen, wird – in Einschränkung der Allgemeinheit: siehe Diskussion in Abschnitt 5 – angenommen, dass die c_i räumlich unkorreliert sind.¹⁰

Bezüglich des Verhaltens der Landnutzer bzw. Agenten wird angenommen, dass sie ihren Gewinn maximieren. Bei Entscheidungen, die den Gewinn über mehrere Zeitperioden beeinflussen, wird diejenige gewählt, die den Nettobarwert maximiert, der durch die Summe der abdiskontierten erwarteten Gewinne aller zukünftigen Zeitperioden gegeben ist. Bei der Modellierung des Marktes für diese Rechte wird angenommen, dass dieser vollkommen ist (Feess 1997: S. 256, Baumol & Blinder 2003: S. 227). Insbesondere wird damit die Präsenz von Monopolisten ausgeschlossen, und der Preis der Landnutzungsrechte ermittelt sich in jeder Zeitperiode durch ein Gleichgewicht von Rechte-Angebot und -Nachfrage. Je nach Ausgestaltung des Naturschutzinstruments (räumlich homogene oder differenzierte Kompensationszahlungen, räumliche Anreizkomponenten, Besteuerung der Umwandlung von Habitaten in landwirtschaftliche Fläche, verfügbares Naturschutzbudget, etc.) ergeben sich verschiedene raumzeitliche Landnutzungsdynamiken $\mathbf{x}(t)$.

Im Allgemeinen wird angenommen, dass eine für den Naturschutz genutzte Fläche als Habitat für die zu schützende Art geeignet ist. In einigen Analysen wird dagegen berücksichtigt, dass die Renaturierung, also die Umwandlung von landwirtschaftlicher Fläche in ein Habitat, Zeit braucht. Während dieser Zeit wirft die Fläche also weder landwirtschaftliche Erträge ab, noch ist sie als Habitat für die zu schützende Art geeignet. Abgesehen davon besitzen alle Habitatflächen dieselbe Habitatqualität für die betrachtete Art. Mit diesen Annahmen bestimmt die Landnutzungsdynamik unmittelbar die räumliche Verteilung der Habitate, und wie sich diese über die Zeit ändert. Diese raumzeitliche Habitatdynamik wiederum bestimmt die Überlebensfähigkeit der in der Landschaft lebenden Art, die über das Naturschutzinstrument kosteneffizient geschützt werden soll.

Die Abschätzung der Überlebensfähigkeit der zu schützenden Art in der durch die Vektoren $\mathbf{r}$ und $\mathbf{x}(t)$ definierten Landschaft basiert auf dem in der Ökologie häufig verwendeten Metapopulations-Konzept von Levins (1969) und Hanski & Gilpin (1991). Eine Metapopulation wird dabei als Ensemble von Teil- oder lokalen Populationen betrachtet, von denen jede eine Habitatfläche besetzt. Einzelne lokale Populationen können aufgrund verschiedener ökologischer Faktoren wie z.B. ungünstiger Witterungsbedingungen aussterben. Im Gegenzug können, sofern die Art zwischen den einzelnen Habitatflächen wandern kann (d.h. einzelne Individuen eine Habitatfläche verlassen können, um eine andere aufzusuchen), leere Habitatflächen wiederbesiedelt werden. Das Metapopulationskonzept

¹⁰ Das heißt, dass beispielsweise die Wahrscheinlichkeit, auf Fläche i hohe Kosten zu beobachten, unabhängig davon ist, welche Kosten auf den anderen Flächen beobachtet werden.

wird häufig zur Beschreibung der Dynamik von Arten in räumlich strukturierten Landschaften verwendet.

In Anlehnung an die Betrachtungen in Abschnitt 1.4.1 wird die raumzeitliche Dynamik der Landschaft ($\mathbf{r}$, $\mathbf{x}(t)$) durch drei Landschaftsindizes charakterisiert:

1. die Gesamtzahl der Habitatflächen (Habitatmenge),
2. die räumliche Konnektivität der Habitate (Habitatkonnektivität), und
3. die zeitliche Kontinuität der Habitate (Habitatkontinuität).

Zur Abschätzung der Überlebensfähigkeit einer Art als Funktion ihrer biologischen Eigenschaften und der drei genannten Landschaftsindizes wird eine eigens entwickelte mathematische Formel verwendet (Aufsatz I in Abschnitt 3.1). Konkret erlaubt diese Formel die Berechnung der mittleren bzw. erwarteten Überlebensdauer einer Metapopulation in Abhängigkeit der genannten Faktoren. Einer Landnutzungsdynamik ($\mathbf{r}$, $\mathbf{x}(t)$) kann damit insgesamt sowohl ein ökologischer Benefit (Überlebensfähigkeit einer Art) als auch ökonomische Kosten (beispielsweise die Summe über alle Produktionskosten c_i) zugeordnet werden, was eine Bewertung der Kosteneffizienz ermöglicht.

2.2 Einbeziehung der ökonomischen Produktionstheorie

2.2.1 Allgemeine Betrachtungen

Die ökonomische Produktionstheorie beschäftigt sich mit der effizienten Produktion von Gütern aus einer Menge von Produktionsfaktoren und analysiert Substitutions- und Transformationsbeziehungen zwischen diesen Gütern und Produktionsfaktoren. Die in Abschnitt 1.4.2 andiskutierten Trade-offs zwischen den Landschaftsindizes lassen sich daher mit Hilfe der ökonomischen Produktionstheorie sehr gut analysieren.

Die Produktionstheorie gehört zum ökonomischen Standardrepertoire und findet sich in praktisch allen mikroökonomischen Lehrbüchern wie z.B. Varian (2004: S. 326 ff.), Wiese (2005: S. 193ff.) oder Endres & Martiensen (2007: S. 199 ff.). Bei der Zusammenstellung der für die vorliegende Fragestellung relevanten Aspekte orientiere ich mich im Folgenden an dem Lehrbuch von Feess (1997), das als repräsentativ für die ökonomischen Standard-Betrachtungen zur Produktionstheorie angesehen werden kann. In Kapitel 3 dieses Buches wird die Produktion eines Guts mit Hilfe zweier Produktionsfaktoren betrachtet. Die Menge des produzierten Guts sei mit z bezeichnet, die Mengen der beiden Produktionsfaktoren mit y_1 bzw. y_2 . Die substitutionale Produktionsfunktion $z(y_1, y_2)$ gibt die Outputmenge z an, die bei Einsatz der Mengen y_1 und y_2 produziert werden kann. Als Grenzproduktivität wird die partielle Ableitung von z nach den Faktoren y_1 und y_2 bezeichnet. Sie gibt an, um wie viele Einheiten die Outputmenge z erhöht werden kann, wenn y_1 bzw. y_2 um eine Einheit erhöht wird. Der Begriff „substitutional“ meint, dass die Faktoren 1 und 2 substituiert werden können, also dass beispielsweise eine Verminderung von y_1 durch eine Erhöhung von y_2 ausgeglichen werden kann, so dass nach wie vor dieselbe Outputmenge $z = \bar{z}$ produziert werden kann. Um wie viele Einheiten y_2 erhöht werden muss, um eine bestimmte Reduktion in y_1 auszugleichen, wird durch die Grenzrate der Substitution („marginal rate of substitution – MRS),

$$MRS_{21} = \left| \frac{dy_2}{dy_1} \right|_{z=\bar{z}} = \frac{\frac{\partial z}{\partial y_1} \Big|_{z=\bar{z}}}{\frac{\partial z}{\partial y_2} \Big|_{z=\bar{z}}},$$

gegeben. Sie ist das Verhältnis der Grenzproduktivitäten $\partial z/\partial y_1$ und $\partial z/\partial y_2$ bei festgehaltener Outputmenge $\bar{z}$.

Die Funktion $y_2(y_1 | z = \bar{z})$ wird als Isoquante bezeichnet und gibt an, wie viele Einheiten des Faktors 2 eingesetzt werden müssen, wenn y_1 Einheiten des Faktors 1 eingesetzt werden und die Outputmenge $\bar{z}$ produziert werden soll. Geometrisch ist die Grenzrate der Substitution, MRS_{21} , die (totale) Ableitung von y_2 nach y_1 . Unter der Annahme fallender Grenzproduktivitäten ($\partial^2 z/\partial y_1^2 < 0$ und $\partial^2 z/\partial y_2^2 < 0$), die bei technischen Produktionsprozessen im Allgemeinen erfüllt ist, ist die Isoquantenkurve konvex: $d^2 y_2/dy_1^2 > 0$.

In Kapitel 7 erweitert Feess (1997) seine Betrachtung auf die Produktion zweier Güter mit Hilfe zweier Produktionsfaktoren. Die Outputmengen der beiden Güter werden mit y_1 und y_2 bezeichnet, die Mengen der beiden Produktionsfaktoren mit X_1 und X_2 . Der Anteil von X_1 , der für die Produktion von Gut 1 (2) verwendet wird, wird mit x_{11} (x_{12}) bezeichnet, so dass $x_{11} + x_{12} = X_1$; für Produktionsfaktor 2 gilt analoges. Die substitutionalen Produktionsfunktionen $y_1(x_{11}, x_{21})$ und $y_2(x_{12}, x_{22})$ geben an, wie viele Einheiten y_1 und y_2 bei Einsatz der Mengen x_{11} , x_{21} , x_{12} und x_{22} produziert werden können.

Man kann zeigen, dass bei effizienter Produktion die Grenzzraten der Substitution für beide Güter gleich sind:

$$\frac{\frac{\partial y_1}{\partial x_{11}}}{\frac{\partial y_1}{\partial x_{21}}} = \frac{\frac{\partial y_2}{\partial x_{12}}}{\frac{\partial y_2}{\partial x_{22}}}.$$

Aus dieser Bedingung folgt die Gleichung

$$MRT_{21} = \left| \frac{dy_2}{dy_1} \right| = \frac{\frac{\partial y_2}{\partial x_{12}}}{\frac{\partial y_1}{\partial x_{11}}} = \frac{\frac{\partial y_2}{\partial x_{22}}}{\frac{\partial y_1}{\partial x_{21}}}$$

Die Ableitung $|dy_2/dy_1|$ wird als Grenzrate der Transformation („marginal rate of transformation“ – MRT) bezeichnet und gibt an, um wie viele Einheiten (bei effizienter Produktion beider Güter) die Produktion von Gut 2 abgesenkt werden muss, wenn die Produktion des Gutes 1 um eine Einheit erhöht wird. Die Gleichung sagt aus, dass die Grenzrate der Transformation gegeben ist durch den Quotienten der Grenzproduktivitäten der beiden Güter, wobei es egal ist, ob man diesen bezüglich Faktor 1 ($\partial y_i/\partial x_{1i}$) ($i=1,2$) oder bezüglich Faktor 2 ($\partial y_i/\partial x_{2i}$) ($i=1,2$) bildet.

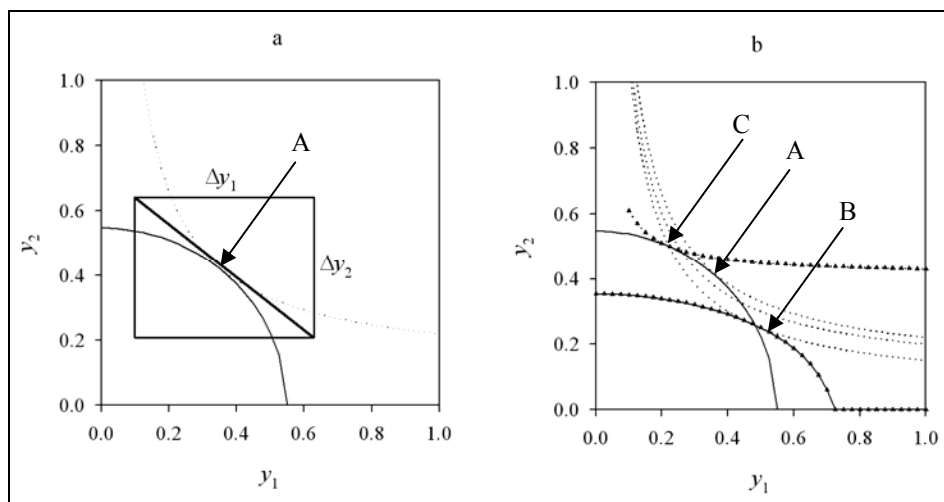
Die Funktion $y_2(y_1 | x_{11} + x_{12} = X_1, x_{21} + x_{22} = X_2)$ wird als Transformationskurve bezeichnet und gibt an, wie viele Einheiten des Gutes 2 produziert werden können, wenn y_1 Einheiten des Gutes 1 produziert werden und die beiden Faktoren 1 und 2 mit jeweiligen Mengen X_1 und X_2 eingesetzt werden. Geometrisch ist die Grenzrate der Transformation, MRT_{21} , die (totale) Ableitung von y_2 nach y_1 . Unter der Annahme fallender Grenzproduktivitäten $\partial^2 y_i/\partial x_{ij}^2 < 0$ ($i,j=1,2$), die bei technischen Produktionsprozessen im Allgemeinen erfüllt ist, ist die Transformationskurve konkav: $d^2 y_2/dy_1^2 < 0$.

Diese Betrachtungen lassen sich nun kombinieren in dem Sinne, dass aus den Produktionsfaktoren mit jeweiligen Mengen X_1 und X_2 in effizienter Weise zwei Zwischenprodukte mit jeweiligen Mengen y_1 und y_2 produziert werden, aus denen schließlich das Endprodukt mit Menge z produziert wird. Man kann leicht zeigen (s. Anhang A), dass bei effizienter Produktion (und fallenden Grenzproduktivitäten) die Grenzrate der Transformation

$MRS_{21}=dy_2/dy_1$ (bezüglich der Produktion von y_1 und y_2 aus X_1 und X_2) gleich der Grenzrate der Substitution $MRT_{21}=dy_2/dy_1$ (bezüglich der Produktion von z aus y_1 und y_2) ist (Abb. 3a).

Die effizienten Mengen y_1 und y_2 der Zwischenprodukte lassen sich nun in eleganter Weise durch die Formen der Transformations- und Isoquantenkurven erklären. Je flacher beispielsweise der Abfall der Transformationskurve, desto niedriger ist ceteris paribus das effiziente Niveau von y_2 im Vergleich zu dem von y_1 (Abb. 3b). Dies ist plausibel, da bei einem flachen Abfall der Transformationskurve die Reduktion von Zwischenprodukt 1 um eine Einheit die Produktion nur weniger weiterer Einheiten des Zwischenprodukts 2 ermöglicht. Analog erhöht ein flacher Abfall der Isoquantenkurve das effiziente Niveau von y_2 gegenüber dem von y_1 (Abb. 3b), da bei einem flachen Abfall der Isoquantenkurve die Reduktion des Zwischenprodukts 1 um eine Einheit durch die Produktion nur weniger weiterer Einheiten des Zwischenprodukts 2 ausgeglichen werden kann, um dieselbe Menge des Endprodukts z erzeugen zu können.

Abbildung 3: Beispiele für Transformationskurven (durchgezogene Linien) und Isoquantenkurven (gepunktete Linien) zweier Zwischenprodukte mit Mengen y_1 und y_2 .*



* Links: Die kosteneffizienten Niveaus der beiden Zwischenprodukte befinden sich an dem Punkt A, an dem sich Transformations- und Isoquantenkurven berühren, d.h. wo die Grenzrate der Transformation gleich der Grenzrate der Substitution ist. Rechts: Reduziert man die Steigung der Produktionskurve (durchgezogene Linie mit Dreiecken), so wandert bei den gegebenen Isoquantenkurven (gepunktete Linien) der kosteneffiziente Punkt nach rechts unten (B), also zu höheren Mengen y_1 und geringeren Mengen y_2 . Reduziert man die Steigung der Isoquantenkurve (gepunktete Linie mit Dreiecken), so wandert bei gegebener Transformationskurve (durchgezogene Linie) der kosteneffiziente Punkt nach links oben (C), also zu geringeren y_1 und höheren y_2 .

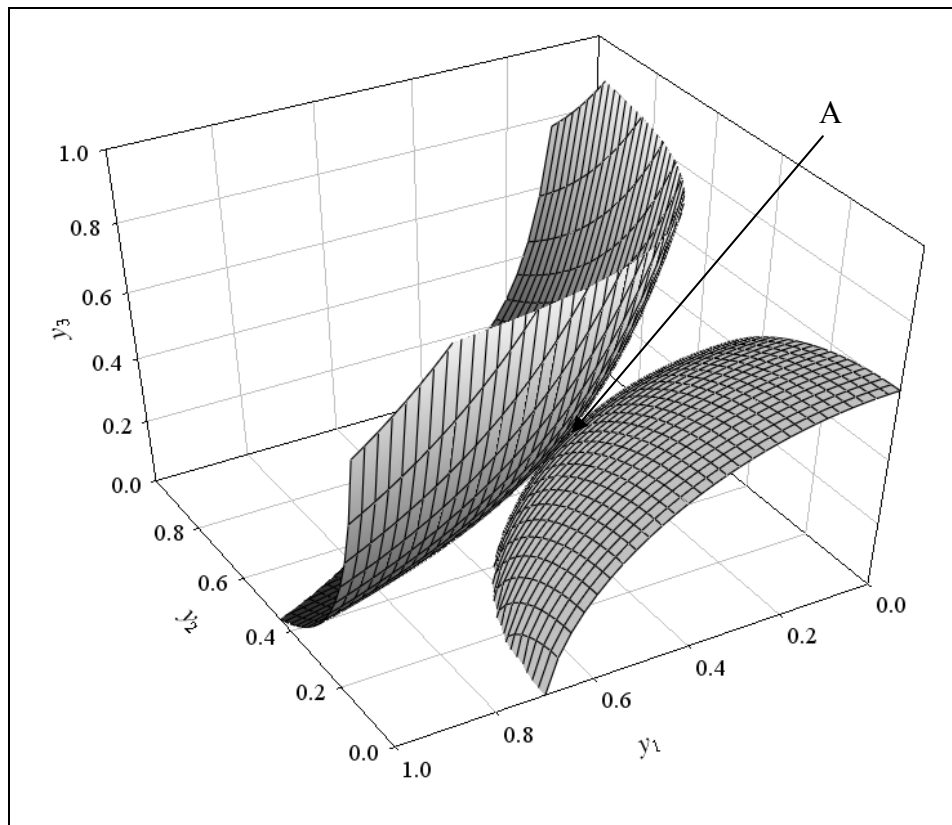
Diese grundlegenden mikroökonomischen Zusammenhänge werden im folgenden Abschnitt zur Strukturierung der in dieser Arbeit betrachteten Artenschutzprobleme angewandt.

2.2.2 Anwendung auf den kosteneffizienten Artenschutz

Der im vorangegangenen Abschnitt beschriebene zweistufige Produktionsprozess ($x_i \rightarrow y_i \rightarrow z$) entspricht mit ein wenig Abstraktion dem in Abschnitt 2.1 vorgestellten Ansatz zur Analyse von Landschaftsdynamiken im Hinblick auf die mittlere Lebensdauer von Metapopulationen. Die Flächen $i=1, \dots, N$ können als Produktionsfaktoren betrachtet werden, mit jeweiligen Mengen $x_i=1$ (Habitat) oder $x_i=0$ (landwirtschaftliche Produktion). Die Kosten einer (der

einzig möglichen) Einheit von x_i zum Zeitpunkt t sind durch die Funktion $c_i(t)$ gegeben. Der Einsatz der Produktionsfaktoren x_i zu den Zeitpunkten t entspricht der in Abschnitt 2.1 definierten Landnutzungsdynamik $\mathbf{x}(t)$, welche durch die drei Landschaftsindizes Habitatmenge, Habitatkonnektivität und Habitatkontinuität charakterisiert wird. Diese drei Landschaftsindizes können als Zwischenprodukte und ihre quantitative Ausprägung als deren Mengen $y_1=y_1(\mathbf{x})$, $y_2=y_2(\mathbf{x})$ und $y_3=y_3(\mathbf{x})$ betrachtet werden. Aus diesen drei Zwischenprodukten wird schließlich das Endprodukt, die mittlere Lebensdauer der Metapopulation generiert, wobei die Formel in Aufsatz I (siehe Abschnitt 3.1) die Rolle der Produktionsfunktion $z(y_1, y_2, y_3)$ einnimmt. Sind die Grenzproduktivitäten der Produktionsfunktionen $y_j(\mathbf{x})$ ($j=1,2,3$) und $z(y_1, y_2, y_3)$ fallend, (vgl. Abschnitt 2.2.1), so ergeben sich die effizienten Niveaus von y_1 , y_2 und y_3 durch den Berührungspunkt von Transformations- und Isoquantenfläche (Abb. 4).

Abbildung 4: Transformationsfläche (rechts unten) und Isoquantenfläche (links oben) dreier Zwischenprodukte mit Mengen y_1 , y_2 und y_3 und kosteneffizientem Punkt A



Die Formel in Aufsatz I eignet sich gut zur Bestimmung von Isoquantenkurven für die oben genannten Landschaftsindizes, so dass man angeben kann, um welchen Betrag ein Landschaftsindex erhöht werden muss, um die Reduktion in einem anderen auszugleichen, so dass die mittlere Lebensdauer der Metapopulation erhalten bleibt. Beispiele für Transformationskurve zeigt Abbildung 3 von Aufsatz I. In Tafel a dieser Abbildung wird beispielsweise eine Transformationskurve bezüglich zweier Parameter, N und R , diskutiert. Der Parameter N steht dort für die Anzahl der Habitatflächen, während Parameter R den Radius des kleinstmöglichen Kreises, der alle Habitatflächen umfasst, repräsentiert. Dieser

Radius wird in dem Aufsatz als Maß für die Habitatkonnektivität verwendet, da ein großer (kleiner) Radius einer geringen (hohen) Habitatkonnektivität entspricht.

Die obigen Betrachtungen haben deutlich gemacht, wie ökonomische Grundsachverhalte auf die Ökologie übertragen werden können. Auf dieser Basis können nun die Aufsätze dieser Dissertationsschrift eingeordnet und zusammengefasst werden.

3 Zusammenfassungen der Aufsätze

In die vorliegende Arbeit gehen sieben Zeitschriftenartikel ein, die jeweils unterschiedliche Aspekte der beschriebenen Trade-offs, der kosteneffizienten Niveaus der Landschaftsindizes und der Rolle des für die Umsetzung der Naturschutzmaßnahmen gewählten politischen Instruments beleuchten. Die Hauptgedanken dieser sieben Aufsätze werden im Folgenden skizziert.

3.1 Aufsatz I

Drechsler M, Johst K, 2010. Rapid viability analysis for metapopulations in dynamic landscapes. Proceedings of the Royal Society B 277, 1889-1897.

Die im vorangegangenen Abschnitt erwähnte Überlebensfähigkeit einer Art kann durch verschiedene Messgrößen ausgedrückt werden. Da die Dynamik von Populationen im Allgemeinen Zufallseinflüssen ausgesetzt ist (Wissel et al. 1994), sind diese Messgrößen meist statistischer Natur. Insbesondere kann man ausschließen, dass eine Art oder Population unendlich lange persistieren kann. Stattdessen wird sie (ähnlich dem Ausspruch von John Maynard Keynes, „Langfristig sind wir alle tot“) irgendwann mit Sicherheit ausgestorben sein. Dazwischen ist es sinnvoll, von der Wahrscheinlichkeit $P(t)$ zu sprechen, dass die Population bis zum Zeitpunkt t überlebt. In diversen theoretischen Arbeiten hat sich gezeigt (z.B. Grimm & Wissel 2004), dass die Überlebenswahrscheinlichkeit oft exponentiell mit der Zeit abnimmt:

$$P(t) \approx \exp(-t/T).$$

Dabei ist $1/T$ die Aussterberate bzw. T die mittlere Lebensdauer der Population.

In dem vorliegenden Aufsatz wird eine mathematische Formel entwickelt, mit deren Hilfe diese mittlere Lebensdauer für eine Metapopulation in einer räumlich strukturierten und dynamischen Landschaft abgeschätzt werden kann. Es zeigt sich, dass die mittlere Lebensdauer der Metapopulation in guter Näherung als Funktion von drei Landschaftsindizes ausgedrückt werden kann: der Anzahl der Habitate, deren räumlicher Konnektivität (ausgedrückt durch den Radius eines Kreises, der alle Habitat umfasst) und deren zeitlicher Kontinuität (ausgedrückt durch den Anteil an Habitaten, der von einem Zeitschritt zum nächsten nicht realloziert wird). Dies sind genau die drei in Abschnitt 1.4.1 vorgestellten Landschaftsindizes, zwischen denen Trade-offs untersucht werden sollen.

Neben diesen drei Landschaftsindizes hängt die mittlere Lebensdauer auch von den Arteigenschaften ab. Berücksichtigt werden in der Formel hierbei unter anderem

- a. die Rate, mit der lokale Populationen auf einzelnen Habitatflächen aussterben,
- b. die Ausbreitungsfähigkeit der Art, charakterisiert durch die mittlere Distanz, die wandernde Individuen zwischen Habitatflächen zurücklegen können,

- c. ein „Replikationsfaktor“¹¹, der angibt, wie viele leere Habitatflächen bei unendlicher Ausbreitungsdistanz durch eine lokale Population während ihrer mittleren Lebensdauer besiedelt werden können. Er ist gegeben durch die Rate, mit der Individuen aus einer lokalen Population emigrieren, multipliziert mit der Wahrscheinlichkeit, dass ein in ein leeres Habitat eingewandertes Individuum dort eine lokale Population etablieren kann, dividiert durch die obige Rate, mit der eine lokale Population ausstirbt.

Dieser erste Aufsatz bildet die ökologische Basis, auf der die ökonomischen Betrachtungen aufbauen können. Die Ergebnisse dieses Aufsatzes fließen in mehrere der folgenden Aufsätze ein.

3.2 Aufsatz II

Johst K, Drechsler M, van Teeffelen AJA, Hartig F, Vos CC, Wissel S, Wätzold F, Opdam P. Conservation planning for dynamic landscapes – tradeoffs between spatial and temporal landscape attributes. Journal of Applied Ecology, eingereicht.

Dieser Aufsatz verwendet die Formel aus Aufsatz I zur Analyse ökologischer Trade-offs zwischen verschiedenen Landschaftsindizes. Der Fokus liegt dabei auf der Rolle von Landschaftsdynamik. Es wird argumentiert, dass sich diese aufgrund von globalem Wandel ändern kann, was Auswirkungen auf die Überlebensfähigkeit der in der Landschaft lebenden Arten hat. Im Kontext ökologischer Trade-offs werden zwei Fragestellungen untersucht. Zum einen: kann eine erhöhte Landschaftsdynamik mit verringerter Habitatkontinuität durch eine Verbesserung statischer Landschaftsindizes wie Habitatmenge und -konnektivität ausgeglichen werden, und zum anderen: ändern sich Trade-offs zwischen statischen Landschaftsindizes wie der zwischen Habitatmenge und -konnektivität, wenn eine vormals statische Landschaft (mit quasi unendlicher Habitatkontinuität) dynamisch wird (die Habitatkontinuität also endlich wird).

Die Analysen zeigen zunächst grundsätzlich, dass die Trade-offs zwischen den Landschaftsindizes nicht-linear, die Grenzzraten der Substitution also nicht konstant sind. Dies bedeutet, dass der Betrag, um den ein Landschaftsindex erhöht werden muss, um die Reduktion eines anderen Landschaftsindizes zu kompensieren, von den aktuellen Niveaus der Landschaftsindizes abhängt, und mag aus mathematischer Sicht nicht besonders verwundern; es steht jedoch im Widerspruch zu diversen ökologischen Ansätzen zur Landschaftsplanung, die von konstanten Substitutionsraten zwischen Landschaftsindizes ausgehen. Betrachtet man die Trade-offs zwischen Habitatmenge und -konnektivität einerseits für statische und andererseits für dynamische Landschaften, so ist der Grad der Nichtlinearität bei statischen Landschaften höher als bei dynamischen.

Darüberhinaus hängen die Grenzzraten der Substitution zwischen den Landschaftsindizes von den Eigenschaften der zu schützenden Art ab. So zeigt sich, dass man zwischen zwei Typen von Arten unterscheiden muss: den sogenannten „r-Strategen“ (Begon et al. 1990), die sich durch eine gute Ausbreitungsfähigkeit, einen hohen Replikationsfaktor (vgl. Abschnitt 3.1) und eine geringe Empfindlichkeit gegenüber Schwankungen in den Umweltbedingungen, etwa der Witterung oder dem Nahrungsangebot, auszeichnen, und den sogenannten „K-Strategen“ (Begon et al. 1990), die eine geringe Ausbreitungsfähigkeit, einen niedrigen Replikationsfaktor und eine hohe Empfindlichkeit gegenüber Umweltschwankungen besitzen.

¹¹ In den Originalarbeiten wurde diese Größe mit dem Begriff „local colonisation-extinction ratio“ bezeichnet. Der Begriff Replikationsfaktor ist möglicherweise anschaulicher und lehnt sich etwas an die Epidemiologie an: ein Krankheitserreger kann sich dann ausbreiten, wenn im Mittel ein infiziertes Individuum bis zum Zeitpunkt, an dem seine Infektiosität endet, mehr als ein gesundes Individuum infizieren kann.

Vergleicht man den relativen Einfluss verschiedener Landschaftsindizes miteinander, so zeigt sich, dass sich die Überlebensfähigkeit von K-Strategen am besten durch eine Erhöhung der Zahl und räumlichen Konnektivität der Habitate steigern kann. r-Strategen lassen sich dagegen besser durch eine Erhöhung der mittleren Größe¹² der Habitatflächen und/oder eine Erhöhung der Habitatkontinuität steigern.

Insgesamt zeigt sich an diesem Aufsatz, dass das ökonomische Konzept des Trade-offs bzw. der Grenzrate der Substitution auch für die Untersuchung rein ökologische Fragestellungen wie der ökologischen Wirksamkeit von Naturschutzmaßnahmen sehr gut geeignet ist.

3.3 Aufsatz III

Drechsler M. Trade-offs in the design of cost-effective habitat networks when conservation costs are variable in space and time. Biological Conservation, im Druck.

Das Wissen über die ökologischen Trade-offs bzw. Grenzzraten der Substitution allein ermöglicht noch keine Aussagen zu den kosteneffizienten Niveaus der Landschaftsindizes. Dazu werden, wie in den Abschnitten 2.2.1 und 2.2.2 erläutert, noch die Grenzzraten der Transformation benötigt, die angeben, um welchen Betrag ein Landschaftsindex vermindert werden muss, damit bei gegebenem Budget ein anderer Landschaftsindex um einen bestimmten Betrag erhöht werden kann. Die Grenzzraten der Transformation werden in diesem Aufsatz über ein mathematisches Modell bestimmt. Das Modell geht davon aus, dass die (Produktions-) Kosten c_i der Naturschutzmaßnahmen auf den Flächenstücken $i=1, \dots, N$ räumlich unkorreliert und aus einer für alle i identischen Wahrscheinlichkeitsverteilung gezogen werden. Mit diesen Annahmen lässt sich eine Grenzkostenfunktion $c(N')$ bestimmen, mit deren Hilfe durch Summation bzw. Integration die Gesamtkosten für die Durchführung von Naturschutzmaßnahmen auf den $N' \leq N$ „billigsten“ Flächen errechnet werden kann. Diese N' billigsten Flächen sind aufgrund der räumlichen Unkorreliertheit der Kosten zufällig über die Landschaft verteilt und die räumliche Konnektivität der erzeugten Habitat gering. Eine Erhöhung der räumlichen Konnektivität wird dadurch simuliert, dass nur Flächen in einer kreisförmigen Zone mit einem bestimmten Radius R für Naturschutzmaßnahmen in Frage kommen. Diese Einschränkung erhöht die Steigung der Grenzkostenfunktion $c(N')$ und damit die Durchschnittskosten pro Habitat, was zu dem bereits in Abschnitt 1.4.2 postulierten ökonomischen Trade-off zwischen Habitatmenge und Habitatkonnektivität (bei gegebenem Budget) führt.

Das beschriebene Modell ermöglicht die analytische Bestimmung der Grenzzrate der Transformation zwischen Habitatmenge und -konnektivität als Funktion der räumlichen Variabilität der Kosten (σ) und des zur Verfügung stehenden Naturschutzbudgets. Zusammen mit den Grenzzraten der Substitution, die über die Formel in Aufsatz I bestimmt werden, werden nun über eine einfache numerische Optimierung die kosteneffizienten Niveaus von Habitatmenge und Habitatkonnektivität ermittelt. Neben der Kostenvariabilität und dem Budget hängen sie von den Eigenschaften der zu schützenden Art ab – betrachtet werden hier die Ausbreitungsfähigkeit und der Replikationsfaktor (vgl. Abschnitt 3.1). Im Detail werden diese Ergebnisse in Abschnitt 5 vorgestellt und diskutiert.

In ähnlicher Weise wird die Grenzkostenfunktion für eine dynamische Landschaft, in der sich die c_i zufällig (und zeitlich unkorreliert) ändern, bestimmt. Nimmt man an, dass in jeder Zeitperiode Naturschutzmaßnahmen stets auf den „billigsten“ Flächenstücken durchgeführt

¹² Da in der vorliegenden Arbeit die Größe der einzelnen Habitatflächen als unveränderlich angenommen wird, ist die Habitatmenge ausschließlich durch die der Anzahl der Habitate bestimmt. Die Substitutionsrate zwischen Anzahl und mittlerer Größe der Habitate bei gegebener Habitatmenge, in der Ökologie als SLOSS-(„single large or several small patches“)-Problem bezeichnet, wird nicht betrachtet.

werden, so ergibt sich wieder die obige Funktion $c(N')$. Für diese Allokationsstrategie muss aufgrund der sich permanent ändernden Kosten stets ein bestimmter Prozentsatz von Naturschutzmaßnahmen realloziert werden, was zu einer Reduzierung der Habitatkontinuität (von quasi unendlich auf einen endlichen Wert) führt. Alternativ kann man die Anzahl der Naturschutzmaßnahmen, die pro Zeitperiode realloziert werden darf, einschränken. Dies erhöht einerseits die Habitatkontinuität aber andererseits auch die Steigung der Grenzkostenfunktion $c(N')$, was zu dem in Abschnitt 1.4.2 postulierten ökonomischen Trade-off zwischen Habitatmenge und -kontinuität (bei gegebenem Budget) führt.

Analog zum Trade-off zwischen Habitatmenge und -konnektivität wird wieder eine Transformationskurve für die beiden Landschaftsindizes Habitatmenge und -kontinuität analytisch ermittelt. Durch Zusammenführung mit der Isoquantenkurve, die sich durch die Formel in Aufsatz I bestimmt, werden die kosteneffizienten Niveaus der beiden Landschaftsindizes errechnet. Sie hängen von der zeitlichen Variabilität der Kosten und dem Budget einerseits und den Arteigenschaften (berücksichtigt werden der Replikationsfaktor und die Rate, mit der lokale Populationen aussterben: vgl. Abschnitt 3.1) andererseits ab. Details zu den Einflüssen dieser Parameter finden sich in Abschnitt 5.

Zuletzt wird in Aufsatz III noch der Fall betrachtet, dass die Naturschutzmaßnahmen über Kompensationszahlungen (vgl. Abschnitt 1.3.2) induziert werden. Aus Akzeptanzgründen und um Transaktionskosten nicht ausufern zu lassen, ist es üblich, dass alle Landnutzer dieselbe Zahlung für die Durchführung von Naturschutzmaßnahmen erhalten. Die Gesamtkosten für N' Habitate sind daher nicht die Summe bzw. das Integral über die Grenzkostenfunktion sondern das Produkt $c(N')N'$ aus den Kosten des „teuersten“ Habitats und der Zahl der Habitate. Landnutzer mit Kosten $c_i < c(N')$ erhalten dadurch eine Produzentenrente, was bei gegebenem Naturschutzbudget zu geringerer Habitatmenge und/oder Habitatkonnektivität führt.

3.4 Aufsatz IV

Drechsler M, Wätzold F, Johst K, Bergmann H, Settele J, 2007. A model-based approach for designing cost-effective compensation payments for conservation of endangered species in real landscapes. Biological Conservation 140, 174-186.

Dieser Aufsatz beschäftigt sich mit Kompensationszahlungen für Naturschutzmaßnahmen. Es handelt sich bei diesem Aufsatz um eine Fallstudie, bei der es um den Schutz des gefährdeten Wiesenknopf-Ameisenbläulings im Kreis Landau in Rheinland-Pfalz geht. Hauptziel des Aufsatzes ist die Ermittlung eines kosteneffizienten Mahdregimes. Betrachtet wird eine Ausgangsmenge verschiedener Mahdregimes, die definiert sind durch die Mahd-Häufigkeit (ein bzw. zwei Mal pro Jahr) und die Zeitpunkte der ersten und ggf. der zweiten Mahd.

Die verschiedenen Mahdregimes haben unterschiedliche Kosten, vor allem aufgrund unterschiedlicher Erträge aus dem geernteten Mahdgut. Betriebswirtschaftlich optimal sind in der Untersuchungsregion zwei Mahdtermine, der erste Ende Mai und der zweite Mitte Juli. Der zweite Mahdtermin fällt jedoch genau in die Flugzeit, während der die Schmetterlinge ihre Eier auf einer bestimmten Pflanze, dem Gemeinen Wiesenknopf, ablegen. Durch die Mahd werden die Eier zerstört bzw. von der Wiese entfernt und der Weiterbestand der Schmetterlingspopulation verhindert. Eine Verschiebung der zweiten Mahd auf einen anderen Zeitpunkt, bei dem die Reproduktion der Schmetterlinge nicht beeinträchtigt wird, würde jedoch Einnahmeverluste für die Landwirte verursachen. Um die Landwirte zur freiwilligen Durchführung einer solchen Schmetterlingsschutzmaßnahme zu bewegen, müssen sie für diese Einnahmeausfälle kompensiert werden.

Die ökonomische Modellierung in diesem Aufsatz basiert auf agrarökonomischen Kostenberechnungen, die sowohl die Kosten als auch die Erträge der verschiedenen Mahdregimes abschätzen. Bei diesen Werten handelt es sich um Durchschnittswerte, von denen der einzelne Landwirtschaftsbetrieb bzw. die einzelne Wiese abweichen kann. Dies wird durch Addition einer Zufallskomponente zu den ermittelten Werten berücksichtigt. Die Naturschutzbehörde kann nun ein bestimmtes Mahdregime wählen und für dieses eine für alle Wiesen identische Zahlung (pro Hektar) anbieten. Auf Wiesen, deren Kosten einschließlich der Zufallskomponente unterhalb der angebotenen Zahlung liegen, wird das geförderte Mahdregime durchgeführt, auf allen übrigen das oben beschriebene konventionelle. Die sich daraus ergebene Landnutzungsdynamik beeinflusst die Populationsdynamik des Wiesenknopf-Ameisenbläulings. Diese wird über ein Simulationsmodell beschrieben, welches den jährlichen Lebenszyklus des Schmetterlings (Imago – Ei – Larve – Puppe – Imago) nachstellt und auch die Bewegung der Schmetterlinge in der Landschaft berücksichtigt. Die ökologische Eignung der simulierten Landnutzungsdynamik wird über die (erwartete) Gesamtfläche der vom Schmetterling bevölkerten Wiesen gemessen.

Durch die systematische Analyse des ökologisch-ökonomischen Modells lassen sich zwei Mahdregimes mit vergleichsweise hoher Kosteneffizienz identifizieren. Das eine zeichnet sich durch zwei sehr frühe Mahdtermine vor der Flugzeit des Schmetterlings aus, das zweite durch eine erste Mahd vor der Flugzeit und eine zweite Mahd unmittelbar danach. Des Weiteren zeigt die Analyse, dass beträchtliche Effizienzgewinne erzielt werden könnten, wenn man die Kompensationszahlungen nach den Kosten der einzelnen Wiesen differenzieren könnte anstatt für alle Wiesen dieselbe Zahlung anzubieten, da hierdurch die im vorangegangenen Abschnitt erwähnte Produzentenrente minimiert werden könnte. Auch eine Steuerung der räumlichen Anordnung der mit den schmetterlingsfreundlichen Mahdregime bewirtschafteten Wiesen birgt nach den Modellanalysen ein Potenzial für Effizienzsteigerungen. Sie kann über die betrachteten räumlich homogenen Kompensationszahlungen jedoch nicht erreicht werden.

3.5 Aufsatz V

Drechsler M, Wätzold F, Johst K, Shogren JF, 2010. An agglomeration payment for cost-effective biodiversity conservation in spatially structured landscapes. Resource and Energy Economics 32, 261-275.

Dieser Aufsatz knüpft an die obige Kritik räumlich homogener Kompensationszahlungen an: dass sie zu aus Sicht der Behörde unerwünschten Produzentenrenten auf Seiten der Landnutzer führen, und dass eine räumliche Steuerung der Naturschutzmaßnahmen nicht möglich ist. Zur Verbesserung wird, auf Basis der Arbeit von Parkhurst et al. (2002), eine Agglomerationszahlung vorgeschlagen, deren Auszahlung sich daran knüpft, dass genügend andere Landnutzer in der Nachbarschaft ebenfalls die Maßnahme durchführen. Konkret muss in einem von den Landnutzern frei wählbaren Landschaftsausschnitt die „Habitatdichte“, also der Anteil der Fläche, auf dem die Maßnahme durchgeführt wird, einen bestimmten Mindestwert überschreiten. Die „konventionelle“ räumlich homogene Kompensationszahlung wird dabei mathematisch durch eine Mindest-Habitatdichte von Null und eine Agglomerationszahlung durch eine positive Mindest-Habitatdichte repräsentiert.

Die Kosteneffizienz dieser Agglomerationszahlung wird mit Hilfe eines konzeptionellen und eines angewandten Modells untersucht. In dem konzeptionellen Modell wird eine hypothetische Landschaft mit Flächenstücken auf einem quadratischen Raster betrachtet. Die (Produktions-) Kosten der Naturschutzmaßnahmen variieren zwischen den Flächen und sind wie in Aufsatz III zufällig verteilt. Die Behörde bietet eine räumlich homogene Zahlung an,

die jedoch an die Erzeugung der oben erwähnten Mindest-Habitatdichte in einem frei wählbaren Landschaftsausschnitt geknüpft ist. Unter der Annahme, dass die Landnutzer ihren aggregierten Gewinn, d.h. die Summe der erhaltenen Zahlungen über alle Landnutzer abzüglich der Summe aller Kosten, maximieren, entscheiden die Landnutzer, auf welchen Flächen Naturschutzmaßnahmen durchgeführt werden. Ökologisch bewertet wurde das Landnutzungsmuster durch eine einfache ökologische Benefitfunktion, die sowohl Habitatmenge als auch Habitatkonnektivität honoriert. Bei der Bewertung der Habitatkonnektivität wird berücksichtigt, dass die räumliche Nähe zwischen Habitaten bei Arten mit geringer Ausbreitungsfähigkeit im Vergleich zur Habitatmenge wichtiger ist als bei Arten mit hoher Ausbreitungsfähigkeit.

Die systematische Analyse verschiedener Niveaus von Zahlungen und Mindest-Habitatdichten zeigt, dass Agglomerationszahlungen im Sinne obiger Definition stets kosteneffizienter sind als räumlich homogene Zahlungen. Die Kosteneffizienz wächst mit zunehmender Mindest-Habitatdichte bis zu einem Punkt, an dem die geforderte Dichte bei der angebotenen Höhe der Zahlung nicht mehr erreicht werden kann. Die Effizienzsteigerung durch Agglomerationszahlungen konnte für verschiedene Kostenvariabilitäten (σ) und Arten unterschiedlicher Ausbreitungsfähigkeit beobachtet werden. Dass auch für Arten mit einer hohen Ausbreitungsfähigkeit eine Effizienzsteigerung beobachtet werden konnte, verwundert zunächst, wenn man bedenkt, dass der Einfluss der Habitatkonnektivität auf das Überleben einer Art mit hoher Ausbreitungsfähigkeit relativ gering, eine Erhöhung der Habitatkonnektivität bei gegebenem Budget jedoch eine beträchtliche Reduktion der Habitatmenge erfordert. Erwartet hätte man stattdessen eine Schwelle für die Ausbreitungsfähigkeit, unterhalb derer die Agglomerationszahlung kosteneffizienter als die homogene Kompensationszahlung ist, und oberhalb derer das Gegenteil der Fall ist. Der Grund für die Überlegenheit der Agglomerationszahlung auch bei ausbreitungsstarken Arten liegt in ihrer Fähigkeit, Produzentenrenten bei den Landnutzern abzuschöpfen. Um die Mindest-Habitatschwelle zu erreichen, kann es nämlich sein, dass Landnutzer einen Teil ihrer Produzentenrente über Seitenzahlungen benachbarten Landnutzern zukommen lassen müssen, damit diese einen positiven Gewinn aus der Durchführung der Naturschutzmaßnahme ziehen (näheres hierzu findet sich in Abschnitt 4.1).

Nach der Analyse des konzeptionellen Modells wird die vorgeschlagene Agglomerationszahlung auf die in Aufsatz IV betrachtete Landschaft zum Schutz des Wiesenknopf-Ameisenbläulings angewendet. Auch hier führt die Agglomerationszahlung zu einer höheren Kosteneffizienz als homogene Kompensationszahlungen.

3.6 Aufsatz VI

Drechsler M, Wätzold F, 2009. Applying tradable permits to biodiversity conservation: effects of space-dependent conservation benefits and cost heterogeneity on habitat allocation. Ecological Economics 68, 1083-1092.

Dieser Aufsatz untersucht die Landnutzungsdynamik, die sich ergibt, wenn man in einem Markt für handelbare Landnutzungsrechte (vgl. Abschnitt 1.3.2) die Menge der durch Erzeugung eines Habitats erworbenen Zertifikate an die Umgebung koppelt, in der das Habitat angelegt wurde. Je mehr Habitate schon in der unmittelbaren Nachbarschaft vorhanden sind, desto mehr Zertifikate kann man durch Anlegen eines Habitats erwerben bzw. desto mehr Zertifikate müssen aufgewendet werden, um ein Habitat zerstören zu dürfen.

Es wird postuliert, dass die resultierende Landnutzungsdynamik von einem Widerstreiten zweier Kräfte geprägt ist. Zum einen sollte der Anreiz, Habitate in der Nachbarschaft anderer Habitat anzulegen bzw. Habitate, die in der Nachbarschaft anderer Habitate liegen, nicht zu

zerstören, zu einer Agglomeration von Habitaten in der Landschaft, analog zu Parkhurst et al. (2002) und obigem Aufsatz V, führen. Andererseits besteht ein Anreiz, die Habitate an den kostengünstigsten Standorten anzulegen, was wegen der zufälligen räumlichen Verteilung der Kosten zu einer verstreuten Allokation der Habitate in der Landschaft führen sollte. Dieser zweite Anreiz ist umso stärker, je größer die räumliche Variabilität der Kosten ist.

Zur Untersuchung der Landnutzungsdynamik wird ein konzeptionelles dynamisches räumlich strukturiertes agentenbasiertes Modell entwickelt. Ähnlich wie in Aufsatz V sind die zu bewirtschaftenden Flächenstücke auf einem quadratischen Raster angeordnet. Die mit dem Anlegen bzw. dem Erhalt eines Habitats verbundenen Kosten können räumlich und zeitlich variieren. Es wird angenommen, dass jeder Agent genau ein Flächenstück besitzt und dieses unter den gesetzten Rahmenbedingungen so bewirtschaftet, dass der eigene Gewinn maximiert wird.¹³ In jeder Zeitperiode wird eine gewisse Anzahl an Zertifikaten bzw. Landnutzungsrechten an die Agenten verteilt, die ihren Besitzern erlauben, innerhalb der jeweiligen Zeitperiode ihre Fläche landwirtschaftlich zu nutzen¹⁴. Alle anderen Agenten müssen ihre Flächen für den Naturschutz nutzen. Ermöglicht man den Agenten, mit diesen Zertifikaten zu handeln, so werden Agenten mit hohen Kosten (oberhalb des Marktpreises für Landnutzungsrechte) und ohne Zertifikat eine Kaufbereitschaft signalisieren (um ihre Fläche landwirtschaftlich nutzen zu können), während Besitzer eines Zertifikats bei niedrigen Kosten (unterhalb des Marktpreises für Zertifikate) eine Verkaufsbereitschaft signalisieren werden. Unter der Annahme eines vollkommenen Marktes (Feess 1997: S. 256, Baumol & Blinder 2003: S. 227) bildet sich ein Gleichgewichtspreis p^* heraus, bei dem Angebot und Nachfrage nach Zertifikaten im Gleichgewicht sind.¹⁵

Die Modellanalyse zeigt, dass je nach Größe des Verhältnisses von räumlichem Agglomerationsanreiz und Kostenvariabilität die Habitate entweder räumlich stark geklumpt (wenn das Verhältnis einen bestimmten kritischen Wert überschreitet) oder verstreut sind (wenn das Verhältnis den kritischen Wert unterschreitet). Im ersten Fall ist der Zertifikateumsatz ferner gering, es werden trotz sich ändernder Kosten wenige Habitate erzeugt oder vernichtet, und die Habitatkontinuität ist entsprechend hoch; im zweiten Fall ist der Zertifikateumsatz hoch und die Habitatkontinuität niedrig. Dies bedeutet, dass bei zeitlich veränderlichen Rahmenbedingungen rein räumliche Anreize nicht nur die räumliche Struktur sondern auch die zeitliche Dynamik der Landnutzung beeinflussen können, was für das Überleben von Arten sehr bedeutsam sein kann (Hartig & Drechsler 2009).

3.7 Aufsatz VII

Drechsler M, Hartig F, 2011. Conserving biodiversity with tradable permits under changing conservation costs and habitat restoration time lags. Ecological Economics 70, 533-541.

Dieser Aufsatz widmet sich einem Aspekt, der in Aufsatz VI unberücksichtigt geblieben ist: der Tatsache, dass die Erzeugung eines Habitats lange Zeit benötigen kann und nicht nur

¹³ Die hier verwendeten Modelle lassen sich in die Klasse der agentenbasierten Simulationsmodelle einordnen, die vor allem dann eingesetzt werden, wenn die Komplexität des Problems eine analytische Beschreibung unmöglich macht (Nolan et al. 2009). Im vorliegenden Fall entsteht die Komplexität u.a. durch die Heterogenität der Agenten, deren räumliche Wechselwirkung in dem Sinne, dass die Entscheidung eines Agenten von den Entscheidungen benachbarter Agenten abhängt (Aufsätze II und III), und Pfadabhängigkeiten (zeitliche Verzögerungen bei der Erzeugung von Habitat in Aufsatz IV). Da komplexe Verhaltensweisen der Agenten wie etwa Lernverhalten nicht berücksichtigt werden, ähneln sie nichtsdestotrotz typischen ökonomischen Prinzipal-Agenten-Modellen, wie sie beispielsweise zur Berücksichtigung asymmetrischer Informationsverteilung eingesetzt werden (Feess 1997: S. 585, Baumol & Blinder 2003: S. 247).

¹⁴ Im Rahmen der Analysen ist die genaue Art der Zuteilung der Rechte (vgl. Abschnitt 1.3.2) irrelevant.

¹⁵ Damit fällt das Modell in die Klasse der partiellen Gleichgewichts-Modelle (Chiang 1984: S. 36).

Kosten durch entgangene land- oder forstwirtschaftliche Gewinne verursacht sondern auch aktive und kostenbehaftete Renaturierungsmaßnahmen benötigen kann, die mit „Restaurierungskosten“ verbunden sind. Wieder wird ein Markt für handelbare Landnutzungsrechte modelliert. Im Gegensatz zu Aufsatz VI können die Kosten zeitlich korreliert sein, räumliche Aspekte spielen dagegen in Aufsatz VII keine Rolle.

Während in Aufsatz VI angenommen wird, dass Zertifikate in jeder Zeitperiode zugeteilt werden, wird in Aufsatz VII nur dann ein Zertifikat zugeteilt, wenn die Erzeugung eines Habitats abgeschlossen ist. Um ein Habitat zerstören zu dürfen, muss ein entsprechendes Zertifikat bei der Behörde eingereicht werden. Um zu entscheiden, ob es gewinnbringend ist, eine zur Zeit landwirtschaftliche Fläche in ein Habitat umzuwandeln oder nicht, sind folgende Kosten und Erlöse gegeneinander abzuwägen: die abdiskontierten Produktionskosten, die abdiskontierten Restaurierungskosten bis zur Fertigstellung des Habitats und der abdiskontierte (erwartete) Erlös aus dem Verkauf des nach Fertigstellung des Habitats zugeteilten Zertifikats. Übersteigt letzterer die Summe der ersten beiden Kosten, so wird mit der Restaurierungsmaßnahme begonnen, andernfalls wird die landwirtschaftliche Produktion beibehalten. Diese Entscheidungsregel ist zum eine ökonomisch plausible, andererseits kann man sie, wie in diesem Aufsatz dargelegt, mit Hilfe dynamischer Optimierung (Clark 1990: S. Kap. 4) herleiten.

Kann ein Habitat instantan erzeugt werden, so zeigt die Analyse des Modells unter anderem, dass bei einer Erhöhung der Restaurierungskosten erwartungsgemäß die Restaurierungsaktivitäten abnehmen, was zu geringerer Marktaktivität und höherer Habitatkontinuität führt. Da sich die Produktionskosten auf den einzelnen Flächenstücken jedoch von Zeitperiode zu Zeitperiode ändern, führt eine hohe Habitatkontinuität dazu, dass die durchschnittlichen Produktionskosten pro Habitat ebenfalls hoch sind (vgl. Aufsatz III). Dieser Trade-off zwischen Habitatkontinuität und Produktionskosten kann jedoch verschwinden, wenn die Erzeugung von Habitat nicht instantan ist sondern Zeit braucht. In diesem Fall müssen die Landnutzer die zukünftigen Zertifikatepreise und Produktionskosten schätzen. Geschehen dabei Fehler, so können Marktfluktuationen entstehen, die die Effizienz des Marktes, also seine Fähigkeit, die geforderte Habitatmenge zu den geringstmöglichen Kosten bereitzustellen, vermindern kann. Als Folge können im Extremfall Habitatkontinuität und Produktionskosten negativ korreliert sein und damit eine adäquate Erhöhung der Restaurierungskosten – beispielsweise über eine Steuer – sowohl die Habitatkontinuität erhöhen als auch die Produktionskosten senken.

4 Ergebnisse und Synthese

Im Folgenden werden Ergebnisse aus den sieben in Abschnitt 3 genannten Aufsätzen zusammengeführt, die für die Betrachtung der Trade-offs zwischen Habitatmenge, -konnektivität und -kontinuität relevant sind. Zunächst wird in Abschnitt 4.1 die Transformation zwischen den drei Landschaftsindizes diskutiert und danach in Abschnitt 4.2 die Substitution.

4.1 Zur Grenzrate der Transformation

Die Aufsätze III, V und VI befassen sich mit der Grenzrate der Transformation zwischen den Landschaftsindizes Habitatmenge und -konnektivität, d.h. mit der Frage, um welchen Betrag bei gegebenem Naturschutzbudget (bzw. volkswirtschaftlichen Kosten) ein Landschaftsindex reduziert werden kann, damit ein anderer Landschaftsindex um einen bestimmten Betrag

erhöht werden kann.. Alle Aufsätze bestätigen den in Abschnitt 1.4.2 postulierten Trade-off zwischen diesen beiden Indizes. Die Form dieses Trade-offs wird nach den Ergebnissen von Aufsatz III maßgeblich durch die Stärke σ , mit der die Kosten räumlich variieren, bestimmt (vgl. Abb. 3a in Aufsatz III). Der Grund liegt darin, dass vor allem bei hoher Kostenvarianz σ die mittleren Kosten pro Habitatfläche gesenkt werden können, wenn stets die kostengünstigsten Flächen für den Naturschutz genutzt werden. Um dies zu verstehen, betrachte man zwei extreme Habitatkonfigurationen. Die erste sei bestimmt durch die Maximierung der Habitatkonnektivität, indem alle Habitatflächen nebeneinander liegen. Bei der gemäß Abschnitt 2.1 angenommenen zufälligen Verteilung der Kosten enthält eine solche Konfiguration, die sich nicht an einer Minimierung der Kosten orientiert, sowohl Habitatflächen mit hohen als auch solche mit geringen Kosten, und die mittleren Kosten pro Habitatfläche sind nach den Annahmen aus Abschnitt 2.1 gleich 1. Nutzt man stattdessen nur die kostengünstigsten Flächen in der Landschaft für den Naturschutz, so erhält man die andere extreme Habitatkonfiguration, die durch eine geringe Habitatkonnektivität ausgezeichnet ist. Die Kosten pro Habitat sind in dieser Konfiguration gemäß den Annahmen aus Abschnitt 2.1 etwa $1 - \sigma$. Die Konfiguration mit maximaler Habitatkonnektivität kostet pro Habitat also den Betrag σ mehr als diejenige mit minimalen Kosten. Die Kostenvarianz σ bestimmt damit die Grenzrate der Transformation zwischen Habitatmenge und -konnektivität. Konkret nimmt die Zahl der Habitatflächen, die für eine zusätzliche Einheit an Habitatkonnektivität aufgewendet werden müssen, mit wachsendem σ zu. Nach den Überlegungen in Abschnitt 2.2.1 sollte daraus folgen, dass das kosteneffiziente Niveau der Habitatkonnektivität mit zunehmendem σ sinkt – was in Abbildung 2 von Aufsatz III bestätigt wird. Da die Grenzrate der Transformation positiv ist, steigt gleichzeitig das kosteneffiziente Niveau der Habitatmenge, wenn σ vergrößert wird.

Aufsatz III betrachtet zwei verschiedene Naturschutzzinstrumente. Im ersten trägt jede Habitatfläche zu den Gesamtkosten bzw. zum Gesamtbudget gemäß ihren Kosten bei, während im zweiten Fall jede Fläche denselben Betrag beisteuert. Der erste Fall entspricht räumlich differenzierten Kompensationszahlungen (vgl. Wätzold & Drechsler 2005), der zweite räumlich homogenen. Aufsatz III zeigt, dass der Trade-off zwischen Habitatmenge und -konnektivität in seiner qualitativen Form nicht davon abhängt, ob räumlich differenziert wird oder nicht. Natürlich sind die Gesamtkosten (aus Sicht der Naturschutzbehörde) bei homogenen Zahlungen höher als bei differenzierten Zahlungen. Der Differenzbetrag kommt denjenigen Landnutzern als Produzentenrente zugute, die im Vergleich zu den anderen Landnutzern nur geringe Kosten haben. Wie Aufsatz IV für einen konkreten Anwendungsfall zeigt, kann dieser Betrag beträchtlich sein.

In Aufsatz V, das sich mit räumlichen Agglomerationsanreizen beschäftigt, zeigt sich, dass die Produzentenrenten, die bei homogenen Kompensationszahlungen an die Besitzer der kostengünstigen Habitatflächen fließen, vor allem in Habitatkonfigurationen hoher räumlicher Konnektivität hoch sind, da hier die Spreizung der Kosten (wie oben argumentiert) besonders hoch sind. Aufsatz V hat nun einen Weg aufgezeigt, wie man die Höhe dieser aus Sicht der Naturschutzbehörde unerwünschten Produzentenrenten reduzieren kann: indem man – wie in Abschnitt 3.5 beschrieben – die Auszahlung der Kompensationszahlung an die Bedingung knüpft, dass die eigene Habitatfläche in der Nachbarschaft anderer Habitatflächen liegt. Für den Besitzer einer Fläche mit geringen Kosten aber zu geringer Habitatdichte in der Nachbarschaft kann es sich daher lohnen, einen Teil seiner Produzentenrente benachbarten Landnutzern anzubieten, die zwar aufgrund hoher Kosten ihre Flächen landwirtschaftlich nutzen, sich aber durch den vom Nachbarn angebotenen Betrag (plus die von der Behörde angebotene Kompensationszahlung) dazu bewegen lassen, ihre Flächen für den Naturschutz zu nutzen. Durch diese Seitenzahlungen beteiligen sich die Besitzer kostengünstiger Flächen an den Naturschutzmaßnahmen auf teureren Flächen. Vor allem Habitatkonfigurationen mit

hoher räumlicher Konnektivität werden dadurch für die Behörde günstiger, so dass die Anzahl an Habitatflächen, die für eine zusätzliche Einheit Habitatkonnektivität gezahlt werden muss, sinkt. Durch diesen Effekt erhöht sich (vgl. Abschnit 2.2) *ceteris paribus* das kosteneffiziente Niveau der Habitatkonnektivität – wie in Aufsatz V gezeigt wird.

Aufsatz VI betätigt den in den Aufsätzen III und V identifizierten Trade-off zwischen Habitatmenge und -konnektivität, zeigt jedoch, dass bei Einsatz eines marktwirtschaftlichen Instruments die Transformationskurve aufgrund der begrenzten Rationalität der Landnutzer un stetig sein kann in dem Sinne, dass nicht alle Kombinationen von Habitatmenge und -konnektivität, die rein rechnerisch möglich wären, produziert werden können. Stattdessen konnten in dem modellierten Markt für handelbare Landnutzungsrechte – je nach Ausgestaltung der räumlichen Anreize – nur zwei mögliche Kombinationen produziert werden: eine Habitatkonfiguration mit maximaler Habitatmenge und minimaler Habitatkonnektivität und eine Habitatkonfiguration mit minimaler Habitatmenge und maximaler Habitatkonnektivität. Der Übergang zwischen diesen beiden Extremen ist sprunghaft, so dass etwa Habitatkonfigurationen mit mittelgroßer Habitatmenge und mittelhoher Konnektivität nur selten erreicht wurden. Hartig & Drechsler (2010) zeigen überdies, dass die begrenzte Rationalität der Landnutzer zu Effizienzverlusten führen kann in dem Sinne, dass das Niveau an Habitatkonnektivität, das bei gegebener Habitatmenge (und gegebenen Gesamtkosten) erzielt wird, geringer ist als dasjenige, das sich unter perfekter Rationalität einstellen würde.

Aufsatz III beschäftigt sich ferner mit dem Trade-off zwischen Habitatmenge und -kontinuität, wenn die (Produktions-) Kosten von Naturschutzmaßnahmen räumlich heterogen und zeitlich veränderlich sind. Aufsatz III findet unter diesen Annahmen eine positive Grenzrate der Transformation zwischen diesen beiden Größen, deren Höhe von der zeitlichen Variabilität der Kosten abhängt. Die Erklärung für diese Beobachtung ist praktisch dieselbe wie die oben angeführte Erklärung für die Positivität der Transformationsrate zwischen Habitatmenge und -konnektivität: Erlaubt man die Reallokation von Naturschutzmaßnahmen, nimmt also eine Verringerung der Habitatkontinuität in Kauf, so können die Naturschutzmaßnahmen zu jeder Zeitperiode auf den kostengünstigsten Flächen durchgeführt werden, was die Durchschnittskosten pro Habitat senkt. Bei gegebenem Budget sinkt mit zunehmender Habitatkonnektivität also die Habitatmenge. Je größer die zeitliche Kostenvariabilität, desto stärker sinken die Durchschnittskosten pro Habitat mit abnehmender Habitatkontinuität, und desto mehr Habitatflächen müssen für eine zusätzliche Einheit an Habitatkontinuität aufgewendet werden. *Ceteris paribus* senkt zunehmende Kostenvariabilität damit nach Abschnitt 2.2.1 das kosteneffiziente Niveau an Habitatkontinuität, während das kosteneffiziente Niveau der Habitatmenge zunimmt.

Aufsatz VII untersucht unter anderem, ob die Grenzrate der Transformation zwischen Habitatmenge und -kontinuität auch dann positiv ist, wenn die Allokation der Naturschutzmaßnahmen über das Instrument handelbarer Landnutzungsrechte umgesetzt wird. Hier ist die Habitatmenge vorgegeben, und eine positive Transformationsrate würde vorliegen, wenn die mit der Bereitstellung dieser Habitatmenge verbundenen Kosten für die Landnutzer mit zunehmender Habitatkontinuität steigen würden.

Gesteuert wird in Aufsatz VII die Habitatkontinuität durch die Höhe der mit der Erzeugung von Habitat verbundenen Restaurationskosten. Je höher diese sind, desto weniger profitabel ist die Erzeugung von Habitat, desto weniger Zertifikate werden angeboten und desto geringer ist die Marktaktivität und die Häufigkeit, mit der Naturschutzmaßnahmen realloziert werden. Im Einklang mit den Ergebnissen aus Aufsatz III sind die Gesamtkosten des Zertifikatemarktes bei vorgegebener Habitatmenge hoch, wenn aufgrund hoher Restaurationskosten der Zertifikateumsatz gering und die Habitatkontinuität hoch ist. Dies entspricht auch der Erwartung, da bei (zu) geringem Zertifikateumsatz die

Artenschutzmaßnahmen nicht vollständig auf die kostengünstigsten Flächen alloziiert werden können, so dass auch teurere Flächen für den Artenschutz bewirtschaftet werden müssen. Dies erhöht die Durchschnittskosten pro Habitat und führt zu der positiven Grenzrate der Transformation zwischen Habitatmenge und -kontinuität.

Die Grenzrate der Transformation zwischen Habitatmenge und -kontinuität kann, wie in Aufsatz VII gezeigt, jedoch auch negativ werden (das heißt, eine Zunahme des einen der beiden Landschaftsindizes impliziert bei gegebenen volkswirtschaftlichen Kosten eine Zunahme des anderen), nämlich wenn die Restaurierung von Habitaten nicht instantan mit dem Einsatz von Naturschutzmaßnahmen erfolgt, sondern mehrere Zeitperioden benötigt, und wenn die Landnutzer keine Informationen über die zukünftige Entwicklung der Kosten und des Zertifikatspreises haben. In diesem Fall begrenzter Rationalität kann es zu Fehlentscheidungen – insbesondere zu Fehlinvestitionen in dem Sinne, dass zuviel Habitat restauriert wird – kommen, mit der Folge, dass die Gesamtkosten des Zertifikatemarktes steigen¹⁶. Die erwartete Anzahl von Fehlentscheidungen korreliert natürlicherweise mit der Zahl der getroffenen Entscheidungen, so dass eine Erhöhung der Restaurationskosten, die die Restaurationsfähigkeit bremst, auch die Häufigkeit von Fehlinvestitionen und die damit verbundenen Kosten vermindert. Zwar führen hohe Restaurationskosten wie oben erwähnt auch dazu, dass die Durchschnittskosten pro Habitat zunehmen, diese Kostenerhöhung ist nach den Analysen in Aufsatz VII jedoch geringer als die mit den Fehlinvestitionen verbundenen Kosten. Damit besteht bei vorgegebener Habitatmenge eine positive Korrelation zwischen Habitatkontinuität und Gesamtkosten, d.h. bei festgehaltenen Gesamtkosten steigt die Habitatmenge mit wachsender Habitatkontinuität.

4.2 Zur Grenzrate der Substitution

Mit der Substitution zwischen den Landschaftsindizes Habitatmenge und -konnektivität bzw. Habitatmenge und -kontinuität beschäftigen sich die Aufsätze II und III. Die Grenzrate der Substitution zwischen Habitatmenge und -konnektivität, also der Betrag um den einer der beiden Landschaftsindizes erhöht werden muss um eine Reduktion des jeweils anderen Landschaftsindex um einen bestimmten Betrag auszugleichen, hängt vor allem von der Ausbreitungsfähigkeit der Art ab. Je größer diese Ausbreitungsfähigkeit, desto weniger ist die Art auf eine hohe räumliche Konnektivität angewiesen. Dies bedeutet, dass der Verlust an Konnektivität um eine Einheit bereits durch eine geringe Erhöhung der Habitatmenge ausgeglichen werden kann, so dass die Überlebensfähigkeit der Metapopulation erhalten bleibt. Damit ist bei einer hohen Ausbreitungsfähigkeit *ceteris paribus* das kosteneffiziente Niveau der Habitatkonnektivität verhältnismäßig niedrig und das kosteneffiziente Niveau der Habitatmenge verhältnismäßig hoch.

Ein hoher Replikationsfaktor bedeutet, dass die Art (bei ausreichender Ausbreitungsfähigkeit) sehr gut leere Habitate besiedeln kann. Die Zahl der Habitate ist in diesem Fall sehr wichtig, so dass eine Verringerung der Habitatkonnektivität gut durch eine Erhöhung der Habitatmenge ausgeglichen werden kann. Das kosteneffiziente Niveau der Habitatkonnektivität sinkt daher mit zunehmendem Replikationsfaktor, während das kosteneffiziente Niveau der Habitatmenge wächst.

Bei der Substitution zwischen Habitatmenge und -kontinuität ist entscheidend, ob die Art von Natur aus eine hohe lokale Extinktionsrate (vgl. Abschnitt 3.1) aufweist oder nicht. Auch bei einer hohen lokalen Extinktionsrate können Metapopulationen überleben, wenn gleichzeitig der Replikationsfaktor (vgl. Abschnitt 3.1) oder die Ausbreitungsfähigkeit genügend hoch ist.

¹⁶ Hier besteht eine gewisse Analogie zum zuerst von Hanau (1928) beobachteten und von Kaldor (1934) modellierten „Schweinezyklus“.

Ist die lokale Extinktionsrate also hoch, so ist die Metapopulation von Natur aus darauf angewiesen, immer wieder leer gewordene Habitatflächen wiederzubesiedeln, um das Aussterben lokaler Populationen zu kompensieren. Die Reallokation von Naturschutzmaßnahmen und die damit verbundenen Auslöschungen lokaler Populationen sind für solche Arten damit verhältnismäßig leicht zu kompensieren, so dass der Verlust einer Einheit Habitatkonnektivität durch wenige zusätzliche Habitate ausgeglichen werden kann. Je größer die naturbedingte lokale Extinktionsrate desto geringer ist damit das kosteneffiziente Niveau der Habitatkontinuität und desto höher ist das kosteneffiziente Niveau der Habitatmenge.

Aus der Betrachtung im vorangegangenen Absatz ist es plausibel, dass das kosteneffiziente Niveau der Habitatkontinuität auch mit zunehmendem Replikationsfaktor und zunehmender Ausbreitungsfähigkeit sinkt, da Arten mit hohem Replikationsfaktor und hoher Ausbreitungsfähigkeit ein verhältnismäßig hohes Potential zur Wiederbesiedlung leerer Habitate besitzen und die Reallokation von Naturschutzmaßnahmen besser verkraften können. Der Verlust einer Einheit Habitatkontinuität kann daher gut durch einer Erhöhung der Habitatmenge ausgeglichen werden.

5 Diskussion und Schlusswort

In dieser Arbeit werden ökologisch-ökonomische Modelle zur kosteneffizienten räumlichen und zeitlichen Allokation von Naturschutzmaßnahmen entwickelt. Die ökonomischen Komponenten der Modelle erklären vor allem, wie die räumliche und zeitliche Landnutzungsdynamik von ökonomischen Rahmenbedingungen und Anreizen für die Landnutzer abhängen. Ferner identifizieren sie Trade-offs zwischen ökologisch relevanten makroskopischen Eigenschaften der Landschaft (Landschaftsindizes) in dem Sinne, dass bei gegebenem Naturschutzbudget bzw. volkswirtschaftlichen Kosten ein Landschaftsindex vermindert werden muss, wenn ein anderer erhöht werden soll. Schließlich wird die Abhängigkeit dieser Trade-offs von den ökonomischen Rahmenbedingungen untersucht. Die ökologischen Komponenten der Modelle ermitteln vor allem, wie die Überlebensfähigkeit von Arten von der Landnutzungsdynamik und den biologischen Eigenschaften der Art abhängt und ermitteln Trade-offs zwischen den erwähnten Landschaftsindizes in dem Sinne, dass ein Landschaftsindex erhöht werden muss, um eine Verminderung in einem anderen auszugleichen, damit die Überlebensfähigkeit der Art erhalten bleibt. Die genannten Trade-offs werden mit Hilfe der ökonomischen Produktionstheorie systematisiert und Implikationen für die kosteneffiziente räumliche und zeitliche Allokation von Naturschutzmaßnahmen sowie die kosteneffiziente Ausgestaltung von Naturschutzinstrumenten abgeleitet.

Die Analyse der ökologisch-ökonomischen Modelle und die Systematisierung der Ergebnisse mit Hilfe der Produktionstheorie geben wertvolle Hinweise darauf, wie die kosteneffiziente räumlich-zeitliche Allokation von Artenschutzmaßnahmen von ökologischen und ökonomischen Rahmenbedingungen abhängt. Aus diesen Hinweisen lassen sich, wie in Abschnitt 1.3.3 angedeutet, Schlussfolgerungen für die kosteneffiziente Ausgestaltung marktwirtschaftlicher Naturschutzinstrumente ableiten. Bei der Einrichtung einer Zone, in der Artenschutzmaßnahmen förderfähig sind (Parkhurst & Shogren 2005), lässt sich beispielsweise die räumliche Konnektivität von Habitaten durch die Größe der Zone beeinflussen. Sollen räumliche Agglomerationsanreize zum Einsatz kommen, so bestimmt, wie in Aufsatz VI gezeigt, die Höhe des Agglomerationsanreizes im Verhältnis zur räumlichen Variabilität der Kosten den Grad der Habitatkonnektivität. Die Rate, mit der Artenschutzmaßnahmen realloziert werden (die „Inverse“ zur oben diskutierten Habitatkontinuität), lässt sich, wie in Abschnitt 1.3.3 und Aufsatz VII argumentiert, durch die

Länge von Verträgen zwischen Naturschutzbehörde und Landnutzern oder auch durch die Besteuerung von Landnutzungsänderungen beeinflussen. Auch wenn die vorliegenden Ergebnisse keine quantitative Bestimmung der kosteneffizienten Höhe eines Agglomerationsanreizes oder einer Steuer auf Landnutzungsänderungen in konkreten Anwendungsfällen erlauben, so zeigen sie doch auf, welche Rolle verschiedene ökologische und ökonomische Faktoren bei der kosteneffizienten Ausgestaltung dieser Anreize spielen.

Insgesamt leistet die vorliegende Arbeit damit einen wichtigen Beitrag zur Weiterentwicklung marktwirtschaftlicher Naturschutzinstrumente. Neu ist dabei vor allem, dass nicht nur die Menge des von den privaten Akteuren bereitgestellten Gutes (die Anzahl der Habitate), sondern auch dessen raum-zeitliche Verteilung gesteuert wird. Möglich ist dies aufgrund der in Aufsatz I entwickelten Erkenntnis, dass für die Sicherstellung der ökologischen Effektivität der Naturschutzmaßnahmen die Steuerung von Landschaftsindizes wie z.B. der räumlichen Habitatkonnektivität weitgehend ausreichend ist, was mit sehr viel geringeren Transaktionskosten verbunden ist als etwa eine flächen- und zeitpunktscharfe Steuerung der Landnutzungsdynamik. Damit löst sich ein Stück weit der in der Umweltpolitik immer wieder auftretende Trade-off zwischen der Maximierung der ökologischen Effektivität einerseits und der Minimierung der Transaktionskosten andererseits, und es zeigt sich, dass die Berücksichtigung ökologischer Theorie die Entwicklung ökonomischer Naturschutzinstrumente befruchten kann. Umgekehrt demonstriert die vorliegende Arbeit die Nützlichkeit der ökonomischen Produktionstheorie bei der Analyse rein ökologischer Zusammenhänge, insbesondere der Frage, wie schädliche Landnutzungsänderungen in einer Landschaft kompensiert werden können, um die Überlebensfähigkeit der dort lebenden Arten auf einem gewünschten Niveau zu erhalten.

Die in der Arbeit beschriebenen Analysen und Ergebnisse basieren auf einer Reihe von Annahmen. Eine der wesentlichsten ist die Annahme räumlich unkorrelierter Kosten, da in der Realität Kosten im Allgemeinen räumlich korreliert sind. Die landwirtschaftliche Ertragsfähigkeit variiert meist auf größeren räumlichen Skalen als von Schlag zu Schlag, ökonomische Entwicklungen und damit einhergehende Steigerungen der Bodenpreise geschehen häufig in räumlich konzentrierter Form (Henderson, 2003), und die Bodenpreise sind in der Nähe von Städten im Allgemeinen höher als auf dem Land.

Die Berücksichtigung räumlicher Korrelationen in einer theoretischen Analyse ist eine große Herausforderung, da Korrelationen (auch gleichzeitig) auf mehreren Skalen auftreten können, deren Wirkungen auf die kosteneffiziente räumliche Allokation von Naturschutzmaßnahmen voneinander abhängen können. Eine Wechselwirkung wird auch mit der Höhe des Budgets bestehen: bei einem sehr kleinen Budget und genügend großer räumlicher Korrelationslänge wird die Grenzrate der Transformation zwischen Habitatmenge und -konnektivität beispielsweise nicht positiv sein, da alle durch das Budget finanzierbaren Naturschutzmaßnahmen in einem einzigen „Kosten-Tal“ Platz finden. Erst wenn das Budget größer ist als zur Finanzierung aller Habitate in dem Kosten-Tal nötig, stellt sich die Frage, ob die weiteren Mittel für Naturschutzmaßnahmen auf einem benachbarten „Kosten-Berg“ oder in einem weiter entfernten Kosten-Tal ausgegeben werden sollten. Eine erste Erweiterung des Modells von Aufsatz V zur Berücksichtigung räumlicher Korrelationen ist in Arbeit.

Ein weiteres offenes Feld ist die adäquate Modellierung des Verhaltens der Landnutzer bei der Analyse marktwirtschaftlicher Instrumente. In den Aufsätzen IV – VII wurde von gewinnmaximierenden Agenten ausgegangen, obwohl Profitmaximierung erwiesenermaßen nicht das einzige Entscheidungskriterium realer Akteure darstellt (vgl. Fußnote 6). Des Weiteren haben die modellierten Agenten eine relativ geringe Intelligenz. So sind sie beispielsweise nicht in der Lage, sich an vergangenen Preis- und Kostenentwicklungen zu

erinnern und daraus nichttriviale¹⁷ Prognosen abzuleiten. Auch die Möglichkeit zu strategischem Verhalten, das sowohl bei räumlichen Kooperation der Landnutzer in Aufsatz V als auch bei Investitionen und Marktinteraktionen¹⁸ in Aufsatz VII eine Rolle spielen könnte, wurde den modellierten Agenten verwehrt. Eine Erweiterung der Modelle hin zu realistischeren Agenten ist eine lohnenswerte Aufgabe für die Zukunft – mit interessanten Anknüpfungspunkten zur empirischen und experimentellen Ökonomik (Parkhurst et al. 2002, Janssen et al. 2010). Ein erster Schritt in diese Richtung ist hier die Entwicklung eines Online-Spiels zu handelbaren Landnutzungsrechten (Hartig et al., 2010) auf Basis des Modells in Aufsatz VI, das zurzeit für Experimente genutzt wird.

Auf ökologischer Seite wurden in der vorliegenden Arbeit ebenfalls beträchtliche Vereinfachungen vorgenommen. So wurde angenommen, dass das Naturschutzziel in dem Schutz einer einzigen Art besteht. Grundsätzlich lassen sich mit demselben Ansatz zwar auch mehrere Arten berücksichtigen, indem beispielsweise eine Naturschutz-Zielfunktion definiert wird, die durch die gewichtete Summe oder ein gewichtetes Produkt der Überlebensfähigkeiten der einzelnen Arten gebildet wird (Nicholson & Possingham 2006, Hartig & Drechsler 2009). Die genaue Form der Zielfunktion könnte über eine ökonomische Bewertung, z.B. durch Choice-Experimente (Meyerhoff et al. 2009) ermittelt werden. Damit wären die Ergebnisse der Analyse allerdings kontext-spezifisch und ihre Übertragbarkeit auf andere Regionen eingeschränkt. Eine Herausforderung bei solchen Mehrartenbetrachtungen ist die Berücksichtigung ökologischer Wechselwirkungen zwischen den Arten. Während es bei zwei Arten schon acht mögliche Kopplungen¹⁹ gibt, für deren mathematische Modellierung es praktisch beliebig viele biologisch plausible Möglichkeiten gibt, so steigt die Zahl möglicher Kopplungen exponentiell mit zunehmender Artenzahl an. Nichtsdestotrotz muss in der Zukunft diese Herausforderung angenommen werden, um Biodiversität und nicht nur einzelne Arten kosteneffizient schützen zu können.

Bei Mehrartensystemen, in denen Arten sich auch negativ beeinflussen können, gilt dann auch die in dieser Arbeit verwendete Beziehung nicht mehr, dass die Reallokation, also das Zerstören und Wiederherstellen von Habitaten, aus ökologischer Sicht stets negativ zu bewerten ist. Stattdessen maximiert in Mehrartensystemen häufig eine moderate Rate an Reallokationen die Anzahl der überlebenden Arten (Grime 1973, Begon et al. 1990). Reallokationen von Habitat können auch in Einartensystemen ökologisch notwendig sein, wenn die Art auf „junge“ Habitate angewiesen ist.

Trotz der erhöhten Komplexität lassen sich all diese Erweiterungen nach dem in dieser Arbeit angewendeten Vorgehen behandeln: indem die Ergebnisse ökologisch-ökonomischer Modelle unter Zuhilfenahme der ökonomischen Produktionstheorie systematisiert und interpretiert wurden. Insbesondere die Unterscheidung zwischen Transformations- und Substitutionsrate und deren separate Diskussion in den Abschnitten 4.1 und 4.2 – erweist sich dabei als zielführend für das Verständnis der ökologischen und ökonomischen Trade-offs zwischen den Landschaftsindizes. Es lohnt sich daher, die oben angedeuteten weiterführenden Arbeiten auch durch die Brille der ökonomischen Produktionstheorie zu betrachten, um einer Theorie der kosteneffiziente Allokation von Artenschutzmaßnahmen einen weiteren Schritt näher zu kommen.

¹⁷ Prognosen spielen in Aufsatz IV eine Rolle, und hier gehen die Agenten davon aus, dass sich Kosten und Preise gegenüber den aktuellen Niveaus nicht ändern werden.

¹⁸ Beispielsweise können Zertifikate gehortet werden („banking“) mit dem Ziel, Preise günstig zu beeinflussen, oder der Aussicht, die Zertifikate später zu einem günstigeren Zeitpunkt nutzen zu können (Tietenberg 2006: S. 107 ff., Wissel & Wätzold 2008).

¹⁹ Jede der beiden Arten kann die jeweils andere Art positiv, negativ oder gar nicht beeinflussen. Von diesen neun Möglichkeiten repräsentiert eine den Fall, dass es keinerlei Wirkung einer Art auf die jeweils andere gibt.

Anhang A

Zu lösen ist folgendes Maximierungsproblem: Die Gütermenge z wird gemäß der Produktionsfunktion $z(\tilde{y}_1, \tilde{y}_2)$ aus den Mengen $\tilde{y}_1$ und $\tilde{y}_2$ der Faktoren 1 und 2 produziert. Die Mengen $\tilde{y}_1$ und $\tilde{y}_2$ werden wiederum gemäß den Produktionsfunktionen $y_1(x_{11}, x_{21})$ und $y_2(x_{12}, x_{22})$ aus den Mengen x_{11}, x_{12}, x_{21} und x_{22} produziert, so dass gilt:

$$\tilde{y}_1 = y_1(x_{11}, x_{21}) \text{ und } \tilde{y}_2 = y_2(x_{12}, x_{22})$$

mit den Nebenbedingungen

$$x_{11} + x_{12} = X_1 \text{ und } x_{21} + x_{22} = X_2.$$

Mit diesen vier Beziehungen kann man nun die Lagrangefunktion zur Maximierung der Gütermenge z bilden:

$$L = z(\tilde{y}_1, \tilde{y}_2) - \lambda_1 [\tilde{y}_1 - y_1(x_{11}, x_{21})] - \lambda_2 [\tilde{y}_2 - y_2(x_{12}, x_{22})] - \lambda_3 [x_{11} + x_{12} - X_1] - \lambda_4 [x_{21} + x_{22} - X_2]$$

Aus den Maximierungsbedingungen erster Ordnung ergeben sich die Gleichungen

$$\frac{\partial z}{\partial \tilde{y}_1} - \lambda_1 = \frac{\partial z}{\partial \tilde{y}_2} - \lambda_2 = \lambda_1 \frac{\partial y_1}{\partial x_{11}} + \lambda_3 = \lambda_1 \frac{\partial y_1}{\partial x_{21}} + \lambda_4 = \lambda_2 \frac{\partial y_2}{\partial x_{12}} + \lambda_3 = \lambda_2 \frac{\partial y_2}{\partial x_{22}} + \lambda_4 = 0,$$

deren Lösung zu

$$\frac{\frac{\partial z}{\partial \tilde{y}_1}}{\frac{\partial z}{\partial \tilde{y}_2}} = \frac{\frac{\partial y_1}{\partial x_{12}}}{\frac{\partial y_1}{\partial x_{11}}}$$

führt. Nach Abschnitt 2.2.1 repräsentiert die linke Seite dieser Gleichung die Grenzrate der Substitution (MRS_{21}) bezüglich der Produktion von z aus $\tilde{y}_1$ und $\tilde{y}_2$ und die rechte Seite die Grenzrate der Transformation (MRT_{21}) bezüglich der Güter $\tilde{y}_1 = y_1(x_{11}, x_{21})$ und $\tilde{y}_2 = y_2(x_{12}, x_{22})$ aus X_1 und X_2 , so dass

$$MRS_{21} = MRT_{21}.$$

Unter der Annahme fallender Grenzproduktivitäten ist das gefundene Extremum $MRS_{21}=MRT_{21}$ ein Maximum, das die Gütermenge z unter den gesetzten Nebenbedingungen maximiert.

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Angaben zu den Beiträgen des Autors

1. Drechsler M, Johst K, 2010. *Rapid viability analysis for metapopulations in dynamic landscapes. Proceedings of the Royal Society B* 277, 1889-1897.

MD entwickelte die Idee des Aufsatzes und die mathematische Formel für die Überlebensfähigkeit der Metapopulation; KJ führte die numerische Validierung der Formel durch; MD und KJ schrieben das Manuskript, wobei MD den überwiegenden Beitrag beigesteuert hat.

2. Johst K, Drechsler M, van Teeffelen AJA, Hartig F, Vos CC, Wissel S, Wätzold F, Opdam P., 2011. *Conservation planning for dynamic landscapes – tradeoffs between spatial and temporal landscape attributes. Journal of Applied Ecology* 48, 1227–1235.

MD entwickelte die Idee des Aufsatzes und das Konzept zur Analyse der Trade-offs; KJ führte die Analysen durch und berechnete die Trade-offs; KJ und MD diskutierten die Ergebnisse; alle Autoren schrieben das Manuskript unter Federführung von KJ, die den überwiegenden Beitrag beigesteuert hat.

3. Drechsler M. (2011) *Trade-offs in the design of cost-effective habitat networks when conservation costs are variable in space and time. Biological Conservation* 144, 479-489.

4. Drechsler M, Wätzold F, Johst K, Bergmann H, Settele J, 2007. *A model-based approach for designing cost-effective compensation payments for conservation of endangered species in real landscapes. Biological Conservation* 140, 174-186.

FW entwickelte die Idee des Aufsatzes; HB führte die agrar-ökonomische Kostenberechnung durch; KJ entwickelte das ökologische Modell unter Mithilfe von JS und MD; MD modellierte die Kompensationszahlungen und ihre Wirkung auf das Landnutzungsmuster in der Untersuchungsregion, integrierte alle Modellkomponenten und führte die Analysen durch; MD und FW diskutierten die Ergebnisse; alle Autoren schrieben das Manuskript, wobei der Umfang der Beiträge durch die Autorenreihenfolge gegeben ist.

5. Drechsler M, Wätzold F, Johst K, Shogren JF, 2010. *An agglomeration payment for cost-effective biodiversity conservation in spatially structured landscapes. Resource and Energy Economics* 32, 261-275.

FW entwickelte die Idee des Aufsatzes; MD entwarf die Agglomerationszahlung, modellierte ihre Wirkung auf das Landnutzungsmuster und führte die Analysen durch; KJ entwickelte das ökologische Modell für die Fallstudie; MD, FW und JS diskutierten die Ergebnisse; alle Autoren schrieben das Manuskript mit Hauptbeiträgen von MD und FW.

6. Drechsler M, Wätzold F, 2009. *Applying tradable permits to biodiversity conservation: effects of space-dependent conservation benefits and cost heterogeneity on habitat allocation. Ecological Economics* 68, 1083-1092.

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Rapid viability analysis for metapopulations in dynamic habitat networks

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Abstract

For land-use planning numerically fast and easily applicable tools are urgently needed that allow us to assess how landscape structure and dynamics affect biodiversity. To date such tools exist only for static landscapes. We provide an analytical formula for the mean life time of species in fragmented and dynamic habitat networks where habitat patches may be destroyed and created elsewhere. The formula is able to consider both patch size heterogeneity and dynamics additionally to patch number and connectivity. It is validated through comparison with a dynamic and spatially explicit simulation model. It can be used for the optimisation of spatiotemporal land-use patterns in real landscapes and for advancing our general understanding of key processes affecting the survival of species in fragmented heterogeneous dynamic landscapes.

Key words: dynamic landscapes, habitat network, habitat turnover, mean life time, metapopulation, viability.

Introduction

Landscapes and ecosystems are dynamic due to various ecological and economic drivers. For instance, flooding of wetlands leads to a continuous sequence of habitat creation and destruction, or economic development leads to the destruction of habitats at some places while habitats are restored at others. Climate change is likely to alter these dynamics in the future with substantial impacts on biodiversity (e.g., Thuiller 2007; Buisson *et al.* 2008).

Managing land for conservation in dynamic landscapes is currently a hot topic in the conservation literature (Pressey *et al.* 2007). A major challenge in this context is the assessment of species viability in dynamic habitat networks. Relatively complex numerical (e.g., DeWoody *et al.* 2005; Ross *et al.* 2008) and simulation models (e.g., Johst *et al.* 2002; Wintle *et al.* 2005; Hodgson *et al.* 2009) have been developed to analyse the survival of fragmented populations (so-called metapopulations: Hanski 1999b) in dynamic habitat networks. As time and effort required for the parameterization and analysis of these models is large, they have limitations with respect to both general theoretical analysis and application in conservation management. For exploring general concepts and for devising specific management plans more rapid approaches are urgently needed.

A promising alternative to numerical and simulation models are analytical formulae that effectively integrate the synergistic effects of network structure and dynamics. On the one hand, these formulas explicitly reveal general relationships between spatial and temporal components of metapopulation survival furthering our theoretical understanding of metapopulation viability in dynamic landscapes. On the other hand, they are urgently needed for conservation planning and the cost-effective allocation of conservation resources (e.g., Nicholson *et al.* 2006; Nelson *et al.* 2008).

Only few analytical approaches have been developed for metapopulation viability analysis in dynamic and spatially heterogeneous habitat networks (e.g., Gyllenberg & Hanski 1997; Hanski 1999a; Johnson 2000; Keymer *et al.* 2000; Amarasekare & Possingham 2001; Hastings 2003; DeWoody *et al.* 2005). To our knowledge all of them focus on occupancy thresholds that tell us under which conditions the mean occupancy (mean number of occupied patches) in a metapopulation is nonzero. Since these thresholds ignore variations in occupancy through time, they underestimate the true extinction risk and can lead to false conservation management recommendations (Frank 2005). Another practical disadvantage of considering occupancy thresholds is that they allow distinguishing only between zero and non-zero mean patch occupancy associated with metapopulation extinction and survival, respectively. Any further differentiation among different levels of non-zero mean occupancy and thus different levels of metapopulation viability is not possible. Such

differentiation, however, is indispensable for optimising landscapes which involves a weighting of the improvements in species viability and the associated (finite, often even marginal) financial costs (e.g., Naidoo *et al.* 2006; Nelson *et al.* 2008). Cornell & Ovaskainen (2008) developed an analytical expression for the mean patch occupancy in dynamic landscapes which allows such differentiation. Their expression has the advantage that patches can be destroyed and created in a spatially correlated manner. However, patch size heterogeneity characteristic for many real landscapes is not included.

An alternative measure of metapopulation viability is the expected life time, or mean time to extinction of a metapopulation (Grimm & Wissel 2004). Analytical formulae for calculating this mean metapopulation life time (MMLT) in static habitat networks have been developed by Frank & Wissel (2002) and Drechsler (2009). We take the formula for the MMLT by Drechsler (2009) and derive new estimates for its parameters that extend the applicability of the formula to dynamic networks where habitat patches may be destroyed through natural or anthropogenic influences and new habitat patches may be created elsewhere.

Assuming a balance between patch destruction and patch creation (e.g., Hanski 1999a; Keymer *et al.* 2000; Amarasekare & Possingham 2001; Briers & Warren 2000; Wahlberg *et al.* 2002; Biedermann 2004), we can describe the network dynamics by effective parameters that enter the formula for dynamic habitat networks. In particular, we take into account that patches may differ in size and/or quality independent of their dynamics. Metapopulation extinction times in static habitat networks are known to be exponentially distributed so that the magnitude of their mean determines the entire distribution of extinction times (Grimm & Wissel 2004). We show that the same is true for dynamic networks.

Below we present the modelling approach and the derived formula, a numerical validation of the formula, and examples that demonstrate its parameterisation and application. Our formula does not explicitly account for non-stationary and spatially correlated dynamics of patch destruction and creation. However, we hypothesise that it is still applicable to such kind of network dynamics if the degree of temporal variation and spatial correlation of patch creation and destruction are within certain limits. An objective of the numerical validation is to identify these limits.

Often, the processes of patch creation or patch destruction are induced and/or accompanied by succession in the patches so that habitat quality does not switch between habitable and uninhabitable but continuously changes with time (e.g., Wu & Levin 1994; Stelter *et al.* 1997; Johnson 2000; Johst *et al.* 2002; Hastings 2003; Wintle *et al.* 2005; Matlack 2005; Hodgson *et al.* 2009). We provide and demonstrate a practical approach for considering succession in a convenient manner and incorporating it into our model framework.

Material and Methods

Predicting the MMLT in static networks

Consider a metapopulation on a static habitat network of N habitat patches ($i=1, \dots, N$) with patch sizes A_i and inter-patch distances r_{ij} ($i, j=1, \dots, N$). The extinction rate e_i and the colonisation rate c_i of a local population on patch i may depend on patch size A_i . A standard model for c_i and e_i has been provided by Hanski (1999b).

$$e_i = \varepsilon A_i^{-\eta} \quad (1)$$

$$c_i = m A_i^b \quad (2)$$

where ε , η , m and b are species-specific constants (for empirical examples, see below and Hanski (1999b) as well as Nicholson *et al.* (2006)). In the present notation, c_i measures the rate by which individuals emigrate from patch i , divided by the number of individuals required to colonise an empty patch. Under infinite dispersal range and infinite number of patches ("Levins limit": Levins (1969) c_i represents the rate by which a local population colonizes another patch. If the patch sizes A_i differ, so do the colonisation and extinction rates c_i and e_i . An appropriate measure of patch size heterogeneity is the ratio Q of the maximum and minimum local extinction rates $e_i^{(\max)}$ and $e_i^{(\min)}$, which via eq. (1) are associated with the smallest and largest patches in the network, respectively.

Based on Frank & Wissel (2002) and Drechsler (2009) we calculate the MMLT as

$$T = \frac{1}{\tilde{e}} \sum_{i=1}^N \sum_{k=i}^N \frac{1}{k} \frac{(N-i)!}{(N-k)!} \frac{1}{(N-1)^{k-i}} q^{k-i} \quad (3)$$

where $\tilde{e}$ is the geometric mean over the local extinction rates e_i :

$$\tilde{e} = \prod_{i=1}^N (e_i)^{1/N}, \quad (4)$$

and q is the so-called aggregated colonisation extinction ratio, which represents a spatially aggregated ratio of the colonisation and extinction rates:

$$q \approx \frac{\bar{c}}{\tilde{e}} H. \quad (5)$$

In eq. (5), $\bar{c}$ is a power mean with

$$\bar{c} = \left(\frac{1}{N} \sum_{i=1}^N c_i^{\eta/b} \right)^{b/\eta} \quad (6)$$

and

$$H = \prod_{i=1}^N \left(\frac{1}{N-1} \sum_{\substack{j=1 \\ j \neq i}}^N \exp(-r_{ij}/d) \right)^{1/N} \approx \min \left\{ \frac{10^{-R/(15d)}}{(R/d)^2} \frac{3(R/d)^{1.65}}{(R/d)^{1.65} + 5}, 1 \right\}. \quad (7)$$

is a connectivity measure which considers that the mean dispersal distance d of individuals is finite and can be much smaller than R . Parameter R represents the spatial extent of the network. With Δx and Δy measuring the distances between the most eastern and most western, respectively the most northern and most southern patches, R is calculated as

$$R = \sqrt{\Delta x \Delta y / \pi}, \quad (8)$$

so that we denote R as “network radius”. Quantity H in eq. (7) which depends only on the ratio of network radius and species mean dispersal distance can be regarded as a measure of spatial connectivity. The approximation on the right hand side of eq. (7) represents a slight refinement of the approximation provided by Drechsler (2009). If d becomes large compared to the network size R the connectivity measure H reaches 1, reproducing the “Levins limit” (Levins 1969).

Equation (3) (derived by Drechsler (2009)) is the central formula that describes the MMLT. It is dependent on four key macroscopic parameters: the number (N) of habitable patches, the mean colonisation rate ($\bar{c}$) and the mean extinction rate ($\tilde{e}$), and the ratio (R/d) of the average network radius and the species’ mean dispersal distance. Equation (3) has previously been applied to static networks, which may be uncharacteristic of many real metapopulations. Our major advance in this paper is to relax the assumption that networks are static and to provide statistical estimates of the mentioned key macroscopic parameters in dynamic networks. This facilitates the application of equation (3) to a broader class of more realistic metapopulation models in which patches may be created and destroyed and in which habitat quality of a patch may vary over time.

Predicting the MMLT in dynamic networks

In this section we extend the work of Frank and Wissel (2002) and Drechsler (2009) that applies only to static networks, and include network dynamics. We distinguish between two types of network dynamics. In the first type, habitat patches randomly disappear at a rate μ and new patches are randomly recreated elsewhere (e.g., Wu & Levin 1994; Stelter *et al.* 1997; Amarasekare & Possingham 2001; Wahlberg *et al.* 2002; Biedermann 2004). As we consider patch size heterogeneity, recreated patches can have sizes differing from those of the destroyed ones. Assuming a balance of habitat destruction and creation, the stationary (expected) number of patches is denoted as N_{dyn} . Patch destruction (μ) effectively increases the local extinction rates e_i ($i=1, \dots, N$) to

$$e_i^{(\text{dyn})} = e_i + \mu \quad (9)$$

(e.g., DeWoody *et al.* 2005; Keymer *et al.* 2000). To calculate the MMLT for this type of dynamic network, e_i of eq. (1) needs to be replaced by $e_i^{(\text{dyn})}$ and all occurrences of N in eqs. (3) – (7) need to be replaced by N_{dyn} . Parameter R in eq. (8) represents half of the average diameter of the region within which new patches are created.

In the second type of dynamic networks, there are N patches with fixed locations and sizes. An uninhabitable patch randomly becomes habitable at a rate λ and a habitable patch becomes uninhabitable at a rate μ (e.g., Briers & Warren 2000; Ellner & Fussmann 2003). The expected number of habitable patches then is

$$N_{\text{dyn}} = \text{round}\left(\frac{\lambda}{\lambda + \mu} N\right) \quad (10)$$

(DeWoody *et al.* 2005; Keymer *et al.* 2000), where function $\text{round}()$ rounds its argument to the next nearest integer number. Like for the previous type of network, the MMLT is determined by replacing e_i by $e_i^{(\text{dyn})}$ of eq. (9) and all occurrences of N in eqs. (3) – (7) by N_{dyn} . In addition, in this type of network dynamics it may be that dispersers do not only immigrate into habitable patches but also into uninhabitable ones. In that case only a fraction $(N_{\text{dyn}}-1)/(N-1)$ of the dispersers contributes to the metapopulation dynamics and $\bar{c}$ in eq. (6) needs to be replaced by $\bar{c}(N_{\text{dyn}} - 1)/(N - 1)$.

Verification of the formula for dynamic networks

To test the validity of the analytical formula (eqs. (3) – (10)) for dynamic networks we compared its output with that of a spatially explicit stochastic computer simulation where the creation and destruction of habitat patches as well as the extinction of local populations and the colonisation of empty patches is simulated as Markov processes (see Appendix A). We varied all model parameters systematically within specified ranges (Table 1) and for each parameter combination plotted the predicted MMLT against that obtained from the simulation model.

Table 1: The ranges of all model parameters used in Fig. 1. The geometric mean local extinction rate was set to $\tilde{e} = 0.05$ - an arbitrary choice, since $\tilde{e}$ simply determines the time scale of the metapopulation and network dynamics. Rate λ is fixed via eq. (10) by choosing N_{dyn}/N and μ .

$N \in \{10, 20, \dots, 100\}$	Patch number
$\gamma \in \{4, 8, 12\}$	$\gamma = m(\tilde{e}/\varepsilon)^{-b/\eta}/\tilde{e}$ is the geometric mean over the patch-specific colonisation-extinction ratios c_i/e_i and through eqs. (1) and (2) related to the average patch size
$Q = \frac{e_i^{(\text{max})}}{e_i^{(\text{min})}} \in [1, 3]$	Degree of patch size heterogeneity, where of $e_i^{(\text{max})}$ and $e_i^{(\text{min})}$ represent the local extinction rates of the smallest and largest patches, respectively.
$b/\eta \in \{0.25, 0.5, 1.0, 1.5, 2.0\}$	Scaling exponent. Typical values of b range from 0.5 (emigration proportional to patch perimeter) to 1.0 (emigration proportional to patch area). η typically ranges from 0.5-2 (Lande 1993).
$d/R \in \{0.1, 0.5, 1\}$	Species mean dispersal distance (relative to the network radius R)
$\mu/\tilde{e} \in \{0.2, 0.4, \dots, 2.0\}$	Ratio of patch destruction and local extinction rates
$N_{\text{dyn}}/N \in \{0.5, 0.75, 1\}$	Ratio of the number of habitable patches to the total number of patches.
$w \in [0, 2]$	Range of temporal variation of the patch destruction and creation rates, measured relative to their respective long-term means
$\rho/R \in [0, 0.2]$	Spatial correlation length of patch destruction and creation (relative to the network radius R)

Essentially, our formula captures network and metapopulation dynamics by appropriate averages over space and time. Large levels of variability and spatial correlations naturally constrain the applicability of this kind of approach. Therefore we investigated how our formula performs if the heterogeneity in patch sizes (Q) increases beyond the ranges considered in Table 1. Further, in the simulations we allowed for non-stationary network dynamics in the sense that patch destruction and creation rates (λ and μ) randomly vary in time and

the processes of patch destruction and creation are spatially correlated (see Appendix A). As a measure of prediction error we plotted the standard deviation of our formula on a $\log_{10}$ scale between simulated and predicted MMLT as a function of patch size heterogeneity, the range of temporal fluctuations in the patch destruction and creation rates, and the range of spatial correlation in patch destruction and creation events. The log standard deviation was calculated by taking the logarithm (to the base of 10) of the simulated and predicted (i.e. analytically calculated) MMLT and calculating the standard deviation between these two quantities over all parameter combinations. A log-scale was chosen, so a prediction of 90 years where the true MMLT is 100 years, e.g., is regarded equivalent to a prediction of 900 years where the true value is 1000 years.

How to incorporate habitat succession on the patches

So far we have assumed that all habitable patches have a temporally constant habitat quality: when a patch is created its habitat quality h jumps from zero to $h_{\max}$, remains at that level and drops to zero again as the patch is destroyed. However, the quality of a habitat patch may change in time, e.g., due to succession so that habitat quality is a function of the patch age τ , i.e. the time after patch creation: $h=h(\tau)$. Assuming $h=h_{\max}$ throughout the life time of the patch obviously overestimates the patch quality. A more appropriate choice is the average habitat quality h_m . To calculate h_m we consider that for a patch destruction rate μ the probability that the patch has not yet been destroyed exponentially decreases with increasing patch age τ by $\exp(-\mu\tau)$. Because at small τ the patch is most likely not yet destroyed, habitat qualities at these times contribute more to h_m than habitat qualities associated with larger ages. Denoting by $P(\mu; \tau) = \mu \exp(-\mu\tau)$ the probability of a patch not being destroyed (the normalisation factor μ was included to ensure that the integral of $P(\mu, \tau)$ over time equals 1), the average habitat quality h_m is

$$h_m = \int_{\tau=0}^{\infty} P(\mu, \tau) h(\tau) d\tau \quad (11)$$

for continuous time, or for discrete time steps:

$$h_m = \sum_{n=0}^{\infty} P(\mu, \tau_n) h(\tau_n) = \mu \Delta t \sum_{n=0}^{\infty} \exp(-\mu n \Delta t) h(n \Delta t) \cdot \quad (12)$$

where Δt is the length of the time step.

To calculate the MMLT in a dynamic network shaped by succession, it has to be specified how the local extinction rate e_i and the colonisation rate c_i depend on habitat quality. A plausible model would be to replace patch size A_i in eqs. (1) and (2) by the product of patch size and expected habitat quality, $h_m A_i$. Clearly, there are other ways to modelling local extinction and colonisation rates than eqs. (1) and (2) (see the empirical example in the following section). The general principle, however, remains the same: we consider succession through an averaged patch quality that takes the probability of observing a patch of a particular age into account.

Results

Verification of the formula for dynamic networks

For stationary network dynamics with patch destruction rates of up to twice the average local extinction rate, and heterogeneity in local extinction rates e_i of up to a factor of $Q=3$ we observed good agreement between formula and simulation model (Fig. 1). The standard deviation of the life times on a $\log_{10}$ -scale is 0.14 (an interpretation of this number is given in the Discussion). Smaller errors are obtained for networks with short dispersal ranges, low ratios of colonisation and extinction rates (c_i/e_i) and low patch size heterogeneity. The validation results are independent of whether patches are recreated where they had been destroyed, or elsewhere within the spatial range ($\Delta x, \Delta y$) defined after eq. (8).

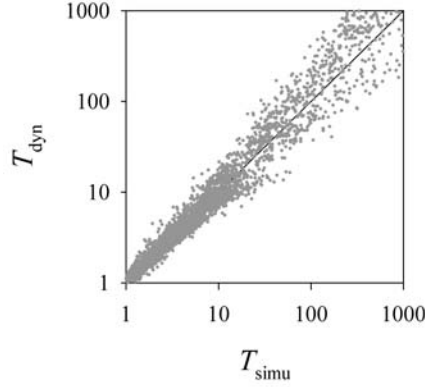


Figure 1: Mean metapopulation life time obtained from the formula (eqs. (3) – (10)) vs. the expected life time obtained through numerical simulations (100 simulation runs per parameter combination), both plotted in units of $\tilde{\epsilon}^{-1}$ (the geometric mean of the expected life times of all local populations in the absence of network dynamics: eq. (4)). If, e.g., local populations on average survive for $\tilde{\epsilon}^{-1} = 20$ years, the dots between 1 and 1000 correspond to mean metapopulation life times between 20 and 20,000 years. All parameters are systematically varied according to Table 1 with $w=0$ and $\rho=0$).

Figure 2 shows the effect of patch size heterogeneity and non-stationary network dynamics on the precision of the formula. Patch size heterogeneity beyond about $Q=3$ measurably increases the error of the approximation formula (Fig. 2a). While temporal variability in the patch destruction and creation rates (w) only moderately increases the error of our approximation formula (Fig. 2b) a spatial correlation ρ of patch destruction and creation that extends over more than about 25% of the network radius (R) can lead to substantial error (Fig. 2c).

Theoretical application and biological insights

The derived formula (eqs. (3) – (10)) allows users to rapidly calculate MMLTs for a variety of different landscapes and species attributes. Such broad and differentiated analyses are indispensable for advanced biological insights. We demonstrate this on the example of trade-offs between different landscape parameters. Knowledge of such tradeoffs is of high relevance for conservation planning and the optimisation of landscapes (Nicholson *et al.* 2006; Nelson *et al.* 2008), because they tell how much change in one landscape parameter (such as mean patch size, patch size heterogeneity, connectivity, patch dynamics, etc.) must be compensated by changing another one in order to maintain the same MMLT. Figure 3a illustrates that increasing patch size heterogeneity or decreasing patch turnover (μ) increase the MMLT. As a consequence, an increase in patch turnover can be compensated for by a sufficient increase in patch size heterogeneity. The numerical simplicity of the formula allows calculating this trade-off rapidly (more than 30 times faster than with a simulation model) and in a systematic manner. Figure 3b presents such a systematic analysis. It shows that patch size heterogeneity Q needs to be increased by about 3 units to compensate for an increase in patch destruction μ by $0.1\tilde{\epsilon}$ (to recall, $\tilde{\epsilon}$ is the geometric mean of the local extinction rates: eq. (4)).

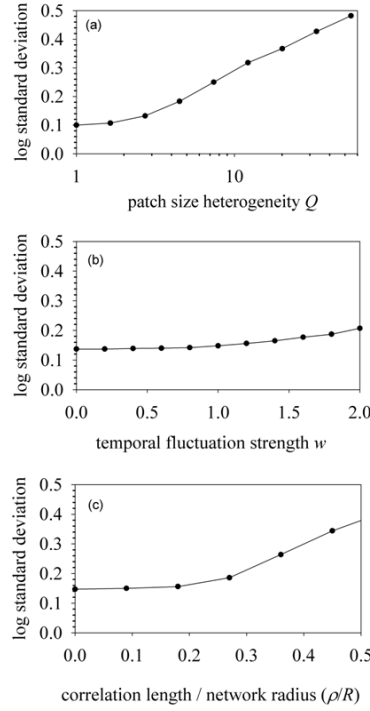


Figure 2: Log standard deviation of the formula (standard deviation of the predicted mean metapopulation life time on $\log_{10}$ scale) as a function of (a) the patch size heterogeneity Q , (b) the temporal variation w of the patch creation and destruction rates (relative to their means), and (c) the length of the spatial correlation ρ of patch destruction and creation relative to the network radius R . Other parameters as in Fig. 1.

Figure 3a provides yet further biological insights. It shows that the capacity of habitat networks to buffer landscape dynamics depends on the patch size heterogeneity. Metapopulations in networks with patch size heterogeneity ($Q > 1$) turn out to be less robust to patch turnover (μ) than metapopulations in homogenous networks ($Q = 1$) because at $Q > 1$ the MMLT decreases more strongly with increasing patch turnover (μ) than at $Q = 1$. For instance, an increase of the patch destruction rate μ from $0.2\tilde{\epsilon}$ to $0.4\tilde{\epsilon}$ reduces T_{dyn} by a factor of about 3 at $Q = 1$, and by a factor of 40 at $Q = 7$.

Another option to compensate for patch destruction is to create more patches by increasing the patch creation rate λ (Fig. 3c). However, the systematic analysis (Fig. 3d) reveals that the effectiveness of this measure is limited, particularly if the patch destruction rate is high. At small patch destruction rates an increase in the patch destruction rate μ by $0.5\tilde{\epsilon}$ can be compensated by an increase in the patch creation rate by about $0.2\tilde{\epsilon}$ while at large patch destruction rates the patch creation rate would have to be increased by $\tilde{\epsilon}$ or more.

Example for the parameterisation of the formula for a static network

Drechsler *et al.* (2003) consider a metapopulation of butterflies, *Melitaea cinxia*, inhabiting a static network of $N = 48$ habitat patches on the Finnish Åland Islands. The estimation of the parameters of eqs. (1) and (2) is provided in Drechsler *et al.* (2003); the mean dispersal distance estimated by the authors is $d = 2.5$ km. Below we focus on the remaining step: the calculation of the connectivity H (eq. (7)). According to Fig. 1 of Drechsler *et al.* (2003), the 48 patches are spread over an area with east-west and north-south dimension of about $\Delta x = \Delta y = 6$ km. With eq. (8) we obtain a network radius of about $R = 3.4$ km and with eq. (7) a connectivity of about $H = 0.3$.

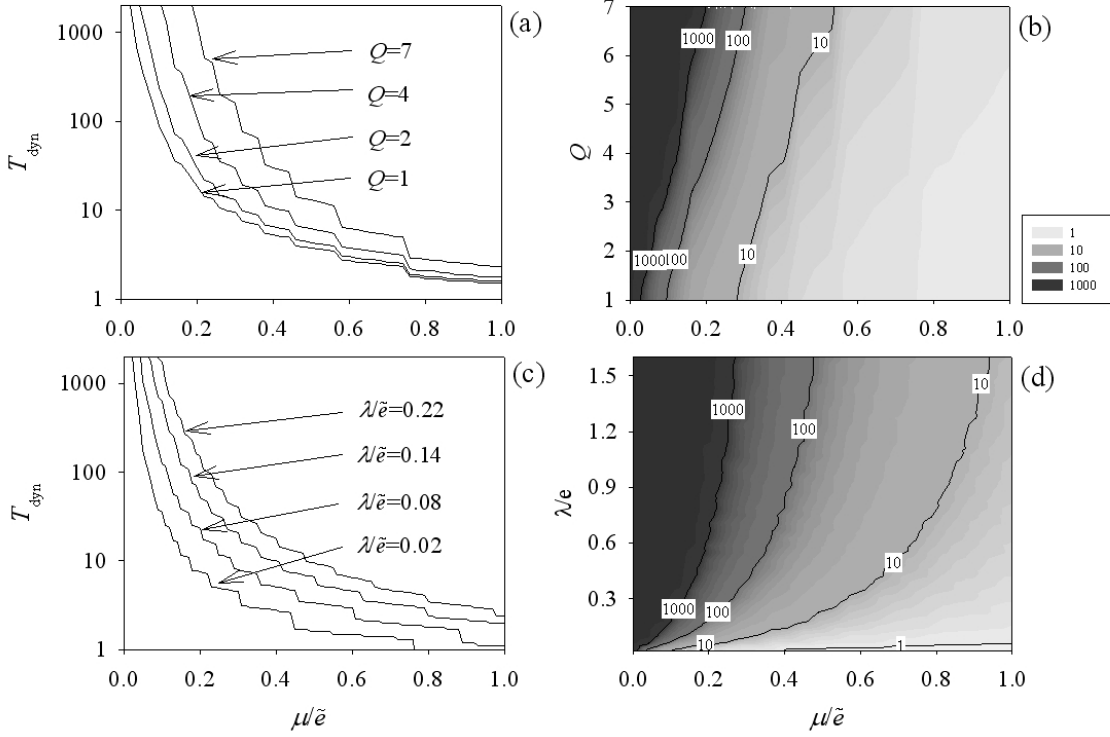


Figure 3: (a) Mean metapopulation life time (MMLT) (eq. (3)) in units of $\tilde{e}^{-1}$ (eq. (4)) as a function of the patch destruction rate μ (in units of $\tilde{e}$) for four levels of patch size heterogeneity Q . (b) MMLT (indicated by colour) as a function of the patch destruction rate μ (in units of $\tilde{e}$) and patch size heterogeneity Q . The solid lines mark so-called iso-MMLT lines, so that all points (combinations of Q and μ) lead to the same MMLT. (c) MMLT in units of $\tilde{e}^{-1}$ as a function of the patch destruction rate μ (in units of $\tilde{e}$) for four levels of the patch creation rate λ (in units of $\tilde{e}$). (d) MMLT (indicated by colour) as a function of the patch destruction rate μ and the patch creation rate λ (both in units of $\tilde{e}$). The model parameters are: $N=30$, $d=0.25$, $b/\eta=2$, $\bar{c}/\tilde{e}=12$, $\tilde{e}=0.05$ and $\lambda/\tilde{e}=0.1$ (for panels a and b) and $Q=3$ for panels c and d). The steplike run of the curves is due to the rounding of the patch number in eq. (10).

Example of the parameterisation of the formula for a dynamic network in the presence of succession

Stelter *et al.* (1997) consider a metapopulation of plant hoppers, *Bryodemus tuberculata*, inhabiting a dynamic network of vegetated gravel banks with identical sizes in the River Isar, Germany. We focus here on the establishment of the colonisation and extinction rates, c and e , which depend on the network dynamics. Floods destroy local populations and recreate bare gravel banks at a frequency μ . After creation of a gravel bank it takes 3 years for vegetation to establish and for the gravel bank to become habitable. In the model of Stelter *et al.* (1997) this is modelled by a jump in the local carrying capacity for the plant hoppers (only females are considered in the model) from zero to $K_{\max}=50$. Due to succession, the quality of the vegetation declines with time, associated with a decline of the local carrying capacity by 1 per year. This continues for 45 years after which the local carrying capacity assumes a value of $K_{\min}=5$ where it remains constant until the gravel bank is washed away. Mathematically, the dynamics of the carrying capacity of gravel banks are described by

$$K(\tau_n) = \begin{cases} 0 & 0 \leq n \leq 3 \\ 53 - n & 3 \leq n \leq 48 \\ 5 & n \geq 48 \end{cases} \quad (13)$$

(with time step length $\Delta\tau = 1$ year). Inserting eq. (13) into eq. (12) (identifying $K(\tau_n)$ with $h(\tau_n)$) delivers the expected carrying capacity as a function of μ : $K_m(\mu)$ (Fig. 4). It is small for very frequent floods, because in

the first three years the patch is inhabitable, and small for very infrequent floods, because the carrying capacity declines with increasing patch age (eq. (13)). Stelter *et al.* (1997) assume that local extinction is caused by two processes: Environmental stochasticity and demographic stochasticity lead to local extinction with annual probabilities of 0.1 and $1/K$, respectively. The (annual) local extinction rate is therefore

$$e(\mu) = 1 - (1 - 0.1) \left(1 - \frac{1}{K_m(\mu)} \right) = 1 - 0.9 \left(1 - \frac{1}{K_m(\mu)} \right) \quad (14)$$

The annual probability of a female plant hopper leaving a gravel bank is 0.1. Each female immigrating into an empty gravel bar is assumed to establish a local population, leading to a colonisation rate (cf. eq. (2)) of

$$c = 0.1 K_m(\mu). \quad (15)$$

Inserting K_m of eq. (13) into eqs. (14) and (15) yields the colonisation and extinction rates c and e (identical for all patches, since these have identical sizes) as functions of the patch destruction rate μ . These two parameters include the indirect effects of the flood dynamics and, like the expected carrying capacity, are “optimal” (i.e., c maximal and e minimal) for flood rates around $\mu=0.1$. The additional direct effect, the destruction of local populations due to patch destruction at rate μ , is considered through the dynamic local extinction rate e_{dyn} which is obtained by adding μ to e (eq. (9)). Inclusion of this direct and adverse effect shifts the optimal flood rate from 0.1 (associated with the minimum of e) to a smaller value around 0.02 (Fig. 4). The flood rate that maximises the ratio of colonisation and dynamic extinction rates, c/e_{dyn} , is a compromise between maximising c and minimising e_{dyn} and is located around a value of 0.05.

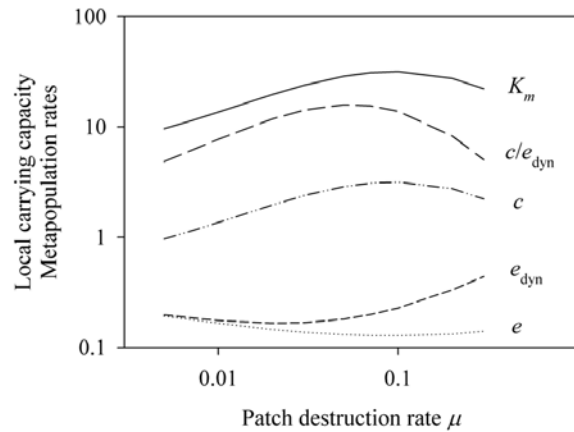


Figure 4: Parameters of the metapopulation dynamics as functions of the patch destruction rate μ for the metapopulation of (Stelter *et al.* 1997). Solid line: expected patch carrying capacity; dotted line: the static local extinction rate e (but considering the indirect effect of patch destruction on the average patch carrying capacity); short-dashed line: the dynamic local extinction rate $e_{\text{dyn}}=e+\mu$ (considering direct and indirect effects of patch destruction); dash-dotted line: the colonisation rate c ; long-dashed line: the ratio c/e_{dyn} .

As mentioned above, Stelter *et al.* (1997) assume that floods destroy and create gravel banks at the same time and with the same numbers so that the total number of gravel banks in the system is constant at $N_{\text{dyn}}=30$ and independent of the flooding frequency. The patch destruction rate that maximises the ratio c/e_{dyn} therefore maximises the life time of the metapopulation. In the simulation model analysis of Stelter *et al.* (1997) the patch destruction rate is given by the product $\text{Flood} \times \text{Wash}$ where Flood is the flood rate and Wash the proportion of gravel banks affected by a flood. The authors set $\text{Wash}=0.25$, meaning that in each flood one forth of all gravel banks is affected, and find that the mean life time of the *Bryodema* metapopulation is maximised by $\text{Flood}=0.2 \dots 0.3$. So the optimal patch destruction rate is $(0.2 \dots 0.3) \times 0.25$, which very well agrees with our approximation.

Discussion

We provide a formula for the expected life time of a metapopulation in a dynamic habitat network with heterogeneous patch sizes. The validity of the formula over large parameter ranges confirms our initial hypothesis that the life time of a metapopulation in a dynamic habitat network can be estimated by casting the stationary properties of network dynamics into effective parameters and inserting these appropriately into a static metapopulation formula.

Previously developed formulae for heterogeneous and dynamic landscapes are based on occupancy thresholds. They ignore stochasticity and predict that below a certain level of network dynamics a metapopulation persists indefinitely and above it goes extinct with certainty. Focussing on the mean metapopulation life time (MMLT), our formula provides a more differentiated view on the impact of network dynamics on metapopulation viability (e.g. Fig. 3a) and allows the rapid assessment of different spatiotemporal landscape structures and tradeoffs between them in a continuous manner (e.g. Fig. 3b). Such broad and differentiated analyses are indispensable for both advanced biological insights and conservation management. Another important consequence of focussing on the MMLT is that (meta)population extinction times are generally exponentially distributed. This has been proven for static landscapes (Grimm and Wissel 2004) but we found this to be true also under the considered network dynamics (Fig. A1 in Appendix A). Thus, the mean of this exponential distribution - the MMLT - captures all essential information required to assess (meta)population viability (Grimm and Wissel 2004).

The way of its derivation implies that our formula can be applied only in metapopulations where the landscape dynamics are stationary (e.g., where floods destroy patches and vegetation growth recreates them at constant rates throughout the landscape). Transient dynamics where e.g. patches are destroyed at one end of the landscape and recreated on the other (e.g., Travis 2003), or where patches are lost on net (e.g., Bascompte & Solé 1996; Casagrandi & Gatto 2002) cannot be considered with our formula. However, we found that temporal variation in the patch destruction and creation rates has relatively little influence on the precision of our formula.

Succession dynamics on the patches can be considered in a statistical manner (another example is Hastings (2003) for homogenous successional landscapes). We propose a relatively simple approach for heterogeneous successional landscapes based on temporal averages of local patch qualities and implied local extinction and colonisation rates that can be inserted into our formulae. As demonstrated on the example of a plant hopper metapopulation, the simplicity of the approach allows us to derive insights into the role of disturbance in successional landscapes that could not be obtained with the original simulation model.

Another limitation of the formula is that it assumes that there is no spatial correlation in the network dynamics of patch destruction and recreation (Johst & Drechsler 2003; Vuilleumier *et al.* 2007). We found that our formula approximates the simulated MMLT with acceptable precision if the correlation length is less than about 25% of the network radius. Cornell & Ovaskainen (2008) developed an analytical expression for mean patch occupancy for these cases, however, without consideration of patch size heterogeneity. Developing analytical approaches for both heterogeneous and correlated landscapes is still an unresolved challenge.

A final limitation is the degree of patch size heterogeneity, which via eqs. (1) and (2) reflects in heterogeneity in the extinction and colonisation rates of the local populations. We found that if local extinction rates differ by more than a factor of 3, the error in the output of the formula may be judged unacceptable. The definition of unacceptable is of course subjective. In the notion of the present paper a standard deviation between predicted and simulated MMLT on a $\log_{10}$ scale of less than 0.14 is considered acceptable. The 95% confidence interval associated with a standard deviation of 0.14 comprises true MMLTs between ± 0.28 of the predicted value on a $\log_{10}$ scale. With a predicted MMLT of 100 years, for instance, this means that the true MMLT lies between $100 \cdot 10^{-0.28} = 52$ and $100 \cdot 10^{0.28} = 190$. This error may seem substantial but in fact is not larger, or even smaller, than that produced by many other models used for (meta)population viability analysis (McCarthy *et al.* 2003; Drechsler *et al.* 2003; Lindenmayer *et al.* 2003). Like the cited authors we suggest to use our formula for comparing and ranking of conservation strategies rather than making crisp predictions of the future of a particular metapopulation.

Within the stated limits of application the formula represents a straightforward tool for rapidly assessing metapopulation survival under a variety of spatiotemporal network structures. Thus it is valuable for conservation management and for optimising large spatiotemporal landscape structures with multiple species where detailed simulation models are not applicable because of long computation times (see e.g., Nicholson *et al.* 2006; Nelson *et al.* 2008). Once a basic understanding has been obtained about what constitutes an optimal landscape more sophisticated models may be employed to refine the optimum (Polasky *et al.* 2008). Our formula is also useful for general analyses of metapopulation viability in heterogeneous and dynamic

landscapes to advance our theoretical understanding of population ecology in dynamic fragmented landscapes. Systematic evaluation of the formula, e.g., revealed that metapopulations with heterogeneous patch sizes are more vulnerable to network dynamics than metapopulations with homogenous patch sizes, and patch creation can effectively compensate for patch destruction only if the patch destruction rate is not too high. This type of comprehensive understanding of the synergistic effects of landscape structure and dynamics is crucial for both ecological theory and conservation management.

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Appendix A: Verification of the formula for dynamic networks

To test the validity of the analytical formula (eqs. (3) – (10)) for dynamic networks we compared its output with that of a spatially explicit stochastic computer simulation where the creation and destruction of habitat patches is simulated as a Markov process with rates λ and μ . Local populations go extinct stochastically at rates e_i and/or when the habitat patch gets destroyed. Empty patches become recolonized according to

$$C_i = \frac{1}{N_{\text{tp}} - 1} \sum_{\substack{j=1 \\ (j \neq i)}}^N c_j p_j \exp(-r_{ij} / d) \quad (\text{A1})$$

Here $p_j=1$ if patch j is occupied and $p_j=0$ otherwise, c_j is the colonisation rate of patch j (cf. eq. (2)), r_{ij} is the Euclidian distance between habitat patches i and j , d the species specific mean dispersal distance; $N_{\text{tp}}=N_{\text{dyn}}$, except for the case where dispersers immigrate into uninhabitable patches so that $N_{\text{tp}}=N$. By this, C_j is the rate by which dispersers immigrate into patch i divided by the number of individuals required for the successful colonisation of an empty patch.

For the analysis of randomly varying patch destruction and creation rates (cf. Fig. 2) we draw these rates from a uniform distribution with means μ and λ , and widths $w\mu$ and $w\lambda$, respectively. For demonstrating the consequences of spatial correlation in patch destruction and patch creation processes we used a simple but

reasonable algorithm based on two quantities: the patch destruction (creation) rate and the conditional probability that a neighbour patch of an affected patch is also destroyed (recreated) (e.g., Ovaskainen *et al.* 2002; Hiebeler 2004). This conditional probability exponentially decreases with increasing distance from the affected patch thereby ensuring that on average the proportion of destroyed (created) patches is the same in spatially uncorrelated and correlated dynamics. The range of the spatial correlation is given by the correlation length ρ . It is assumed to be identical for patch destruction and creation.

To simplify the numerical validation of the formula we introduced a parameter δ_i that measures the deviation of the local extinction rate e_i from the geometric mean of all patch sizes $\tilde{\varepsilon}$,

$$\delta_i = e_i / \tilde{\varepsilon} . \quad (\text{A2})$$

Inserting eq. (1) into eq. (2) and using eq. (A2) one can calculate the corresponding colonisation strengths c_i as

$$c_i = m \left(\frac{e_i}{\varepsilon} \right)^{-b/\eta} = m \left(\frac{\delta_i \tilde{\varepsilon}}{\varepsilon} \right)^{-b/\eta} . \quad (\text{A3})$$

The N patches were randomly allocated in a unit square (other shapes such as circles and ellipses with axis ratios (semi-major / semi-minor) of up to 10) were tested, as well, and lead to the same results). The parameters measuring patch size heterogeneity, δ_i , were drawn from a log-uniform distribution: $\ln \delta_i \in [-0.5 \ln Q, 0.5 \ln Q]$. By this, Q is the ratio between the local extinction times of the smallest and the largest patches in the network (denoted as $e_i^{(\max)}$ and $e_i^{(\min)}$, respectively). A value of $Q = e_i^{(\max)} / e_i^{(\min)} = 1$ represents patch size homogeneity and an increasing Q represent increasing heterogeneity in the local extinction times, which by eq. (1) is associated with increasing patch size heterogeneity. We systematically varied all model parameters (Table 1) and for each parameter combination plotted the MMLT obtained from the formula against the MMLT obtained in the simulation.

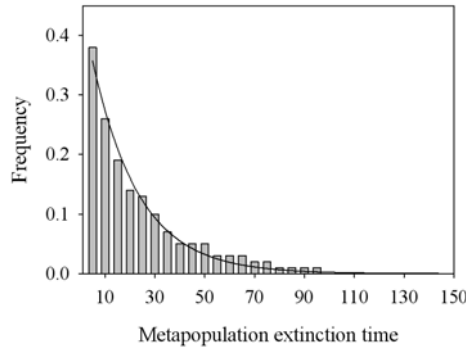


Figure A1: In our numerical simulations of the metapopulation dynamics we recorded not only the MMLT but the entire distribution of metapopulation life times. The panel shows a typical example obtained for a dynamic network with parameters $d/R=0.5$, $Q=7$, $\beta=1$, $\gamma=12$, $\mu/\tilde{\varepsilon} = 1.5$, $\tilde{\varepsilon} = 0.05$, $N=30$). The solid line represents an exponential fit to the distribution.

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Biodiversity conservation in dynamic landscapes: trade-offs between number, connectivity and turnover of habitat patches

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Summary

1. Many species are adapted to landscapes with characteristic dynamics generated by ongoing habitat destruction and creation. Climate change and human land use, however, may change the dynamics of these landscapes. Studies have repeatedly shown that many species are not able to cope with such changes in landscape dynamics. Conservation policies must, therefore, explicitly address this threat. The way in which management should be modified when formerly static landscapes become dynamic or when landscape dynamics change is unclear.

2. Using an analytical formula for the rapid assessment of metapopulation lifetime in dynamic landscapes, we investigate if and how changes in one landscape attribute may be compensated by changes in another attribute to maintain species viability. We study such trade-offs considering both spatial (number, connectivity of patches) and temporal (patch destruction and creation rates) landscape attributes.

3. We show that increasing patch destruction can be compensated to a certain extent by improvements in other spatial and/or temporal landscape attributes. Focusing on trade-offs between management options reveals two key factors essential for management decisions: First, the trade-offs are generally nonlinear irrespective of considering spatial or temporal landscape attributes. Secondly, species can be grouped according to their response to particular management options.

4. *Synthesis and applications.* We demonstrate the usefulness of an analytical formula for calculating trade-offs between landscape attributes for a variety of landscapes and species. Two practical and robust management recommendations can be derived: (i) The nonlinearity of trade-offs implies that the effectiveness of conservation measures depends explicitly on the current level of landscape attributes. It must, therefore, be taken into account in conservation decision making. In particular, the existing level of patch turnover is decisive: if it is already high, improvements in other landscape attributes are ineffective in maintaining species viability. Thus, monitoring the current level of landscape attributes is indispensable for effective biodiversity conservation. (ii) Compensation of increased patch destruction by increased patch creation is only suitable for species with high dispersal propensity adapted to variable environments (aside from habitat patch turnover). This implies that conservation policies which rely on such compensation, like offsetting and conservation banking, are feasible only for this type of species.

Key-words: climate change, conservation planning, environmental stochasticity, landscape attributes, landscape dynamics, management, metapopulation

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Introduction

Many ecosystems are characterised by continuous changes in habitat structure creating spatial and temporal habitat heterogeneity with ongoing habitat destruction and creation. Fire, for example, creates spatiotemporal vegetation structures in many savannas and forest ecosystems (e.g. Groeneveld, Enright & Lamont 2008; Zinck, Johst & Grimm 2010). In arid regions, patchy and stochastic rainfall is responsible for habitat conditions that are extremely heterogeneous in space and time (e.g. Fahse, Dean & Wissel 1998). Gap formation in forests by insect outbreaks or windfall and weather events such as droughts and floods may create similar structures (e.g. Stelter *et al.* 1997; Briers & Warren 2000). Last but not least, human impacts shape landscapes through agricultural land use such as harvesting, grazing, mowing or habitat restoration (e.g. Johst *et al.* 2006; Hodgson, Moilanen & Thomas 2009; Meulebrouck *et al.* 2009). Habitat dynamics in terms of habitat destruction and creation are a key characteristic of these landscapes.

Many species are specifically adapted to the spatiotemporal heterogeneity of their habitat (e.g. Stelter *et al.* 1997; Briers & Warren 2000; Wahlberg, Klemetti & Hanski 2002; Biedermann 2004; Hodgson, Moilanen & Thomas 2009). However, the rapid economic and social development during the last century and the resulting global change, particularly the changing climate and impact of human land use, may alter the characteristic of habitat dynamics. For example, mowing or logging patterns may change, floods and fire may be suppressed, or habitat succession rates may alter. Both theoretical and field studies suggest that many species are not able to cope with such changes without conservation measures (e.g. Johst, Brandl & Eber 2002; Matlack & Leu 2007; Thuiller 2007). Thus, biodiversity conservation that accounts for landscape dynamics and responses to the foreseeable impacts of global change is an important challenge for research (e.g. Wintle *et al.* 2005; Jäkäläniemi, Tuomi & Sikamaki 2006; Drechsler & Wätzold 2007; Leroux *et al.* 2007; Pressey *et al.* 2007; Ross *et al.* 2008; Possingham, Moilanen & Wilson 2009).

In this article, we consider landscapes characterised by patchy habitats that are destroyed and created by natural and/or anthropogenic influences. Patch destruction and creation occur at constant rates resulting in stationary landscape dynamics with ongoing patch turnover (Hanski 1999a). Populations of species living in these patchy landscapes can be described as metapopulations. Metapopulation models assume that local populations inhabit (habitat) patches and may colonise other patches but are otherwise independent of each other (e.g. Gyllenberg & Hanski 1997; Keymer *et al.* 2000; Wilcox, Cairns & Possingham 2006; Cornell & Ovaskainen 2008).

Many studies have considered metapopulation survival in static landscapes (in which habitat patches are permanently present) and investigated how changing, for example, the number, size or connectivity of habitat patches influences species viability (Verboom *et al.* 2001; McCarthy, Thompson & Possingham 2005). As landscape attributes can interact in their

impact on species, a change in one landscape attribute can be compensated for by changes in another attribute. This interaction is important for management decisions and can be analysed by so-called trade-offs between two attributes. The corresponding trade-off curves visualise and quantify the extent of compensation necessary to maintain the species persistence. In static landscapes, trade-offs between spatial landscape attributes such as the number and size of habitat patches (the so-called SLOSS problem, e.g. Ovaskainen 2002) or between the number and connectivity of patches (e.g. Moilanen & Hanski 1998; Vuilleumier *et al.* 2007) have been discussed frequently.

For dynamic landscapes, however, the use of general landscape attributes for conservation is much less developed, and, in particular, interactions between landscape attributes and related trade-offs are unclear or absent (Van Teeffelen *et al.*, unpublished data). This concerns especially trade-offs between spatial landscape attributes (number, connectivity of patches) and temporal landscape attributes (rates of patch destruction and creation). These temporal attributes impact species in a different way as they lead to temporally varying patch configurations that species have to cope with. Specifically, there is a lack of knowledge in three directions.

It is often unclear how the effectiveness of conservation measures depends on the level of landscape dynamics (e.g. Possingham, Moilanen & Wilson 2009) and whether traditional rules of network design in static landscapes can be transferred to dynamic landscapes. Thus, the question arises: (1) How do trade-offs between spatial landscape attributes differ in static vs. dynamic landscapes? To address this question, we compare static (with zero patch turnover) and dynamic (with nonzero patch turnover) landscapes with respect to the trade-off between number and connectivity of habitat patches based on species viability. If the differences between the trade-offs in static vs. dynamic landscapes were small, management guidelines that are optimal in static or very low level dynamic landscapes might be retained in highly dynamic landscapes. If the differences were large, dynamic landscapes would require different management.

As compensation measures for dynamic landscapes may consist of alterations of the spatial attributes of the landscape such as the number and connectivity of habitat patches, the question arises: (2) Can an increasing patch destruction rate be compensated by changes in spatial landscape attributes? To answer this question, we focus on the trade-offs between temporal and spatial landscape attributes: (i) the trade-off between habitat destruction rate and patch number (at given connectivity) and (ii) the trade-off between habitat destruction rate and patch connectivity (at a given patch number).

Many current conservation policies like offsetting and conservation banking allow habitat destruction provided that it is compensated by habitat creation or restoration elsewhere (Cuperus *et al.* 1999; Bishop *et al.* 2009; Schippers *et al.* 2009; Wissel & Wätzold 2010). However, it is unclear under which conditions such policies can ensure the survival of species (e.g. Drechsler & Wätzold 2009; Hartig & Drechsler 2009). We therefore ask: (3) Can an increasing patch destruction rate be

compensated by an increasing habitat creation rate? To address this question, we focus on trade-offs between temporal landscape attributes and investigate how well an increased habitat destruction rate can be compensated by increasing the rate of patch creation.

The survival of metapopulations in dynamic landscapes has been subject to repeated simulation studies (e.g. Boughton & Malvadkar 2002; Johst, Brandl & Eber 2002; Ellner & Fussmann 2003; Johst & Drechsler 2003; Wintle *et al.* 2005; Wilcox, Cairns & Possingham 2006; Vuilleumier *et al.* 2007; Hodgson, Moilanen & Thomas 2009). However, stochastic simulation models require a lengthy numerical analysis, making a systematic exploration of trade-offs between landscape attributes particularly cumbersome. Alternatively, approximation formulae have been derived to calculate the mean metapopulation lifetime as a function of static (Frank & Wissel 2002; Drechsler 2009) and dynamic landscape attributes (Drechsler & Johst 2010). Trade-offs can be analysed conveniently and rapidly with these formulae. In particular, the shape of these trade-off curves provides important insights into the impact of spatial and temporal landscape attributes on metapopulation survival in dynamic landscapes. For instance, highly nonlinear trade-off curves would indicate thresholds beyond which viable populations can be sustained (for details see below). The shape of the curves is likely to depend on the species to be protected. Species differ, for example in their dispersal ability, individual area requirements and their sensitivity to environmental stochasticity (e.g. Vos *et al.* 2001; Jacquemyn, Butaye & Hermy 2003). Therefore, we also investigate the influence of species traits on the trade-offs and discuss the consequences for biodiversity conservation in dynamic landscapes.

Materials and methods

Our description of the methods is divided into three subsections. In the first part, we present the formula for the mean metapopulation lifetime from Drechsler & Johst (2010) on which our analysis is based. In the second part, we explain the trade-offs between landscape parameters that were considered. In the third part, we discuss the parameterisation of the formula and the parameter combinations for which trade-offs were explored. For calculating the trade-offs, the analytical formula was implemented in Delphi 5.0 (Borland 1999).

ANALYTICAL FORMULAE FOR THE MEAN METAPOPOPULATION LIFETIME

In the following, we review the results of Drechsler & Johst (2010) who derived a formula for the mean time to extinction in dynamic landscapes based on analytical approaches for static landscapes (Frank & Wissel 2002; Drechsler 2009). Our starting point is a habitat network of given spatial extent (given a network radius R) containing N habitat patches affected by ongoing patch destruction and patch creation. Parameter R may be regarded as $R = \sqrt{\Delta x \Delta y / \pi}$ where Δx and Δy are the distances between the most eastern and most western or the most northern and most southern patches, respectively. If patches are created at positions other than those at which they had been destroyed, Δx and Δy represent the geographic range within which patches can be created.

The formula for the mean metapopulation lifetime in a dynamic habitat network allows rapid assessment of metapopulation survival as a function of both spatial and temporal landscape attributes (Drechsler & Johst 2010):

$$T_{\text{dyn}} \approx \frac{1}{\bar{e}_{\text{dyn}}} \sum_{i=1}^{N_{\text{dyn}}} \sum_{k=1}^{N_{\text{dyn}}} \frac{1}{k} \frac{(N_{\text{dyn}} - i)!}{(N_{\text{dyn}} - k)!} \frac{1}{(N_{\text{dyn}} - 1)^{k-i}} q_{\text{dyn}}^{k-i} \quad \text{eqn 1}$$

Here, N_{dyn} is the number of patches, q_{dyn} is the so-called aggregated colonisation/extinction ratio, and $\bar{e}_{\text{dyn}}$ is the geometric mean over the local extinction rates e_i including patch destruction at rate μ

$$\bar{e}_{\text{dyn}} = \frac{N}{\prod_{i=1}^N (\mu + e_i)^{1/N}} = \bar{e} \prod_{i=1}^N (1 + \mu/e_i)^{1/N} \quad \text{eqn 2}$$

$\bar{e}$ denotes the geometric mean of the local extinction rates in the absence of network dynamics. The patch number N_{dyn} in dynamic landscapes is determined by the total number of patches N and the patch destruction and creation rates (μ and λ):

$$N_{\text{dyn}} = \text{round} \left(\frac{\lambda}{\lambda + \mu} N \right) \quad \text{eqn 3}$$

q_{dyn} is the aggregated colonisation/extinction ratio:

$$q_{\text{dyn}} = \frac{\bar{c}}{\bar{e}_{\text{dyn}}} H \quad \text{eqn 4}$$

where $\bar{c}$ is the power mean of the colonisation strengths c_i of the patches:

$$\bar{c} = \left(\frac{1}{N} \sum_{i=1}^N c_i^{1/\beta} \right)^{\beta} \quad \text{eqn 5}$$

The colonisation strengths c_i represent the rate by which individuals emigrate from a local population i divided by the number of immigrants required for successful colonisation of an empty patch. The parameter

$$\beta = b/\eta \quad \text{eqn 6}$$

summarises the species-specific parameters η and b . These parameters together with species-specific parameters ε , m describe how colonisation strengths and extinction rates of local populations, c_i and e_i in eqns 2 and 5, relate to the patch sizes A_i (Drechsler 2009):

$$e_i = \varepsilon A_i^{-\eta} \text{ and } c_i = m A_i^b. \quad \text{eqn 7}$$

Typical values of b range from 0.5 (emigration proportional to patch perimeter) to 1.0 (emigration proportional to patch area) and η typically ranges from 0.5 to 2 according to high and low (sensitivity to and level of) environmental stochasticity (e.g. Lande 1993). The parameter β of eqn 6 hence varies among species between about 0.25 and 2. See the next section for more details on the biological explanation and numerical estimation of these parameters.

Quantity H in eqn 4 is a measure of patch connectivity, where d is the mean dispersal distance of species, and R is the 'network radius' as defined previously:

$$H = \min \left\{ \frac{3 \cdot 10^{-R/(15d)}}{(R/d)^2} \frac{(R/d)^{1.65}}{(R/d)^{1.65} + 5}, 1 \right\} \quad \text{eqn 8}$$

H lays between zero and one and measures – relative to a network with perfectly connected patches – the ability of dispersers to reach the other patches of the network. If the species dispersal range d is

large compared to the network radius R , all patches can be reached by the dispersers. Then, the network consists of N perfectly connected patches and H takes its maximum of one. If in contrast, d is small compared to R species dispersal is very local compared to the network radius such that only nearby patches can be recolonised. In this case, the network consists of N very poorly connected patches and H is close to zero.

Altogether, metapopulation lifetime depends on the following landscape attributes: total number (N) of (inhabitable and uninhabitable) patches, patch destruction rate (μ), patch creation rate (λ) and patch areas (A_i), the species parameters m , ε , β and η and the species-specific 'network permeability' R/d described by the ratio of the average network radius R and the species' dispersal range d . The landscape-related parameters of the formula may be subject to management. For example, 'network permeability' may be managed by decreasing network radius R or decreasing dispersal mortality (resulting in increasing connectivity H , see eqn 8). Moreover, patch destruction and/or creation rate may be altered e.g. via controls on logging or mowing patterns, controlled burning or flood suppression.

TRADE-OFFS BETWEEN LANDSCAPE ATTRIBUTES

The landscape attributes exhibit trade-offs with respect to the expected metapopulation lifetime. For example, a lower patch number may be compensated by increasing connectivity, or a higher patch destruction rate may be compensated by a larger patch number.

We analyse the trade-offs between two landscape attributes x and y , where x and y are any of the parameters involved in the three trade-off types above, by plotting the mean metapopulation lifetime as a function of x and y (Fig. 1). Combinations (x, y) that lead to the same mean metapopulation lifetime are termed iso- T lines. The shape of an iso- T line contains information about the trade-off between landscape attributes x and y . Assuming that current values of x and y are x_1 and y_1 [point (x_1, y_1) in Fig. 1a], a reduction in y by Δy can be compensated by an increase in x by Δx [ending at point (x_2, y_2) in Fig. 1a] that is located at the same iso- T line as point (x_1, y_1) . The ratio $\Delta y/\Delta x$ measures the relative importance of the two variables x and y . Between points (x_1, y_1) and (x_2, y_2) of the present example, variable y is more important, because a relatively large increase in x is required to compensate for a relatively small decline in y . If the slope of the iso- T line is constant (Fig. 1b), the relative importance of x and y is constant

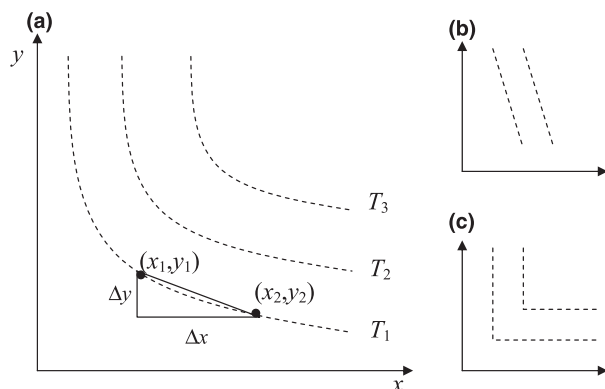


Fig. 1. Conceptual example of a trade-off between variables x and y with regard to mean metapopulation lifetime T_i . Panel (a) shows three iso- T lines, i.e. each combination (x, y) located on curve T_i leads to a mean metapopulation lifetime of T_i . Panels (b) and (c) show variants of iso- T lines.

and independent of the actual values of x and y . If the iso- T lines are nonlinear, this is not the case, instead, the relative importance of the variables depends on their current values. Figure 1a represents a typical situation where the relative importance of variable y increases with decreasing magnitude of y . For example, if y is large, a large decline in y can be compensated by just a small increase in x whereas if y is small, even a small decline in y can only be compensated by a large increase in x . In the extreme cases shown in Fig. 1c, a decline in y can no longer be compensated by an increase in x . This means that if the objective is to keep the mean metapopulation lifetime above a certain target level, y must not fall below a certain threshold. The same holds for x . Thus, highly nonlinear trade-off curves entail thresholds for landscape attributes to maintain a certain metapopulation lifetime.

PARAMETERISATION OF THE FORMULA AND DEFINITION OF SCENARIOS

To apply the formula, the species-specific parameters m , ε , b , η and d have to be known or have to be estimated from field observations (e.g. Hanski 1999b; Drechsler *et al.* 2003; Nicholson *et al.* 2006). To simplify the analysis of this article, we do not vary all of these parameters, but summarise the species-specific properties in two aggregated parameters: β and γ .

Species parameter γ is defined as

$$\gamma = \prod_{i=1}^N \gamma_i^{1/N} \quad \text{where} \quad \gamma_i = \frac{c_i}{e_i} = \frac{m}{\varepsilon} A_i^{b+\eta}. \quad \text{eqn 9}$$

γ_i represents the mean number of individuals emigrating from local population i during its expected lifetime $1/e_i$, divided by the number of immigrants required for the successful colonisation of an empty patch. It depends on species characteristics as well as the patch area A_i (cf. eqn 7) and may be determined in (at least) three ways: (i) through direct measurement of the number of emigrants during the lifetime of the local population plus an estimate of how many immigrants are required for the successful colonisation of an empty patch, (ii) through eqn 7 (assuming the parameters m , ε , b and η are known), and (iii) through a Bayesian Calibration with a Markov Chain Monte Carlo (MCMC) algorithm (O'Hara *et al.* 2002; Drechsler *et al.* 2003) of a time series of patch occupancy data (which patch is occupied and which is not) which, among others, allows estimating c_i and e_i .

The aggregated species parameter γ then is the geometric mean over the γ_i (eqn 9) and can be interpreted as the mean number of emigrants from an average-sized local population during the expected lifetime of this local population, divided by the number of immigrants required for the successful colonisation of an empty patch. Thus, species with high values of γ are characterised by a high dispersal propensity compared to species with low values of γ . This explains the increase in metapopulation lifetime T with increasing γ (see also Results section).

The second aggregated species parameter, β may be determined through eqn 6 (assuming b and η are known), or again from the rates c_i and e_i obtained from field data. For the latter approach, we use the two equations of eqn 7 to eliminate the patch area A_i and write

$$c_i = m \varepsilon^\beta e_i^{-\beta} \Rightarrow \ln(c_i) = \ln(m \varepsilon^\beta) - \beta \ln(e_i). \quad \text{eqn 10}$$

Equation 10 means that $-\beta$ is the slope of the regression line if we plot c_i vs. e_i . As already mentioned in the context of eqn 7, large values of β are associated with species experiencing high environmental stochasticity whereas small values of β represent species experiencing low environmental stochasticity (Lande 1993). Thus, in a landscape with a certain level of environmental stochasticity, the value of β is a

measure of species sensitivity to environmental stochasticity. Large values of β also imply higher heterogeneity in the colonisation rates at given heterogeneity in the local extinction rates (Drechsler & Johst 2010). As high colonisation rates contribute overproportionally to metapopulation survival, this explains the increase in metapopulation lifetime T with increasing β (see also Results section).

We consider two values each for β and γ and combine these systematically into four scenarios: ($\beta = 0.25, \gamma = 4$), ($\beta = 0.25, \gamma = 12$), ($\beta = 2, \gamma = 4$), ($\beta = 2, \gamma = 12$).

According to eqns 2 and 5, the mean metapopulation lifetime also depends on the rates c_i and e_i (note that c_i and e_i are related via eqn 10). For the present analysis, we assume that the e_i vary around their geometric mean $\bar{e}$, so that the largest and smallest e_i have a ratio of $Q = e_{\max}/e_{\min} = 3$. Other values of Q lead to qualitatively similar results. Thus, the parameter Q represents patch size heterogeneity, whereas the parameter $\bar{e}$ defines the relative timescale of metapopulation extinction.

Lastly, the patch destruction rates μ and creation rates λ can be determined by observing the network over time and recording how many patches are destroyed respectively created per time step. The parameters μ and λ then are the number of patches destroyed respectively created divided by the number of patches recorded in the previous time step.

Results

1. How do trade-offs between spatial landscape attributes differ in static vs. dynamic landscapes?

Figure 2 compares trade-offs between patch number N (eqn 3) and connectivity H (eqn 8) for different species-specific parameters $\beta = b/\eta$ (eqn 6) and γ (eqn 9) in static (without patch turnover) vs. dynamic (with patch turnover) landscapes. The curves of equal metapopulation lifetime (iso- T lines; curves of equal grey scale) are generally nonlinear but the degree of nonlinearity differs between static and dynamic landscapes. Nonlinearity in the N - H trade-offs is generally higher in static than in dynamic landscapes.

The shape of the N - H trade-off curves also depends on the aggregated species attributes γ and β (Fig. 2). Species with high γ show strongly nonlinear N - H -trade-offs in static landscapes. Thus, threshold behaviour is important and compensation between N and H is impossible over a wide range of N and H : at low patch number, increasing connectivity is ineffective whereas at low connectivity increasing high patch number is useless. Thus, either the number or the connectivity of patches is important depending on the current level of these landscape attributes. In contrast, the more linear N - H trade-off of species with high γ in dynamic landscapes indicates that compensation between connectivity and patch number is possible for a wider range of N and H .

Species with low γ generally show more linear N - H trade-offs, irrespective of whether the landscapes are static or dynamic. As a consequence, threshold behaviour is less important and compensation between N and H is generally possible.

Species with higher γ and β generally have higher metapopulation lifetimes. Metapopulation lifetime quickly increases for these species with increasing connectivity H and increasing patch number N , irrespective of landscape dynamics (Fig. 2).

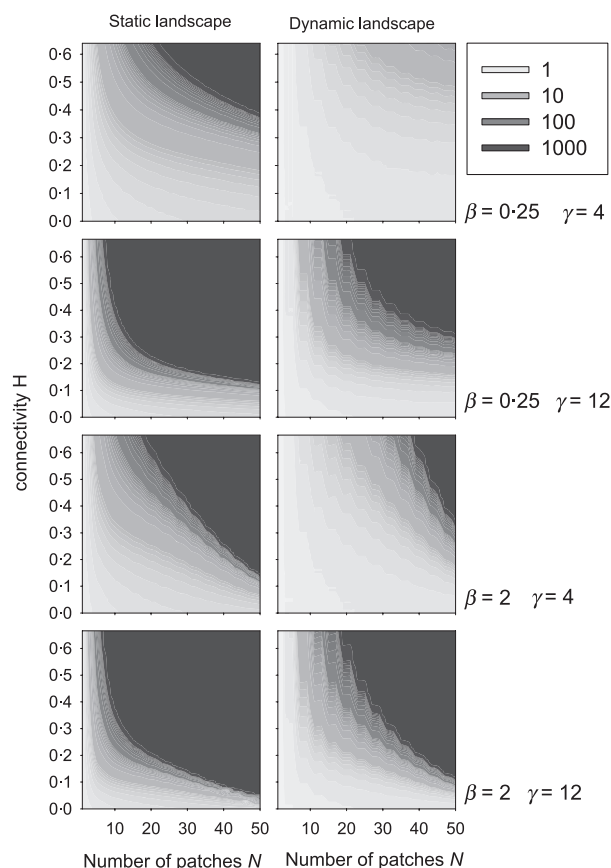


Fig. 2. H - N trade-offs (connectivity H vs. patch number N) in static ($\mu = 0$, left panel) vs. dynamic ($\mu = 0.5 \bar{e}$, right panel) landscapes for different species attributes γ and β (see Materials and methods section). T is given in units of $\bar{e}$. Other parameters are $\bar{e} = 0.05$, $\lambda = \mu$, $Q = 3$.

2. Can an increasing patch destruction rate be compensated by changes in spatial landscape attributes?

Figure 3 shows trade-offs between patch destruction rate μ and the spatial landscape attributes patch number N (Fig. 3, left panel), and connectivity H (Fig. 3, right panel) for different species-specific parameters $\beta = b/\eta$ (eqn 6) and γ (eqn 9). The curves of equal metapopulation lifetime (iso- T lines; curves of equal grey scale) are again generally nonlinear. Nonlinearity is especially pronounced in the μ - H trade-offs. Note that the maximum $H = 0.6$ on the x -axis corresponds to high species' mean dispersal distance of approximately double the network radius R . Similarly to Fig. 2, the shape of the curves depends on the aggregated species attributes γ and β (Fig. 3). Species with low values of β and γ have short metapopulation lifetimes in dynamic landscapes (i.e. the proportion of dark shading in Fig. 3 is lowest for this type of species; see also Fig. 2), whereas species with high values of β and γ can generally cope with higher levels of patch destruction. An increase in patch number N to compensate for increasing patch destruction is very effective for species with high β (i.e. species experiencing high environmental stochasticity). An increase in connectivity H to compensate for increasing patch destruction is only effective for species with high γ .

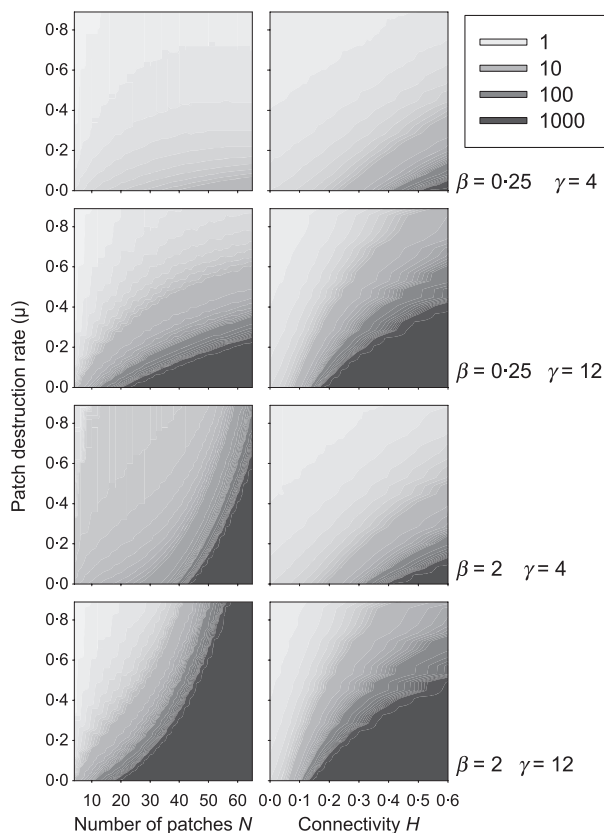


Fig. 3. μ - N trade-offs (patch destruction rate μ vs. number of patches N , left panel) and μ - H trade-offs (patch destruction rate μ vs. connectivity H , right panel) for different species attributes γ and β . T is given in units of $\bar{e}$. Other parameters are $\bar{e} = 0.05$, $\lambda = 0.2\bar{e}$, $Q = 3$, $H = 0.21$ (left panel), $N = 30$ (right panel).

3. Can an increasing patch destruction rate be compensated by an increasing habitat creation rate?

Regarding the two temporal landscape attributes (patch destruction rate μ and creation rate λ), an increase in patch creation rate can generally compensate for increasing patch destruction (Fig. 4). Our results reveal that this compensation is very effective when the starting value of patch destruction rate μ is low and the species parameters γ and β are large. Otherwise this option has little effect. Because of the strong nonlinearity of this trade-off, in already highly dynamic landscapes, it is much more efficient to increase metapopulation persistence by decreasing patch destruction than by increasing patch creation.

Discussion

Knowledge of the trade-offs between different landscape attributes based on species viability is indispensable for effective management and policy decisions. Quantification of these trade-offs for dynamic landscapes with ongoing habitat destruction and creation usually requires extensive computer simulations. Using an analytical formula for the rapid assessment of metapopulation lifetime in dynamic landscapes (for general applicability and validity of the formula see Drechsler

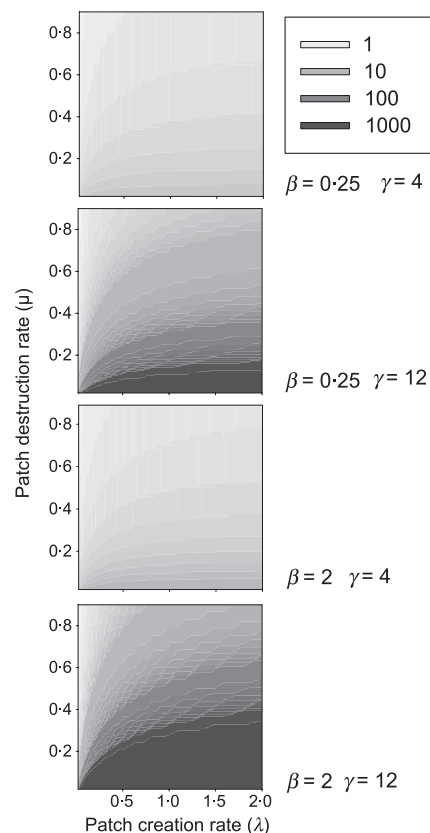


Fig. 4. μ - λ trade-offs (patch destruction rate μ vs. patch creation rate λ) for different species attributes γ and β . T is given in units of $\bar{e}$. μ and λ are given as proportion of $\bar{e}$. Other parameters are $\bar{e} = 0.05$, $Q = 3$, $H = 0.21$, $N = 30$.

& Johst 2010), we demonstrate that trade-offs for a variety of combinations of spatial and temporal landscape attributes and species parameters are quickly accessible. In the following, we discuss first our results with respect to the three questions posed in the introduction and then consider their implications to biodiversity conservation.

1. How do trade-offs between spatial landscape attributes differ in static vs. dynamic landscapes?

Our results confirm and quantify that landscapes with high habitat turnover (i.e. high rates μ and λ compared to the rate of local population extinction $\bar{e}$) generally require a higher number and better connectivity of patches to maintain species viability compared to static landscapes (e.g. Gyllenberg & Hanski 1997; Keymer *et al.* 2000; Johst, Brandl & Eber 2002; Matlack & Leu 2007; Hodgson, Moilanen & Thomas 2009). A frequently discussed management question is, therefore, whether the number of patches N or their connectivity H is more valuable, i.e. has a greater impact on metapopulation survival in dynamic landscapes (Etienne & Heesterbeek 2000; McCarthy, Thompson & Possingham 2005). Our results clearly show that this question cannot be answered in a general fashion. The answer depends on the current level of these landscape attributes, i.e. on the actual values of N and H . This is a consequence of the nonlinearity of the trade-offs between number N and connectivity H of patches in both static and dynamic

landscapes. The degree of this nonlinearity is influenced by the aggregated species-specific traits γ and β (Fig. 2). Species with low values of γ and β cannot cope with highly dynamic landscapes.

2. Can an increasing patch destruction rate be compensated by changes in spatial landscape attributes?

For management decisions, it is important to know which of the spatial landscape attributes, such as connectivity or patch number can better compensate for increasing patch destruction rate μ (at a given patch creation rate). We found that trade-offs between temporal (patch destruction rate μ) and spatial (connectivity H , number of patches N) landscape attributes are likewise nonlinear (Fig. 3). As a consequence, the effectiveness of increasing H or N depends on the current level of these landscape attributes and both options are useless in highly dynamic landscapes. Besides this general observation, there are interesting differences between species. An increase in connectivity H to compensate for increasing patch destruction is only effective for species with high γ (i.e. species with high dispersal propensity). An increase in patch number N to compensate for increasing patch destruction is only effective for species with high β (i.e. species experiencing high environmental stochasticity).

3. Can an increasing patch destruction rate be compensated by an increasing habitat creation rate?

Another option to compensate for increasing patch destruction is to increase the patch creation rate λ . This increases the mean number of habitable patches in the landscape (see eqn 3). We found, however, that this option fails in highly dynamic landscapes because of the strong nonlinearity of the corresponding trade-off curves (Fig. 4). We also found that this option is inefficient for species with low values of γ and β . Therefore, the question of whether patch destruction is compensated more effectively by increasing the patch creation rate or by decreasing the patch destruction rate itself cannot be answered straightforwardly but depends on the level of landscape dynamics and the type of species.

IMPLICATIONS TO BIODIVERSITY CONSERVATION IN DYNAMIC LANDSCAPES

Our results show the importance of considering both spatial and temporal landscape attributes when designing conservation measures in dynamic landscapes. For conceptual guidance of policy design in dynamic landscapes, two key factors have been found to be important:

Firstly, we found that the trade-offs are strongly dependent on the aggregated characteristics of species in a given landscape (Figs 2–4): the value of γ describing the dispersal propensity of a species and the value of β describing how much environmental stochasticity a species experiences in a certain landscape (depending on the environmental variability of this landscape aside from patch turnover and species sensitivity to it). Dependency of policy design on species traits is not new (e.g. Wätzold & Drechsler 2005; Drechsler *et al.* 2010). Our analytical formula confirms this and shows how single species-specific parameters (ϵ , m , η , b , eqn 7) determine metapopula-

tion lifetime (eqn 1). However, it also shows that combinations of them (γ and β , eqns 6 and 9) are already sufficient to explain differential responses of species to certain compensation measures. Such conceptual grouping of species into species types characterised by aggregated characteristics (such as low/high γ and β , respectively) simplifies the transition from single to multi-species conservation (Opdam *et al.* 2008). It is often unavoidable as data information on the single parameters of many species is generally scarce. Our results suggest that species with high dispersal propensity adapted to highly variable environments (aside from patch turnover, corresponding to large values of γ and β) can generally cope with high habitat turnover. For this type of species increasing patch number, connectivity and/or patch creation rate are effective options to compensate for increasing habitat destruction. In contrast, species with low values of γ and β generally have a low survival probability in dynamic landscapes even with a considerable increase in patch number and connectivity. For this type of species decreasing patch destruction would be the best option.

Secondly, we found that the trade-offs between the above mentioned landscape attributes are generally nonlinear. This means that the relative importance of the landscape attributes is not constant but dependent on the current situation (see also Materials and methods). This insight has important implications for biodiversity conservation in dynamic landscapes and the further development of conservation planning software packages that aim to support it. Current up-to-date software packages (e.g. Marxan, ConsNet, see also Ball, Possingham & Watts 2009; Ciarleglio, Wesley Barnes & Sarkar 2009) generally assume constant (linear) trade-off ratios between landscape attributes. Our results can be used to improve such software packages. The rapid quantitative assessment of trade-offs between landscape attributes by the presented formula (eqn 1) makes it possible to optimise complex landscapes for multiple species.

The nonlinearity of the trade-off curves implies that the *actual* spatial and temporal landscape properties strongly determine the effectiveness of a conservation measure. We identified that compensation of increasing habitat destruction by increasing patch creation is only efficient for landscapes in which habitat destruction rate is still low (compared to the rate of local population extinction $\bar{\epsilon}$). This means that a conservation strategy which is effective in a landscape with presently low dynamics is not necessarily effective in a highly dynamic landscape or vice versa. These findings imply that conservation strategies should not only be *landscape type* specific requiring a different strategy in dynamic compared to static landscapes, but in fact, conservation strategies should be attuned to *individual landscapes*. As a consequence, monitoring of the current state of the landscape (e.g. amount of habitat, current level of habitat turnover) is indispensable for effective management.

Policies that require compensation measures for habitat destruction like offsetting and conservation banking are increasingly implemented in many developed countries (Drechsler & Wätzold 2009; eftec, IEEP IEEP 2010; Wissel & Wätzold 2010). Our results are directly relevant for the design and implementation of such policies. They show that they are

appropriate only for a certain type of species (good dispersers adapted to variable environments, i.e. species with high values of γ and β) and in certain landscapes (with sufficient number and connectivity but presently low turnover of patches). Furthermore, for offsetting and conservation banking, 'trading rules' need to be designed which stipulate in what ways and to what extend destroyed habitat has to be compensated by restored habitat. Handbooks have been developed for this purpose (BBOP 2009), and our findings are directly relevant for the further development of these handbooks. They may, for example, help to design differentiated rules for certain species types and landscapes specifying which compensation measures are effective under which conditions.

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Trade-offs in the design of cost-effective habitat networks when conservation costs are variable in space and time

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ABSTRACT

The consideration of economic costs can dramatically influence the cost-effective allocation of resources spent on the conservation of biodiversity. In the face of ecological and economic data scarcity, simple rules are needed for the design of cost-effective habitat networks. A conceptual semi-analytical ecological-economic model is developed that is based on metapopulation theory and takes into account that the costs of conservation may be spatially heterogeneous and changing in time. The model is used to study trade-offs between amount, spatial connectivity and temporal continuity of habitat. The cost-effective levels of habitat connectivity and continuity are determined as functions of species attributes and economic parameters like the distribution of conservation costs. The results are relevant for the design of cost-effective conservation instruments.

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1. Introduction

In the past decade an increasing number of articles has illustrated that the consideration of economic costs can dramatically influence the cost-effective allocation of resources spent on the conservation of biodiversity (Ando et al., 1998; Bode et al., 2008; Bladt et al., 2009). The reason for this is that conservation costs often vary substantially over space and time and resources should be allocated to ecologically beneficial areas only if the costs are not too high (Naidoo et al., 2006). It is widely acknowledged now that ignoring this simple fact can lead to an enormous waste of scarce conservation resources (Ando et al., 1998).

The importance of conservation costs poses new challenges to conservation planning and policy design. Many endangered species and ecosystems are located on private land and conservation costs are difficult to observe, because they are generally only known to the landowners and these have an incentive to hide this private information (Polasky and Doremus, 1998; Parkhurst and Shogren, 2003; Wätzold and Schwerdtner, 2005). In the face of data scarcity, rules for landscape design are needed that do not require explicit knowledge of the conservation costs on each individual land patch but use information like the spatial variation of conservation costs in the region of concern. As a consequence, such landscape design

rules abstract from individual patches and focus on landscape attributes, such as total habitat area and spatial connectivity of habitat patches. Another advantage of landscape design rules is that they can be more directly used in the design of market-based conservation instruments, which are the first choice for implementing conservation on private land (Panayotou, 1994; Chomitz, 2004; Drechsler et al., 2007; Jack et al., 2008). These instruments usually do not specify for each land patch the type of land use but attempt to control the regional land-use pattern as a whole by setting the right economic incentives. The desired land-use pattern then emerges as the response of the landowners to these incentives (Hartig and Drechsler, 2009).

Landscape design rules are not an entirely new invention but have been developed in the past. One of the most popular examples where landscape design rules have been discussed is the SLOSS (“single large or several small”) debate (Quinn and Hastings, 1987; Ovaskainen, 2002; McCarthy et al., 2005): a total habitat area K is divided among N patches of size K/N each and the question is what the optimal magnitude of N is. Even though knowledge of the optimal N does not fully define the optimal reserve system (because the locations of the individual habitat patches are not specified) some understanding is provided about the optimal degree of fragmentation, which can be used as a guideline for the optimal design of the landscape.

Economics enters the landscape design problem by acknowledging that managing land for conservation imposes costs (e.g., in terms of foregone agricultural benefits) and that such costs

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usually differ in space (Lubowski et al., 2008). In this case it is not sufficient to know the optimal degree of fragmentation but also the optimal spatial allocation of the habitat patches. However, being interested in landscape design rules, I do not focus here on the cost-effective location of each individual habitat patch but on the level of spatial connectivity of the habitat patches in the landscape.

At a given budget a trade-off may appear between maximising the amount of land managed for conservation and the spatial connectivity of the created habitat: managing the cheapest sites (in terms of cost per area) for conservation maximises the amount of habitat for a given budget, but unless these cheapest sites are all located next to each other, the connectivity of the created habitat network will not be maximal. Alternatively, placing the habitat patches most closely to each other maximises their connectivity but will in general imply that some of these patches have higher costs, increasing the average cost per habitat patch. As a consequence, the number of patches that can be protected at a given budget will be smaller. It is of interest which configuration of habitat patches is most cost-effective (maximising species survival for a given budget): the one with high number and low connectivity of habitat patches, or the one with high connectivity and low number, or some compromise solution with medium number and medium connectivity. This cost-effective allocation may depend on economic factors, such as the level of cost variation, and ecological factors, such as the dispersal range of the species. To date there exists no systematic understanding on this issue.

Another trade-off arises if one considers that conservation costs do not only vary in space but may change over time, as well. For instance, urban development may raise the price of land (Chicoine, 1981; Lubowski et al., 2008). Or, changes in agricultural policy and markets may increase or decrease the agricultural profitability of land so that the opportunity costs of conservation change. As an example, the introduction of a market for bioenergy is likely to increase opportunity costs of alternative land uses (Walsh et al., 2003). Many other causes for changing conservation costs may be thought of. Not all of them act everywhere and push costs in the same direction (Lubowski et al., 2008) so that conservation costs may increase in one part of a landscape and decrease in another. To maximise the amount of habitat in such an economically changing world, conservation measures should be continuously reallocated from high-cost to the lowest-cost sites. This however, creates permanent habitat turnover that is often detrimental for species (Hanski, 1999a; DeWoody et al., 2005). Alternatively, maintaining habitat patches indefinitely would lead to zero turnover but imply that patches are managed for conservation even if their costs are currently high – increasing the average cost per patch and reducing the number of patches that can be managed for conservation at a given budget. Again a trade-off exists: between maximising the amount of habitat on the one side and maximising habitat continuity, i.e. the longevity of habitat patches, on the other. The cost-effective level of habitat continuity is likely to depend on the dynamics of the conservation costs, the sensitivity of the species to habitat turnover and other ecological and economic factors, such as the cost and time required to restore a habitat patch. Again no systematic understanding exists about this issue so far.

In this paper I analyse the two outlined trade-offs between amount and spatial connectivity of habitat, and between amount and continuity of habitat and determine how the cost-effective levels of these landscape attributes depend on important ecological (such as the species dispersal range and habitat restoration time) and economic parameters (such as spatial and temporal cost variation and the conservation budget). For this I numerically combine an analytical formula for the mean lifetime of a metapopulation (a population fragmented into interacting subpopulations, Hanski,

1999b) with an analytical economic cost model. For the analysis of the first trade-off I consider a static network with limited species dispersal range and spatial variation of conservation costs. For the second trade-off I consider a dynamic network with infinite species dispersal range (but discuss how the results change when the dispersal range is finite) and temporal variation of conservation costs.

The analysed trade-offs not only occur in the design of habitat networks but also in the design of instruments for biodiversity conservation. For instance, conservation activities are often concentrated in target zones (Parkhurst and Shogren, 2003), and analysing the trade-off between number and connectivity of habitat patches helps in answering the question of how large such a zone should be. Tradable land-use permits (Drechsler and Wätzold, 2009) may involve the reallocation of conservation activities, and analysing the trade-off between number and turnover of habitat patches helps answer how much trading activity should be allowed in the permit market. In Section 4 I therefore relate the results of the model analyses to existing conservation instruments.

2. Methods

2.1. The two network design problems

I consider a landscape with N_{tot} land parcels, numbered $i = 1, \dots, N_{tot}$, with identical size and quality. At a given time t each land patch can be managed for conservation (habitat, $x_i(t) = 1$), or other, economic purposes (non-habitat, $x_i(t) = 0$). The vector $\mathbf{x}(t) = (x_1(t), \dots, x_{N_{tot}}(t))$ fully characterises the management in the landscape at time t . Managing a patch i as habitat incurs a cost $c_i(t)$ that varies among patches and in time. The cost may be the sum of several cost components, such as opportunity costs (forgone profits compared to economic land use) and management costs. The average distance between neighboured patches is δ . Without loss of generality I set $\delta = 1$, implying that I scale all distances (e.g., the network radius R and the species mean dispersal range d introduced below) in units of δ .

The objective is to protect a species that has the capacity to disperse between individual habitat patches in the landscape and whose dynamics can be described by metapopulation dynamics: local populations can become extinct while empty habitat patches can be recolonised by dispersing individuals (Hanski, 1999b). A budget B is available in each time period t to manage a subset of the land parcels as habitat, so that the budget covers the costs $c_i(t)$ of the habitat patches:

$$B(t) = \sum_{i=1}^{N_{tot}} x_i(t) c_i(t), \quad (1)$$

for all periods t . I assume that, subject to Eq. (1), a decision maker wishes to maximise the mean lifetime of the metapopulation and searches for the corresponding – cost-effective – habitat network. The mean lifetime (Frank and Wissel, 2002; Drechsler and Johst, 2010) is a useful measure for metapopulation viability that takes the stochasticity of the dynamics into account and relates to various other important measures of metapopulation viability such as extinction risk (Grimm and Wissel, 2004). I consider two complementary network design problems.

1. Static network with limited species dispersal range. In order to maximise the mean lifetime of the metapopulation at a given number N of habitat patches the habitat patches should be spatially clustered. To maximise the number patches that can be managed for conservation at a given budget the least costly patches should be selected which implies a more scattered spatial distribution of the habitat patches. To analyse the trade-off between number and spatial connectivity of habitat patches I

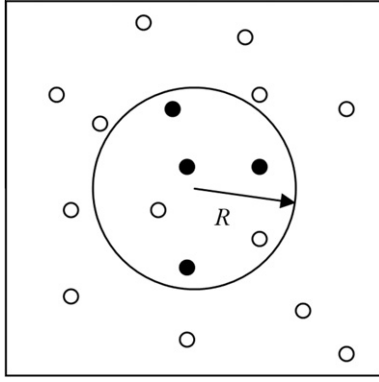


Fig. 1. Example of landscape with $N_{tot} = 17$ patches, $N_R = 6$ patches within a circle of radius R , $N = 4$ of which are habitat (filled circles).

introduce a network radius R so that all N habitat patches are located within a circle of radius R (Fig. 1). This radius may be regarded as a target zone for conservation activities, for instance to compensate for economic development associated with habitat loss in other regions (see Section 4). At a given conservation budget, a large (small) radius implies low (high) connectivity and vice versa. The task is to identify the cost-effective magnitude of R and determine how it depends on the ecological and economic parameters introduced below.

2. Dynamic network with infinite species dispersal range. If the cost of restoring a habitat patch is zero and the cost c_i incurred by managing patch i as habitat changes between time periods the number of patches that can be managed for conservation at a given budget is maximised if in each time period the least costly patches are managed for conservation. This requires a reallocation of at least some habitat between time periods where some habitat patches are destroyed and an equal number of non-habitat patches is restored. I assume that on net no habitat is lost so that for each destroyed habitat patch another patch is restored to become habitat. This assumption mimics “no-net-loss policies”, such as biodiversity off-set schemes (Fox and Nino-Murcia, 2005) where each acre of lost habitat must be compensated for by an acre of equivalent restored habitat. To maximise the mean metapopulation lifetime, there should be no habitat turnover, but this may mean that at a given budget fewer patches can be managed for conservation. To analyse the trade-off between temporal continuity of habitat (absence of turnover) and number of habitat patches I determine the cost-effective level of X and determine how it depends on the ecological and economic parameters, including the cost and time required for habitat restoration.

2.2. Model description and analysis

2.2.1. Rationale

In this section I outline the ecological model for the determination of the mean lifetime of the metapopulation (T) and develop a model for the budget B of Eq. (1). Since the objective of the analysis is to develop general network design rules, the developed models abstract from the specific patch locations but estimate mean metapopulation lifetime and budget as functions of the macroscopic network properties introduced above: the network radius R and the amount of habitat turnover X . With regard to the mean metapopulation lifetime I make use of results of Drechsler and Johst (2010) which estimate the mean lifetime of a metapopulation in static as well as dynamic habitat networks. The conservation budget B is expressed as a function of the macroscopic network parameters, as well.

2.2.2. The mean metapopulation lifetime

According to Drechsler and Johst (2010), the mean lifetime of a metapopulation in a habitat network with N patches is estimated by

$$T = T_l \sum_{i=1}^N \sum_{k=i}^N \frac{1}{k} \frac{(N-i)!}{(N-k)!} \frac{1}{(N-1)^{k-i}} q^{k-i}, \quad (2)$$

where T_l is the mean lifetime of a local population in a single habitat patch (identical for all patches) and q the so-called aggregated colonisation–extinction ratio (as coined by Frank and Wissel (2002)). Quantity q is the product of two factors:

$$q = \gamma H, \quad (3)$$

where $\gamma = cT_l$, and c is the rate by which individuals emigrate from local populations divided by the number of immigrants required for successful colonisation of an empty patch (Drechsler and Johst, 2010). Henceforth, γ is termed the local colonisation–extinction ratio, because it considers all aspects of the aggregated colonisation–extinction ratio except for the spatial arrangement of the habitat patches and at infinite dispersal range would equal Levins’ (Levins, 1969) famous turnover ratio. The spatial arrangement of the habitat patches is considered by the function

$$H = \prod_{i=1}^N \left(\frac{1}{N-1} \sum_{\substack{j=1 \\ j \neq i}}^N \exp(-d_{ij}/d) \right)^{1/N} \\ \approx \frac{3 \times 10^{-R/(15d)}}{(R/d)^2} \frac{(R/d)^{1.65}}{(R/d)^{1.65} + 5}. \quad (4)$$

Parameter d in Eq. (4) is the species mean dispersal range and d_{ij} the Euclidian distance between habitat patches i and j . As can be seen, H depends only on a single quantity: the ratio $s = d/R$ of dispersal range and network radius (for a more details, see Drechsler (2009)). The mean metapopulation lifetime then is a function of three parameters: the local colonisation–extinction ratio γ , the dispersal range d , and the two network design parameters which are the number of habitat patches N and the network radius R . Further details, e.g., about the locations of individual patches, are not required to estimate the mean metapopulation lifetime in good approximation (Drechsler and Johst, 2010).

As outlined above, habitat may be destroyed in the course of land-use change. If habitat destruction is accompanied by an equal number of restored habitat patches so that the total number of habitat patches is constant at level N then habitat turnover has in good approximation only one effect (Drechsler and Johst, 2010): it increases the extinction rate of local populations. If $e = 1/T_l$ is the extinction rate of a local population in the absence of habitat turnover (henceforth termed the “natural local extinction rate”) and Δt the length of a time period, the extinction rate in the presence of habitat turnover is $e_{dyn} = e + X/\Delta t$. The aggregated colonisation–extinction ratio then becomes

$$q = \frac{c}{e_{dyn}} = \frac{c}{e(1 + X/(e\Delta t))} = \frac{\gamma}{1 + X/(e\Delta t)}. \quad (5)$$

One can see that q depends on γ and the proportion of habitat reallocated per period (X) divided by the expected number of local populations becoming extinct during that period ($e\Delta t$).

2.2.3. The budget function

I assume that the costs $c_i(t)$ are spatially and temporally uncorrelated random numbers drawn uniformly from the interval $[1 - \sigma, 1 + \sigma]$. A deterministic trend in the costs can be ignored if the budget is assumed to change with the same trend. Setting

the mean cost to 1 means that the costs of all patches c_i and the budget B are scaled to the average over all c_i and imposes no loss of generality.

Considering the first network design problem (temporally constant costs) the budget B needs to be expressed as a function of the number of habitat patches N and the network radius R . Assuming the network is roughly of circular shape and the average distance between neighbouring patches is $\delta = 1$, the number of patches (habitat or non-habitat) contained within radius R is approximately

$$N_R = \pi R^2. \quad (6)$$

Now assume a proportion $q = N/N_R$ of these patches is managed for conservation. Assuming that the least costly patches are managed for conservation, the total cost of this management strategy is (Appendix A):

$$B = N_R[(1 - \sigma)q + \sigma q^2] = N \left[(1 - \sigma) + \sigma \frac{N}{N_R} \right]. \quad (7)$$

Inserting Eq. (6) into Eq. (7) I obtain for the budget

$$B = N \left[(1 - \sigma) + \frac{\sigma N}{\pi R^2} \right]. \quad (8)$$

For $\sigma = 0$ one obtains $B = N$, because each habitat incurs a cost of 1. In that case the budget is independent of the network radius. Given that the mean metapopulation lifetime increases with decreasing network radius it is most cost-effective to cluster the habitat patches as closely as possible within a circle of radius $R = (N/\pi)^{1/2}$.

In the second network design problem costs c_i change randomly between time periods. The budget required to manage N patches as habitat while allowing a fraction X of these to be destroyed in each time period (with an according number of patches being restored simultaneously) is (Appendix B)

$$B = N \left(1 + \sigma X \left(\frac{X}{1 - N/N_R} - 2 \right) + c_X X \right). \quad (9)$$

Parameter c_X is the restoration cost per patch and N_R is the total number of patches; at maximum $N = N_R$ patches can be managed for conservation.

2.2.4. Calculation of the cost-effective network design

For the static network I am interested in the cost-effective combination of network radius R and number of habitat patches N and maximise T of Eq. (2) as a function of R and N subject to the budget constraint, Eq. (8). Eq. (8) relates R and N , and by solving it for R the network radius can be uniquely expressed for given budget B and cost variation σ as a function of the number of habitat patches:

$$R = \left(\frac{\pi}{\sigma N} \left[\frac{B}{N} - (1 - \sigma) \right] \right)^{-1/2}, \quad (10)$$

(for numerical examples see Fig. 3a). By inserting Eq. (10) into Eq. (4), the mean metapopulation lifetime is a function of the ecological parameters γ and d , the economic parameters B and σ , and the decision variable N . Systematically varying N , I determine the level of N that maximises T (for given γ , d , B and σ) and insert this value into Eq. (10) to determine the associated cost-effective network radius. I analyse how this cost-effective network radius depends on the parameters γ , d , B and σ .

For the dynamic network I am interested in the cost-effective combination of habitat turnover X and number of habitat patches N . Analogously to the analysis of the static network, I solve Eq. (9) for X :

$$X = (1 - N/N_R)(1 - c_X/(2\sigma)) \left\{ 1 - \left(1 - \frac{1 - B/N}{\sigma(1 - N/N_R)(1 - c_X/(2\sigma))} \right)^{1/2} \right\}, \quad (11)$$

(for numerical examples see Fig. 3b). Inserting Eq. (11) into Eq. (5) and Eq. (5) into Eq. (2), the mean metapopulation lifetime T is expressed as a function of the patch number N , and the ecological and economic parameters γ , $e\Delta t$, B , σ and c_X . For given levels of these parameters I numerically determine the level of N that maximises T and insert that level into Eq. (11) to determine the cost-effective level of X . I analyse how this cost-effective level of X depends on the ecological parameters γ and $e\Delta t$ and the economic parameters B , σ and c_X .

So far I have assumed that restoration is instantaneous. If N patches are managed for conservation instantaneous restoration implies that the metapopulation can utilise N habitat patches. If in contrast, it takes one time period for a patch to restore, a patch is suitable for the metapopulation only if it has been managed for conservation for the current time period and the previous time period. The probability that a patch managed for conservation in the previous period is not destroyed is $1 - X$. So the expected number of habitat patches available for the metapopulation is $N(1 - X)$. To generalise, if it takes k periods for a patch to be restored it must have been managed for conservation for the k previous periods and the expected number of habitat patches available to the metapopulation is

$$N_{\text{eff}} = N(1 - X)^k. \quad (12)$$

To determine the cost-effective level of X under delayed restoration, I insert Eq. (11) into Eqs. (5) and (12), insert Eq. (5) into Eq. (2), replace N in Eqs. (2) and (4) by the effective number of habitat patches N_{eff} of Eq. (12) and proceed as described above for the case of instantaneous restoration.

3. Results

3.1. First network design problem: static network with spatially heterogeneous costs

Fig. 2 shows the cost-effective network radius (R^*) as a function of the ecological parameters (Fig. 2a) and the economic parameters (Fig. 2b). First, R^* increases with increasing local colonisation-extinction ratio γ , because a large colonisation-extinction ratio γ increases the relative importance of the habitat patch number N for metapopulation survival (Drechsler and Wissel, 1998). Since for a fixed budget an increase in N has to be paid for by an increased network radius R (Fig. 3a), a relatively large network radius is cost-effective at large γ .

Second, R^* increases with increasing dispersal range d , because a large dispersal range quite obviously supports metapopulation dynamics even on spatially extended habitat networks, so it is cost-effective to choose a rather large R , which allows financing more habitat patches N at a given budget.

Third, R^* increases with increasing cost variation σ . To understand the reason, consider an infinitely large network radius. To protect N patches one can choose the least expensive ones which have cost of about $1 - \sigma$ each (cf. the subsection on the budget function above), so the required budget is about $N(1 - \sigma)$. On the other extreme, consider a network with a small radius $R = (N/\pi)$ so that all patches within that radius are protected. Since there is no choice to select the cheapest patches, the cost of each patch can be any random number from the interval $[1 - \sigma, 1 + \sigma]$ (cf. the subsection on the budget function), so the average cost per patch is 1 and the required budget is N . The cost of “squeezing” N patches into a small circle equals the difference between the two configurations: $N - N(1 - \sigma) = N\sigma$. Fig. 3a confirms this argument numerically: at a large cost variation σ , a reduction of the network radius R has to be paid for by a substantial decrease in habitat patch number N , making larger levels of R more cost-effective.

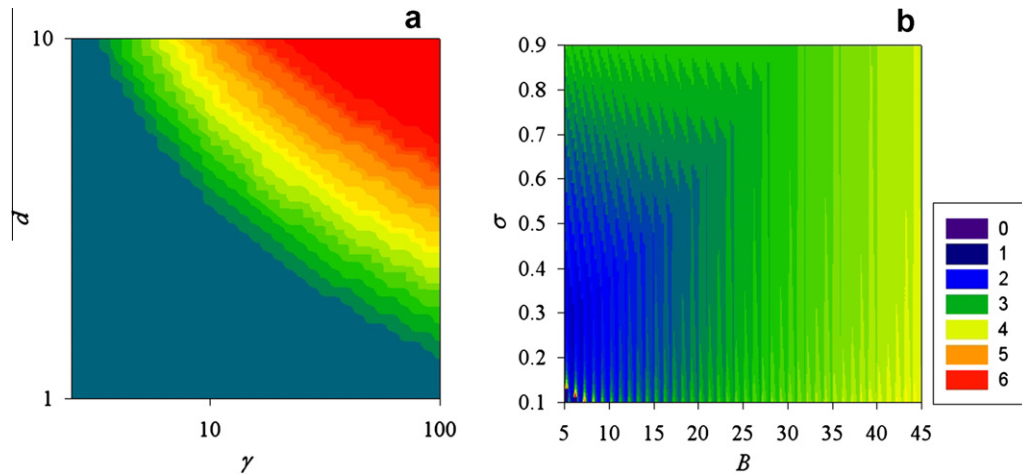


Fig. 2. Cost-effective network radius (R^*) as a function of the ecological parameters (panel a: local colonisation–extinction ratio (γ) and dispersal range (d), both on logarithmic scale) and the economic parameters (panel b: budget (B) and spatial cost variation (σ)). The magnitude of R^* is given by colour. Model parameters: $B = 20$, $\sigma = 0.5$ (panel a); $\gamma = 10$, $\delta = 3.16$ (panel b).

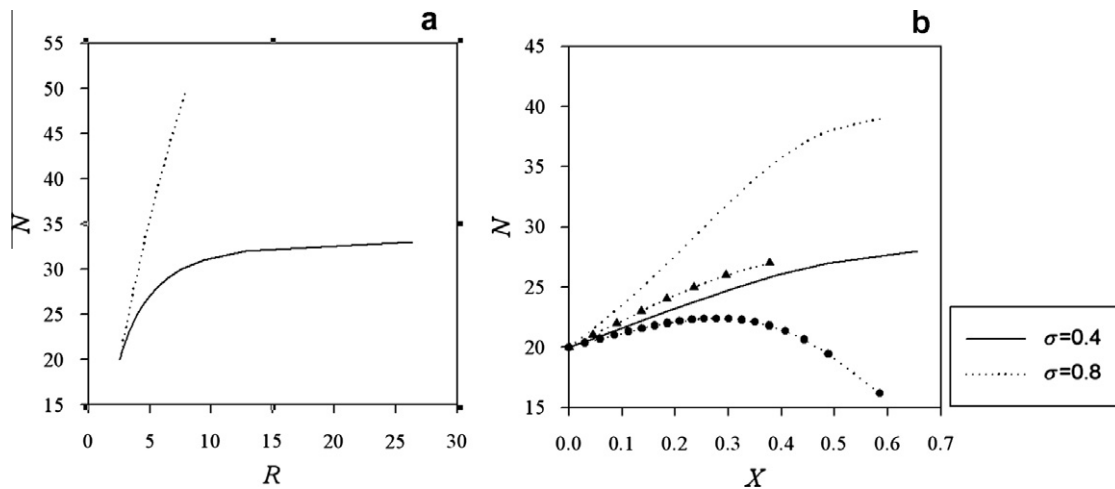


Fig. 3. Budget lines. Panel a: number of patches (N) that can be managed for conservation at budget $B = 20$ as a function of the network radius (R). Panel b: number of patches (N) that can be managed for conservation at a given budget $B = 20$ as a function of the maximum allowed habitat turnover (X). Lines without symbols: restoration is instantaneous and incurs no cost; line with triangles: restoration cost is $c_X = 0.5$; line with circles: restoration takes $k = 1$ period. The budget lines for the two panels were obtained by Eqs. (10) and (11), respectively.

Fourth and last, R^* increases with increasing budget B , because additional patches can be protected but due to the above discussed “cost of squeezing” it is not cost-effective to place all of these into the initial network but to expand the network in space. Unpublished analyses reveal that the density of patches, i.e. the number of patches per unit area, is roughly independent of the budget.

3.2. Second network design problem: dynamic network with changing costs (habitat restoration is instantaneous and incurs no cost)

Fig. 4 shows the cost-effective amount of habitat turnover (X^*) as a function of the ecological parameters (Fig. 4a) and the economic parameters (Fig. 4b). First, and similar to the cost-effective network radius (R^*), X^* increases with increasing local colonisation–extinction ratio γ , because a large colonisation–extinction ratio γ increases the relative importance of the habitat patch number N for metapopulation survival (Drechsler and Wissel, 1998). Since for a fixed budget an increase in N has to be paid for by an increased amount of habitat turnover X (Fig. 3b), a relatively large amount of habitat turnover is cost-effective at a large γ .

Second, X^* increases with increasing natural local extinction rate e , because at large e the additional local extinctions caused by habitat turnover represent only a small contribution to the total amount of local extinction per time step (Eq. (5)). Therefore the larger e the less adverse to the metapopulation is an increase in X , and it becomes cost-effective to choose a rather large X , because this allows financing more habitat patches N at a given budget.

Third, X^* increases with increasing spatio-temporal cost variation (σ). The explanation is analogous to that for the impact of σ on the optimal network radius R^* in the previous section. Again, consider the protection of N patches in two extreme cases. If there is no constraint on X , at each time step the N least costly patches can be selected for protection, leading to a total cost of around $N(1 - \sigma)$. If no habitat turnover is allowed ($X = 0$) there is no freedom to select the least costly ones. Instead the cost of each patch is a random number from the interval $[1 - \sigma, 1 + \sigma]$, so the average cost per habitat patch is 1 and the total cost for N habitat patches is N . The cost of avoiding habitat turnover equals the difference between the two cases: $N - N(1 - \sigma) = N\sigma$. Fig. 3b confirms this argument numerically: at large cost variation σ , a reduction in

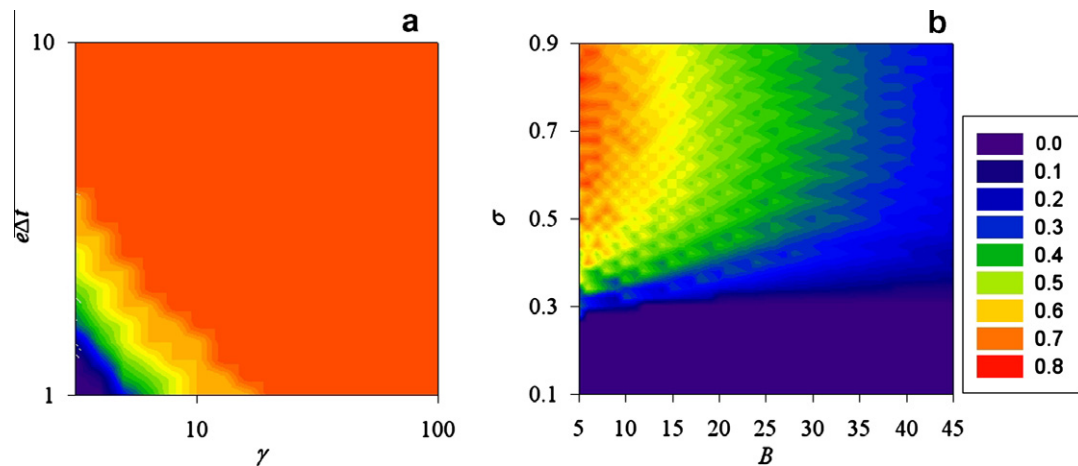


Fig. 4. Cost-effective amount of habitat turnover (X^*) as a function of the ecological parameters (panel a: local colonisation–extinction ratio (γ) and number of “natural” local extinctions per time step ($e\Delta t$), both on logarithmic scale) and the economic parameters (panel b: budget (B) and spatio-temporal cost variation (σ)). The magnitude of X^* is given by colour. Restoration is instantaneous and incurs no cost. Model parameters: $B = 20$, $\sigma = 0.5$ (panel a); $\gamma = 10$; $e\Delta t = 1$ (panel b).

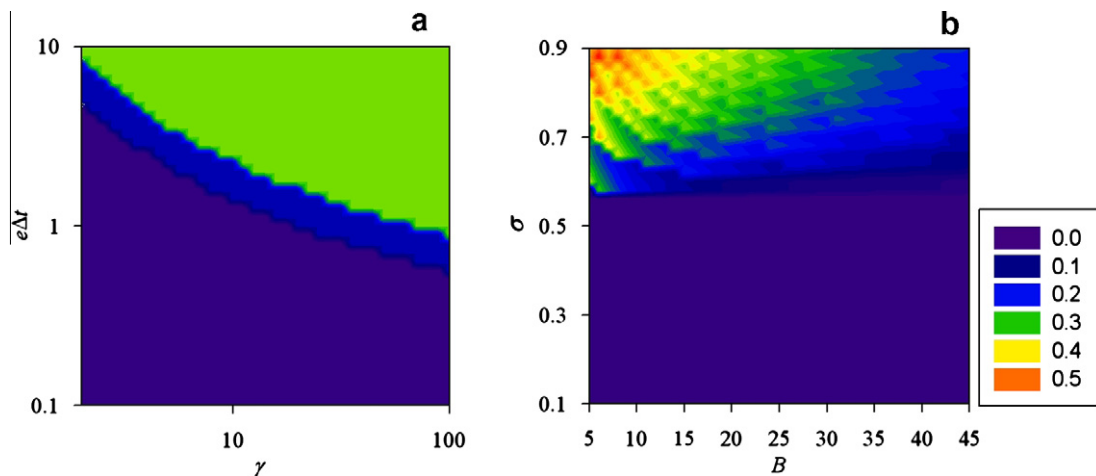


Fig. 5. Cost-effective amount of habitat turnover (X^*) as a function of the ecological (panel a) and economic (panel b) parameters. Same as in Fig. 4 but with restoration cost $c_X = 0.5$.

the amount of habitat turnover X has to be paid for by a substantial decrease in habitat patch number N , making larger levels of X more cost-effective.

Fourth and last, X^* decreases with increasing budget B . This means that an increase in the budget would be invested in reducing habitat turnover rather than increasing the number of patches.

3.3. Second network design problem: dynamic network with changing costs (habitat restoration is delayed by one period and costly)

Fig. 5 shows the cost-effective amount of habitat turnover (X^*) as a function of the ecological (Fig. 5a) and economic (Fig. 5b) parameters for a restoration cost of $c_X = 0.5$ (which means that the restoration cost is half the average opportunity cost c). The dependence of X^* on the ecological and economic parameters is the same as in the case of zero restoration cost, but the level of X^* is smaller throughout the entire parameter space. The reason is that for non-zero c_X turnover is associated with additional costs, which reduces the amount of habitat that can be managed for con-

servation at a given level of X and given budget (cf. Fig. 3b, dotted line with triangles).

Fig. 6 shows the cost-effective amount of habitat turnover (X^*) as a function of the ecological (Fig. 6a) and economic (Fig. 6b) parameters for a restoration time of $k = 1$ period. The dependence of X^* on the parameters is very similar to that in the case of instantaneous restoration, but the cost-effective level of X^* is much lower throughout the parameter space. This is despite the choice of a high level of environmental variation ($\sigma = 0.8$) which was found in Section 3.2 to favour high levels of X^* . If I had chosen a medium level of $\sigma = 0.5$, as in Figs. 4a and 5a, X^* would have been zero for all considered levels of γ and $e\Delta t$.

The reason why the cost-effective turnover rate is so small under delayed habitat restoration is the following. Although an increased turnover rate allows managing more patches as habitat for given budget (Fig. 3b dotted line without circles), an increased turnover rate reduces the effective number of habitat patches relative to the number of patches managed for conservation (Eq. (12)). The latter effect largely neutralises the former, so the effective number of habitat patches N_{eff} only moderately increases with increasing turnover rate X (Fig. 3b, dotted line with circles).

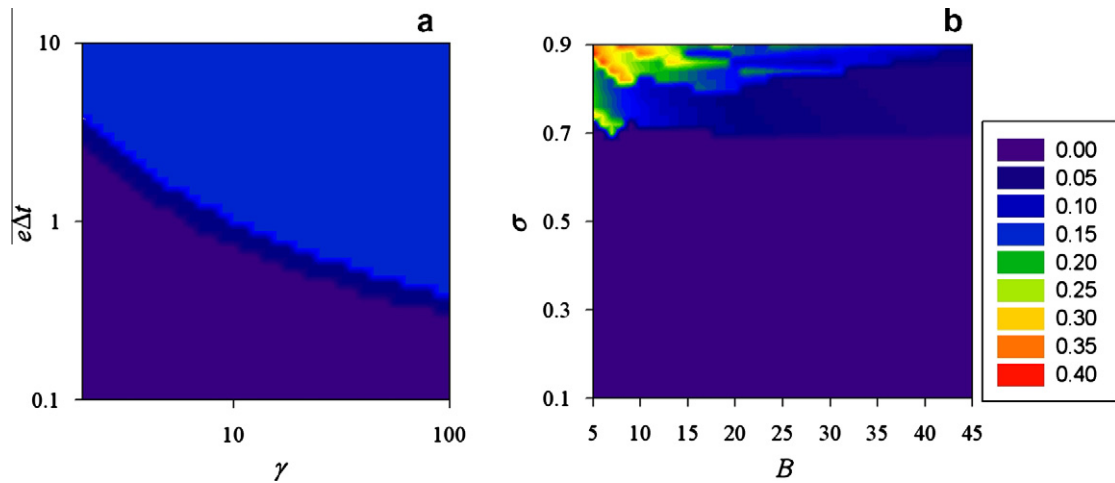


Fig. 6. Cost-effective amount of habitat turnover (X^*) as a function of the ecological (panel a) and economic (panel b) parameters. Same as in Fig. 4 but with restoration time $k = 1$.

Furthermore, it does so only for small levels of X while for larger levels N_{eff} even declines with increasing X . So altogether, increasing habitat turnover not only adds to local population extinction (Eq. (5)) but also reduces the effective number of habitat patches. Within the scope of the present model, large turnover rates therefore are disadvantageous in all respects. It is surprising that this outcome appears already at a small restoration time of $k = 1$. For larger k it would be hardly possible to find any parameter combination for which $X^* > 0$.

4. Discussion

In this paper a conceptual ecological-economic model was built on the basis of metapopulation theory and some basic economic assumptions. The model was analysed to develop general design rules for cost-effective habitat networks when conservation costs are spatially heterogeneous and change in time. The objective here was to provide an understanding of the dependence of cost-effective habitat networks on ecological and economic constraints rather than provide quantitative predictions. The analysis focused on the trade-offs between amount and spatial connectivity of habitat (static network) and between amount and temporal continuity (dynamic network). The trade-off between amount and connectivity of habitat was analysed by identifying the cost-effective radius (R^*) of a habitat network. For a given conservation budget, a large radius allows protecting more habitat patches, because there is more freedom to select patches with low conservation costs and so the cost per patch is smaller than for a small network radius. On the other hand, a large network radius implies relatively low habitat connectivity. The cost-effective network radius exactly balances these pros and cons and generally lies in between the radius that would maximise connectivity (selecting relatively costly patches) and the radius that would maximise habitat area (selecting only the least costly patches). In particular, the cost-effective radius was found to increase with increasing local colonisation-extinction ratio γ , increasing species dispersal range d , increasing spatial cost variation σ and increasing budget B (explanations for these results are provided in Section 3.1).

The trade-off between amount and continuity of habitat was analysed by identifying the cost-effective turnover rate (X^*) of a habitat network. For a given conservation budget, a high turnover rate allows protecting more habitat patches, because there is more freedom to manage patches with low costs as habitat and so the

average cost per patch is smaller than that for a low turnover rate. On the other hand, a high turnover rate leads to additional extinctions of local populations and increases the extinction risk of the metapopulation inhabiting the habitat network. The cost-effective turnover rate exactly balances these pros and cons, and in particular was found to increase with increasing local colonisation-extinction ratio γ , increasing natural extinction rate of local populations (e), increasing spatio-temporal cost variation σ and decreasing budget B (explanations for these results are provided in Section 3.2). In the analysis of dynamic habitat networks I assumed unlimited dispersal: $H = 1$ in Eq. (3). A finite dispersal range would decrease H by some factor which, according to Eq. (3) would be equivalent to a reduction of the local colonisation-extinction ratio γ by the same factor.

The balance between the pros and cons of habitat turnover is heavily disturbed if habitat restoration takes time, because here increased turnover reduces the ratio of the number of patches available for the species and the number of patches managed for conservation. That largely neutralises – or even overrides – that habitat turnover increases the number of patches that can be managed for conservation at a given budget (the pro of habitat turnover). Within the present analyses the cost-effective level of habitat turnover for non-zero restoration times therefore turns out to be very small or even zero. The cost-effective level of habitat turnover also declines if the cost of habitat restoration is increased. Larger levels of habitat turnover would be cost-effective if habitat turnover was less detrimental than assumed in the present study. A moderate level of habitat turnover may even be beneficial in ecosystems shaped by disturbances (Moloney and Levin, 1996). Nevertheless, the ecological risks have to be born in mind when installing policies that attempt to reduce economic costs by allowing for habitat turnover.

The decision variables of the analysis, network radius R and habitat turnover rate X , relate well to some of the major existing conservation instruments (an extensive overview of relevant instruments is given by Parkhurst and Shogren (2003), but see also Sterner (2002)). The network radius R may be identified with the spatial extent of a target zone for conservation. As noted by Parkhurst and Shogren (2003), zoning is the “traditional approach... to guide [economic] development towards existing infrastructure and away from environmentally sensitive areas.” Such a zoning policy only specifies that conservation areas are located within the zone but it does not specify where exactly in the zone these areas are located, just as it is assumed in the present

study. Recently zoning has been combined with market-based instruments, such as tradable development rights (Parkhurst and Shogren, 2003). Here economic development is restricted in so-called “sending zones” while developers in so-called “receiving zones” buy development rights from property owners in a sending zone. The optimal network radius R^* analysed in the present paper may be identified with the optimal radius of such a sending zone.

In a sending zone, as it was outlined above, habitat is only created or conserved but never destroyed. Other instruments, however, exist where the permanency of conservation efforts is less certain. Payment schemes (Parkhurst and Shogren, 2003; Jack et al., 2008), e.g., involve contracts between a conservation agency and landowners who agree to manage their land for conservation. Such contracts usually have a finite duration, and when the contract terminates it is not clear whether current economic conditions will be so that the landowner is willing to renew the contract. If opportunity costs are too high the landowner is likely to use the land for other purposes than conservation and refuse to renew the contract. On the other hand, for another landowner it may be profitable to enter a contract and manage his land for conservation. This process of entering and exiting conservation contracts creates habitat turnover whose amount may be controlled by the lengths of the contracts.

Habitat turnover may also occur in biodiversity off-set schemes (Fox and Nino-Murcia, 2005) if sending and receiving zones are identical, so that each landowner is free to buy or sell land-use permits and accordingly create or destroy habitat (Drechsler and Wätzold, 2009). Hartig and Drechsler (2009) discuss the importance of habitat turnover in markets for tradable development rights which may be controlled by putting a tax on habitat destruction (Drechsler and Hartig, *in press*). The present analysis of the optimal habitat turnover rate X^* may contribute to the optimal design of market-based instruments in a changing world and help, e.g., in the selection of the optimal length of conservation contracts in payment schemes or the optimal control of habitat turnover in markets for tradable development rights.

While there are a lot of ecological-economic analyses on the cost-effective allocation of conservation efforts (cf. Section 1), few studies exist that foster our general understanding of the relevant factors. Such a general understanding is not only of interest to theoreticians but also valuable in the design of reserve networks where it is not possible to determine the ecological value and economic cost of each individual site but information is available only on a coarser, statistical level (such as the conservation cost variation σ considered in the present analysis). Even if detailed information on costs and benefits is available, in working landscapes transaction costs may prevent individual negotiations with each landowner. Coarser approaches like zoning or payment schemes that do not exactly specify where and when conservation measures are carried out but only specify the size of the region and the total amount of habitat turnover within that region are likely to be more appropriate.

In the analysis I made the simplifying assumption that extinctions of local populations are not correlated (Harrison and Quinn, 1989). Frank and Wissel (2002) provided an extension of the model used in this paper that allows considering correlated local extinctions. Correlations in the local extinctions can increase the optimal distance between patches (Frank and Wissel, 1998) which would translate into a larger network radius being cost-effective. Although the mean metapopulation lifetime was used to measure the ecological benefit of a habitat network similar results would be obtained for other benefit functions which increase with increasing area, connectivity, and continuity of habitat. Such a benefit function might also take different levels of habitat quality into account to discuss, e.g., the trade-off between quantity and quality of habitat.

In addition, the conservation costs were assumed to be spatially uncorrelated, as well. In reality profits or land prices depend on various factors, such as distance to settlements and soil quality (for agricultural production), which vary on certain spatial scales (Lubowski et al., 2008). These scales will determine the scale of conservation cost correlations. Such cost correlations may favour multiple small habitat clusters located in the low cost areas. However, the correct prediction of the cost-effective network structure is not trivial in such a case, because several ecological scales (ranges of dispersal and extinction correlation) interact with the scale of the cost correlation. The analysis of such interactions will be a matter of future research.

In the analysis of the trade-off between amount and continuity of habitat I assumed that no habitat is lost on net. No habitat net-loss is the aim of many conservation policies, such as biodiversity off-set schemes (see above). In the real world this goal is often not reached and extending the model to consider net gain or net-loss of habitat may be worthwhile. However, the obtained qualitative rules for the dependence of the cost-effective network radius and the cost-effective level of habitat turnover on the considered ecological and economic parameters are largely independent of the number of habitat patches. Therefore I am confident that these qualitative rules will also apply in the cases of net habitat gain and net habitat loss.

Lastly, I largely abstracted from the question of how the conservation measures are implemented. As mentioned above, economic incentives are a common approach to induce conservation measures on private land. The response of the landowners to these incentives must be considered carefully to avoid unwanted outcomes (Innes et al., 1998; Polasky and Doremus, 1998; Smith and Shogren, 2002). Another problem is that the costs of conservation measures are often known only to the landowners (Polasky and Doremus, 1998; Smith and Shogren, 2002). For this reason (and other reasons such as equity concerns) payments for environmental services (Drechsler et al., 2007; Engel et al., 2008), are generally homogenous in that each landowner receives the same payment (per unit area) regardless of his or her costs. A landowner will carry out the conservation measure if the payment exceeds the cost, and if the cost is substantially lower than the payment the landowner earns a producer rent. Although this producer rent is undesirable from the point of view of the conservation agency and the society (Innes et al., 1998), the presence of producer rents affects the dependence of the cost-effective network radius on the ecological and economic parameters only marginally (Appendix C). In fact, some of the trade-offs that were analysed in the present study have been observed by Drechsler and Wätzold (2009) in a modelled market for tradable land-use permits (although the trade-offs were not investigated systematically in that paper). Nevertheless, a detailed analysis of the effects of landowner behaviour and asymmetric information is a fruitful avenue for future research.

Acknowledgments

The paper substantially benefitted from the helpful comments of two anonymous reviewers.

Appendix A

Assuming the costs are uniformly distributed between $1 - \sigma$ and $1 + \sigma$, the probability density function of the costs is given by

$$p(c) = \begin{cases} (2\sigma)^{-1} & 1 - \sigma \leq c \leq 1 + \sigma \\ 0 & \text{otherwise} \end{cases} \quad (\text{A1})$$

This leads to the cumulative density function $q(c)$

$$q(c) \equiv \int_{-\infty}^c p(c')dc' = \begin{cases} (c-1+\sigma)/(2\sigma) & 1-\sigma \leq c \leq 1+\sigma \\ 0 & \text{otherwise} \end{cases}, \quad (\text{A2})$$

which equals the proportion of land patches with cost below c . The inverse function of Eq. (A2) is given by

$$c(q) = 1 - \sigma + 2q\sigma. \quad (\text{A3})$$

It can be identified with the marginal cost function, i.e. it gives the cost of the most expensive patch out of the qN_R least costly patches, where N_R is the total number of patches. Integration of Eq. (A3) delivers the average cost $C(q)$ required to manage the qN_R least costly parcels as habitat:

$$C(q) = \int_0^q c(q')dq' = (1-\sigma)q + \sigma q^2. \quad (\text{A4})$$

Multiplying Eq. (A4) with the total number of land patches, N_R , leads to the total budget required to manage the qN_R patches as habitat (Eq. (7)).

Appendix B

Assume a landscape with N_R patches. Protection of patch i incurs a cost c_i ($i = 1, \dots, N_R$). Costs are assumed to be uniformly distributed on the interval $[1-\sigma, 1+\sigma]$. They are assumed to change randomly between periods. Temporal correlation is assumed to be zero.

Let N be the number of patches that are managed for conservation, which is assumed constant in time. Let Q be the total number of patches that are allowed to switch land use from one period to the next. The objective is to manage N patches as habitat at least cost, taking the constraint on habitat turnover into account.

Consider the landscape just after costs have changed. Since there is no temporal correlation in the costs (so no correlation, too, between the current land use and the current cost of a patch), for each patch the cost is entirely random and the frequency distribution of the costs of the N habitat patches is the uniform distribution

$$f(c) = \begin{cases} N(2\sigma)^{-1} & 1-\sigma \leq c \leq 1+\sigma \\ 0 & \text{otherwise} \end{cases}. \quad (\text{B1})$$

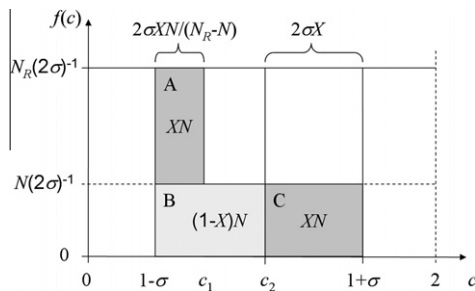


Fig. B1. Illustration of the costs associated with habitat turnover. In each period a number of N patches is managed for conservation. After randomisation of the costs in the beginning of each period the frequency distribution of the costs of the N habitat patches is represented by rectangles B and C. Allowing for a habitat turnover rate of magnitude X (so a number of XN patches may change their land use) costs are minimised if the XN most expensive habitat patches (rectangle C) are developed and the XN least expensive non-habitat patches (rectangle A) become habitat. After this reallocation, the frequency distribution of the costs of the habitat patches is represented by union of rectangles A and B.

(note that the frequency distribution equals the number of habitat patches, N , times the probability density function of the costs, $p(c) = (2\sigma)^{-1}$). Managing these N patches as habitat would cost

$$B = \int_{1-\sigma}^{1+\sigma} cf(c)dc = \frac{N}{2\sigma} \int_{1-\sigma}^{1+\sigma} cdc = N. \quad (\text{B2})$$

It is allowed to change the land use on $Q = XN$ patches to minimise total cost B . Total cost is minimised if the XN most costly habitat patches are developed and the XN least costly economically used patches become habitat. The frequency distribution of the costs of the XN least costly economically used patches is (Fig. B1)

$$g_1(c) = \begin{cases} N_R(2\sigma)^{-1} & 1-\sigma \leq c \leq c_1 \\ 0 & \text{otherwise} \end{cases} \quad \text{where } c_1 = 1 - \sigma + \frac{2\sigma X}{1 - N/N_R}, \quad (\text{B3})$$

and the frequency distribution of the costs of the XN most costly habitat patches is

$$g_2(c) = \begin{cases} N(2\sigma)^{-1} & c_2 \leq c \leq 1+\sigma \\ 0 & \text{otherwise} \end{cases} \quad \text{where } c_2 = 1 + \sigma - 2\sigma X. \quad (\text{B4})$$

It is not reasonable to put a relatively costly patch under conservation management in order to develop a less costly patch, which means that $c_2 \geq c_1$, implying that

$$X \leq 1 - N/N_R. \quad (\text{B5})$$

(Eq. (B5) means that if, e.g., 20% of all N_R patches are managed for conservation then less than 80% of these are developed per time step). After developing the XN most costly patches and putting the XN least costly patches under conservation management, the frequency distribution of the costs of the habitat patches is

$$h(c) = \begin{cases} N_R(2\sigma)^{-1} & 1-\sigma \leq c \leq c_1 \\ N(2\sigma)^{-1} & c_1 < c < c_2 \\ 0 & \text{otherwise} \end{cases}, \quad (\text{B6})$$

and the cost of managing these patches as habitat is

$$\begin{aligned} B &= \int_0^1 ch(c)dc = \frac{N_R}{2\sigma} \int_{1-\sigma}^{c_1} cdc + \frac{N}{2\sigma} \int_{c_1}^{c_2} cdc \\ &= \frac{N_R}{4\sigma} (c_1^2 - (1-\sigma^2)) + \frac{N}{4\sigma} (c_2^2 - c_1^2) \\ &= N \left(1 + \sigma X \left(\frac{N_R X}{N_R - N} - 2 \right) \right). \end{aligned} \quad (\text{B7})$$

Eq. (B7) assumes that the restoration of a habitat patches incurs no cost. Denoting the restoration cost per patch as c_X and considering that in each time period a number of XN patches is restored, the budget becomes

$$B = N \left(1 + \sigma X \left(\frac{N_R X}{N_R - N} - 2 \right) + c_X X \right). \quad (\text{B8})$$

Appendix C

In the analysis of the cost-effective network radius (Section 3.1) I assumed that each habitat patch i contributes to the budget according to its cost c_i (Eq. (1)). In the practice of conservation policy this may be overoptimistic. One of the most common policy instruments for biodiversity conservation are payments for environmental services (PES) (Drechsler et al., 2007; Engel et al., 2008) where a conservation agency offers payments to landowners who manage their land in a biodiversity-friendly manner. For various reasons, including asymmetric information and equity

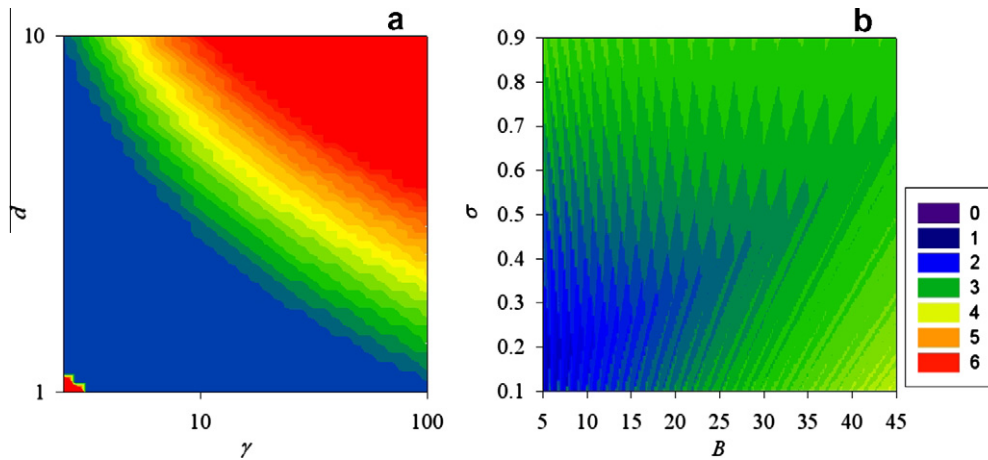


Fig. C1. Cost-effective network radius (R^*) as a function of the ecological (panel a) and economic (panel b) parameters. Same as in Fig. 2, but all habitat patches receive the same payment p . The red colour in the lower left corner is a model artefact.

concerns, it is common to pay all landowners the same payment p regardless of the cost c_i (which implies that landowners with costs $c_i < p$ are over-compensated and earn a producer rent). As a consequence, the total cost for the conservation agency is not given by the sum over all costs c_i but by the product of the number of patches managed for conservation and the payment p : $C = pq$. To induce a proportion of q landowners to manage their land for conservation the payment must be equal to (or precisely: marginally above) the cost of the most costly patch in that set, which is given by Eq. (A3):

$$p = c(q) = 1 - \sigma + 2q\sigma. \quad (C1)$$

The total cost becomes

$$C(q) = p \cdot q = q(1 - \sigma + 2q\sigma) = (1 - \sigma)q + 2\sigma q^2. \quad (C2)$$

This is identical to Eq. (A4), except that the quadratic term carries an additional factor of 2, which implies that the budget required for managing qN patches for conservation is higher. Replacing Eq. (A4) by Eq. (C2) and repeating the calculations that led to Eqs. (7), (8), and (10) delivers the network radius as a function of the budget and the number of habitat patches (the analogue to Eq. (10)):

$$R = \left(\frac{\pi}{2\sigma N} \left[\frac{B}{N} - (1 - \sigma) \right] \right)^{-1/2}. \quad (C3)$$

Replacing Eq. (10) by Eq. (C3) and repeating the calculations described in Section 2.2.4 delivers the cost-effective network radius R^* for the case where conservation management is induced by a homogenous payment p . The dependence of R^* on the ecological parameters γ and d is shown in Fig. C1 (the analogue to Fig. 2). Qualitatively both figures look identical, except that in Fig. C1 the cost-effective network radius is slightly higher than in Fig. 2.

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A model-based approach for designing cost-effective compensation payments for conservation of endangered species in real landscapes

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ABSTRACT

An approach is presented which integrates an economic and an ecological model for designing cost-effective compensation payments for conservation of endangered species in real landscapes. The approach is used to develop a cost-effective payment scheme for conservation of an endangered butterfly species (*Maculinea teleius*) protected by the EU Habitats Directive in the region of Landau, Germany. The results of the case study are used to analyse the effect of metapopulation dynamics on the cost-effectiveness of payment schemes, to compare spatially homogeneous and heterogeneous payments, and to evaluate existing conservation policies.

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1. Introduction

Conservation of endangered species is demanded by legislation in many parts of the world. Examples of such legislation are the Endangered Species Act of 1973 in the USA and the European Union Habitats Directive of 1992. Some of the species protected by such legislation require reserves in order to survive, but others require particular types of human land use to be carried out on a regular basis. Such human land-use was often profitable in the past, but today, due to technologi-

cal and economic development, this is no longer the case. For example, much of the biodiversity-rich land in the EU depends on low-intensity farming which is no longer economically viable (Bignal and McCracken, 2000). As the political will often exists that landowners should not be forced to carry out a certain type of land-use, they have to be compensated (Hanley et al., 1998). Experience with the USA Endangered Species Act has also shown that forcing owners of land with endangered species to carry out conservation measures may encourage them to eradicate the species concerned in order

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to avoid the conservation costs (Brown and Shogren, 1998). Compensation payment schemes for conservation measures now play an important part in conservation efforts in Europe, the USA and other parts of the world, particularly in the context of agri-environmental policy (e.g. Pywell et al., 2006; Walker et al., 2007). Examples of such schemes include the Countryside Stewardship and the Moorland schemes in the UK (Hanley et al., 1998), nature protection contract schemes (Vertragsnaturschutzprogramme) in Germany (Hampicke and Roth, 2000) and the Fish and Wildlife Service Spending on endangered species recovery in the USA (Simon et al., 1995).

So far, little research has been carried out with respect to the cost-effectiveness of compensation payment schemes, i.e. with respect to their ability to achieve a maximum conservation output for a given financial budget. One reason may be that addressing the scheme's cost-effectiveness requires the integration of knowledge from ecology and economics, and that with respect to the evaluation of conservation policies, such interdisciplinary work has evolved only recently (Wätzold et al., 2006 cf.).

Some examples of such work deal with cost-effective reserve site selection. For instance, Ando et al. (1998) and Polasky et al. (2001) analyse the extent to which improvements in efficiency can be achieved by integrating economic costs (land prices) into the selection criteria of conservation sites compared to an approach that only considers ecological parameters such as the number of endangered species. Other examples estimate trade-offs between economic activities and conservation objectives on forested landscapes (Lichtenstein and Montgomery, 2003; Nalle et al., 2004), and on landscapes that can be used either as reserves, or for agricultural or forestry production (Polasky et al., 2005). To address the issue of identifying cost-effective conservation options in agricultural landscapes, Holzkämper and Seppelt (2007) developed a spatially explicit optimisation approach to identify optimum land-use patterns with respect to an ecological-economic objective function. The approach can take into account site specific conditions like soil quality which influence the economic as well as the ecological functions.

With regard to the instrument of compensation payments Hanley et al. (1998) as well as Oglethorpe and Sanderson (1999) integrate an economic and an ecological model and generate quantitative data of the costs and benefits of certain specific conservation measures. The combined ecological-economic models are able to determine the benefits and the costs of conservation measures (and thus the necessary compensation payments) simultaneously, but do not address the issue of how to allocate conservation measures cost-effectively in space or time.

Our research is close to Johst et al. (2002) who combine economic data, an ecological model and a numerical optimisation procedure to quantitatively determine cost-effective compensation payments for species conservation which are differentiated in space and over time. To illustrate the operation of their approach, Johst et al. apply it to the design of a payment scheme for the protection of the White Stork (*Ciconia ciconia*) in a hypothetical landscape. This research shows how cost-effective payments may be developed in principle, but the hypothetical case study is rather simple, and neglects

many complexities that are relevant for actual conservation problems.

The aim of this paper is to further develop the research regarding the cost-effectiveness of compensation payments for biodiversity conservation measures. We do this with the help of a case study: the development of a cost-effective payment scheme for the conservation of an endangered butterfly species (*Maculinea teleius*, protected by the EU-Habitats Directive) in the region of Landau, Germany, a spatially structured agricultural landscape. The paper advances the research on the cost-effective design of compensation payments in four areas:

(1) *Designing a modelling approach for cost-effective payments in a real landscape:*

We go beyond Johst et al. (2002) by developing an ecological-economic modelling approach for designing cost-effective compensation payment schemes for species conservation in real landscapes. The landscape data were obtained from the GIS analysis of a satellite image. Furthermore, in Johst et al. data on conservation costs were gained through a survey of farmers who were aware that the data were collected solely for scientific research. The survey method is problematic if the farmers know that the data are used for designing actual payments as then they have an incentive to answer strategically and, e.g. overstate the costs of conservation measures. To avoid such problems in the present study, costs are calculated based on estimated profit losses of farmers.

(2) *Analysing the influence of metapopulation dynamics:*

The butterfly population exhibits *metapopulation dynamics*, which means that the local dynamics of the butterflies in the individual meadows interact through the exchange of individuals. This interaction usually leads to a mutual stabilisation of the local populations and – in case local populations go extinct – may lead to the re-colonisation of empty meadows (e.g. Hanski, 1999). The influence of metapopulation dynamics on optimal land-use decisions has been thoroughly analysed in ecology. However, with a few exceptions (e.g. Groeneveld, 2004) economic aspects have not been considered in these analyses. The present case allows for a discussion regarding how the existence of metapopulation dynamics affects the cost-effective design of compensation payments for conservation measures.

(3) *Spatial heterogeneity of compensation payments:*

It has been emphasised in the literature that conservation measures should be spatially heterogeneous if benefit functions (e.g. Babcock et al., 1997; Wätzold and Drechsler, 2005) and cost functions (e.g. Innes, 2000; Smith and Shogren, 2002) differ in space. We compare the cost-effectiveness of spatially homogeneous and heterogeneous payments for the case study and analyse how much the cost-effectiveness of compensation payments may be improved if spatially heterogeneous benefits and costs are taken into account.

(4) *Evaluation of existing payment scheme:*

The case study contributes to the evaluation of existing conservation policies. A payment scheme for conservation measures exists in the region of Landau and we use the ecological-economic modelling approach to analyse the scheme's contribution to *Maculinea* conservation and to derive some

general conclusions regarding German conservation policies in agricultural landscapes.

The paper is structured as follows: Section 2 introduces the conservation problem and its relation to different types of land use in the region of Landau. Based on knowledge of the butterflies' requirements for survival in the landscape, alternative land use strategies are suggested. Following these considerations, the model-based approach that determines cost-effective land use strategies and compensation payments to achieve them is described. The approach consists of three components that are presented in the following sections. The agri-economic calculations that are introduced in Section 3 determine the costs of alternative land use strategies for each meadow as well as the overall costs and the compensation payments necessary to induce land users to adopt these strategies. The cost structure – together with the conservation budget – shapes the land use and the spatio-temporal structure of the landscape in the region. The ecological effects of the alternative land use strategies are determined by an ecological model describing the metapopulation dynamics of the butterflies in the landscape (Section 4). In Section 5, the ecological and economic components discussed in Sections 3 and 4 are considered in an integrated manner to identify cost-effective land-use strategies and the corresponding compensation payments. These are defined by maximising the viability of the butterfly metapopulation for a given budget. In Section 6 the model results are discussed.

2. Land-use and conservation of *M. teleius*

Maculinea teleius is a meadow-dwelling butterfly that relies on the presence of open landscapes. Most adults fly in the weeks of July and lay their eggs on the plant *Sanguisorba officinalis*. Larvae are adopted by ants of the species *Myrmica scabrinodis*. Both plant and ant species are found only if a meadow is mowed in a certain way.

The dependence of *M. teleius* on a certain type of mowing largely explains why the butterfly was quite common in Germany until the 1950s, but since then its population size has steadily declined. In former times meadows were used rather extensively. In particular, the meadows of a region were not mowed all at once but the mowing season extended over the whole summer. Therefore, even if some meadows were unsuitable for the butterflies at a particular time, enough other suitable meadows were available to which butterflies could disperse and deposit their eggs. Today in contrast, all meadows in a region typically are mowed simultaneously twice a year with the first session being at the end of May and the second session six to eight weeks later. This mowing regime (henceforth referred to as the “conventional mowing regime”), however, is relatively unsuitable for the reproduction of the butterflies as, in particular, the second session of mowing falls exactly into the weeks during which the butterflies deposit their eggs on the *Sanguisorba* plants.

The concentration of mowing on two points in time maximises the farmer's profit and has been made possible due to the development of machinery which allows mowing of a large area within a short period of time. In order to induce

farmers to adopt a mowing regime that is more beneficial to the butterflies, the farmers have to be compensated.

In the present paper a cost-effective compensation payment scheme for a region east of the town of Landau in the Rhine Valley is developed. Our geographic data base comes from a digitised satellite image of this area ($10 \times 6 \text{ km}^2$ with a resolution of $20 \times 20 \text{ m}^2$). The image allows one to distinguish between 14 different landscape types in each pixel, such as settlements, traffic ways, lakes and rivers, forests, meadows, arable land, etc. For the ecological model below we structure the 14 landscape types into four main types as they are experienced by the species: meadows, open land (e.g. traffic ways, lakes and rivers, arable land), forests (including shrubland), and settlements. Fig. 1 shows the model landscape.

Having identified the individual meadows (whose total number is 347) in the landscape, their areas a_i are determined by counting the pixels belonging to each meadow. The location of each meadow is defined by its midpoint, or centre of weight, such that the $x(y)$ – co-ordinate of a meadow is the average of the $x(y)$ – co-ordinates of all pixels belonging to that meadow. From these $x - y$ locations the Euclidian distances, $d_{ij} = ((x_i - x_j)^2 + (y_i - y_j)^2)^{1/2}$ are calculated for all pairs (i, j) of meadows. The meadow sizes are required as an input into the cost assessment as well as the ecological model, whereas the pair-wise distances are only needed as an input into the ecological model.

A large variety of alternative mowing regimes is considered. A mowing regime is coded by three numbers, $x - y - z$. The first number tells whether a meadow is mowed every year ($x = 1$) or every second year ($x = 2$). The second number ($y = 0, 4, 6$, or 8) tells whether there is only a single mowing event in a mowing year ($y = 0$), or whether there is a second cut 4, 6, or 8 weeks after the first cut. By this, the first two numbers characterise the frequency of mowing. The third number ($z = -1, 0, \dots, 12$) consecutively codes the week of the first mowing where -1 stands for the week before the last week of May, 0 for the last week of May, and so on. For instance, the conventional mowing regime introduced above is coded as $(1, 6, 0)$. Altogether, we consider $2 \times 4 \times 14 = 112$ different mowing regimes.

It is assumed that a conservation agency selects one of the 112 mowing regimes and offers a certain payment to farmers. The farmers either accept the payment and adopt the selected mowing regime (henceforth denoted as the “promoted mowing regime”) or stick to the conventional one. Whether the promoted or the conventional mowing regime is adopted on each individual meadow is determined by the agri-economic cost assessment.

3. Agri-economic cost assessment

3.1. Description

The aim of the agri-economic cost assessment is to determine the compensation that has to be paid to induce a farmer to adopt a certain promoted mowing regime. We assume that this compensation is determined by three components: (I) Compensation for the foregone profit that arises because

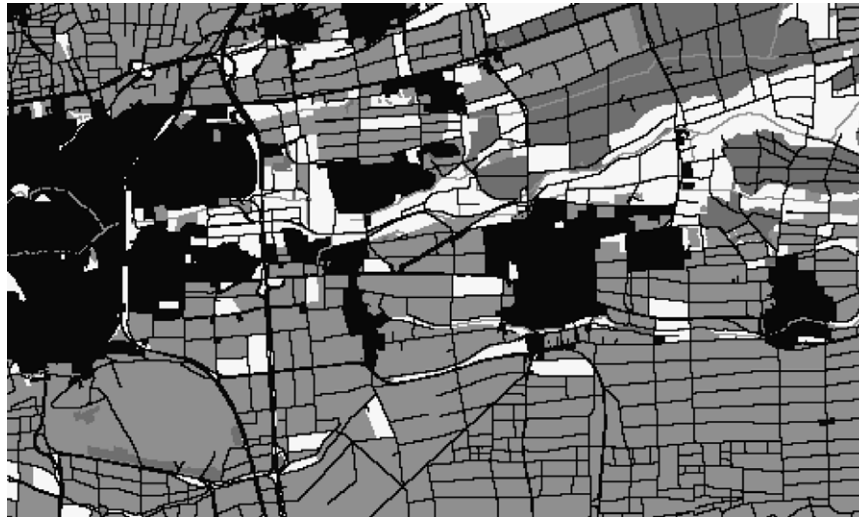


Fig. 1 – The model landscape (black: settlement/roads; dark grey: forest; light grey: open land, water bodies; white: meadows). The dimension of the map is $10 \times 6 \text{ km}^2$.

the farmer cannot carry out the profit-maximising mowing regime, (II) compensation for the farmer's transaction costs arising from scheme participation, and (III) individual farm characteristics and the farmer's personal attitude towards conservation.

(I) We only provide a brief description here of how the field specific profit losses have been calculated. A detailed description of the calculations and how the underlying assumptions are derived can be found in [Bergmann \(2004\)](#).

In the region of Landau, grassland is used intensively in dairy and cattle production. Farmers usually harvest silage (or less frequently hay) with a first cut approximately at the end of May, a second cut about six weeks later and a third cut in August/September. As an alternative to the third cut, the grassland is often used for grazing. The most important factor that determines the quality of the silage and the hay is its energy content, which is maximised by the prevalent, conventional mowing regime in the region.

For this reason, the reduction in energy yields per ha that is caused by the different mowing regimes compared to the conventional mowing regime forms the basis of the calculations of the payments for the foregone profits. As most farmers use silage, the calculations are based on silage production. The impact of the various mowing regimes on the energy content of silage have been determined on the basis of a literature review on data from field research, in particular on functions estimated by [Opitz von Boberfeld \(1994, p. 262\)](#).

We assume that the farmers purchase concentrates as an additional fodder to compensate for the loss of energy yields in the silage and calculate the compensation payments accordingly. However, due to its low quality, silage harvested with a first cut late in the season (e.g. in August) can no longer be used in cattle nutrition and farmers have to be compensated for the complete loss of silage.

The energy yields of the various mowing regimes have been estimated for each meadow based on information about medium grassland yields in the region taking into account soil quality and soil humidity, which have a positive influence

on productivity, and altitude which has a negative influence. All variables are relatively homogenous throughout the study region. Soil quality number is about 35, the humidity level is "high" (as compared to "low"), as the region can be regarded as riparian, intersected by several rivers, and the altitude is below 250 msl.

We further take into account variable costs of the various mowing regimes such as costs for transport, machinery and fertiliser. As part of these costs (calculated on a per hectare basis) decreases with an increase in meadow size, we distinguish between three meadow sizes ($a < 0.75 \text{ ha}$; $0.75 \text{ ha} < a < 1.5 \text{ ha}$; $a > 1.5 \text{ ha}$) and assume different variable costs for the three sizes. The meadow size as well as the soil quality, the humidity level and the altitude are known for each individual meadow and stored in the data base described in Section 2.

The necessary compensation for the foregone profit is then calculated for each mowing regime and each meadow taking into account the necessary purchase of concentrates, and, if necessary, other additional fodder and the variations in variable costs.

(II) There are different types of transaction costs for a farmer who participates in a compensation payment scheme. The farmer has to gather information about the scheme, fill out administrative documents and spend some time with the conservation manager in case the farmer's compliance with the scheme's requirements is monitored. To provide sufficient incentives for participation the farmer needs to be compensated for the transaction costs. Following common practise in many EU countries (see also EU-Regulation 1698/2005) we calculate the amount of transaction cost compensation to be a fixed amount per ha of land enrolled in an agri-environmental scheme and estimate the compensation to be 100€ per ha.

(III) Due to different characteristics of individual farms such as equipment with machinery, farm size, and experience of the farmer with conservation programmes, administrative costs as well as costs for conservation measures

differ among farms. Furthermore, personal benefits from participating in conservation programmes may differ among farmers (Smith and Shogren, 2002 cf.). To take into account the effects of personal benefits and farm characteristics we introduce a “farm parameter” u , where a positive (negative) u indicates that lower (higher) than average payments are required to induce a farmer to participate in the programme. Obviously, it is difficult to get information about the distribution of u . Therefore, we assume that for each meadow u is a uniform random variable $u \in [-u_0, +u_0]$ with values for u_0 of €50 and €200. With more information available one could also consider more sophisticated models where u varies among mowing regimes and/or farmers in a deterministic manner.

3.2. Model analysis and results

To determine the mowing regime on a given meadow, a value for u is drawn from the distribution and the promoted mowing regime is adopted if the compensation payment $p > c + a - u$, where c represents the foregone profit and a the compensation for transaction costs. We assume that all participants receive the same payment which is the common approach of many payment schemes in the EU and also of the existing scheme in Landau. The total amount of money that has to be spent by the agency is the total area of all meadows with the promoted mowing regime multiplied by the payment.

To determine p for a given budget B (the amount of money that can be spent on conservation in the region of interest) we start with $p = 1\text{€}/\text{ha}$ and successively increase the payment in steps of $1\text{€}/\text{ha}$. In each step we determine which meadows adopt the promoted mowing regime and determine how much the agency has to spend for these meadows. We proceed until this amount is just below the budget B , such that in the next step the budget would be exceeded. The result is the payment that leads to maximum possible exhaustion of the available budget B . The difference between B and the actual amount of money spent is negligible within the scope of the analysis. Next to p , the analysis determines which individual meadows adopt the promoted mowing regime as well as the total area A of such meadows.

As the decision to adopt the promoted mowing regime on a given meadow depends on the farm parameter u , payment p and total area A are random, too. To account for this randomness, costs for all meadows are sampled randomly 10 times. Each time the compensation payment and the total area adopting the promoted mowing regime are determined and an average is taken over the 10 replicates.

Fig. 2 shows the expected area with the promoted mowing regime for all 112 mowing regimes. Mowing regimes that have a mowing frequency of 1–4, 1–6 or 1–8 (= mowing twice every year with 4, 6 or 8 weeks between the first and second cuts) and a (first) mowing week between –1 and 3 (= mowing between mid May and mid June) are adopted on a relatively large area (light colour in Fig. 2), because they are similar to the conventional mowing regime (1–6–0). Profit losses are small and their implementation is relatively inexpensive, so the limited budget suffices for promoting a large number of meadows.

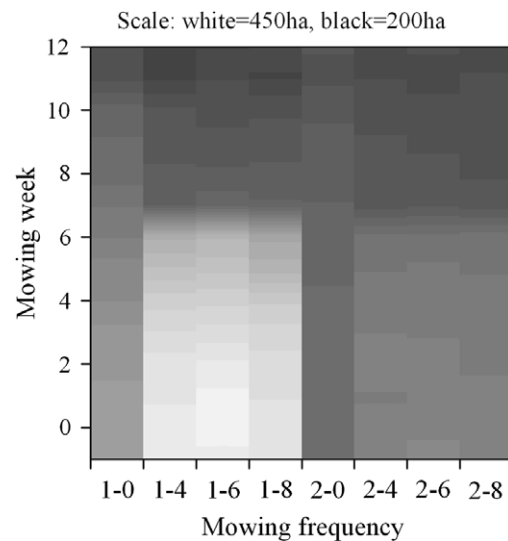


Fig. 2 – The expected meadow area with the promoted mowing regime as a function of the promoted mowing regime for a budget of €64,000 with $u_0 = €50$. The promoted mowing regime is characterised by the mowing frequency (x-axis) and the mowing week (y-axis). Mowing frequency: the first number of each pair of numbers stands for mowing every single (1) or every second (2) year; the second number indicates whether in a mowing year there are two cuts, separated by 4, 6, or 8 weeks, or only one cut (0). Mowing week: The week of the first mowing event (1 is the first week of June). The promoted meadow area is indicated by the colour where black colour represents an area of 200 ha, white colour an area of 450 ha; grey colours represent intermediate values on a linear scale.

In contrast, if the first cut is late in the season (week 11 or 12, i.e. second half of August) the harvest cannot be used and profit losses are high. Therefore such a mowing regime can be implemented only on a small area (black colour in Fig. 2 for weeks 11 and 12), regardless of whether mowing takes place every (mowing frequencies 1–...) or every second (2–...) year, or whether the second cut is 4, 6 or 8 weeks after the first cut (mowing frequencies ...–4, ...–6, ...–8). A single late cut (mowing frequency 1–0 or 2–0; week 11 or 12) can be implemented on a slightly larger area (dark grey), since the cost of the (useless) second cut is saved.

4. Ecological model

4.1. The local dynamics

The local dynamics of the butterfly *M. teleius* on each individual meadow is dependent on two resources: Plants of species *Sanguisorba officinalis* for egg deposition and ant nests (species *Myrmica scabrinodis*) for pupation. As we concentrate on the impact of mowing, the life cycle is modelled as simply as possible and follows in principle the model of Hochberg et al. (1992). The model used in this study is a stochastic simulation model. Details are described in Johst et al. (2006) and here only a brief overview of the model is given.

The life of the butterfly (Thomas and Settele, 2004) is divided into an over-ground phase on the meadow and an underground phase in the ant nests. The over-ground phase encompasses approximately three months (June, July and August) and is considered on a weekly scale, and the underground phase includes nine months considered as one whole period. The over-ground phase involves the eclosion of adults followed by egg deposition and death of adults, and the development of three different larvae stages on the *Sanguisorba* plants. All larvae which get older than 3 weeks successively fall to the ground where they are adopted by the ants. The underground phase in the ant nests includes three processes: (1) larval survival due to the winter mortality of ant nests, (2) intra-specific competition for food in the ant nest characterised by scramble competition and (3) survival after possible parasite infestation. Then the life cycle switches to the over-ground phase again.

Mowing influences the population dynamics in a direct and an indirect way. The direct effect is that during a mowing event eggs and larvae that are currently on the *Sanguisorba* plants are destroyed, and that the abundance of *Sanguisorba* will be insufficient for egg deposition for the next four weeks. The indirect effect of mowing (Thomas, 1984) is that it stops succession of the vegetation of the meadow, i.e. keeps the meadow open and the composition of plant species relatively constant. If meadows are mowed too rarely the abundance of *Sanguisorba* declines. Furthermore, rarely mowed meadows with thick vegetation become unsuitable for *M. scabrinodis*. On the other hand, field data show that too frequent mowing harms the ants as well, so the mowing frequency that maximises the abundance of ant nests is once per year.

4.2. The landscape dynamics and the dispersal model

The local dynamics on the individual meadows are coupled in the landscape through the dispersal of butterflies among different meadows which leads to metapopulation dynamics. The dispersal model describes the emigration of butterflies from their “home”, or “source”, meadow as well as their movement to other patches which includes the possibility of dying, e.g. due to predators, during the flight.

Emigration of the butterflies to deposit their eggs on a meadow different from their eclosion location, depends on the quality of the meadow i.e. on the abundance of the *Sanguisorba* plants (see above). Based on field observations, we assume that the butterflies emigrate with a high probability (0.9) if the habitat quality is low; otherwise there is only little emigration (0.1). The decision to emigrate is made after eclosion on a weekly time scale leading to a certain number of butterflies leaving the meadow.

Now it has to be determined which of these emigrants reach which of the other meadows. The share of emigrants that reaches a particular target meadow is determined by two factors: the “attractiveness” of the target meadow, and the probability that a butterfly survives the flight to the target meadow. The attractiveness again is composed of a “distance preference factor” and a “thinning factor”.

To calculate the attractiveness factor we assume that dispersing butterflies prefer closer meadows. This means that, e.g. a meadow twice as far away as another has half the

attractiveness. However, attractiveness depends not only on the distance but also on the landscape types between source and target patch (e.g. settlements or forests). Therefore, we introduce a landscape resistance, $\bar{\alpha}_{ij}$, between meadow i and j and assume that the preference for a certain target meadow decreases with distance d_{ij} via $(\bar{\alpha}_{ij}d_{ij})^{-1}$. Thus, target meadows with higher resistance (e.g. settlement) between themselves and the source meadow have accordingly lower attractiveness than a target meadow separated with lower resistance (e.g. open land).

If more than one landscape type crosses the path of a butterfly the easiest way is to draw a straight line between source and target patches, determine the distances d_x travelled through each landscape type x with $x \in \{m, l, f, s\}$ (see below) and $d_m + d_l + d_f + d_s = d_{ij}$ and calculate mean resistance of the four landscape types by

$$\bar{\alpha}_{ij} = \sum_{x \in \{m, l, f, s\}} d_x \alpha_x / d_{ij} \quad (1)$$

As Eq. (1) indicates, the average landscape resistance is the mean of the landscape specific resistances α_x weighted by the proportion d_x/d_{ij} of the dispersal path that falls into landscape type x . We distinguish four types of land: meadow with $\alpha_m^{-1} = 3$ km, open land with $\alpha_l^{-1} = 2$ km, forest with $\alpha_f^{-1} = 1$ km and settlements with $\alpha_s^{-1} = 0.5$ km. The numerical values are based on expert knowledge and arguments of plausibility.

Even if closer meadows were not preferred, meadows further away would receive fewer butterflies than meadows closer to the source due to the thinning factor. This indicates that a meadow farther away covers a smaller angle than a closer meadow and just statistically receives fewer butterflies. Precisely, viewed from the source patch, the arc spanned by a target patch diminishes with d_{ij}^{-1} . Altogether, the attractiveness of a target meadow, composed of preference and thinning factor, decreases with increasing distance as $\bar{\alpha}_{ij}^{-1}d_{ij}^{-2}$. If no dispersal mortality is assumed, all butterflies reach some meadow, so the sum $S_i = \sum_j \bar{\alpha}_{ij}^{-1}d_{ij}^{-2}$ (where $j = 1 \dots$ number of patches, and $j \neq i$) must be one. Thus the factor $\bar{\alpha}_{ij}^{-1}d_{ij}^{-2}$ has to be normalised by dividing it by S_i and the attractiveness of a target patch j for butterflies emigrating from a source patch i becomes $\bar{\alpha}_{ij}^{-1}d_{ij}^{-2}/S_i$.

Now we consider the probability of surviving a flight to a given target meadow. We adopt the exponential relationship $P = \exp(-\bar{\alpha}_{ij}d_{ij})$ most commonly used (e.g. Hanski, 1999) and assume the inverse of the mean landscape resistance $\bar{\alpha}_{ij}^{-1}$ as mean dispersal distance a butterfly can reach alive. At high $\bar{\alpha}_{ij}$ therefore most butterflies already die after short travel distances. Including dispersal mortality along with attractiveness factor, the total share of emigrants from a source meadow i that reaches a particular target meadow j is

$$\Phi_{ij} = \frac{\exp(-\bar{\alpha}_{ij}d_{ij})}{\bar{\alpha}_{ij}d_{ij}^2} \sum_j \bar{\alpha}_{ij}d_{ij}^2 \quad (2)$$

with $\bar{\alpha}_{ij}$ being determined by Eq. (1).

4.3. Model analysis and results

The objective of the following analysis is to understand the behaviour of the ecological model without consideration of the spatial arrangement of the meadows. For this we consider

a simple and fictitious landscape in which all patches have equal size, and the distances between all possible pairs of patches are identical. Although such a configuration is geometrically impossible to achieve in a two-dimensional landscape, it is nevertheless frequently used in ecological research as a reference model or starting point for more complex research questions (e.g. Tilman et al., 1994). In the present study, the objective of such an analysis is to gain a general understanding of the effects of the 112 mowing regimes on the viability of a population inhabiting an ensemble of meadows. For our purpose, a suitable indicator for metapopulation viability is the total meadow area occupied by the butterfly after a certain number of model years. As the dynamics of the species are stochastic, it is appropriate to use the expected area of meadow occupied (unpublished results show that it is strongly correlated to the quasi-extinction risk (Ginzburg et al., 1982)).

A landscape of 40 meadows, each of 1 ha size is considered. On each meadow either the conventional or the promoted mowed regime is applied. To make the analysis comparable to the analysis of the ecological-economic model (described in the next section) we consider that less costly mowing regimes can be implemented on accordingly larger proportions of the total meadow area than more costly ones. The distance between the 40 meadows is set such that the probability to survive the flight from one patch to the other is 0.5 for all pairs of meadows and all meadows have the same attractiveness. For all 112 possible mowing regimes the proportion of all meadows that are occupied after 20 years (this proportion is henceforth referred to as “occupancy”) is recorded. Each simulation is repeated 100 times to account for the stochasticity in the ecological dynamics and an average occupancy is determined.

Fig. 3 shows the occupancy of the meadows as a function of the applied mowing regime. Eggs and larvae are especially abundant on the plants in the weeks 6–9 (second week of June till first week of July). Thus, mowing in these weeks is very detrimental irrespective of the mowing frequency which is indicated by the black colour in Fig. 3 for these weeks. Furthermore in mowing scenarios with two cuts, mowing in earlier weeks is detrimental, too, if the second cut falls into the weeks of high larvae abundance and thus causes severe larvae mortality. Therefore, the occupancy of scenarios with two cuts is very sensitive both to the time of first mowing and the time between the cuts. The highest occupancy (white colour) is achieved by mowing twice every year with the second cut 8 weeks after the first cut (frequency 1–8) and the first cut in the third week of June (week 3). By this choice the first cut is early enough so plants will have recovered when the eclosion periods starts and the second cut takes place after the eclosion period. Relatively beneficial mowing regimes are also to mow *once* every year (frequency 1–0) early enough before the eclosion period. In these mowing regimes the mowing frequency is high enough to ensure sufficiently high plant and ant nest abundance and at the same time larvae mortality due to mowing is sufficiently low. Mowing only every second year (frequency 2–...) is often more beneficial than mowing every year (frequency 1–...), because this means that larvae and eggs are killed only every second year. In some cases it is, however, less beneficial, because it also reduces the

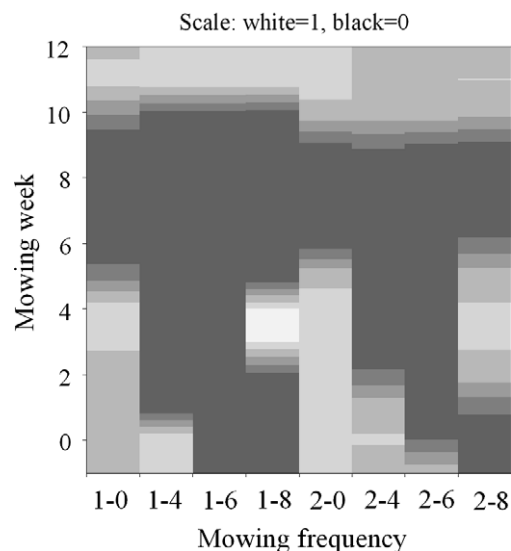


Fig. 3 – The occupancy as obtained from the ecological model component as a function of the mowing regime. The occupancy is given by the colour on a linear scale where white colour represents a value of one and black colour a value of zero. Other details as in Fig. 2.

abundance of ant nests, so there is a trade-off (Section 4.1 c.f.). The results of Fig. 3 are very robust against variations in the dispersal survival (a range of 0.1...0.9 was tested) and the total number of meadows, as long as the latter was larger than about 40.

An interesting observation is that the occupancy is very sensitive to the applied mowing regime and ranges from zero (for the worst) to one (for the best mowing regimes). In comparison, the proportion of meadow area with promoted mowing regime varies much less (only by a factor of about 2) from the cheapest to the most expensive mowing regimes (Fig. 2). This indicates that the cost-effectiveness of a promoted mowing regime depends more on its ecological suitability than the proportion of meadow area on which it is applied (i.e. on the cost structure).

The motivation for this ecological model analysis within the ecological-economic analysis of this paper was that the “economics” has two effects in our system: first the cost of a mowing regime determines the proportion of meadow area in the landscape that adopts this mowing regime (Fig. 2), and second the choices of the individual farmers (which depend on costs and payments) affect the spatial arrangement of the promoted meadows. In the analysis of this section we have considered only the first effect of economics: the total promoted meadow area. In the following Section 5 we will, among other, focus on the second effect: the spatial distribution of promoted meadows.

5. The ecological-economic model

5.1. The cost-effective land-use measure

We now turn to the ecological-economic model to identify the cost-effective mowing regime, i.e. the mowing regime that achieves the highest ecological benefit for a given

conservation budget. The analysis considers the cost assessment and the ecological model component as well as the structure of the landscape with the different sizes and locations of the meadows.

The optimisation is carried out for 20 different budget sizes. In order to have a higher resolution at low budget sizes we increase the budgets in a quadratic manner as $B = 1000 n^2 \text{€}$ where $n = 1 \dots 20$. For each budget B we determine the promoted mowing regime that maximises the expected meadow area occupied by butterflies. For this we consecutively analyse each of the 112 mowing regimes and (for each) determine the expected occupied meadow area as follows: First we determine which meadows adopt the mowing regime. On the resulting landscape the butterfly population dynamics are simulated for 20 years and the final total meadow area containing butterflies is recorded. To account for the randomness in the incentive component u of the costs and the randomness in the butterfly population dynamics, the simulation is repeated 100 times and an average, the expected meadow area occupied by butterflies, is taken. Carrying out this analysis for all 112 mowing regimes and comparing the resulting expected occupied meadow areas delivers the most cost-effective mowing regime(s) for the budget considered.

Fig. 4 shows the cost-effectiveness of all promoted mowing regimes for various budgets. A comparison with Fig. 3 reveals that the colour pattern of the two figures is nearly identical, which means that the ecologically most effective mowing regime is also the most cost-effective one and vice versa. The most effective mowing regimes have been discussed in Section 4.3. Recalling the discussion in the last paragraph of Section 4.3, the similarity between Figs. 3 and 4 suggests that the costs of the mowing regimes affect their cost-effectiveness only in that expensive mowing regimes can be implemented on less total area than inexpensive ones. The spatial distribution of the promoted meadows which is considered in Fig. 4 but not in Fig. 3 seems to play no role.

Since all three panels have the same colour pattern and only differ by the scale, we can further conclude that the budget only affects the meadow area occupied for a given mow-

ing regime but not the rank order of mowing regimes in terms of their cost-effectiveness. Again, possible consequences of a budget increase on the spatial distribution of the promoted meadows seem to be negligible.

The compensation payments that correspond to the mowing regimes are shown in Fig. 5 for several budgets. They are basically the inverse to the promoted meadow area (Fig. 2), i.e. light (dark) colour in Fig. 2 corresponds to dark (white) colour in Fig. 3. The reason is that an expensive (inexpensive) mowing regime requires a high (low) payment and can therefore be implemented on a small (large) area. As already discussed on Fig. 2, mowing regimes similar to the conventional one are inexpensive and require low payments while late cuts (weeks 11 and 12) require high payments.

Comparison of the three panels of Fig. 5 reveals that for a given mowing regime the payment increases with increasing budget (compare panels from left to right). The rank order the mowing regimes in terms of payment size, however, is independent of the budget.

5.2. The role of space

The results above suggest that the main effect of budget and costs is that at a higher budget more meadows adopt the mowing regime and that for a given budget inexpensive mowing regimes can be implemented on a larger area than expensive ones. Changes in the spatial arrangement of the promoted meadows obviously play only a minor role. Below we explore in more detail the impact of space on the cost-effectiveness of the mowing regimes. For this we compare the results of the ecological-economic model with those of another model, henceforth termed “product model”, that combines the economic model of Section 3 and the ecological model of Section 4 in a simplified manner. The product model estimates the meadow area occupied by butterflies by calculating the product of the meadow area adopting the promoted mowing regime (determined by the cost assessment: Fig. 2) and the occupancy (obtained from the ecological model in the fictitious landscape: Fig. 3). By this the product model

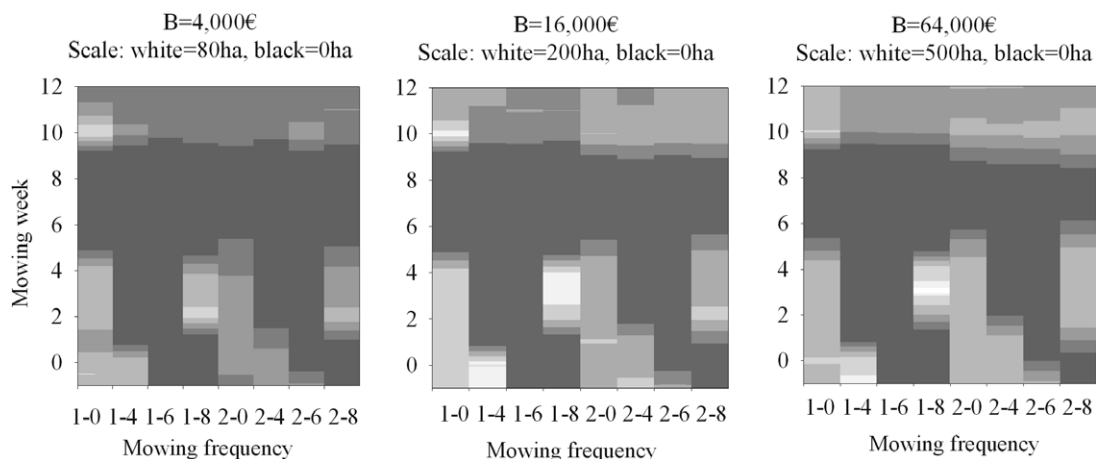


Fig. 4 – The meadow area occupied by butterflies as a function of the promoted mowing regime. The budget sizes are €4000, €16,000, and €64,000. The area is given by the colour on a linear scale where black colour represents all meadows being unoccupied and white colour indicates occupied areas of 80 ha, 200 ha and 500 ha, respectively. Other details as in Fig. 2.

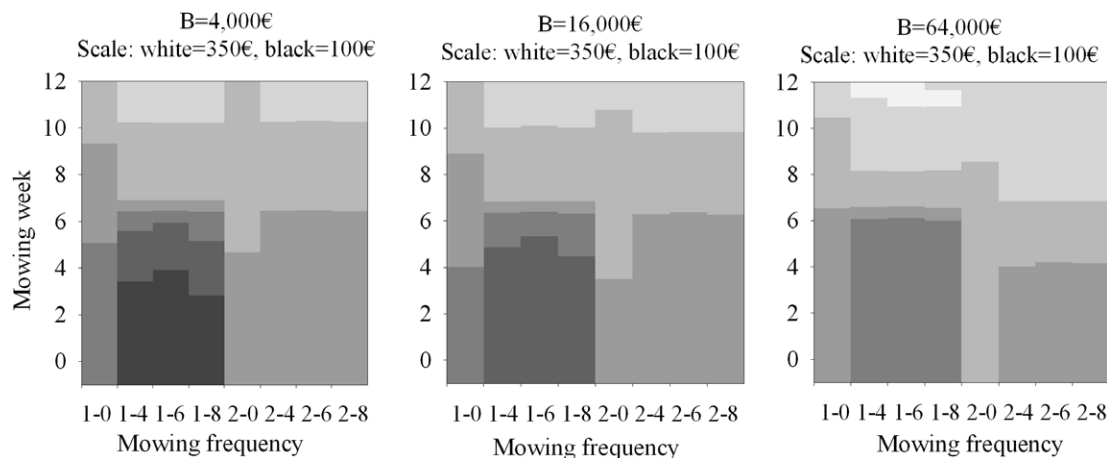


Fig. 5 – Compensation payments in € as a function of the mowing regime for three budget levels: €4000, €16,000, €64,000. The payments are given by the colour on a linear scale where black and white colour represent about €100 and €350, respectively. Other details as in Fig. 2.

considers that the economic parameters (budget and cost of mowing regime) affect the total area of the meadows with promoted mowing regime, but it ignores the particular locations of these meadows. A good (poor) agreement between the ecological-economic model of Section 5.1 and the product model thus indicates low (high) importance of spatial arrangement.

Fig. 6 shows the area of occupied meadow obtained from the ecological-economic model plotted against the occupied area obtained from the product model, each dot representing one of the 112 mowing regimes. The dots are aligned quite well along the diagonal (slightly above it, which indicates that the product model underestimates the occupied meadow area; the reason is that in the full model butterflies can spill over from promoted to neighboured conventional meadows, which cannot occur in the product model where all meadows have some distance between each other).

For all budgets, the deviation from the diagonal, i.e. relative error between the two models, is generally largest for

the mowing regimes located close to the origin, i.e. those with low performance. Furthermore, the error is largest if the budget is low (4,000€). Obviously, in these cases the spatial arrangement of the meadows with promoted mowing regime matters.

5.3. Cost-effectiveness of spatially differentiated compensation payments

Following the dominant approach for compensation payments for conservation measures in Europe we assumed that every farmer in the region receives the same payment. However, the question arises how well such an approach performs in comparison to a spatially heterogeneous policy. Such a policy may lead to a more cost-effective solution because (a) the spatial configuration of promoted meadows affects the survival probability of the butterfly population and (b) the agency can compensate each farmer for his or her individual costs

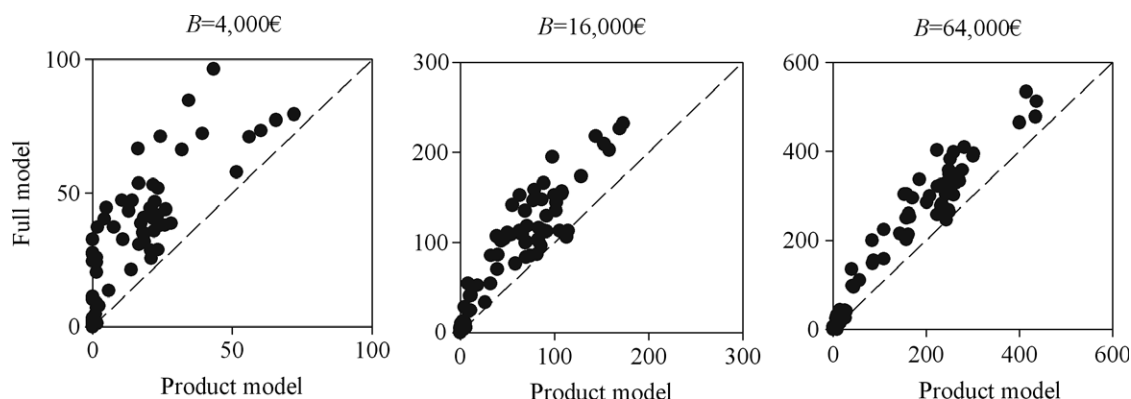


Fig. 6 – Meadow area occupied by butterflies according to the product model versus area occupied according to the ecological-economic model (measured in ha). The area in the product model is the product of the area adopting the promoted mowing regime and the occupancy as it is obtained from the ecological model component. Each dot represents one of the 112 different promoted mowing regimes. The budgets are €4000, €16,000, and €64,000.

rather than paying all farmers the same amount of compensation.

Although a detailed analysis of option (a) is beyond the scope of this paper we are able to provide a conservative estimate on how much a policy that takes into account the spatial configuration of conservation measures leads to higher cost-effectiveness. As described in Section 5.1, we sampled and evaluated several landscape configurations in order to capture the randomness of u . Comparing the performances of the mowing regime over these landscape configurations provides an estimate on how much the spatial optimisation of the location of promoted meadows would increase the performance of the mowing regime. Fig. 7a shows the result for one of the most cost-effective mowing regimes, “mowing in the third week of May and four weeks later” (1,4,-1). For small budgets below €10,000 the coefficient of variation of the performances is about 0.25. As plus/minus two times the coefficient of variation roughly mark the bounds of a 95% confidence interval, this means that good spatial configurations perform at least 50% better than average configurations. With an increasing budget the coefficient of variation decreases indicating that spatial optimisation of meadows becomes less important.

To analyse option (b), consider that in the case of uniform payments the budget is the product of the payment and the promoted meadow area. This means that the payment is the ratio of budget and area: $p(A) = B_u(A)/A$. It is generally a function of the area A . In the case of heterogeneous payments the budget is not the product of payment and area but the integral of the payment over the area: $B_h(A) = \int p(A) dA$. Inserting $p(A)$ from above delivers the budget B_h (heterogeneous payments) as a function of the budget B_u (homogenous payments): $B_h(A) = \int [B_u(A)/A] dA$. Fig. 7b shows how much money ($B_u - B_h$) could be saved with heterogeneous payments. The saved amount increases with increasing budget and variation in the farm parameter (u_0). At small areas A , increasing u_0 decreases the required budget, because the costs of the cheaper meadows where conservation measures are carried out first decrease with increasing u_0 . For larger budgets the opposite is found, because the costs of the expensive meadows increase with u_0 . Except for very small budgets and low varia-

tion u_0 , the amount saved by spatial differentiation of payments is quite substantial.

6. Discussion

The aim of this paper is to advance the research on the cost-effectiveness of compensation payments in four areas (cf. Section 1). We will discuss each area separately.

6.1. A model-based approach for designing cost-effective payments in real landscapes

Using the example of the conservation of a butterfly species protected by the EU Habitats Directive, a model-based approach is presented which is able to develop cost-effective compensation payment schemes for conserving endangered species in real landscapes. Although the results from our case study are specific to the area and species studied, the methodology is general and applicable elsewhere. The landscape data are obtained from the GIS analysis of a satellite image. Agri-economic calculations determine the costs of different conservation measures. The costs, together with the available budget, determine the spatial structure and temporal dynamics of the landscape. An ecological model simulates the population dynamics of the species in the landscape and determines the effect of various conservation measures on the population. In the example, we calculate the effect of different mowing regimes on the (expected) meadow area occupied by butterflies after 20 model years. As a result, for a given budget the ecological benefit is known for each conservation measure which allows identification of the most cost-effective one(s) and the corresponding compensation payment(s).

6.2. Analysing the influence of metapopulation dynamics

In analysing the relative contributions of economic and ecological parameters in our example, we find that the cost-effectiveness of a mowing regime is more determined by its ecological suitability than by its cost – an interesting counter-example to studies where cost-differences dominate differences in ecological benefits (e.g. Naidoo et al., 2006).

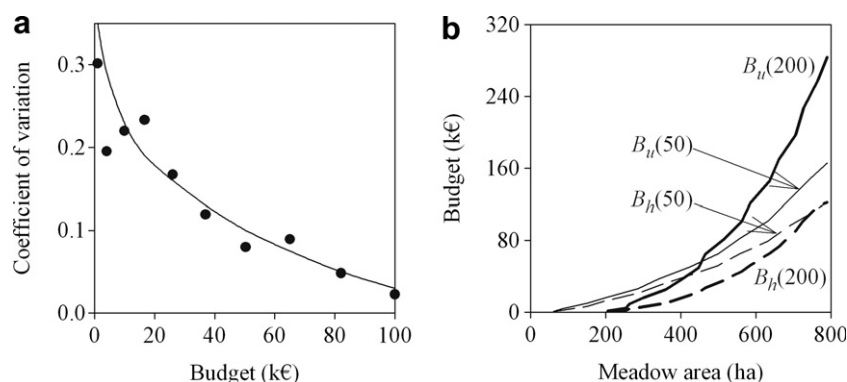


Fig. 7 – (a) Coefficient of variation of the performance of the mowing regime (1,4,-1) as a function of the budget; (b) Budget required to obtain a particular occupied meadow area for uniform (solid lines) and heterogeneous payments (dashed lines). The variation of the farm parameter u_0 (capturing cost differences among farms) is €50 and €200 (thin and bold lines, respectively).

In good approximation we also find that the meadow area occupied by butterflies in the real landscape is the product of the meadow area adopting the promoted mowing regime and the occupancy (proportion of area occupied by butterflies under this mowing regime) as determined from a simplified, non-spatial ecological model. This result stems mainly from the limited importance of spatial configuration, such that the location where a particular mowing regime is applied does not significantly affect the survival of the butterfly. The simple picture, however, changes when the budget is small or when the cost-effectiveness of the mowing regime is low, such that altogether the area of occupied meadows becomes small. Then the product model does not well approximate the ecological-economic model, indicating that the spatial location of meadows matters (Fig. 7a).

This result can be explained with the ecology of metapopulations. Metapopulations are composed of subpopulations, each inhabiting individual meadows and interacting via the exchange of individuals. Metapopulation dynamics are governed by three central processes: the extinction of subpopulations, the re-colonisation of empty habitats, and the stabilisation of subpopulations through immigrants from neighbouring populations (Hanski, 1999). As the cost-effectiveness of a mowing regime is mainly determined by its ecological suitability, there is a strong correlation between the cost-effectiveness of a mowing regime and the stability of the local populations. Depending on budget and choice of mowing regime we may, therefore, be confronted with very different types of butterfly metapopulation dynamics.

If the cost-effectiveness of the promoted mowing regime is very low, the local populations on the individual meadows are critically unstable irrespective of the available budget. Even the interaction of different local populations cannot prevent the metapopulation from rapid extinction (Drechsler and Wissel, 1998). Spatial configuration has no influence.

Now consider slightly more cost-effective mowing regimes. Here the local populations are still unstable and cannot persist in isolation. However, if the meadows with promoted mowing regimes are close enough to each other, there is sufficient exchange of individuals between meadows and the species can survive as a metapopulation. For small budgets only few meadows with the promoted mowing regime exist in the landscape, and it is important to have these meadows arranged together in one part of the landscape: spatial configuration matters. For high budgets there are so many meadows with the promoted mowing regime that even under random allocation the distances between neighbouring meadows are so small that butterflies can disperse between them. Metapopulation dynamics exist regardless of the spatial configuration of meadows. In between these two extremes of large and small budgets the importance of spatial configuration increases with decreasing budget.

Now consider the most cost-effective mowing regimes. Such mowing regimes lead to relatively stable local populations which are less reliant on immigrating butterflies. Therefore, the species can survive as a metapopulation even if the meadows are further apart than would be optimal. Spatial configuration still matters, but it matters less than in the above case of less cost-effective mowing regimes with unstable local populations.

Our findings confirm Groeneveld (2004) who emphasizes the role of local population stability but adds that the dispersal ability of the individuals can be equally important when assessing the importance of spatial configuration. We further conclude that the importance of spatial configuration increases with decreasing budget – more strongly if the promoted mowing regime is less cost-effective and less strongly if the promoted mowing regime is more cost-effective. We observe that an economic parameter – the budget – governs via the ecology of metapopulations the importance of spatial configuration of meadows, with implications for instrument design are outlined below.

6.3. Spatial heterogeneity of compensation payments

Research has emphasised that spatially differentiated benefit functions (a) and cost functions (b) call for spatially heterogeneous policy instruments. Our case study contributes to this mostly theoretical research with empirical results.

(a) Conceptual models have shown that for spatially differentiated benefit functions the criterion of cost-effectiveness requires spatially heterogeneous conservation measures and compensation payments (e.g. Babcock et al., 1997; Wu and Bogess, 1999; Wätzold and Drechsler, 2005). The case study result shows that well-designed spatial configurations of the meadows with promoted mowing regimes may lead to ecological benefits which are 50% higher than benefits from average configurations (Fig. 7a). This result suggests that the issue of spatial heterogeneity of conservation policies can be of significant practical importance.

The case study draws attention to two aspects that have not been addressed in the above mentioned conceptual ecological-economic research. First, metapopulation dynamics lead to spatial heterogeneity of the benefit functions. Second, designing cost-effective heterogeneous payments may prove difficult for some conservation problems. The reason is that the (added) benefit of a meadow – and so the cost-effective compensation payment for that meadow – depends on the presence and the locations of other meadows with promoted mowing regimes in the region which are not known a priori to the conservation energy. Higher marginal benefits of a meadow with the promoted mowing regime only arise if the meadow is closely located to other meadows with the promoted mowing regime. To initiate such agglomeration one possible option for the agency may be to randomly choose a particular area where payments are higher. However, there is a risk that an area is selected where costs are comparatively high, for example due to a negative attitude of farmers towards conservation (cf. Smith and Shogren, 2002). Furthermore, it may be perceived as unfair by farmers if there is an arbitrary differentiation of payments. An alternative to such a differentiation of compensation payments may be an agglomeration bonus (Parkhurst et al., 2002) where a bonus is paid on top of a compensation payment when a conservation measure like mowing is carried out close to an area where other conservation measures are carried out. It is a matter of further research to analyse to what extent and under what circumstances an agglomeration bonus provides a better solution than spatially differentiated payments.

(b) Several authors emphasised that compensation payments lead to an additional monetary gain for some land-users (a producer surplus) if conservation costs differ among land users but payments are uniform (e.g. Innes, 2000; Smith and Shogren, 2002). If producer surpluses exist, a higher financial budget for achieving a given conservation aim is required compared to an identical situation where payments are differentiated based on true costs. A higher budget, in turn, leads to a welfare loss as the taxation required to finance public funds has a distortionary effect on consumption and/or production. In the present study, we found (Fig. 7b) that depending on the variation (u_0) in the farm parameter the production surplus may be substantial. Payments differentiated according to individual farmers' costs may require up to only half the budget than homogeneous payments. This result demonstrates the importance of cost-based differentiation, as we may find even higher savings for other agriculture-related conservation measures in Europe. In our study costs only differ due to meadow size, farm characteristics and the different attitudes of farmers towards conservation whereas in other circumstances costs may additionally differ according to the natural factors considered in the cost assessment (soil quality, soil humidity, altitude). This calls for an increasing consideration of payment schemes that aim to reduce producer surpluses such as auctions (Latacz-Lohmann and van der Hamsvoort, 1997).

6.4. Evaluation of existing payment scheme

The case study allows analysing a payment scheme that already exists in the region of Landau. Farmers may participate in a programme where they receive a compensation of €200 per ha when they commit themselves not to mow before 15 June. Similar schemes exist all over Germany and in many other parts of Europe. Their aim is to improve the conservation of meadows in general and of meadow birds in particular. With this restriction on the mowing date, it is profit maximising for farmers if the first cut is in the third week of June and the second cut six weeks later (coded as (1,6,3) in this paper). As Fig. 4 shows, such a mowing regime is ranked very low in terms of cost-effective conservation of *M. teleius*. In fact, it has a negative impact on the *Maculinea* population, as here the second cut falls into the critical phase where the butterflies deposit their eggs on the *Sanguisorba* plants. While a criticism of the existing scheme has to take into account that it is not explicitly focused on *M. teleius*, our analysis demonstrates that the existing scheme fails to cover all relevant ecological objectives. *M. teleius* protected by the EU Habitats Directive and, therefore, has a high priority for conservation in Europe. This criticism is all the more important as schemes similar to the programme in Landau exist all over Germany, whereas to our knowledge no programme is specifically directed at *M. teleius*. There are no studies that analyse the reasons for this uniformity of conservation programmes across Germany. Anecdotal evidence suggests that conservation programmes that are implemented in one region are just copied in other regions. Scientific research like this study can be used to demonstrate that spatially heterogeneous conservation programmes that take into account the needs of many species

are better than the uniform approach that currently dominates conservation policies in Germany.

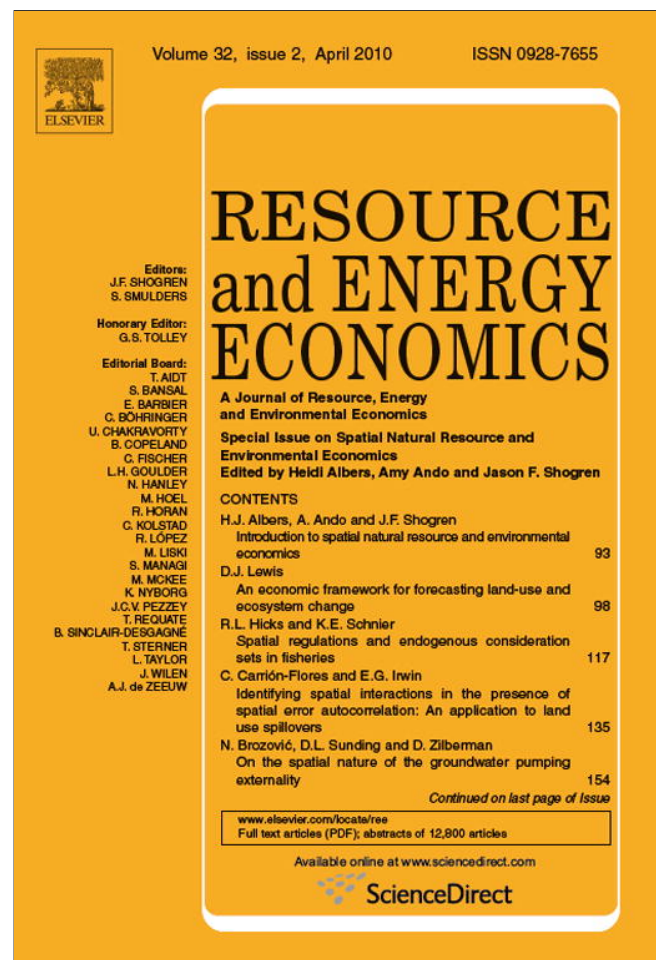
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An agglomeration payment for cost-effective biodiversity conservation in spatially structured landscapes

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ABSTRACT

Connected habitats are ecologically more valuable than isolated habitats for many species. A key challenge when designing payments for biodiversity in fragmented landscapes is to increase the spatial connectivity of habitats. Based on the idea of an agglomeration bonus we consider a scheme in which land-owners only receive payments if habitats are arranged in an ecologically favourable configuration. We compare the cost-effectiveness of agglomeration payments to spatially homogeneous payments on a conceptual level. Our results suggest that positive efficiency gains exist for agglomeration payments. We use Large Blue butterfly habitat in Germany as a specific case study, and find the agglomeration payments may lead to cost-savings of nearly 70% relative to homogenous payments.

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1. Introduction

Compensation schemes in which land-owners receive payments for voluntarily managing their land in a biodiversity-enhancing manner have become one of the most important instruments for biodiversity conservation worldwide. In the United States, the US Fisheries and Wildlife Service and over a thousand non-profit land trusts promote habitat conservation by using voluntary incentive mechanisms to elicit the cooperation of private land-owners. Based on a survey of state incentive

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programs, George (2002) found about 400 incentive programs enrolling some 70 million private acres already exist in the 50 states—50% of which were created within the last decade. The typical state offers four to six conservation incentives, usually in some form of direct payment and easement with tax relief (also see the overview in Shogren, 2005). In Europe, farmers receive several billion Euros annually in the context of agri-environmental schemes for applying biodiversity-enhancing farming measures (cf. European Commission, 2005). Increasingly, payment schemes for conservation measures are also applied in developing countries (e.g., Landell-Mills and Porras, 2002).

These voluntary schemes are necessary because property rights are frequently allocated so land-owners have considerable latitude to manage their land in their own private interest. Experience with the US Endangered Species Act also demonstrates that forcing owners of land with endangered species to carry out conservation measures might encourage them to eradicate these species to escape the burden of conservation costs (Brown and Shogren, 1998).

One key challenge when designing effective biodiversity conservation compensation schemes is to account for the spatial arrangement of habitats.¹ Gustafson et al. (2007, p. 141) make this point with force: "...developing protocols to practice effective environmental stewardship across ownership boundaries is recognized as one of the great challenges of our time." The ecological literature addresses how specific habitats should be spatially allocated to maximise the targeted ecological benefit, such as population size and species viability (see, e.g., McDonnell et al., 2002; Frank and Wissel, 2002; Drechsler et al., 2003). The design needs to consider that the contribution of a habitat to an overall conservation objective depends on both its spatial extent and its location relative to other patches (see for instance Gustafson et al., 2007; Schulte et al., 2008). In spatially structured landscapes, species populations exist as so-called *metapopulations*, which consist of subpopulations each of which inhabits a habitat patch. If individual members of the species can move between patches, the subpopulations interact. In general, this exchange of individuals is beneficial for the survival of the metapopulation,² resulting in the general rule for given total habitat area connected habitats are ecologically more valuable than isolated habitats (e.g., Simberloff, 1988; Hanski, 1999).

Given the voluntary nature of payment schemes, the question is how to induce land-owners to select land for conservation so that habitats are connected? Many payments are spatially homogeneous—every land-owner receives the same payment for a particular conservation measure. Such homogeneous payment schemes generate an ecologically valuable spatial configuration only if it contains the least costly patches. In contrast, Parkhurst et al. (2002) suggested an alternative scheme—the 'agglomeration bonus.' The agglomeration bonus provides an incentive to land-owners to generate a valuable configuration. The idea of an agglomeration bonus is a premium—a bonus—is paid on top of a standard payment for managing land in a biodiversity-enhancing manner if the managed patches are arranged in a specific spatial configuration. This requires cooperation among land-owners and research about the agglomeration bonus has so far focused on the cooperation problem (e.g., Parkhurst et al., 2002; Parkhurst and Shogren, 2007, 2008).³

Herein we bypass the cooperation problem and explore the cost-effectiveness question: does an agglomeration bonus lead to a higher ecological output for a given budget⁴ than homogeneous payments? This question raises the concern that the agglomeration bonus leads to higher ecological benefits but it can also lead to higher costs. It may be necessary to include costly patches to achieve a desired spatial configuration. This suggests a trade-off exists between maximising total habitat size with inferior spatial configuration and optimising spatial configuration with less habitat size.

¹ See for example Knight and Landres (1998), Fairfax et al. (2005), and Raymond (2006).

² In some cases, the exchange of individuals among subpopulations may be adverse, e.g., spread of disease.

³ See also discussions of the pros and cons of the agglomeration bonus idea in Michael (2003), Stoneham et al. (2005), Chomitz et al. (2006), Smith et al. (2007), and Zhang et al. (2007).

⁴ An alternative approach is to maximise ecological benefits subject to a cost constraint. The difference between a cost and a budget constraint is that the latter includes producer surpluses arising from payments that exceed costs. We chose the budget constraint because producer surpluses from payments cannot be considered as transfer payments without welfare effects. Payments need to be financed from taxes which leads to administrative costs of tax collection and indirect costs due to deadweight losses from distortionary effects of taxes (which have been estimated to be in the order of 10–30 cents per dollar (Innes, 2000, p. 197)). There is also a significant amount of research on the design of incentive mechanisms to reduce producer surpluses (e.g., Latacz-Lohmann and Van der Hamsvoort, 1997).

This paper addresses this question—we compare the cost-effectiveness of an agglomeration bonus against a spatially homogeneous payment. We compare two ‘pure’ payment schemes: (i) payments are only made when an ecologically beneficial spatial configuration is generated (agglomeration payment), and (ii) payments are made independent of habitat location (spatially homogeneous payment).⁵ We first explore a conceptual analysis on a fictitious landscape to gain insight into how economic and ecological parameters affect the cost-effectiveness of an agglomeration payment. We then compare the cost-effectiveness of homogeneous and agglomeration payments for a real conservation problem: the protection of an endangered butterfly species (Large Blue, *Maculinea teleius*) in a region around the city of Landau, Germany.

Our conceptual analysis shows that the cost-effectiveness of agglomeration payments compared to homogeneous payments is determined by the interaction of three effects: the *connectivity effect* captures the ecological benefits of agglomeration payments: spatially aggregated habitats are usually better for species survival than spatially dispersed habitats. In contrast, the *patch restriction effect* makes homogeneous payments comparatively more cost-effective. This effect arises because under homogeneous payments the most inexpensive patches in the landscape are selected; whereas with the agglomeration payment the selection is restricted which thereby induces the choice of more costly patches.

The cost-effectiveness of agglomeration payments is increased because they reduce land-owners’ producer surpluses—which leads to the third effect, the *surplus transfer effect*. To generate ecologically valuable spatial configurations, it may require the participation of land-owners who would lose money from participating. Their contribution can only be assured with side payments from other land-owners, which would reduce their producer surpluses. In our model, the patch restriction effect never dominates the other two effects, and agglomeration payments are always more cost-effective than homogeneous payments. In the butterfly case study, we find cost-savings of 30–70% can be achieved with agglomeration payments.

Our work is related to the economics literature on the spatial allocation of conservation activities.⁶ This work has focused primarily on adding economic considerations into the biological mindset that has dominated reserve selection. In an influential paper Ando et al. (1998) showed how the cost-effective spatial allocation of reserves depends on both the cost and benefits of land parcels (see e.g., Polasky et al., 2000, 2001; Balmford et al., 2003; Groeneveld, 2004 for extensions of this type of research). In related vein, Babcock et al. (1997), Ferraro (2003) and Wätzold and Drechsler (2005) explore efficiency losses if the regulator spatially allocates funds for environmental purposes not according to the cost-effectiveness rule (cf. also Wu and Boggess, 1999). In a series of related papers, Lewis and Plantinga (2007), Nelson et al. (2008), and Lewis et al. (2008) have explored in detail the efficient use of economic incentives and economic methods to protect biodiversity given fragmentation exists on the landscape (also see Goodin, 1994; Albers and Ando, 2005; Ferraro, 2007; Thoyer and Saïd, 2006). Robalino and Pfaff (2004), Tikkanen and Kurttila (2007) and Schulte et al. (2008) raised the idea of the agglomeration bonus as a potential solution to overcome coordination problems between land-owners for several practical conservation problems. Overall, this literature has provided useful insight into how economics can make bio-centric conservation policy better by showing how to get more protection for fewer resources. We extend this research by addressing the supporting role the agglomeration bonus can play as an incentive tool to generate ecologically desired spatial configurations cost-effectively.

2. Introduction of agglomeration payments

Consider a landscape with N habitat patches. Let $\mathbf{r}_i = (x_i, y_i)$ denote the spatial location and a_i the size of patch i ($i = 1, \dots, N$) and z_i the land-owner’s decision to manage patch i in a species-friendly “green” manner ($z_i = 1$) or conventional manner ($z_i = 0$). The vector $\mathbf{z} = (z_1, \dots, z_N)$ then characterises the spatial

⁵ For the sake of analytical clarity, we do not explore mixed schemes with a space-independent component and an agglomeration bonus.

⁶ The agglomeration benefit idea is related to the idea of a network externality and has been addressed in different economic contexts in which the “whole is greater than the sum of the parts” (see e.g., Wan and Cheng, 2001; Banks et al., 2003).

arrangement of green patches. The opportunity cost (per habitat patch) to manage patch i in a green manner is denoted as c_i . For convenience, assume each land-owner possesses one patch so the words 'patch' and 'land-owner' can be used synonymously.

Without a detailed specification, we assume an ecological benefit function $\Pi(a_i, \mathbf{r}_i, z_i; i = 1, \dots, N)$ that increases if the distances between the patches, determined by their locations $\mathbf{r}_i$, decrease. Rather than considering complicated frequency distributions of these pairwise distances, we focus on a simple surrogate variable, habitat density, which (for given number of habitat patches) is inversely related to the patch distances. We consider the ecological benefit Π can be larger by increasing the density of green patches, ρ , in some part of the landscape, denoted as R . The density of green patches in landscape part R is defined as the total area of green patches contained in R divided by the total area ($|R|$) of R :

$$\rho(R) = \frac{\sum_{\mathbf{r}_i \in R} z_i a_i}{|R|} \quad (1)$$

The sum in Eq. (1) runs over all patches contained in R . If R , e.g., is a square of size $|R| = 100$ ha and it contains 20 ha of green patches, then $\rho = 0.2$. To achieve a desired green patch density, the conservation manager offers a payment p (money per patch area) to each land-owner who:

- (1) manages the habitat patch in a green manner, and
- (2) in cooperation with other land-owners produces a density of green habitat patches ρ above a given threshold $\rho_{\min}$. The threshold has to be reached in a certain part of the landscape. For simplicity this landscape part, denoted as R , has a rectangular shape. To ensure that there is a single contiguous large area with the desired density *only one* single rectangle may be formed. The choice of size and location of that rectangle is for the land-owners to decide.

Patches outside the rectangle do not receive any payment and are managed conventionally. In mathematical terms, a payment p is paid to land-owner i if and only if $z_i = 1$ and $\mathbf{r}_i \in R$ and

$$\rho(R) > \rho_{\min} \quad (2)$$

A payment scheme is defined by the payment p and the threshold density $\rho_{\min}$. Note for purpose of simplification we assume there is only a payment if the conditions of Eq. (2) are met, i.e., no other, space-independent payment is considered. We assume that the agency only knows the mean and variance of the costs (m_c and σ_c) but has no information about the individual conservation costs c_i .

For the response of the land-owners to the payment scheme ($p, \rho_{\min}$) we assume that land-owner i only participates in the scheme if the profit from participation is positive ($\pi_i > 0$) with π_i being determined by

$$\pi_i = p - c_i. \quad (3)$$

Side payments s_i arise if the individual profit of land-owner i from scheme participation is negative but her contribution is required to generate a desired rectangle. In this case, $s_i > 0$ means land-owner i receives side payments and $s_i < 0$ means she offers them. We assume that land-owners know other land-owners, conservation costs c_i and cooperate. This implies that land-owners select a rectangle if the *aggregated* profit from all land-owners, i.e., the sum over all π_i , is positive. They eventually decide so the total profit from participation of all land-owners in the landscape:

$$\Pi = \sum_{i=1}^N z_i a_i (p - c_i + s_i) = \sum_{i=1}^N z_i a_i (p - c_i), \quad (4)$$

is maximised. The side payments drop out in Eq. (4) as the sum over all side payments is zero. Having agreed upon a rectangle, the land-owners inform the agency about its location and size as well as the locations of the green patches. The resulting budget that has to be spent is

$$B = \sum_{i=1}^N z_i a_i p. \quad (5)$$

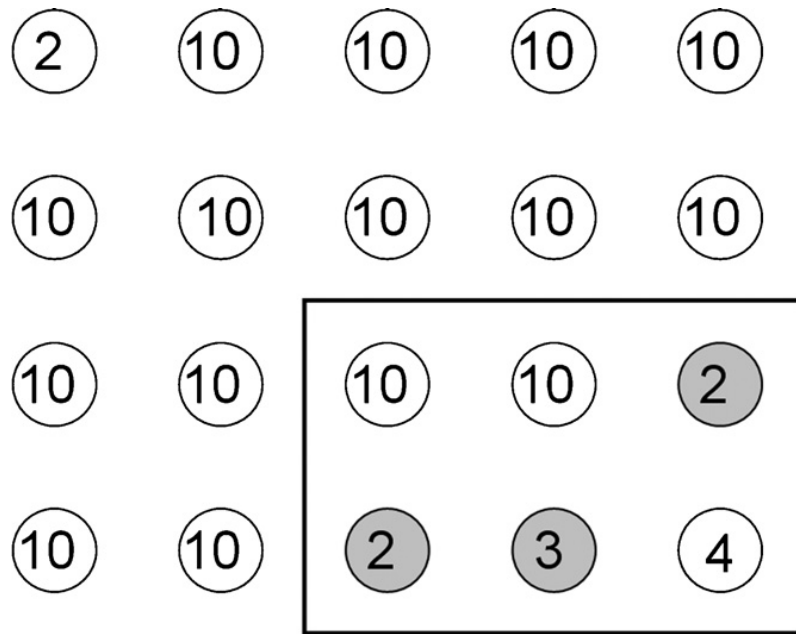


Fig. 1. Artificial landscape of patches of identical size with different costs (given by the numbers). Patches filled grey are “green” patches managed as habitat. For further details, see text.

The spatial configuration of green patches that maximises Π and represents the farmers' choice is determined by forming all possible distinctive rectangles in the landscape (two rectangles are distinctive if they contain a different subset of patches). In each rectangle, profit is maximised under the constraint Eq. (2).⁷ If the threshold density is too high or p too small compared to c_i , a positive profit may be unachievable. Here the maximum profit is zero and is achieved through $z_i=0$ for all i and the corresponding ecological benefit is zero.

3. Functioning of the agglomeration payment

3.1. Illustration of basic principle

To demonstrate the idea behind the agglomeration payment, consider now the artificial landscape in Fig. 1, in which all patches have equal size a and are arranged on a regular grid. The numbers in the circles represent the costs c_i . With a payment of $p=2.1$ and a density threshold $\rho_{\min}=0$ (representing homogenous compensation payments) the three patches with $c=2$ are turned into green patches for a budget of 6.3. These three patches, however, are distant from each other and it would be desirable ecologically to have them closer together. This is achieved, e.g., by offering a payment of $p=3.1$ under the constraint that a green patch density of $\rho_{\min}=0.5a/d^2$ is exceeded, where d represents the distance between two adjacent grid points.

A number of possible rectangles R can be formed that fulfil Eq. (4). The one that maximises the landowners' total profit is in the lower right corner with $\Pi=3p-2-2-3=2.3$ (Eq. (4)). The required budget (Eq. (5)) for these three green patches is $B=3p=9.3$. It is higher than the budget required for $p=2.1$ without density threshold, because not the three least expensive patches are selected. We call this budget-increasing impact the *patch restriction* effect. In contrast, the connectivity between the patches, and the ecological effectiveness, has increased—an outcome we call the *connectivity effect*. Since the two effects point into opposite directions, it is unclear a priori whether the agglomeration payment is more cost-effective than homogenous payments. In the next section we investigate this question in a comprehensive manner on a general model.

⁷ Technically this works as follows: start with all patches in the rectangle participating: $z_i=1$. Then one by one remove all green patches (i.e. set $z_i=0$) that have negative profits $\pi_i < 0$. Start with the patch that has the most negative profit, followed by the one with the second most negative profit and proceed until having either reached the marginal meadow ($\pi_i = -0$) or the density threshold $\rho_{\min}$.

3.2. Description of a conservation problem in a fictitious landscape

We now consider the conservation problem in a fictitious landscape which we use to illustrate the cost-effectiveness of an agglomeration payment in a general manner. Defining an ecological benefit function without any loss of generality is impossible; so instead we use a general function to measure the connectivity of green habitat patches:

$$\Gamma = \sum_{i=1}^N z_i \sum_{j=i+1}^N z_j \exp(-\alpha d_{ij}) \quad \text{with} \quad d_{ij} = \sqrt{(x_i - x_j)^2 + (y_i - y_j)^2} \quad (6)$$

where d_{ij} is the distance between two patches i and j . Eq. (6) is based on a standard ecological model for the dispersal of individuals from one habitat patch to another (e.g., Hanski, 1999). The model assumes if an individual emigrates from a patch i it has to move through inhabitable area (called the “matrix” by landscape ecologists) which implies an increased mortality. The longer an individual moves through the matrix the more likely it is killed. The probability p_{ij} of reaching a patch j at a distance d_{ij} is assumed to decline with increasing d_{ij} . A frequently used functional shape for modelling this decline is $p_{ij} = \exp(-\alpha d_{ij})$, where α is determined by the dispersal ability of the species (e.g., Hanski, 1999). Small α means that p_{ij} declines slowly with increasing d_{ij} so individuals of the species are able to reach distant patches, while large α means they can only reach nearby patches. From Eq. (6) for given α , we see the connectivity Γ increases with increasing habitat area and with decreasing distances between habitat patches. Habitat patches close to a cluster of patches contribute more to connectivity than isolated ones. According to the theory of metapopulations (e.g., Hanski, 1999), Γ is a good predictor for the survival probability of a metapopulation inhabiting the landscape.

With this measure of ecological benefit, an agglomeration payment scheme [defined as a combination of payment and density threshold ($p, \rho_{\min}$)] is more cost-effective than another agglomeration payment scheme if and only if it leads to higher patch connectivity Γ for a given budget. For the general analysis we consider a landscape where the patches are arranged on a regular square grid with length and width given by $dN^{1/2}$ (cf. Fig. 1). Here N is the total number of patches and d is the distance between two adjacent grid points. The costs of patches c_i are drawn randomly from a uniform distribution with mean m_c and width $2m_c\sigma_c$. Costs are assumed to be spatially uncorrelated (we discuss this assumption in Section 5).

We consider a landscape of 100 patches, and we assume two levels of the dispersal parameter α : $\alpha_1 = 1/d$ for a species with short-range dispersal that cannot travel on average much farther than from one patch to one of its next neighbours; and $\alpha_2 = 1/(dN^{1/2})$ for a species that can travel a mean distance of $dN^{1/2}$ and can reach any patch in the landscape with high and nearly equal probability.

3.3. Analysis of the demonstrational conservation problem

We now define a landscape by the number of patches (N), the distance between grid points (d), patch size (a), and mean and variation of costs (m_c and σ_c). For several different landscapes (see below) we investigate 200 different payment schemes ($p, \rho_{\min}$). For $\rho_{\min}$, we consider values k times a/d^2 with $k \in \{0.0, 0.05, 0.1, 0.2, 0.4, 0.6, 0.8, 0.9, 0.95, 1.0\}$. At the lowest density level, $\rho_{\min} = 0$, all patches that fulfil Eq. (3) participate in the scheme. This represents the *homogenous payment scheme* that does not induce any explicit agglomeration. At the highest level of $\rho_{\min} = a/d^2$ each patch in the landscape must be a green patch. Values for the payment p are chosen so they encompass the entire range of costs $[m_c(1 - \sigma_c), m_c(1 + \sigma_c)]$. We set these at $p = m_c(1 + l\sigma_c)$ with $l \in \{-0.95, -0.9, -0.8, -0.7, -0.6, -0.5, -0.4, -0.3, -0.2, -0.1, 0.0, 0.1, 0.2, 0.3, 0.4, 0.5, 0.6, 0.7, 0.8, 0.9\}$. Systematic combination of the 10 levels for k and 20 levels for l leads to the 200 possible payment schemes.

Since the costs c_i are uncertain, for a given payment scheme the size and location of the rectangle R and particularly the resulting connectivity Γ are also uncertain. We account for this by randomly sampling the costs c_i for all patches 100 times. Each of the 100 random sets of costs $\{c_i\}_{i=1, \dots, N}$ may be denoted as a “cost landscape”. For each cost landscape $\{c_i\}$ we examine the 200 payment schemes. Means and standard deviations of the resulting connectivity, the corresponding

budget and the land-owners' total profit are calculated for each payment scheme over the 100 random cost landscapes.

Some of the model parameters have a trivial effect on the results. Doubling patch size a quadruples the ecological benefit Γ ; doubling next-neighbour inter-patch distance d has the same effect as halving the species dispersal range ($1/\alpha$); and doubling the mean cost m_c doubles the budget. Without loss of generality we reduce the dimensionality of the problem by eliminating these parameters by measuring:

1. Connectivity Γ (Eq. (6)) in units of a^2 , which is achieved by formally setting $a=1$.
2. Species dispersal range ($1/\alpha$) in units of the next-neighbour inter-patch distance d which is achieved by formally setting $d=1$ (by this, habitat density ρ (Eq. (2)) is measured in units of a/d^2).
3. The budget B and the cost variation σ_c in units of the mean cost, m_c , which is achieved by formally setting mean cost $m_c=1$.

The only parameters that affect the cost-effectiveness of the agglomeration payment in a non-trivial manner are the cost variation (σ_c) and the species dispersal range ($1/\alpha$). Starting from a base scenario and varying each parameter independently, we consider the following three scenarios for $N=100$:

- a. $\sigma_c=0.1$, $\alpha=1$;
- b. $\sigma_c=0.1$, $\alpha=1/(N^{1/2})$;
- c. $\sigma_c=0.5$, $\alpha=1/d$.

In scenario a, the cost variation is small (10% of the mean) and the species dispersal range ($1/\alpha$) is small and equals the distance d between neighboured patches. In scenario b the species dispersal range is increased to about the diameter ($dN^{1/2}$) of the landscape; in scenario c the cost variation is increased to 50% of the mean.

3.4. Results

Fig. 2a–c show the results for the three scenarios. All figures show the connectivity Γ as a function of the budget for various density thresholds $\rho_{\min}$. The *density threshold* $\rho_{\min}=0$ (solid line in Fig. 2) represents homogeneous payments; the expected cost-effectiveness improvements of the agglomeration payment are presented in Fig. 2 for various $\rho_{\min}$.

In all scenarios of Fig. 2 the cost-effectiveness of a payment scheme increases with $\rho_{\min}$, so all agglomeration payment schemes with $\rho_{\min}>0$ lead to efficiency gains compared to homogenous payments. Why is this so, given the patch restriction effect increases the cost of the spatially aggregated patch arrangements? The reason is the presence of a third effect that has not been considered yet: a *surplus transfer effect*. The agglomeration payment not only aggregates patches in space but also reduces the producer surplus of the land-owners. Without a density threshold ($\rho_{\min}=0$), only land-owners with positive individual profits, $\pi_i>0$, participate. If a positive density threshold is set and only land-owners with positive individual profits participate, their number may be too small to reach the density threshold $\rho_{\min}>0$ and so they may not get any payments at all (Eq. (2)). To get at least some profit individual land-owners have to sacrifice some of their producer surplus and transfer it through side payments (Eq. (4)) to the land-owners whose individual profits would otherwise be negative. Now the density threshold is reached and a positive total profit obtained. To give a numerical example, set $p=2.6$ instead of $p=3.1$ in Fig. 1. The profit maximising patch configuration can be achieved only if the owners of the two ($c=2$)-patches offer a side payment to the owner of the ($c=3$)-patch. Both the required budget (7.8) and the total profit ($7.8-7=0.8$) are reduced compared to the case of $p=3.1$.

Two questions remain: (i) how does the magnitude of the efficiency gain depend on key model parameters: budget, dispersal range ($1/\alpha$), and level of cost variation (σ)? (ii) Why do surplus transfer effect plus connectivity effect dominate the patch restriction effect? We now address each question in turn.

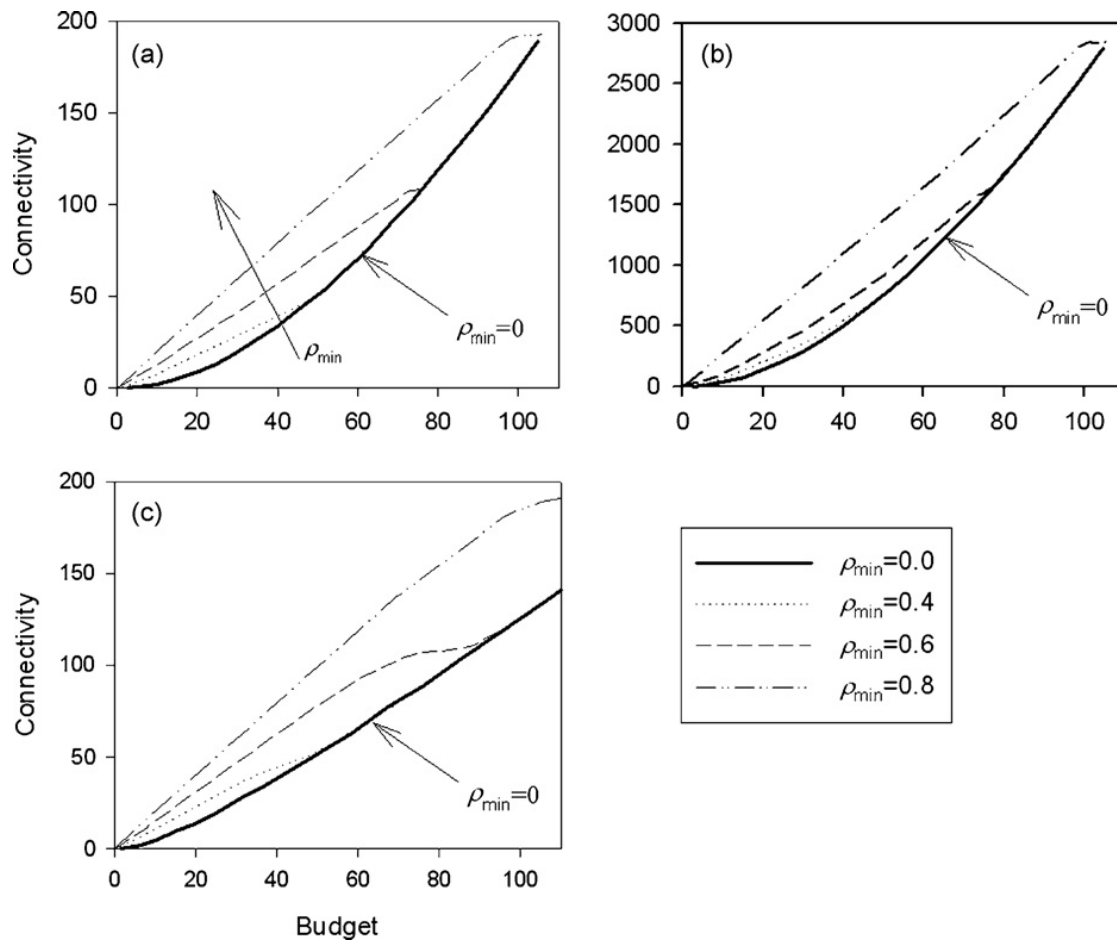


Fig. 2. Mean connectivity versus mean budget (measured in units of mean patch cost m_c) for the different levels of $\rho_{\min}$. Solid bold line: $\rho_{\min}=0$ (equivalent to homogeneous payments). Dashed lines: $\rho_{\min}$ increasing from bottom to top with levels 0.2, 0.3, 0.4, 0.6, and 0.8. Panels (a)–(c) represent scenarios (a)–(c). Budget and connectivity are averages over the 100 random cost landscapes $\{c_i\}$.

3.4.1. The effect of the budget on the efficiency gain

Fig. 2 shows that high efficiency gains exist only if the budget is below a specific value (Fig. 2a). For instance, in the case of $\rho_{\min}=0.6$ the connectivity (long-dashed line) exceeds the connectivity obtained from homogenous payments (solid line) only for budgets below $80m_c$, while for higher budgets both curves are identical, indicating zero efficiency gain. The reason is that at high budgets there are already many green patches in the landscape and selecting one patch instead of another will not increase connectivity considerably (the connectivity effect is small).⁸ Furthermore, in such a situation the density threshold can be reached in the entire landscape already with those patches that have $\pi_i > 0$. In this case, there is no incentive for the owners of these patches to share their producer surplus (the surplus transfer effect is small). Each of them gains his full amount $p - c_i$, which is just what one obtains under homogenous payments. Overall, the highest efficiency gain in relative terms occurs with small budgets and decreases with increasing budget.

3.4.2. The effect of the dispersal range

Comparison of Fig. 2a and b reveals that for species with long-range dispersal efficiency gains are smaller than for species with short-range dispersal. This is plausible given that good dispersers are less dependent on the spatial configuration of habitat than poor dispersers (e.g., Drechsler et al., 2007), which means that for good dispersers the connectivity effect is smaller than for poor dispersers.

⁸ This result is similar to Lewis and Plantinga (2007) who also find that the percentage of the landscape covered with land use beneficial to conservation has a significant impact on the relative performances of different conservation policies.

3.4.3. The effect of the cost variation (σ)

We find this effect to be ambiguous. For small budgets higher variation in the costs c_i slightly reduces the cost-effectiveness of the agglomeration payment (compare the distances between the solid and dashed lines near the origins of Fig. 2a and c) while for high budgets it increases the cost-effectiveness of the agglomeration payment. The reason for the ambiguity is that for small budgets the patch restriction effect is relatively strong, because a small budget means that patches that in the case of homogenous payments are dispersed over the entire landscape have to be in a very small rectangle, which leads to a high likelihood that costly patches have to be selected. For increasing budgets the rectangle becomes larger and the patch restriction effect decreases to zero (reached when the rectangle covers the entire landscape). The surplus transfer effect, in contrast, increases with the budget and a point exists where both effects have the same magnitude, so that for relatively small (large) budgets the patch restriction (surplus transfer) effect dominates and increases (decreases) the costs of the agglomeration payment compared to homogenous payments.

3.4.4. The dominance relations between the three effects

The source of patch restriction and surplus transfer effects is the variation among the costs (one can show that for uniformly distributed costs with range 2σ the magnitudes of both effects are proportional to σ). Since both effects point into opposite directions, they at least partly compensate each other, and their combined effect is smaller than the connectivity effect associated with the limited dispersal range of the species. With the dispersal ranges selected in the model (we discuss possible effects of longer dispersal ranges in Section 5), the efficiency gain of the agglomeration payment is positive.⁹

4. Empirical study: conserving endangered butterflies with an agglomeration payment

4.1. The conservation problem

We now apply the idea of an agglomeration payment to a case study, the conservation of an endangered butterfly species (Large Blue, *M. teleius*) in an area near the town of Landau in Rhineland-Palatinate, Germany. The butterfly species is highly relevant for conservation as it is protected by the EU Habitats Directive.¹⁰ *M. teleius* is a butterfly that requires the presence of spatially connected meadows for its survival (see Thomas and Settele, 2004 for details of the butterfly's ecology). Every July, the adult butterflies deposit their eggs on the plant *Sanguisorba officinalis*. After a few weeks the larvae fall onto the ground where they are adopted by ants (*Myrmica scabrinodis*) which feed them in their nests over winter. For the survival of the butterfly, it is important when and how frequently meadows are mowed. Mowing may destroy the eggs and larvae on the *Sanguisorba* plant, and the abundance of the plant will be insufficient for egg deposition for the next couple of weeks. Too frequent mowing may also harm *M. scabrinodis*. Mowing is necessary, however, because it avoids succession and preserves an open landscape. Furthermore, rarely mowed meadows become overrun with thick vegetation which is unsuitable for the ants.

The butterfly's dependence on a certain mowing regime explains why *M. teleius* was common in Central Europe until the 1950s, but since then has become endangered. Prior to 1950s, meadows of a region were not mowed all at once; rather mowing took place over the whole summer. Even if some meadows were unsuitable for *M. teleius* at a particular time, there were always other meadows to which butterflies could disperse and deposit their eggs. The development of machinery, however, made it possible to mow all meadows in a region simultaneously twice a year, first at the end of May and second six to eight weeks later. This mowing regime maximises the farmers' profits but is

⁹ We have focused on mean values over 100 random landscapes. How does the variation among these landscapes affect these results? Our work shows that especially for small agglomeration payments the variation in the corresponding budgets and connectivities can be substantial; however, budget and connectivity are almost perfectly correlated. This means that in some landscapes a certain payment may deliver less connectivity than in another landscape, but at the same time the required budget will be smaller by the same factor. So the peculiarity of the landscape affects the effectiveness (connectivity) of the agglomeration payment scheme but not its cost-effectiveness.

¹⁰ We selected this case study given the intersection of data availability and high policy relevance.

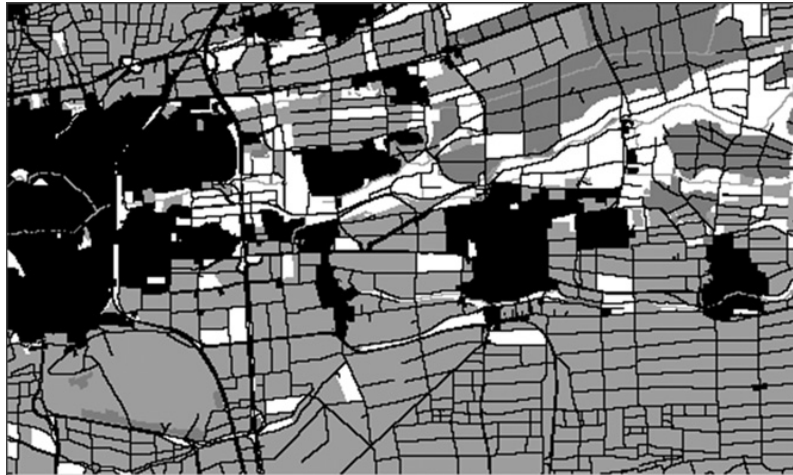


Fig. 3. The model landscape (black: settlement/roads; dark grey: forest; light grey: open land, water bodies; white: meadows). The dimension of the map is 10 km × 6 km. Source: Drechsler et al. (2007, p. 177).

unsuitable for the reproduction of the butterflies as the second mowing date falls into the weeks during which the butterflies deposit their eggs on the *Sanguisorba* plants.

Following the practise of German agricultural policy, we assume property rights are such that farmers cannot be forced to adopt conservation-enhancing mowing practises. This implies a regulator will have to provide compensation to induce farmers to adopt a mowing regime beneficial to the butterflies. The farmers' opportunity costs of mowing at some other date differ depending on the mowing regime. As a general rule, opportunity costs rise with a later mowing date because the energy content of swath and its quality as fodder decreases.

4.2. Analysis

We identify a cost-effective mowing regime for the region by relying on results from Drechsler et al. (2007). The authors developed an approach to design a cost-effective payment scheme for the conservation of *M. teleius* in the case study region we now consider. The approach integrates an agro-economic cost assessment and an ecological model.¹¹ The agro-economic cost assessment determines the opportunity costs of the mowing regimes for each meadow in the case study region and the ecological model quantifies the effects of these mowing regimes on the butterfly population on a regional level. By comparing the ecological effects of different mowing regimes, the cost-effective mowing regime and the corresponding payments may be determined as a function of the conservation budget. In line with the current agricultural policy approach in Germany, Drechsler et al. assume for a particular mowing regime payments are not differentiated according to farmers' opportunity costs but every farmer receives the same payment. In the current analysis we extend this work by determining the efficiency gains that can be achieved if the homogeneous payments analysed by Drechsler et al. are replaced by an agglomeration bonus.

For this we consider the most cost-effective mowing regime analysed in Drechsler et al. that is not in conflict with other endangered species (mowing once every second year at the end of August) and compare its cost-effectiveness with a scheme based on an agglomeration payment. The geographic data base for the analysis comes from a digitised satellite image of the case study area (10 by 6 km² with a resolution of 20 by 20 m²). With the image one can distinguish between different landscape types in each pixel. We structure the landscape types into four types as experienced by the butterfly species: meadows, open land (e.g., traffic ways, lakes and rivers, arable land), forests (including shrubland), and settlements. Fig. 3 shows the model landscape.

We determine the areas of the individual meadows in the landscape by counting the pixels belonging to each meadow. The location of each meadow is defined by its midpoint such that the x

¹¹ See Bergmann (2004) and Johst et al. (2006) for a detailed description of the agro-economic cost assessment and the ecological model.

(y)—co-ordinate of a meadow is the average of the x (y)—co-ordinates of all pixels belonging to that meadow. From these x – y locations the Euclidian distances, $d_{ij} = ((x_i - x_j)^2 + (y_i - y_j)^2)^{1/2}$ are calculated for all pairs (ij) of meadows. The meadow sizes are required as an input for the ecological model and the cost assessment, and the pairwise distances are needed for the ecological model.

The opportunity costs of implementing the above introduced mowing regime on the meadows come from Bergmann (2004). Following Drechsler et al. (2007) we account for both opportunity cost and the farmer's administrative costs arising from scheme participation. The costs accrue, for example, from taking time to fill out forms and participate in monitoring activities of the conservation agency. In addition, farm specific characteristics may differ and different farmers may have different attitudes towards biodiversity conservation and may request slightly higher (if they are opposed) or slightly lower payments (if they are in favour). Assumed farm characteristics and personal attitude are random among farmers and uniformly distributed between plus and minus 10% of the real (opportunity plus administrative) costs.¹²

We perform the analysis in the same manner as the general analysis in the previous section. First we select a critical density $\rho_{\min}$ (where $\rho_{\min}=0$ represents the homogenous payment scheme) and determine the number and arrangement of butterfly-friendly mowed meadows that maximise the farmers' profits. Again we assume farmers generate rectangles in the landscape and identify the one that maximises their profit. In a real landscape the number of rectangles to be considered would be too large to analyse. We consider a large subset of rectangles of different sizes, shapes and locations that systematically cover the entire landscape. For this we lay a regular grid with 50 by 50 cells on the entire landscape with the grid cells' north-south and east-west dimension being 120 m and 200 m respectively. To find the outcome of the farmers' negotiations we form all possible rectangles whose borders lie on the grid lines (which includes all 2500 rectangles made of one grid cell, all 4900 rectangles made of two adjacent grid cells, etc., ... up to the largest possible rectangle that includes all 2500 cells). For each agglomeration payment, from these rectangles we determine the one that maximises the farmers' total profit and the corresponding budget and area of meadows occupied by butterflies. The area occupied by butterflies is calculated using a spatially explicit stochastic simulation model (Johst et al., 2006) which considers the life cycle of the species, the dispersal between the meadows, weather fluctuations and the landscape dynamics caused by the mowing events.

As the costs of implementing the mowing regime contain a random element, we consider four different random cost landscapes and determine mean area of occupied meadows and the mean budget.

4.3. Results

Fig. 4 shows the efficiency gains achieved by the agglomeration payment compared to a homogeneous payment scheme. The efficiency gain increases with the density threshold $\rho_{\min}$. A maximum of $\rho_{\min}=0.02$ (equivalent to 2 ha of green meadow per km²) is considered in the figure, as higher thresholds do not lead to further efficiency gains. Efficiency gains of agglomeration payments are substantial for low and medium sized budgets. They range from about 70% for a budget of 3000€ to about 30% for a budget of 10,000€. Wätzold et al. (2008) found that with 10,000€ the extinction risk of *M. teleius* could be strongly reduced in the case study region.

The observation that efficiency gains are largest for low budgets is in line with results from the conceptual model (cf. Section 3.4; Fig. 2). The reason is that with low budgets only few meadows are managed in a green manner. Under homogeneous payments these would be dispersed over the entire landscape and agglomerating them strongly increases their connectivity. In contrast, for high budgets there are many green meadows in the landscape whose connectivity would be sufficient even under homogeneous payments.

¹² We only consider medium sized meadows between 0.75 ha and 1.5 ha. European legislation allows compensation for farmers' administrative costs only as a percentage of opportunity costs and the administrative effort to participate in conservation schemes with small meadows may be too high. Large meadows are excluded, because their areas are likely to be overestimated. We do not have data about ownership of meadows and the satellite image which forms the data base of the analysis can depict roads that separate meadows but not fences.

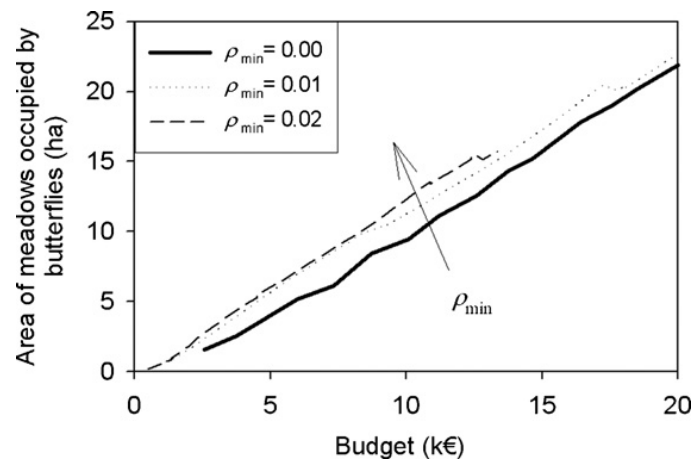


Fig. 4. Area of occupied meadows versus budget (means over four random landscapes) for three different density thresholds $\rho_{\min}$ ($\rho_{\min}=0$ representing the homogenous payment scheme). The density threshold increases from bottom to top.

5. Summary and discussion

Designing effective compensation payment schemes for biodiversity conservation requires accounting for the spatial configuration of habitat patches. One scheme that has been proposed to generate an ecologically valuable configuration is the *agglomeration bonus* (see Parkhurst et al., 2002). Land-owners receive an agglomeration payment if habitat patches are arranged in an ecologically beneficial configuration. While ecological benefits increase with the bonus scheme, the costs are expected to increase, too, as more costly patches tend to be selected. This raises the open question of how cost-effective an agglomeration payment is relative to spatially homogeneous payments. Herein we address this question at both a conceptual level and for a specific conservation study—the design of payments for butterfly-friendly grassland management in the region of Landau, Germany. We find the cost-effectiveness of an agglomeration payment is determined by the interaction of three mechanisms: (i) the connectivity effect, (ii) the patch restriction effect, and (iii) the surplus transfer effect.

The connectivity effect (i) arises because *ceteris paribus* a spatially aggregated arrangement of habitats usually leads to higher survival rates of endangered species than spatially dispersed habitats and the agglomeration bonus increases the ecological effectiveness of the habitat network. The ecological reason for this is that the viability of most endangered species inhabiting fragmented landscapes increases when the dispersal of individuals among the habitat patches is increased. The connectivity effect is strongest when the conservation budget or the dispersal range of the species is small, or both. The reason is that in the case of a small budget, only few habitats are created which under homogenous payments are dispersed all over the landscape. The distances between these patches are too large for the species to cross, especially if the species has a small dispersal range. Spatial aggregation of these few patches strongly improves the dispersal among them. The dispersal range of the Large Blue butterfly analysed in the case study is so small (on average ca. 1 km) that for homogeneous payments and small budgets the distances between habitat patches are often larger than the species' dispersal distances, and so the connectivity effect is relevant.

The patch restriction effect (ii) arises, because different patches are selected under homogeneous payments and under the agglomeration payment. Under homogeneous payments the most inexpensive patches out of all patches in the landscape are chosen. In contrast, under the agglomeration payment selection is restricted and can be made only from the patches contained in a smaller compartment (rectangle R) of the landscape. As a consequence, selecting N patches from the compartment is more expensive than selecting the same number of patches out of the entire landscape. This cost increase, or the patch restriction effect, is largest when the cost heterogeneity (σ) among the patches in the landscape is high.

The surplus transfer effect (iii) is a consequence of the density threshold $\rho_{\min}$ that has to be exceeded by the land-owners to receive a payment. Depending on the specific situation, some of the

land-owners will be confronted with the choice between not receiving any payment and offering side payments to farmers whose participation in the programme is necessary to reach the density threshold but whose individual profits would be negative without the side payments. The side payments reduce the overall producer surplus—an effect that is largest when the cost heterogeneity (σ) among the patches in the landscape is high.

The surplus transfer effect is responsible for our unexpected result that the efficiency gain of the agglomeration payment is always positive (Fig. 2). Without the surplus transfer effect there would be the expected trade-off between connectivity and patch restriction effect, and too high cost variation would cause the patch restriction effect to dominate the connectivity effect, leading to negative efficiency gains. Lewis and Plantinga (2007) identify similar mechanisms to our *patch restriction* and *connectivity effect*. They find a spatially targeted policy is not always better than a spatially uniform policy. But since the surplus transfer effect also increases with increasing cost variation but points into the opposite direction, it at least partly neutralises the patch restriction effect.

Our result that the agglomeration payment leads to a positive efficiency gain is unambiguous within the parameter range considered. The open question is whether different parameters would make things worse than the status quo, i.e., negative efficiency gains. Efficiency might be negative if the species dispersal range is vast. This implies the connectivity effect is close to zero and, as a consequence, the patch restriction effect may dominate the surplus transfer effect. The agglomeration payment, however, is not designed for such situations. Rather the purpose of the bonus is to provide incentives to generate a certain spatial arrangement of habitats which is unnecessary for vast dispersal ranges.

Efficiency gains may also become negative if costs are spatially correlated. In our study we assumed the costs are uncorrelated among patches. But with spatial cost correlations the implied clustering of low-cost patches in space may induce ecologically sufficient clustering of habitats even with homogenous payments. An agglomeration payment would not improve the ecological benefit and the additional costs associated with the patch restriction effect could render the agglomeration payment less cost-effective than homogeneous payments. A detailed analysis of the effects of spatial correlation is worthy direction for future research.

A possible alternative to the agglomeration bonus may be that the regulator negotiates individually with those land-owners whose land would be needed for a certain spatial configuration. This, however, requires that the regulator has a high level of information about each individual land-owner's conservation costs which seems unrealistic (cf. Lewis and Plantinga, 2007). In contrast, for the agglomeration payment the regulator only needs to know mean and variance of the costs. The negotiation partners are neighbouring land-owners and conditions do arise in which each land-owner might know more about his or her neighbour than the regulator. In local rural agricultural communities many producers are adjacent to each other, know each others' preferences and have a vested interest in knowing what their neighbours are doing—e.g., in pest control decisions. Varian (1994) makes a similar point—people and firms with similar activities have better knowledge than the regulator about each others' cost functions and preferences.

For the agglomeration payment to work, however, land-owners need to co-ordinate with each other about side payments and their actions. This implies additional transaction costs arise relative to standard homogeneous payments. These transaction costs might reverse our result that agglomeration payments are more cost-effective than homogeneous payments. To what extent these transactions costs arise is an empirical matter and depends on factors such as the local tradition of cooperation between land-owners, the information disparity across land-owners about conservation costs and the number of land-owners that need to participate in negotiations. Our analysis indicates this number is likely to be small because efficiency gains are highest in relative terms for small conservation budgets. A small budget implies only a few land-owners need to participate in negotiations, which makes negotiation less costly than for a large number of land-owners.

We appreciate the limits of our results—the agglomeration bonus is less likely to be successful the greater the information disparity across neighbouring producers, and the more severe the problems of cooperation. Assessing the robustness of the agglomeration bonus idea based on the determinants and degrees of shared knowledge and cooperation across neighbouring producers remains an important

area for future empirical research. That said, our real world case study on the conservation of the Large Blue butterfly confirms the general results. We find efficiency gains of up to 70% may be achieved with agglomeration payments. For the conservation of species with smaller dispersal ranges than the Large Blue efficiency gains may be even larger. Bearing in mind that in Europe and the US several billion Euro and dollars are spent each year on conservation this result suggests that significant improvements in conservation management could be made if agglomeration payments are used in practise.

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ANALYSIS

Applying tradable permits to biodiversity conservation: Effects of space-dependent conservation benefits and cost heterogeneity on habitat allocation

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ABSTRACT

This paper is concerned with the cost-effective allocation of habitat for species under spatio-temporally heterogeneous economic development. To address the dynamic dimension of the problem we consider tradable development rights as the instrument of choice. A particular challenge in applying tradable development rights is that the conservation benefit of an individual habitat patch depends on its spatial relationship with other habitat patches and thus is an emergent rather than a fixed property. We analyse with a conceptual model the spatial and temporal dynamics of habitats in a region under a tradable development rights market that takes spatial interaction of habitats explicitly into account. In our analysis two different outcomes may emerge depending on the levels of spatial interaction and cost heterogeneity: an “ordered” structure where habitat patches are clustered in space and are stable over time, and a “disordered” structure where habitat patches are scattered in space and subject to high turnover of destruction and recreation. A high level of spatial interaction or a low level of cost heterogeneity favours an ordered structure while a low level of spatial interaction or a high level of cost heterogeneity favours a disordered structure.

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1. Introduction

This paper is concerned with the problem that a conservation agency wishes to cost-effectively allocate a certain proportion of a region as conservation areas in a dynamic setting. With a dynamic setting we mean that economic development exists and land prices (representing opportunity costs of designating an area for conservation in terms of foregone economic de-

velopment) change in a spatially heterogeneous manner. Cost-effectiveness is here understood as the achievement of an ecological target at least costs. At least in principle, the agency is able to select the cost-effective spatial allocation of conservation areas in a static setting (e.g. Ando et al., 1998; Polasky et al., 2001). In a dynamic perspective, however, changing land prices may lead to a situation where the initially cost-effective selection is not cost-effective anymore. In order to re-establish a cost-

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effective allocation, the agency would be confronted with the problem of designating new areas for conservational purposes and allowing economic development in former conservation areas. Such a bureaucratic approach requires a high level of information about cost changes on the side of the agency and is also very sensitive to political lobbying activities regarding the questions which areas shall be released for economic development and which areas shall be designated for conservation.

An alternative to this bureaucratic approach to addressing changing land prices are tradable development rights. Based on the concept of tradable permits, such a system would allow economic development of a formerly conservation area if a permit is submitted to the conservation agency which certifies that an area with previously no conservation value has been transformed back into a conservation area of ecological value equal to the area to be destroyed. There is no requirement that developers establish new habitats themselves, but the permit can be bought from other landowners. This allows a market for tradable development rights to emerge.

The instrument of tradable permits has gained increasing popularity in environmental policy. It has been applied in a wide range of fields in air pollution control (see [Tietenberg, 2006](#) for an overview) and is moving increasingly into other areas with the EU CO₂-emissions trading scheme being the most prominent example of a recent application (e.g., [Hansjürgens, 2005](#)). However, until now there are only a few schemes related to biodiversity conservation that exhibit at least some elements of trading. One example is species conservation banking in the United States ([Fox and Nino-Murcia, 2005](#)). A conservation bank is a piece of private land that is conserved and managed in perpetuity under a conservation easement to protect rare species. The party that holds the easement is granted credits by a federal or state agency for the land's conservation value. These credits may be used to address a bank owner's mitigation required by law. However, it may also be sold to other landowners with mitigation requirements. Another example of conservation related trading opportunities exists in Brazil where regulations require each rural property to maintain a proportion of forest under natural vegetation ([Chomitz et al., 2004](#)). Recent provisional regulations allow landowners to satisfy the requirement for one property through a forest reserve located on another. The reserve site may be owned by another party, opening the possibility of trading land development rights.

One of the challenges of applying tradable permits to biodiversity conservation arises because the ecological value of habitat patches for the survival of species is space dependent, i.e. it depends on the presence and location of other habitat patches (e.g. [Hanski, 1999](#); [Vos et al., 2001](#); [Ovaskainen and Hanski, 2003](#)). In this paper we develop a conceptual model to analyse how these spatial interdependencies influence the allocation of habitat patches and areas for economic development over time, if a market for tradable development rights exists. The role of spatial dependencies in tradable development rights has been largely ignored so far and the purpose of the model analysis is to provide some first general insights.

This paper is related to the literature on applying tradable permits to environmental pollutants whose emission location strongly influences their damage size. There is a significant

body of literature on how to optimally design trading areas and rules when emission location matters (see [Tietenberg, 2006](#) for an overview). An example of such research is [Atkinson and Morton \(2004\)](#) who analysed the cost-effective size of an emission trading region taking into account that for small areas there is less potential for cost-saving trades and for large areas emissions may be reduced at locations where they contribute little to damage reduction. Our paper is also related to the literature on models that specifically address issues arising when tradable permits are applied to conservation. [Chomitz et al. \(2004\)](#) investigated with a spatially explicit simulation model for a hypothetical forest trading program in the Brazilian state of Minas Gerais how the size of the trading domain influences cost savings that arise from trading. [Saeed \(2004\)](#) developed a systems dynamic model for helping to design effective conservation banking institutions. This model has been further developed by [Arquitt and Johnstone \(2008\)](#) with the purpose of analysing the design of a restoration banking scheme for coastal mangroves in Thailand. However, none of these models focuses on spatial interdependencies.

Our model considers a setting with stochastic changes in costs, and the flexibility of the market for development rights is used to adapt to this change. We will show that within the model the space-dependency of the conservation benefit and the dynamics in the costs substantially affects the dynamics in the market for tradable development rights and, particularly, the spatio-temporal dynamics of the habitat network in the landscape. The next section presents the model, which is solved partly analytically and partly numerically in Section 3. The results are discussed in the final Section 4.

2. The model

The model presented in this section is a grid-based stochastic cellular automaton. We are interested in comprehensibility and, where possible, analytical tractability and thus choose a parsimonious model structure. First we introduce the landscape and the conservation benefit function, then the trading and decision rules of the market, and finally the economic dynamics that drive the market. All model parameters and state variables are compiled in [Table 1](#).

Consider a landscape with $N \gg 1$ land patches, numbered $i = 1 \dots N$, of identical sizes. Whether a patch can serve as a habitat depends on the type of use. Land may be either used for economic purposes and is of no conservational value, or it may be used for conservation which leads to opportunity costs in terms of foregone economic development c_i .¹ Let x be a vector with N elements that can take values of 1 and 0, where $x_i = 1$ indicates that patch i is a habitat and $x_i = 0$ otherwise. Let $r = (r_1, \dots, r_N)$ be an N -element vector containing the spatial coordinates r_i of the patches $i = 1 \dots N$. Let $V(x, r)$ be the conservation benefit of the

¹ In order to create a habitat patch in the real world, not only opportunity costs in terms of foregone economic development but other costs such as transaction costs and costs for restoration and management activities may be relevant as well. However, for reasons of simplification we only consider opportunity costs in terms of foregone economic development in the model.

Table 1 – Model parameters and state variables

Symbol	Meaning
N	Number of patches
$\mathbf{r}=(\mathbf{r}_1,\mathbf{r}_2,\dots,\mathbf{r}_N)$	Vector of N 2-dimensional vectors, each containing the spatial coordinates of a patch
$\mathbf{x}=(x_1,x_2,\dots,x_N)$	Vector of N binary numbers where $x_i=1(0)$ indicates that patch i is habitat (non-habitat)
$V(\mathbf{x},\mathbf{r})$	Conservation benefit of the habitat network $(\mathbf{x},\mathbf{r})$
$v_i(\mathbf{x},\mathbf{r})$ ($i=1\dots N$)	Benefit of habitat on patch i
ε	Idiosyncratic benefit of a habitat
$\mu_i(\mathbf{x},\mathbf{r})$ ($i=1\dots N$)	Location benefit of a habitat on patch i
m	Maximum possible location benefit of a habitat
Y	Target benefit set by the conservation agency for the landscape
$y=Y/N$	Target benefit per patch
c_i ($i=1\dots N$)	Cost of habitat on patch i
p (p^*)	Permit price (in market equilibrium)
w	Importance of neighbouring habitat for benefit v_i
σ	Magnitude of cost variation
A	Total area of habitat in the landscape
C	Total cost of habitat in the landscape
M	Total location benefit in the landscape
$\bar{\mu}$	Average location benefit of a habitat patch
η	Temporal correlation between patch states over the entire landscape

landscape structure defined by $\mathbf{x}$ and $\mathbf{r}$. We assume it can be written as the sum of local benefits² $v_i(\mathbf{x})$:

$$V(\mathbf{x},\mathbf{r})=\sum_{i=1}^N x_i v_i(\mathbf{x},\mathbf{r}) \quad (1)$$

The local benefit that is realised if patch i is turned into and/or maintained as habitat ($x_i=1$) then can be broken down into

$$v_i(\mathbf{x},\mathbf{r})=\varepsilon+\mu_i(\mathbf{x},\mathbf{r}) \quad (2)$$

where ε is the “idiosyncratic benefit” of a habitat, i.e. the habitat’s value in the absence of other habitats, independent of the landscape structure $(\mathbf{x},\mathbf{r})$. The “location benefit” μ_i in contrast depends (only) on the presence of other habitats and thus on the landscape structure $(\mathbf{x},\mathbf{r})$.

Being interested in species survival, we consider that individuals of the species can disperse more easily between habitats if these habitats are closely together. This generally improves the viability of species inhabiting the habitat network (e.g., [Hanski, 1999](#)). Edge effects (e.g., [Murcia, 1995](#)) are smaller when habitats are adjacent to each other. These arguments strongly motivate the assumption for our model that the location benefit of a habitat i increases with decreasing distance to other habitats:

$$\frac{d\mu_i(\mathbf{x},\mathbf{r})}{d|\mathbf{r}_j-\mathbf{r}_i|}<0 \text{ for all } j\in J=\{j=,\dots,N;j\neq i|x_j=1\} \quad (3)$$

In the numerical analysis of Section 3.2 below we will consider a specification of Eq. (3) that is widely used in the

analysis of complex systems. For this we will assume that the N patches are located on a regular square grid and that

$$\mu_i(\mathbf{x},\mathbf{r})=w\sum_{j\in M_i}x_j \quad (4)$$

where M_i is the so-called Moore neighbourhood of patch i (e.g., [Codd, 1968](#)) which contains the eight adjacent patches. The interaction parameter w determines the importance of habitats in the Moore neighbourhood for the local benefit v_i . Eq. (4) represents an example of Eq. (3) where the location benefit is large for very small distances and drops to zero for larger distances.

Regarding the initial allocation of development rights we assume that the regulator sets a target value Y for the conservation benefit $V(\mathbf{x},\mathbf{r})$ of the whole landscape and requires each land owner to contribute an (average) target value $y=Y/N$. The owner of patch i can now decide to create and/or maintain the patch as habitat ($x_i=1$) and earn a certificate of value $z_i=v_i-y$ which may be offered on the market at a price p (measured in monetary units per unit of conservation benefit). To simplify the analysis we assume that habitats can be created instantaneously (cf. Discussion). Alternatively, the owner may not wish to have a habitat on the patch ($x_i=0$). To fulfil the rules of the scheme in this case, the owner has to buy a certificate of value y at price p on the market. Given the cost of selecting patch i as habitat, c_i , the choice between these two options is made with the aim of maximising the profit

$$\pi_i(x_i)=-c_i x_i+p[v_i(\mathbf{x},\mathbf{r})x_i-y] \quad (5)$$

Whether $x_i=1$ or 0 maximises π_i depends on the market price of certificates, p :

$$x_i(p)=\begin{cases} 1 & p>c_i/v_i \\ 0 & \text{otherwise} \end{cases} \quad (6)$$

The value of the certificate bought or sold by the owner of patch i is

$$z_i=x_i v_i(\mathbf{x},\mathbf{r})-y \quad (7)$$

where a positive (negative) value represents a situation where the owner is a seller (buyer). The equilibrium market price p^* is given by an equality of supply and demand of certificates:

$$\sum_{i=1}^N z_i=\sum_{i=1}^N (x_i(p^*)v_i(\mathbf{x},\mathbf{r})-y)=0, \quad (8)$$

which automatically leads to the fulfilment of the regulator’s objective:

$$V(\mathbf{x},\mathbf{r})=\sum_{i=1}^N x_i(p^*)v_i(\mathbf{x},\mathbf{r})=\sum_{i=1}^N y=Y \quad (9)$$

We now put this model into a dynamic setting by assuming heterogeneous economic development within the region. This leads to spatially heterogeneous variations of the opportunity costs in terms of foregone economic development, c_i . To model the temporal dynamics of c_i in the simplest way, we consider discrete time periods and assume that in each time period the

² Note that this assumption does not imply any assumption of linearity. The non-linear function $V=\sum_i v_i$, e.g., can be transformed into $V'=\ln(V)=\sum_i \ln(v_i)$ and V' considered instead of V . Also, despite its formulation as a sum over all patches, V is not additive, since v_i is a function of the states of the other patches $j\neq i$.

costs c_i are sampled randomly and independently from a uniform distribution with mean 1 and width 2σ :

$$f(c) = \begin{cases} (2\sigma)^{-1} & |c-1| \leq \sigma \\ 0 & \text{otherwise} \end{cases} \quad (10)$$

Within the scope of the model analysis, the assumption of a constant mean does not impose a loss of generality and so we can set it to 1 and consider the costs c_i as dimensionless quantities. Finally, we introduce three aggregated variables that will be of interest: the total number of habitat patches,

$$A = \sum_{i=1}^N x_i, \quad (11)$$

the total cost over all patches

$$C = \sum_{i=1}^N x_i c_i \quad (12)$$

(which due to Eqs. (5) and (8) is equal to minus the sum over all profits π_i), and the total location benefit

$$M = \sum_{i=1}^N x_i \mu_i(\mathbf{x}, \mathbf{r}) \quad (13)$$

Eqs. (11) and (13) allow determining the average location benefit of a habitat patch,

$$\bar{\mu} = \frac{M}{A} \quad (14)$$

which is a measure of spatial agglomeration of habitat: for a given functional form of μ_i , a large (small) value indicates a high (small) level of agglomeration. For the example of Eq. (4), it equals w times the expected number of habitats in the Moore neighbourhood around a habitat. This allows writing the ecological target Y as

$$Y = V = \sum_{i=1}^N v_i = \varepsilon \sum_{i=1}^N x_i + \sum_{i=1}^N x_i \mu_i(\mathbf{x}, \mathbf{r}) = \varepsilon A + M = (\varepsilon + \bar{\mu})A \quad (15)$$

Eq. (15) shows that for fixed conservation benefit Y there is a unique, inverse relationship between location benefit $\bar{\mu}$ and habitat area A .

3. Model analysis

In this section we present some analytical (Section 3.1) and numerical (Section 3.2) results of the model. Section 3.1 focuses on the spatial pattern of habitats and identifies two important types of model behaviour. Section 3.2 confirms the results of Section 3.1 and adds insights into the dynamics of the habitat arrangement in the landscape.

3.1. Analytical investigations

Some of the model dynamics can be deduced analytically if the arrangement of the patches is regular (e.g., if the patches are arranged on a square lattice), or – in the case of an irregular,

amorphous patch arrangement – if the spatial range of the location benefit is large enough that spatial irregularities can be ignored. Considering such a landscape, if all patches in the northern half (for instance) of the landscape were habitat ($x_i=1$, all $i=1\dots N$) the location benefits of the patches in this “habitat cluster”, $\mu_i(\mathbf{x}, \mathbf{r})$, would be approximately identical and given by $\mu_i(\mathbf{x}, \mathbf{r})=m$.³ Since the habitat patches in the habitat cluster are packed as densely as possible, m is the maximum possible location benefit that a patch can attain. In the case of Eq. (4), for instance, the location benefit is maximised if all eight patches in the Moore neighbourhood are habitat: $m=\mu_i(\mathbf{x}, \mathbf{r})=8w$.

Having these reflections in mind, consider the special case of zero variation in the costs: $\sigma=0$, i.e. $c_i=1$, for all i . Here the total cost becomes (Eqs. (11) and (12))

$$C^{(0)} \equiv C(\sigma=0) = A = \sum_{i=1}^N x_i \quad (16)$$

and with Eq. (15)

$$C^{(0)} = \frac{Y}{(\varepsilon + \bar{\mu})} \quad (17)$$

As the land owners attempt to maximise their profits, they attempt to minimise C , which is achieved by maximising the level of spatial agglomeration $\bar{\mu}$ (Y and ε are exogenous). Spatial agglomeration is maximised when all patches are arranged in a single large cluster. If the patch number N (and by this: M) is large enough, the cluster boundary (footnote 3) can be ignored and only two types of patches exist in the landscape:

- (1) Habitat patches ($x_i=1$) that belong to a habitat cluster and therefore have location benefit $\mu_i(\mathbf{x}, \mathbf{r})=m$.
- (2) Non-habitat patches ($x_i=0$) that belong to a cluster that contains only non-habitat, and therefore have location benefit $\mu_i(\mathbf{x}, \mathbf{r})=0$.

With this Eq. (13) simplifies to

$$M^{(0)} \equiv M(\sigma=0) = m \sum_{i=1}^N x_i \quad (18)$$

and the average location benefit (Eq. (13)) takes its maximum possible value:

$$\bar{\mu}^{(0)} \equiv \bar{\mu}(\sigma=0) = m \quad (19)$$

confirming the above reasoning and indicating that all habitats (except for those negligibly few habitats on the cluster boundary) are completely surrounded by habitat. Now gradually increase σ . As long as the clusters remain stable and are sufficiently large ($N, M \gg 1$), we can assume that the probability of a patch i having cost c_i is relatively independent of whether the patch contains habitat ($x_i=1$) or not. The distribution of the c_i , in particular the mean cost, then is the same in habitat and

³ Next to the above-mentioned small-scale spatial heterogeneities in the patch arrangement, deviations from m can also arise, because some habitats are located on the boundary of the habitat cluster and have fewer neighbours. If the habitat cluster is large enough, however, the number of these boundary patches is so small compared to the total number of habitat patches in the cluster that their deviation from m can be ignored.

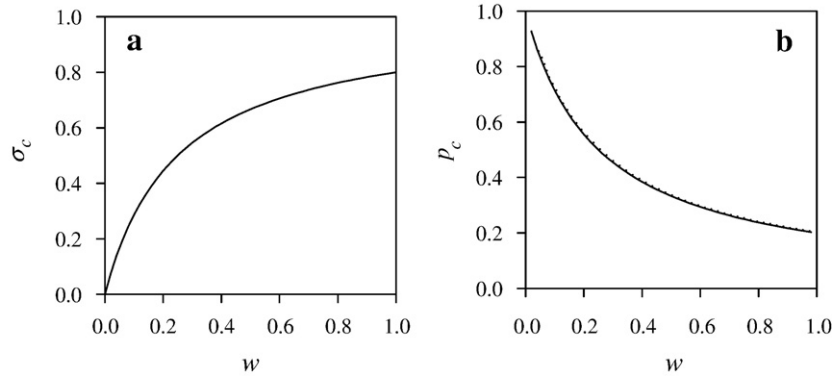


Fig. 1 – Critical cost variation σ_c (Eq. (20); panel a) and critical price $p_c = p(\sigma_c)$ (Eq. (21); panel b) as functions of the interaction parameter $w = m/8$ (cf. Eq. (3)). Dotted line in panel b: simulation results (Section 3.2).

non-habitat clusters and equal to the mean cost ($=1$) in the entire landscape.

The habitat cluster which contains certificate suppliers becomes unstable as soon as suppliers switch to become buyers. As μ is identical for all suppliers, the first suppliers to switch are those with the highest cost (Eqs. (5) and (6)), i.e. those that have cost $c_i = 1 + \sigma$. The certificate price p where these land owners are indifferent between supplying and buying is given by $p_s = (1 + \sigma)/(\varepsilon + m)$ (Eq. (6)). Analogously, the non-habitat cluster containing buyers becomes unstable if buyers switch to become suppliers. The first buyers to switch are those with minimal costs ($c_i = 1 - \sigma$) which are indifferent between buying and supplying if the price is $p_b = (1 - \sigma)\varepsilon$. Equating $p_s(\sigma) = p_b(\sigma)$ delivers a critical cost level (Fig. 1a)

$$\sigma_c = \frac{m}{2\varepsilon + m}, \quad (20)$$

which has the following meaning: For $\sigma < \sigma_c$ we find $p_b(\sigma) - p_s(\sigma) > 0$ and there is a finite range of market prices $p_s < p^* < p_b$ where the equilibrium of demand and supply leads to stable clusters and where total cost and total location benefit are given by Eqs. (17) and (18). At the critical point $\sigma = \sigma_c$ the feasible interval $p_s < p^* < p_b$ contracts to a single unique market price (Fig. 1b)

$$p_c = \frac{2\varepsilon}{2\varepsilon + m}. \quad (21)$$

For $\sigma > \sigma_c$ some buyers and sellers switch their behaviour, meaning that some habitat patches in the habitat cluster are developed and some non-habitat patches in the non-habitat cluster are transformed into habitat. As a consequence, the formerly clear boundaries between the clusters start to dissolve.

It is difficult to estimate at what level of cost variation the cluster will have dissolved completely. “Completely dissolved” means that the locations of the habitats are entirely determined by the costs, so that only the least expensive patches are habitat (under the constraint, Eq. (9)). Since the costs are uncorrelated, those habitats are allocated completely randomly and the average number of habitats around a (habitat) patch equals the proportion of habitat patches in the landscape, denoted as $A^{(1)}/N$ (the superscript (1) indicates total disorder). The average location benefit (Eqs. (4) and (14)) then

is given by $A^{(1)}/N$ multiplied by the maximum location benefit ($m = 8w$, obtained if all neighbour patches were habitat):

$$\bar{\mu}^{(1)} = \frac{mA^{(1)}}{N}. \quad (22)$$

Inserting this into Eq. (15), $Y = (\varepsilon + \bar{\mu}^{(1)})A^{(1)}$, and solving for $A^{(1)}$ delivers

$$A^{(1)} \equiv A(\sigma > \sigma_c) = \frac{N\varepsilon}{2m} \left\{ \left(1 + \frac{4mY}{\varepsilon^2 N} \right)^{1/2} - 1 \right\}, \quad (23)$$

and with Eq. (22)

$$\bar{\mu}^{(1)} \equiv \bar{\mu}(\sigma > \sigma_c) = \frac{\varepsilon}{2} \left\{ \left(1 + \frac{4mY}{\varepsilon^2 N} \right)^{1/2} - 1 \right\} \quad (24)$$

To summarise, for $\sigma < \sigma_c$ the ecological-economic system is in an “ordered phase”⁴ with stable clusters and total cost, habitat area and location benefit given by Eqs. (17) and (19). For larger σ we observe a disordered phase. The critical cost variation σ_c increases with the maximum location benefit m (Fig. 1a). For $m \ll \varepsilon$ we have $\sigma_c \approx m/\varepsilon$; for larger m , σ_c asymptotically approaches a value of 1. For $m \ll \varepsilon$ the critical price is $p_c \approx 1$ (Fig. 1b); for larger m it decreases with increasing m and asymptotically approaches a value of 0.

3.2. Numerical investigations

As the analytical investigation of the disordered phase, $\sigma > \sigma_c$, is very demanding and would be beyond the scope of the present paper, we employ numerical simulation on the basis of a

⁴ This behaviour is similar to that of various physical systems that undergo a so-called phase transition when the temperature crosses a critical level (e.g., Landau and Lifshitz 1969). Consider, e.g., a ferromagnet. If the temperature is below a critical level, so-called clusters form in which all spins (“elementary magnets”) point in the same direction. One speaks of an ordered phase. If the temperature is increased beyond the critical level, the high thermal energy destroys the magnetic order, the clusters disappear and the directions of the spins become random. One speaks of a disordered phase.

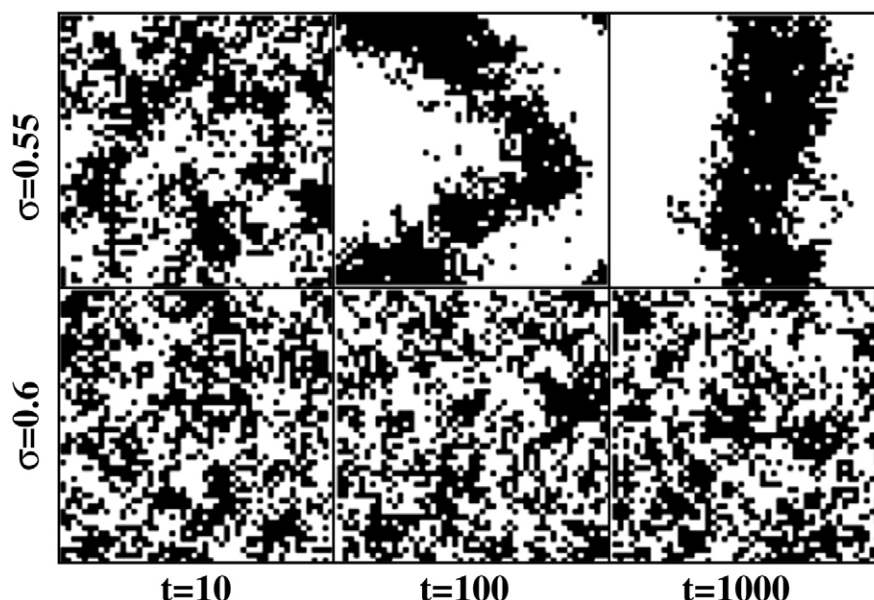


Fig. 2 – Pattern of habitat (black) and non-habitat (white) areas after 10, 100, and 1000 simulation periods for $\sigma < \sigma_c = 0.58$ and for $\sigma > \sigma_c$. Other parameters: $w = 0.36$ and $Y = (\varepsilon + 8w)/2$ (the latter meaning that the target Y is fulfilled if each patch has half its maximum value, given by Eq. (2) with $\max(\mu_i) = m = 8w$).

specific location benefit function. We choose the Moore neighbourhood function introduced in Eq. (4) and assume that the patches are located on a regular square grid with cyclical boundaries. The dimension of the grid is 50×50 unless stated otherwise. The maximum location benefit here is $m = 8w$. For each patch we draw the costs c_i from a random distribution according to Eq. (10). The initial distribution of habitat x in the landscape is chosen randomly; it plays no role for the long-term behaviour of the model as long as there is at least one patch with $x_i = 0$ and one patch with $x_i = 1$. From the x_i we determine the local benefits, v_i which together with the c_i form the inputs for the habitat trade. To determine the equilibrium permit price p^* we scan the range of economically sensible prices in small steps from $1 - \sigma$ to $1 + \sigma$ until a unique p^* is found that satisfies⁵ Eq. (8). Knowing for each patch whether it remains habitat/non-habitat or switches its state, we update the x_i and enter the next time period. In this and all following time periods we proceed as in the initial period, i.e. we start by randomly drawing the costs c_i and end with the determination of the market equilibrium.

We are interested in the long-term behaviour of the model where price p^* , total cost C and total location benefit M are stationary. To determine the stationary values we simulate for 1000 periods to reach the stationary state and then for another 200 periods to calculate a temporal average of the variables of interest which are the equilibrium price p , the total habitat area A and the average location benefit $\bar{\mu}$.

Fig. 2 shows the development of the habitat pattern for two different levels of cost variation σ . For $\sigma = 0.55 < \sigma_c = 0.58$ an ordered phase with separated habitat and non-habitat clus-

ters is reached relatively quickly whereas for $\sigma = 0.6 > \sigma_c$ no order can be observed, even after long simulation time.

Disorder means a reduced level of spatial habitat agglomeration, measured by a reduced average location benefit $\bar{\mu}$ (Eq. (14)). Fig. 3a shows that just above the critical level of cost variation σ_c the average location benefit sharply drops from close to $m = 8w$ (Eq. (19)) to a smaller value. The larger the total number, N , of patches the steeper is the drop. Since a smaller expected location benefit requires more habitat area to fulfil the conservation target Y (Eq. (15)), the habitat area A jumps from just above A_0 to a higher value (Fig. 3b). Fig. 4 confirms for all possible combinations of model parameters w and σ that the landscape is either in an ordered (with high spatial aggregation and small total habitat area) or a disordered phase (with low spatial aggregation and high total habitat area) which are clearly separated from each other.

Analogous results can be obtained for other values of conservation target Y . The numerical results of Fig. 4 very well agree with the theoretical calculations (Fig. 1a); the agreement between analytical calculations and numerical simulations is further confirmed by the results for the “critical” price p_c (Fig. 1b).

So far we have considered the spatial aspects of the habitat dynamics. To complete the analysis we turn to the temporal dimension of the habitat dynamics. To quantify this we consider the “turnover rate” of habitats, i.e. the rate by which a habitat patch turns into a non-habitat patch or vice versa. We measure habitat turnover by the correlation coefficient

$$\eta(t) = \frac{4}{N} \sum_{i=1}^N [x_i(t) - 0.5] \times [x_i(t-1) - 0.5] \quad (25)$$

If there is no turnover in patch i such that x_i remains constant between two consecutive periods t and $t+1$ then patch i contributes an amount $1/N$ to the quantity η . If there is turnover, such that x_i changes from 0 to 1 or from 1 to 0 then patch i

⁵ The procedure is uncritical, because the l.h.s. of Eq. (8) is negative for the lowest sensible price, $p = 1 - \sigma$ (where $x_i = 0$ for all i), positive for the highest sensible price, $p = 1 + \sigma$ (where $x_i = 1$ for all i), and monotonically increases with increasing p in between, so that a unique solution of Eq. (8) exists.

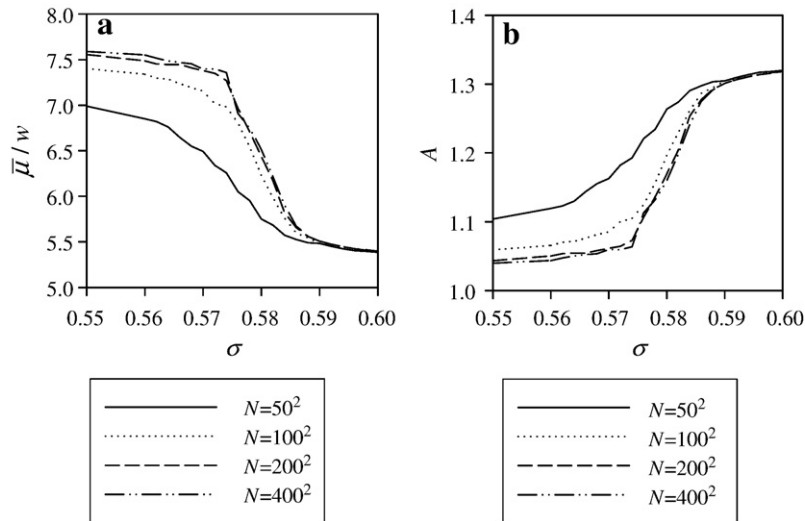


Fig. 3 – Average location benefit $\bar{\mu}$ scaled in units of w (measuring the expected number of habitats in the Moore neighbourhood of a habitat; panel a) and total habitat area A (scaled in units of A_0 ; panel b) as functions of the cost variation σ for various numbers of patches: $N=50^2$, 100^2 , 200^2 and 400^2 . Other parameters: $w=0.36$ and $Y=(\epsilon+8w)/2$ (cf. Fig. 2).

contributes an amount of $-1/N$ to η . The correlation coefficient therefore ranges from -1 where there is turnover in all N patch to $+1$ where there is no turnover at all. An alternative interpretation is: for $\eta=1$ a given patch switches its state x_i with probability 0, for $\eta=0$ it switches with probability 0.5 and for $\eta=-1$ it switches with probability 1.

Fig. 5 shows the correlation coefficient as a function of w and σ . In the ordered phase (cf. Fig. 3) habitat turnover is very small (η close to 1), i.e. the habitat structure is not only clustered in space but also stable in time. In the disordered phase, habitat turnover is almost exclusively triggered by the random fluctuations of the costs c_i and therefore the correlation of x_i between subsequent periods is close to $\eta=0$ (i.e. the probability of switching states is 0.5).

4. Discussion

We modelled a market for development rights in a landscape where land patches can either be used as habitat or for eco-

nomical purposes. Land owners trade rights to destroy habitat and use it for economic development. The costs (in terms of foregone economic development) of using a patch as habitat differ among patches and vary over time. Space plays an important role in that the ecological value of a habitat patch depends on its location; in particular, to what extent other habitat patches exist in its vicinity. Based on ecological theory (e.g., Hanski, 1999; Vos et al., 2001; Ovaskainen and Hanski, 2003), we assumed that the ecological value of a habitat patch increases when more habitat patches are found in its neighbourhood. A similar assumption has been made by Parkhurst et al. (2002) who designed a payment scheme for conservation measures which contains a bonus payment for habitat adjacency. In our model, this spatial interaction leads to self-organised dynamics of habitat creation and destruction in the considered landscape.

Being interested in the stationary behaviour of the model, we found two possible phases the dynamics can be in: an ordered or a disordered phase. In the ordered phase the patches containing habitat are clustered in space, while in the disordered phase

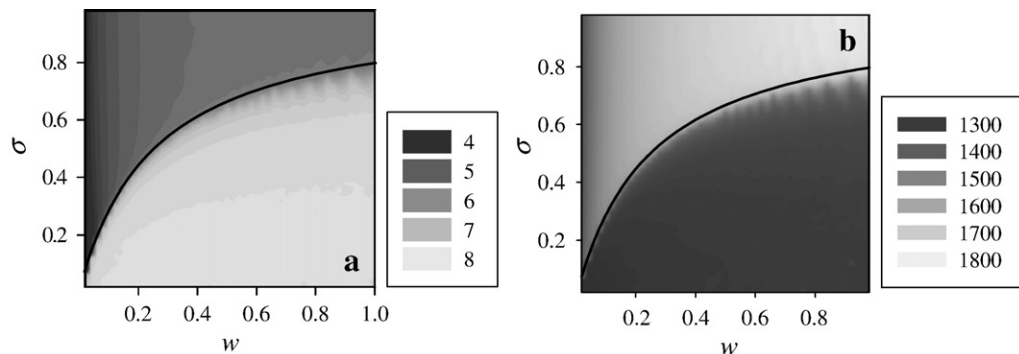


Fig. 4 – Average location benefit $\bar{\mu}$ scaled in units of w (measuring the expected number of habitats in the neighbourhood of a habitat) (panel a) and total habitat area A (panel b) as functions of w and σ . The conservation target is set at $Y=(\epsilon+8w)/2$ (cf. Fig. 2). The concave lines mark the set of critical points $(w, \sigma_c(w))$ after Eq. (20) which separate the ordered and disordered phases. The number of patches is $N=2500$.

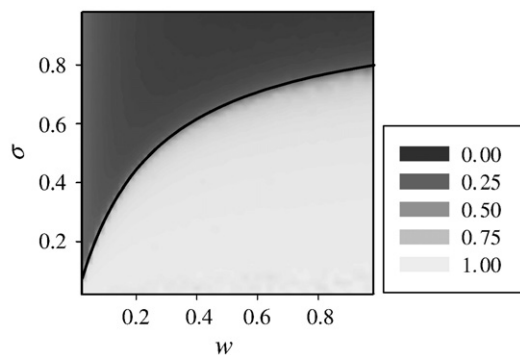


Fig. 5 – Correlation coefficient η of states x_i between two subsequent time periods as a function of w and σ . Similar to Fig. 2 the line separating the ordered phase with high correlation and the disordered phase with low correlation is given by Eq. (20). The conservation target is $Y = (\epsilon + 8w)/2$ (cf. Fig. 2). The number of patches is $N = 2500$.

they are scattered. The ordered phase is obtained if the variation in the costs lies below a critical value that is determined by the spatial interaction between the ecological values of the habitats. If the value of a habitat patch very strongly depends on the presence of other habitat patches in its neighbourhood, the ordered phase is maintained even at high cost variation.

If the variation in the costs exceeds the critical value, the system switches into a disordered phase. In a way, the dynamics can be seen as a struggle between two forces: the interaction between the ecological values of the habitat patches is the ordering force that leads to a clustering of habitat patches; the random variation in the costs tends to tear habitat clusters apart and lead into disorder. The outcome of the dynamics is determined by the prevailing force.

The analysis further showed a correlation between spatial order and stability of habitat, or equivalently, between spatial disorder and high level of habitat turnover. This is plausible, because inside a habitat cluster the loss of conservation benefit associated with the development of a habitat is large compared to the economic gain and so there is little risk that the habitat is developed.

The analysis contains a number of assumptions which are worth discussing. The first is that the conservation benefit of the landscape structure can be written as the sum of local benefits over all habitat patches (Eq. (1)). Each local benefit is composed of an idiosyncratic component and a component that depends on the spatial habitat configuration around the habitat patch (Eq. (2)). These assumptions may impose a loss of generality, but Eqs. (1) and (2) appear general enough to capture the essential factors that determine the suitability of a habitat network for species survival.

Another important assumption is that the spatial range of interaction between the ecological values of habitat patches is very short. To consider species with better dispersal abilities the range of interaction could be increased, so that not only adjacent but also habitat patches further apart contribute to the value of a habitat. This would mean that more surrounding patches contribute to the value of the habitat patch implying that the relative contribution of each surrounding habitat patch is reduced. The chance of non-habitat patches appearing in a habitat

cluster would increase, destabilising the cluster. On the other hand, at a longer interaction range a habitat patch contributes to the values of more patches, favouring more clustering. It is a matter of future research to analyse which effect prevails.

We further made the assumption that habitats can be successfully restored within a short time period. However, in reality habitat restoration may take time. This implies that a time lag exists between the decision to restore a habitat and the selling of the created permit which prevents land owners from immediately reacting to price changes. The land owner has to decide on the land-use type without perfectly knowing future prices which may give rise to complex dynamics in the market like the so-called pork cycle (see, e.g., Rosen et al., 1994). Next to the presence of time lags, the success of habitat restoration is uncertain (Moilanen et al., in press) with the degree of uncertainty depending on the habitat type. In addition, habitat turnover means that individuals are chased away or killed where habitat is destroyed. Even if at the same time another habitat is created this has to be colonised by individuals from other habitats, which requires sufficient time and dispersal ability of the species. In any case, habitat turnover leads to a disruption of species dynamics and increases the extinction risk of most species (e.g., Gyllenberg and Hanski, 1997; Johst et al., 2002). One possible way to counteract this increase in extinction risk may be a modified trading rule which demands that for the destruction of a conservation area an area with higher ecological value has to be restored and not with equal ecological value as assumed in this paper. Analysing such trading rules and other mechanisms to counteract the negative aspects of habitat turnover are important future research topics.

In our analysis we randomly sampled land price changes and assumed that they are independent of the current price level and of the land-use type of the surrounding areas. This is an assumption that needs to be modified in future studies. For instance, economic development is often spatially concentrated due to positive externalities (e.g. Henderson, 2003). This means that land prices close to an area with economic development are more likely to increase than land prices in other areas. Such spatial land price correlations may be a driver of habitat clustering which would appear on the spatial scale given by the range of the land price correlations. If this scale is small compared to the landscape scale, however, clustering on the landscape scale may be hindered; instead the landscape would consist of multiple small habitat clusters located in the low-cost regions.

Further research may also consider feedback loops that arise when land prices not only affect land-use change but also the opposite relationship exists. For instance, Armsworth et al. (2006) pointed out that reserves can increase the overall attractiveness of an area due to conservation amenities which may also lead to an increase in land prices. Such a feedback would certainly hamper the formation of habitat clusters.

Altogether, the spatial and temporal pattern of habitats is an outcome of a complex interaction of various factors and processes and under modified assumptions the transition between ordered and disordered configurations may have a different shape and occur at different parameter values than predicted in our model analysis. However, the magnitudes of location benefit and cost variation considered as key factors in our study (represented by w and σ in Fig. 4) are of general

importance. A large (small) ratio of the two will favour a more (less) ordered habitat structure in the landscape.

A key assumption of this paper is that the value of a habitat patch depends on the number of habitat patches within some neighbourhood. This is a useful assumption for the purpose of this paper because it captures the effects of space-dependency on land allocation in the context of tradable development rights. However, when designing rules for tradable development schemes, the schemes' effectiveness might be improved by employing ecologically more realistic benefit functions that address the above mentioned issue of habitat turnover and more complex spatial interactions. Next to sophisticated analytical formulas (e.g., Frank and Wissel, 2002), simulation models (e.g. Grimm and Railsback, 2005; Johst et al., 2006) may be used to measure conservation benefit. Such assessments, however, mean more complicated trading rules and, hence, are likely to incur higher transaction costs. A challenge of future research, therefore, is the design of benefit functions that are simple enough to be implemented and still provide a sufficiently good approximation of the true conservation benefit of a habitat patch.

The implementation of a scheme for tradable development rights where the value of a habitat patch depends on the land-use type of neighbouring areas may be difficult to implement in practice. The main reason is that it requires a re-evaluation once the land-use of adjacent areas changes. Re-evaluations are costly and they may be perceived as unfair, because they are not a result of the actions of the land owners themselves but of other land owners. They may also be unpopular with conservation groups, because if an area is partly economically developed those land owners who still keep their areas as habitats not only do not profit from transferring their land but additionally get 'punished' by having to acquire additional development rights. Furthermore, in some countries legal reasons of protection of confidence may prevent such a scheme. A scheme that takes these concerns into account, and where the conservation benefit of a habitat depends, e.g., only on its size, however, is naturally less cost-effective. Further research may address the extent of the loss in cost-effectiveness under various benefits functions.

Implementing tradable permits for biodiversity conservation in practice faces a number of challenges that cannot be all discussed here. If, in order to overcome these challenges, trading rules get too complex transaction costs for market participants may become too high and the trading system may not work (cf. Mansfield, 2004). Tradable permits are certainly not a panacea for biodiversity conservation but they may improve current policies under specific ecological and socioeconomic circumstances. For the benefit of biodiversity conservation a better understanding is required of what these circumstances are.

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Analysis

Conserving biodiversity with tradable permits under changing conservation costs and habitat restoration time lags

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ABSTRACT

Tradable permits are a common environmental policy instrument that has recently been applied also to the conservation of biodiversity. Biodiversity conservation differs in many respects to the classical applications of tradable permits like emissions control. One particularity is that, even if the permit system maintains a constant total amount of species habitat, habitat turnover (the destruction of a habitat and restoration elsewhere) affects the ecosystem. Another particularity is that the restoration of habitats often takes much time, leading to time lags between the initiation of restoration activities and the time when restored habitat is available for trading. We use an agent-based model of a tradable permit market to study the influence of heterogeneous and dynamic conservation costs and habitat restoration time lags on key variables of the market, such as the costs incurred to the market participants and the amount of habitat turnover. Our results show that there may be trade-offs between these key variables. We also find that restoration time lags can lead to fluctuations in permit prices that reduce the efficiency of the permit market. We conclude that temporal lags deserve a careful analysis when implementing tradable permit systems for the preservation of natural habitats and biodiversity.

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1. Introduction

In the last decades, tradable permits have gained increasing popularity as a flexible and cost-effective policy instrument for limiting the use of natural resources such as fish or water, and for limiting the emission of pollutants like SO₂ and CO₂ (Tietenberg, 2006). A more recent development, often referred to as habitat banking, is to use tradable permit systems to protect rare habitats and biodiversity (see *eftec*, IEEP et al. (2010) and Wissel and Wätzold (2010) for a detailed discussion of these schemes and their current use). Under these systems, a degradation or destruction of a natural habitat requires possession of a permit which can only be acquired by restoring a habitat of equal ecological value elsewhere or by buying a permit on the market.

Controlling the amount of natural habitat in a region by means of a tradable permit system raises a number of challenges as opposed, for example, to the control of carbon emissions. For climate protection, it is of minor importance at which locations greenhouse gas emissions are reduced or whether reduction efforts are constant in time or not, as long as total emissions are reduced on an intermediate time scale. The persistence of biodiversity, in contrast, is highly sensitive both to the spatial and temporal allocation of natural habitat (Hanski, 1999a;

Roy et al., 2004; With and King, 2004; Wilson et al., 2007). A number of studies has therefore addressed the spatial allocation of conservation measures with tradable land-use permits, such as (Drechsler and Wätzold, 2009; Hartig and Drechsler, 2009).

For the temporal allocation, however, much less research has been done. In the present paper we focus on two temporal issues. The first is the presence of long time lags. The restoration of many relevant habitats takes several years (e.g., to create an oligotrophic meadow on formerly intensively used agricultural land) up to decades or even centuries (e.g., to create an old-growth forest). If the production of a market good involves a time lag, market participants must decide on their production level in advance without knowing at what price they will be able to sell. The relevance of time lags in markets has already been emphasized about 80 years ago by Hanau (1928) and Kaldor (1934). For the example of pork production, the authors found that, under certain conditions, markets with time lags may exhibit cyclic fluctuations of prices and supply. The reason is that at a temporary oversupply of a good prices fall and production levels drop. This leads to an undersupply of the good in the near future. The rising prices that are caused by this undersupply trigger high production levels which lead to an oversupply of the good in the near future, and so on. These cycles are not only undesirable from the consumers' point of view but may also be inefficient in the sense that the same total amount of the good could be produced at lower costs if productions levels were held constant in time.

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The second problem is more specific to market-based conservation instruments: while tradable permits lead to more flexibility and to cost savings, the associated market activity has the potential to harm species. The reason is that each trade implies the destruction of a habitat patch and its local species populations, while created habitat patches have to become occupied by local populations before they can contribute to species survival. Even if the total number of habitat patches remains constant, and even if species are able to disperse between habitats (e.g., so-called metapopulations: Hanski (1999b)), this spatial reallocation of habitats, called habitat turnover, is often detrimental for the species (Hanski, 1999a; Keymer et al., 2000). In (Hartig and Drechsler, 2009), we showed that turnover can affect species survival as strongly as does the spatial allocation of habitat (see also Schrott et al., 2005) and is a decisive factor when considering tradable permits for biodiversity protection. It is therefore important to understand how much turnover a market will produce and which factors influence and determine the amount of turnover.

Dynamics in permit markets have been studied so far mainly within the context of carbon emissions trading. For instance, Stevens and Rose (2002) as well as Godal and Klaassen (2006) investigate how the absence or presence of constraints on intertemporal trade in the form of permit borrowing and banking affects the cost-effectiveness of the permit market. Hagem and Westskog (2008) analyze how restrictions on intertemporal trade affect the ability of a dominant agent to exploit its market power. The mentioned studies, however, do not consider that changing management actions may take time and be associated with transaction costs (in the sense that the management change per se incurs a cost). Given that the restoration of habitat is often costly and very time consuming, it is of interest to understand how restoration costs and time delays affect the dynamics of a tradable permit scheme for biodiversity conservation.

In this study, we develop a non-spatial agent-based model of a tradable permit scheme to conserve habitat. Important parameters of this scheme are habitat restoration time, restoration costs, and the variation of opportunity costs between sites and in time. Opportunity costs are the forgone profits if a patch is not used for the production of conventional market goods (henceforth termed: “for economic production”) but managed for conservation. We investigate how habitat turnover, the total opportunity cost (the sum of the opportunity costs over all patches) and the total restoration expense (the sum of the restoration costs over all patches) depend on these parameters. In addition, we analyze whether permit schemes for biodiversity may develop cyclic fluctuations, similar to other markets with production time lags. The following Section 2 introduces the model. The results are presented in Section 3 and discussed, together with their practical implications, limitations and questions for future research, in Section 4.

2. Methods

2.1. Model Description

2.1.1. Model Region, Land-use Options and Economic Framework

We assume that the model region consists of $N=1000$ land patches, each of which is owned by one agent and managed in discrete time steps. During each period t , a patch can be either used for economic production, $r_i(t)=0$, or for conservation, $r_i(t)=1$. Conservation management incurs a patch-specific opportunity cost c_i per period. Opportunity costs $c_i(t)$ are modeled as a temporally correlated random walk with mean 1, standard deviation σ and temporal correlation α (Appendix A). A correlation of $\alpha=1$ means perfect temporal correlation so that $c_i(t+1)=c_i(t)$, and a correlation of $\alpha=0$ means that the costs between consecutive periods are uncorrelated. Costs are further assumed to be uncorrelated among different patches.

The ecological state x_i of patch i is represented by a value between 0 and 1, with 1 being a habitat of maximum ecological value. The ecological state of a patch changes according to the type of man-

agement applied. Using the patch for economic production ($r_i=0$) immediately changes the ecological state to $x_i=0$. When managed for conservation, the ecological state is assumed to recover with a speed of $1/K$ per time step, so starting from state $x_i=0$ it takes K periods to reach the habitat state ($x_i=1$; see Fig. 1). Uncertainty in the restoration success (cf. Moilanen et al., 2008) is ignored for simplicity. We assume that agents may have to support restoration actively. In this case, they bear an additional restoration cost of magnitude d per time period during restoration, in addition to the opportunity cost c_i .

If a patch has fully recovered to $x_i=1$, its owner receives a land-use permit. The possession of a permit by agent i is denoted by $z_i=1$; otherwise $z_i=0$. Any agent who destroys a habitat patch requires a permit. Permits are traded among agents on a perfectly-competitive market. Banking of permits for the purpose of speculation ($z_i>1$) is not considered in our model. Agents decide on their market and land-use actions under the objective of maximizing their long-term profit. This long-term profit is assumed to be the difference between the discounted economic benefits and costs realized in each period. The discounting factor is denoted as $q=1/(1+\delta)$, where δ is the discount rate per time period. Agents have information neither about the future development of the permit price nor about their future opportunity costs. Their decisions are taken under the assumption that permit price and opportunity costs remain on their current levels.

The number of patches initially managed for conservation is denoted as Z . Since no land-use permits are allocated initially and the destruction of a habitat requires a new habitat to be restored elsewhere, Z is constant in time. The initial allocation of the Z habitat patches is described in Section 2.2. A summary of the state variables and model parameters is given in Table 1.

2.1.2. Agents's Decisions and Market Interactions

We assume that all agents are fully informed about their current opportunity costs $c_i(t)$ and the current market price for permits. Based on this information, as well as the ecological state $x_i(t-1)$ and the number of owned permits $z_i(t-1)$, agents decide on their land-use r_i and whether to buy a permit, sell a permit, or neither buy nor sell. The three choices buy, sell, and neither buy nor sell are denoted by $b_i=1$, $b_i=-1$ and $b_i=0$, respectively. The following decision rules maximize the expected long-term profit of agent i under the above-described assumptions (details of the derivation of the decision rules can be found in Appendix B):

- (a) If the patch is not habitat ($x_i<1$) the agent can choose between restoration ($r_i=1$) or use of the patch for economic production ($r_i=0$). For the decision, the agent has to weight the discounted benefit of selling the permit at price p after completed restoration against the sum of the discounted restoration costs that accrue from the present period until completed restoration, and the discounted opportunity costs from the present period until infinity (the latter is henceforth termed the

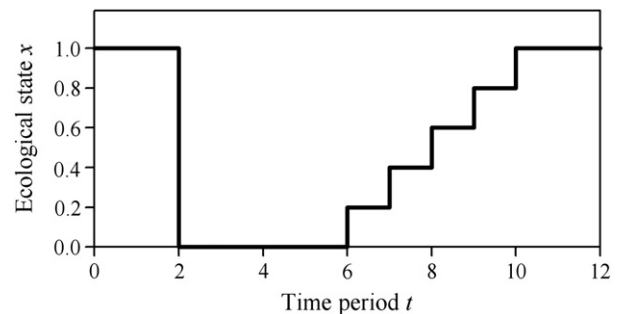


Fig. 1. Schematic illustration of the development of the ecological state of a patch over time. Initially, the patch is habitat and managed for conservation ($x=1$, $r=1$). At time $t=2$, the patch is developed and used for economic production ($r=0$) until $t=5$. At $t=5$ restoration activities start ($r=1$) and the ecological state recovers to the habitat state ($x=1$) which is reached after $K=5$ time periods. During restoration the ecological state increases by $1/K=0.2$ in each time period.

Table 1

State, decision, and aggregated variables as well as model parameters. Note that instantaneous habitat restoration (“zero time periods required for habitat restoration”) is considered in this study, as well, but parameter K has no meaning in that case.

Symbol	Connotation	Range
<i>State variables</i>		
x_i	Ecological state of patch i	$\{0, \dots, 1\}$
z_i	Number of land-use permits associated with patch i	$\{0, 1\}$
$Y_i = (x_i, z_i)$	State of patch i	$\{0, \dots, 1\} \times \{0, 1\}$
c_i	Opportunity cost of patch i	≥ 0
p^*	Permit price in market equilibrium	≥ 0
<i>Decision variables</i>		
b_i	Market action of agent i (sell/none/buy)	$\{-1, 0, 1\}$
r_i	Land-use activity on patch i (economic production or conservation)	$\{0, 1\}$
<i>Aggregated variables</i>		
T	Habitat turnover	≥ 0
C	Total opportunity cost	≥ 0
D	Total habitat restoration expense	≥ 0
$\bar{X}$	Long-term temporal average of variable X	≥ 0
<i>Model parameters and their values and ranges considered in the analysis</i>		
N	Number of patches	1000
Z	Initial number of habitat patches	250
σ	Standard deviation of opportunity costs c_i	$\{0.1, \dots, 0.5\}$
α	Temporal correlation of opportunity costs c_i	0.8
d	Habitat restoration cost	$\{0, \dots, 0.5/(1-q)\}$
q	Discounting factor	0.95
K	Number of time periods required for habitat restoration	$\{1, 2, \dots, 10\}$

(expected) land price of the patch). If the discounted benefits exceed the discounted costs $r_i = 1$ is optimal, otherwise the agent chooses $r_i = 0$ (cf. Eq. (B9b) in Appendix B).

- (b) If the patch is habitat and no permit is held ($x_i = 1$ and $z_i = 0$) the agent can choose between buying a permit and converting the patch to economic production ($b_i = 1$ and $r_i = 0$), or buy no permit and conserve the patch as habitat ($b_i = 0$ and $r_i = 1$). If the current permit price p exceeds the land price of the patch the latter option is chosen; otherwise the former option is chosen (cf. Eqs. (B9c) and (B9d)).
- (c) If the patch has just recovered to habitat and the agent has received a permit ($x_i = z_i = 1$) the agent can choose between selling the permit and conserving the patch as habitat ($b_i = -1$ and $r_i = 1$) or using the permit to convert the patch back to economic production ($b_i = r_i = 0$). If the current permit price p exceeds the land price the former option is chosen; otherwise the latter option is chosen (cf. Eqs. (B9e) and (B9f)).

For the case of instantaneous restoration an additional rule applies: in case (a) the permit can be sold immediately after the decision to restore. Thus, the choice is between restoring and selling on the one side and not restoring on the other (cf. Eqs. (B9a) and (B9b)).

The described decision rules can be regarded as a function $b_i(x_i, z_i, c_i, p)$ that determines for a given permit price p whether agent i is willing to buy a permit on the market ($b_i = 1$), sell a permit ($b_i = -1$) or do nothing ($b_i = 0$) (for simplicity of notation we suppress the time index here). To derive the equilibrium price p^* and the market dynamics from this function, we equate demand and supply and solve the equation

$$\sum_{i=1}^N b_i(x_i, z_i, c_i, p^*) = 0.$$

The solution for p^* is straightforward because $\sum_i b_i(x_i, z_i, c_i, p)$ increases monotonically with increasing p from negative values (obtained for very small p) to positive values (obtained for large p).

By inserting the equilibrium price p^* into the function $b_i(x_i, z_i, c_i, p)$ we calculate for each agent whether he buys or sells or stays passive ($b_i = 1, -1$ or 0) and update the number of owned permits, $z_i(t)$, by adding or subtracting bought respectively sold permits from $z_i(t-1)$. The ecological state x_i is updated from $x_i(t-1)$ to $x_i(t)$ as described in the previous Subsection 2.1.1. A graphical representation of the updating of x_i and z_i can be found in Fig. 2.

2.2. Model Initialization and Analysis

We initialize the model by assigning a random cost c_i to each patch and assuming that the Z least costly patches are managed for conservation. No land-use permits are allocated initially, which may be regarded as “grandfathering” of permits, meaning that those agents who currently use their patch for economic production have the permission to do so in the future, and those whose patches are habitat must maintain their patch in that state (unless they acquire a land-use permit). Because of the restoration time lags, the initial allocation may have a short-term influence on the land use in the model. To avoid any influence of this on the results of our analysis, we run the model for 1000 “burn-in” periods until we generate data. For the considered parameter combinations, this time is sufficient for the market to reach a stationary state that is independent of the initial levels of the c_i and the allocation of the conserved patches. After the burn-in time, the data for the analysis are generated by running the model for another 1000 periods. We use a base parameter combination $\sigma = 0.3$ (medium variation of opportunity costs), $\alpha = 0.8$ (large level of temporal correlation in the opportunity costs), $q = 0.95$ (which corresponds to a discount rate of about five percent per period), $d = 5$ (restoration cost per time period equals 25 percent of the average land price, $1/(1-q)$). The number of patches managed for conservation is $Z = 250$. We record the temporal development of the following aggregated variables during the simulation: the amount of habitat turnover (number of habitat patches destroyed between consecutive periods (T)), the total opportunity cost (C) which sums the opportunity costs (c_i) of all patches under conservation or restoration (i.e., $r_i = 1$), and the total restoration expense (D) that sums the restoration costs (d) of all patches under restoration (i.e., $r_i = 1$ and $x_i < 1$). In addition we calculate the 1000-period temporal average of these variables, denoted by $\bar{T}$, $\bar{C}$ and $\bar{D}$.

From the defined base parameter combination we then vary d between 0 and $0.5/(1-q)$ (half the average land price), and σ

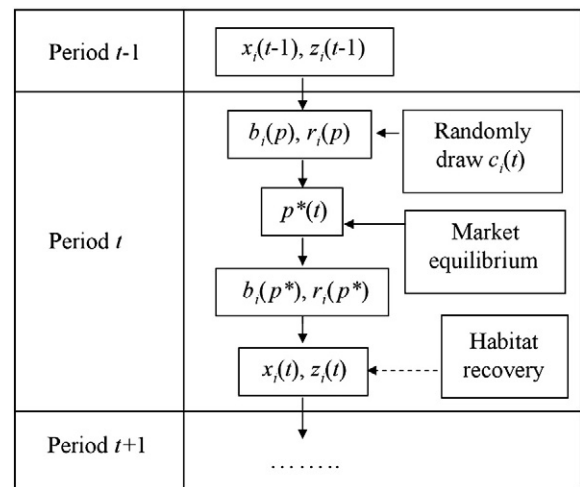


Fig. 2. Schematic representation of model scheduling within one time period. Habitat recovery applies if the patch is managed for conservation ($r_i = 1$) and the patch has not yet fully recovered to habitat ($x_i < 1$). After full recovery of a patch, its owner receives a land-use permit ($z_i = 1$).

between 0.1 and 0.5. Since σ represents the coefficient of variation of the normally distributed opportunity costs, a value of 0.1 (0.5) corresponds to a confidence interval of about [0.8, 1.2] respectively [0, 2]. The described analyses are carried out for instantaneous restoration and for restoration delayed by one time period ($K=1$). We lastly consider cases of $K>1$.

3. Results

3.1. Temporal Evolution of the Aggregated Variables T , C and D

Fig. 3 shows the temporal development of the total opportunity cost C , the total restoration expense D and habitat turnover T for the base parameter combination (other parameter combinations lead to similar trajectories). While in the case of instantaneous restoration (Fig. 3a), T , C and D are fairly constant in time, all three variables fluctuate in the case of delayed restoration (Fig. 3b). Also, the temporal averages of T , C and D are higher for the case of delayed restoration as compared to the case of instantaneous restoration (note that the variables are plotted on a log scale).

3.2. Influence of Opportunity Cost Variation and Restoration Costs on the Market Behavior

To analyze the influence of opportunity cost variation and restoration costs on the market behavior, we focus on the temporal averages of turnover and costs: the average amount of habitat turnover, $\bar{T}$, the average total opportunity cost, $\bar{C}$, and the average total cost which is the sum of average total opportunity cost and average total restoration expense, $\bar{C} + \bar{D}$.

For the case of instantaneous restoration, Fig. 4a shows that average habitat turnover $\bar{T}$ increases with increasing cost variation σ (moving from left to right the color changes from blue/green to green/red). The reason is that at large σ , cost savings from reallocating

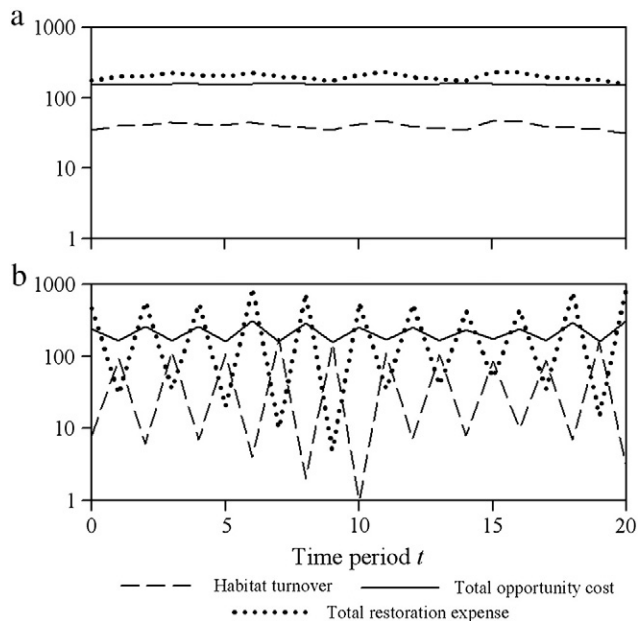


Fig. 3. Habitat turnover (number of habitat patches destroyed between consecutive time periods) (T , dashed line), total opportunity cost (sum of the opportunity costs over all patches) (C , solid line) and total restoration expense (sum of the restoration costs over all patches) (D , dotted line) as functions of time for the case of instantaneous habitat restoration (panel a) and for the case of delayed habitat restoration ($K=1$; panel b). The variables T , C and D are plotted on a logarithmic scale to the base of 10. The model parameters are: $N=1000$, $Z=250$, $\sigma=0.3$, $\alpha=0.8$, $d=0.25/(1-q)$ and $q=0.95$.

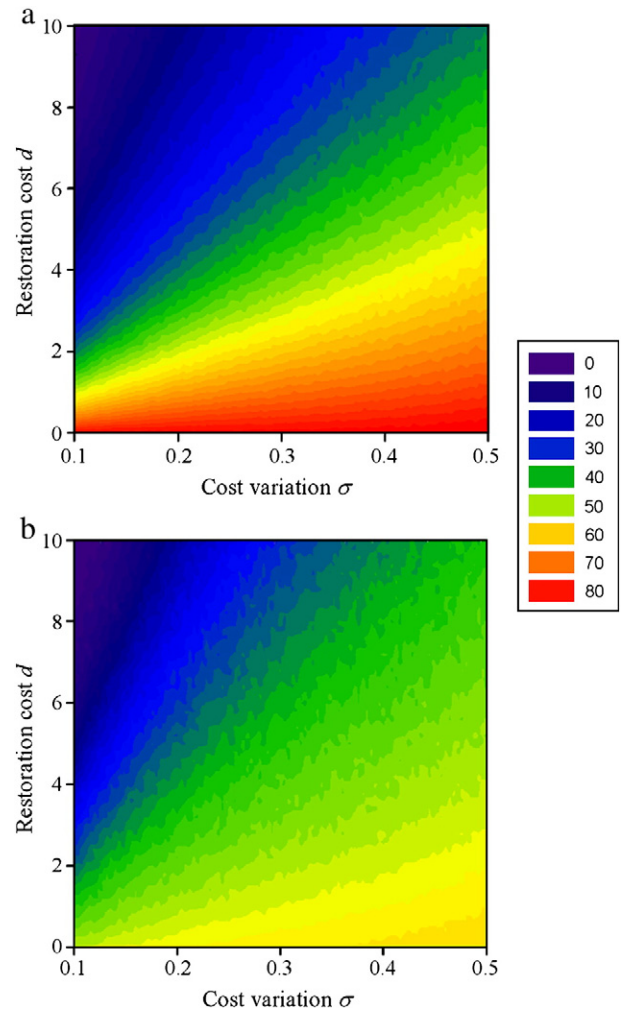


Fig. 4. Average habitat turnover ($\bar{T}$) for instantaneous habitat restoration (panel a) and delayed restoration ($K=1$; panel b) as functions of the opportunity cost variation (σ) and the restoration cost (d). $\bar{T}$ is represented by color scale. Other model parameters are chosen as in Fig. 3.

habitat are large and agents have a strong incentive to trade permits and reallocate habitat. Average habitat turnover further increases with decreasing restoration cost d (moving top to bottom), because at small d the costs associated with the habitat reallocation are small. The same results are obtained for the case where restoration is delayed by one time period (Fig. 4b).

Since large restoration costs imply low habitat turnover (Fig. 4), one would expect that they also imply a high total opportunity cost, because at low habitat turnover it is not possible to allocate conservation activities to the least costly patches. This is indeed observed for instantaneous restoration (Fig. 5a): moving from bottom to top the average total opportunity cost increases. For delayed restoration, however, we observe the opposite: increasing restoration cost d decreases the average total opportunity cost (Fig. 5b) even though it reduces turnover (Fig. 4b). This decrease of the total opportunity cost can be explained by the fluctuations observed Fig. 3. The fluctuations reflect “excess” restoration activities that lead to a periodic oversupply of permits. The additional opportunity costs that arise from these excess restoration activities outweigh the above-mentioned cost savings that are associated with the reallocation of conservation measures. Altogether, in the case of delayed restoration an increase in the restoration cost reduces the total opportunity cost, because it reduces excess restoration.

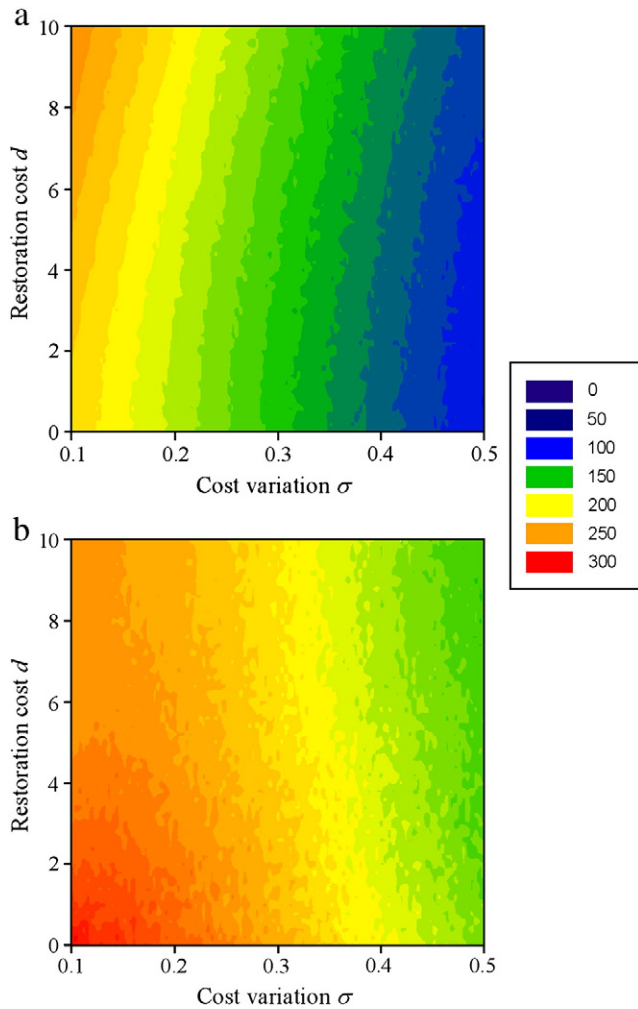


Fig. 5. Average total opportunity cost ($\bar{C}$) for instantaneous habitat restoration (panel a) and delayed restoration ($K=1$; panel b) as functions of the opportunity cost variation (σ) and the restoration cost (d). $\bar{C}$ is represented by color scale. Other model parameters are chosen as in Fig. 3.

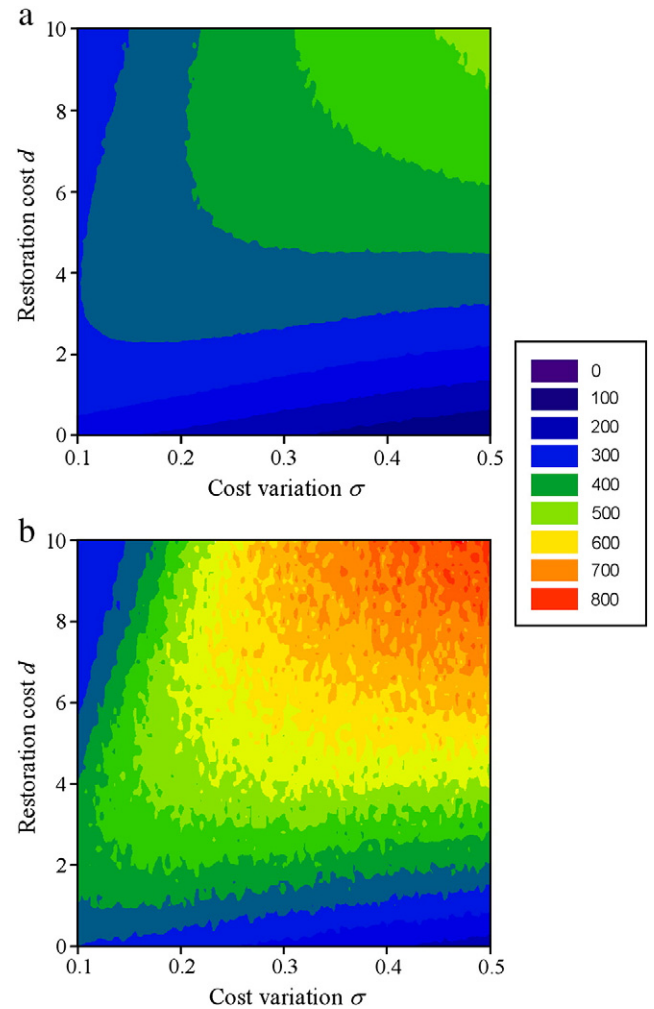


Fig. 6. Average total cost (total opportunity cost plus restoration expense, $\bar{C} + \bar{D}$) for instantaneous habitat restoration (panel a) and delayed restoration ($K=1$; panel b) as functions of the opportunity cost variation (σ) and the restoration cost (d). $\bar{C} + \bar{D}$ is represented by color scale. Other model parameters are chosen as in Fig. 3.

At small opportunity cost variation $\sigma < 0.2$, the average total cost ($\bar{C} + \bar{D}$) first increases, approaches a maximum and then decreases with increasing restoration cost d (moving from the bottom to the top of Fig. 6a and b). The reason is that the restoration expense D is the product $d \cdot T$ of the restoration cost d and habitat turnover T . At small d , turnover T only weakly depends on d (cf. Fig. 4a and b) so the product $d \cdot T$ increases with increasing d . At large d , however, turnover T steeply declines with increasing d (cf. Fig. 4a and b) and it declines so fast that the product $d \cdot T$ declines as well. This non-monotonic dependence of the total cost on the restoration cost is observed only for small opportunity cost variation while for larger values of σ we observe a monotonic increase. This increase is caused by the increase in the total opportunity cost observed in Fig. 5.

The effect of the opportunity cost variation σ on the total cost depends on the magnitude of the restoration cost. At $d < 2$, the total cost decreases with increasing σ (moving from left to right in the bottom part of Fig. 6a and b), because the total cost is dominated by the average total opportunity cost $\bar{C}$ that was found to decline with increasing σ (Fig. 5a and b). At large d we find the opposite: the total cost increases with increasing σ . The reason is that at large d the average total cost is dominated by the average total restoration expense $\bar{D}$, and $\bar{D}$ increases with increasing average habitat turnover $\bar{T}$ which increases with increasing σ (Fig. 4a and b).

3.3. The Effects of the Restoration Time (K)

Fig. 7 shows that habitat turnover declines with increasing restoration time K . The reason for this is that increasing K reduces

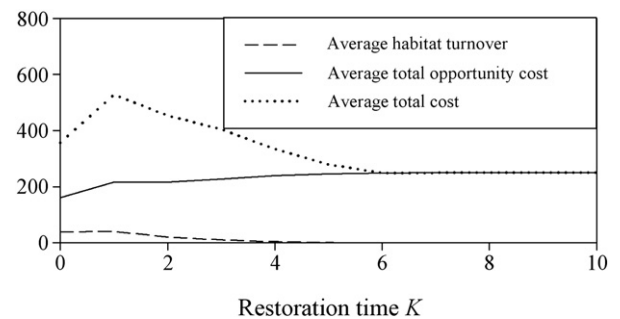


Fig. 7. Average habitat turnover (number of habitat patches destroyed between consecutive time periods) ($\bar{T}$, dashed line), average total opportunity cost ($\bar{C}$, solid line) and average total cost (summing opportunity cost and restoration expense: $\bar{C} + \bar{D}$, dotted line), as functions of the habitat recovery time (K) ($K=0$ here represents instantaneous restoration). Other model parameters are chosen as in Fig. 3.

the profitability of habitat restoration. This is associated with an increase of the average total opportunity cost $\bar{C}$, because conservation is not carried out on the patches with the lowest opportunity costs. Total cost exhibit a maximum at $K=1$, because delayed restoration leads to excess restoration activities so total cost is higher than for instantaneous restoration ($K=0$). At larger K , however, habitat turnover decreases so steeply that average total restoration expense and average total cost decrease with increasing K . The maximum can also occur at larger K if the restoration cost d is small (not shown), but the general pattern prevails.

4. Discussion

We developed an agent-based model for the dynamics of a permit scheme with a special focus on conservation applications where reallocations of conservation measures (“habitat turnover”) and time lags between the initiation of a conservation measure and its positive environmental effect (“habitat restoration time”) are of particular relevance. The model considers that conservation of a habitat leads to opportunity costs and that opportunity costs exogenously change in time and vary among sites. An additional cost of magnitude d arises during the restoration of a habitat.

Within the considered parameter ranges habitat turnover generally increases with increasing cost variation, because the larger the cost variation the higher the cost savings that can be achieved through the reallocation of conservation activities. Habitat turnover decreases with increasing restoration cost d and habitat recovery time, because large restoration costs and recovery times make restoration unattractive to landowners, reducing the supply of permits on the market. For the case of instantaneous restoration we further found that low habitat turnover leads to high total opportunity costs, because not all conservation measures can be allocated to the sites with the lowest costs. Considering that habitat turnover is often harmful for species, a trade-off exists between minimizing the amount of habitat turnover and minimizing the total opportunity cost.

The fact that turnover is affected by the restoration cost d provides a potential for market regulation. So far, we have interpreted d as a restoration cost that is determined by biological or technological conditions and cannot easily be influenced. It would be possible, however, to increase d by introducing a tax on restoration. Therefore, d could be used to adjust habitat turnover depending on the ecology the species of concern: the higher the sensitivity of the species to habitat turnover the higher should be the tax.

If restoration is not instantaneous but includes a time lag the modeled permit market exhibits fluctuations of habitat turnover and costs. The reason for these fluctuations is that the decision to restore a habitat is made in period t on the basis of the current permit price and opportunity cost, but the habitat and the associated land-use permit are obtained only in a later period when cost and permit price may have changed. At that time it may not be profitable to keep the habitat and sell the permit, but instead the patch is converted to economic production again. This process is similar to the well-known pork cycle (e.g., Hanau, 1928; Kaldor, 1934). Since restoration is associated with both opportunity and restoration costs, restoring too much habitat is costly. Decreasing excessive restoration, e.g. by taxing restoration activities, may therefore reduce habitat turnover as well as the total cost of the policy.

The length of the time lag (restoration time) has a decisive influence, as well. Large time lags render restoration unattractive and reduce restoration activity. That reduces habitat turnover and the associated total restoration expense but increases the total opportunity cost, because conservation is no longer allocated to the patches with the lowest opportunity costs. At very large restoration times

market activity ceases and we end up in a static landscape without any trading activity or land-use change.

In the presentation of the model results we have kept some model parameters fixed in order to focus on opportunity cost variation, restoration time, and restoration cost. Those were regarded by us to be the most relevant parameters in the context of this paper. We nevertheless varied the other parameters, too, and found that the main results presented in this paper are quite robust to these variations. The main effects of the other parameters were: (i) decreasing the temporal correlation of the opportunity costs leads to faster changes in the opportunity costs and increases average habitat turnover and the associated total restoration expenses in the model landscape; (ii) increasing the (initial) number of habitat patches increases average habitat turnover but decreases “relative turnover,” i.e. the ratio of average habitat turnover and number of habitat patches; (iii) changes in the discount rate lead to ambiguous results and require further scrutiny.

Our model makes a number of assumptions that may limit the generality of the results. One is that landowners base their expectations about future costs and prices solely on their current observations. Using current costs and prices may be a sensible strategy especially in the face of long restoration times and severe uncertainty in costs and prices. On the other hand, it appears also plausible to assume that agents are able to look further back to the past, observe the long-term behavior of costs and prices and include this information into their decision making. Such a memory of agents would most probably reduce the excessive restoration that was found to increase habitat turnover and costs.

Another consequence of the steady-state expectation model of the agents is that banking of permits for the purpose of speculation (Tietenberg, 2006) is not efficient from the agents' point of view. When costs and prices are assumed not to change, it is optimal for any agent who owns a habitat patch and a permit either to immediately convert the habitat or to sell the permit. Banking by keeping habitat and permit is not profitable (cf. Eqs. (B9e)–(B9f)). Modeling smarter agents would be an interesting opportunity for further research on the effect of banking on the dynamics and efficiency of permit schemes.

An assumption which concerns both the ecological and the economic side of the model is that spatial issues are neglected. In the context of conservation space is often important, because conservation benefits as well as conservation costs may show substantial spatial heterogeneity (e.g., Ando et al., 1998; Polasky et al., 2008). Moreover, if species individuals or populations on different habitats interact, this interaction is likely to be distance-dependent (Hanski, 1999b), leading to spatially external effects in the permit scheme (Bruggeman and Jones, 2008). These can be internalized through spatial trading rules (Bruggeman et al., 2005, 2009) which may have consequences on the dynamics of a permit scheme (Drechsler and Wätzold, 2009; Hartig and Drechsler, 2009, 2010). An avenue of future research could therefore be to study the interaction between spatial trading rules and rules that target the market dynamics, such as a restoration tax. One can, however, expect that the general conclusions of the present analysis will be retained even if spatial interactions and trading rules are included.

Acknowledgement

We are grateful for the helpful comments of two anonymous reviewers.

Appendix A

The opportunity cost $c_i(t)$ for patch i is sampled randomly with mean 1 and standard deviation σ , and temporally correlation α , where $\alpha=0$ represents no correlation and $\alpha=1$ perfect

correlation. We use the following algorithm to create this cost distribution:

$$c_i(t) = 1 + \left[\alpha \cdot (c_i(t-1) - 1) + (1-\alpha) \frac{\sigma}{G(\alpha)} \xi \right]. \quad (\text{A1})$$

Here $G(\alpha)$ is the standard deviation of the following first-order autoregressive process:

$$c_i(t) = \alpha c_i(t-1) + (1-\alpha) \xi, \quad (\text{A2})$$

where ξ is a normally distributed random variable with zero mean and standard deviation 1 (e.g., Mills (1990)). Since G depends on α , for a chosen level of α we simulate Eq. (A2) to determine G and then run the market model using Eq. (A1). An example of a cost trajectory is shown in Fig. A1.

Appendix B

We define a patch state $Y=(x,z)$ that comprises the ecological state x and the number of owned permits z . We denote the number of the present period with an index 0, so that the present state, opportunity cost and permit price are denoted as Y_0 , c_0 and p_0 . For simplicity, we also suppress the agent number i . We further introduce a quantity $s_0=(\beta_0, \rho_0)$ that represents the chosen actions in the present period. These include $\beta_0 \in \{1, -1, 0\}$, representing purchase or sale of a permit or inactivity, respectively, and $\rho_0 \in \{0, 1\}$, representing management of the patch for economic production or for conservation, respectively. We use the small letter s and the Greek letters β and ρ to indicate that they represent possible actions, while capital letters $S=(b, r)$ used in Section 2.1 represent the strategy that gives the optimal response to a given permit price p_0 at given costs c_0 in a given patch state Y_0 .

To consider agents' expectations of the future, we define a vector $Y=(Y_0, Y_1, Y_2, \dots, Y_k, \dots)$ that contains the states of the present and all future periods, $\dots, \infty$, a vector c that correspondingly contains the present and anticipated conservation management costs for all periods, a vector p that contains the present and anticipated permit prices, and a vector s that contains the present and future actions.

We assume that the profit of the agent (Π) can be written as the sum of the discounted profits, π_t , earned in the present ($t=0$) and future ($t>0$) periods

$$\Pi(Y, c, p, d, s) = \sum_{t=0}^{\infty} q^t \pi_t(Y_t, c_t, d, p_t, s_t) \quad (\text{B1})$$

where the discounting factor $q<1$ measures how agents discount future profits. The profit π_t earned in period t is composed of

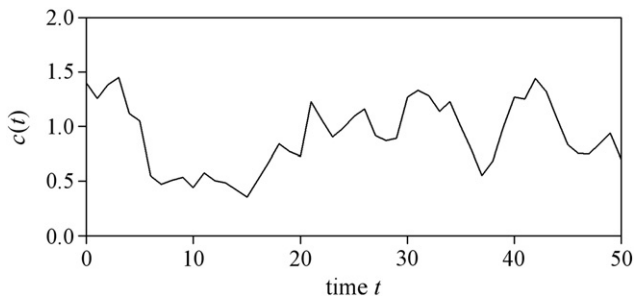


Fig. A1. Random cost trajectory with cost variation $\sigma=0.3$ and temporal correlation $\alpha=0.8$.

the opportunity costs c_t , habitat restoration costs d and the cost or revenue from buying or selling a permit:

$$\pi_t = -\beta_t p_t - \rho_t (c_t + d \cdot \Theta(K - x_t)) \quad (\text{B2})$$

The first term in Eq. (B2) considers that buying ($\beta_t=1$) or selling ($\beta_t=-1$) of permits decreases or increases the profit by the permit price of the present period. Opportunity costs c_t arise if the patch is managed for conservation ($-\rho_t c_t$). The quantity $\Theta(y)$ represents the so-called Heaviside function that yields 1 if $y>0$ and zero otherwise. This implies that the last term of Eq. (B2), $\rho_t d \Theta(1 - x_t)$, equals d if restoration takes place (i.e., if $\rho_t=1$ and $x_t<1$), and zero otherwise.

We assume that agents expect future costs and permit prices to maintain constant in time:

$$c_t = c_0, p_t = p_0 \text{ for all } t > 0. \quad (\text{B3})$$

Π of Eq. (B1) is maximized through dynamic programming (e.g., Clark, 1990). As a result, we obtain the optimal actions in the present period, b and r , as functions of the present patch state, opportunity cost, permit price, restoration cost, and discount factor.

Inserting the obtained b and r for each patch into function $b_i(x_i, z_i, c_i, p)$ in Section 2.1 yields the market transactions and the equilibrium permit price for the present period. This determines the distribution of land use and land-use permits in the region and the states of the patches.

To maximize the profit function of Eq. (B1), we start by considering a finite number of T periods, assuming that the agent is currently in period $t=0<T$, with present opportunity costs c_0 and permit price p_0 , and introduce a value function for some other later period $0 \leq T-k \leq T$:

$$V(T-k) = \max_{s_{T-k}} \left\{ \sum_{i=0}^k q^i \pi_{T-k+i}(Y_{T-k+i}, c_{T-k+i}, d, p_{T-k+i}, s_{T-k+i}) \right\} \quad (\text{B4})$$

The term in parentheses represents the sum of the discounted (with regard to period $T-k$) profits earned from period $T-k$ on until the final period T , given that opportunity cost and permit price are given by c_0 and p_0 , respectively (Eq. (B3)). To obtain $V(T-k)$, this sum has to be maximized as a function of the actions s_{T-k} in period $T-k$, which are participation in the permit market (β_{T-k}) and land use (ρ_{T-k}). The maximization is subject to the constraints described in Section 2.1. For the final period T the value function reads

$$\begin{aligned} V(Y_T) &= \max_{s_T} \{ \pi_T(Y_T, c_0, d, p_0, s_T) \} \\ &= \max_{\beta_T, \rho_T} \{ -\beta_T p_0 - \rho_T (c_0 + d \cdot \Theta(1 - x_T)) \} \end{aligned} \quad (\text{B5})$$

The solution of Eq. (B5) depends on the patch state $Y_T=(x(T), z(T))$. Noting that b and r are the optimal actions, the solution of Eq. (B5) is

$$\begin{aligned} b(T; x(T)<1, z(T)=1) &= 0 \\ r(T; x(T)<1, z(T)=1) &= 0 \\ V(x(T)<1, z(T)=1) &= 0 \end{aligned} \quad (\text{B6a})$$

$$\begin{aligned} b(T; x(T)=1, z(T)=0) &= \begin{cases} 0 & p(t) > c(t) \\ 1 & \text{otherwise} \end{cases} \\ r(T; x(T)=1, z(T)=0) &= \begin{cases} 1 & p(t) > c(t) \\ 0 & \text{otherwise} \end{cases} \\ V(x(T)=1, z(T)=0) &= \begin{cases} -c(t) & p(t) > c(t) \\ -p(t) & \text{otherwise} \end{cases} \end{aligned} \quad (\text{B6b})$$

$$\begin{aligned}
 b(T; x(T) = 1, z(T) = 1) &= \begin{cases} -1 & p(t) > c(t) \\ 0 & \text{otherwise} \end{cases} \\
 r(T; x(T) = 1, z(T) = 1) &= \begin{cases} 1 & p(t) > c(t) \\ 0 & \text{otherwise} \end{cases} \\
 V(x(T) = 1, z(T) = 1) &= \begin{cases} p(t) - c(t) & p(t) > c(t) \\ 0 & \text{otherwise} \end{cases}
 \end{aligned} \quad (B6c)$$

The value function for the penultimate period is

$$V(Y_{T-1}) = \max_{\beta_{T-1}, \rho_{T-1}} \{-\beta_{T-1} p_0 - \rho_{T-1} (c_0 + d \cdot \Theta(1 - x(T-1)/K)) + qV(Y_T)\} \quad (B7)$$

(note that the state $Y_T \equiv (x(T), z(T))$ depends on the actions, $\beta(T-1)$ and $\rho(T-1)$ in the penultimate period. The solution of Eq. (B7) delivers the optimal actions $b(T-1)$ and $r(T-1)$ for the penultimate period. For an arbitrary period $T-k$ the value function $V(Y_{T-k})$ can be expressed recursively by the Bellman equation

$$V(Y_{T-k}) = \max_{\beta_{T-k}, \rho_{T-k}} \{-\beta_{T-k} p_0 - \rho_{T-k} (c_0 + d \cdot \Theta(1 - x_{T-k}/K)) + qV(Y_{T-k+1})\} \quad (B8)$$

(Clark, 1990). Eq. (B8) is applied repeatedly backwards in time until the present period $t=0$ is reached. Letting T numerically approach infinity, $V(Y_T)$ approaches the maximum profit (Eq. (B1)) that can be obtained in the present period, with the associated optimal actions b and r . A typical result is shown in Fig. B1.

With T approaching infinity the optimal strategy converges to that presented in Eqs. ((B9a)–(B9f)) for instantaneous and delayed habitat restoration.

$$b(x < 1) = \begin{cases} -1 & \left(\text{instant. restor. and } p > c \sum_{j=0}^{\infty} q^j = \frac{c}{1-q} + d \right) \\ 0 & \text{otherwise} \end{cases} \quad (B9a)$$

$$r(x < 1) = \begin{cases} 1 & \left\{ \begin{array}{l} \left(\text{instant. restor. and } p > \frac{c}{1-q} + d \right) \text{ or} \\ \left(\text{delayed restor. and } q^{K-x} p \geq c \sum_{j=0}^{\infty} q^j + d \sum_{j=0}^{K-x-1} q^j = \frac{c + d(1-q^{K-x})}{1-q} \right) \end{array} \right\} \\ 0 & \text{otherwise} \end{cases} \quad (B9b)$$

$$b(x = 1, z = 0) = \begin{cases} 0 & p > \frac{c}{1-q} \\ 1 & \text{otherwise} \end{cases} \quad (B9c)$$

$$r(x = 1, z = 0) = \begin{cases} 1 & p > \frac{c}{1-q} \\ 0 & \text{otherwise} \end{cases} \quad (B9d)$$

$$b(x = 1, z = 1) = \begin{cases} -1 & p > \frac{c}{1-q} \\ 0 & \text{otherwise} \end{cases} \quad (B9e)$$

$$r(x = 1, z = 1) = \begin{cases} 1 & p > \frac{c}{1-q} \\ 0 & \text{otherwise} \end{cases} \quad (B9f)$$

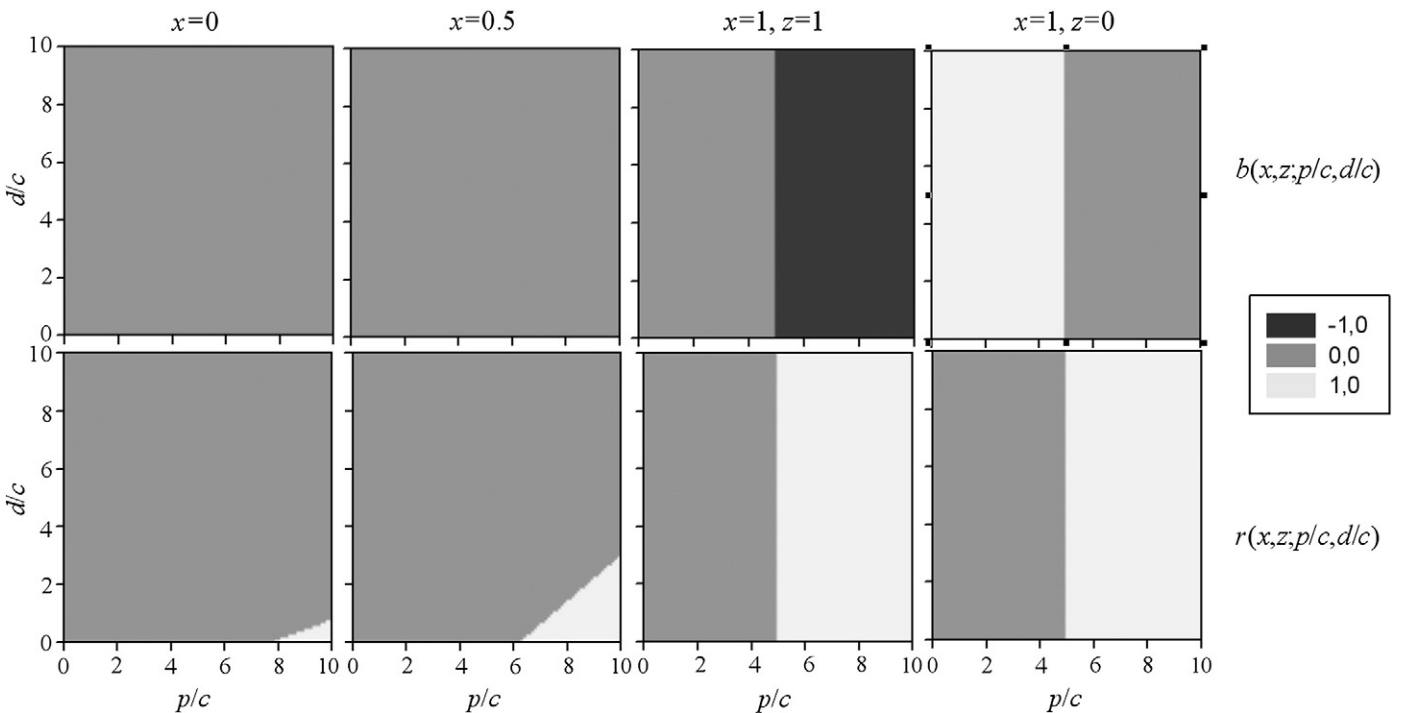


Fig. B1. Optimal strategy $b(x,z)$ (top row) and $r(x,z)$ (bottom row) for the case of $K=2$ as a function of the patch state $Y=(x,z)$, ($x \in \{0, 0.5, 1\}, z \in \{0, 1\}$), the ratio of price and opportunity cost (p/c) and the ratio of restoration and opportunity costs (d/c). The levels of $b \in \{-1, 0, 1\}$ and $r \in \{0, 1\}$ are represented by grey scale.

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