

**Space for Species:
Spatial Ecological-Economic Analyses
of Biodiversity Conservation**

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**Space for Species:
Spatial Ecological-Economic Analyses of Biodiversity Conservation**

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Voorwoord

Als kind wist ik dat het boegbeeld van het Wereldnatuurfonds, de panda op uitsterven stond. De afgelopen jaren heb ik geleerd dat de panda maar een schakeltje is in het veelzijdige probleem van biodiversiteitverlies. Die complexiteit maakt de effectiviteit en doelmatigheid van biodiversiteitbehoud tot een interessant vraagstuk. De keerzijde is dat de juiste vragen stellen, laat staan de juiste antwoorden vinden, geen gemakkelijke opgave is. Voor de begeleiding van mijn eerste stappen in dit onderzoeksveld ben ik een aantal mensen dankbaar.

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1. Introduction

1.1. Motivation

Ordovician, Devonian, Permian, Triassic and Cretaceous. To many readers, these will be uncommon terms. They signify five periods in the Earth's history in which a large share of life on earth was extinguished. Clearly, extinctions are a normal part of life on Earth: fossil records suggest that the 'natural' rate of extinction is about one to three species per year (May et al., 1995). The current rate of extinction, however, may be 1,000 to 10,000 times as high (Heywood, 1995, p. 235). Although this estimate should be used with due care, most environmental scientists agree that dire times are ahead for many of Earth's species.

The cause of this 'Sixth Extinction' is *Homo sapiens*, or more specifically, the way humanity exploits the Earth's natural resources to accommodate its consumption. Demands placed on environmental resources are often found to exceed the capacity of the Earth to provide for them (e.g., Lenzen and Murray, 2001; Zhao et al., 2005). Other species bear the burden by having to survive under degraded circumstances. For both economic and moral reasons, efforts are made to conserve natural areas of good quality so that threatened species may survive. Such nature reserves, however, require scarce and costly space. This thesis aims to gain insight into economically efficient use and allocation of space to satisfy both human and natural needs.

The International Union for the Conservation of Nature (IUCN) keeps track of the extinction risk of species in the 'Red List', which covers all sorts of species, from plants to elephants (see Table 1.1). Worldwide, a recorded total of 886 species have gone extinct, while –save for specimens in zoos– 14,926 species are considered extremely likely to be lost, and another 11,000 species may soon require human protection if they are to survive (IUCN, 2004). Such numbers are not very promising.

The predominant media image of extinction is as a problem limited primarily to Asian, African and South American countries. Coral reefs and tropical rain forests dominate the extinction debate. And it is true that such places –often referred to as 'biodiversity hotspots'– house many more species that occur on the Red List than Western countries do. In the West, however, the extinction problem is also very pressing, much more so than one would expect. The United States have recorded 237 extinctions, which is over a quarter of all recorded extinctions (IUCN, 2004). In

Europe, only 22 species are officially extinct, but no less than 1,759 species require our close attention and protection if they are to persist into the future (IUCN, 2004).

Table 1.1. Changes in the number of globally threatened species per taxonomic group and threat level; 1996 – 2006

<i>Taxonomic group</i>	<i>Critical</i>			<i>Endangered</i>			<i>Vulnerable</i>		
	1996/98	2004	2006	1996/98	2004	2006	1996/98	2004	2006
Mammals	169	162	162	315	352	348	612	587	583
Birds	168	179	181	235	345	351	704	688	674
Reptiles	41	64	73	59	79	101	153	161	167
Amphibians	18	413	442	31	729	738	75	628	631
Fishes	157	171	253	134	160	238	443	470	682
Insects	44	47	68	116	120	129	377	392	426
Molluscs	257	265	265	212	221	222	451	488	488
Plants	909	1,490	1,541	1,197	2,239	2,258	3,222	4,592	4,591

Source: IUCN Red List (2004, 2006).

The existence of these species is at risk through human, economic behaviour. Four mechanisms of species loss are conventionally recognised, which in no particular order are (e.g., Barbier et al., 1995):

- climate change
- exotic species
- harvesting and hunting
- habitat loss

Normally, climate change is a slow process without major effects on species in the short run. If climate change is rapid, however, a species that is unable to adapt quickly or to migrate to more affable areas becomes extinct (e.g. Maciver, 1998). The introduction of exotic species to a country or region often follows the opening of trade and may be intentional or coincidental (e.g. Jenkins, 1996). These introduced species often have no natural predator in their new environment and can easily overtake native species. Harvesting and hunting are possibly the oldest human-induced causes of species loss and have been studied intensively by economists in the last decades.

This thesis addresses the fourth cause of species extinction, namely habitat loss. It analyses economic efficiency in choices between habitat loss and habitat protection. A habitat, according to the Merriam-Webster dictionary, is the place or

environment where a plant or animal naturally or normally lives and grows. Habitats provide the specific ecological conditions to which a species has adapted, such as temperature, humidity, and food items, (e.g., Wilson, 1975; Begon et al., 1990). A species such as the domestic pigeon can flourish both in natural and (especially) built-up areas. The pigeon exploits a wide niche, and its habitat comprises a heterogeneous landscape. The badger, on the other hand, prefers to build its underground nest (or 'sett') in dry areas with cover (Feore and Montgomery, 1999). These requirements make its ecological niche smaller than that of the pigeon, and its habitat contains more homogeneous landscapes.

A species cannot exist without its habitat and therefore maintaining habitat availability is a crucial aspect of biodiversity conservation. This task is easier the more heterogeneous is a species' habitat. In the example above, the badger has fewer options for relocation if its habitat is destroyed for economic production than the domestic pigeon would have. Habitat preservation, however, is more complicated than simply preventing human activity in crucial habitats. The loss of habitat includes, according to Armsworth et al. (2004), three distinct processes:

- conversion
- fragmentation
- degradation

These notions indicate, respectively, the loss of habitat availability, loss of spatial coherence of habitat areas, and loss of ecological quality in habitat areas due to processes like pollution or drainage of groundwater. In the following chapters, each of these issues is addressed in more detail.

1.2. Scales and indicators of biodiversity

The overarching issue of this thesis is biodiversity conservation. Biodiversity itself is possibly also this thesis' most complicated concept. The broader context of biodiversity will be surveyed in this section, and a number of related issues and terms explained. This lays the basis for the expositions in the following chapters.

Lovejoy (1980) is often attributed as the first to use the term biological diversity, abbreviated later to biodiversity. Lovejoy essentially refers to the number of variations at the species level. Wilson (1992) expands the scope of biodiversity to the number of variations at either the genetic, species or ecosystem level. He argues in favour of a hierarchical view of biodiversity, where genes are the smallest and ecosystems are

the largest units of biodiversity.¹ These levels at which biological diversity exists have been extended further with the functional level by Walker (1992). According to him, biodiversity is not just a matter of species and ecosystems, but more importantly of the services they provide, such as water cleaning or capturing and storing solar energy. All of these aspects are more or less covered by the Convention on Biological Diversity (UNEP, 1992; art. 2), which comprehensively defines biodiversity as “the variability among living organisms from all sources including, *inter alia*, terrestrial, marine and other aquatic ecosystems and the ecological complexes of which they are part; this includes diversity within species, between species and of ecosystems.”

To express differences between regions in the biological variation they contain, a number of methods have been devised (Magurran, 1988). These measures of biodiversity generally emphasise two distributional aspects of biodiversity at its various scales. The first is ‘richness’, which is the total number of variations (genes, species, etc) in a given area. Richness is easily understood as well as measured and is therefore a popular indicator of biodiversity. The second aspect is the ‘evenness’ of biodiversity, which refers to the relative abundance of variations. This means that, compared to common species, rare species make relatively large contributions to the level of biodiversity.

Measures of biodiversity that describe the overall level of biodiversity in a region may not provide the necessary information to decide which species or ecosystem needs conservation. In practice, other considerations influence decisions on whether efforts are made to save a species. Margules and Pressey (2000) argue that conservation decisions must be based on ‘representativeness’, the extent to which a species or ecosystem historically belongs to a region, and ‘persistence’, the extent to which conservation of a species is feasible in the long term. Whether it is the better conservation strategy to consider richness and evenness, or to emphasise aspects such as representativeness currently remains a topic of debate among ecologists (e.g., Brooks et al., 2004; Cowling et al., 2004).

Focusing on any one level or aspect of biodiversity is not as straightforward as it sounds, since levels of biodiversity interact. To save any one species requires the protection of its habitat. The habitat itself, however, is an ecosystem of which the species itself is a part. Franklin (1993), therefore, argues in favour of using an ecosystem perspective, rather than the species-oriented approach to biodiversity

¹ Although definitions of ecosystems abound, roughly speaking an ecosystem is a dynamic and interacting complex of biotic (living) organisms and their abiotic (non-living) environment.

conservation. Furthermore, he acknowledges that an ecosystem is dependent on the environmental effects of nearby human activities. Scientists and conservationists should therefore consider the 'landscape matrix', or the whole spatial pattern of human activities, habitats and the ecological connections that exist between them. It is particularly the ecological connections that complicate the development of reserve sites and human activities. Locating biodiversity reserve sites far from polluting activities is the obvious solution. If any human activities other than biodiversity conservation already occupy a region, such a solution may not be available.

1.3. Policy context

The Habitat and Bird Directives (HBD) of the European Union aim to preserve species by protecting their habitats in the 'Natura 2000' network.² The HBD, however, also notes that the social and economic costs of such protection may be insurmountable, in which case alternative means or locations for conservation must be sought. In intensively used areas, which are common in industrialised countries, this caveat may be invoked rather easily. If land is very scarce, nature reserves do not constitute an economically productive usage of land. Little, if any, monetary revenue will be generated by nature reserves. As the scarcity of space and land prices increase, it becomes harder to protect species that cannot earn their keep by being harvested or providing other monetary value (see Swanson, 1994). If, however, it is decided that species should not be lost to posterity, choices must be made about how many and which species to preserve, and where to preserve them.

The HBD requires all EU countries to leave the essential habitat areas undeveloped and in good ecological quality. In the Netherlands, these obligations are difficult to fulfil, because almost all land area is intensively used. The competition for space between economic activities and habitat reserves, and the environmental impact of economic activities all force Dutch environmental policy and spatial planning to collaborate closely. Long-term environmental goals are set out in the report 'Nature for people' (NvM; LNV, 2000) and the Fourth National Environmental Plan (NMP4; VROM, 2001). The spearhead of Dutch biodiversity conservation is the establishment of the National Ecological Network (EHS), a network of natural areas of high ecological quality.

To achieve this EHS, conservation of natural areas is based on an ecosystem approach, with 'core' areas and buffer zones. Economic activities are only allowed in these buffer zones. One important activity in the Netherlands is agriculture, which

² The counterpart of the HBD in the United States is the Endangered Species Act (ESA).

NMP4 acknowledges has important, negative impacts on the EHS: ammonia (NH₃) emission, nitrate (NO₃) leaching into groundwater and surface water, and lowering of groundwater tables degrade the ecological conditions in neighbouring natural areas. These effects can be far-reaching and complex. The EHS has been designed to limit the environmental effects from economic activities through reserving large natural areas that are connected via corridors to allow migration of species.

Reality, however, has proven quite resistant to the well-intentioned plans of the NMP4. The National Institute for Public Health and the Environment (RIVM) has already shown in 2002 that a large discrepancy exists between the continuous, planned EHS and the fragmentation that characterises the network of natural areas (RIVM, 2002). Since then, the goals and instruments for the EHS set out in NMP4 have been scaled down or even been abandoned (MNP, 2004). According to that same document, even the adjusted goals require increased efforts in order to be achieved within the timeframe set. Economic activities are still being located inside of 20% of the appointed Natura 2000 reserve sites (MNP, 2005), which only adds to the problem of habitat fragmentation. The ecological quality of many Dutch natural areas, however, appears to have improved in the last few years (MNP, 2006). At the same time, however, a planned slackening of national instruments designed to limit environmental effects from economic activities implies that this achievement is at risk. As a result, the costs of maintaining a good ecological quality in natural areas may well increase.

If anything, this brief history of Dutch environmental policy shows that biodiversity conservation currently has difficulty competing for space with economic activities. Two very general explanations can be given for this lack of competitiveness. Either the number and set of species targeted for conservation are not socially optimal, or unobserved or unpriced environmental effects of economic activities cause misallocations of space. These explanations point out two trade-offs that can be taken into account in biodiversity conservation. The one trade-off concerns the number and composition of species and ecosystems to be preserved, whereas the other relates to the locations and sizes of biodiversity reserve sites and economic activities. But, as has been argued above, these two aspects of biodiversity are related, and ideally these two trade-offs are considered together.

1.4. Research context

1.4.1. Historical background of this thesis

That policies to preserve current levels of biodiversity have been only partially successful may be the result of a lack of knowledge about the interactions between the ecological and economic systems. The importance of these interactions has increasingly been recognised by ecologists and economists alike. The motivation for the current study has been a large research program on the ecological-economic connections, the 'Ecological-economic analysis of wetlands: functions, values and dynamics' (ECOWET) program. It shall be briefly discussed here.³

This program was financed under the Fifth Framework Programme of the European Commission and ran from 1996-1999. Participants in the project were the University of East Anglia, the Vrije Universiteit Amsterdam, the Tilburg University, the Beijer International Institute of Ecological-Economics and the University of the Aegean. The purpose of the ECOWET-program was to provide more detailed information to policy makers about the costs and benefits of wetland conservation and restoration. The research tiers were refining (non-)monetary valuation methods and techniques, as well as developing scenarios of environmental change to model possible future states of wetlands and appropriate policy responses (see, e.g., Turner et al., 2000). This thesis can be viewed as a follow-up to the latter tier.

In the main publications that have resulted from the ECOWET program, Van den Bergh et al. (2001, 2004), a spatially explicit simulation model is described that has been developed to analyse wetland conservation in the Vechtstreek region in the Netherlands. An innovative feature of this model is that it integrates two spatial scales. At the aggregated spatial scale, scenarios are defined that reflect choices made in physical planning, nature and agricultural policy and regulation of recreation. These choices affect local economic indicators, such as revenue from recreation and agriculture, under the various scenarios. Moreover, such policy decisions cause changes in the ecological system, which are simulated at the disaggregated spatial scale. Simulated changes concern hydrological conditions, such as ground water level and eutrophication of ground- and surface water, which then determine the composition of vegetation. The ecological results are subsequently aggregated to the

³ Broadly speaking, wetlands are ecosystems that 1) are distinguished by the presence of water at the surface or within the root (of vegetation) zone, 2) have unique soil conditions different from adjacent uplands, and 3) are characterised by the absence of flooding-intolerant vegetation (Mitsch and Gosselink, 2000; chapter 2).

spatial scale at which the economic indicators have been calculated, so that the combined social welfare effects can be assessed through multi-criteria analysis.

The study of which this thesis is the end product has been financed under the NWO 'Stimulation Programme Biodiversity' as a part of three research projects. The first focuses on developing scenarios for the Vechtstreek area and promoting the integration of economics and ecology in the other two projects.⁴ The second improves upon the ecological modelling of ECOWET by introducing ecological dynamics and allowing for spatial interactions between natural areas.⁵ The third project, of which this thesis is the end result, aims to get a better understanding of the interdependency between economic production and biodiversity conservation.

1.4.2. Economic analysis of biodiversity conservation

Aside from providing the project's history, it is also important to position this thesis in relation to (environmental) economics. Because land allocation plays a central role in this thesis, the economics literature that considers biodiversity conservation in a spatial context is considered to be the most relevant. The importance of natural resources in general has long been recognised by economists (e.g., Boulding, 1966; Krutilla, 1967), but biodiversity loss specifically has only started to generate discussion among economist since the 1990's. This is not to say, however, that earlier environmental economics lacks all applicability to biodiversity conservation. Environmental economics basically offers three approaches to model biodiversity conservation that incorporate land allocation decisions. Other approaches, such as the determination of cost-effective allocation of conservation funds (Weitzman, 1998), are not addressed in this section.

A first approach focuses on the trade-off that exists between the conservation of a finite, non-renewable resource and the level of economic production. This non-renewable resource can be assumed to represent a habitat. An early contribution comes from Fisher et al. (1972), who develop a macroeconomic growth model in which land is valued both as an input to production and as a natural resource stock. In contrast to earlier models, however, land used for production cannot be reverted back to its natural state. As a result, a larger quantity of land must be preserved than previous models indicated. In Miller (1981), undeveloped land explicitly serves as

⁴ This project was performed by the Institute of Environmental Studies at the Vrije Universiteit Amsterdam.

⁵ This research is being done at the Department of Innovation and Environmental Sciences at the Utrecht University.

habitat to a single species, while Rowthorn and Brown (1999) focus on total habitat availability, which generates species richness. In all these models land is a homogeneous resource, both ecologically and spatially, which does not correspond to the heterogeneous nature of real habitats.

A second, more recent body of literature emphasises exactly this heterogeneous nature of habitats. One of the earlier applications of this modelling approach is found in Ando et al. (1998). It can determine, for any region, the combination of reserve sites that protects the maximum number of species, given budget constraints (the 'maximum coverage problem'). Newer models include a trade-off between conservation of species richness and economic objectives (e.g., Liechtenstein and Montgomery, 2003), or consider the impact of habitat fragmentation on species persistence (e.g., Nalle et al., 2004). A predetermined minimum level of economic production limits the level of ecological protection that is found in these models. They thus show the most efficient way of preserving a preset level of biodiversity, but cannot indicate whether that level of biodiversity is socially optimal.

The third modelling approach concerns models in which harvesting effort can be used to control the size of a renewable resource stock, such as a species or ecosystem. Gordon (1954) and Schaeffer (1954) independently developed the prototype of these models, and Clark (1973) added the concept of economic efficiency to the framework. Swanson (1994) extends these models with habitats as an additional instrument for control, while Perrings and Walker (1997) investigate the stability of habitats. The abundance of this literature, however, cannot hide the fact that this type of model is not easily adapted to express the heterogeneity of real habitats. Moreover, two species at most have been considered in a single model. This restricts the usefulness of these models for analysing possible trade-offs between species or ecosystems at any level of biodiversity.

1.5. Research approach

The primary goal of this thesis is to study the economics of biodiversity conservation. Much emphasis has been placed on the connections that exist between spatial patterns of land use and the ecological indicators and mechanisms that determine biodiversity. This thesis develops extensions to the traditional spatial-economic models, and addresses the following main research question

How can environmental economic modelling be employed to address spatial issues in biodiversity loss and conservation, and what policy recommendations result from modelling adaptations?

This question gives rise to a number of subquestions:

- 1) To what extent do current economic studies of biodiversity conservation include relevant concepts and theories from ecology?
- 2) What impact does the composition of urban land use have on biodiversity in neighbouring natural areas?
- 3) How do the spatial requirements of economic production affect the degree of habitat fragmentation in optimal biodiversity conservation?
- 4) Does the spatial distribution of economic production and biodiversity conservation in the Netherlands change when the damage costs of fragmentation and acidification of habitats are internalised?

The main improvements in economic modelling of biodiversity conservation suggested in this thesis are that landscapes and ecosystems, rather than individual species, are considered. As a result, spatial heterogeneity is incorporated in all models developed in this thesis, but each model applies a different approach and considers alternative aspects of ecosystems and biodiversity conservation.

The first model emphasises differences in habitat conditions required by four sets of species. The second model focuses instead on asymmetries in the spatial distributions of two different habitat types and the consequences in fragmentation of biodiversity reserve sites. In the third and final model, degradation and fragmentation of habitats are integrated into an economic land use model. Here, the focus is on achieving more efficient patterns of land use and biodiversity conservation by pricing the environmental damage arising from land use.

1.6. Outline

The remainder of this thesis is organised into six chapters. Chapter 2 provides the theoretical underpinnings of the study. It contains a review of the relevant economic literature on biodiversity conservation, and addresses the extent to which such studies integrate ecological concepts and theories relating to biodiversity. Chapter 3 develops a bid-rent model of urban expansion that includes the loss and degradation of natural areas for several types of ecosystem and the species within them. The composition of biodiversity determines the value of the land surrounding the city, affecting its size in the steady state. Additionally, a survey of the literature on land

use modelling sets the stage for the approaches taken in this thesis. Chapter 4 presents a two-region, general equilibrium model to determine the interaction of labour migration and fragmentation of nature reserves. This model is extended with land use and habitat loss, where the distribution of species over space is not uniform. Workers' preferences for income and biodiversity are assumed to affect the size of biodiversity reserve sites. In chapter 5, an equilibrium model of the Dutch land market, the Ruimtescanner (Land Use Scanner), is extended with fragmentation and habitat degradation. Internalisation of damage costs associated with these impacts on habitats affect the pattern of land use and biodiversity conservation. Chapter 6 concludes by drawing policy lessons for biodiversity conservation from the various studies performed.

2. Ecological theories and indicators in economic models of biodiversity loss and conservation¹

2.1. Introduction

It is by now common knowledge that biodiversity is under serious threat from human activities that increase land use, fragmentation, harvesting, hunting, pollution and climate change (e.g., Sala et al., 2000). Continued economic growth makes it likely that pressure on current biodiversity will increase. Nonetheless, conservation efforts – including public expenditures – are not growing enough to adequately respond to this pressure (Emerton et al., 2005). In addition to moral arguments for conservation aside, biodiversity also provides direct and indirect economic benefits to mankind. To make increased conservation politically acceptable, it should do as little harm to the economy and its growth as possible. Economists are exceptionally equipped to analyse this issue, but only if they incorporate appropriate biodiversity indicators and related ecological theories in their models.

Biological diversity is a multidimensional concept. It includes genes, species, ecosystems and ecosystem functions (UNEP, 1992; Wilson, 1992; Turner et al., 1999). Biodiversity has even been so broadly defined as to include not only biotic elements but also abiotic factors, such as the ground water level and nutrient availability (e.g., Noss, 1990). The definition of biodiversity merits careful consideration by economists. Does it concern, for instance, the total number of entities, their relative abundance or their representativeness (Magurran, 1988; Margules and Pressey, 2000)? Then there is the issue of which conservation strategy to follow. Conservation efforts can emphasise the preservation of individual species, as the US Endangered Species Act does, of landscapes, as specified in the EU Habitat Directive, or of an indicator species whose presence is inherently connected with that of other species (Margules and Pressey, 2000).

The aim of this chapter is to evaluate how well economic models of biodiversity conservation apply ecological knowledge of biodiversity. In order to do so, a framework is required that determines relevant theories and indicators of biodiversity

¹ This chapter also appears as: Eppink, F.V. and J.C.J.M. van den Bergh, 2006, Ecological theories and indicators in economic models of biodiversity loss and conservation: a critical review, Ecological Economics, in press.

and their connection to economic activity. The first step here is to determine which theories and indicators of biodiversity are relevant for each type of economic model. For this purpose we discuss ecological theories that explain biodiversity changes at the four levels of biodiversity. Some of these theories provide a very direct link with economic activities, such as hunting, habitat destruction and fragmentation. Other theories suggest that biodiversity loss comes from more indirect effects of various environmental pressures, such as climate change, nitrogen deposition and land use.

We develop the framework in section 2.2 and give a review of interesting cases of each of four types of economic models in section 2.3. Here, we examine the way these models incorporate the biodiversity indicators and theories. The conclusions are presented in section 2.4.

2.2. Developing a framework to incorporate biodiversity into economic models

The models of biodiversity conservation that will be reviewed here can be divided into four types: cost-effectiveness (CE) models, renewable resource extraction (RR) models, macroeconomic growth (MG) models with natural resources, and general equilibrium (GE) models with natural resource externalities (discussed in detail in section 2.3). These are the four major approaches used by economists when studying environmental issues in general. For each model type we have attempted to collect all representative models. In addition, there are models that do not fit into any of the four categories. Although we do not give much attention to these individual approaches for reasons of space, we will mention the most original cases.

Our approach to collecting literature has been a systematic article search via ISI “web of science”, using a wide range of relevant key words. In addition, we have followed references listed in the articles. We have given special attention to publications in economic journals, in particular the best-known environmental economics journals. A number of original contributions in (environmental) science journals have also been included.

The four economic model types use varying, partially implicit assumptions. As a result, each model is equipped to answer specific questions relating to biodiversity loss and conservation. The ecological indicators and theories of biodiversity underlying the models vary among the model categories. We develop a framework to evaluate the extent to which the models apply relevant biodiversity theories. This framework connects four aspects, namely levels and indicators of biodiversity, spatial scale, and ecological theories of biodiversity change.

Figure 2.1 represents the framework. The first column in Figure 2.1 lists the scales of analysis that are common in economics. The two scales address both spatial and agent characteristics. We consider a small scale to be any area that is considered in the decision-making by firms (or individuals). Areas governed by policy makers often are of a large scale (e.g., from a municipality up to a nation).

Scale	Relevant level of biodiversity	Relevant indicator of biodiversity	Corresponding theories of biodiversity
Small	Species	Representativeness	Species interaction Metapopulation
	Genetic	Genes & alleles	-
Large	Function	Quality	Resilience
	Ecosystem	{ Richness Evenness Representativeness	Resilience Abiotic
	Species		Species interaction Metapopulation
	Genetic	Genes and alleles	-

Figure 2.1. A framework for evaluating economic models of biodiversity loss and conservation

The second column of Figure 2.1 gives the relevant levels of biodiversity for each scale. These include genetic, species, ecosystem and functional diversity. An individual can only partially observe the effects of his activities on the environmental conditions governing biodiversity outside his land, or control the activities of outside individuals that affect biodiversity on his land. If this individual is managing a genetic or species stock, he may clearly notice the impacts that such processes have on this resource and adapt his management accordingly. Individuals rarely manage ecosystems or ecosystem functions, however, and therefore changes at these levels will tend to go unnoticed. In contrast, models of government planners can include all levels of biodiversity, because governments can be interested in ecosystem and functional diversity.

The third column in Figure 2.1 lists five indicators of biodiversity. These are genes/alleles, representativeness, richness, evenness and quality. Representativeness denotes whether a species or ecosystem has historically existed in an area. Species richness, the number of species, is an indicator of biodiversity that is easy to understand and often used. Species evenness refers to the relative

distributions of species populations, another important aspect of biodiversity. The term 'quality' is meant to indicate the degree to which ecosystem functions are performed. At the level of genetic diversity, species' genes can be compared to those of other species to indicate the genetic uniqueness, or be used to assess the extent of genetic dynamics caused by selection processes. At the species level, an individual economic agent may be interested in the representativeness – culturally or historically – of a species. Assuming that the individual does not manage multiple species simultaneously, he does not assess a species' contribution to richness or evenness. A government does manage many species at once, and may be interested in several indicators, including also richness and evenness. Some biodiversity indicators, such as the Shannon or Simpson's indices, are entropy measures that combine richness and evenness (Magurran, 1988).

The fourth column in Figure 2.1 mentions four established ecological theories that explain biodiversity loss or the effect of biodiversity loss on ecosystem composition and functions.¹ First, by 'metapopulation' we refer to the theory developed by Hanski and Gilpin (1991) and Hanski (1994), which describes the spatial dynamics of species' populations. The theory addresses species' populations, where individuals move between habitat patches. The relative spatial positioning of these patches, as well as their size, is important to the viability of the overall population. Such habitat issues also are considered here, because they are crucial to a good understanding of the options and limits of biodiversity conservation.

A second theory is 'multi-species interactions'. With this theory, we indicate dynamics of competition, mutualism and predation. These interactions influence the population dynamics of ecologically related species. Such theories can be used to trace the impacts of diversity changes in one species on another.

A third theory concerns competitive interactions between flora for abiotic resources, such as nutrients, sunlight and water. A plant that is the best competitor for a limiting resource becomes dominant, as described for instance in Tilman (1982). Changes in abiotic conditions may lead to succession and large-scale changes in ecosystem types. We refer to this dynamic in Figure 2.1 as 'abiotics'.

Finally, at the levels of ecosystem and functional biodiversity, 'resilience' is used to refer to several theoretical issues dealing with ecological thresholds and stability. Ecosystems may shift between multiple stable states (e.g., Holling, 1973; Scheffer et al., 2001). In a 'pristine' state the ecosystem may have aesthetic value and provide

¹ This is limited to theories that are relevant in an economic context. For example, evolutionary theories that explain increases in (genetic) biodiversity (e.g., neutral genetic drift) are not addressed here.

ecological functions. Incremental changes in abiotic conditions, however, may cause the system to approach a threshold level. An incidental shock may then relatively easily push the ecosystem into an alternative, possibly less attractive state. In evaluating resilience, two dimensions or interpretations are relevant: the degree of disturbance an ecosystem can endure without flipping to an alternative state (Holling, 1973) and the speed with which the ecosystem may return to its pristine state after a disturbance (Pimm, 1984). It should also be noted that resilience of ecosystems is studied in two directions: namely, the effect of biodiversity loss on resilience and ecosystem functions, and the impact of reduced resilience on biodiversity (e.g., Holling et al., 1994; Loreau et al., 2002; Tilman et al., 2005).

Many of the above theories and indicators are connected to human activities. Armsworth et al. (2004) summarise the main threats to biodiversity from human activity: introduction of exotic species, climate change, harvesting, and habitat loss (including fragmentation and degradation). Although Figure 2.1 does not list these threats, we will give some attention to the role of these threats in choosing a particular type of economic model.

2.3. Review of economic models of biodiversity conservation

2.3.1. Cost-effectiveness models

The class of cost-effectiveness (CE) models is defined to contain all models of biodiversity conservation in which a budget restriction determines the level of conservation effort. This broad definition implies that this group of models is diverse, but two main topics can be discerned. First, a large share of CE models look for a cost-effective spatial distribution of habitat patches. Second, several CE models address the prioritising of species for conservation. Although many of these models do not explicitly define the decision maker, given these topics, we may safely regard him to be a conservation manager. CE models can be applied to large spatial scales to study conservation of genetic, species, ecosystem as well as functional biodiversity.

Some CE models focus on prioritising species that can be conserved. Weitzman (1992) argues that conservation priorities must be based on a species' contribution to total biodiversity. Using the genetic uniqueness of species, he develops a way to measure this contribution at the species level. Applications of this tool can be found for instance in Solow et al. (1993), Montgomery et al. (1999) and Reist-Marti et al. (2003). This use of genetic diversity in biodiversity (species) conservation, however, has received some criticism for ignoring other attributes of

species that may have economic value (e.g., Humphries et al., 1995; Crozier, 1997; Mainwaring, 2001). Accordingly, several additions to Weitzman's measure have been suggested. For instance, Nehring and Puppe (2002) include qualitative attributes of species in the biodiversity measure, while Weikard (2002) describes an application of the biodiversity measure to the ecosystem level. Önal (2003) develops an indicator in which species richness as well as genetic uniqueness contributes to the level of biodiversity.

By themselves, the above models do not indicate cost-effective conservation solutions. Weitzman (1998) adds changes in species' survival probabilities due to conservation efforts to this type of model. Interestingly, he shows that it is not necessarily the most unique species that must be preserved, but rather those species with the best combination of genetic uniqueness and chance of long-term survival. Again, some authors have suggested extensions to make this model more realistic, which mostly have focussed on including species interactions. In Witting et al. (2000) and Van der Heide et al. (2005) species' survival probabilities are determined by conservation effort as well as the survival of other species. Baumgärtner (2004) also models interdependent survival probabilities in the species set. Additionally, he includes the provision of ecosystem services that is dependent on the survival of a specific species.

While the setting of priorities is important in the design of conservation policies, policy makers are also interested to know where to preserve these species. Many CE models therefore investigate the reserve site selection problem, often formulated as a maximum coverage problem (MCP). This MCP is that conservation funds are directed towards habitat reserves containing the most species. This is a static, deterministic approach as used in Ando et al. (1998) and Polasky et al. (2001). In reality, however, the MCP is dynamic, because the funds needed to acquire all selected reserve sites may not be immediately available. By the time they are, potential reserve sites may already have been developed. Costello and Polasky (2004) and Snyder et al. (2004) develop the MCP with regard to uncertainty about future land use. In many of these models, reserve sites are stand-alone units. Drechsler (2005) incorporates the spatial coherence of reserve sites in the MCP. Furthermore, not all types of land use are equally detrimental to the existence of a species. Hence, uncertainty about species coverage in the MCP may also arise from land use pressure that is spatially heterogeneous as in Arthur et al. (2002) and Pfaff and Sanchez-Azofeifa (2004). Finally, it is not just land use that determines the survival of a species, as this may also be dependent on the presence of other species. One way to approximate species interaction is to use correlations between

the occurrences of species in which one species is used as an indicator for the presence of other species (e.g., Juutinen and Mönkkönen, 2004).

The reserve site selection problem becomes more complex when ecological as well as economic targets are pursued. Typically, a higher standard achieved in one type of target entails a loss for the other. A production possibilities frontier (PPF) may be constructed by maximising a function that encompasses both an ecological and an economic variable.² This PPF shows possible combinations of the two variables that achieve the maximum level of the target function. Lichtenstein and Montgomery (2003) trace the PPF for a forest that on the one hand is used for wood production, but on the other hand must contain at least a minimum level of species richness. They use a large set of species, each of which requires a minimum amount of contiguous habitat to survive. Nalle et al. (2004) and Groeneveld et al. (2005) employ metapopulation dynamics and spatial distributions of reserve sites in their determination of the PPF.

So far, the CE models we have reviewed specifically deal with prioritising species and the spatial design of conservation policies. Some models are more concerned with other aspects of policy design. For instance, conservation policies often assume constant marginal returns to conservation expenditures. Ecosystems, however, may be subject to non-linearities due to threshold effects. Wu and Boggess (1999) and Wu and Skelton-Groth (2002) show that threshold effects influence the allocation of conservation funds to different ecosystems. Another issue is the cost-effectiveness of conservation policies that require the cooperation of private landowners.³ These may need financial incentives to allocate their land or use techniques that benefit the conservation goal. Since individuals have different land endowments and preferences, the cost-effectiveness of compensation schemes can be increased by implementing heterogeneous, rather than homogeneous, payments. Several authors consider this issue, looking at both spatial and temporal aspects in land use (e.g., Drechsler and Wätzold, 2001; Johst et al., 2002; Wätzold and Drechsler, 2005; Groeneveld, 2005).

² Strictly speaking, recent modelling efforts discussed in this paragraph have moved this type of model beyond our definition of CE modelling, as the budget constraint has been dropped in favour of a multi-criteria maximisation problem. Given the history of these models, it seems justifiable to discuss these models under this heading.

³ This type of model addresses issues that are closely related to the principal-agent problem. It is outside the scope of this chapter to go into this literature as well. We refer the reader to, for instance, Smith and Shogren (2002).

Table 2.1. Frequency of biodiversity theories and concepts in CE models ^a

Biodiversity level	N	Biodiversity theories				Biodiversity concepts				
		Meta-population	Inter-action	Abiotic	Resilience	Genes	Rich-ness	Even-ness	Represen-tativeness	Quality
Genetic	0	-	-	-	-	0	-	-	-	-
Species	25	5	4	-	-	(11)	10	0	1	(1)
Ecosystem	3	-	-	2	2	-	0	0	0	-
Function	0	-	-	0	0	-	-	-	-	0

^a N is the total number of models found. Numbers in parentheses indicate the number of models that use biodiversity theories or indicators that apply to levels of biodiversity not consistent with our framework.

Table 2.1 summarises the results of our review of CE models, which seem to emphasise the threats of habitat loss and habitat fragmentation.⁴ Twenty-five of the CE models reviewed consider biodiversity conservation at the species level. Of these, three models employ metapopulation theory in that both size and location of habitat area matter, whereas two others only consider habitat size. Species interactions are covered in three of the models, one of which does so implicitly by use of indicator species.

With respect to biodiversity concepts, Table 2.1 paints a complex picture. As it turns out, some models are applied at one level of biodiversity, but also use theories that apply to other levels of biodiversity. Eleven models, for instance, follow the Weitzman (1992) model and prioritise species for conservation, based on genetic information. Similarly, one model suggests priorities for species conservation by looking at their role in the provision of ecosystem functions. With respect to biodiversity indicators, there are ten models of species biodiversity that use the indicator species richness. Most of these models deal with the MCP problem and inherently maximise the number of protected species. One model uses a weighting function to determine the level of biodiversity of a species set. This weighting can be regarded as a tool for expressing representativeness.

Conservation of biodiversity at the ecosystem and functional levels has received relatively little attention. Of the two levels, only biodiversity at the ecosystem level is considered. Ecosystem biodiversity, however, appears explicitly in only three models.

⁴ One remark on these results is in order, as in this section we mix analytical with numerical models. As a rule, the more complex a model is, the harder it is to arrive at analytical solutions. Some of the analytical models in our review, however, integrate quite complex, but stylised ecological processes. Numerical methods are used mainly for (dynamic) models with large (spatial) data sets.

Of these, two consider both resilience and ecosystem interactions. None of the models at the ecosystem level takes biodiversity indicators into account.

2.3.2. Renewable resource extraction models

Renewable resource extraction (RR) models are built on the consideration that a species' population may have economic value, particularly when harvested. With fisheries in mind, Gordon (1954) and Schaefer (1954) find that complete depletion of such populations, i.e. extinction, is suboptimal. Clark (1973), however, shows that extinction is optimal if a species is unable to generate a competitive return, as determined by economic and biological parameters (see also Clark and Munro, 1975). RR models can be used to study two types of problems. One is that of an individual resource owner who determines his private optimal rate of harvesting, whereas the other is that of a government planner who wants to achieve socially optimal harvesting. CE models can thus be used to study all four levels of biodiversity at both small and large spatial scales.

Irrespective of which sort of optimality is analysed, it is important to know the biological parameters of the target species' population dynamics. Many factors influence these parameters and much attention has gone towards integrating these factors into RR models. One first extension is to include the effect of species interactions. Hannesson (1983) considers a case in which both a predator and a prey are harvested. Alternatively, one can study a situation where just the predator (Ragozin and Brown, 1985; Wilen and Brown, 1986) or the prey (Hoekstra and van den Bergh, 2004) is harvested. Competition is another possible interaction between species. Flaaten (1991) models two harvested species that compete directly with each other for resources. Additionally, models can be extended to include evolutionary dynamics at the genetic level. An example of such dynamics is a case of intra-species competition of a diploid species that contains varieties with different genetic resistance to a pest (Munro, 1997; Brock and Xepapadeas, 2003). While evenness of genetic variety within a species is not a typical conservation target, the relative distributions of genetic varieties can form an important aspect of species management.

Wacker (1999) studies the optimal harvesting of a resource that has a mutually beneficial relation with a non-harvested resource. According to the author, this particular model is applicable to the Amazonian rainforest and climate change. The formal specification of the model, however, does not immediately suggest this. The model of Brock and Xepapadeas (2002) seems more specifically designed for analysing biodiversity at the ecosystem and functional level. A main part of this model is an area that is spatially heterogeneous with respect to abiotic conditions,

which are the resources for vegetation. In each patch of this area, flora compete for a limiting resource with the result that all but the most competitive species are lost, as well as many ecosystem functions. In this model, the management problem is to preserve enough species to maintain the ecological functioning in the entire area. Perrings and Walker (1997) present a model of a relatively complete ecosystem with grazers, competition between two types of vegetation and the abiotic event of fire. Formally, in this model the conservation target is the population of grazers. The main point of the model, however, is to show the impact of grazing on the composition of the vegetation, and its impact on the probability of crossing an ecosystem threshold in case of a fire event (see also Janssen et al., 2004).

Much effort has gone into extending RR models with metapopulation dynamics between habitat patches. Sanchirico and Wilen (1999) present an early model that explicitly integrates metapopulation dynamics into an RR type of model. In this model, there is multidirectional movement of individuals of the species, i.e. emigration and immigration both occur in each patch. More recent models tend to focus on the management implications of setting up select patches as reserve sites where harvesting is not allowed. Schnier (2005) considers the effect of reserve sites under the assumption that the resource has different intrinsic growth rates in the various patches. Populations may moreover be structured into distinct age groups, which may affect harvesting rates and the location of reserve sites. In Smith and Wilen (2003), the age structure of the population is continuous, but more models look at populations that have distinct life cycle stages (Brown and Roughgarden, 1997; Pezzey et al., 2000; Imeson and van den Bergh, 2004; Sanchirico, 2005).

RR models can also be formulated to further investigate the cost structure of resource harvesting. Harvesting costs themselves are differentiated over species (Agar and Sutinen, 2004) or over patches (Sanchirico and Wilen, 2005). The harvested population may also generate costs or benefits that have not yet been discussed. Swanson (1994) incorporates the opportunity cost of a habitat area in RR models, which has a negative impact on a species' economic return. Furthermore, non-use values do have a significant impact on a species' economic return.⁵ Horan and Shortle (1999) examine non-use value in a multi-patch habitat without metapopulations effects, but most analyses of non-use values have looked at a single habitat area (Skonhofs, 1999; Alexander, 2000; Dyar and Wagner, 2003) or none at all (Rondeau, 2001; Hoekstra and van den Bergh, 2004). RR models can be

⁵ Although non-use values affect the optimal management of a harvested species, the RR model type seems unsuitable to species that generate non-use values only (Alexander and Shields, 2002).

used to study many more economic aspects of resource management. A complete account of the possibilities is beyond the scope of this chapter, but we suggest Bulte and van Kooten (1999) or Bulte and Horan (2003).

The focus of RR models is the threat of harvesting, with a secondary concern for habitat loss and fragmentation. Given that RR models consider only a small number of species, it is not surprising that they rarely include biodiversity indicators. Nonetheless, a species may also generate non-use value in that it contributes to the overall level of biodiversity. In Li et al. (2001), the level of biodiversity is indicated by species richness. The results of the two RR models that integrate evolutionary dynamics are partially dependent on the even distribution of a species' genetic varieties. This evenness, however, is not explicitly used as a conservation target.

Table 2.2 shows the results of our review of thirty-two RR models. We evaluated thirty models of biodiversity management at the species level. Two of these include information on genetic biodiversity and another two emphasise the importance of abiotic conditions in the ecosystem. Metapopulation dynamics are explicitly used in eight models, whereas a contiguous habitat area is included in another five models. The effects of species interactions on optimal management have also received a fair amount of attention in nine models. Biodiversity indicators are not a major issue in RR modelling. Species' contributions to overall biodiversity are considered in two papers, of which one uses species richness and the other applies Weitzman's (1992) approach. Finally, two papers are intended to provide insight into managing ecosystems and functions. One of these has a fairly general structure, but the other clearly focuses on the role of abiotic conditions and spatial heterogeneity. Neither of these models considers any biodiversity indicators.

Table 2.2. Frequency of biodiversity theories and concepts in RR models^a

<i>Biodiversity level</i>	<i>N</i>	<i>Biodiversity theories</i>				<i>Biodiversity concepts</i>				
		Meta- population	Inter- action	Abiotic	Resilience	Genes	Rich- ness	Even- ness	Represen- tativeness	Quality
Genetic	0	-	-	-	-	0	-	-	-	-
Species	30	13	10	(2)	(2)	(2)	1	0	0	-
Ecosystem	2	-	(1)	1	0	-	0	0	0	-
Function	0	-	-	0	0	-	-	-	-	0

^a *N* is the total number of models found. Numbers in parentheses indicate the number of models that use biodiversity theories or indicators that apply to levels of biodiversity not consistent with our framework.

2.3.3. Macroeconomic growth models with natural resources

Macroeconomic growth (MG) models are used to analyse optimal growth paths of an economy over time. When they are extended to include the effects of growth on the environment, MG models can indicate whether or not this growth is sustainable. Since economic growth is a macroeconomic variable, the decision-maker who desires optimality or sustainability generally is a government planner, but even our selective survey comprises models that use various assumptions and model specifications. Older MG models tend to focus on non-renewable resources and irreversibility, whereas newer models mainly consider renewable resources. Regardless of these distinctions, all MG models are applied at a large spatial scale and suitable for analysing biodiversity at all levels.

The original context of older MG models would be, for instance, the extraction of diamonds or oil, in which the resource provides a direct use value. It has no economic value in its natural state. Fisher et al. (1972) consider a non-renewable resource that may either be irreversibly developed or left in a natural state.⁶ Contrary to previous models, however, if the resource is left undeveloped, it generates a non-use value. This development of the model type allows that the definition of resources can be broadened to include land or even ecosystems and functions. Given the simple representations of environmental resources in many models, however, such interpretations must be made with due care.

Nonetheless, in MG models there is a potential for extensions into these levels of biodiversity. As far as the integration of biodiversity theories and concepts is concerned, not much progress has been made since Fisher et al. (1972). Instead, attention has been directed to relaxing the underlying assumptions of the model with respect to, e.g., the role of technology (Krautkraemer, 1985; Barrett, 1992), the irreversibility of development (Rubio and Goetz, 1998) or the degree to which the government planner is risk-averse (Smith and Son, 2005).

We found only two models that explicitly include biodiversity theories and concepts in an MG model. One of these is Rowthorn and Brown (1999), who consider the potential for preservation of natural land. In its natural state land produces biodiversity, which is expressed as species richness. Species richness is modelled as a concave function of the amount of natural land that is available. The other model analyses land preservation under the restriction that natural land must be available to a renewable resource. Using an MG model with biological dynamics

⁶ A related literature deals with the economic valuation of environmental goods and services when there is irreversibility and uncertainty. It is not our aim to give a review of valuation theory, but suggest the reading of, for instance, Arrow and Fisher (1974) and Kassari and Laspere (2004).

reminiscent of RR models, Miller (1981) studies the effects of a species' population on the potential to preserve natural land. This species generates a non-use value only. Similar to the development seen in MG models with non-renewable resources, recent developments in MG models with renewable resources focus on relaxing certain model assumptions (e.g., Eliasson and Turnovsky, 2004; Valente, 2005). In these models, the renewable resource is represented in a relatively simple fashion, making their application to ecosystem and functional biodiversity difficult.

Table 2.3. *Frequency of biodiversity theories and concepts in MG models*^a

<i>Biodiversity level</i>	<i>N</i>	<i>Biodiversity theories</i>				<i>Biodiversity concepts</i>				
		Meta- population	Inter- action	Abiotic	Resilience	Genes	Rich- ness	Even- ness	Represen- tativeness	Quality
Genetic	0	-	-	-	-	0	-	-	-	-
Species	30	13	10	(2)	(2)	(2)	1	0	0	-
Ecosystem	2	-	(1)	1	0	-	0	0	0	-
Function	0	-	-	0	0	-	-	-	-	0

^a *N* is the total number of models found. Numbers in parentheses indicate the number of models that use biodiversity theories or indicators that apply to levels of biodiversity not consistent with our framework.

In Table 2.3, we present the results of our review. Interest in biodiversity in MG modelling is low, with only two articles that explicitly model issues related to biodiversity management. Many models have functional specifications that could be considered to touch on biodiversity, but we did not include these in our review, because the majority focuses on economic, rather than ecological, extensions. In the two models we have considered, the incorporated threat to biodiversity is habitat loss. Both models consider biodiversity at the species level. One model looks at the management of a single species that requires an amount of habitat to exist. In the other model, habitat is needed to maintain species richness. Neither model looks at metapopulation dynamics or species interactions. We have not found a model of economic growth where the environmental restrictions are based on the preservation of biodiversity at the ecosystem or functional level.

2.3.4. General equilibrium models with natural resource externalities

General equilibrium (GE) models are systems of input-output relations, or markets, where prices and volumes of traded goods are determined simultaneously. If the production of a traded good requires an input for which there is no market, such as many natural resources, then the production and consumption levels of that traded

good will be inefficient. GE models can be used to study such inefficiencies and policies to remedy them. GE models describe the behaviour of an individual, but it is assumed that this individual is representative of a large group of individuals. Therefore GE models essentially describe complete economic systems and thus apply to a large spatial scale.

Hannon (1976) argues that the principle of flows of inputs and outputs in GE models of economies is equally applicable to ecosystems. In an ecosystem, a species functions much like an economic agent: the species attempts to maximise its cumulative biomass by expending and accumulating units of energy. Crocker and Tschirhart (1992) present a GE system of an ecosystem that is affected by economic behaviour. In this model, humans hunt a pest species, whose existence conflicts with human consumption.⁷ The pest, however, is also the prey of a species with a positive non-use value. Crocker and Tschirhart show how this ecological connection affects market prices and the optimal population levels of both species. Recent advances in this type of model have extended into the ecological as well as the economic realm. An elaborate ecological system with eight species, one of which is harvested, is simulated in Finnoff and Tschirhart (2003a, 2003b). Jin et al. (2003) analyse the impact of changing technological parameters where both the economic and the ecological systems contain four sectors, or species.

Aside from their application to regional markets of economies and ecosystems, GE models have also been applied to issues in interregional trade. Insofar as such models address the management of natural resources, the emphasis is on the role of property rights and the welfare effects of trade regulations. Similar to our observation of MG models, this particular type of GE model uses fairly simplistic representations of environmental goods. Usually, the production of a traded good requires the input of a renewable resource that is connected to the production sector, but not to other natural resources (e.g., Brander and Taylor, 1998; Datta and Mirman, 1999; Emami and Johnston, 2000). This makes the application of the model results to many issues in biodiversity conservation, particularly at the ecosystem or functional levels, relatively problematic.

We have found two recent GE models of interregional trade in which the approximation of ecological complexity is increased beyond the usual level. Smulders et al. (2004) describe a system where a traded good requires inputs of a renewable resource and land. The resource, however, also needs some undeveloped land as its habitat. A similar trade-off in land allocation is modelled in Polasky et al. (2004), but

⁷ Mice that feed on grain are a good example.

here the motivation to leave some land undeveloped is for the non-use value that habitat generates by producing species richness.

Table 2.4 shows the results of our review of GE models. As in the previous section, we did not include models that use highly abstracted representations of biodiversity. If we had, the number of relevant GE models, particularly of the type that describes interregional trade, would be much higher. As it is, the list comprises six papers that consider aspects of biodiversity conservation. These look at the threats of harvesting and habitat loss. Four of these include very detailed and complex species interactions. Habitat availability is used in two of the models, although each case does not include metapopulation dynamics. Only one of the five models considers a basic biodiversity indicator, i.e. species richness. Neither ecosystem nor functional diversity has been analysed.

Table 2.4. Frequency of biodiversity theories and concepts in GE models^a

<i>Biodiversity level</i>	<i>N</i>	<i>Biodiversity theories</i>				<i>Biodiversity concepts</i>				
		Meta- population	Inter- action	Abiotic	Resilience	Genes	Rich- ness	Even- ness	Represen- tativeness	Quality
Genetic	0	-	-	-	-	0	-	-	-	-
Species	6	2	4	-	-	-	1	0	0	-
Ecosystem	0	-	-	0	0	-	0	0	0	-
Function	0	-	-	-	0	-	-	-	-	0

^a *N* is the total number of models found. Numbers in parentheses indicate the number of models that use biodiversity theories or indicators that apply to levels of biodiversity not consistent with our framework.

2.4. Conclusion

The purpose of this chapter has been to establish the current state of economic modelling and theoretical analysis of biodiversity loss and conservation. We review studies within four economic model categories: cost-effectiveness (CE) models, renewable resource extraction (RR) models, macroeconomic growth (MG) models with natural resources and general equilibrium (GE) models with natural resource externalities. We also examine how often specific biodiversity theories and indicators are being applied. Although the diversity of modelling approaches turns out to be high, we have been able to make several general observations about economic modelling of biodiversity conservation.

Overall attention to biodiversity conservation, in terms of number of studies performed, tends to decline as models gain economic complexity. While many CE and RR models cover biodiversity at some level, MG models and interregional GE

models are less frequently used to study aspects of biodiversity conservation. Admittedly, there are a large number of models that describe an unspecified, ecologically isolated renewable resource within the latter two model categories. This resource can equally denote a species, an ecosystem or an ecological function. In other words, these models are of a very general nature, with all obvious advantages and disadvantages.

This observation suggests that there are opportunities to develop MG and GE models of biodiversity conservation. Models of these types emphasise harvesting and habitat loss as the major threats to biodiversity caused by human activity. Threats such as habitat fragmentation, habitat degradation and climate change may conceivably be included as well. CE models also have a limited application range, focusing mostly on habitat loss and fragmentation. Ventures into modelling habitat degradation appear to be fruitful directions and further extensions may prove useful. In principle, the same holds for RR models, although these models were developed specifically to study harvesting. Regardless of type, the increased ecological realism of the resulting models is likely to frustrate analytical solutions.

The models that deal with biodiversity in more detail present a very strong emphasis on biodiversity at the species level. This makes sense, as there is relatively much more knowledge about species, as compared to our understanding of genetics, ecosystems and functions. The emphasis on species is also understandable in the case of RR models, considering their original purpose. We find that CE, MG and GE models are used exclusively in the context of government planning, and therefore were expected to address all levels of biodiversity. Yet species diversity is dominant in these models as well. With respect to the level of biodiversity that is considered, chances for improvement lie largely in extending the CE, MG and GE model types.

In all four model categories, surprisingly little attention is devoted to the biodiversity indicators of evenness and representativeness. It can be argued that these models are used to analyse and support the protection of rare and representative species and ecosystems. But within particular groups of fragile species and ecosystems, trade-offs in conservation of specific species may be possible to improve the efficiency and effectiveness of conservation efforts. It may, for instance, be beneficial to allocate conservation funds to fewer, but rarer species or ecosystems, and vice versa. To analyse such considerations, however, requires that larger sets of species are modelled than currently is being achieved.

Compared to analysing the conservation of individual species, considering biodiversity at the ecosystem level and qualitative aspects of biodiversity (such as evenness and representativeness) increases the implied spatial scale of the analyses. It has been suggested above that GE and MG models are suitable to deal

with this larger spatial scale, but an alternative option also presents itself. Conserving ecosystems means that environmental externalities resulting from land used for non-conservation purposes must be taken into account, and that decisions on socially optimal biodiversity conservation ideally include the costs and benefits of alternative allocations of land. Hence, another promising way to proceed in economic modelling of biodiversity conservation may be to pay attention to spatial-economic models.

It is easy to recommend incorporating more ecological complexity in economic models of biodiversity, as we have done above. It is fair to add a disadvantage, namely that theoretical, analytical solutions will often become impossible. Fortunately, numerical solutions will always be possible and perhaps this is the direction that this type of research must be taken in. The fine balance between ecological relevance and analytical tractability requires compromise, as well as good communication between economists and ecologists.

3. An ecological-economic model of biodiversity and land use: urban growth, agriculture and nature in a wetland area¹

3.1. Introduction

Biodiversity loss is a growing concern. Important causes of biodiversity losses are habitat destruction and alteration of abiotic conditions in natural areas. These effects are caused by land use, which is an inevitable consequence of economic activity. Wetland have been severely diminished throughout human history (Hook, 1993). In densely populated areas, such as much of Western Europe, wetlands and wetland species are under continued high pressure from land use. This chapter analyses the sustainability of urban growth and wetland biodiversity.

Society derives many benefits from economic growth and land use. The benefits of biodiversity, however, are often overlooked (Barbier et al., 1994, Chapter 4). Many models of wetland-economy interactions therefore identify stakeholder interests (e.g. Turner et al., 2000; Söderqvist, 2003; Kaplowitz and Kerr, 2003). Such models, however, do not entirely solve issues of social optimality and sustainability of land use and wetland conservation. To analyse sustainability of economic growth with respect to wetland biodiversity, models are needed which simultaneously describe the linkages between economic growth, land use and their effects on wetland biodiversity. Example of such models can be found in Van den Bergh et al. (2004), Simonit et al. (2002), and Chopra and Adhikari (2004).² Preserving habitats in reserve sites is essential to species conservation.³ Broadly speaking, there are two approaches to reserve site management: the single-species and the landscape view. In a single-species approach, the population number of an indicator species is

¹ This chapter has also appeared as: Eppink, F.V., J.C.J.M. van den Bergh, P. Rietveld, 2004, Modelling biodiversity and land use: urban growth, agriculture and nature in a wetland area, *Ecological Economics* 51: 201-216.

² The model by Chopra and Adhikari (2004) is somewhat similar to our own, but emphasises wetland hydrology rather than land use.

³ Another approach would be to restore ecosystems and habitats (e.g. Perrings and Walker, 1997; Janssen et al., 2004). In ecosystem restoration and management, irreversibility, resilience and hysteresis effects are important. These effects can occur in case of multiple equilibria and may cause excessively high restoration costs. The level of biodiversity, however, is not necessarily an equilibrium phenomenon (e.g. Chesson, 2000; Hubbell, 2001). Our model, however, is not concerned with restoration, but with sustainability and optimal conservation as an endogenous outcome of equilibrium land use.

assumed to reflect the status of other species in the reserve. The representativeness of the indicator species, however, is questionable (Andelman and Fagan, 2000). Moreover, habitat requirements of the indicator species may conflict with the needs of other species (Simberloff, 1998). In the landscape approach, it is assumed that species at all trophic levels benefit from pristine habitat conditions (Franklin, 1993; Noss, 1990). Hence, reserve site management from a landscape perspective aims to approximate natural habitat conditions and does not explicitly focus on species management. Although the latter approach does have its own problems, there is a growing interest in the landscape perspective (Goldstein, 1999).

According to Franklin (1993), there is a strong relation between human land use and (abiotic) conditions in nearby nature reserves. He argues that conservationists should consider the landscape matrix, the spatial mix of land use and reserve sites. Land use allocation thus becomes an important variable in biodiversity conservation. Reconciling economic goals, such as increasing production and maximising land values with wetland biodiversity conservation requires a model that integrates 'land economics' and 'biodiversity ecology'.

This chapter first identifies dominant approaches in land use modelling and evaluates their characteristics. One modelling approach is then selected for its ability to integrate concepts from both ecology and economics. This modelling approach is then applied to develop a general, dynamic model that can be used to simulate the conflict between land use and wetland biodiversity conservation. We use the model to trace the effects of various policy options to conserve biodiversity and to improve social welfare.

The model presented in this chapter builds on the recommendations in chapter 2 by incorporating various impacts of land use on abiotic conditions in two types of ecosystems, which affect their sizes and the species they contain. The chapter is organised as follows: section 3.2 surveys approaches to models of land use and wetland-land use interactions, section 3.3 develops the ecological-economic model of land use and biodiversity, simulation results are presented in section 3.4, and the conclusion follows in section 3.5.

3.2. Approaches to land use modelling

3.2.1. A classification scheme

This section presents a non-exhaustive survey of spatial economic analyses of land use. Considering the importance of the landscape matrix, we are interested in the emergence of land use patterns and the underlying economic decisions. Hence, this

review only lists modelling approaches that explicitly cover land use allocation. This limitation means that many other spatial economic models, such as multi-regional models and spatial equilibrium models are excluded. Neither model type is intended for the type of spatially explicit analysis envisioned in this chapter.

A multitude of classification schemes for land use change models has been suggested (e.g. Kaimowitz and Angelsen, 1998; Briassoulis, 2000; Veldkamp et al., 2001; Irwin and Geoghegan, 2001). The classification scheme presented here distinguishes between pure optimisation, non-optimisation, and hybrid models (see Table 3.1). Our classification system reflects the presence of decision variables, exogenous forces, or both in the model structure.

Table 3.1. A classification of land use models

Primary characteristic	Pure optimisation			Non-optimisation		Hybrid	
Secondary characteristic	Analytical	Numerical	Statistical	Heuristic decisions	Cellular automata	Theoretical	Statistical

In pure optimisation models, a public decision maker or an economic agent optimises one or more decision variables so as to maximise or minimise a goal function that describes, for instance, utility, income, profits or costs. Typical decision variables in land use modelling are volume, spatial allocation, and timing of land development. The spatial scale of the represented decision process typically is small, ranging from the level of individuals or households to the level of local areas. Large scale exogenous forces are absent from this model type. While in many of these models space is homogeneous and abstract, inclusion of distance dependent costs (e.g. transport costs) or land quality introduces some degree of spatial differentiation. The resulting models are mostly static.

This model class can be subdivided into analytical, numerical and statistical models. Analytical models capture land use decisions in an abstract framework that allows for mathematical solutions. Numerical models take parameter values from real world situations. Statistical models within this class, used to estimate parameter values from empirical data are based on the assumption that the data were generated by rational, optimising economic agents. Without this assumption, more degrees of freedom would lead to different estimation results.

Non-optimisation and hybrid models are generally characterised by inclusion of large scale exogenous forces. Hence, they describe large scale (regional, national or even global) land use patterns. The difference between the two model types is that land patterns in non-optimisation models are not consistent with microeconomic theory. Instead, these models use heuristic decision rules or cellular automata to

allocate land use. Hybrid models, on the other hand, produce optimal land allocation patterns under the constraints imposed by exogenous forces. Geographic Information System (GIS) techniques are common to both model classes. As a result, model solutions are usually numerically calculated. Models in both classes are either dynamic or static-comparative.

3.2.2. *Pure optimisation models*

Tropical deforestation and urban development are very prominent issues in the subgroup of analytical pure optimisation models. Models of tropical deforestation analyse the land use decisions of farm households. The solutions to these models indicate the optimal timing or the extent of forest conversion and field maintenance (e.g. López, 1998; Coxhead et al., 2002). Economic models of urban development analyse the economic rationale of a social planner or a collective of individuals that underlies the optimal sizes of cities (e.g. Martinez, 1992) or location (e.g. Fujita et al., 1989).

Analytical pure optimisation models that address the impact of land use on species and wetland presence are rare. This rarity may be partially explained by the increased complexity arising from incorporating the ecological and the hydrological relations associated with wetland modelling. A recent model is presented by Simonit et al. (2002). They develop a model structure of several economic sectors that affect and are dependent on the ecological services provided by wetlands. The model is then used in a numerical study of the economic impact of wetland loss.

High complexity in optimisation problems can be compensated for by using numerical pure optimisation models. Musacchio and Grant (2002) model a farmer's decision to allocate land to either (wetland) rice paddies or cattle pastures, when rice crops are less profitable than husbandry. The rice paddies, however, attract geese that can be hunted for additional revenue. While the ecological and economic relations in this model are rather detailed, the model cannot deal with spatially explicit land allocation.

The use of GIS-techniques implies a further increase in complexity. Many models that use GIS optimise the spatial characteristics of wildlife habitats within budget constraints (for example, see Nevo and Garcia, 1996; Van Langevelde et al., 2002). Such models yield a cost-effective type of optimality. An alternative is presented by Seppelt and Voinov (2002). Their model maximises an ecological-economic performance criterion that compares environmental quality, which is approximated by nutrient outflows, against farmer income. The optimisation algorithm suggests a spatially explicit solution of optimal land allocation.

Pure optimisation models that use statistical techniques often concern land use or land prices. Models of land use typically attempt to determine the socio-economic factors that influence tropical deforestation (e.g. Chomitz and Gray, 1996). In models of land prices (hedonic pricing) studies infer values of non-marketed environmental characteristics from prices of marketable goods, such as houses (e.g. Bockstael, 1996). A small number of such studies concerns wetlands and biodiversity. For example, Geoghegan et al. (1997) estimate the value of landscape diversity in an urban area, the value of urban wetlands is assessed by Mahan et al. (2002) and the value of services provided by a tropical wetland is studied by Barbier (1994).

3.2.3. Non-optimisation models

Non-optimisation models are often part of climate change models, such as IMAGE (Alcamo, 1994) and AIM (Matsuoka et al., 1995) or of integrated assessment models such as TARGETS (Rotmans and de Vries, 1997). In these models, land use often is a proxy for human activities, and forms the basis for predictions on the impact these will have on environmental resources. Total demand for land use is determined by exogenous factors, such as demographic and economic changes, which serve as inputs to the land use module. Non-optimisation models use several techniques to spatially distribute this demand for land use.

Heuristic decision rules are one way of generating land use patterns. Expert knowledge is often used to translate historical land use patterns into simplified qualitative statements. It is assumed that these statements adequately represent the complex decision processes that determine actual land use patterns. An example of a set of heuristic decision rules is given in Table 3.2.

Table 3.2. Examples of heuristic decision rules for land allocation from the IMAGE model

Hierarchy of satisfying land use demands: agriculture, rangeland, exploited forest;
New agriculture is allocated to land with highest crop yield potential;
New grassland is allocated adjacent to agriculture, grassland or savanna;
Agricultural land taken out of production will revert to its climate-potential cover.

Source: Zuidema et al. (1994).

A more common technique in non-optimisation models is the use of cellular automata. Here, transition rules define the state of a grid cell as a probabilistic function of the state of neighbouring cells. Especially when integrated with GIS and large data sets, cellular automata are capable of creating endogenous land use

patterns over time. Examples of cellular automata in land use models are Engelen et al. (1995), De Kok et al. (2001) and Sui and Zheng (2001).

3.2.4. Hybrid models

Hybrid models combine the characteristics of optimisation and non-optimisation models: both exogenous forces and microeconomic decision variables are included. Thus, the models maximise the economic value of the land that is being allocated. Hybrid models are spatially explicit and very often make use of GIS. As with non-optimisation models, the spatial scale of these models is often restricted to national, regional and global patterns of land use.

Hilferink and Rietveld (1999) present an application of microeconomic bid-rent theory in a comparative static equilibrium model, the Land Use Scanner. The Land Use Scanner has been developed around the concept of suitability, which is an indication of how well-adapted a grid cell is to various land use types. Suitability is based on, for example, the cost of converting the current land use to a new type or proximity of identical land use. For the whole area, a suitability map is calculated. Land use types then 'bid' for grid cells. In this process of competitive bidding, a land use type with a high suitability value for a grid cell can place a relatively high 'bid' for this cell. As a result of this high bid, this type of land use has a higher chance of being allocated to this grid cells than land use types with a lower suitability value. The bidding process continues until the restriction of zero excess demand is met.

The CLUE (Conversion of Land Use and its Effects) approach, developed by Veldkamp and Fresco (1996), employs statistical estimation techniques. Regression analysis identifies socio-economic and biophysical determinants of land use. These results are then used to predict land use allocation at both coarse and fine spatial resolutions. Corrections to predictions of land use in grid cells are made for excessive deviations from the average values. Land use of a given type in a grid cell is increased if the grid cell is initially allocated a below-average amount of that land use type.

3.2.5. Selection of a land use modelling approach

There are both direct and indirect effects of land use on biodiversity in wetlands. The direct effects of wetland conversion for urban, agricultural and infrastructural development are loss and fragmentation of habitat areas. McArthur and Wilson (1967) have studied the relationship between habitat size and species numbers in the context of islands. They find that the level of biodiversity on islands is related to

their sizes. The smaller the habitat, the fewer and smaller the plant and animal populations it can support. Thus, as habitats shrink, species numbers are reduced.

Indirect impacts of land use affect abiotic conditions and change landscape composition. Tilman (1982) argues that abiotic conditions can determine competitive hierarchies between plant species. For wetland persistence, nutrient availability and groundwater levels are important abiotic factors. Persistent nutrient loading and ground water drainage in wetlands shift the competitive balance in favour of non-wetland vegetation. These human-powered changes in competitive hierarchies mean that wetlands necessarily lose out to other landscape types.

A desirable model of land use and wetland biodiversity includes both the direct and the indirect effects of land use. As we have already mentioned in section 3.2.2, the resulting complexity would make it almost impossible to employ an analytical pure optimisation modelling approach. This ideal model can also represent dynamics of land allocation decisions and biodiversity change. Pure optimisation models usually are static and therefore less suited to the task. Hence, the choice set can be limited to non-optimisation and hybrid models.

While non-optimisation models are dynamic, they are not based on fully rational, optimising behaviour. Thus they cannot adequately take into account the costs and benefits of land use and habitat conservation. The land use pattern suggested by non-optimisation models may well be inconsistent with economically optimal land use patterns. A hybrid modelling approach, combining a certain amount of ecological complexity with economic behaviour, thus appears to be the best option for a general dynamic model of wetland biodiversity and land use.

3.3. A model of land use and wetland biodiversity

3.3.1. Overview

In the following sections, we develop a dynamic hybrid model that simulates urban expansion and its effects on wetland biodiversity. Imagine an isolated city, surrounded by a finite amount of natural area, which in a complete undeveloped state contains only wetland. The property rights to this area are owned by individual land owners. These land owners sell their property rights to the highest bidder. City inhabitants can be divided into two groups of bidders. The first group, referred to as

'expansionists', favours urban expansion, while the second group, the 'conservationists', prefers conservation of the natural area.¹

The driving factor of the model is population growth, which occurs entirely within city limits. A growing population brings economic benefits because of positive agglomeration effects. Population growth, however, also has a negative effect: population density increases. To alleviate population density, expansionists attempt to buy right to the surrounding natural area in order to convert it to urban land use. This increase in human land use is at the loss of wetland biodiversity.

As biodiversity is reduced, conservationists' valuation of the remaining biodiversity increases. They raise funds, which consequently are used to buy property rights to the natural area. Once conservationists have property rights to the natural area, this purchased area becomes a nature reserve that cannot be used for further urban development. In this fashion, increased valuation of the environmental resource is capitalised into the property rights to the wetland. City growth thus becomes more expensive.

Biodiversity is a composite term that comprises many aspects of natural areas. Basically, biodiversity measures all species, from micro-organisms up to big mammals, and their relative abundance. By partitioning biodiversity into a few key aspects, we can capture its conceptual scope. Four levels of biodiversity exist: the genetic, the species, the ecosystem, and the functional level. The latter three levels of biodiversity relate to species and ecological communities in their abiotic environments, respectively. We focus attention on species and ecosystems, because they are the most studied in relation to human activities. Furthermore, we assume our biodiversity indicators can be expressed in monetary units.

The model is shown schematically in Figure 3.1. It consists of four modules. Changes in stocks of land use are tracked in the 'Land use accounting' module. The magnitudes of the environmental pressures resulting from the various types of land use and their implications for biodiversity are determined in the 'Biodiversity changes' module. The dynamics of urban expansion, affected by biodiversity change and population pressure, are modelled in the module labelled 'Land use decision'. The module 'Social evaluation' collects the performance indicators used to evaluate policy scenarios (presented in section 3.4). Below, these four modules are discussed in more detail, along with definitions of model variables and equations in general form.

¹ Hence, the value of the surrounding area is variable in our model. Including an external effect of urban growth on urban land prices is a deviation from standard urban economics in which returns to undeveloped land are fixed (such as Martinez, 1992).

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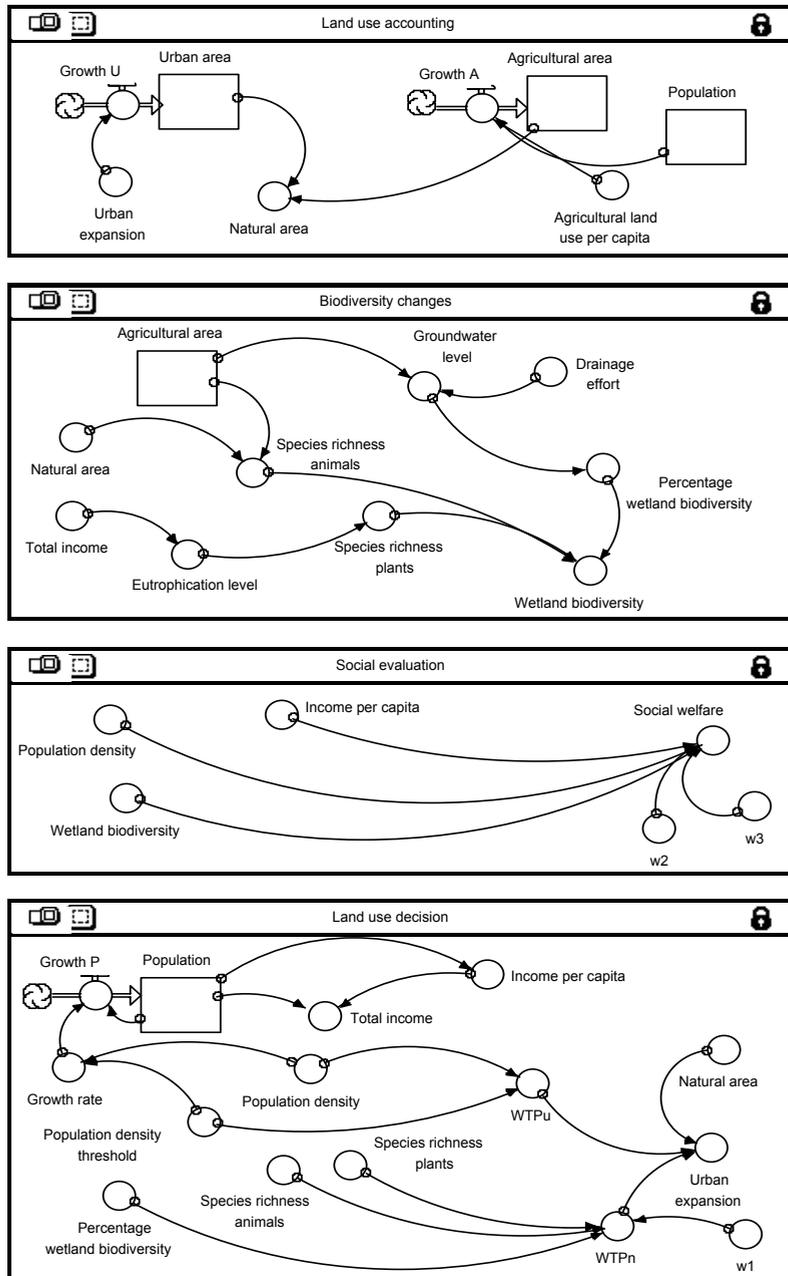


Figure 3.1. A schematic representation of the model

The complete structure of the simulation model, with functional specifications, parameter values and initial conditions, is given in Appendix 3.A.

3.3.2. Land accounting

The land use accounting module describes the development over time of the areas of urban and agricultural land use, as well as of land cover. The extent of urban land use, or city size, is a stock variable

$$U_t = U_{t-1} + \Delta U_t \quad U(0) = U_0 \quad (3.1)$$

and

$$\Delta U_t = f_U(WTP^u, WTP^n) \quad \frac{\partial \Delta U}{\partial WTP^u} \geq 0, \frac{\partial \Delta U}{\partial WTP^n} \leq 0 \quad (3.2)$$

where U_t is the area allocated to urban land use in period t and ΔU_t represents urban growth in period t .² Respectively, WTP^u and WTP^n are the prices expansionists and conservationists are willing to pay for property rights to the wetland. The decision to develop wetland area in favour of urban and agricultural land use is described in more detail in section 3.4. The agricultural area is modelled as

$$A_t = A_{t-1} + \Delta A_t \quad A(0) = A_0 \quad (3.3)$$

and

$$\Delta A_t = c \Delta P_t \quad c \geq 0 \quad (3.4)$$

where A_t is the area allocated to agriculture in period t , ΔA_t is agricultural growth in period t and ΔP_t is population change in period t (see section 3.4). To avoid unnecessary complexity in the model, we assume fixed agricultural yields and per capita agricultural demand that is constant over time. Thus, the area allocated to agriculture increases proportionally with population size. All area not in economic use is (semi-) natural habitat

² In Figure 3.1, urban growth is represented by both the variable 'Growth U' and the variable 'Urban expansion'. This is a modelling technicality; these variables have a 1:1 relation.

$$N_t = K - U_t - A_t \quad N(0) = N_0 \quad (3.5)$$

Here, N_t is natural land in period t and K is a fixed supply of land. Since U and A grow over time, N can only decrease. Consequently, natural area stabilises when urban growth stops.

3.3.3. Biodiversity changes

The biodiversity module describes the impacts of land use on biodiversity. Within overall biodiversity, Magurran (1988) distinguishes between species richness and species evenness. The former relates to the total number of species, whereas the latter reflects the composition, the relative abundance, of all species. Our model covers both aspects of biodiversity. First, total natural area consists of two types of land cover: wetland and some other non-wetland ecological community, such as forest or grassland. Second, species richness of both vegetation and animals is considered.

Modelling population responses for a set of species would make the model very cumbersome. Instead, we use empirical ecological studies that fit the rather general biodiversity indicators in this model. Furthermore, we normalise initial numbers of both plant and animal species to 100. Plant species richness is determined by

$$R_t^p = f_{Rp}(E_t) \quad \frac{df_{Rp}}{dE} \leq 0 \quad (3.6)$$

where R_t^p represents species richness of plant populations and E_t is nutrient availability in the ecosystem. Tilman (1982) suggests that the number of plant species decreases with nutrient availability. Wilson and Tilman (2002) show that this process can be described by a quadratic function. Because this function is increasing only over very low nutrient concentrations, our model considers just the downward sloping part of the curve.

Atmospheric deposition of nutrients is a very important mechanism of increased nutrient supplies in natural areas (Olde Venterink, 2000; Chapter 7). We assume atmospheric deposition, and hence nutrient availability increases with economic activity, which is indicated by total income.

$$E_t = f_E(Y_t) \quad \frac{df_E}{dY} \geq 0 \quad (3.7)$$

where Y_t is total income (see section 3.3.4). There is a saturation point of nutrient availability above which only species that flourish in nutrient-rich situations exist.

Animal species richness is dependent on habitat availability. Hence, species richness of higher trophic levels is

$$R_t^a = f_{Ra}(N_t, A_t) \quad \frac{\partial f_{Ra}}{\partial N} \geq 0, \frac{\partial f_{Ra}}{\partial A} \geq 0 \quad (3.8)$$

where R_t^a is species richness of animal populations. Results from Andrén (1994) and (2001) suggest that species richness is linearly related to habitat size. Since agricultural fields can support some wildlife, total habitat size is the sum of natural and agricultural areas. We assume, however, that few species prefer agricultural fields to natural areas. Hence, the contribution of A_t to R_t^a is smaller than of N_t .

Species composition, i.e. how many of the plant and the animals species are typical wetland species, is determined by

$$WD_t = f_{WD}(W_t, R_t^a, R_t^p) \quad \frac{\partial WD}{\partial W} \geq 0, \frac{\partial WD}{\partial R^a} \geq 0, \frac{\partial WD}{\partial R^p} \geq 0 \quad (3.9)$$

Here, WD_t is the (normalised) number of wetland species in period t and W_t is wetland area as a percentage of total natural area in period t . Since many animal species are adapted to particular types of habitat, species composition can be determined the relative abundance of land cover types. These are identified by dominance of vegetation adapted to specific abiotic conditions. The percentage of wetland area is calculated by

$$W_t = f_W(G_t) \quad \frac{df_W}{dG} \geq 0 \quad (3.10)$$

where W_t is wetland area as a percentage of total natural area. Hence, $(1-W_t)$ is the percentage of non-wetland natural area. G_t represents ground water depth in the surrounding ecosystem. As the ground water is lowered, wetland plants lose the competitive struggle with non-wetland plant species. A sigmoid function is used to determine W_t , following Runhaar et al. (1997).

Ground water depth is determined by drainage activities. Farmers drain ground water from their fields to increase yields. Pumping activities affect hydrology in surrounding areas. Hence, ground water depth in the natural area is linked to the amount of agricultural area

$$G_t = f_G(A_t, e) \quad \frac{\partial f_G}{\partial A} \leq 0, \frac{\partial f_G}{\partial e} \leq 0 \quad (3.11)$$

where e is an indicator for drainage effort. The value for drainage effort is set between 0 and 1, where 1 is maximal drainage. G_t is a bounded variable, its upper bound indicating surface level. The impact of drainage on the ecosystem is proportional to the volume of agricultural land use.

3.3.4. Land use decision

This module describes the processes that lead to decisions regarding urban expansion. In every period at which the actual population density exceeds the threshold density, there is a demand from expansionists for urban growth. The owners of the property rights to the natural area then offer a set amount of natural area, which they sell to the highest bidder. If $WTP_t^u > WTP_t^n$, then urban expansion occurs. If the reverse holds, it does not. The price that expansionists offer for the property rights, WTP_t^u , is

$$WTP_t^u = f_{WTP_u}([P/U]_t, TD_t) \quad \frac{\partial f_{WTP_u}}{\partial [P/U]} \geq 0, \frac{\partial f_{WTP_u}}{\partial TD} \leq 0 \quad (3.12)$$

where P_t is the urban population size in period t and TD_t is the threshold level of urban population density. Population density is defined as P_t/U_t . The urban population size is described by

$$P_t = P_{t-1} + \Delta P_t \quad P(0) = P_0 \quad (3.13)$$

and

$$\Delta P_t = g_t P_t \quad (3.14)$$

where P_t is the population stock in period t , ΔP_t is the population change in period t and g_t is the population growth rate in period t .

Population density can increase only up to a threshold density level. Since we consider an isolated city, people cannot move away from the city. Crowding is the result, which reduces the population growth rate. This dynamic is reminiscent of a habitat with a limited carrying capacity. The growth rate is determined by

$$g_t = f_g([P/U]_t, TD_t) \quad \frac{\partial g}{\partial [P/U]_t} \leq 0, \frac{\partial g}{\partial TD} \geq 0 \quad (3.15)$$

City inhabitants have two ways of overcoming this limit on population size and growth. The one is urban expansion, the core issue of this model. The other option is

to research new infrastructural technologies that allow more people to occupy a given urban area. We model the state of technology as an autonomous process driven by the demand for urban expansion

$$TD_t = f_{TD}(WTP_{t-1}^u) \quad \frac{dTD}{dWTP^u} \geq 0 \quad (3.16)$$

A growing population size carries with it economic benefits that arise from agglomeration effects. Increased innovation and complementarity effects raise the standard of living (Mills and Hamilton, 1984). Hence, we include an effect on per capita income

$$y_t = f_y(P_t) \quad \frac{dy}{dP} \geq 0 \quad (3.17)$$

where y_t is per capita income. Total income, Y_t is defined as $y_t * P_t$. The price that conservationists offer for property rights, WTP_t^n , is

$$WTP_t^n = f_{WTP^n}(R_t^a, R_t^p, W_t) \quad \frac{\partial WTP^n}{\partial R^a} \geq 0, \frac{\partial WTP^n}{\partial R^p} \geq 0, \frac{\partial WTP^n}{\partial W} \geq 0 \quad (3.18)$$

Conservationists are assumed to prefer animals over plants. The use value of a natural area as recreational space is generally increased by the presence of birds or mammals, more than by the presence of plants. Furthermore, we assume that non-use motivations cause conservationists to value wetland species over non-wetland species. Since wetlands disappear disproportionately quickly, remaining wetland species carry existence and bequest value.

3.3.5. Social evaluation

We use a measure of social welfare to assess scenario outcomes. Here, social welfare is composed of three output variables: income per capita, population density and the state of wetland biodiversity. Income per capita and wetland biodiversity contribute positively to social welfare, while population density has a negative effect on social welfare. Social welfare is

$$S_t = f_S(y_t, WD_t, [P/U]_t) \quad \frac{\partial S}{\partial y} \geq 0, \frac{\partial S}{\partial WD} \geq 0, \frac{\partial S}{\partial [P/U]} \leq 0 \quad (3.19)$$

where S_t is social welfare. In the social welfare function, there are only limited possibilities for substitution among performance indicators.

3.4. Scenario analysis

3.4.1. Description of scenarios

The model was calibrated to run for 100 time steps, each time step representing one year. For this time limit, five scenarios are developed and examined. The scenarios reflect exogenous developments and policy alternatives. The business-as-usual (B) scenario is the reference scenario. It assumes a maximum population growth rate of 3 percent per year. The threshold level of population density is 2 inhabitants per hectare of urban land, and each inhabitant requires 0.3 hectares of agricultural land. Furthermore, there are no restrictions on drainage effort. Agglomeration effects and research effort into infrastructural technology are set at a base level.

There are two scenarios of exogenous developments. Under the 'high growth' (G) scenario, the population growth rate is increased to 5 percent per year. In the 'high productivity' (P) scenario, economic benefits from agglomeration effects increase so that they have a doubled impact on per capita income. Two scenarios assess the impacts of policy alternatives. The high population density (D) scenario incorporates increased research efforts into urban infrastructural technology, doubling the threshold population density. Drainage efforts are restricted to half of the maximum level in the 'hydrological restriction' (H) scenario.

3.4.2. Simulation results

Model outcomes for wetland biodiversity are given by biodiversity component in Table 3.3. Species richness of animals is best preserved in the D scenario, whereas the H scenario performs poorest. Low environmental impacts of urban land use in the D scenario initially suppress large rises in WTP^n . The population growth rate, however, is relatively high, cancelling the benefits of low urban land use with agricultural volume. The swift decrease in wetland biodiversity results in a quick increase of the price of urban expansion. This process forces population growth to slow down immediately and hence, a relatively large share of the natural area is preserved. Analogously, the H scenario is characterised by sustained population and city growth.

The direct and indirect effects of land use (see section 3.5) may have opposite effects on urban size in economic equilibrium. On the one hand, direct effects limit urban land use, mainly by affecting animal species richness. On the other hand, indirect effects may actually increase equilibrium city size. Indirect effects have a positive effect on city size when they are limited and preserve relatively large areas

of desired types of natural area. The variance in final values for animal species richness suggests that this influence of indirect effects may be strong.

The end values for plant species richness under the various scenarios show less variance than for animal species richness. Preservation of plant species richness is most successful in the B scenario and least successful in the P scenario. The B scenario yields the lowest final level of total income and hence the lowest level of nutrient availability. As the two scenarios do not differ much with respect to total population level, the main explanatory factor here is per capita income, which is much higher in the P scenario.

Table 3.3. Final normalised values of biodiversity components in various scenarios^a

<i>Scenario</i>	<i>Species richness animals</i>	<i>Species richness plants</i>	<i>Wetland species in total species richness</i>
Business-as-usual (B)	39.63	59.22	22
High growth (G)	35.84	53.09	5
High population density (D)	42.84	58.89	21
Hydrological restriction (H)	15.21	56.80	61
High productivity (P)	44.16	52.35	0.26

^a Initial value of species richness of animals and plants is 100; of wetland species 90 due to initial allocation of agriculture.

The percentage of wetland biodiversity of total biodiversity is best preserved in the H scenario, while the G scenario performs by far the worst in this respect. This result derives from a relatively large demand for agriculture, caused by a high population level. Drainage activities have a severe impact on the surrounding natural area in this scenario. The reduction in drainage effort, on the other hand, apparently counters the negative effect of sustained urban growth in the H scenario.

Figure 3.2 presents the time paths for social welfare and the performance indicators under the business-as-usual scenario. Social welfare initially increases. Wetland biodiversity is still at a high level, which allows population density to remain constant around the threshold level. Hence, the increase in income per capita that follows from population growth is the major factor driving the welfare increase.

An important increase in the valuation of wetland biodiversity can be seen in period 25, where population density makes a slight jump. This jump is caused by the absence of urban expansion at that point. Population density jumps again in period 37, after which there is an almost continuous increase in population density. This behaviour indicates that after periods 25 en 37, biodiversity loss starts to have a real effect on the value of the rights to undeveloped natural area.

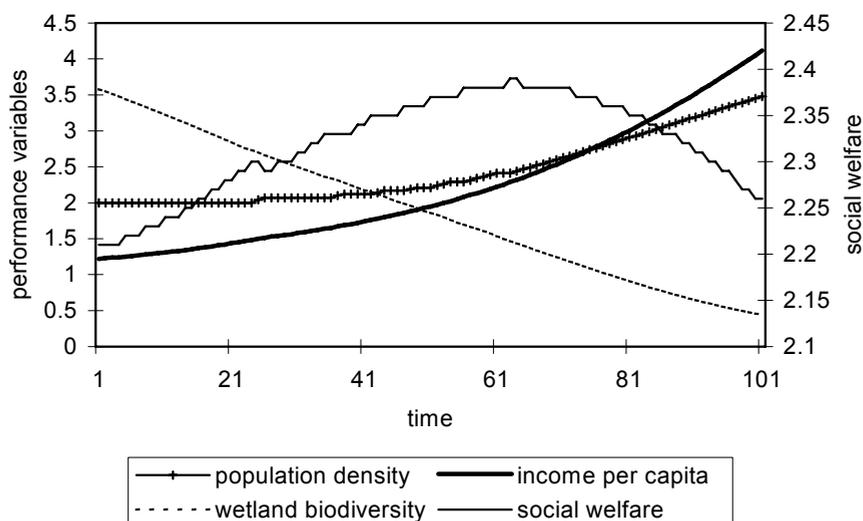


Figure 3.2. Time paths of social welfare and its components in the business-as-usual scenario; population density is in population/area unit; income per capita is in monetary units; wetland biodiversity is the sum of normalised species richness of animals and plants multiplied by the percentage of wetland in nature; social welfare is in utility units.

Herein lies the fundamental cause of the downturn in social welfare. Loss of wetland biodiversity leads to increasing costs of urban expansion. Consequently, population density increases. At some point, willingness to pay for the remaining biodiversity prohibits new instances of urban expansion. The combined negative effects of increasing population density and biodiversity loss eventually overshadow the benefits of increasing income per capita, and social welfare starts to decline.

This time pattern is not identical for all scenarios. The D scenario is almost identical development to the B scenario in the development of social welfare over time. In the G scenario, the inverted U shape is much more pronounced. The H and P scenarios generate a non-decreasing time path for social welfare.

Table 3.4 gives the outcomes for each of the scenarios in terms of social welfare and its components. Under the P scenario, social welfare reaches by far the highest level, while the G scenario performs the worst in this respect. The H scenario appears to be a compromise, offering a combination of relatively high wetland biodiversity and low population density. The P scenario performs by far the best with respect to income per capita, followed by the G scenario. Population density is lowest

under the H scenario, and highest in the G scenario. Wetland diversity is best conserved under the H scenario, as was already implied by Table 3.4. The G scenario performs the worst in this respect.

Table 3.4. Final values of social welfare components in various scenarios^a

<i>Scenario</i>	<i>Income per capita</i>	<i>Population density</i>	<i>Wetland biodiversity</i>	<i>Social welfare</i>
Business-as-usual (B)	4.12	3.48	11.06	2.26
High growth (G)	7.23	5.02	2.42	1.98
High population density (D)	4.22	3.78	10.81	2.22
Hydrological restriction (H)	5.03	2.85	22.09	3.04
High productivity (P)	14.72	3.57	12.52	4.11

^a Income per capita is in monetary units; population density is in population/area unit; wetland biodiversity is the sum of normalised species richness of animals and plants multiplied by the percentage of wetland in nature; social welfare is in utility units.

3.4.3. Sensitivity analysis

The model makes a number of simplifying assumption. Here, we test the robustness of the model under the B scenario for a number of assumptions. First, in the version of the model presented in this chapter, the number of property rights that becomes available is fixed. We have tested a model version in which the number of property rights that becomes available is just enough to maintain the threshold population density. Simulation outcomes do not diverge much, aside from a different expansion pattern (see Figure 3.3).

We have also assessed the impact of changing 1) the relation between total income and eutrophication level, 2) agricultural land use per capita, 3) the relation between agricultural land area and animal richness, and 4) initial values for population and land use. The latter simply affects the pace of the dynamic patterns, shortening or lengthening the growth period of the model. The model does prove sensitive to changes in the other three parameters, however (see Table 3.5).

As Table 3.5 shows, strengthening the impact of agricultural area on animal richness has very little impact on wetland biodiversity and slightly increases social welfare, but is crucial to animal species richness. Increasing the parameter value to 4.5 changes the monotonically decreasing time path for animal species into a U-shape. While the parameter is somewhat hard to interpret, a value 4.5 implies that the impact of agriculture on animal species richness is 4.5% of the impact of natural habitat.

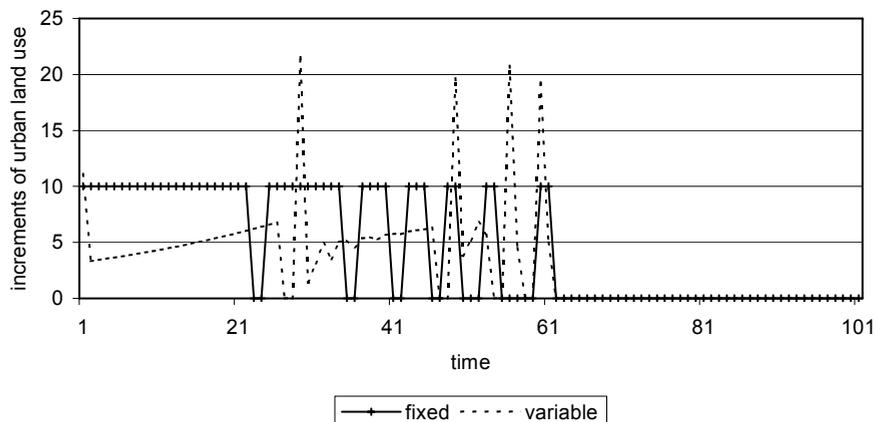


Figure 3.3. Patterns of urban expansion in area units when property rights are sold in fixed and in variable amounts

Changing the impact of total income on nutrient availability has very little effect on social welfare. Reducing the parameter value by half or more, however, exponentially increases the initial value of wetland biodiversity. As a result, the time path of wetland biodiversity becomes less linear (compare Figure 3.2). This effect is caused by the specification of the relationship between eutrophication and plant species richness.

The model is very sensitive to downward adjustments of the amount of agricultural land required per city resident. A reduction from 0.3 units per head to 0.25 units per head changes the time path of social welfare to a continuously increasing pattern (compare Figure 3.2). Essentially, the effect of reducing the agricultural needs of city residents is similar to the effects seen in the reduced drainage scenario.

Table 3.5. Sensitivity analysis: calibrated and critical parameter values

	<i>Calibrated value</i>	<i>Critical value</i>
Contribution of agriculture to animal species richness	0.01	> 4.5
Contribution of total income to eutrophication	0.05	< 0.02
Agricultural land use per capita	0.3	< 0.25

3.5. Conclusion

This chapter has studied the interactions of population growth, land use and wetland biodiversity in a limited spatial area. Land use affects species numbers of both plants and animals, and furthermore impacts species composition by changing the landscape. We develop a hybrid simulation model to assess the (un)sustainability of urban growth and optimal levels of biodiversity. In the model, owners of property rights choose to sell their rights for the purpose of either urban expansion or biodiversity conservation. In economic equilibrium, the areas allocated to urban and agricultural land use on the one hand and to biodiversity conservation on the other, are set.

Several scenarios were simulated and their outcomes assessed using a social welfare indicator. This measurement was comprised of income per capita, urban population density and level of wetland biodiversity. The scenarios describe exogenous increases in the population growth rate and elevated agglomeration effects on productivity. Also assessed are policy alternatives to increase the threshold population density and to restrict hydrological effects of agriculture. With respect to social welfare, the high productivity scenario outperforms all other scenarios, while the scenario of high population growth yields the lowest score. A compromise is the scenario with hydrological restrictions on agriculture, yielding average per capita income, low population density, and high wetland biodiversity.

Under the scenario of high population growth, on the other hand, overall wetland biodiversity is almost completely lost. The other scenarios occupy the middle ground in wetland preservation. The results differ, however, for individual biodiversity components. Animal species richness, for instance, is severely reduced in the scenario with hydrological restrictions, while the number of plant species does not vary much in the different scenarios.

A few conclusions on biodiversity conservation can be drawn from the scenario results. First, the model suggests that increasing land use is unsustainable in the long run. In economic equilibrium, there is at least some remaining biodiversity. How much biodiversity is preserved depends on the economic values land generates in use for either income growth or biodiversity conservation. Even with technological progress in city infrastructure, a growing population size puts pressure on biodiversity via indirect mechanisms, such as groundwater drainage and nutrient availability. If biodiversity is positively valued, at some point the environmental cost of biodiversity loss makes further urban and economic growth prohibitively expensive.

Second, direct and indirect effects of land use may work in opposite directions in biodiversity conservation effort. While direct effects serve to limit urban land use,

low indirect impacts may actually increase a city's size. Reducing drainage per capita preserves a relatively high proportion of wetland in the total natural area. Since wetlands are valued higher than non-wetland areas, the cost of urban expansion remains relatively low. Hence, a conflict between conserving sensitive wetland area and maintaining high numbers of animal species may occur.

Our model is a first step in improving our understanding of how economic development affects biodiversity through various channels. Compared with other models of wetland-economy interactions (e.g. Simonit et al., 2002), the economic impacts of wetland loss in our model are highly stylised. The influence of land use on biodiversity, on the other hand, is modelled more elaborately (as in Chopra and Adhikari, 2004). In particular, we consider a wide concept of biodiversity. Our biodiversity indicators take into account that biodiversity is a multi-faceted environmental good, each aspect of which generates economic value.

Appendix 3.A. Functional specification of the model in the B scenario

Land use accounting

Initial values

$$K(0) = 1500$$

$$U(0) = 100$$

$$A(0) = 60$$

Parameter values

$$\text{Agricultural land use per capita} = 0.3$$

Stocks

$$\text{Agricultural area} = \text{Agricultural area}(t-dt) + \text{Growth A} \cdot dt$$

$$\text{Natural area} = 1500 - \text{Urban area} - \text{Agricultural area}$$

$$\text{Urban area} = \text{Urban area}(t-dt) + \text{Growth U} \cdot dt$$

Flows

$$\text{Growth U} = \text{Urban expansion \{see Land use decision\}}$$

$$\begin{aligned} \text{Growth A} = & \text{Agricultural land use per capita} \cdot \text{Population} \\ & - \text{DELAY}(\text{Agricultural land use per capita} \cdot \text{Population}, 1) \end{aligned}$$

Biodiversity changes

Parameter values

$$\text{Drainage effort} = 1$$

Converters

$$\text{Species richness plants} = 20 / ((\text{Eutrophication level} / 10) + 0.0913)$$

$$\text{Nutrient availability} = \text{LOG}_{10}(0.05 \cdot \text{Total income})$$

$$\begin{aligned} \text{Species richness animals} = & 100 \cdot \text{Natural area} / \text{INIT}(\text{Natural area}) \\ & + 0.01 \cdot \text{Agricultural area} / \text{INIT}(\text{Agricultural area}) \end{aligned}$$

$$\text{Wetland percentage} = 1 / (1 + \text{EXP}(-8 \cdot \text{Groundwater level}) / 15)$$

$$\text{Groundwater depth} = -\text{Agricultural area} / 850 \cdot \text{Drainage effort}$$

$$\text{Wetland biodiversity} = \text{Wetland proportion} \cdot (\text{Species richness animals} + \text{Species richness plants}) / 2$$

Appendix 3.A

Land use decision

Parameter values

$$w1 = 0.7 \text{ \{preference for animals and wetland in WTP}^n \text{ function\}}$$

Initial values

$$P(0) = 200$$

Stocks

$$\text{Population} = \text{Population}(t-dt) + (\text{Growth P}) * dt$$

Flows

$$\text{Growth P} = \text{Growth rate} * \text{Population}$$

$$\text{Growth rate} = \text{IF}(\text{Population density} / \text{Population density threshold} > 1) \\ \text{THEN}(0.03 * (1 - ((\text{Population density} / \text{Population density threshold}) - 1)) / 1.5) \text{ ELSE}(0.03)$$

Converters

$$\text{Income per capita} = \text{EXP}(\text{Population} / 1000)$$

$$\text{Population density} = \text{Population} / \text{Urban area}$$

$$\text{Population density threshold} = \text{LOGN}(\text{WTPu})$$

$$\text{Total income} = \text{Income per capita} * \text{Population}$$

$$\text{Urban expansion} = \text{IF}(\text{Natural area} > 0) \text{ AND}(\text{WTP}^u > \text{WTP}^n) \\ \text{THEN}(10) \text{ ELSE}(0)$$

$$\text{WTPu} = \text{Population density} / \text{Population density threshold}$$

$$\text{WTPn} = -0.19 + w1 * \text{EXP}(0.009 * w1 * (100 / (\text{Percentage wetland biodiversity} * \text{Species richness animals}))) \\ + 0.5 * (1 - w1) * (100 / (\text{Percentage wetland biodiversity} * \text{Species richness plants}))) \\ + (1 - w1) * \text{EXP}(0.009 * (w1 * (100 / ((1 - \text{Percentage wetland biodiversity}) * \text{Species richness animals}))) \\ + 0.5 * (1 - w1) * (100 / (1 - \text{Percentage wetland biodiversity}) * \text{Species richness plants}))))$$

Social evaluation

Parameter values

w2 = 0.5 {preference for income in S function}

w3 = 0.2 {preference for wetland biodiversity in S function}

Converters

Social welfare = Income per capita^{w2}*Wetland biodiversity^{w3}
*Population density^(1-w2-w3)

4. Spatial patterns of biodiversity conservation in a multiregional general equilibrium model¹

4.1. Introduction

The spatial arrangement of biodiversity reserve sites is of paramount importance in biodiversity conservation. Ecologists have long grappled with the question whether the best approach to biodiversity conservation is to establish a Single Large or Several Small reserves, the so-called SLOSS debate (see Kingsland, 2002, for a review). Economists can make a valuable contribution to this debate, by analysing the optimality of these two conservation strategies from a social, rather than an ecological perspective. Our chapter contributes to this literature by introducing biodiversity to a model of location choices by firms and workers.

One approach to the SLOSS-problem that economists may take is to maximise an environmental goal, such as the number of conserved species, within a fixed budget constraint. This environmental goal is attained by determining which currently undeveloped natural areas generate the greatest contribution and protecting them from future developments in non-natural land use (the reserve site selection problem). For instance, Polasky et al. (2000) consider the effects of information about species distributions on the selection of biodiversity reserve sites, whereas Arthur et al. (2004) look at the impacts of using various biodiversity indicators to define the environmental goal. In this type of model, non-natural land use patterns are typically exogenous, but uncertainty about future developments in such land use can be taken into account (e.g., Costello and Polasky, 2004).

Making land use patterns endogenous to the model may lead to very different conclusions to the SLOSS debate. In renewable resource management much progress has been made with spatial aspects of biodiversity conservation. Swanson (1994) addresses the opportunity costs of reserving land for a resource, for instance a species, which exists in a single patch of habitat. With species that are spread over multiple patches, dispersal effects and habitat heterogeneity influence the patch-specific optimal management regime (e.g., Sanchirico and Wilen, 1999). These models may also be employed to investigate the consequences for resource management of establishing some patches as reserve sites (Sanchirico and Wilen,

¹ This chapter has been written in cooperation with C.A. Withagen.

2001; Smith and Wilen, 2003; Sanchirico, 2005). Models of renewable resource management, however, are not suitable for analyses of biodiversity conservation when species generate only non-use values and land allocation is the only policy instrument (Alexander and Shields, 2002). These conditions apply to many instances of species conservation.

To focus the analysis of biodiversity protection on land use, consider land allocated to the protection of biodiversity as a public good. It is difficult to centrally determine optimal protection of natural areas, because preferences are likely to be misrepresented. According to the Tiebout hypothesis, consumers of a public good move to the particular region that best meets their preferences for that good and thus the optimal provision of public goods can be approximated at the local level, provided that population mobility between regions is possible. Environmental conditions are public goods, and their effect on population concentration is analysed in, e.g., Sandmo and Wildasin (1999) and Hoel and Shapiro (2003). Given that people require land to sustain them, population mobility may provide insights into the SLOSS debate. When a population is concentrated in one region, this implies that another region contains only natural areas. Such regional specialisation would indicate that the socially optimal strategy for biodiversity conservation is a single large biodiversity reserve site.

Models of regional specialisation rarely explicitly integrate ecological theories of biodiversity change. One exception is Polasky et al. (2004), who use a two-region trade model with no labour mobility to analyse the effects of regional specialisation on biodiversity. The level of biodiversity changes with the composition of regional land use, for example as a forest, for agriculture, or a combination of the two. Regional biodiversity consists of two types of species that depend on habitats in forest or agricultural lands. Polasky et al. (2004) find that the degree to which regions specialise determines the level of biodiversity. Whether specialisation has a positive or a negative effect on biodiversity depends on the overlap in species between the two regions.

Polasky et al. (2004) make use of the so-called species-area curve, which gives the number of species as a concave function of the availability of natural areas. Their model assumes that all species are equally affected by habitat loss, and that all species have an identical risk of extinction. This is a fairly strong assumption. If all species run the same risk of extinction, then all species warrant similar amounts of conservation effort. Conservation effort then amounts to maximising the number of species. Obviously, the goal of biodiversity conservation is to preserve as many species as possible. Conservation laws such as the Endangered Species Act and the Habitat and Bird Directives, however, have a very strong focus on species with

elevated extinction risks. To our knowledge, no economic model of biodiversity conservation reflects such differences in extinction risks.

In this chapter, we investigate the implications for the SLOSS debate of different extinction risks of species and population mobility, using a general equilibrium model of regional specialisation. We adapt the model described in chapters 4 and 5 in Fujita, Krugman and Venables (2001; henceforth FKV), which endogenously determines the extent of regional specialisation through simultaneous location choices of firms and labour. Similar to the model in Elbers and Withagen (2004), we adapt the FKV model so that regional environmental conditions partially determine labour migration decisions. The focus here, however, is explicitly on biodiversity conservation. Biodiversity consists of two types of species that are related to population concentration by a finite stock of habitat. Contrary to Polasky et al. (2004), however, we include species with different extinction risks. The two types of species respond differently to habitat loss.

Our results suggest that the FKV results are partially overturned by including biodiversity with different extinction risks for two sets of species. We find that above the minimum marginal utility of biodiversity, a symmetric pattern of manufacturing and biodiversity conservation has increased stability. Furthermore, additional equilibria may emerge. The socially optimal equilibrium may be symmetric or asymmetric, where one region has the larger share in manufacturing and the other region maintains a higher level of biodiversity. This depends on the preferences for the two types of species. Only if the first-best solution is symmetric, then it may be maintained when governments do not cooperate.

The model presented in this chapter builds on the recommendations in chapter 2 by incorporating the fragmentation of biodiversity reserve sites, where this fragmentation differently affects the species richness of two types of ecosystem. Section 4.2 describes the model. It also contains a more elaborate description of the two types of species and their responses to habitat loss. We compare the basic results with those in FKV and provide in-depth analyses of parameter settings and policy measures in section 4.3. Conclusions and implications for the SLOSS debate are presented in section 4.4.

4.2. Model outline

4.2.1. Production and consumption

The model includes two regions, here named domestic and foreign. Below, we describe the behaviour of a representative manufacturing firm and consumer in the domestic region. Where needed, an asterisk $*$ marks variables pertaining to the foreign region. Consumers from both regions share identical preferences and all firms have access to the same technology.¹ In both regions, there is production of an agricultural good and of manufactured goods. All goods require inputs of labour and land. The total supply of labour in the economic system is $\bar{L} = \bar{L}_A + \bar{L}_M$. Respectively, \bar{L}_A and \bar{L}_M indicate supplies of labour for agriculture and manufacturing. Regional stocks of land S and S^* are fixed and are the property of the respective governments. They may rent the land to the manufacturing and agricultural sectors. The revenue is redistributed in a lump-sum fashion to all regional inhabitants. Land that is not used in agriculture or manufacturing is a natural area in which biodiversity exists. The level of biodiversity influences migration decisions of labour.

The homogeneous agricultural good q_A is produced under perfect competition and with constant-returns-to-scale in unskilled labour L_A , so $q_A = L_A$, and no transportation costs are associated with trade of agricultural goods. Hence, the wage rate for unskilled labour is identical in both regions, $w_A = p_A = w_A^* = p_A^*$. Moreover, we want the agricultural good to function as the numeraire, so we set $p_A = 1$. The supply of unskilled labour is inelastic and equal in both regions, $L_A = L_A^* = 1/2\bar{L}_A$. Agricultural production also requires land as an input with a constant land-to-labour ratio, but we assume that the rent for agricultural land is zero. Furthermore, since unskilled labour is immobile across regions, agricultural land use is fixed. These assumptions ensure that agriculture does not affect the location choices of firms and skilled workers and keep the model simple.

The manufacturing sector of the economy is characterised by monopolistic competition. There is a continuum of manufactured commodities of \hat{n} varieties, where each firm produces only one variety $i \in [0, \hat{n}]$ in only one region. The range of domestic varieties is $[0, n]$ and foreign varieties n^* belong to the interval $(n, \hat{n}]$.

¹ Because both regions are homogeneous in these respects, the terms 'domestic' and 'foreign' can be somewhat misleading. The assumed homogeneity is reasonable only for regions at similar levels of economic development. Hence, the model is not intended to analyse North-South issues and conservation of biodiversity 'hot spots'. It is, for instance, more applicable to biodiversity conservation trade-offs within a country at the level of provinces.

Varieties of the manufactured good are subject to transport costs only when transported between the two regions. Production of all varieties requires skilled labour, which is mobile between the two regions. Moreover, land is also an input to production and firms rent units of land from the regional government. Total production q_M of variety i has a labour demand l_M with fixed input F and marginal input c_M ²

$$l_M = F + c_M q_M \quad (4.1)$$

A firm's demand for land is determined by the land-to-labour ratio b_M , which is constant and identical for all firms. The results of our model are partially dependent on the definition of this parameter, as we shall discuss later on. Note that this technological specification implies increasing returns to scale.

The domestic region's supply of surface area S can be allocated either to manufacturing S_M or habitat S_H :

$$S = S_M + S_H = ns_M + S_H \quad (4.2)$$

where s_M indicates a firm's demand for land $s_M = b_M l_M$. The firm faces wage costs w_M and land rent τ . The firm's profits are

$$\pi = p_M q_M - (w_M + \tau b_M)(F + c_M q_M) \quad (4.3)$$

where p_M is the mill price of manufactured goods. Monopolistic competition allows firms to earn economic rents by applying mark-up pricing. Since each firm uses the same technology, all domestic firms set the same price p_M . With costless entry and exit, firms enter the market for manufactured goods until profits are zero. With an isoelastic demand function, to be derived below, profit maximisation implies that all firms set the mill price at

$$p_M = c_M (w_M + \tau b_M) / \rho \quad (4.4)$$

where the parameter ρ ($0 < \rho < 1$) indicates the degree of consumer preference for variety in manufactured goods. It is discussed in more detail below. In equilibrium, profits are zero, so output and demand for labour and land are, respectively

² We dispense with subscript i , except where it is necessary for the exposition.

$$q_M = F(\sigma - 1) / c_M \quad (4.5)$$

$$l_M = F\sigma \quad (4.6)$$

$$s_M = b_M F\sigma \quad (4.7)$$

with σ indicating the elasticity of substitution between varieties, defined by $\sigma = 1/(1-\rho)$, so that $\sigma > 1$.

Total domestic demand for skilled labour is $L_M = nF\sigma$ and total land used in manufacturing is $S_M = nb_M F\sigma$. Hence, habitat area is $S_H = S - nb_M F\sigma$. Clearly, both the number of firms and the intensity of land use in manufacturing determine when depletion of the habitat area occurs.

Now we turn to consumer behaviour. Both skilled and unskilled consumers in the domestic region have the following Cobb-Douglas type welfare function

$$U(M, A, B) = M^\mu A^{1-\mu} + \varphi B(C, E) \quad (4.8)$$

where M is a composite index of the consumption of \hat{n} varieties of the manufactured good, A is consumption of the agricultural good, and μ ($0 \leq \mu \leq 1$) is a constant. The local level of biodiversity B is a function of the local number of generalist species C and the local number of specialist species E . We return to this composite biodiversity indicator below. The marginal benefit of biodiversity, φ ($\varphi \geq 0$), is assumed constant. Consumption of the composite manufactured good is defined by a constant-elasticity-of-substitution function

$$M = \left[\int_0^{\hat{n}} m(i)^\rho di \right]^{1/\rho} \quad (4.9)$$

with $m(i)$ consumption of variety i . As mentioned above, the parameter ρ indicates the degree of consumer preference for variety in manufactured goods. If ρ goes to unity, varieties of manufactured goods become perfect substitutes; if it approaches zero, varieties are complements. Given a consumer price $p_m(i)$ for variety i of manufactured goods and per capita income y , all consumers face the budget constraint

$$y \geq p_A A + \int_0^{\hat{n}} m(i) p_m(i) di \quad (4.10)$$

From equations (4.8) – (4.10), we can derive the total demand functions for the agricultural good and for variety i of the manufactured good:

$$A = (1-\mu)Y / p_A \quad (4.11)$$

where Y indicates total income of the domestic region and G is that region's composite price index for manufactured goods:

$$Y = w_M L_M + w_A L_A + \tau S_M \quad (4.12)$$

$$G = \left[\int_0^{\hat{n}} p_m(i)^{1-\sigma} di \right]^{1/(1-\sigma)} \quad (4.13)$$

The first two terms on the right hand side of equation (4.12) are labour incomes of skilled and unskilled workers. The third term expresses the lump-sum redistribution of total revenue from renting land to firms. The form of equation (4.13) is easily interpreted if $p_m(i) = p_M$ for all varieties i . It then collapses to $G = p_M \hat{n}^{1/(1-\sigma)}$. The latter form clearly indicates that since $\sigma > 1$, G is negatively dependent on the number of varieties \hat{n} . The higher the elasticity of substitution σ , the stronger is this effect.

So far, we have actually described a one-region economy. In a two-region system, mill prices may differ across regions, so $p_m(i) = p_M$ for goods that are produced domestically and $p_m^*(i) = p_M^*$ for foreign goods. The domestic market price of goods produced in the foreign region, is affected by transport costs. These costs take the form of Samuelson's "iceberg": for each unit delivered $T \geq 1$ units must be shipped. Consequently, for $i \in [0, n]$, equation (4.12) becomes

$$m(i) = \mu \left[Y p_M^{-\sigma} G^{\sigma-1} + Y^* p_M^{*-\sigma} T^{1-\sigma} G^{*\sigma-1} \right] \quad (4.14)$$

and equation (4.13) turns into

$$G = \left[n p_M^{1-\sigma} + n^* (p_M^* T)^{1-\sigma} \right]^{1/(1-\sigma)} \quad (4.15)$$

Next, we address the migration decision of skilled labour. In FKV, skilled workers migrate to the region where firms offer the highest real wage, because that enables them to attain the highest utility from consumption. From earlier results, we can derive that indirect utility from consumption for a skilled worker is $\mu^\mu (1-\mu)^{1-\mu} G^{-\mu} y_m$ with y_m as per capita income of skilled labour:

$$y_m = w_M + \frac{\tau S_M}{L_M + L_A} \quad (4.16)$$

The second term on the right hand side is the lump-sum redistribution of land rents per capita, total domestic revenue divided by the domestic population.

In this model, migration decisions of skilled workers are based on the broader concept of per capita utility of skilled labour u_m , which is dependent on both real income and regional biodiversity. Equilibrium is characterised by the absence of migration flows, which occurs when $u_m = u_m^*$. Per capita welfare of skilled labour u_m , total welfare U and domestic per capita welfare u in the domestic region are, respectively

$$u_m = \psi G^{-\mu} \left[w_M + \frac{\tau S_M}{L_M + L_A} \right] + \varphi B \quad (4.17)$$

$$U = \psi G^{-\mu} [w_M L_M + L_A + \tau S_M] + \varphi B [L_M + L_A] \quad (4.18)$$

$$u = \frac{\psi G^{-\mu}}{L_M + L_A} [w_M L_M + L_A + \tau S_M] + \varphi B \quad (4.19)$$

where $\psi = \mu^\mu (1-\mu)^{1-\mu}$ for notational brevity.

4.2.2. Species with different extinction risks

Many formal economic models of biodiversity conservation define the level of biodiversity by the number of species, species richness (e.g., Barbier and Schulz, 1997; Rowthorn and Brown, 1999; Polasky et al., 2004). These models apply the species-area curve, which is an empirically established relationship between the total number of species R and habitat size S_H (MacArthur and Wilson, 1967). The species-area curve is typically specified as

$$R = \eta S_H^\kappa \quad (4.20)$$

with $\eta \geq 0$ and $0 \leq \kappa \leq 1$ as region-specific ecological parameters. The species-area curve displays decreasing returns to scale in the 'production' of biodiversity. According to the theory of the species-area curve, all species suffer equally when habitat is lost (see, e.g., the discussion in chapter 1 of Hubbell, 2001). This assumption of ecological similarity of species, however, is unrealistic for a number of reasons. One important reason, according to Pimm et al. (1995), is that the species-area curve assumes a uniform spatial distribution of species over an area. Some species, however, are present throughout the area, whereas others occur only in specific areas. The latter are more susceptible to habitat loss than the former. Hence, the species-area curve overestimates the extinction risk of widely present species and underestimates the risk of species that are limited to only certain natural areas.

The use of multiple types of habitat, such as in Polasky et al. (2004) does not account for such effects.

To approximate the different extinction risks of species, we distinguish between generalist species and specialist species. Generalist species use a wide range of resources and hence can compete successfully in various habitat types. Consequently, generalist species are present in many types of habitat. If one particular type of habitat is destroyed individuals of a generalist species may adapt relatively easily to remaining types of habitat. A specialist species, on the other hand, is limited to habitats with narrowly defined, pristine resource conditions. It cannot compete successfully in other types of habitat. If the specific habitat of a specialist species is degraded or lost, individuals of that species may not relocate so easily.

The difference in extinction risks of generalist and specialist species in response to overall habitat loss may be derived from the species-area curve (Harte and Kinzig, 1997). They show that a power function such as equation The difference in extinction risks of generalist and specialist species in response to overall habitat loss may be derived from the species-area curve (Harte and Kinzig, 1997). They show that a power function such as equation (4.20) exists for specialist species

$$E = \chi S_H^\zeta \tag{4.21}$$

with E as the number of specialist species, and $\chi > 0$ and $\zeta > 1$ as region-specific ecological parameters relevant to specialist species. The ‘specialist-area’ curve differs from the conventional species-area curve in that the former is convex, rather than concave (Harte and Kinzig, 1997; Kinzig and Harte, 2000). This form expresses the spatial restrictions on specialist species: the probability of finding one in relatively small areas is low, because it is unlikely that the area has the characteristics amenable to a specialist species.

For generalist species we assume the following ‘generalist-area’ curve:

$$C = \gamma S_H^\theta \tag{4.22}$$

with $\gamma > 0$ and $0 < \theta \leq 1$ as region-specific biological parameters relevant to generalist species. Together generalists and specialists constitute all species, so we have

$$R = C + E \tag{4.23}$$

Given the above components of biodiversity, we can describe how the biodiversity function enters the migration decision of skilled workers. Important conservation acts, such as the Endangered Species Act and the Habitat and Bird Directives, aim to maintain species numbers primarily by preserving species that are rare and vulnerable. The biodiversity function in this model allows for a similar attitude to species conservation. Skilled workers perceive the regional level of biodiversity as a combination of generalist species richness and specialist species richness in their region. The resulting biodiversity function is

$$B = \alpha_C C + \alpha_E E \quad (4.24)$$

with parameters α_C and α_E as weighting factors, where $\alpha_C + \alpha_E = 1$. When $\alpha_C = \alpha_E$, then the level of biodiversity is proportional to the total number of species. Substituting the demand for land from equation (4.24) gives the perceived level of biodiversity. With some rewriting, equilibrium biodiversity becomes

$$B = \alpha_C \gamma (S - nb_M F \sigma)^\theta \left[1 + \left(\frac{\alpha_E \chi}{\alpha_C \gamma} \right) (S - nb_M F \sigma)^{\zeta - \theta} \right] \quad (4.25)$$

The first term on the right hand side of equation (4.25) is the species-area curve for generalist species as a function of the number of varieties produced in a region and the land-to-labour ratio. The term in brackets describes the effect of specialist species richness on the perceived level of biodiversity relative to the effect of generalist species numbers. Perceived biodiversity increases as the potential species set consists of more specialist species, as shown by the ratio χ / γ . The exponent $(\zeta - \theta)$ indicates the elevated extinction risk of specialist species relative to that of generalist species. The higher the relative extinction risk of specialist species, the higher their contribution to the perceived level of biodiversity.

4.2.3. Normalisation and equilibrium

We choose units of measurement that simplify the above equations without loss of generality (FKV, p. 54). Setting $c_M = \rho$ implies that the pricing equation (4.4) becomes $p_M = w_M + \tau b_M$ and that, from equation (4.5), $q_M = l_M$. Furthermore, fixed costs are set at $F = \mu / \sigma$, which gives zero-profit output $q_M = l_M = \mu$. Normalisation of the total labour supply gives $\bar{L} = \bar{L}_A + \bar{L}_M = 1$ and we choose units for the total supply of skilled labour $\bar{L}_M = \mu$. The regional demand for skilled labour becomes $L_M = n\mu$, which implies that $n\mu + n^*\mu = \mu$ or $\hat{n} = n + n^* = 1$. It is convenient to also normalise the regional stocks of land, $S = S_M + S_H = 1$ and

$S^* = S_M^* + S_H^* = 1$. Clearly, each firm demands $s_M = b_M \mu$ of land. Since there are n domestic and n^* foreign firms, the domestic and foreign areas of land allocated to biodiversity conservation are, respectively, $S_H = 1 - nb_M \mu$ and $S_H^* = 1 - n^* b_M \mu$. Finally, the agricultural good is used as the numeraire, $p_A = 1$. So simplified, equilibrium is described by the following set of equations

$$Y = n\mu w_M + \left(\frac{1-\mu}{2}\right) + \tau n b_M \mu \quad (4.26)$$

$$Y^* = n^* \mu w_M^* + \left(\frac{1-\mu}{2}\right) + \tau^* n^* b_M \mu \quad (4.27)$$

$$G = \left[n[w_M + \tau b_M]^{1-\sigma} + n^* [w_M^* + \tau^* b_M] T^{1-\sigma} \right]^{1/(1-\sigma)} \quad (4.28)$$

$$G^* = \left[n([w_M + \tau b_M] T)^{1-\sigma} + n^* [w_M^* + \tau^* b_M]^{1-\sigma} \right]^{1/(1-\sigma)} \quad (4.29)$$

$$w_M = \left[Y G^{\sigma-1} + Y^* T^{1-\sigma} (G^*)^{\sigma-1} \right]^{1/\sigma} - \tau b_M \quad (4.30)$$

$$w_M^* = \left[Y T^{1-\sigma} G^{\sigma-1} + Y^* (G^*)^{\sigma-1} \right]^{1/\sigma} - \tau^* b_M \quad (4.31)$$

For the domestic region, the reduced form functions of per capita utility of skilled labour, total regional welfare and regional biodiversity in terms of the number of varieties are

$$u_m(n) = \psi G^{-\mu} \left[w_M + \frac{2\tau n b_M \mu}{2n\mu + (1-\mu)} \right] + \varphi B(n) \quad (4.32)$$

$$U(n) = \psi G^{-\mu} \left[n\mu w_M + \left(\frac{1-\mu}{2}\right) + \tau n b_M \mu \right] + \varphi \left[n\mu + \left(\frac{1-\mu}{2}\right) \right] B(n) \quad (4.33)$$

$$B(n) = \alpha_C \gamma (1 - nb_M \mu)^\theta + \alpha_E \chi (1 - nb_M \mu)^\zeta \quad (4.34)$$

Equation (4.32) contains the three factors that influence the migration decision of skilled labour. The first term in brackets is the real wage rate in manufacturing. The second factor is the per capita income from redistributed revenues from land rents. Both are directly related to utility from consumption. Biodiversity is the third contribution to utility. The combined effect of the latter two factors on a skilled worker's utility when concentration of firms occurs, is unclear. On the one hand, the concomitant revenues from land rent increase utility from consumption. On the other hand, utility derived from biodiversity decreases as habitat area is developed for production.

4.3. Simulation results on the geographic pattern of biodiversity conservation

4.3.1. Introduction and parameter settings

The geographic pattern of manufacturing depends on the relative strengths of centripetal forces and centrifugal forces. The FKV model contains two economic centripetal forces. Due to the ‘home market effect’, firms prefer to settle in the region with the larger market because of better access, i.e. no transport costs for reaching this larger market. The ‘price effect’ draws workers to the region with the larger share of production. Since only a small share of consumed products bears transport costs, the price index is low. Consequently, the real wage is high, making the region attractive to skilled workers. In these two effects, transport costs are shown to be a centrifugal force: when transport costs are low, centripetal forces prevail and vice versa.

If skilled workers also care about biodiversity, as they do in this model, then biodiversity is operative as an additional centrifugal force. Skilled labourers prefer a region with biodiversity to a region with no biodiversity, *ceteris paribus*. Of course, workers in the region with the smaller market require jobs, but firms prefer to stay in the region with the larger market because of the home market and price effects. To persuade firms to move to the smaller market, skilled workers accept a lower real wage. Because the region with the smaller market has a higher level of biodiversity, skilled labour achieves the same level of utility while firms are compensated for incurred transport costs by the lower real wage.

FKV find two possible equilibrium patterns of manufacturing: an asymmetric equilibrium with manufacturing that is concentrated in either region ($n=1$ or $n^*=1$) and a symmetric equilibrium where both regions have an equal share of manufacturing ($n=n^*=1/2$). In this extension to the FKV model, these solutions indicate degrees of fragmentation: the more asymmetric the solution, the lower is the degree of fragmentation. Using numerical simulations, we analyse the robustness of these results when biodiversity also matters to location choices.

Following FKV (chapter 5), we use these settings for the economic parameters: $\sigma = 5$, $\mu = 0.4$, and $T = 2.1$, $T = 1.7$ and $T = 1.5$ for high, intermediate and low transport costs, respectively. It is convenient to define the land-to-labour ratio $b_M = S / \bar{L}_M = 1 / \mu = 2.5$. This setting has implications for the results, as we discuss later on. Both regions potentially have the same species richness and species composition with $\gamma = \gamma^* = 2$, $\chi = \chi^* = 3$, $\theta = \theta^* = 0.35$, and $\zeta = \zeta^* = 7$. These parameter values in no way indicate the regional types of habitat and species. It may

well be that one region is a river delta, whereas the other contains mountain ranges. No assertion is made to the effect of such qualitative aspects of biodiversity on migration decisions. In the base simulations we set the marginal utility of biodiversity at $\varphi = 0.006$. Initially, we use $\alpha_C = 1$ and introduce specialist species later.

First, there is a comparison of the FKV results to those of this model for our positive value of marginal utility of biodiversity φ . In that scenario, $\tau = \tau^* = 0$, which means that neither regional government implements any environmental policy. The consequences of varying the weighting factors of both types of species in the biodiversity function are also briefly addressed. Next, we briefly discuss the robustness of the results under relaxed assumptions about the technology in land use and the role of specialist species. Finally, regional environmental policy by use of land rent τ is analysed. We consider what would constitute socially optimal policy and assess whether the resulting outcome is still attainable when the regional governments display strategic behaviour.

4.3.2. Patterns of biodiversity conservation with a positive marginal utility of biodiversity

In the general equilibrium framework of FKV with no role for biodiversity ($\varphi=0$) three types of equilibria emerge: $n = 1$, $n = 0$ or $n = 1/2$. We first investigate the effect of including biodiversity on the appearance of equilibria on the boundary. For $n = 1$ we have $\varphi B(1) = 0$ and $\varphi B^*(0) = \varphi[\alpha_C \gamma + \alpha_E \chi]$. This implies that for large enough φ and $n = 1$ we have $u_m - u_m^* < 0$. For a large enough marginal utility from biodiversity, therefore, full concentration of manufacturing in the home country cannot be an equilibrium, because skilled workers will move to the foreign region.

If transport costs are high, FKV find that the only stable equilibrium is the symmetric distribution of manufacturing over both regions ($n=n^*=1/2$). Biodiversity would accordingly be preserved in several, i.e. two, small reserves of identical size in both regions.³ When the model is extended with biodiversity, this result holds a fortiori as is illustrated by Figure 4.1. At $n = 1$, the difference between u_m and u_m^* becomes more negative. In the case of high transport costs, therefore, biodiversity merely reinforces the centrifugal force exerted by transport cost.

³ As it is presented, the model cannot explicitly analyse spatial patterns of land use within each region. We exclude the possibility that the biodiversity reserves of both regions are located adjacently on the border between the regions, effectively forming a single large reserve site.

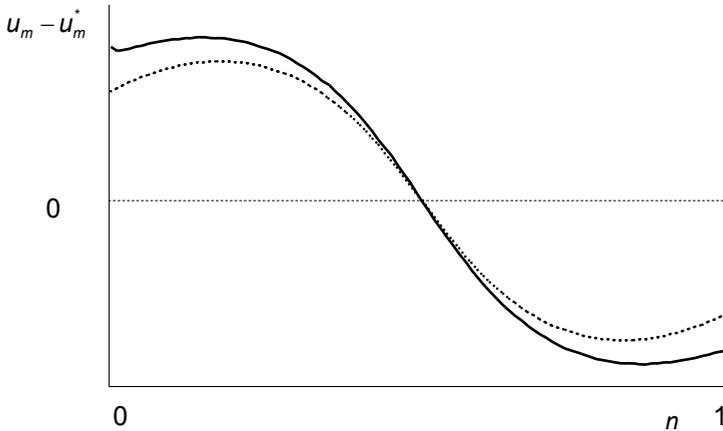


Figure 4.1. Utility differential as a function of the domestic number of firms, $T=2.1$, $\varphi=0.006$ (dotted line shows $\varphi=0$)

For intermediate transport costs, FKV find that both concentration of manufacturing in either region ($n=1$ or $n^*=1$) and identical regional shares in manufacturing ($n=n^*=1/2$) are stable equilibria. Which situation prevails when $\varphi=0$ depends on the initial distribution of manufacturing. Biodiversity would be preserved in either a single large or in two small reserves. If φ is kept at a very low level, no qualitative changes occur. Figure 4.2 shows the effect of increasing the marginal utility of biodiversity. For relatively high levels of marginal utility from biodiversity, only the symmetric solution is stable. This is the case because, as we have seen, skilled workers want to migrate out of the region without biodiversity.

A new result is that for intermediate marginal utility of biodiversity ($0.0056 \leq \varphi \leq 0.0064$), there are both quantitative and qualitative changes in the distributions of biodiversity reserve sites. Complete regional specialisation in manufacturing and biodiversity conservation is no longer a stable solution. Two additional equilibria emerge, located just off the boundary solutions of a single large reserve. The occurrence of these 'new' equilibria is a consequence of the non-linearity of the biodiversity function. If biodiversity were to enter the utility function in a linear way, as in Elbers and Withagen (2004), this phenomenon would not appear. The new equilibria dictate that, although biodiversity is preserved in several reserves, there is only a small degree of fragmentation. One region will have a larger share in manufacturing and the other region will have a larger area allocated to biodiversity conservation.

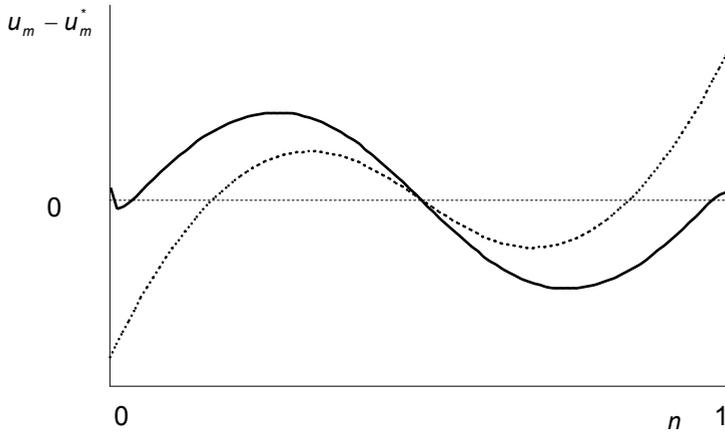


Figure 4.2. Utility differential as a function of the domestic number of firms, $T=1.7$, $\varphi=0.006$ (dotted line shows $\varphi=0$)

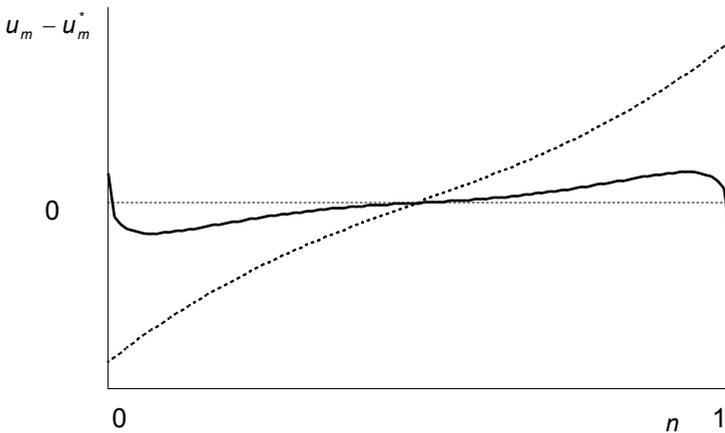


Figure 4.3. Utility differential as a function of the domestic number of firms, $T=1.5$, $\varphi=0.017$ (dotted line shows $\varphi=0$)

For low transport costs, FKV find that complete concentration of manufacturing in either region ($n=1$ or $n^*=1$) is a stable pattern of production. Biodiversity, therefore, would be preserved in a single large reserve. In Figure 4.3, we illustrate how this

result is affected when skilled workers derive utility from regional biodiversity. Again our model can produce distinctly different results from the FKV results for intermediate values of the marginal utility of biodiversity.

If $0.0152 \leq \varphi \leq 0.0193$, two additional equilibrium patterns of biodiversity conservation again appear. As in the previous instance, these new solutions are stable and imply that one region preserves a small biodiversity reserve site while the other region maintains a large reserve site. For $0.0194 \leq \varphi \leq 0.0212$, two more equilibria emerge, similar to Figure 4.2. If the marginal utility from biodiversity exceeds these intermediate values, the symmetric equilibrium with maximal fragmentation is the stable solution.

4.3.3. Sensitivity analyses when transport costs are intermediate

In this section, we address the effects of varying the values of two parameters: the land-to-labour ratio and the weighting factors of generalist and specialist species in the biodiversity function. The chosen setting for the land-to-labour ratio, $b_M = S/\bar{L}_M$, has implications for the robustness of the results that were presented in the previous section. This setting has the convenient property that production concentration in, for instance, the domestic region, i.e. $n=1$ and $L_M = \bar{L}_M$, implies that $S_M = (S/\bar{L}_M)L_M = S$. All firms together require precisely all the land available in the domestic region. Two other values for b_M are conceivable, namely $b_M > S/\bar{L}_M$ and $b_M < S/\bar{L}_M$. To start with the former, it implies that production is more land-intensive than in the simulations performed above. Since more land is needed per worker, $n=1$ requires that $S_M > S$. This is infeasible, because in that case $S_H < 0$. Therefore, one region cannot contain all firms, and the other region must also maintain a small manufacturing sector. Both regions, therefore, necessarily lose at least some of their biodiversity. Alternatively, given the less intensive land use technology in production, $b_M < S/\bar{L}_M$, full concentration of manufacturing in the domestic region implies that S_H is always positive.

Figure 4.4 shows the effect of increasing the weight of specialist species α_E in the biodiversity function on equilibrium patterns of biodiversity conservation for $\varphi = 0.006$. For a given marginal utility of biodiversity, a higher value of α_E implies that only the symmetric solution is stable. This result, however, holds only under the condition that specialist species are more numerous than generalist species if regions are completely undeveloped. Recall that if all manufacturing is concentrated in the home region, then $\varphi B(1) = 0$ and $\varphi B^*(0) = \varphi[\alpha_C\gamma + \alpha_E\chi]$. Increasing α_E while keeping $\alpha_C + \alpha_E = 1$ has a positive effect on $\varphi B^*(0)$ only if $\chi > \gamma$. Clearly, if α_C and α_E can take any (positive) value, then $\chi > \gamma$ is not a necessary condition.

In either case, the differential in utility of skilled workers between regions, $u_m - u_m^*$, for high α_E is more negative than for low α_E , which makes clustering of manufacturing in the home region is less likely. The presence and preference for specialist species increase the degree of regional fragmentation for any given marginal utility of biodiversity.

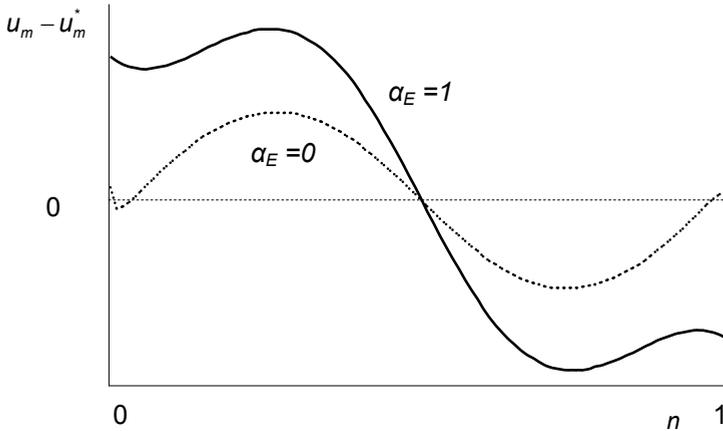


Figure 4.4. Utility differential as a function of the number of domestic firms for various α_E ; $T=1.7$ and $\varphi=0.006$

4.3.4. Policy analysis

In this section, the effect of regional environmental policy is analysed for the situation of intermediate transport costs. Regions can implement environmental policies by raising the rent τ that firms have to pay for the use of land. The coordinated optimum is compared with a non-coordinated Nash game of tax competition. In this game, each region takes the rent of the other region as given and sets its own optimal rent. Policies are determined at the outset of the game with full commitment of both governments. We ignore transition costs of changing policies and assume that governments care only about the steady-state pay-offs. Negative land rents are infeasible, as we do not allow governments to subsidise biodiversity loss. Rents are moreover bounded by the requirement that the manufacturing wage is positive. As $p = w_M + \tau b_M$, the upper bound on rents is equal to $(p - w_M) / b_M$. Finally, governments' pay-offs consist of aggregate average per capita utility of all inhabitants of the region, both skilled and unskilled. In evaluating the outcome of the game,

therefore, governments also care about the utility of foreign skilled workers that would move to their region.

Coordinated optimal policy

Here, we look at land allocation under a coordinated environmental policy that aims to maximise welfare summed over both regions. When specialist species do not enter the biodiversity function, $\alpha_E = 0$, the coordinated optimal solution is a symmetric distribution of manufacturing and biodiversity conservation in both regions. In other words, it is optimal to preserve biodiversity in two biodiversity reserve sites of similar size. To achieve this pattern of land use, there is no need for environmental policy. All environmental policies with equal rents (including zero rents) will support the first-best outcome.

When skilled workers value the presence of specialist species, a different result emerges. For $\alpha_E = 0.7$, the coordinated optimal pattern of land use is achieved when $n = S_H^* = 0.9940$ or, conversely, $n = S_H^* = 0.0060$. From a welfare perspective, full regional specialisation is not optimal. Each region, however, will specialise to a large extent in either manufacturing or biodiversity conservation. Hence, biodiversity is preserved in two reserve sites, but one of these is much larger than the other. This outcome corresponds closely to the pattern of land use that maximises biodiversity, $n = S_H^* = 0.9986$, which requires a somewhat lower degree of fragmentation. Obviously, these patterns of land use cannot be achieved when both governments implement identical environmental policies. Again, however, there is no unique solution to the appropriate combination of land rents.

Non-coordinated optimal policy

The Nash equilibrium now is addressed in a game where each individual government maximises average per capita welfare of all its inhabitants, using the rent as an instrument. It is impossible to give a full account of all the possible Nash equilibria that arise. Therefore we shall concentrate on a few cases. We maintain the distinction between $\alpha_E = 0$ and $\alpha_E = 0.7$.

Consider Figure 4.4, where there are three stable equilibria for $\alpha_E = 0$ and $\tau = \tau^* = 0$. Starting from the right-hand side equilibrium at $n = 0.9992$, the domestic government wants to drive a number of firms away to arrive at $n = 0.9854$. It will therefore increase the rent, given $\tau^* = 0$, to $\tau = 0.0010$. The foreign government observes that per capita welfare increases and therefore takes no action. Because of symmetry, the converse holds for the left-hand side stable equilibrium. Alternatively, if the initial position is the symmetric equilibrium and $\tau = \tau^* = 0$ then the home region will not increase its rent. That course of action

would lead to a larger habitat area and lower per capita welfare. On the other hand, a decrease in the rent rate is infeasible by assumption (and would moreover be matched by the foreign government). Hence, neither government can escape the symmetric equilibrium. It follows that if $\alpha_E = 0$, first-best outcomes may be supported as Nash equilibria, but this is dependent on initial conditions.

When $\alpha_E = 0.7$, we reach a different conclusion to the sustainability of first-best outcomes. In the absence of other equilibria, the symmetric pattern of land use is the starting point of the policy game. This equilibrium does not correspond to the first-best solution, nor to the second-best solution, which for the domestic region is characterised by $n = 0.9978$ given that $\tau^* = 0$. The domestic government, however, is unable to escape the symmetric equilibrium for the same reason outlined above: doing so entails subsidising land use without retaliation from the foreign government (and vice versa). If $\alpha_E = 0.7$, the pattern of land use desired by non-cooperating governments, characterised by a high degree of asymmetry in regional specialisation, is not attainable.

The conclusion we draw is that first-best allocations of land may be supported as a Nash equilibrium if generalist species alone contribute to perceived biodiversity. Otherwise, attaining the first-best degree of fragmentation is infeasible. In either case, the possibility of achieving the first-best outcome depends on initial conditions.

4.4. Conclusion

The model outlined in this chapter aims to contribute to the Singe-Large-or-Several-Small debate in biodiversity conservation from an economic perspective. We have adapted the spatial Fujita-Krugman-Venables (FKV) model with two regions and labour mobility to consider biodiversity conservation. Biodiversity has been included by giving both regions biodiversity endowments and by linking habitat availability to the location choice of firms and labour. Moreover, we modelled two types of species: generalists and specialists. These types of species react differently to loss of overall habitat. Skilled workers value regional numbers of both generalist and specialist species. Numerical simulations were used to study the behaviour of the model with respect to patterns of manufacturing and biodiversity conservation.

The results show that a positive marginal utility of biodiversity may produce new results. First, compared to the FKV results for intermediate and low transport costs, two or four additional equilibria may emerge. The new stable equilibria imply that biodiversity is conserved in several biodiversity reserves that are characterised by very low degrees of fragmentation. With increasing relative preferences for specialist species, the degree of fragmentation of biodiversity reserves sites increases.

Second, compared to the FKV result, the symmetric equilibrium, which indicates the maximum degree of fragmentation, is shown to have increased stability for all levels of transport costs and a marginal utility of biodiversity above some minimum level. Third, if the marginal utility of biodiversity is large enough, then the symmetric equilibrium is the only stable pattern of manufacturing regardless of the level of transport costs. Our extension of the FKV model suggests that when unregulated economic agents determine land allocation, there is a tendency towards a high degree of fragmentation of biodiversity reserve sites.

We have also considered environmental policies and looked at strategic behaviour of the regional governments. When governments cooperate to maximise total welfare and specialist species do not enter the biodiversity function, the optimal pattern of biodiversity conservation is to have two reserve sites with maximal fragmentation. As preferences for specialist species increase, the optimal distribution of biodiversity reserve sites becomes increasingly asymmetric. This is a result of the non-convexity in the biodiversity function. Whichever region maintains the higher level of biodiversity also has the lower level of per capita welfare. Accordingly, our analysis of non-coordinated environmental policy shows that both regions try to attain the larger share in manufacturing. These asymmetric solutions may not be achieved, however, depending on initial conditions. The symmetric pattern of biodiversity conservation, on the other hand, may be sustained as a Nash equilibrium, but does not necessarily correspond to the optimal solution.

A macroeconomic model such as the one presented in this chapter is well suited for including changes in biodiversity composition on the scale of landscapes or ecosystems. We have done so by exploring species numbers for species sets with different extinction risks. Of course, many alternative factors that determine biodiversity are also affected by labour migration and land use patterns. Some relevant issues are introduction of exotic species, fragmentation and degeneration of habitat quality. Including these issues in large-scale models, e.g., macroeconomic models is quite a difficult task. As understanding of biodiversity dynamics grows, economists are provided with new perspectives on integrating biodiversity in macroeconomic models.

5. Internalising the costs of nutrient deposition and fragmentation in a decision support tool for spatial planning: an application to the Netherlands¹

5.1. Introduction

A useful concept in biodiversity conservation is the landscape matrix, i.e. the spatial allocation of land to the various human, economic, and natural purposes (Franklin, 1993). The costs of biodiversity conservation can be reduced by rearranging the landscape matrix to minimise the impacts of human land development on natural areas, such as loss, fragmentation and abiotic degradation of natural areas (e.g., Barbier et al., 1995; Armsworth et al., 2004). Recent studies indeed suggest that reducing nutrient deposition and ground water drainage can lead to considerably lower expenses for biodiversity conservation (Wamelink et al., 2005; van Walsum et al., 2005). By internalising these damage costs generated by human land use in spatial planning, the efficiency of biodiversity conservation can be increased. In this chapter, we study the effects of including externalities in a tool for spatial planning that is widely used in the Netherlands.

Clearly, to minimise the environmental impacts of economic activities, these activities must be located as far as possible from biodiversity-rich areas. One effective instrument for achieving this is implementation of zoning regulations. The corresponding policy issue is to determine which areas to protect from development. For this purpose, Wear et al. (1996) have estimated transition probabilities in natural areas from historical data based on location characteristics. They have simulated future developments for several policy scenarios and compared the resulting landscapes using metrics that indicate degrees of fragmentation. Similar work can be found in Swenson and Franklin (2000); and Conway and Lathrop (2005). Such models indicate how to reduce the threats to biodiversity, but they do not consider all costs of conservation, such as opportunity costs of appointing biodiversity conservation sites.

¹ This chapter has been written in cooperation with P. Rietveld, J. van den Bergh, J. Vermaat, M. Wassen en M. Hilferink.

Conceivably, land use zoning can bar economic activities from locations that are economically optimal. As a result, there are efficiency losses in land allocation that should be considered when developing a socially efficient strategy for biodiversity conservation. Ando et al. (1998), Haight et al. (2002), and Snyder et al. (2004), for instance, take into account opportunity costs in determining cost-effective biodiversity conservation. By increasing existing natural areas or creating new ones, these models arrange the landscape matrix to maximise the probability of sustainable populations of protected species. The number and sizes of the reserve sites that can be created are usually restricted by a budget, which is spent on the acquisition of land. Variations in land attributes are included in these models as an approximation of the opportunity costs of biodiversity conservation. Some models go a step further and optimise the landscape matrix for a performance indicator that combines economic and ecological goals (e.g., Nalle et al., 2004; Polasky et al., 2005). These and many similar models, however, often rely on spatial distributions of species, and disregard the environmental impacts of economic activities on the ecological and spatial qualities of the ecosystems inhabited by species (see chapter 2).

In this chapter, we present a model of a land market that internalises the damage costs of human land use on the environment into land prices. To this purpose, the Land Use Scanner (LUS) is extended with approximations of market instruments, i.e. taxes and subsidies, to account for environmental externalities that are relevant to biodiversity conservation. The LUS is a spatially explicit, economic equilibrium model that can consider many types of land use simultaneously, including both economic activities and natural areas. In previous configurations of the LUS, natural areas - and the biodiversity they represent - do not participate in the market, but serve as restrictions on the allocation of economic activities. This zoning approach has been used because, as a result of market failures, economic activities are likely to usurp all desirable natural areas. In densely populated areas where natural and economically important areas are located quite close to each other, such as the Netherlands, this is a very realistic concern (LNV, 2000; RIVM, 2002). If market prices are corrected for environmental externalities, then the efficiency of equilibrium in the land market increases.

The extension of the LUS presented here considers two main environmental externalities of land use, both of which are spearheads of Dutch environmental policy: eutrophication and fragmentation of natural areas (VROM, 2001). Eutrophication, i.e. accumulation of nutrients, is incorporated through modelling the ecological damage caused by nitrogen (N) deposition. Worldwide N-addition to the environment has increased fivefold since 1960 (World Resources Institute, 2005). Increased N-eutrophication reduces biodiversity in terrestrial ecosystems (Sala et al.,

2000; Stevens et al., 2004). In the model in this chapter, local variation in N-deposition is caused by the spatial distribution of several types of agriculture. Fragmentation of natural areas is the process of breaking up contiguous natural areas into smaller, unconnected areas. This loss of spatial coherence of natural areas compromises the long-term viability of the species that inhabit these areas (Hanski and Gilpin, 1991). Many natural areas are increasingly characterised by fragmentation, not just in the Netherlands (RIVM, 2002), but also in other regions of the world (e.g., Skole and Tucker, 1993; DeFries et al., 2005). The model in this chapter counteracts fragmentation by promoting agglomeration of existing natural areas.

The analyses performed in this chapter take two different approaches. The first considers the environmental quality generated in four scenarios that reflect, among other things, varying assumptions about developments in the agricultural sector and the strictness of environmental policy.¹ The environmental quality of the scenarios is evaluated using a measure for spatial coherence of natural areas developed for this purpose. Second, sensitivity analysis is performed to assess the impact of different levels of the two environmental externalities on the economic value of the resulting land use patterns. For each pattern of land use, we also consider the cost-effectiveness of the implemented market instruments.

The model presented in this chapter builds on the recommendations in chapter 2 by combining both fragmentation and changes in abiotic conditions of ecosystems in a spatially explicit model that incorporates the allocation of multiple types of land use. The chapter has the following structure. Section 5.2 gives an outline of the LUS allocation mechanism and describes the approach adopted to model the environmental externalities and the measures used for the various analyses. Section 5.3 presents the data used for crucial parameters. Next, section 5.4 briefly introduces the scenarios, evaluates the scenario simulations, and presents the results from the sensitivity analyses. The conclusions from this study are given in section 5.5.

5.2. Environmental externalities in the Land Use Scanner

5.2.1. Grid cell suitability and the allocation mechanism

The Dutch National Institute for Public Health and Environment initiated the development of the Land Use Scanner (LUS) to assist long term spatial planning

¹ The scenarios were developed using the IPCC-SRES method, which is described in Nakicenovic et al. (2000).

(Scholten et al., 2001). The LUS output is spatially explicit and shows patterns of land use that correspond with an economic equilibrium in the (future) land market. Allocation of individual grid cells to land use types is based on bid-rent theory, which states that parcels of land are allocated to the use in which they generate the highest economic value. The LUS approximates the economic value, or bid price, of grid cells for various land use types by a suitability score.

Suitability maps for all land use types $j = \{1, 2, \dots, k\}$ play an important role in the allocation outcome. As the suitability of grid cell c to land use type j increases relative to other types of land use, the likelihood of allocating grid cell c to land use j also increases. For land use types that represent economic activities, henceforth land use, the suitability maps are determined by a number of economic, geographic and policy-related variables. To list just a few examples, these include foregone economic revenues in agriculture, distance to major centres of transit (e.g., the Amsterdam airport or the port of Rotterdam) and noise generated by highways, trains and planes. For the various types of nature, hereafter land cover, suitability is mainly determined by policies to conserve biodiversity.

The LUS allocation mechanism is extensively described in Hilferink and Rietveld (1999) and Scholten et al. (2001), but a short outline is provided here. For each grid cell, the LUS calculates expected land use according to

$$M_{cj} = a_j b_c \exp(\gamma s_{cj}) \quad (5.1)$$

where M_{cj} ($M_{cj} > 0$) is the expected allocation of hectares in grid cell c ($c=1, 2, \dots, i$) to land use type j . The balancing factors a_j and b_c ensure that supply meets demand, and s_{cj} is the suitability of grid cell c to land use j in €/m². The parameter γ determines the role of suitability in the allocation process. If γ is zero, suitability is not important and all land uses j have identical expected allocations in a cell, i.e., land use in each grid cell is highly heterogeneous. The probability that grid cell c is allocated to the land use type that has the highest suitability score approaches unity as γ goes to infinity. In this case, the allocation of land use types is homogeneous.²

² The probabilistic algorithm is described here, as it clearly shows the economic intuition behind the LUS. For this chapter, however, a more recent configuration of the LUS has been used, which employs an algorithm for discrete allocation of grid cells, \bar{M}_{cj} . Discrete allocation has two advantages: it maximises the summed suitability of grid cells, and it calculates shadow prices more accurately. It can be shown, nevertheless, that $\lim_{\gamma \rightarrow \infty} M_{cj} = \bar{M}_{cj}$. The higher the spatial resolution of the model, the stronger the case for discrete allocation, but conceptually there is little distinction between the model described and the model used.

The balancing factors a_j and b_c are derived from the following two constraints, respectively

$$\sum_c M_{cj} \geq D_j \quad (5.2)$$

$$\sum_j M_{cj} \leq L_c \quad (5.3)$$

where D_j is the total demand for land use j , and L_c is the amount of land available in cell c . The first constraint states that total land allocated to a land use class must at least equal its demand (economic constraint), and the second implies that land use allocation per grid cell cannot exceed the area of that cell (physical constraint). D_j is an exogenous factor that differs between scenarios, whereas L_c may vary for individual grid cells due to their predetermined land use, such as infrastructure, water or administrative borders.

From equations (5.1) – (5.3), it follows that the balancing factors a_j and b_c can be expressed as

$$a_j = \frac{D_j}{\sum_c b_c \exp(\gamma s_{cj})} \quad (5.4)$$

$$b_c = \frac{L_c}{\sum_j a_j \exp(\gamma s_{cj})} \quad (5.5)$$

Setting a_j initially to 1, i.e. not placing any restrictions on the claims for land use, enables a value for b_c to be determined. The resulting land use pattern probably will not satisfy the economic constraint, and the model is reiterated with adjusted a_j . Each iteration can be interpreted as a round of bidding. The variable a_j approximates economic shadow prices. Suppose that initially all grid cells are relatively unsuitable to land use j compared to land use types $k \neq j$. In the first round of bidding, land use j cannot place high bids. This makes it likely that land use j is allocated to too few grid cells relative to the demand, D_j in this round. For the next iteration, the economic constraint for j increases the balancing factor a_j relative to $a_{k \neq j}$. This means that the shadow price of land use j has risen: the cost of allocating too few grid cells to land use j has increased. The higher shadow price raises the maximum bid land use j can place for grid cells during the next round of bidding, thus increasing M_{cj} . Iterations continue until the predicted pattern of land use satisfies equations (5.4) and (5.5).

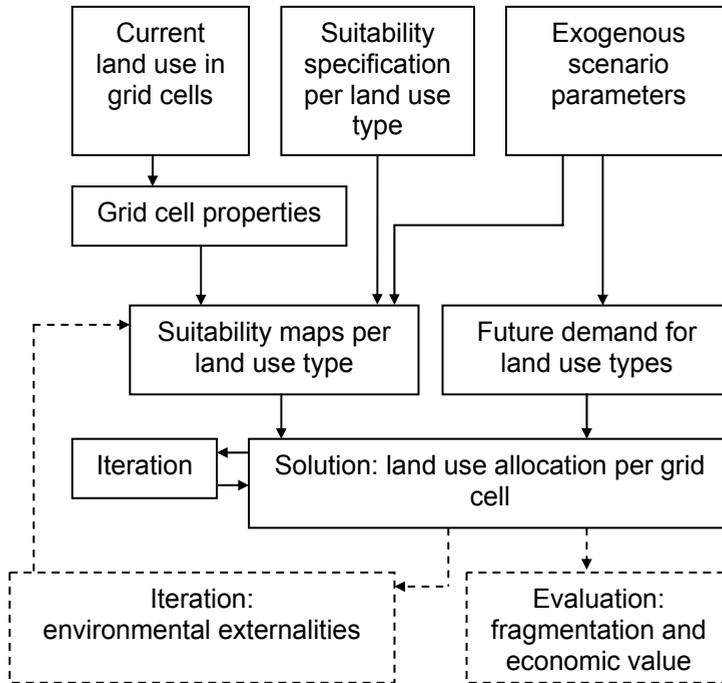


Figure 5.1. Structure of the Land Use Scanner with environmental externalities

5.2.2. Environmental externalities of land use

In the basic version of the LUS, indicated by the solid lines in Figure 5.1, suitability maps do not take into account the environmental externalities. The main purpose of this chapter is to illustrate and develop a means to internalise such externalities in spatially explicit models such as the LUS. The dotted lines in Figure 5.1 show how the LUS has been extended to account for such externalities. The spatial externalities implied by a solution are assessed and used to update the previous suitability maps via penalties and bonuses. This structure of bonuses and penalties reflects the assumption that a non-market party, for instance the (Dutch) government, has the property rights to nature. This party can enforce taxes on land use that causes environmental damage, in order to discourage this kind of land use in some locations. Similarly, subsidisation can be used to stimulate or support patterns of land use or land cover that would have beneficial environmental effects. Tax and subsidy rates are calculated per m^2 of area allocated to land use or cover types, are location-

dependent, and are determined by several environmental factors described in detail below. In addition, we include maps of groundwater tables and soil types in the suitability maps of land cover that are used in the first iteration. The implementation of these maps discourages the allocation of land cover types to grid cells that are physically unsuitable.

All land use types $j = \{1, 2, \dots, k\}$ are classified as either land use or land cover, as defined in section 5.2.1. The subset U comprises types of land use u , and the subset N contains land cover types n . Any land use pattern predicted by the LUS consists of a vector Φ of land use cells and a vector Ξ of land cover cells. In this configuration of the LUS, the subset U consists of nineteen types of land use, of which four types of agriculture cause eutrophication of land cover cells. These types of agriculture are: landscape management, arable land, intensive livestock farming, and bio-industry (see Table 5.2). The subset N contains nine types of land cover: swamp, peat grassland, dune, salt grassland, rain-fed mire, heath, coniferous forest, deciduous forest, and other.

The ecological quality of natural areas depends, among other things, on the level of eutrophication resulting from nitrogen (N) deposition (Sala et al., 2000; Stevens et al., 2004). N-deposition can be modelled as a function of the intensity of N-emissions, the spatial dispersion of emissions, the presence of natural areas, the amount of N captured by land cover types n , and the sensitivity of land cover types n to N-deposition. Together, these factors determine the penalty used to adapt the suitability map, or the tax on land use u in grid cell c

$$p_{cu} = \sum_i \sum_n \alpha_n m_{ic} r_{in} e_u M_{cu} \quad (5.6)$$

where p_{cu} is the tax on land use u in cell c in €/m² (the unit of the suitability maps). The parameter $\alpha_n \leq 0$ is a monetary approximation of the decrease in ecological quality in grid cells for land cover types caused by a unit of N-deposition in (€/m²)/(molN/ha.yr). The larger $|\alpha_n|$, the more ecological damage N-deposition causes in type n . The source-receptor matrix, indicated by m_{ic} , converts a point-source emission of ammonia (NH₃) into a spatial pattern of nitrogen (N) deposition. Although emissions of other substances could also be incorporated, at present a source-receptor matrix exists only for emissions of NH₃, as only these emissions show high local variation in the time period of the LUS (Van Hinsberg et al., 2004). The unit of m_{ic} is (molN/ha.yr)/(gramNH₃/sec), which is simply output (a spatial pattern of deposition) divided by input (a point-source emission). Actual N-deposition depends on the roughness of the land cover type allocated to a grid cell, r_{in} . This parameter, which has no unit, is a correction on the source-receptor matrix, which

expresses that, for instance, a forest captures more airborne N than a mown lawn. Finally, the parameter e_u is the amount of NH_3 emitted by land use u in $\text{gramNH}_3/\text{ha}\cdot\text{sec}$. Amortisation has been used to convert the dynamic parameters to values suitable to the static model.

The model also considers the spatial quality of the landscape, indicated by the degree of fragmentation of natural areas. In a well-known article, Hanski and Gilpin (1991) describe how fragmentation threatens the long-term viability of species. The formalisation of their model by Hanski (1994), however, cannot easily be incorporated in the LUS, as this would be computationally cumbersome. More importantly, it would not fully match the structure of the LUS suitability maps (see the discussion under equation (5.8)). Instead, proximity to land cover cells that have already been allocated to identical land cover determines the suitability of grid cells to land cover types:

$$f_{cn} = \beta_n \sum_{i \in \Psi} (M_{in} / d_{ci}) / \sum_{i \in \Psi} (1 / d_{ci}) \quad (5.7)$$

where f_{cn} is the bonus, or subsidy on land cover type n in grid cell c in $\text{€}/\text{m}^2$. The parameter $\beta_n > 0$ indicates in $\text{€}/\text{m}^2$ the increase in suitability that grid cell c receives from being near to cells i in the vector Ψ of grid cells that contain the same type of land cover. Alternatively, the value of β_n is a monetary approximation of the improvement in spatial quality of land cover types due to decreased fragmentation. The distance between land cover cells as measured from their centres is indicated by the variable d_{ci} . The functional form of equation (5.7) has been chosen to reflect the disproportionately higher success rate of species dispersal at smaller distances between habitat patches (e.g., With and King, 1999). Accordingly, the bonus is relatively large for grid cells that are close to land cover cells.

5.2.3. Measures of environmental and economic value of landscape patterns

With the extension to the LUS presented above, we will perform two alternative types of analysis on the allocation of land use and land cover. The first analysis is an evaluation of the land use patterns that emerge under the various land use scenarios, described in section 5.4.1. The second type of analysis focuses on the effectiveness of market instruments in guiding the land market to spatial patterns that are more beneficial to biodiversity conservation. Sensitivity analyses of the environmental externalities are performed by assessing the resulting increases in monetary value of allocated land. These are compared with the total marginal

revenues and costs of the concomitant tax and subsidy, which are an indication of the required policy effort.

As indicators of the overall state of the environment, ideally both the ecological quality of land cover cells and the degree of fragmentation would be considered. Changes in the suitability of grid cells could be interpreted to indicate such changes. This is in fact the underlying assumption of this model, albeit that these changes are expressed as monetary values that are subsequently interpreted as taxes (subsidies) on land use (cover). If the model and all parameters values are correct, then these interpretations of suitability changes can be freely substituted.³ Nevertheless, separate indicators are preferable to multiple interpretations of variables. With respect to ecological quality, however, this configuration of the LUS does not provide any means to consider the quality of land cover in grid cells. The model may show that a grid cell contains a particular type of land cover, but not, for instance, how much biomass its vegetation produces, or its abundance of desirable species. Such indicators require more sophistication in the ecological areas of the model.

Fragmentation, on the other hand, can be considered separately. Several indices for the degree of fragmentation have been suggested, each of which emphasises different aspects of fragmentation, such as interior size of habitat patches, edge length and patch isolation (see, e.g., Debinski and Holt, 2000). None of the aforementioned measures, however, gives an integral assessment of both size and relative location of habitat patches. Here, these two aspects of landscape fragmentation are captured in a single measure. These aspects, as has been discussed above, are crucial to the survival of species in fragmented landscapes. Suppose that species z uses land cover type(s) n_z as habitat. Then, the vector of land cover cells Ξ contains a vector of habitat cells Ω_z for species z . Some of these habitat cells form contiguous areas of various sizes, which are numbered $h = \{1, 2, \dots, g\}$. Contiguous areas below some minimum size are disregarded. The degree of fragmentation of the landscape as far as species z is concerned, F_z , is approximated by

$$F_z = \sum_h \left[S_h^2 + \sum_{g \neq h} S_g S_h \left(1 - \frac{d_{gh}}{d_z^{\max}} \right) \right] \quad (5.8)$$

where S_h is the size of the h th habitat patch, d_{gh} is the distance between habitat patches h and g as measured from the patch edges, and d_z^{\max} is the maximum dispersal distance of species z . The value of F_z decreases with increasing

³ It is acknowledged that putting a monetary value on the environment has its methodological problems.

fragmentation. Equations (5.7) and (5.8) consider the degree of fragmentation from very different perspectives, but they are nonetheless related. Equation (5.8) describes the environmental quality for a single species, and thus corresponds to some degree to the Hanski model.⁴ Equation (5.7), on the other hand, targets environmental quality at the level of land cover types and thus applies to many species simultaneously. The bonus awarded to land cover types in any one grid cell, f_z , should correspond to the change in the value of F_z that would arise from actually allocating land cover to that grid cell, summing over all species z that would benefit from this change in land cover allocation.

In order to assess the impact of the implementation of market instruments on LUS results, we consider the following issues: changes in land allocation patterns, changes in the economic value of these patterns, and the extent to which taxes and subsidies on land use and land cover types are required for achieving improvements in land allocation. The suitability maps for land use and land cover types are the key to calculating these indicators. The economic value of land allocation is

$$V = \sum_c \sum_j s_{cj} M_{cj} \quad (5.9)$$

with V in €. Letting asterisk $*$ indicate variables in the basic model, then $V - V^*$ gives the change in V that arises from internalising environmental effects of land use, where V^* is first corrected for the externalities implied by the land use pattern. For each grid cell and land use or cover type, the tax and subsidy rates required to achieve efficient changes in land allocation are denoted by p_{cj} and f_{cj} , respectively. The total marginal tax revenue and subsidy cost per land use and cover type are calculated by summing the suitability differences over grid cells that change allocation due to the implementation of market instruments.

5.3. Data description

5.3.1. Ammonia emission rates and nitrogen deposition

Nitrogen deposition in the Netherlands mainly stems from emissions of NO_x and NH_3 (see Table 5.1). The main sources of NO_x are traffic and neighbouring countries.

⁴ The measure presented in equation (5.8) is of our own devising, and lacks the strong connection to metapopulation theory of the measure suggested by Hanski (1999). Our measure, nevertheless, is successful in capturing the main characteristics of fragmentation: smaller and more isolated habitat patches imply a higher degree of fragmentation.

Nitrogen emissions from these sources may change and result in different spatial patterns of N-deposition in the long run. In the short run, only emissions of NH₃ show high local variation (Van Hinsberg et al., 2004). Within the Netherlands, the main source of NH₃ is agriculture. Emission patterns from agriculture may conceivably be changed more easily than those from infrastructure and other countries. It is assumed, therefore, that no significant shifts in the latter sources of nitrogen occur in the time span of the LUS simulations. Consequently, the focus here is on the spatial allocation of agricultural activities.

Table 5.1. Sources of NH_x and NO_y deposition in the Netherlands as predicted for 2010

Source	NH _x	NO _y
Industry	32.3	29.9
Traffic	28.5	129
Agriculture	864.4	4.8
Consumers	82.2	7.5
Other countries	306.6	276.1

Source: MNP, personal communication, 2005.

In this model, every grid cell containing agricultural land use types is considered as a point source of NH₃ emissions (although at 500x500m, the spatial resolution is arguably too low for this assumption to hold). The spatial gradient of N-deposition around each emitting grid cell has an oblong shape that stretches to the north-east. This pattern of deposition is caused by the wind, which in the Netherlands generally comes from the southwest. The source-receptor matrix as calculated by Van Hinsveld et al. (2004) lets the effect that agriculture has on land cover types be simulated. Equation (5.6), which calculates the penalty, or tax on N-deposition, however, entails the reverse, so the matrix has been inverted.

For the rate of NH₃ emissions per hectare of the various types of agriculture, yearly national emissions data were made available by the MNP. Most of these data could be linked to specific agricultural sectors, but there was some difficulty in distinguishing between emissions from landscape management and emissions caused by intensive livestock farming. Both types of farming are included in a single aggregate, and allocating emissions by acreages yields only a negligible difference in emission rates due to an averaging effect. Emissions from agricultural landscape management, however, are bound to be much lower than those from intensive livestock farming. It is assumed that the rate of NH₃ emissions per hectare from

landscape management activities is a tenth of that from intensive livestock farms. Table 5.2 shows the emission rates for the four agricultural sectors.

Table 5.2. *NH₃ emission rates from four types of agricultural land use (grNH₃/ha.sec)*

<i>Landscape management</i>	<i>Arable land</i>	<i>Livestock farming</i>	<i>Bio-industry</i>
0.000181	0.000919	0.001809	0.059079

Changes in the pattern of N-deposition caused by different spatial allocations of agriculture are modelled using the source-receptor matrix. This matrix has been derived from Operational Priority Substances (OPS) model. The OPS model was developed by the National Environmental Assessment Agency (MNP) to describe the spatial distribution of deposition for many types of acidifying emissions (e.g., Van Jaarsveld, 2004). It distinguishes between local and non-local sources of emission, but operates at a spatial resolution that is too low to be used with the LUS. Van Hinsberg et al. (2004) describe a method to approximate the results of the OPS model at a finer spatial resolution. The result is the source-receptor matrix as used in equation (5.6). In fact, several source-receptor matrices were calculated to reflect differences in the altitude of emission and meteorological characteristics of various areas in the Netherlands. In this study, only matrices for the middle-eastern part of the Netherlands have been used. Presumably, this area largely approximates the average Dutch meteorological condition.⁵ Two matrices of this region are used that distinguish between emissions from stables and from meadows. The study by Van Hinsberg et al. (2004) shows that deposition decreases more quickly with distance in the case of meadows, as the altitude of the emission is less than it is of stables.

5.3.2. *Suitability changes due to N-deposition and fragmentation*

To approximate the suitability change from a unit of N-deposition, indicated in equation (5.6) by α_n , results from De Jong et al. (2004) have been used. This study estimates the management costs of maintaining the ecological quality of various land cover types, both at the current level of deposition, as well as at an assumed lower level of deposition. For each land cover type, the difference indicates the damage cost of a unit of N-deposition. De Jong et al. (2004) take nine types of land cover into

⁵ Erik Noordijk, MNP, personal communication, 2005.

account: dry and wet heathland, dry, moist and wet grassland, reed and roughland, forest, salt grassland and moorland pools.

Most, but not all, of these land cover types correspond perfectly to the land cover types present in the LUS. If the land cover types match, then results from De Jong et al. (2004) have been used to calculate α_n . If not, then the average of the damage costs from a number of land cover types from De Jong et al. (2004) is the value of α_n for LUS land cover types. Table 5.3 clarifies by showing the correspondence among the land cover types, as well as the resulting suitability parameter α_n for all land cover types in the LUS.⁶ There is a certain measure of uncertainty surrounding the calculated values for α_n , which arises, for instance, from the method used to transfer results from De Jong et al. (2004) to the LUS or the discount rate used to amortise the data. To give expression to such uncertainty, we later assess the impact of increasing the values for α_n tenfold.

Table 5.3. Suitability changes for land cover types per unit of N deposition

<i>Land cover types in the LUS</i>	<i>Land cover types in De Jong et al. (2004)</i>	α_n (€/m ²)/(molN/ha.yr)
Swamp	Reed and roughland	- 1.098 10 ⁻³
Peat meadow	Moist grassland Wet grassland	- 1.858 10 ⁻³
Dune	Dry heath Wet heath	- 3.029 10 ⁻⁴
Salt marsh	Salt grassland	- 2.533 10 ⁻⁴
Rain-fed mire	Moorland pools	- 6.902 10 ⁻⁴
Heath	Dry heath Wet heath	- 3.029 10 ⁻⁴
Coniferous forest	Forest	- 2.056 10 ⁻⁵
Broad-leafed forest	Forest	- 2.056 10 ⁻⁵
Other	-	0

As discussed in equation (5.8), the parameter β_n from equation (5.7) ideally reflects the change (loss) in spatial quality of land cover types that is caused by an extra unit of fragmentation summed over all species. Only a few studies have estimated the cost of fragmentation. Geoghegan et al. (1997), for instance, use a hedonic pricing model to show that fragmentation (of land cover and land use) generally has a negative effect on housing prices. Van der Heide (2005, chapter 8) estimates the

⁶ The values in Table 5.3 were derived using a reduction of N-deposition of 908 mol/ha.yr for all types of land cover (p. 31, De Jong et al., 2004).

willingness-to-pay for less fragmentation in a large Dutch nature reserve. He elicits the value of the change in a visitors' enjoyment of the reserve due to a reduction in fragmentation, rather than the actual cost of preserving species in fragmented landscapes. For our purpose, the study of van der Heide (2005; chapter 8) is the most relevant study available. Assuming that its results apply to all of the Netherlands and to all land cover types equally, we can use it here. Both the mean and the median are considered, $\beta_n = 1.1 \text{ €/m}^2$ and $\beta_n = 0.123 \text{ €/m}^2$, respectively, to express possible uncertainty in the results of van der Heide (2005).

To assess the environmental quality of land allocation in each scenario, the fragmentation measure presented in equation (5.8) is used. As has been explained, this measure requires data on species dispersal and habitat preferences. Because of the low spatial resolution and ecological detail of this study, however, the use of data on real species seems superfluous. At a large spatial scale, for instance, an endangered species of damselfly (*Coenagrion mercuriale*) is present in systems of meadows and ditches, but small-scale physical attributes of these ditches have significant influence on local presence of this damselfly (Rouquette and Thompson, 2005). Here, to illustrate the functioning of equation (5.8) in assessing the spatial quality of land cover patterns, these following values for parameters are assumed: the model only considers spatial interactions between areas of identical land cover that are no more than 5 kilometres apart, while it disregards land cover areas smaller than 125 hectares.

5.3.3. Suitability maps and geophysical attributes

The land cover types in the LUS are an aggregation of the many land cover types that conservationists discern within the Netherlands. One commonly used classification of land cover types is described in Bal et al. (2001) in the 'Handbook Nature Target Types' (HNT). This detailed classification is largely based on important geophysical attributes, such as soil type and hydrological conditions. Here, the more detailed land cover types from the HNT were aggregated to correspond to the nine land cover types in the LUS. From this aggregating procedure, the amenable soil type and hydrological conditions were determined for the land cover classification used in the LUS (see Tables Table 5.4 and Table 5.5).

Although already part of the LUS dataset, maps for these attributes have not yet been used in an integrated assessment of land use and land cover allocation. Such maps, however, can be crucial in achieving better predictions of land cover allocation. They may prevent land cover types from being allocated to grid cells with unsuitable geophysical conditions. Accordingly, grid cells receive a suitability penalty

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for land cover types that cannot grow given the soil type in the grid cells. The penalty is constant for all soil and land cover types, which implies, to take an example from Table 5.4, that loess is as unsuitable to swamps as it is to coniferous forests. For hydrological conditions, the penalty increases with deviation from the optimal groundwater level.

Table 5.4. Land cover types and amenable soil conditions

<i>Land cover type</i>	<i>Sand</i>	<i>Loess</i>	<i>River clay</i>	<i>Sea clay</i>	<i>Peat</i>	<i>Sand with organic material</i>
Swamp	x	-	x	x	x	x
Peat meadow	-	-	-	-	x	x
Dune	x	-	-	-	-	x
Salt marsh	x	-	-	x	-	x
Rain-fed mire	x	-	-	-	x	x
Heath	x	-	-	-	-	-
Coniferous forest	x	-	-	-	-	x
Broad-leafed forest	x	x	x	x	x	x
Other	x	x	x	x	x	x

Source: Bal et al. (2001). An 'x' indicates which soil type is required for each land cover type.

Table 5.5. Land cover types and amenable hydrological conditions

<i>Land cover type</i>	<i>I</i>	<i>II</i>	<i>III, IV</i>	<i>V, VI, VII</i>
Swamp	x	x	-	-
Peat meadow	-	x	x	-
Dune	-	-	-	x
Salt marsh	x	x	-	-
Rain-fed mire	x	x	-	-
Heath	-	-	x	x
Coniferous forest	-	x	x	x
Broad-leafed forest	x	x	x	x
Other	-	x	x	x

Source: Bal et al. (2001). Roman numerals indicate standardised groundwater levels relative to surface area; I: 0 to -50 cm; II: -50 to -80 cm; III, IV: -80 to -120 cm; V, VI, VII: -120 cm and less. An 'x' indicates which hydrological regime is required for each land cover type.

These penalties are supposed to reflect transition costs, e.g., the costs of replacing sandy soil with peat soil to accommodate peat meadows in a cell, or changing the

groundwater level from level II to level V, VI or VII for dunes. Estimates of such costs, however, have not been found. Some testing with parameter values showed that increasing the penalties quickly leads to improbable results. Dunes, for instance, which in the original LUS occur only on the coast, were relocated to the east of the Netherlands. The coast itself became populated with broad-leafed and pine forests. Clearly, the addition of these two suitability factors has a big impact on the original suitability maps, but this matter is not investigated further here. For now, the penalties for both inappropriate soil types and groundwater conditions have been set at 2 €/m².

5.4. Scenario and sensitivity analyses

5.4.1. Brief description of land use scenarios

This section considers the environmental quality generated under various scenario assumptions. The LUS configuration used in this study is the one employed in the 'Spatial impressions' project (Borsboom-van Beurden et al., 2005). The 'Spatial impressions' project analyses scenarios for the Netherlands that were developed using the IPCC method (De Mooij and Tang, 2003; Lejour, 2003, see also Nakicenovic et al., 2000). According to this method, two societal choices, the extent of government responsibility and the degree of international (economic) cooperation, underlie all possible future developments. This gives rise to four scenarios. The macroeconomic data provided by De Mooij and Tang (2003) and Lejour (2003), however, cannot be used as direct input to the LUS. The necessary parameters, e.g., future demand for all land use types j and weighting parameters for the suitability maps, have been derived by Borsboom-van Beurden et al. (2005).

The four scenarios are named A1, B1, A2 and B2. Letters indicate the degree of government responsibility (centralistic versus individualistic), and the numbers give the extent of global economic integration (regional versus global). Scenarios A1 and B2 are the extreme cases, indicating an individualistic society with a global orientation, and a centralistic one with a regional focus, respectively. The A2 and B1 scenarios form combinations of these attributes. With respect to land use, the A scenarios assume that global competition drives the demand for agricultural types of land use to large-scale production with relatively large environmental impacts. Additionally, the suitability maps show little attention to protecting natural areas. The B scenarios express a relatively high demand for less environmentally damaging, small scale agriculture as well as increased consideration for environmental

preservation. In the following scenario simulations, the low settings for α_n and β_n are used. Sensitivity analysis of these parameters is performed in the next section.

5.4.2. Assessment of fragmentation in the scenarios

Starting with the fragmentation of land cover types, results per scenario are given in Table 5.6.⁷ With respect to individual land cover types, the scenarios generate varied results. In the B2 scenario, four of eight land cover types have the lowest fragmentation, namely peat meadow, salt marsh, heath and broad-leafed forest. Two land cover types are rated with the lowest level of fragmentation in the B1 and A2 scenarios each, and no land cover type ranks first in this respect under the assumptions of the A1 scenario. As the B2 and A1 scenarios are, respectively, the most and least environmentally oriented scenarios, this result conforms to expectations.

Table 5.6. Normalised values of the measure of fragmentation, F_z , per scenario^a

<i>Land cover type</i>	<i>A1</i>		<i>B1</i>		<i>A2</i>		<i>B2</i>	
Swamp	0.63	(44)	1.00	(125)	0.60	(50)	0.69	(91)
Peat meadow	0.46	(25)	0.39	(56)	0.65	(28)	1.00	(38)
Dune	0.98	(28)	0.87	(30)	1.00	(29)	0.99	(28)
Salt marsh	0.91	(19)	0.90	(20)	0.94	(18)	1.00	(20)
Rain-fed mire	0.09	(13)	1.00	(55)	0.04	(12)	0.53	(63)
Heath	0.95	(46)	0.90	(48)	0.70	(48)	1.00	(51)
Coniferous forest	0.95	(138)	0.18	(127)	1.00	(136)	0.27	(120)
Broad-leafed forest	0.54	(451)	0.77	(456)	0.23	(366)	1.00	(406)

^a Number of habitat areas in parentheses

Rain-fed mire appears to be an exceedingly fragile type of land cover in the A scenarios, as the number of contiguous areas is very low compared to both B scenarios. This is to a large extent attributable to a very low demand for this type of land cover in the A scenarios. Note, however, that even though the B2 scenario allocates more areas of rain-fed mire than the B1 scenario does, the fragmentation of these areas is almost twice as low in the latter. Similar effects can be discerned for swamps, peat meadows and broad-leafed forests. This shows that the measure for

⁷ The values of F_z differ only marginally between the LUS configurations with and without market instruments.

fragmentation presented in equation (5.8) does not increase strictly with the number of habitat patches. Apart from rain-fed mire, other land cover types that perform very poorly in several scenarios are peat meadow and coniferous forest.

5.4.3. Sensitivity analysis of externalities and implications for taxes and subsidies

In this section, the implications of adding market instruments to the basic LUS configuration, which relies only on zoning to guide land use developments, are studied in the A1 scenario. Regarding patterns of types of land use and land cover, both changes in the volume and the spatial distribution are considered separately. Moreover, the increase in the economic value of allocated land that arises from internalising environmental externalities is considered, as well as the costs and benefits associated with implementing these market instruments.

Adjustments of relative prices in general will affect the volumes of land use and land cover in equilibrium. Such changes, however, are not prominent in this particular configuration of the LUS. A technical explanation is that the minimum demands for many of the land use and land cover types considered here are binding model restrictions of the LUS (see equation (5.4)). In that case, the extended configuration may easily yield the same volumes of these land use types. In scenarios where the minimum demand is not binding for all land use types, however, volume effects are small. To the extent that volume effects do occur, these are more easily generated by increases in α_n than in β_n . If this LUS configuration accurately reflects future conditions in the land market, then it appears that the environmental impacts of N-deposition and fragmentation on land cover areas are insufficiently large to affect allocated volumes of land use types. A likely explanation of this is the scarcity of land in the Netherlands, which causes high shadow prices of land use types. Alternatively, altering definitions of suitability maps or claims for land use can provide the LUS with more flexibility to deal with taxation and subsidisation of environmental externalities.

Although volume effects are small, the implementation of taxes and subsidies can have large impacts on the spatial distribution of land use and land cover types. Table 5.7 compares the LUS results of the original and extended configurations, given the parameter settings α_n as shown in Table 5.3 and $\beta_n = 0.123$. For each type of land use and land cover, the first column shows the percentage of grid cells that change allocation due to the implementation of taxes and subsidies. At these levels of the two environmental impacts of land use, there are only small effects on the allocation of land cover types. Of the agricultural types of land use, landscape management (7.6%) and livestock farming (2%) show the largest changes in

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allocation due to taxation of environmental damage. Bio-industry, the most polluting type of agriculture, is hardly affected. Grid cells with bio-industry are apparently not in locations where the economic valuation of their environmental impacts is large enough to warrant their relocation.

Table 5.7. Comparison of allocation results from extended and original LUS for α_n and $\beta_n = 0.123$

<i>Land cover type</i>	<i>Grid cells changed dominance (%)</i>	<i>Land use types predominantly substituted</i>	<i>Corresponding suitability difference (€/ha)</i>	<i>Predominantly substituted by land use types</i>	<i>Corresponding suitability difference (€/ha)</i>
Swamp	0.4	-	-	-	-
Peat meadow	0.9	-	-	-	-
Dune	0	-	-	-	-
Salt marsh	0	-	-	-	-
Rain-fed mire	0.3	-	-	-	-
Heath	0.1	-	-	-	-
Coniferous forest	0.2	-	-	-	-
Broad-leafed forest	0.3	-	-	-	-
Landscape management	7.6	Livestock farming	0	Livestock farming	0
Arable land	0	-	-	-	-
Livestock farming	2.0	Landscape management	-1.9	Landscape management	-60.5
Bio-industry	0.5	-	-	-	-

The remaining columns give information only for land use and land cover types of which more than one percent of grid cells change dominance. These columns are to be read pair-wise: columns two and three show results for grid cells in which the various land use and land cover types gain dominance, whereas columns four and five apply to grid cells where dominance has been lost.

In grid cells where any given type of land use or cover gains dominance, other types lose dominance. If these latter are predominantly of one type, this is given in column two. Analogously, the fourth column shows the land use or cover types to which any specific type loses its dominance. These columns indicate if land use and cover types compete for the same locations. The instance of such competition that is most clear from Table 5.7 exists between livestock farming and landscape

management. Landscape management mostly gains dominance in grid cells allocated to livestock farming in the basic LUS, and vice versa. The process of this competition is explained in more detail below.

Although the LUS calculates tax and subsidy rates for all grid cells individually (see Figure 5.2), columns three and five in Table 5.7 show averages of these rates only in grid cells where land use and land cover types gain or lose dominance, respectively.⁸ The values indicate bounds on the marginal rates for subsidies and taxes on land cover and land use. For example, subsidies in this model are intended to encourage the placement of land cover in new locations. Since land cover types would not have become dominant in new grid cells with lower subsidies, the values in the third column are upper bounds on the average subsidy rate. Similarly, as land cover types would not have lost dominance in grid cells if subsidies were higher, values in the fifth column indicate lower bounds on the subsidy. For the average tax rates on agricultural land use types, the third and fifth columns, respectively, show lower and upper bounds.

The ranges of the marginal tax and subsidy rates can be large. For instance, the upper and lower bounds of the tax rate for livestock farming are €60.5 and €1.9 per hectare. This range for the marginal tax rate is the result of supply and demand conditions, as well as the initial suitability maps. Livestock farming is sometimes initially located in grid cells where it causes high environmental damage, because without environmental externalities these grid cells are very suitable to this type of agriculture. Consequently, a high tax rate is necessary to cause livestock farming to bid unsuccessfully for these grid cells. Livestock farming can, however, bid successfully for grid cells where it would cause less environmental damage and would be subject to a lower tax rate. Since the suitability map of livestock farming is very similar to that of landscape management, relocation of the former is likely to drive the latter from its initial locations. Simultaneously, landscape management is likely to relocate to grid cells previously allocated to landscape management. It can do this successfully, because it emits very little NH₃ and is thus confronted with a zero marginal tax rate in these locations.⁹

⁸ Numbers are given only if the allocation changes in more than 1% of grid cells.

⁹ Landscape management nevertheless competes for grid cells initially allocated to livestock farming with other types of land use and land cover, most significantly peat meadow and swamp. As these land cover types also successfully bid for some grid cells, the tax on remaining nearby livestock farming increases, reinforcing the process described above. With successive iterations, the mean and variance of the tax on livestock farming indeed take on increasingly negative values.

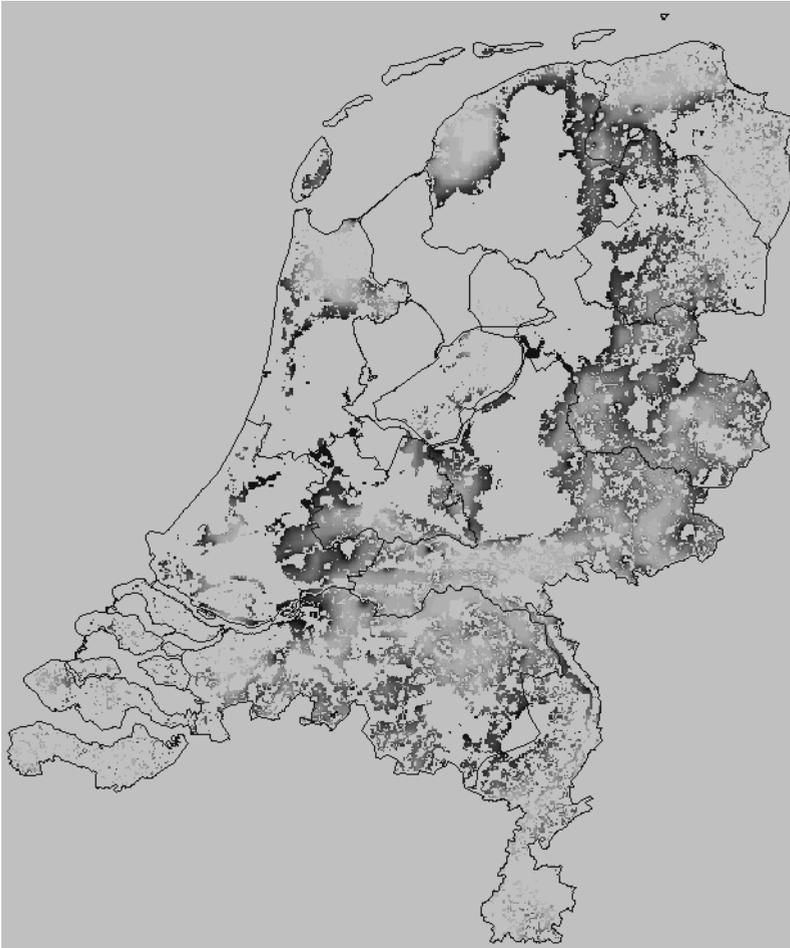


Figure 5.2. Spatial pattern of tax rates on allocated livestock farming in 2030 for $10x \alpha_n$ (darker areas indicate higher tax rates)

The average marginal rates of taxes and subsidies in Table 5.7 are derived from the spatial distribution of tax and subsidy rates in all grid cells, shown for livestock farming in Figure 5.2. The level of taxation is indicated by shades of grey, with darker areas signalling higher tax rates. The areas with higher tax rates are near to areas that contain land cover types which are sensitive to N-deposition. The blank areas in the northern part of the Netherlands, for instance, correspond to large concentrations of swamp and peat meadow. Livestock farming in the surrounding grid cells is

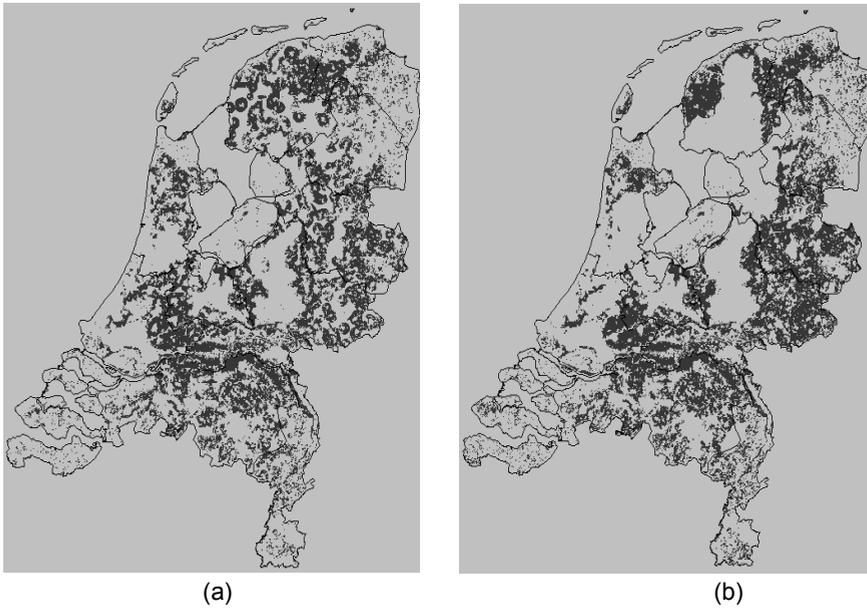


Figure 5.3. Allocation of landscape management under zoning (a) and market-based (b) policy regimes

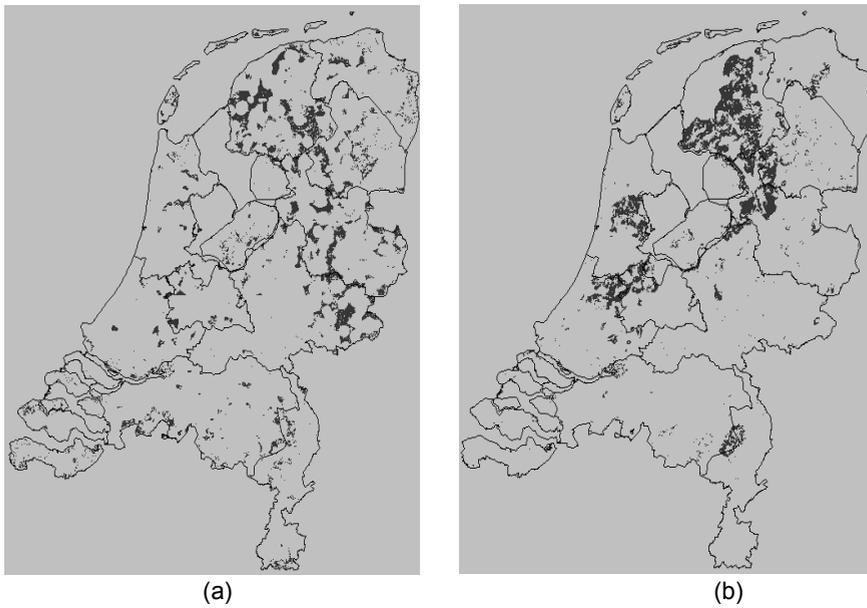


Figure 5.4. Allocation of livestock farming under zoning (a) and market-based (b) policy regimes

subject to a higher tax rate compared to grid cells that are farther from these land cover areas.

Table 5.8. Comparison of allocation results from extended and original LUS for $10x \alpha_n$ and $\beta_n = 0.123$

<i>Land cover type</i>	<i>Grid cells changed dominance (%)</i>	<i>Land use types predominantly substituted</i>	<i>Corresponding suitability difference (€/ha)</i>	<i>Predominantly substituted by land use types</i>	<i>Corresponding suitability difference (€/ha)</i>
Swamp	0.5	-	-	-	-
Peat meadow	1.2	Livestock farming	978.3	Landscape management	198.7
Dune	0	-	-	-	-
Salt marsh	0	-	-	-	-
Rain-fed mire	0.3	-	-	-	-
Heath	0.1	-	-	-	-
Coniferous forest	0.2	-	-	-	-
Broad-leaved forest	0.3	-	-	-	-
Landscape management	36.1	Livestock farming	0	Livestock farming	0
Arable land	0.1	-	-	-	-
Livestock farming	9.4	Landscape management	-10.7	Landscape management	-389.7
Bio-industry	3.8	Diverse	-324.2	Diverse	-2959.7

In Table 5.8, results are shown when the environmental impact of N-deposition, α_n , is increased tenfold. Impacts on landscape management and livestock farming, which remain strong competitors for locations, are in this instance severe. Respectively, 36% and 9.5% of grid cells allocated to these land use types change dominance. Figure 5.3 and Figure 5.4 show where and how the majority of these changes take place. The corresponding rate of taxation remains zero for landscape management, but increases to €10.7 - € 389.7 per hectare for livestock farming. Furthermore, of the grid cells with bio-industry as the dominant land use type, 3.8% are in a new location when damage from N-deposition is internalised. The tax rate that is required to bring about these reallocations of land is significantly higher than for livestock farming: bio-industry must be taxed by €324.2 - €2959.7 per hectare. These relocations occur on the basis of individual grid cells, rather than groups, and

no single type of land use type can be identified as the major competitor for bio-industry. Pricing the environmental damage due to N-deposition has a limited impact on land cover types. Only in the case of peat meadows are 1.2% of the grid cells in a new location under the subsidy scheme. This change requires a subsidy of €198.7 - €978.3 per hectare. Peat meadow drives out livestock farming, and landscape management fills the abandoned grid cells.

Table 5.9. Comparison of allocation results from extended and original LUS for α_n and $\beta_n = 1.1$

Land cover type	Grid cells changed dominance (%)	Land use types predominantly substituted	Corresponding suitability difference (€/ha)	Predominantly substituted by land use types	Corresponding suitability difference (€/ha)
Swamp	1.9	Livestock farming, Peat meadow	7456.9	Livestock farming, Landscape management	9.7
Peat meadow	3.6	Livestock farming, Landscape management	9480.7	Livestock farming, Landscape management	1056.5
Dune	0.4	-	-	-	-
Salt marsh	0.3	-	-	-	-
Rain-fed mire	0.9	-	-	-	-
Heath	1.6	Broad-leafed forest, Coniferous forest	7521.5	Broad-leafed forest, Coniferous forest	533.9
Coniferous forest	1.6	Broad-leafed forest	9036.5	Broad-leafed forest, Heath	841.8
Broad-leafed forest	2.7	Diverse	7905.1	Diverse	389.1
Landscape management	8.0	Livestock farming, Broad-leafed forest	0	Livestock farming, Broad-leafed forest	0
Arable land	0.4	-	-	-	-
Livestock farming	2.3	Diverse	-3.4	Diverse	-60.4
Bio-industry	0.9	-	-	-	-

Table 5.9 shows the impact on allocation results in the third sensitivity analysis, in which the environmental benefit from less fragmentation of natural areas, β_n , is

increased to €1.1 per hectare. The allocation of land cover types is affected to a larger extent than in the previously considered cases. The allocation of dunes, salt marsh and rain-fed mire, however, remains unchanged. These types of land cover are highly specialised and only a few locations in the Netherlands provide the right conditions. Hence, these types of land cover do not compete for locations besides the grid cells they have already been allocated to. The impact on the other types of land cover is not extensive. Peat meadow is the most illustrative example of the effects of the subsidy, shown in Figure 5.5. Concentration of peat meadows increases by adding solitary grid cells to larger peat meadow areas. The concentration of land cover increases, but does so in small increments.

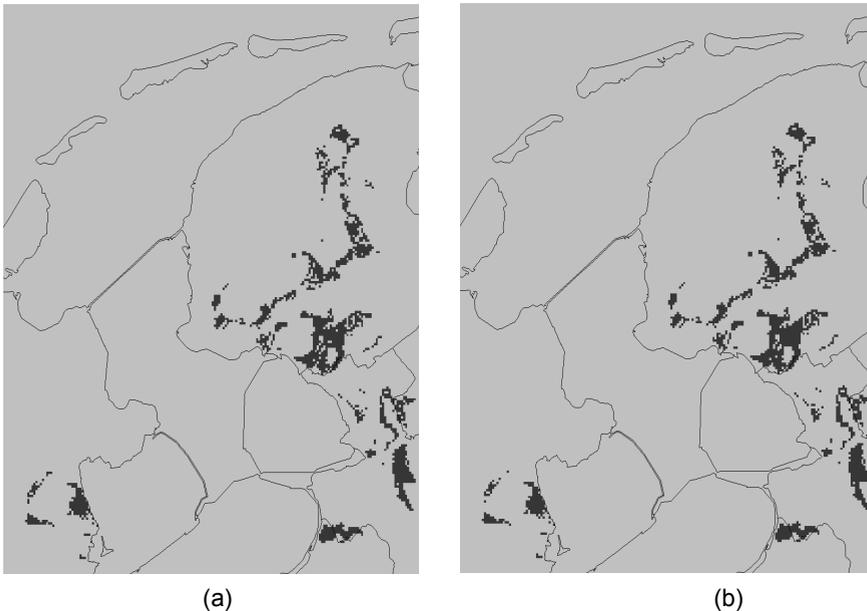


Figure 5.5. Allocation of peat meadow under zoning (a) and market based (b) policy regimes

The impact of increasing β_n has only a small effect on the allocation of agricultural land use, given that the values in the first column of both Table 5.7 and Table 5.9 differ by only 0.3 - 0.4 percentage points. Nonetheless, there is a small increase in the competition between land use and land cover types, as illustrated by columns 2 and 4 in Table 5.9. Peat meadows and swamps together affect the allocation of landscape management and intensive livestock farming. Broad-leafed forest

influences multiple types of land cover and land use. The latter comprise landscape management and intensive livestock farming, but also arable land and, in a few instances, land use not explicitly considered so far: orchards and recreational parks. That high-value land use types are driven out by land cover is rare, as most types of land cover compete for space only among themselves. Accordingly, the rate of subsidisation required to bring about these changes in land cover patterns is steep: the upper bounds on the subsidy range from €7457 per hectare for swamp to €9481 per hectare for peat meadow.

Internalising environmental effects through taxes and subsidies should lead to a higher degree of efficiency in land allocation, and thus to a higher value of land, after correcting for the externalities. Taking this correction into account, this increase in land value constitutes a positive contribution to social welfare. The model outcomes allow us to explore the effectiveness of the tax and subsidy instruments in increasing land value. For the various parameter combinations also used in the previous sensitivity analyses, Table 5.10 shows the increases in the economic value of land, as well as the required changes in tax revenues and subsidy costs.

Comparing the value of land in the initial situation with that under the tax and subsidy schemes considered shows the increase in the economic value of land. When both externalities are set to their low values, this increase is estimated to be €2.6 million. If the environmental impacts of N-deposition and fragmentation, respectively, are high, i.e. increased approximately tenfold as in the sensitivity analysis, the gain in the value of land in the Netherlands increases to €31 million and €130 million. In this configuration of the LUS, the potential to increase the value of land allocation in the Netherlands appears to be relatively limited, as the total value of land in the Netherlands is around €211 billion. Nevertheless, this exercise shows that accounting for environmental externalities in land allocation by tax and subsidy instruments can increase the efficiency of land use.

Table 5.10. Increase in the economic value of land and revenue and cost of tax and subsidy for the previous sensitivity analyses

	α_n, β_n	$10x \alpha_n$	$\beta_n = 1.1 \text{ €/m}^2$
Economic value (€)	$2.605 \cdot 10^6$	$3.102 \cdot 10^7$	$1.301 \cdot 10^8$
Tax revenue (€)	$45,925 - 1.381 \cdot 10^6$	$4.314 \cdot 10^7 - 6.337 \cdot 10^8$	$95,396 - 1.621 \cdot 10^6$
Subsidy expenditure(€)	$132,650 - 1.722 \cdot 10^6$	$259,100 - 2.526 \cdot 10^6$	$7.393 \cdot 10^6 - 1.200 \cdot 10^8$

Table 5.10 also shows the marginal tax revenues and subsidy costs that are required to achieve the monetary gains in land value. For a €2.6 million increase in land value,

at most €1.4 million in taxes and €1.7 million in subsidies are required. In the sensitivity analysis where α_n is increased, a €31 million increase in land value can be achieved, and in the case where β_n is higher the gain is €130 million. The policy effort of implementing the tax exceeds the estimated gain in land value, as the tax revenue is at least €43 million. On the other hand, in the case of subsidies at most €120 million must be spent in subsidies, which is a smaller amount than the increase in land value. The difference in the increase in the value of land between the two cases amounts to almost €100 million. This is explained by the fact that the damage cost of fragmentation is several orders of magnitude larger than that of nitrogen deposition. Even though the allocation of land cover types changes to a lesser degree than of land use types, each reallocated grid cell represents a much larger contribution to V .

In the sensitivity analyses, the environmental impact of one externality has been increased and the other has been kept constant. Table 5.10 shows that the policy effort of the instrument related to the latter externality is roughly doubled in both cases, which is a much smaller change than occurs for the other policy instrument. This confirms a result suggested earlier, that there is little interaction between land use types and land cover types in this configuration of the LUS. It also implies that, with a few exceptions, the taxes and subsidies affect only grid cells allocated to land use and land cover, respectively. Hence, these instruments seem to be able to target specific externalities and the numbers shown in Table 5.10 can be attributed reliably to each market instrument.

5.5. Conclusions

This study presents an extension of the Land Use Scanner (LUS) to address pricing of environmental externalities of land use. The externalities considered here are fragmentation of natural areas and nitrogen deposition. Although the LUS can consider many types of land use and land cover simultaneously, the focus here has been on interactions between land cover and agriculture. The chapter describes the extension, considers for four land use scenarios the variations in fragmentation of land cover types, and it assesses the effectiveness of market instruments in changing patterns of land use and land cover.

Simulation of scenarios derived from the IPCC-SRES studies confirm that the highest number of land cover types benefit from the land use scenario that is most environmentally-oriented. Using the measure for fragmentation developed in the chapter, however, a high level of environmental quality is not the same as having the largest total area allocated to land cover. Indeed, the scenarios that give intermediate

rather than high priority to the environment in land allocation may generate much higher levels of spatial coherence with a lower number of natural areas. The simulations furthermore suggest that rain-fed mire is a very vulnerable type of land cover in three of the four scenarios, as are peat meadows and coniferous forests, albeit to a lesser extent.

Sensitivity analyses on the extents of the environmental externalities show that they may have large impacts on land allocation and the rates of market instruments. When the damage costs of nitrogen deposition and fragmentation are low, implementing taxes and subsidies leads to only small differences in patterns of land allocation. A tax increase due to a higher impact of nitrogen deposition on the ecological quality of natural areas has an effect mainly on the allocation of ammonia-emitting agricultural land use. The type of agricultural land use that has the highest rate of emission, however, is not the type of agriculture that is most affected. Instead, agriculture with lower added-value per hectare, which also emits less nitrogen, is more likely to be relocated. If subsidies are higher to reflect increased losses in the spatial quality of natural areas due to fragmentation, then changes in the spatial distribution of land cover types remain relatively modest. Given how the environmental externalities determine tax and subsidy rates in this model, changes in the damage cost of nitrogen deposition do not affect land cover much, nor do changes in the damage costs of fragmentation have a large impact on land use.

The increase in the economic value of allocated land and the effectiveness of market instruments also depend on the extent of environmental externalities. If externalities are small, then internalisation leads to an increase of €2.6 million. Additional economic value of €31 million and €130 million may be expected when nitrogen and fragmentation, respectively, cause more environmental damage. The effectiveness of higher tax rates, however, is low, as €43 million in taxes must be levied. Addressing increased damage from fragmentation by implementing a higher subsidy is more effective, as €120 million is the resulting expense.

Finally, this extended version of the LUS is not intended as a finished instrument to tune spatial planning to environmental policy, nor should it be viewed as such. We can think of several improvements. First, adjusting the suitability maps provides the LUS with more flexibility to handle externalities. Doing so may well result in larger increases in the value of land and lower levels of policy effort, i.e. lower taxes and subsidies. Second, increasing the spatial resolution of the model enables improvements in other aspects of the model, such as detail in land cover types, inclusion of data on real species, and local fine-tuning of policy measures. Moreover, the model developed here has included two important externalities of land use, but others, such as water quality, are certainly worth consideration in further adaptations

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of this model. Developments in these areas will increase the usefulness of this model as a decision support tool.

6. Conclusion

6.1. Aim and research questions

With increasing economic activity comes a corresponding growth in land development. Currently, this land development is accelerating the rate of biodiversity loss in intensively used regions of the world through the destruction, fragmentation and ecological degradation of habitats. Since land in these regions is scarce, then the competition for space between biodiversity conservation and economic production is evident. The relation between the level of biodiversity and economic productivity, however, is poorly understood and land allocation may very well be suboptimal as a result. The models presented in this thesis describe this conflict and integrate the spatial heterogeneity that characterises both land use and biodiversity. Using this approach, the thesis aims to answer the following main research question:

How can environmental economic modelling be employed to address spatial issues in biodiversity loss and conservation, and what policy recommendations result from modelling adaptations?

In support of the main research question, the following sub-questions are also addressed

- 1) To what extent do current economic studies of biodiversity conservation include relevant concepts and theories from ecology?
- 2) What impact does the composition of urban land use have on biodiversity in neighbouring natural areas?
- 3) How do the spatial requirements of economic production affect the degree of habitat fragmentation in optimal biodiversity conservation?
- 4) Does the spatial distribution of economic production and biodiversity conservation in the Netherlands change when the damage costs of fragmentation and acidification of habitats are internalised?

The research questions combine theoretical and practical issues. Question 1 addresses the former, focusing on methods of integrating biodiversity into economic models. The practical issue of recommending conservation strategies is addressed in questions 2 to 4.

6.2. Conclusions on economic modelling of biodiversity conservation

Turning first to research question 1, chapter 2 establishes that four types of economic modelling have been used in the analysis of cost-effective or efficient biodiversity conservation. We develop a framework to assess to what extent these model types included relevant concepts and theories of biodiversity from ecology. This framework links levels of economic decision making via corresponding spatial scales to levels of biodiversity. These levels range from the genetic to the level of ecosystem functions. The second and third steps considered ecological determinants of the level of biodiversity, such as genes and alleles, fragmentation and abiotic conditions, as well as measures of the level of biodiversity.

Of the four model types found to be commonly used, two modelling approaches are prevalent. The first comprises models of efficient management of renewable resources. Many of these models use concepts and theories about biodiversity and the processes that govern it. Models of this type typically aim for analytical solutions, a difficult goal when more than two species are considered. Moreover, these models are not very suitable to analyse conservation issues when biodiversity does not generate use value. The second model type consists of models that analyse cost-effective strategies for biodiversity conservation, usually applied to large sets of species. Models of this type in general pay little attention to the ecological processes governing biodiversity, and only consider species conservation from the perspective of non-use values. The remaining two frameworks of economic modelling, namely general equilibrium models and models of macroeconomic growth, are to date infrequently used in studies of biodiversity conservation. According to the assessment in this thesis, such models are particularly suited to analyses of biodiversity change at the ecosystem level, since this level of biodiversity can be linked to changes in macro economic activities.

In answer to research question 1, there is still space for improving the integration of concepts and theories of biodiversity into economic models of biodiversity conservation. This conclusion does not apply equally to all current modelling frameworks, but two main characteristics of economic models of biodiversity conservation stand out.

The first is that much effort is put into modelling biodiversity at the species level, with other levels of biodiversity receiving significantly less attention. Given this level of analysis, moreover, either the number of species considered or the inclusion of the ecological processes that determine biodiversity is limited. If models include a small number of species, then the marginal contributions of individual species to aspects of biodiversity such as species richness, species evenness, and historical or cultural

representativeness cannot be considered. If models disregard ecological processes, then the cost of maintaining pristine ecological conditions in natural areas cannot be taken into account. Both aspects, however, are required to achieve economic efficiency in biodiversity conservation.

A second characteristic of popular current economic models of biodiversity conservation is that they tend to emphasise either the use value or the non-use value of biodiversity. In models of the former type, biodiversity is an input to economic production, and the opportunity costs of biodiversity loss are accounted for. Models that emphasise non-use values isolate biodiversity from economic production, and develop conservation recommendations given budget restrictions. Both approaches to the economic role of biodiversity show a one-sided perspective on the reasons for conserving biodiversity, as well as on the policies that could be implemented.

How then, returning to the main research question, can environmental economic models be extended to accommodate biodiversity? The previous paragraphs have indicated two useful directions of economic modelling of terrestrial biodiversity loss and conservation. The first is to try and model multiple components of biodiversity while also addressing the ecological processes governing their existence. The second direction is to search for ways of modelling the economics of biodiversity conservation that can combine the use and non-use values in a single framework.

The incorporation of ecological processes in economic models must reflect that the relationships between the economy and the environment are often asymmetric. This asymmetry arises because any one type of economic production is likely to affect several ecological processes and species in different ways. Conversely, protecting any one species or ecological process may exclude the establishment of some economic activities, but only restrict others. If these asymmetries are not adequately accounted for, they give rise to externalities and cause inefficiencies in land allocation. Modelling the economics of conserving single or small sets of species cannot adequately reflect the extent of these externalities, as biodiversity is addressed only partially. Since biodiversity conservation typically involves many, rather than a few species, the policy recommendations given by models with only a few species, ecosystems or ecosystem functions are necessarily suboptimal solutions.

The suggested comprehensive treatment of biodiversity in economic models is better served by using an ecosystem perspective, since this perspective by definition includes ecological processes, as well as multiple species that depend on and interact with these ecological processes. Addressing all of these distinct components within an integrated framework of ecosystem biodiversity would make it possible to

analyse the economic efficiency of conservation strategies. Using the level of ecosystem biodiversity also gives economic models room to move away from partial indicators of biodiversity, such as species populations or numbers, to indicators that encompass more aspects of biodiversity. The efficiency improvements in biodiversity conservation that may arise from, for instance, allowing losses in species richness in order to gain more species evenness or historical representativeness can be better assessed than current models allow.

In order to find a framework for combining the use and non-use values of biodiversity in modelling, we first turn to the major conservation acts: the Endangered Species Act and the Habitat and Bird Directives. These laws describe the reasons for conservation that are given in the real world. All three texts emphasise that habitats and species are an inheritance for future generations. These laws also acknowledge that use values of species can lead to insurmountable costs of conservation for the current generation. The conservation acts thus indicate that the use and non-use values of biodiversity have different roles in economic considerations of biodiversity conservation. Specifically, they seem to suggest a hierarchy: non-use values are the more important reason to conserve biodiversity, but that use values should not be disregarded.

The problem is how these different roles of the use and non-use values of biodiversity can be reflected in economic models. To find a solution to this problem, consider that in intensively used areas biodiversity conservation does affect economic production. The creation of habitat reserve sites means that these sites and surrounding areas are unavailable to many forms of economic production. Biodiversity conservation thus generates opportunity costs, because production is foregone or occurs in less suitable locations at higher cost. In other words, conservation and economic production are in many cases only indirectly connected. Accordingly, it is our suggestion that the use value of land, rather than of biodiversity itself, should be considered in economic models of biodiversity conservation.

Both of the above conclusions on improvements of economic models of biodiversity conservation suggest that biodiversity conservation is explicitly a spatial economic issue. It can therefore be analysed best by using spatial economic models. This conclusion seems straightforward, but it implies a very different approach than the one that is taken in a large part of the economic literature on biodiversity conservation. Land has often been added as a variable to models that address topics other than the economics of land allocation. Much of the economic literature on biodiversity conservation therefore cannot adequately accommodate the many aspects of biodiversity at the ecosystem level. An additional advantage of spatial economic models is that they are suitable for describing the indirect relation between

biodiversity conservation and economic production. Spatial economics has therefore formed the basis of the models that have been developed in this thesis. This has been a move to bring modelling efforts more in line with the difficulties of biodiversity conservation in regions where space is a scarce resource.

6.3. Conclusions on biodiversity conservation strategies

Research questions 2 to 4 concern the policy aspects of the main research question. The recommendations for biodiversity conservation that can be drawn from the model-based analyses presented in these chapters are discussed below.

Question 2 concerns the impact of the composition of human land use on biodiversity in neighbouring natural areas. It was addressed in chapter 3 using a bid-rent model of city growth. The traditional bid-rent model has been adapted so that an increase in urban land use additionally requires natural area to be taken into use for agricultural purposes. Moreover, the city is located in a finite area, so that increases in human land use cause proportional losses of the natural area or habitat. Urban land use represents industrial production which causes eutrophication of the surrounding natural areas due to emission of nutrients, while drainage from agricultural fields causes lower groundwater tables. Biodiversity in this model consists of the number of animals, which is primarily affected by habitat loss, and the number of plants, which decreases with increasing eutrophication. Additionally, plants and animals are either wetland type species or species that exist in a secondary, non-wetland type of natural area. The relative abundance of these two types of species is determined by the degree of groundwater drainage.

In the model context, increases in land use can be achieved by bidding for property rights to the surrounding natural area. The bid price of expansionists for property rights increases with the marginal disutility derived from increasing population density. Conservationists, however, also bid for property rights to stop such expansion, and their bid price depends on the marginal utility derived from biodiversity. At some critical level of biodiversity loss, urban expansion stops as biodiversity losses raise the bid price of conservationists. Given a positive utility derived from biodiversity, there is a limit to the economically efficient expansion of land use.

Several scenarios were developed and their outcomes for biodiversity and social welfare were compared. These scenarios centred on higher growth rates for the population and economic production, and technologies to reduce the environmental impacts of urban and agricultural land use. Results indicate that pursuing high growth rates is detrimental for all aspects of biodiversity, and can lead

to high levels of social welfare as long as urban population density is not too high. By employing technologies to reduce the environmental impacts of land use, a compromise can be reached in which both welfare derived from economic production and urban population density are relatively low, but welfare from preserved biodiversity is relatively high.

Technologies that reduce the environmental impacts of land use are not necessarily beneficial to biodiversity conservation. In the steady state of each scenario, the composition of biodiversity differs due to interactions between preferences for aspects of biodiversity and the environmental effects of land use. If one preferred component of biodiversity benefits from technological advances in land use, land use can increase more than would otherwise have been the case. This development may result in disproportionately high losses in less-preferred components of biodiversity. The introduction of new technologies that affect the environmental impacts of economic production and land use must be carefully considered regarding their impacts on land use and biodiversity.

Question 3 addresses the interaction between the spatial requirements of economic production and the degree of habitat fragmentation in optimal biodiversity conservation. To answer this question, chapter 4 develops a two-regional spatial equilibrium model in which location decisions of firms and workers depend on economies of scale in production and regional biodiversity. Biodiversity consists of two sets of species, generalists and specialists, which have different extinction risks. Different extinction risks are reflected in the model by allowing habitats suitable for specialist species to exist only in large natural areas. Specialist species are not present if this area falls below a threshold level. The stability of land use patterns is studied by introducing ad-hoc dynamics on location decisions to the equilibrium model.

Model results show that preferences for regional biodiversity can indeed affect settlement and production patterns. When no utility is derived from biodiversity, complete regional specialisation with no habitat fragmentation can occur. The degree of fragmentation is determined by economic parameters and historical location decisions. With increasing marginal utility of biodiversity, a land use pattern without fragmentation becomes impossible. For a given marginal utility of biodiversity, high fragmentation becomes more likely when there is a strong relative preference for specialist species. Without government intervention in the land market, a high degree of fragmentation is likely to occur.

To preserve the highest level of biodiversity, a low level of habitat fragmentation is required. When only the presence of generalist species matters in location decisions, however, this pattern of land use is not socially optimal. Whether or not the

socially optimal land use pattern can be achieved through environmental policies by non-coordinating regional governments depends on historical land use patterns. If, on the other hand, specialist species also generate utility, then low fragmentation of habitat areas also maximises total social welfare. According to the model, however, this first-best solution will not be attained if regional governments do not coordinate their environmental policies. These results demonstrate the need to develop policies on habitat fragmentation at the level of a centralised (inter-) national government.

Question 4 addresses the impact of internalising the damage costs of fragmentation and acidification of habitats on the spatial distribution of economic production and biodiversity conservation in land prices. To study this issue, chapter 5 employs an existing applied equilibrium model of the Dutch land market, currently used in environmental policy analysis in the Netherlands. The model can simulate four land use scenarios that express combinations of two societal developments, namely the degree of government responsibility and the extent of international cooperation. Furthermore, the model accommodates many types of land use and land cover, and can therefore also include many specific interactions between land use and land cover. This allows the particular externalities and their effects on land allocation to be modelled. A model extension developed in this thesis focuses on nitrogen emissions from agricultural land use and on fragmentation of land cover types. Additionally, a fragmentation measure was developed to evaluate the spatial quality, or fragmentation, of land cover patterns.

From the perspective of biodiversity conservation, it is in all likelihood better to concentrate habitat conservation areas than to have many fragmented areas. The extent to which habitats are fragmented in each of the four scenarios has been assessed using the above mentioned measure for fragmentation. Doing so confirms that more land cover does not necessarily imply less fragmentation. Furthermore, a small set of land cover types consistently showed a relatively high degree of fragmentation in scenarios other than the most environmentally friendly scenario. This suggests that these land cover types, namely peat meadow and particularly rain-fed mire, warrant extra attention in policies to limit and reduce fragmentation.

The model results further show that market instruments can be used to address environmental externalities, improve the efficiency of land use patterns, and create significant increases in the value of land. The extent of such increases depends on the environmental damage caused by land use. It appears, however, that there are differences in the effect of internalisation of environmental externalities. These effects vary regionally as well as with respect to externalities and land use types. Internalising the damage costs of nitrogen emissions can effectuate changes in agricultural land use, most noticeably in livestock farming and landscape

management in the north of the Netherlands. Arable land and bio-industry are much less responsive to the implementation of market instruments. Internalising the environmental benefits of less fragmentation, on the other hand, seems to have very little effect on the spatial distribution of land cover. These results suggest that it is less difficult to improve the spatial distribution of nitrogen deposition than to reduce fragmentation through the use of market instruments.

6.4. Discussion

Using the ecosystem level of biodiversity addresses some issues in current economic models of conservation, but it has its own difficulties as well. One significant drawback of the ideal models suggested above is their large information demand. These models require detailed information on the environmental impacts of land use, the resulting changes in ecological processes, as well as species' responses to these changes. If all species and ecological processes are individually regarded, the model becomes a black box. Some degree of aggregation clearly is required. The models in this thesis have done so to various degrees. In chapter 4 the aggregation is extensive, whereas chapters 3 and 5 have employed increasing levels of detail in modelling biodiversity. The degree to which aggregation is acceptable, must be the result of a careful discussion between ecologists and economist.

The degree of ecological detail that can be achieved is partially limited by the economic model that is employed. Some existing spatial economic models, for instance as the one used in chapter 4, describe a relatively complete economic system. Consequently, there is little room for adding ecological detail without compromising the ability to understand the interactions contained within the model. Other models, such as employed in chapters 3 and 5, are models that describe only partial economic systems and they let more facets of biodiversity be modelled. The emphasis of the intended analysis, whether it is on the economic or ecological system partially determines how realistic the other system can be described.

The above restriction on ecological-economic modelling directs the discussion to an important problem in combining the two fields of science. Traditional economics tends to favour abstraction in providing explanations of social phenomena. Ecology has to deal with the heterogeneity and complexity of natural systems and does not offer many (formal) models that are widely accepted. Models such as the species-area curve and concepts of carrying capacity, resilience and metapopulations have managed to achieve this status. As such, they have been embraced by economists and been included in many economic models. At the same time, they have limited

the range of topics addressed by economists, as has been concluded in chapter 2. Chapters 3 and 4 of this thesis in particular have attempted to develop new approaches to integrating concepts of biodiversity into traditional economic models, but this effort has entailed that functional specifications of these models and their ecological parts are more prone to criticism.

It appears that the scope of traditional economic analyses of biodiversity conservation is restricted by a lack of models of the processes that govern biodiversity and ecosystems in general. Insofar as the functioning of ecosystems is understood by ecologists, this currently seems to consist of case studies or selected processes within the ecosystem. Economists may therefore focus on developing models that can use such information, effectively focusing efforts on decision support in local areas. The model in chapter 5 shows, moreover, that this local area need not be a small region, but can cover countries –provided the necessary data are available.

6.5. Recommendations for future research

There clearly is a role for economic analyses of land allocation in improving biodiversity conservation and it provides many opportunities for future research efforts. An overarching problem in environmental and ecological economics is that the interactions between ecosystems and the economic system occur across several administrative, spatial, and temporal scales. So far, these issues have rarely been addressed in spatial (environmental-) economic models. Studying them can bring useful insights into economic efficiency in land use allocation and biodiversity conservation.

In many spatial economic models that do not employ Geographic Information Systems (GIS) techniques, land is an infinite, homogeneous resource. Land, however, is in reality finite and heterogeneous. These characteristic of land affects the conditions for biodiversity, but also human location decisions. Habitat loss, therefore, is not randomly distributed, nor proportional to increases in human land use, as has been assumed in chapters 3 and 4 of this thesis. In order to protect biodiversity better, the factors determining human location choices deserve further attention in spatial economic models of biodiversity conservation.

In this context, the effect of biodiversity conservation in the land market itself is currently becoming an important topic in the economic literature. The main insight here is that by choosing to (not) conserve biodiversity now, future possibilities for conservation are affected. Clearly, to analyse the forms that this interaction may take and its impact on optimal conservation strategies are important issues to address.

Furthermore, in section 6.2 it has been argued that spatial, rather than non-spatial economic models provide a good basis for economic analysis of biodiversity loss and conservation, as they allow for a detailed treatment of land and biodiversity. Many spatial economic models, however, disregard the fact that increases in land use are a by-product of economic and population growth. To some extent, this linkage between economic growth and land use has been integrated into the models developed in this thesis. More realistic modelling of the underlying drivers of land use change will be necessary to develop perspectives on how to deal with increasing pressure from human land use on biodiversity.

Finally, empirical, spatially explicit studies of land use change and biodiversity loss in real-world situations are very much needed. In the long run, strategies for biodiversity conservation cannot be implemented successfully without careful spatial planning, as a continuing worsening of the conflict between human land use and biodiversity protection is likely. Only if interactions between biodiversity and land use are adequately quantified, can alternative policy instruments be analysed and fine-tuned to address this conflict. The resulting models can bring economic considerations about efficiency in fighting biodiversity loss and enhancing conservation much closer to the practice of environmental policy making.

References

- Agar, J.J., J.G. Sutinen, 2004, Rebuilding strategies for multispecies fisheries: a stylized bioeconomic model, *Environmental and Resource Economics* 28: 1-29.
- Alcamo, J. (ed.), 1994, *IMAGE 2.0: integrated modeling of global climate change*, Kluwer, Dordrecht.
- Alexander, R.R., 2000, Modelling species extinction: the case for non-consumptive values, *Ecological Economics* 35: 259-269.
- Alexander, R.R., D.W. Shields, 2002, Using land as a control variable in density-dependent bioeconomic models, *Discussion Paper in Natural Resource and Environmental Economics* 22, Centre for Applied Economics and Policy Studies, Massey University.
- Andelman, S.J., W.F. Fagan, 2000, Umbrellas and flagships: efficient conservation surrogates or expensive mistakes?, *Proceedings of the National Academy of Sciences of the USA* 97: 5954-5959.
- Ando, A., J. Camm, S. Polasky, A. Solow, 1998, Species distributions, land values and efficient conservation, *Science* 279: 2126-2128.
- Andrén, H., 1994, Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review, *Oikos* 71: 355-366.
- Armsworth, P.R., B.E. Kendall, F.W. Davis, 2004, An introduction to biodiversity concepts for environmental economists, *Resource and Energy Economics* 26: 115-136.
- Arrow, K.J., A.C. Fisher, 1974, Environmental preservation, irreversibility and uncertainty, *Quarterly Journal of Economics* 88: 312-319.
- Arthur, J.L., R.G. Haight, C.A. Montgomery, S. Polasky, 2002, Analysis of the threshold and expected coverage approaches to the probabilistic reserve site selection problem, *Environmental Modeling & Assessment* 7: 81-89.
- Arthur, J.L., J.D. Camm, R.G. Haight, C.A. Montgomery, et al., 2004, Weighing conservation objectives: maximum expected coverage versus endangered species protection, *Ecological Applications* 14: 1936-1945.
- Bal, D., H.M. Beije, M. Fellingner, R. Haveman, et al., 2001, *Handboek Natuurdoeltypen* 2nd edition, Report Expertisecentrum LNV nr 2001/020, Den Haag.
- Barbier, E.B., J.C. Burgess, C. Folke, 1995, *Paradise lost: the ecological economics of biodiversity*, Earthscan, London.
- Barbier, E.B., C.E. Schulz, 1997, Wildlife, biodiversity and trade, *Environment and Development Economics* 2: 145-172.
- Barbier, E.B., J.C. Burgess, 2001, The economics of tropical deforestation. *Journal of Economic Surveys* 15: 413-433.

- Barrett, S., 1992, Economic growth and environmental preservation, *Journal of Environmental Economics and Management* 23: 289-300.
- Baumgärtner, S., 2004, Optimal investment in multi-species protection: interacting species and ecosystem health, *EcoHealth* 1: 101-110.
- Begon, M., J.L. Harper, C.R. Townsend, 1990, *Ecology: individuals, populations and communities* (2nd edition), Blackwell, Cambridge.
- Bockstael, N.E., 1996, Modelling economics and ecology: the importance of a spatial perspective, *American Journal of Agricultural Economics* 78: 1168-1180.
- Borsboom-van Beurden, J.A.M., W.T. Boersma, A.A. Bouwman, L.E.M. Crommentuijn, et al., 2005, *Ruimtelijke beelden: visualisatie van een veranderd Nederland in 2030*, RIVM report 550016003/2005, Bilthoven.
- Boulding, K.E., 1966, The economics of the coming spaceship Earth, in: H. Jarret (ed.), *Environmental quality in a growing economy*, Johns Hopkins UP.
- Brander, J.A., M.S. Taylor, 1998, Open access renewable resources: trade and trade policy in a two-country model, *Journal of International Economics* 44: 181-209.
- Briassoulis, H., 2000, *Analysis of land use change: theoretical and modelling approaches*, West Virginia UP.
- Only available at: <http://www.rri.wvu.edu/WebBook/Briassoulis/contents.htm>.
- Brock, W.A., A. Xepapadeas, 2002, Optimal ecosystem management when species compete for limiting resources, *Journal of Environmental Economics and Management* 44: 189-220.
- Brock, W.A., A. Xepapadeas, 2003, Valuing biodiversity from an economic perspective: a unified economic, ecological, and genetic approach, *American Economic Review* 93: 1597-1614.
- Brooks, T.M., G.A.B. da Fonseca, A.S.L. Rodrigues, 2004, Protected areas and species, *Conservation Biology* 18: 616-618.
- Brown, G., J. Roughgarden, 1997, A metapopulation model with private property and a common pool, *Ecological Economics* 22: 65-71.
- Bulte, E.H., G.C. van Kooten, 1999, Economics of antipoaching enforcement and the ivory trade ban, *American Journal of Agricultural Economics* 81: 453-466.
- Bulte, E.H., R.D. Horan, 2003, Habitat conservation, wildlife extraction and agricultural expansion, *Journal of Environmental Economics and Management* 45: 109-127.
- Chomitz, K.M., D.P. Gray, 1996, Roads, land markets and deforestation: a spatial model of land use in Belize, *The World Bank Economic Review* 10: 487-512.
- Clark, C.W., 1973, Profit maximization and the extinction of animal species, *Journal of Political Economy* 81: 950-961.
- Clark, C.W., G.R. Munro, 1975, The economics of fishing and modern capital theory: a simplified approach, *Journal of Environmental Economics and Management* 2: 92-106.
- Conway, T.M., R.G. Lathrop, 2005, Modeling the ecological consequences of land-use policies in an urbanizing region, *Environmental Management* 35: 278-291.

- Costello, C., S. Polasky, 2004, Dynamic reserve site selection, *Resource and Energy Economics* 26: 157-174.
- Cowling, R.M., A.T. Knight, D.P. Faith, S. Ferrier et al., 2004, Nature conservation requires more than a passion for species, *Conservation Biology* 18: 1674-1676.
- Crocker, T.D., J. Tschirhart, 1992, Ecosystems, externalities, and economies, *Environmental and Resource Economics* 2: 551-567.
- Crozier, R.H., 1997, Preserving the information content of species: genetic diversity, phylogeny, and conservation worth, *Annual Review of Ecology and Systematics* 28: 243-268.
- Datta, M., L.J. Mirman, 1999, Externalities, market power, and resource extraction, *Journal of Environmental Economics and Management* 37: 233-255.
- Debinski, D.M., R.D. Holt, 2000, A survey and overview of habitat fragmentation experiments, *Conservation Biology* 14: 342-355.
- DeFries, R., A. Hansen, A.C. Newton, M.C. Hansen, 2005, Increasing isolation of protected areas in tropical forests over the past twenty years, *Ecological Applications* 15: 19-26.
- Dekkers, J.E.C., 2005, Grondprijzen, geschiktheidskaarten en instelling van parameters in het ruimtegebruiksimulatiemodel RuimteScanner, MNP report 550016005/2005, Bilthoven.
- Drechsler, M., F. Wätzold, 2001, The importance of economic costs in the development of guidelines for spatial conservation management, *Biological Conservation* 97: 51-59.
- Drechsler, M., 2005, Probabilistic approaches to scheduling reserve selection, *Biological Conservation* 122: 253-262.
- Dyar, J.A., J. Wagner, 2003, Uncertainty and species recovery program design, *Journal of Environmental Economics and Management* 45: 505-522.
- Elbers, C., C. Withagen, 2004, Environmental policy, population dynamics and agglomeration, *Contributions to Economic Analysis and Policy* 3, Berkely Electronic Press.
- Eliasson, L., S.J. Turnovsky, 2004, Renewable resources in an endogenously growing economy: balanced growth and transitional dynamics, *Journal of Environmental Economics and Management* 48: 1018-1049.
- Emami, A., R.S. Johnston, 2000, Unilateral resource management in a two-country general equilibrium model of trade in a renewable fishery resource, *American Journal of Agricultural Economics* 82: 161-172.
- Emerton, L., J. Bishop, L. Thomas, 2005, Sustainable financing of protected areas: a global review of challenges and options, IUCN, Cambridge.
- Eppink, F.V., J.C.J.M. van den Bergh, 2006, Ecological theories and indicators in economic models of biodiversity loss and conservation: a critical review, forthcoming, *Ecological Economics*.
- Feore, S., W.I. Montgomery, 1999, Habitat effects on the spatial ecology of the European badger (*Meles meles*), *Journal of Zoology* 247: 537-549.

- Finnoff, D., J. Tschirhart, 2003a, Harvesting in an eight-species ecosystem, *Journal of Environmental Economics and Management* 45: 589-611.
- Finnoff, D., J. Tschirhart, 2003b, Protecting an endangered species while harvesting its prey in a general equilibrium ecosystem model, *Land Economics* 79: 160-180.
- Flaaten, O., 1991, Bioeconomics of sustainable harvest of competing species, *Journal of Environmental Economics and Management* 20: 163-180.
- Fisher, A.C., J.V. Krutilla, C.J. Cicchetti, 1972, The economics of environmental preservation: a theoretical and empirical analysis, *The American Economic Review* 62: 605-619.
- Franklin, J., 1993, Preserving biodiversity: species, ecosystems, or landscapes? *Ecological Applications* 3:202-205.
- Fujita, M., P. Krugman, A.J. Venables, 2001, *The spatial economy: cities, regions and international trade*, MIT Press, Massachusetts.
- Geoghegan, J., L.A. Wainger, N.E. Bockstael, 1997, Spatial landscape indices in a hedonic framework: an ecological economics analysis using GIS, *Ecological Economics* 23: 251-264.
- Gordon, H.S., 1954, The economic theory of a common property resource: the fishery, *Journal of Political Economy* 62: 124-142.
- Groeneveld, R., 2005, Economic consideration in the optimal size and number of reserve sites, *Ecological Economics* 52: 219-228.
- Groeneveld, R.A., C. Grashof-Bokdam, E. van Ierland, 2005, Metapopulations in Agricultural Landscapes: A Spatially Explicit Trade-off Analysis, *Journal of Environmental Planning and Management* 48: 527-547.
- Haight, R.G., B. Cypher, P.A. Kelly, S. Phillips, et al., 2002, Optimizing habitat protection using demographic models of population viability, *Conservation Biology* 16: 1386-1397.
- Hannesson, R., 1983, Optimal harvesting of ecologically interdependent fish species, *Journal of Environmental Economics and Management* 10: 329-345.
- Hannon, B., 1976, Marginal product pricing in the ecosystem, *Journal of Theoretical Biology* 56: 253-267.
- Hanski, I., M. Gilpin, 1991, Metapopulation dynamics: brief history and conceptual domain, *Biological Journal of the Linnean Society*: 42:3-16.
- Hanski, I., 1994, A practical model of metapopulation dynamics, *Journal of Animal Ecology* 63: 151-162.
- Hanski, I., 1999, Habitat connectivity, habitat continuity, and metapopulations in dynamic landscapes, *Oikos* 87: 209-219.
- Harte, J., A.P. Kinzig, 1997, On the implications of species-area relationships for endemism, spatial turnover, and food web patterns, *Oikos* 80: 417-427.
- Heide, M.C. van der, J.C.J.M. van den Bergh, E.C. van Ierland, 2005, Extending Weitzman's economic ranking of biodiversity protection: combining ecological and genetic considerations, *Ecological Economics* 55: 218-223.
- Heide, C.M. van der, 2005, *An economic analysis of nature policy*, PhD thesis, Vrije Universiteit, Amsterdam.

- Heywood, V.H. (ed.), 1995, Global biodiversity assessment, United Nations Environment Programme, Cambridge UP.
- Hilferink, M., P. Rietveld, 1999, Land Use Scanner: an integrated GIS based model for long term projections of land use in urban and rural areas, *Journal of Geographical Systems* 1: 155-177.
- Hinsberg, A. van, D.C.J. van der Hoek, M.L.P. van Esbroek, H. Noordijk, et al., 2004, Aansluiting MNP-instrumentarium bij de Vogel- en Habitatrichtlijn, RIVM report 55018001/2004, Bilthoven.
- Hoekstra, J.J., J.C.J.M. van den Bergh, 2004, Harvesting and conservation in a predator-prey system, *Journal of Economic Dynamics and Control* 29: 1097-1120.
- Hoel, M., P. Shapiro, 2003, Population mobility and transboundary environmental problems, *Journal of Public Economics* 87: 1013-1024.
- Hof, J., C. Hull Sieg, M. Bevers, 1999, Spatial and temporal optimization in habitat placement for a threatened plant: the case of the western prairie fringed orchid, *Ecological Modelling* 115: 61-75.
- Holland, E. A., F.J. Dentener, B.H. Braswell, J.M. Sulzman, 1999, Contemporary and pre-industrial global reactive nitrogen budgets, *Biogeochemistry* 46: 7-43.
- Holling, C.S., 1973, Resilience and stability of ecological systems, *Annual Review of Ecology and Systematics* 4: 1-23.
- Holling, C.S., D.W. Schindler, B. Walker, J. Roughgarden, 1994, Biodiversity in the functioning of ecosystems: an ecological primer and synthesis, in C. Perring, K.G. Mäler, C. Folke, C.S. Holling, et al. (eds.), *Biodiversity loss: ecological and economic issues*, Cambridge UP.
- Horan, R.D., J.S. Shortle, 1999, Optimal management of multiple renewable resource stocks: an application to Minke whales, *Environmental and Resource Economics* 13: 435-458.
- Hubbell, S.P., 2001, The unified neutral theory of biodiversity and biogeography, *Monographs in Population Biology*, Princeton UP.
- Humphries, C.J., P.H. Williams, R.I. Vanewright, 1995, Measuring biodiversity value for conservation, *Annual Review of Ecology and Systematics* 26: 93-111.
- Imeson, R.J., J.C.J.M. van den Bergh, 2004, A bioeconomic analysis of a shellfishery: the effects of recruitment and habitat in a metapopulation model, *Environmental and Resource Economics* 27: 65-86.
- Irwin, E.G., J. Geoghegan, 2001, Theory, data, methods: developing spatially explicit economic models of land use change, *Agriculture, Ecosystems and Environment* 85: 7-23.
- IUCN, 2004, 2004 IUCN Red list of threatened species, <http://www.iucnredlist.org>.
- IUCN, 2006, 2006 IUCN Red list of threatened species, <http://www.iucnredlist.org>.
- Jaarsveld, J.A. van, 2004, Description and validation of OPS-Pro 4.1, RIVM report 500045001/2004, Bilthoven.

- Janssen, M.A., J.M. Anderies, B.H. Walker, 2004, Robust strategies for managing rangelands with multiple stable attractors, *Journal of Environmental Economics and Management* 47: 140-162.
- Jenkins, P.T., 1996, Free trade and exotic species introductions, *Conservation Biology* 10: 300-302.
- Jin, D., P. Hoagland, T.M. Dalton, 2003, Linking economic and ecological models for marine ecosystem, *Ecological Economics* 46: 367-385.
- Johst, K., M. Drechsler, F. Wätzold, 2002, An ecological-economic modelling procedure to design compensation payments for the efficient spatio-temporal allocation of species protection measures, *Ecological Economics* 41: 37-49.
- Jong, J.J. de, G.W.W. Wamelink, H.F. van Dobben, M.N. van Wijk, 2004, Benefits of deposition reduction for nature management, Alterra report 1051, Wageningen.
- Juutinen, A., M. Mönkkönen, 2004, Testing alternative indicators for biodiversity conservation in old-growth boreal forests: ecology and economics, *Ecological Economics* 50: 35-48.
- Kaimowitz, D., A. Angelsen, 1998, Economic models of tropical deforestation: a review, CIFOR, Bogor.
- Kassar, I., P. Lassere, 2004, Species preservation and biodiversity value: a real options approach, *Journal of Environmental Economics and Management* 48: 857-879.
- Kingsland, S.E., 2002, Creating a science of nature reserve design: perspectives from history, *Environmental Modeling & Assessment* 7: 61-69.
- Kinzig, A.P., J. Harte, 2000, Implications of endemics-area relationships for estimates of species extinctions, *Ecology* 81: 3305-3311.
- Kok, J-L. de, G. Engelen, R. White, H.G. Wind, 2001, Modelling land-use change in a decision-support system for coastal-zone management, *Environmental Modelling and Assessment* 6: 123-132.
- Krautkraemer, J.A., 1985, Optimal growth, resource amenities and the preservation of natural environments, *Review of Economic Studies* 70: 153-170.
- Krutilla, J.V., 1967, Conservation reconsidered, *American Economic Review* 57: 777-786.
- Langevelde, F. van, F. Claassen, A. Schotman, 2002, Two strategies for conservation planning in human-dominated landscapes, *Landscape and Urban Planning* 58: 281-295.
- Lake, I.R., A.A. Lovett, I.J. Bateman, B. Day, 2000, Using GIS and large-scale digital data to implement hedonic pricing studies, *International Journal of Geographical Information Science* 14: 521-541.
- Lejour, A., 2003, Quantifying four scenarios for Europe, CPB Document 38, CPB, Den Haag.
- Lenzen, M., S.A. Murray, 2001, A modified ecological footprint method and its application to Australia, *Ecological Economics* 37: 229-255.
- Li, C.Z., K.G. Lofgren, M.L. Weitzman, 2001, Harvesting versus biodiversity: an Occam's razor version, *Environmental and Resource Economics* 18: 355-366.

- Lichtenstein, M.E., C.A. Montgomery, 2003, Biodiversity and timber in the Coast Range of Oregon: inside the production possibility frontier, *Land Economics* 79: 56-73.
- LNV, 2000, *Natuur voor mensen, mensen voor natuur: natuur, bos en landschap in de 21e eeuw*, Den Haag.
- Loreau, M., S. Naeem, P. Inchausti (eds.), 2002, *Biodiversity and ecosystem functioning: synthesis and perspectives*, Oxford UP.
- Lovejoy, T.E., 1980, Changes in biological diversity, in: *Global report to the president: entering the twenty-first century* (vol. 2), Government Printing Office, Washington.
- McArthur, R.H., E.O. Wilson, 1967, *The theory of island biogeography*, Princeton UP.
- Maciver, D.C., 1998, Atmospheric change and biodiversity, *Environmental Monitoring and Assessment* 49: 177-189.
- Magurran, A.E., 1988, *Ecological diversity and its measurement*, Croom Helm, London.
- Mahan, B.L., S. Polasky, R.M. Adams, 2000, Valuing urban wetlands: a property price Approach, *Land Economics* 76: 100-113.
- Mainwaring, L., 2001, Biodiversity, biocomplexity, and the economics of genetic dissimilarity, *Land Economics* 77: 79-83.
- Margules, C.R., R.L. Pressey, 2000, Systematic conservation planning, *Nature* 405: 243-253.
- Martínez, F.J., 1992, The bid-choice land-use model: an integrated economic framework, *Environment and Planning A* 24: 871-885.
- Matsuoka, Y., M. Kainuma, T. Morita, 1995, Scenario analysis of global warming using the Asian Pacific Integrated Model (AIM), *Energy Policy* 23: 357-371.
- May, R.M., J.H. Lawton, E.S. Nigél, 1995, Assessing extinction rates, in: J.H. Lawton, R.M. May (eds.), *Extinction Rates*, Oxford UP.
- Miller, J.R., 1981, Irreversible land use and the preservation of endangered species, *Journal of Environmental Economics and Management* 8: 19-26.
- Mills, E.S., B.W. Hamilton, 1984. *Urban Economics*. Scott, Foresman & Co., Glenview.
- Mitsch, W.J., J.G. Gosselink, 2000, *Wetlands*, Wiley, New York.
- MNP, 2004, *Natuurbalans 2004*, Milieu- en Natuurplanbureau, De Bilt.
- MNP, 2005, *Natuurbalans 2005*, Milieu- en Natuurplanbureau, De Bilt.
- MNP, 2006, *Natuurbalans 2006*, Milieu- en Natuurplanbureau, De Bilt.
- Montgomery, C.A., R.A. Pollak, K. Freemark, D. White, 1999, Pricing biodiversity, *Journal of Environmental Economics and Management* 38: 1-19.
- Mooij, R. de, P. Tang, 2003, *Four futures for Europe*, CPB Special Publication 49, Den Haag.
- Munro, A., 1997, Economics and biological evolution, *Environmental and Resource Economics* 9: 429-449.

- Musacchio, L.R., W.E. Grant, 2002, Agricultural production and wetland habitat quality in a coastal prairie ecosystem: simulated effects of alternative resource policies on land-use decisions, *Ecological Modelling* 150: 23-43.
- Nakicenovic, N., J. Alcamo, G. Davis, B. de Vries, et al., 2000, Special Report on Emissions Scenarios, Working Group III, Intergovernmental Panel on Climate Change (IPCC), Cambridge UP.
- Nalle, D.J., C.A. Montgomery, J.L. Arthur, S. Polasky, et al., 2004, Modeling joint production of wildlife and timber, *Journal of Environmental Economics and Management* 48: 997-1017.
- Nehring, K., C. Puppe, 2002, A theory of diversity, *Econometrica* 70: 1155-1198.
- Nevo, A., L. Garcia, 1996, Spatial optimization of wildlife habitat, *Ecological Modelling* 91: 271-281.
- Noss, R.F., 1990, Indicators for monitoring biodiversity: a hierarchical approach, *Conservation Biology* 4: 355-364.
- Olde Venterink, H.G.M., 2000, Nitrogen, phosphorus and potassium flows controlling plant productivity and species richness: eutrophication and nature management in fens and meadows, PhD thesis, Utrecht University.
- Önal, H., 2003, Preservation of species and genetic diversity, *American Journal of Agricultural Economics* 85: 437-447.
- Perrings, C., B. Walker, 1997, Biodiversity, resilience and the control of ecological-economic systems: the case of fire-driven rangelands, *Ecological Economics* 22: 73-83.
- Pezzey, J.C.V., C.M. Roberts, B.T. Urdal, 2000, A simple bioeconomic model of a marine reserve, *Ecological Economics* 33: 77-91.
- Pfaff, A.S.P., G.A. Sanchez-Azofeifa, 2004, Deforestation pressure and biological reserve planning: a conceptual approach and an illustrative application for Costa Rica, *Resource and Energy Economics* 26: 237-254.
- Pimm, S.L., 1984, The complexity and stability of ecosystems, *Nature* 307: 321-326.
- Pimm, S.L., G.J. Russell, J.L. Gittleman, T.M. Brooks, 1995, The future of biodiversity, *Science* 269: 347-350.
- Polasky, S., J.D. Camm, A.R. Solow, B. Csuti et al., 2000, Choosing reserve networks with incomplete species information, *Biological Conservation* 94: 1-10.
- Polasky, S., J.D. Camm, B. Garber-Yonts, 2001, Selecting biological reserves cost-effectively: an application to terrestrial vertebrate conservation in Oregon, *Land Economics* 77: 68-78.
- Polasky, S., C. Costello, C. McAusland, 2004, On trade, land-use, and biodiversity, *Journal of Environmental Economics and Management* 48: 911-925.
- Polasky, S., E. Nelson, E. Lonsdorf, P. Fackler et al., 2005, Conserving species in a working landscape: land use with biological and economic objectives, *Ecological applications* 15: 1387-1401.
- Portela, R., I. Rademacher, 2001, A dynamic model of patterns of deforestation and their effect on the ability of the Brazilian Amazonia to provide ecosystem services, *Ecological Modelling* 143: 115-146.

- Ragozin, D.L., G. Brown, 1985, Harvest policies and non-market valuation in a predator-prey system, *Journal of Environmental Economics and Management* 12: 155-168.
- Rauscher, M., 1994, On environmental dumping, *Oxford Economic Papers* 46: 822-840.
- Reist-Marti, S.B., H. Simianer, J. Gibson, O. Hanotte, et al., 2003, Weitzman's approach and conservation of breed diversity: an application to African cattle breeds, *Conservation Biology* 17: 1299-1311.
- RIVM, 2002, *Natuurverkenningen 2*, De Bilt.
- Rondeau, D., 2001, Along the way back from the brink, *Journal of Environmental Economics and Management* 42: 156-182.
- Rouquette, J.R., D.J. Thompson, 2005, Habitat associations of the endangered damselfly, *Coenagrion mercuriale*, in a water-meadow-ditch system in southern England, *Biological Conservation* 123: 225-235.
- Rosenzweig, M.L., 2001, Loss of speciation rate will impoverish future diversity, *Proceedings of the National Academy of Sciences* 98: 5404-5410.
- Rotmans, J., B.J.M. de Vries, 1997, *Perspectives on global change: the TARGETS approach*, Cambridge UP.
- Rowthorn, R.E., G. Brown, 1999, When a high discount rate encourages biodiversity, *International Economic Review* 40: 315-332.
- Rubio, S.J., R.U. Goetz, 1998, Optimal growth and land preservation, *Resource and Energy Economics* 20: 345-372.
- Runhaar, H.J., J.P.M. Witte, P.H. Verburg, 1997, Ground-water level., moisture supply, and vegetation in the Netherlands, *Wetlands* 17: 528-538.
- Sala, O.E., F.S. Chapin, J.J. Armesto, E. Berlow, et al., 2000, Global biodiversity scenarios for the year 2100, *Science* 287: 1770-1774.
- Sanchirico, J.N., J.E. Wilen, 1999, Bioeconomics of spatial exploitation in a patchy environment, *Journal of Environmental Economics and Management* 37: 129-150.
- Sanchirico, J.N., J.E. Wilen, 2001, A bioeconomic model of marine reserve creation, *Journal of Environmental Economics and Management* 42: 257-276.
- Sanchirico, J.N., 2005, Additivity properties in metapopulation models: implications for the assessment of marine reserves, *Journal of Environmental Economics and Management* 49: 1-25.
- Sanchirico, J.N., J.E. Wilen, 2005, Optimal spatial management of renewable resources; matching policy scope to ecosystem scale, *Journal of Environmental Economics and Management* 50: 23-46.
- Sandmo, A., D.E. Wildasin, 1999, Taxation, migration, and pollution, *International Tax and Public Finance* 6: 39-59.
- Schaefer, M.B., 1954, Some aspects of the dynamics of populations important to the management of commercial marine fisheries, *Bulletin of the Inter-American Tropical Tuna Commission* 1: 25-56.

- Scheffer, M., S. Carpenter, J.A. Foley, C. Folke et al., 2001, Catastrophic shifts in ecosystems, *Nature* 413: 591-596.
- Schnier, K.E., 2005, Biological "hot spots" and their effect on optimal bioeconomic marine reserve formation, *Ecological Economics* 52: 453-468.
- Scholten, H.J., R.J. van de Velde, J.A.M. Borsboom van Beurden (eds.), 2001, Ruimtescanner: informatiesysteem voor de lange termijnverkenning van ruimtegebruik, *Netherlands Geographical Studies* 242, VU/KNAG, Amsterdam.
- Seppelt, R., A. Voinov, 2002, Optimization methodology for land use patterns using spatially explicit landscape models, *Ecological Modelling* 151: 125-142.
- Simberloff, D., 1998, Flagships, umbrellas, and keystones: is single-species management passé in the landscape era?, *Biological Conservation* 83: 247-257.
- Skole, D., C. Tucker, 1993, Tropical deforestation and habitat fragmentation in the Amazon – satellite data from 1978 to 1988, *Science* 260: 1905-1910.
- Skonhofs, A., 1999, On the optimal exploitation of terrestrial animal species, *Environmental and Resource Economics* 13: 45-57.
- Smith, R.B.W., J.F. Shogren, 2002, Voluntary incentive design for endangered species protection, *Journal of Environmental Economics and Management* 43: 169-187.
- Smith, V.K., C. Poulos, H. Kim, 2002, Treating open space as an urban amenity, *Resource and Energy Economics* 24: 107-129.
- Smith, M.D., J.E. Wilen, 2003, Economic impacts of marine reserves: the importance of spatial behavior, *Journal of Environmental Economics and Management* 46: 183-206.
- Smith, W., Y.S. Son, 2005, Can the desire to conserve our natural resources be self-defeating?, *Journal of Environmental Economics and Management* 49: 52-67.
- Smulders, J.A., D. van Soest, C. Withagen, 2004, International trade, species diversity and habitat conservation, *Journal of Environmental Economics and Management* 48: 891-910.
- Snyder, S.A., R.G. Haight, C.S. ReVelle, 2004, Scenario optimization model for dynamic reserve site selection, *Environmental Modeling & Assessment* 9: 179-187.
- Solow, A., S. Polasky, J. Broadus, 1993, On the measurement of biological diversity, *Journal of Environmental Economics and Management* 24: 60-68.
- Stevens, C. J., N.B. Dise, J.O. Mountford, D.J. Gowing, 2004, Impact of nitrogen deposition on the species richness of grasslands, *Science* 303: 1876-1879.
- Suding, K.N., D. Goldberg, 2001, Do disturbances alter competitive hierarchies? Mechanisms of change following gap creation, *Ecology* 82: 2133-2149.
- Sui, D.Z., H. Zheng, 2001, Modeling the dynamic of landscape structure in Asia's emerging desakota regions: a case study in Shenzhen, *Landscape and Urban Planning* 53: 37-52.
- Swanson, T.M., 1994, *The international regulation of extinction*, New York UP.
- Swenson, J.J., J. Franklin, 2000, The effects of future urban development on habitat fragmentation in the Santa Monica mountains, *Landscape Ecology* 15: 713-730.

- Thünen, J.H. von, 1826, *Der isolierte Staat in Beziehung auf Landwirtschaft und Nationalökonomie*. Rostock, English translation by C.M. Wartenberg, 1966, *Von Thünens isolated state*, Pergamon, London.
- Tilman, D., 1982, Resource competition and community structure, *Monographs in Population Biology* 17, Princeton UP.
- Tilman, D., S. Polasky, C. Lehman, 2005, Diversity, productivity and temporal stability in the economies of humans and nature, *Journal of Environmental Economics and Management* 49: 405-426.
- Tschirhart, J., 2000, General equilibrium of an ecosystem, *Journal of Theoretical Biology* 203: 13-32.
- Turner, R.K., K. Button, P. Nijkamp (eds.), 1999, *Ecosystems and nature: economics, science and policy*, Edward Elgar, Cheltenham.
- Turner, R.K., J.C.J.M. van den Bergh, T. Söderqvist, A. Barendregt et al., 2000, Ecological-economic analysis of wetlands: scientific integration for management and policy, *Ecological Economics* 35: 7-23.
- UNEP, 1992, *Convention on Biological Diversity*, Rio de Janeiro.
- UNEP, 1995, *Global biodiversity assessment*, Cambridge UP.
- Valente, S., 2005, Sustainable development, renewable resources and technological progress, *Environmental and Resource Economics* 30: 115-125.
- Vazquez, D.P., D. Simberloff, 2002, Ecological specialization and susceptibility to disturbance: conjectures and refutations, *The American Naturalist* 159: 606-623.
- Veldkamp, A., L.O. Fresco, 1996, CLUE-CR: an integrated multi-scale model to simulate land use change scenarios in Costa Rica, *Ecological Modelling* 91: 231-248.
- Veldkamp, A., P.H. Verburg, K.Kok, G.H.J. de Koning, et al., 2001, The need for scale sensitive approaches in spatially explicit land use change modelling, *Environmental Modelling and Assessment* 6: 111-121.
- VROM, 2001, *Nationaal Milieubeleidsplan 4*, SDU, Den Haag.
- Wacker, O., 1999, Optimal harvesting of mutualistic ecological systems, *Resource and Energy Economics* 21: 89-102.
- Walker, B.H., 1992, Biodiversity and ecological redundancy, *Conservation Biology* 6: 18-23.
- Walsum, P.E.V. van, J. Runhaar, J.F.M. Helming, 2005, Spatial planning for adapting to climate change, *Water Science And Technology* 51: 45-52.
- Wamelink, G.W.W., J.J. de Jong, H.F. van Dobben, M.N. van Wijk, 2005, Additional costs of nature management caused by deposition, *Ecological Economics* 52: 437-451.
- Wätzold, F., M. Drechsler, 2005, Spatially uniform versus spatially heterogeneous compensation payments for biodiversity-enhancing land-use measures, *Environmental and Resource Economics* 31: 73-93.
- Wear, D.N., M.G. Turner, O. Flamm, 1996, Ecosystem management with multiple owners: landscape dynamics in a Southern Appalachian watershed, *Ecological Applications* 6: 1173-1188.

- Weikard, H.P., 2002, Diversity functions and the value of biodiversity, *Land Economics* 78: 20-27.
- Weitzman, M.L., 1992, On diversity, *Quarterly Journal of Economics* 107: 363-405.
- Weitzman, M.L., 1998, The Noahs' ark problem, *Econometrica* 66: 1279-1298.
- Wilén, J., G. Brown, 1986, Optimal recovery paths for perturbations of trophic level bioeconomic systems, *Journal of Environmental Economics and Management* 13: 225-234.
- Wilson, E.O., 1975, *Sociobiology: the new synthesis*, Harvard UP.
- Wilson, E.O., 1992, *The diversity of life*, Harvard UP.
- Wilson, S.D., D. Tilman, 2002, Quadratic variation in old-field species richness along gradients of disturbance and nitrogen, *Ecology* 83: 492-504.
- With, K.A., A.W., King, 1999, Extinction thresholds for species in fractal landscapes, *Conservation Biology* 13: 314-326.
- Witting, L., J. Tomiuk, V. Loeschke, 2000, Modelling the optimal conservation of interacting species, *Ecological Modelling* 125: 123-143.
- World Resources Institute, 2005, *Millennium Ecosystem Assessment: Ecosystems and Human Well-being*, Biodiversity Synthesis.
- Wu, F., 1998, Simulating urban encroachment on rural land with fuzz-logic-controlled cellular automata in a geographical information system, *Journal of Environmental Management* 53: 293-308.
- Wu, J.J., W.G. Boggess, 1999, The optimal allocation of conservation funds, *Journal of Environmental Economics and Management* 38: 302-321.
- Wu, J.J., K. Skelton-Groth, 2002, Targeting conservation efforts in the presence of threshold effects and ecosystem linkages, *Ecological Economics* 42: 313-331.
- Zhao, S., Z.Z. Li, W.L. Li, 2005, A modified method of ecological footprint calculation and its application, *Ecological Modelling* 185: 65-75.
- Zuidema, G., G.J. van den Born, J. Alcamo, G.J.J. Kreileman, 1994, Simulating changes in global land-cover as affected by economic and climatic factors, *Water, Air and Soil Pollution* 76: 163-198.

Nederlandse samenvatting

Ruimte voor Soorten:

Ruimtelijke Ecologisch-Economische Analyses van Biodiversiteitbehoud

Eén van de omvangrijkste milieuproblemen van dit moment is het verlies aan biodiversiteit: plant- en diersoorten sterven uit in een veel hoger tempo dan natuurlijk is. Een scala aan menselijke activiteiten, voornamelijk die activiteiten ten behoeve van materiële productie en consumptie, is hiervoor verantwoordelijk. Planten- en diersoorten zijn via een aantal mechanismen gekoppeld aan de productie van consumptiegoederen. Deze mechanismen zijn: jacht, introductie van vreemde soorten, klimaatverandering en grondgebruik. Om het tempo van biodiversiteitsverlies te verlagen kan beleid gevoerd worden op al deze mechanismen. Dit gaat echter ten koste van economische productie. Dit proefschrift bestudeert de mogelijkheden om grondgebruik in te zetten als instrument om biodiversiteit op efficiënte wijze te beschermen.

De reden dat grondgebruik centraal staat in dit proefschrift is dat er in intensief gebruikte gebieden een groot conflict bestaat tussen het aanwenden van grond voor economische productie en voor biodiversiteitbehoud. Met andere woorden: grond is een schaars goed. De gevolgen van het ontwikkelen van grond voor economische productie zijn bijvoorbeeld de vernietiging en versnippering van natuurgebieden. Deze gebieden vormen de habitats van vele plant- en diersoorten. Daarnaast heeft elk menselijk gebruik van grond een specifieke invloed op de abiotische factoren in habitats. Abiotische factoren zijn alle omstandigheden die betrekking hebben op niet-levende onderdelen van natuurgebieden, zoals de grondwaterstand, zuurgraad en beschikbaarheid van mineralen. Deze abiotische factoren bepalen in belangrijke mate de vegetatie van habitats. De begroeiing op haar beurt heeft een grote invloed heeft op de geschiktheid van habitats voor bepaalde diersoorten.

Het doel van dit proefschrift is om inzicht te verschaffen in de rol die de ruimtelijke verdeling van grondontwikkeling kan spelen in het verhogen van de efficiëntie van biodiversiteitbehoud. Hierbij is het doel om expliciet rekening te houden met de bovenstaande drie invloeden van grondgebruik op biodiversiteit. De centrale vraag van het proefschrift luidt dan ook hoe milieueconomische modellen gebruikt kunnen worden voor de analyse van ruimtelijke aspecten van biodiversiteitbehoud en welke beleidsaanbevelingen vloeien uit modelaanpassingen voort?"

Deze hoofdvraag wordt aan de hand van enkele bijbehorende subvragen beantwoord. In hoeverre houden bestaande economische modellen rekening met theorieën over biodiversiteit? Welke invloed heeft de samenstelling van grondgebruik op de compositie van biodiversiteit in omliggende natuurgebieden? Hoe beïnvloeden de ruimtelijke behoeften van economische productie de optimale mate van habitatfragmentatie? Verandert de ruimtelijke verdeling van economisch grondgebruik en biodiversiteitbehoud in Nederland als de milieuschade die ontstaat door fragmentatie en verzuring verwerkt wordt in grondprijzen?

Allereerst is in hoofdstuk 2 gekeken naar de meest voorkomende soorten modellen die gebruikt worden in economische analyses van biodiversiteitbehoud. Een raamwerk is ontwikkeld om vast te stellen in hoeverre deze modeltypen rekening houden met concepten en theorieën uit de ecologische wetenschap die relevant zijn voor biodiversiteit. Dit raamwerk koppelt in eerste instantie het niveau van economische besluitvorming aan relevante niveaus van biodiversiteit via ruimtelijke schaal. De relevante niveaus van biodiversiteit reiken van genetische diversiteit tot het functioneren van ecosystemen. In tweede en derde instantie worden deze niveaus van biodiversiteit verbonden aan de ecologische determinanten van biodiversiteit, zoals genen en allelen, habitatfragmentatie en abiotische omstandigheden, en aan mogelijke maatstaven van het niveau van biodiversiteit.

Van de vier modeltypen die ingezet worden voor economische analyses van biodiversiteitbehoud blijken er twee het meest frequent te zijn. Deze twee modeltypen zijn modellen voor efficiënt beheer van hernieuwbare hulpbronnen en modellen voor kosteneffectief biodiversiteitbehoud. In modellen van het eerste type worden veel concepten en theorieën over biodiversiteit en veranderingen daarin toegepast. Omdat dit soort modellen vaak analytisch van aard is, wordt het aantal beschouwde diersoorten veelal beperkt tot twee. Bovendien is de gebruikswaarde van soorten, die bijvoorbeeld ontstaat door jacht of oogsten, voor dit soort modellen een onmisbaar onderdeel om tot realistische oplossingen voor biodiversiteitsbeheer te komen. Modellen die de kosteneffectiviteit van biodiversiteitbehoud onderzoeken, maken meestal gebruik van grote verzamelingen diersoorten. In deze modellen besteden over het algemeen weinig aandacht aan de gebruikswaarde van plant- en diersoorten. Tegelijkertijd spelen de ecologische processen die het niveau van biodiversiteit bepalen veelal een kleine rol. De andere twee modeltypen, namelijk algemeen evenwichtsmodellen en modellen van economische groei zijn relatief weinig toegepast in de context van biodiversiteitbehoud. Deze soorten modellen lijken zeer geschikt om biodiversiteitbehoud te beschouwen op een grote ruimtelijke schaal die gekoppeld kan worden aan macro-economische ontwikkeling.

De uitgevoerde evaluatie van de economische literatuur over biodiversiteitbehoud leidt tot de conclusie dat er meer gedaan kan worden om de veelzijdigheid van biodiversiteit tot uitdrukking te laten komen in economische

modellen. Weliswaar zijn ecologische theorieën redelijk goed opgenomen in sommige typen van economische modellen, maar er is relatief veel aandacht voor biodiversiteit op het niveau van (dier-)soorten. In veel modellen is het beschouwde aantal soorten bovendien beperkt, waardoor belangrijke maatstaven als soortenrijkdom, relatieve zeldzaamheid en cultureel of historisch belang van soorten niet goed meegenomen kunnen worden in beslissingen over een efficiënte samenstelling van biodiversiteit. Verder zijn de ecologische processen die biodiversiteit bepalen slechts in beperkte mate terug te vinden in economische modellen. Deze processen zijn onmisbaar voor het modelleren van de eisen die soorten en ecosystemen stellen aan hun omgeving.

Een tweede conclusie luidt dat veel modellen de nadruk leggen op ofwel gebruikswaarden, ofwel op niet-gebruikswaarden van biodiversiteit als reden voor het behoud ervan. In het eerste geval is biodiversiteit een grondstof voor economische productie en worden de opportuniteitskosten van biodiversiteitsverlies in beschouwing genomen. In het tweede geval is biodiversiteitsbehoud volledig geïsoleerd van economische productie en worden kosteneffectieve aanbevelingen ontwikkeld voor biodiversiteitsbehoud gegeven een beperkt budget. Beide aanpakken gebruiken een éénzijdig perspectief op het belang van biodiversiteitsbehoud.

Het eerste deel van de onderzoeksvraag luidt hoe milieueconomische modellen aangepast kunnen worden om biodiversiteit te analyseren. De vorige alinea's hebben twee mogelijke richtingen aangeduid waarin modellen van biodiversiteitsbehoud verder ontwikkeld kunnen worden. De eerste is om te proberen om meerdere aspecten van biodiversiteit in één model te beschouwen, terwijl er ook de ecologische processen van biodiversiteit aan bod komen. De tweede ontwikkelingsrichting is om modellen te vinden waarin gebruikswaarden en niet-gebruikswaarden van biodiversiteit goed gecombineerd kunnen worden.

Wat betreft het opnemen van ecologische processen in economische modellen van biodiversiteit is het zeer belangrijk om deze in de context van milieueffecten van economische productie te plaatsen. In veel opzichten is deze verhouding asymmetrisch, waarmee bedoeld wordt dat elk type grondgebruik uiteenlopende effecten heeft op een groot aantal ecologische processen en plant- en diersoorten. Omgekeerd kan de bescherming van een soort tot gevolg hebben dat sommige typen grondgebruik helemaal niet toegestaan zijn, terwijl andere slechts beperkt worden. In veel gevallen geven dit soort milieueffecten aanleiding tot zogeheten externaliteiten die inefficiënties in grondgebruik tot gevolg hebben. Als economische modellen van biodiversiteitsbehoud individuele soorten of een beperkte verzameling van soorten beschouwen, dan kan de omvang van deze inefficiënties niet afdoende worden meegenomen. Bovendien betreft het beleid voor biodiversiteitsbehoud meestal vele soorten, in plaats van enkele. De beleidsaanbevelingen van modellen die deze punten over het hoofd zien, zijn daarom per definitie suboptimaal.

De voorgestelde alomvattende benadering van biodiversiteit in economische modellen kan beter bereikt worden door ecosystemen te bekijken. De definitie van biodiversiteit op het ecosysteemniveau omvat ecologische processen en bovendien bevatten ecosystemen meerdere soorten die afhankelijk zijn van de kwaliteit van deze processen. Door al deze onderdelen van biodiversiteit in een geïntegreerd raamwerk van ecosystemen te bekijken wordt een analyse mogelijk van de economische efficiëntie van beleidsmaatregelen om biodiversiteit te behouden. Gegeven een patroon van grondgebruik, kan de efficiëntie verbeterd worden door, bijvoorbeeld, soortenrijkdom af te ruilen tegen een meer gelijke distributie van soorten, of tegen het behoud van enkele soorten met bijzondere waarde.

Om een raamwerk te vinden voor het combineren van de gebruikswaarden en niet-gebruikswaarden van biodiversiteit in economische modellen, is het zin eerst te kijken naar belangrijke wetten voor natuurbehoud: de 'Endangered Species Act' en de Habitat- en Vogelrichtlijnen. Deze teksten bevatten de beweegredenen die worden aangevoerd voor biodiversiteitbehoud. Alle drie de teksten benadrukken dat planten, dieren en ecosystemen een erfenis vormen voor toekomstige generaties. Tegelijkertijd erkennen deze wetten dat deze erfenis de huidige generatie voor onoverkomelijke kosten kan stellen. Deze belangrijke juridische teksten geven dus aan dat de gebruikswaarden en niet-gebruikswaarden van biodiversiteit heel verschillende rollen spelen in economische overwegingen over biodiversiteitbehoud. In het bijzonder lijken ze een hiërarchie te suggereren: niet-gebruikswaarden vormen de belangrijkste reden voor behoud, maar gebruikswaarden mogen niet over het hoofd worden gezien.

De uitdaging is om deze verhouding van (niet-)gebruikswaarden in economische modellen op te nemen. Een oplossing voor dit probleem lijkt in de realiteit voorhanden te zijn. In gebieden waar veel land ontwikkeld is of wordt voor menselijk gebruik zou biodiversiteitbehoud wel degelijk een invloed op productie hebben. Natuurgebieden beschermen betekent dat deze en omliggende gebieden niet langer gebruikt kunnen worden voor productie. Biodiversiteitbehoud genereert dus opportuniteitskosten, doordat productie helemaal niet meer plaatsvindt, of moet uitwijken naar minder geschikte locaties. Met andere woorden, biodiversiteitbehoud en economische productie zijn slechts indirect met elkaar verbonden. Derhalve doen we de suggestie dat de gebruikswaarde van land, maar niet van biodiversiteit zelf, in economische modellen van biodiversiteitbehoud opgenomen wordt.

De bovenstaande alinea's hebben aangegeven dat veel economische aspecten van biodiversiteitbehoud een uitgesproken ruimtelijk karakter hebben. Biodiversiteitbehoud kan daarom het beste bestudeerd worden met behulp van ruimtelijk-economische modellen. Deze conclusie lijkt voor de hand liggend, maar wijst wél op een andere aanpak dan in een groot gedeelte van de economische literatuur gehanteerd wordt. Grond is vaak als variabele toegevoegd aan modellen

die niet over grondallocatie gaan. Het resultaat is dat met behulp van dat soort modellen biodiversiteit maar in beperkte mate op het niveau van ecosystemen bekeken kan worden en dat de efficiëntie van bepaalde doelstellingen voor soortenbehoud niet goed geanalyseerd kan worden. Ruimtelijk-economische modellen zijn bovendien zeer geschikt om het indirecte verband tussen biodiversiteitbehoud en economische productie te beschrijven. Deze modellen gaan over de relatie tussen grondgebruik en economische productie en kunnen betrekkelijk eenvoudig met biodiversiteit worden uitgebreid. Ruimtelijke economie heeft daarom de basis gevormd van de modellen die in dit proefschrift ontwikkeld zijn. Op deze manier zijn de modellen meer op één lijn gebracht met de problemen die spelen in gebieden waar grond schaars is.

Door economische aspecten van biodiversiteitbehoud te bekijken op het niveau van ecosystemen lijkt een nuttige doorontwikkeling van huidige economische modellen. Het brengt echter ook een aantal problemen met zich mee. Als ecosystemen worden gemodelleerd met een relatief laag detailniveau, zoals in hoofdstukken 3 en 4, dan gaat veel informatie over individuele soorten verloren. Dit brengt het vermogen om afwegingen te maken tussen verscheidene aspecten van biodiversiteit terug. Als ecosystemen wél gedetailleerd worden weergegeven, dan neemt de complexiteit van het model dramatisch toe. Een zekere aggregatie van biodiversiteitvariabelen is dus onvermijdelijk, maar de mate waarin dit gebeurt moet de uitkomst zijn van discussies tussen ecologen en economen.

Hoofdstuk 3 behandelt de wederzijdse invloed tussen menselijk grondgebruik en het niveau van biodiversiteit. Hiertoe is een model van stedelijke groei gebruikt, waarin de stadsuitbreiding vereist dat natuurgebied omgezet wordt in urbaan en landbouwgebied. De stad ligt in een eindige ruimte, wat betekent dat elke toename in grondgebruik een proportioneel verlies aan natuurgebied betekent. Stedelijk grondgebruik is in dit model een indicator voor het niveau van industriële productie, die via uitstoot voor een toename in de beschikbaarheid van mineralen in natuurgebieden zorgt. Daarnaast verlaagt landbouw het grondwaterpeil in het gebied. In het model is biodiversiteit samengesteld uit het aantal diersoorten, dat bepaald wordt door habitatooppervlakte, en het aantal planten, dat afneemt naarmate er meer mineralen beschikbaar zijn in het natuurgebied. Bovendien is het aantal plant- en diersoorten een samenstelling van twee groepen soorten, waarvan de eerste in moerasgebieden voorkomt en de tweede in een niet nader gedefinieerd type natuur. De verhouding van deze twee groepen wordt bepaald door de landbouw, die grondwater aan natuurgebieden onttrekt.

In het model kan stadsuitbreiding bereikt worden door rechten te kopen om natuurgebied te ontwikkelen. De prijs die 'uitbreiders' bereid zijn te betalen neemt toe met een groeiende bevolkingsdichtheid in de stad. Grondrechten kunnen ook gebruikt worden om de natuur te beschermen. Dit is het geval als

'natuurbeschermers' deze rechten kopen, waarbij hun biedprijs stijgt naarmate het niveau van biodiversiteit afneemt. Indien een kritieke waarde van biodiversiteitverlies overschreden wordt, wordt de prijs van grondrechten dermate hoog dat de stedelijke uitbreiding ophoudt. Als biodiversiteit ook in de echte wereld een economische waarde heeft, duidt dit resultaat erop dat er een grens is aan de toename van stedelijk en ander grondgebruik die nog economisch efficiënt is.

In hoofdstuk 3 is een aantal scenario's gesimuleerd en beoordeeld aan de hand van een maatstaf voor maatschappelijke welvaart. De scenario's richten zich op versnelde groeipaden van de bevolking en de economische productie en op technologieën om de milieueffecten van stedelijk grondgebruik en landbouw te reduceren. De resultaten van het model duiden erop dat hogere groei nastreven relatief slecht uitwerkt voor alle aspecten van biodiversiteit. Aan de andere kant kunnen dergelijke ambities tot hoge maatschappelijke welvaart leiden, onder voorwaarde dat de bevolkingsdichtheid in stedelijke gebieden beperkt blijft. De scenario's waarin technologieën worden toegepast om de milieueffecten van menselijk grondgebruik te beperken blijken compromissen te zijn met relatief lage waarden van economische productie en bevolkingsdichtheid, maar relatief hoge niveaus van biodiversiteit.

Technologieën om de milieueffecten van menselijk grondgebruik te beperken hebben niet een éénduidig positief effect op biodiversiteit. Aan het einde van de simulaties van de verschillende scenario's is de samenstelling van biodiversiteit uiteenlopend. Stel dat één onderdeel van biodiversiteit de voorkeur heeft boven andere onderdelen. Als een technologie op het gebied van landgebruik dit specifieke milieuaspect beschermt of bevordert, kan dat tot gevolg hebben dat het totale grondgebruik verder toeneemt dan anders het geval zou zijn geweest. Dit kan vervolgens leiden tot een buitenproportioneel hoog verlies van het totale biodiversiteitsniveau. Nieuwe technologieën die de milieueffecten van grondgebruik beperken, moeten daarom nauwkeurig beoordeeld worden op hun uitwerkingen op grondgebruik en biodiversiteit.

Hoofdstuk 4 betreft de relatie tussen de ruimtelijke eisen van economische productie en de optimale mate van habitatfragmentatie. Om deze vraag te beantwoorden is een ruimtelijk evenwichtsmodel met twee regio's zodanig aangepast dat bedrijven en werknemers hun besluit zich in een regio te vestigen laten afhangen van zowel schaalvoordelen in economische productie als van regionale biodiversiteit. Biodiversiteit bestaat uit twee verschillende verzamelingen van soorten, generalisten en specialisten, die verschillende risico's van uitsterven hebben. Deze verschillende risico's worden in het model weergegeven doordat de habitatgebieden voor specialisten alleen kunnen bestaan in grote natuurgebieden. Specialistische soorten komen niet in een regio voor als het natuurgebied kleiner is dan een minimumoppervlakte. De stabiliteit van grondgebruikspatronen en

biodiversiteitbehoud kan bekeken worden door ad-hoc dynamiek aan het model toe te voegen.

De modelresultaten geven aan dat voorkeuren voor regionale biodiversiteit inderdaad vestigingsbeslissingen kunnen beïnvloeden. Als biodiversiteit geen economische waarde heeft, kan er een situatie ontstaan waarin er geen fragmentatie van natuurgebieden is. De mate waarin fragmentatie daadwerkelijk optreedt, is afhankelijk van economische parameters en eerdere beslissingen over grondgebruik. Naarmate de economische waardering van biodiversiteit toeneemt, wordt fragmentatie waarschijnlijker, waarbij fragmentatie bovendien waarschijnlijker wordt naarmate de relatieve voorkeur voor specialistische soorten toeneemt. Zonder overheidsingrijpen in de grondmarkt lijkt een hoge mate van fragmentatie onder veel omstandigheden een onvermijdelijke (markt-)uitkomst.

Om het maximale niveau van biodiversiteit te behouden is een lage mate van fragmentatie vereist. Als alleen de aanwezigheid van generalistische soorten gewaardeerd wordt, dan is een dergelijk patroon van grondgebruik niet maatschappelijk optimaal. Of het optimale patroon van grondgebruik bereikt kan worden als regionale overheden concurreren op het gebied van milieubeleid, is afhankelijk van historische ontwikkelingen in grondgebruik en fragmentatie. Als specialistische soorten ook gewaardeerd worden, dan kenmerkt een lage mate van habitatfragmentatie het maatschappelijk optimale grondgebruik. Volgens het model is deze verdeling echter onbereikbaar als regionale overheden niet samenwerken. Deze resultaten suggereren dat ruimtelijk beleid ten aanzien van habitatfragmentatie een aangelegenheid is voor een centrale (inter-)nationale overheid.

Hoofdstuk 5 onderzoekt in hoeverre de verdeling van grondgebruik en biodiversiteitbehoud verandert als milieuschade van grondgebruik verwerkt wordt in de grondprijzen. Hiertoe wordt een bestaand, toegepast evenwichtsmodel van de Nederlandse grondmarkt uitgebreid. Dit model wordt al ingezet voor analyses van (onder andere) milieubeleid. Met het model worden vier scenario's gesimuleerd die twee maatschappelijke ontwikkelingen combineren, namelijk de mate van overheidsingrijpen en van internationale samenwerking. Verder bevat het model meerdere soorten menselijk grondgebruik en verschillende typen natuur. Het model kan daarom gebruikt worden om een groot aantal specifieke interacties tussen al deze soorten grondgebruik te bekijken. Dit maakt het mogelijk om de invloed van het verwerken van milieuschade in grondprijzen te modelleren. De modeluitbreiding die in dit proefschrift gepresenteerd wordt, richt zich op stikstofverrijking en fragmentatie van natuurgebieden als gevolg van grondgebruik. Daarnaast wordt een zelf ontwikkelde fragmentatiemaatstaf gebruikt om de ruimtelijke kwaliteit, ofwel fragmentatie, van natuurgebieden te evalueren.

Voor biodiversiteitbehoud is het waarschijnlijk beter om habitatgebieden samen te voegen dan om meerdere, gefragmenteerde gebieden te hebben. De mate waarin

de vier scenario's leiden tot fragmentatie van natuurgebieden is geëvalueerd met behulp van de eerdergenoemde fragmentatiemaatstaf. Deze evaluatie geeft aan dat een groter aantal natuurgebieden niet per definitie leidt tot minder fragmentatie. Bovendien bleken enkele typen natuur, namelijk veenweide en met name hoogveen, in de overige scenario's aanzienlijk meer gefragmenteerd te zijn dan in het scenario dat het meeste ruimte laat voor milieubehoud. Dit suggereert dat deze typen natuur extra aandacht verdienen in beleidsmaatregelen om fragmentatie terug te dringen.

De resultaten van het model wijzen er verder op dat marktinstrumenten ingezet kunnen worden om milieueffecten van grondgebruik terug te dringen. In hoeverre dergelijke instrumenten effectief zijn, hangt mede af van de milieuschade die grondgebruik veroorzaakt. Het lijkt er op dat de effectiviteit van marktinstrumenten varieert per regio, per type grondgebruik en per milieueffect. Het beprijzen van de milieuschade die ontstaat door uitstoot van stikstof kan veranderingen in landbouw teweeg brengen, voornamelijk van intensieve en extensieve grondgebonden veeteelt in het noorden van Nederland. Akkerbouw en intensieve veeteelt reageren veel minder sterk op de invoering van marktinstrumenten. Het in grondprijzen verwerken van het positieve effect van minder fragmentatie lijkt weinig effect te sorteren op de ruimtelijke verdeling van natuurtypen. Deze resultaten suggereren dat het minder moeilijk is om met marktinstrumenten de ruimtelijke verdeling van de uitstoot van stikstof te verbeteren dan om fragmentatie te reduceren.

De resultaten uit dit proefschrift geven duidelijk aan dat economische analyses van grondgebruik een bijdrage kunnen leveren aan biodiversiteitbehoud en er zijn ruime mogelijkheden om deze rol verder te onderzoeken. Interacties tussen menselijke en natuurlijke systemen overschrijden meerdere administratieve, ruimtelijke en temporele niveaus. Nadere beschouwing van deze aspecten kan nuttige inzichten in economische efficiëntie in grondgebruik en biodiversiteitbehoud opleveren. Verder geven veel ruimtelijk economische modellen grond weer als een oneindige, homogene hulpbron. Deze weergave is echter onjuist en de factoren die de locatie van economisch grondgebruik bepalen, verdienen meer aandacht van economen. Ook maken veel ruimtelijk economische modellen geen gebruik van het feit dat toenemend grondgebruik een neveneffect is van economische en bevolkingsgroei. Een realistischer weergave van deze motoren van veranderingen in grondgebruik zal een beter beeld geven over hoe om te gaan met de toenemende druk die grondgebruik uitoefent op biodiversiteit. Tot slot is er een grote behoefte aan empirische, ruimtelijk economische modellen van grondgebruik en biodiversiteitverlies. Dergelijke modellen kunnen economische overwegingen over efficiëntie in biodiversiteitverlies en het behoud ervan veel dichterbij de beleidspraktijk brengen.