The EFFECTS OF LANDSCAPE STRUCTURE AND BIODIVERSITY *on* ECOSYSTEM SERVICES

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ABSTRACT

Ecosystem services, the benefits that people receive from ecosystems, depend on the movement of organisms and matter across landscapes, as well as the biodiversity and ecosystem functions that are present. Human activities around the world are rapidly and significantly changing ecosystems, landscapes, biodiversity, and, ultimately, ecosystem services. This is particularly true in agricultural systems, where human activities to maximize the ecosystem service of food production often lead to the decline of other important ecosystem services. While we understand that ecosystem services are critical to human well-being, our current knowledge of the provision of ecosystem services across landscapes contains a number of significant gaps that limit our ability to manage for services and human well-being. In particular, we don't fully understand how changes in landscape structure – the composition and configuration of land use types – affect the provision of multiple ecosystem services.

In this thesis, I explore the theoretical and empirical relationships between landscape structure, biodiversity, and ecosystem service provision. I first reviewed our current understanding of these links, finding that while we commonly assume that loss of connectivity between habitat patches in a landscape will have negative effects on ecosystem service provision, we have little empirical evidence that this is the case. In particular, we know little about how this landscape connectivity might simultaneously affect multiple ecosystem services, especially for services other than food, pollination, and pest regulation. I then empirically measured the effects of agricultural landscape structure, including forest fragment connectivity, on six ecosystem services in 34 soybean fields in the Montérégie of southern Québec, Canada. Both the isolation of forest fragments on the landscape, and distances within soybean fields from adjacent forest fragments, had significant effects on the provision of ecosystem services. Importantly, each ecosystem service showed distinct differences in its pattern of provision as these components of landscape structure varied. Therefore, landscape heterogeneity, the variety of forest and field types present in the landscape, was critical to ensure the provision of multiple ecosystem services. Investigating pest regulation in this landscape in more detail, I determined that field width and forest fragments are driving

patterns of diversity and abundance for both beneficial and pest arthropods in this system. However, these patterns are contradictory between these two arthropod functional groups, resulting in inconsistent effects of landscape structure on pest regulation. Finally, using a simple modeling framework, I explored how changing the pattern of habitat loss across a landscape affects ecosystem service provision at different scales. My model reveals that the form of the relationship between habitat fragments and ecosystem services is critical in determining landscape patterns of ecosystem service provision. In addition, there are inherent tradeoffs between service provision in the agricultural matrix and habitat preservation, as well as mismatches between ecosystem service provision at different scales. However, altering the amount and pattern of habitat loss across the landscape can help mitigate these issues.

Overall, my thesis indicates that understanding the connections between landscape structure, biodiversity, and ecosystem service provision will be a critical avenue of research, one that will improve our ability to design multi-functional human-dominated landscapes. Only by understanding how human activities and land use change affect ecosystem services can we generate management tools to maximize multiple ecosystem services at landscape scales. As human demand for ecosystem services and our impacts on natural systems continue to rise, this will be an increasingly important knowledge gap to fill.

RÉSUMÉ

Les services écologiques, les bénéfices que les gens tirent des écosystèmes, dépendent du mouvement des organismes et de la matière à travers le paysage, ainsi que de la biodiversité et des fonctions écosystémiques qui y sont présent. Les activités humaines à travers le monde sont en train de changer rapidement et de façon significative les écosystèmes, les paysages, la biodiversité et par ce billet les services écologiques. Ceci est particulièrement vrai dans les systèmes agricoles, où les activités humaines afin de maximiser le service écologique de la production alimentaire conduisent souvent à la diminution d'autres services écologiques importants. Bien que nous comprenions que les services écologiques sont essentiels au bien-être humain, notre connaissance actuelle de la fourniture des services écologiques contient encore certaines lacunes importantes qui limitent notre capacité à gérer ces services et le bien-être humain. En particulier, nous ne comprenons pas entièrement comment les changements dans la structure du paysage - la composition et la configuration des types d'utilisation des terres - affectent la fourniture de multiples services écologiques.

Dans cette thèse, j'explore les relations théoriques et empiriques entre la structure du paysage, la biodiversité, et l'approvisionnement des services écologiques. J'ai d'abord fait une revue de la littérature pour comprendre nos connaissances actuelles de ces liens, et en constatant que généralement la littérature supporte le fait que la perte de la connectivité entre les parcelles d'habitat dans un paysage aura des effets négatifs sur l'approvisionnement des services écologiques, mais que nous avons peu de preuves empiriques que c'est le cas. En particulier, nous savons peu sur la façon dont cette connectivité du paysage peut affecter simultanément de multiples services écologiques, en particulier pour les services autres que la production de nourriture, la pollinisation, et la régulation des ravageurs. J'ai ensuite empiriquement mesuré les effets de la structure du paysage agricole, y compris la connectivité des fragments de forêt, sur six services écologiques dans 34 champs de soya de la Montérégie au sud du Québec, Canada. L'isolement des fragments de forêt dans le paysage, et la distance à partir de fragments de forêt adjacents dans les champs de soja ont eu des effets significatifs sur la fourniture de services écologiques. Chaque service écologique a été caractérisé par un motif de provision différent avec les configurations variées de ces deux composantes de la structure du paysage. Par conséquent,

l'hétérogénéité du paysage, la variété des types de forêt présents dans le paysage et la variété des types de champs agricoles, sont essentielles pour assurer la fourniture de multiples services écologiques. En regardant en plus de détail la régulation des ravageurs sur le paysage, j'ai déterminé que la largeur de champ et la présence des fragments de forêt sont des facteurs déterminants des motifs de la diversité et de l'abondance des arthropodes bénéfiques et nuisibles présents dans le système. Cependant, le motif des arthropodes bénéfiques et contradictoires avec celui des arthropodes nuisibles, entraînant des effets de la structure du paysage sur la provision du service écologique de la régulation des ravageurs qui sont inconsistants. Dernièrement, à l'aide d'un cadre de modélisation simple, j'ai exploré comment changer les motifs de perte d'habitat dans un paysage affecte la fourniture de services écologique à différentes échelles. Mon modèle révèle que la forme de la relation entre les fragments d'habitat et des services écologiques est essentielle à la determination de l'approvisionnement de services écologiques sur le paysage. De plus, il y a des conflits entre la prestation de services dans la matrice du paysage agricole et la préservation de l'habitat, ainsi que des dissonances entre la prestation de services écologiques à différentes échelles. Cependant, la modification du motif de la perte d'habitat dans le paysage peut contribuer à atténuer ces problèmes.

Dans l'ensemble, ma thèse indique que la compréhension des liens entre la structure du paysage, la biodiversité, et l'approvisionnement de services écologiques sera un élément critique de la recherché qui permettra d'améliorer notre capacité à concevoir des paysages multifonctionnels dominés par l'homme. C'est seulement en comprenant comment les activités humaines et l'utilisation des terres affectent les services écologiques que nous pouvons générer des outils de gestion qui maximise les multiples services écologiques à l'échelle du paysage. Comme la demande humaine pour les services écologiques et nos impacts sur les systèmes naturels continuent d'augmenter, ce sera un manque de connaissances de plus en plus important de remplir.

For Jocelyn & Harriet

and

In memory of Earle Trueman Mitchell (1920-2012)

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PREFACE

Thesis Format

This is a manuscript-based thesis, with connecting statements between manuscript chapters. Overall thesis design borrows considerably from Eivind Uggedal's Masters thesis from the University of Oslo (2008) and the Chicago Manual of Style Online; reference formatting follows the *Journal of Applied Ecology* style. Each manuscript has been published, is in press, has been submitted, or is planned for submission to an academic journal. As such, each manuscript chapter has been written to stand alone. To begin, a brief general introduction provides a summary of the academic context that motivated the research. This followed by four manuscript chapters:

2. A review of the literature linking landscape connectivity with ecosystem service provision. This chapter presents much of the conceptual framework of the thesis. **This chapter has been published**: Mitchell, M.G.E., Bennett, E.M. & Gonzalez, A. (2013) Linking landscape connectivity and ecosystem service provision: current knowledge and research gaps. *Ecosystems*, **16(5)**, 894-908.

3. Results of a field study investigating the effects of forest fragment isolation and size, and distance-from-forest on multiple ecosystem services in an agricultural landscape. **This chapter is under consideration for publication**: Mitchell, M.G.E., Bennett, E.M. & Gonzalez A. (*In Review*) Forest fragments modulate the provision of multiple ecosystem services. *Journal of Applied Ecology*.

4. Results from the same field study describing the relative importance of agricultural landscape- and field-scale structure for arthropod diversity and consequences for ecosystem services. **This chapter is under consideration for publication**: Mitchell, M.G.E., Bennett, E.M. & Gonzalez, A. (*In Review*) Agricultural landscape structure affects arthropod diversity & arthropod-derived ecosystem services. *Agriculture, Ecosystems & Environment*.

5. A modeling study that explores how different patterns of habitat loss might affect landscape and local-scale ecosystem service provision. **This chapter is in preparation for publication**. Mitchell, M.G.E., Bennett, E.M. & Gonzalez, A. (*In Preparation*) Modeling the effects of habitat loss and landscape structure on ecosystem services. *Proceedings of the Royal Society B – Biological Sciences.*

Because chapters 3 and 4 come from the same field study, there is some repetition in methods between the two so that each can stand alone as manuscripts. A final synthesis chapter summarizes the main findings and general conclusions of the thesis with respect to the effects of landscape structure on ecosystem service provision.

Author Contributions

I am first author on each of the chapters, and in each case led development of the research design and conceptual framework, performed the data collection and fieldwork, completed statistical analyses, built and ran the models, and led writing of the manuscripts. Elena Bennett and Andrew Gonzalez provided supervision throughout, contributed to development of the research and experimental designs, and provided guidance on manuscript writing and preparation. Each manuscript notes additional contributions from specific individuals in the acknowledgments.

Statement of Originality

This thesis contains four distinct original contributions to knowledge. First, I provide the first survey of the current primary literature linking landscape connectivity with the provision of ecosystem services (Chapter 2). This is the first work to broadly unite the ecosystem services framework under the concept of landscape connectivity and identify important gaps in our knowledge. Second, I present results from one of the first empirical studies to investigate the effects of landscape structure on multiple ecosystem services (Chapter 3). While studies of single ecosystem services are relatively common, this represents one of the first to measure how landscape structure can alter the relationships between the different ecosystem services provided by agricultural landscapes. Third, I show that understanding the effects of landscape structure on pest regulation depend on measuring patterns of both beneficial and pest arthropods and that these patterns do not necessarily correspond with those of crop production (Chapter 4). The results of this study demonstrate the limitations of studies that focus solely on predator arthropods and which fail to measure crop production. Finally, I provide one of the first spatially explicit landscape-scale models of the effects of landscape structure on ecosystem service provision (Chapter 5). Outputs from this model are relevant for optimizing landscape design for the provision of multiple ecosystem services. Each of these distinct contributions begins to fill some of the gaps in our current understanding of ecosystem service provision at landscape scales and how landscape structure affects biodiversity and in turn, ecosystem service provision.

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I have been extremely fortunate to work with two amazing supervisors during my PhD. Both Elena Bennett and Andrew Gonzalez have been unfailing in their encouragement, positive energy, and guidance over the last four years. I always looked forward to our meetings together, anticipating the range of ideas we would discuss and the progress that would be made on my project in just one short hour. I thank them both for their invaluable contributions to my development as a scientist.

I thank my committee, Martin Lechowicz and Chris Buddle for their thoughtful questions and guidance during committee meetings, help with experimental design and sampling, and insight into the forest, arthropod, and agricultural ecosystems of the Montérégie. In particular, I thank Chris for his help introducing me to the world of arthropod sampling and identification. Jeff Cardille, Terry Wheeler, Tim Moore, Joann Whalen, and Caroline Begg provided advice on specific parts of my research.

Past and current members of both the Bennett and Gonzalez labs have provided amazing energy, support, feedback on presentations, and comments on drafts. Some of them even helped out in the field with counting aphids! I thank Graham MacDonald, Carly Ziter, Kate Liss, Patrick Thompson, Geneviève Metson, Michael Pedruski, Josée Methot, Bronwyn Rayfield, Meagan Schipanski, Aerin Jacob, Shauna Mahajan, Dorothy Maguire, Karine Dancose, and Sylvestre Delmotte. Geneviève also translated my thesis abstract into French. I especially want to thank the Bennett lab for their willingness to put their valuable time and energy towards our group projects, which I always found enriching and worthwhile.

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Hélène Lalande guided me through soil sampling and analysis; Jim Straughton provided the means to thresh my soybean samples; and Hicham Benslim helped with soil C:N analysis. Julia Stepanuk, Sebastian Belliard, Yelena Mitrofanov, and Katriina O'Kane helped process the many samples of soil, litter, soybean, insects, and cotton fabric that resulted from my fieldwork.

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To my parents Warren and Sherry Mitchell, a heartfelt thank-you for your constant support and encouragement throughout the years. Without this I wouldn't be where I am today.

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1 INTRODUCTION

> Everyone in the world depends completely on Earth's ecosystems and the services they provide, such as food, water, disease management, climate regulation, spiritual fulfillment, and aesthetic enjoyment. Over the past 50 years, humans have changed these ecosystems more rapidly and extensively than in any comparable period of time in human history, largely to meet rapidly growing demands for food, fresh water, timber, fibre, and fuel.
>
> Millennium Ecosystem Assessment (2005)

1.1 ECOSYSTEM SERVICES & AGRICULTURE

The past two decades have seen a tremendous increase in our knowledge of the links between human well-being and the natural environment. Realization that ecosystems provide benefits to people and that these benefits can be either enhanced or degraded by human activities occurred as early as Plato (Daily 1997). However, it wasn't until the middle of the 20th century, with authors like Aldo Leopold (1966) and his concept of the land ethic, that these ideas gained general recognition. The term "environmental services" was eventually introduced in 1970 (SCEP 1970), but ecological science didn't fully embrace the idea of "ecosystem services" until the late 1990's with the publications of Daily *et al.* (1997), Vitousek *et al.* (1997), and Costanza *et al.* (1997).

In 2005, the Millennium Ecosystem Assessment (MA 2005) published a global analysis of the status of ecosystem services conducted by over one thousand leading scientists. Its main conclusion was that approximately 60 % of the ecosystem services evaluated were being degraded or used unsustainably, and that this increased to 70 % when only regulating or cultural services were considered (Table 1.1). It also put forward a now widely accepted classification scheme for ecosystem services (but see de Groot, Wilson & Boumans 2002; Wallace 2007; Fisher, Turner &

Table 1.1: Global status of provisioning, regulating, and cultural services evaluated in the Millennium Ecosystem Assessment and their relationship with biodiversity. Adapted from (MA 2005) and Cardinale *et al* (2012).

Service	Status[1]	Relationship with biodiversity[2]	Notes
Provisioning Services			
Crops	+	+/−	Substantial production increase
Fisheries	−	+	Declining production due to overharvest
Wood	+/−	+	Forest los in some regions, growth in others
Fiber	+/−	?	Includes timber, cotton, hemp, silk, etc.
Genetic Resources	−	+[3]	Lost through extinction
Biochemicals, natural medicines, pharmaceuticals	−	+[3]	Lost through extinction, overharvest
Fresh water	−	?	Unsustainable use for drinking, industry, etc.
Regulating Services			
Air quality regulation	−	?	Decline in atmosphere's ability to clean itself
Climate regulation	−	+/−	Positive at global level, negative at regional/local
Water regulation	+/−	?	Varies depending on ecosystem change/location
Erosion regulation	−	?	Increased soil degradation
Water purification & waste treatment	−	?	Declining water quality
Disease regulation	+/−	?	Varies depending on ecosystem change
Pest regulation	−	+/−	Natural control degraded from pesticide use
Pollination	−	+/−	Apparent global decline in pollinator abundance
Natural hazard regulation	−	?	Loss of natural buffers (wetlands, mangroves)
Cultural Services			
Spiritual & religious values	−	?	Rapid decline in sacred groves and species
Aesthetic values	−	?	Decline in quantity/quality of natural lands
Recreation and ecotourism	+/−	?	More areas accessible but many degraded

[1]From the Millennium Ecosystem Assessement (2005)
[2]Results from literature survey from Cardinale *et al.* (2012)
[3]These relationships not evaluated in Cardinale *et al.* (2012), but is assumed as these ecosystem services are directly related to biodiversity.

Morling 2009), dividing them into provisioning, regulating, cultural, and supporting services. The MA ushered in a rapid increase in ecosystem services research (Vihervaara, Ronka & Walls 2010; Seppelt *et al.* 2011). For example, a Web of Science search for articles containing the term "ecosystem services" for 2013 returns over 1 200 results, compared to 90 papers for 2004. With this growth has come a great deal more information about the ecological basis for many ecosystem services, the role that biodiversity plays in ecosystem service provision (Table 1.1), how human activities affect service provision, and how different ecosystem services covary across landscapes. However, a number of critical gaps remain. In particular, our understanding of the effects of landscape structure (the arrangement and pattern of ecosystems across a landscape) on biodiversity, ecosystem function, and ecosystem service provision is incomplete (Kremen & Ostfeld 2005). My thesis helps fill this gap by synthesizing the current knowledge in this area and by contributing new knowledge about these relationships based on studies in an agricultural landscape in southern Québec.

Along with the expansion of ecosystem services research over the last fifteen years, awareness of human impacts on ecosystems and the global environment has grown substantially (Vitousek *et al.* 1997; Kareiva *et al.* 2007). In particular, biodiversity, which underlies and is essential for all ecosystem services (Chapin *et al.* 2000; Balvanera *et al.* 2006; Duffy 2009; Mace, Norris & Fitter 2012), is being lost at unprecedented rates (MA 2005; Butchart *et al.* 2010), and this loss will almost certainly have significant effects on ecosystem service provision worldwide (Cardinale *et al.* 2012). As expansion of our scientific understanding of ecosystem services has occurred, our knowledge of biodiversity loss and its impacts on society has also grown significantly.

A leading driver of biodiversity loss is habitat destruction and fragmentation (Sala *et al.* 2000; Hanski 2005), often due to agricultural expansion for food production (Saunders, Hobbs & Margules 1991; Green *et al.* 2005). Agricultural systems, including croplands, pastures, and rangelands now cover over one-third of Earth's terrestrial surface (Foley *et al.* 2005; Ramankutty *et al.* 2008) and are still one of the principal drivers of land use change around the world (Matson *et al.* 1997; Tilman *et al.* 2001). Land use change driven by agricultural expansion and intensification is a leading driver of biodiversity loss and ecosystem service change worldwide (Rands *et al.* 2010; Foley *et al.* 2011).

While the management of most agricultural landscapes is focused on food production, agroecosystems are in reality multi-functional landscapes that both provide and rely upon numerous ecosystem services and biodiversity (Dale & Polasky 2007; Zhang *et al.* 2007; Power 2010). For example, crop production relies on soil fertility and soil erosion control (Barrios 2007), water quality regulation (Brauman *et al.* 2007), pest regulation (Tscharntke *et al.* 2005), and, for many crops, pollination (Losey & Vaughan 2006; Klein *et al.* 2007). In turn, all of these ecosystem services rely on the biodiversity and ecosystem processes present in agroecosystems (Altieri 1999; Tscharntke *et al.* 2005). For example, soil fertility and structure depends on the diversity of the enormous number of soil micro- and macro-organisms (Barrios 2007), pest regulation often varies with the diversity of pest predators (Bianchi, Booij & Tscharntke 2006; Letourneau *et al.* 2009; Chaplin-Kramer *et al.* 2011), crop species diversity can reduce herbivore damage (Letourneau *et al.* 2011), and pollination services increase with pollinator diversity (Kremen, Williams & Thorp 2002; Hoehn *et al.* 2008). Thus, crop production and agroecosystem multi-functionality relies not only on human activities (*e.g.* tillage, planting, chemical inputs, harvest), but also on the biodiversity present in these systems, much of which is associated with remnant fragments of natural habitat that intersperse agricultural landscapes (Carvalheiro *et al.* 2011; Blitzer *et al.* 2012).

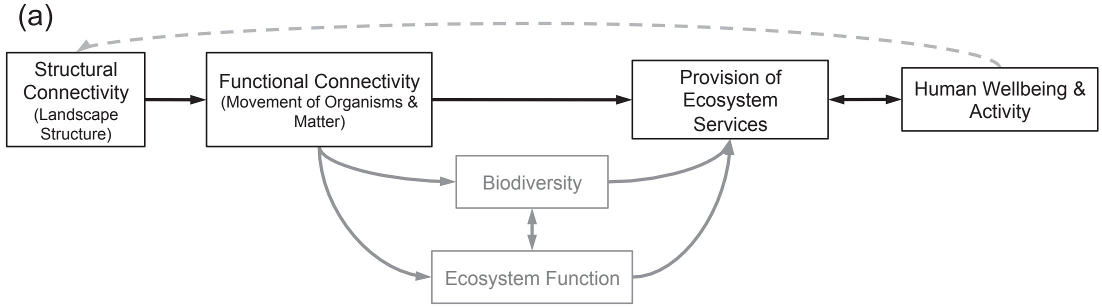
1.2 CURRENT GAPS IN ECOSYSTEM SERVICES RESEARCH & THESIS RATIONALE

People expect agricultural landscapes to provide multiple services – including food, recreational opportunities, carbon storage for climate regulation, and high quality water. The ecosystem services framework provides a way forward to balance the various objectives that society has for human-dominated landscapes like agroecosystems. As such, it is seeing rapid incorporation into policy, land-planning and conservation efforts (Goldman *et al.* 2008; Tallis *et al.* 2009). However, a number of gaps in our scientific understanding limit our ability to use ecosystem service science to manage services and conserve biodiversity across landscapes (Daily & Matson 2008; Carpenter *et al.* 2009; Daily *et al.* 2009). In particular, our lack of understanding of the links among landscape structure, biodiversity, ecosystem function, and the provision of different ecosystem services is a critical gap (Kremen & Ostfeld 2005; Kremen *et al.* 2007; Biggs *et al.* 2012; Figure 1.1a). While we have good understanding that the arrangement of habitat fragments across agricultural landscapes has consequences for biodiversity (Fahrig 2003; Tscharntke *et al.* 2005; Bailey *et al.* 2010), and that increased species diversity is required for multiple ecosystem functions or services (Hooper *et al.* 2005; Balvanera *et al.* 2006; Isbell *et al.* 2011; Cardinale *et al.* 2012), we have relatively few examples that link all three — landscape structure, biodiversity, and ecosystem service provision — at the landscape scales relevant to land managers (but see Bodin *et al.* 2006; Ricketts *et al.* 2008; Farwig *et al.* 2009). Understanding these links is crucial given current rates of habitat loss from human activities and our increasing demand for ecosystem services. Managing landscape structure has the potential to be a key lever by which biodiversity loss and ecosystem service provision can be controlled across agricultural landscapes.

In this thesis, I begin to fill this gap by exploring the theoretical and empirical links between landscape structure, biodiversity, and ecosystem service provision. I take several approaches — including a literature review, empirical field studies, and simulation modeling — to understand how patterns of habitat fragmentation affect multiple ecosystem services in agricultural landscapes.

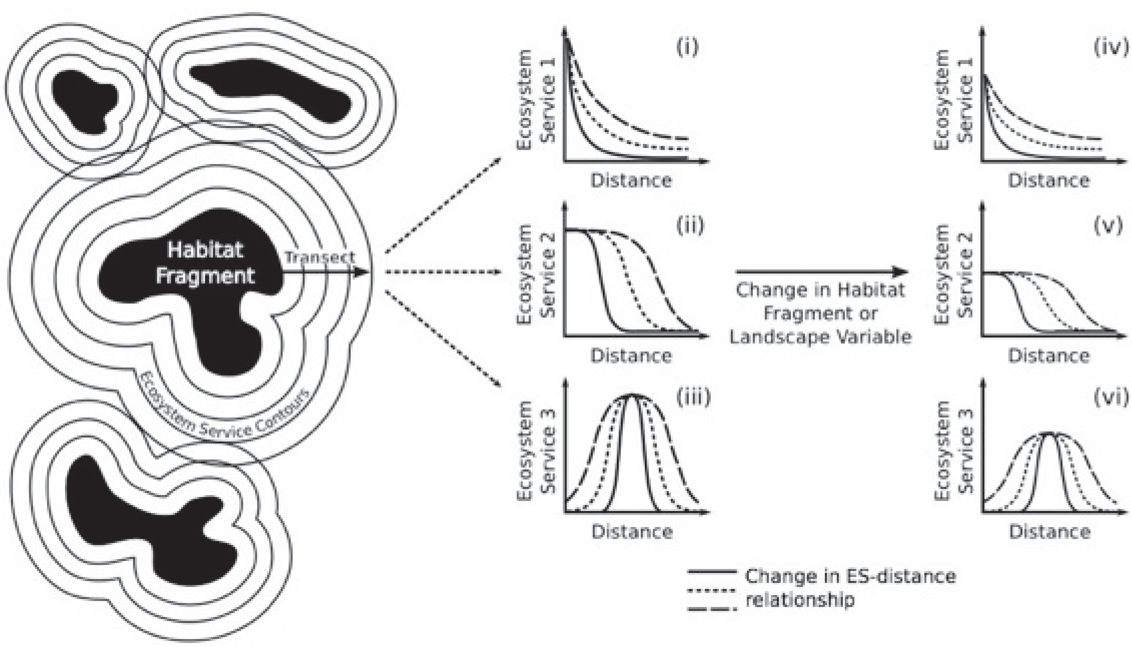
While there is good reason to expect that ecosystem services and biodiversity are affected by landscape structure, in many studies ecosystem services are depicted as site-bound and immobile (Tallis *et al.* 2008). In reality, ecosystem services are heterogeneous and spatially dynamic relationships between ecosystem processes and humans that rely on the movement of organisms, matter, and people for their provision. Pollination, pest regulation, disease regulation, and water quality regulation, among other services, are all influenced by the movement of individual organisms or matter within and between different ecosystems (Kremen & Ostfeld 2005). In addition, the species that provide the ecosystem functions that underlie ecosystem services depend on the ability of individual organisms to move and disperse across landscapes (Loreau, Mouquet & Gonzalez 2003; Leibold *et al.* 2004; Gonzalez, Mouquet & Loreau 2009). Consequently, ecosystem services are likely affected by landscape structure: the types and amounts of different land cover present (*landscape composition*), the spatial arrangement of these land cover types (*landscape configuration*), and the degree to which the landscape facilitates the

(a)



Structural Connectivity (Landscape Structure)
Functional Connectivity (Movement of Organisms & Matter)
Provision of Ecosystem Services
Human Wellbeing & Activity
Biodiversity
Ecosystem Function

(b)



Habitat Fragment
Transect
Ecosystem Service Contours
(i)
(ii)
(iii)
(iv)
(v)
(vi)
Ecosystem Service 1
Ecosystem Service 2
Ecosystem Service 3
Distance
Change in Habitat Fragment or Landscape Variable
Change in ES-distance relationship

Figure 1.1: Conceptual frameworks for landscape structure-ecosystem services research. (**a**) The potential links between landscape connectivity (*i.e.* the degree to which the landscape facilitates movement) and ecosystem service provision. Landscape connectivity can have direct effects on ecosystem service provision by influencing the magnitude of movement of organisms and matter (*black arrows*), and indirect effects by influencing the biodiversity and ecosystem functions that the landscape contains (*gray arrows*). Human activities influence landscape structure by changing land cover and land use (*dashed gray arrows*). (**b**) Fragments of habitat (*black shapes*) across a landscape will likely affect ecosystem service provision in a manner that changes or decays with distance-from-habitat (*contours*). These changes could follow a variety of relationships along transects of distance-from-habitat, including **b**(***i***) exponential decay, **b**(***ii***) logistic decay, or **b**(***iii***) a Gaussian curve, as examples. Changes in either landscape management, landscape structure including connectivity, the specific ecosystem services considered, or societal valuation of an ecosystem service could alter the form of these curves (*solid* and *dashed lines*; **b**(***i***,***ii***,***iii***) versus **b**(***iv***,***v***,***vi***)), which in turn will affect patterns of ecosystem service provision across the landscape.

movement of organisms and matter (*landscape connectivity*). In Chapter 2, I review in detail the theory that links landscape structure and connectivity with ecosystem services and ask: **What is our current level of understanding of the links between landscape connectivity and ecosystem service provision?**

A large number of landscape-scale mapping and modeling studies have been completed for different ecosystem services and regions around the world (*e.g.* Chan *et al.* 2006; Anderson *et al.* 2009; Nelson *et al.* 2009) and various tools have been produced to estimate ecosystem service provision across landscapes (*see* Bagstad *et al.* 2013). However, thus far the majority of these studies and projects estimate service provision solely based on landscape composition. In other words, service provision for a given area is determined solely by the ecosystem or ecosystems present in that location, with little consideration of how the configuration or connectivity of these ecosystems across the landscape might affect ecosystem service provision (Kremen 2005). This despite the fact that there are some well-studied examples of landscape effects on ecosystem services. For example, pollination services in adjacent agricultural fields decay with distance from fragments of natural and semi-natural habitats (Ricketts *et al.* 2008), and pest regulation increases as the diversity and number of fragments of natural habitat increases (Bianchi, Booij & Tscharntke 2006). In addition, the direction and strength of tradeoffs or synergies between ecosystem services are not well known (Kareiva *et al.* 2007; Bennett, Peterson & Gordon 2009), despite the fact that agroecosystems provide and rely on numerous ecosystem services (Power 2010). Filling these gaps requires quantification of the distance-dependent effects of habitat fragments on service provision, how changes in the characteristics of these fragments affect these distance-ecosystem service relationships, and if relationships between ecosystem services vary with landscape structure (Figure 1.1b). In Chapter 3, I ask: **How does landscape structure, specifically distance-from-forest, forest fragment isolation, and forest fragment size, affect the provision of and relationships between multiple ecosystem services in an agricultural landscape?**

Changes to landscape structure are likely to affect ecosystem service provision by altering the patterns of biodiversity and ecosystem function across landscapes (Figure 1.1a). In particular, pest regulation has been widely studied in this context (Bianchi, Booij & Tscharntke 2006;

Letourneau *et al.* 2009; Chaplin-Kramer *et al.* 2011), and it has been generally accepted that landscape structure, and in particular 'landscape complexity', has important effects on pest predator abundance and diversity, driving patterns of pest regulation. However, very few of these studies quantify how landscape structure affects levels of pest pressure, arguably the most direct measure of pest regulation (Chaplin-Kramer *et al.* 2011). Therefore, our understanding of the interplay between landscape structure, crop pests, and the abundance and diversity of pest predators is currently incomplete, hindering management of agricultural landscapes for this service. Additionally, how and under what circumstances crop production is affected by landscape-level changes in pest regulation is rarely determined. In Chapter 4, I delve further into the results from Chapter 3 and ask: **How does landscape structure simultaneously affect the biodiversity and abundance of beneficial and pest arthropods in an agricultural landscape and what effect does this have on pest regulation and crop production?**

The effects of landscape structure on ecosystem services will likely take a variety of forms depending on the ecosystem service and landscape in question (Figure 1.1b). While pollination services generally decline with distance from natural habitat (Ricketts *et al.* 2008) and pest regulation varies with landscape complexity (Chaplin-Kramer *et al.* 2011), the effects of landscape structure on other ecosystem services remain unknown. Moreover, theory and tools to explore how changes in landscape configuration or connectivity might affect service provision have not been widely developed (Kremen & Ostfeld 2005). This makes it difficult to predict whether changes to landscape structure will have significant effects on ecosystem service provision or how to structure landscapes for the optimal provision of different services (Brosi, Armsworth & Daily 2008). We also have limited ability to predict or model the patterns of ecosystem service provision we might expect to see across a landscape given a specific structure. In Chapter 5, I develop a simple modeling framework that starts to address this gap. Specifically, I ask: **How might variation in landscape structure affect ecosystem service provision at different scales?**

Each of my thesis chapters addresses an important gap in our current understanding of the links between landscape structure, biodiversity, and ecosystem service provision. Taken together, my thesis significantly advances our understanding of how changes to landscape structure in agricultural landscapes alter the benefits that we receive from them. My thesis also suggests that landscape structure could be used as a powerful tool to manage multiple ecosystem services, biodiversity, and build multi-functional agricultural landscapes. As human activities and agricultural expansion continue to drive changes in ecosystem service provision worldwide, these types of tools are critically needed to effectively conserve biodiversity and the natural habitats that sustain us.

1.3 REFERENCES

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LINKING LANDSCAPE CONNECTIVITY AND ECOSYSTEM SERVICE PROVISION: CURRENT KNOWLEDGE AND RESEARCH GAPS

2

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2.1 ABSTRACT

Human activities are rapidly changing ecosystems, landscapes and ecosystem service provision, yet there remain significant gaps in our understanding of the spatial ecology of ecosystem services. These gaps hinder our ability to manage landscapes effectively for multiple ecosystem services. In particular, we do not fully understand how changes in landscape connectivity affect ecosystem service provision, despite theory suggesting that connectivity is important. Here, we perform a semi-quantitative review of the literature that investigates how landscape connectivity affects the provision of specific ecosystem services. The vast majority of studies, including reviews, models, and field studies, suggest that decreased connectivity will have negative effects on ecosystem service provision. However, only 15 studies provided empirical evidence of these effects. Average effect sizes from these 15 studies suggest negative effects of connectivity loss on pollination and pest regulation. We identify a number of significant gaps in the connectivity-ecosystem services literature, including: a lack of multiple service studies, which precludes identification of trade-offs between services as connectivity changes; few studies that directly measure organism movement and its effects on ecosystem services; and few empirical studies that investigate the importance of abiotic flows on service provision. We propose that future research should aim to understand how different aspects of connectivity affect ecosystem service provision; which services are most influenced by connectivity; and how connectivity influences how humans access and benefit from ecosystem services. Studies that answer these questions will advance our understanding of connectivity-ecosystem service provision relationships and allow for better ecosystem and landscape management and restoration.

2.2 INTRODUCTION

Worldwide, human activities are rapidly changing land cover and land-use patterns while fragmenting habitat (Foley *et al.* 2005). Humans have fragmented over half of temperate broadleaf and mixed forests and 60 % of large rivers worldwide (MA 2005). These changes to landscape structure affect the movement of organisms and matter, and in turn affect the provision of ecosystem services (MA 2005). Although our understanding of the ecological basis of many ecosystem services has increased significantly over the past decade, much of our knowledge remains rudimentary (Kremen 2005; Nicholson *et al.* 2009), preventing the effective management of landscapes for ecosystem service provision (Tscharntke *et al.* 2005; Daily *et al.* 2009). In particular, ecosystem services are often portrayed as unmoving and site-bound (Tallis *et al.* 2008), ignoring the importance of biotic and abiotic movement for their delivery. The usefulness of the ecosystem services concept for ecosystem and landscape management depends in part on our ability to understand the links between landscape structure, movement of organisms and materials through this landscape, and the subsequent provision of multiple ecosystem services.

A variety of ecosystem services depend on the movement of organisms and materials across landscapes (Tscharntke *et al.* 2005; Kremen *et al.* 2007) and, therefore, are likely influenced by landscape connectivity—the degree to which a landscape facilitates the movement of organisms and matter. Moreover, connectivity also influences biodiversity and ecosystem function (Debinski & Holt 2000; Fahrig 2003; Gonzalez, Mouquet & Loreau 2009), which together are expected to affect ecosystem service provision. Scientists are beginning to recognize that landscape composition (how much of each land cover/use that exists) and landscape configuration (the spatial pattern of these land cover/use types) affect the provision of ecosystem services (for example, Bodin *et al.* 2006; Kremen *et al.* 2007; Brosi, Armsworth & Daily 2008; Bianchi *et al.* 2010). However, both of these landscape components also affect landscape connectivity. Different ecosystem services are likely to respond either positively or negatively to landscape connectivity change, creating and modifying the trade-offs and synergies (negative or positive relationships) between services as connectivity changes. Empirical tests of how connectivity affects different ecosystem services are needed to accurately model and manage ecosystem service provision across human-dominated landscapes. Modeling initiatives like ARIES (Artificial Intelligence for Ecosystem Services - http://www.ariesonline.org/) are developing models for multiple ecosystem services based on a connectivity paradigm. The success of these models depends on our understanding of how landscape connectivity affects the provision of multiple ecosystem services.

We expect connectivity to play a key role in ecosystem service provision because many ecosystem services depend on the promotion or restriction of the movement of organisms and materials across landscapes (Figure 2.1; Lundberg & Moberg 2003). Pollination and pest regulation depend on the movement of insect pollinators, herbivores, and predators from patches of natural habitat to adjacent agricultural fields (Tscharntke & Brandl 2004; Kremen *et al.* 2007); water quality and flood regulation depend on the control of flows of water and nutrients through wetland and riparian ecosystems from neighboring terrestrial and aquatic ecosystems (Brauman *et al.* 2007; Barbier *et al.* 2011); seed dispersal relies on the movement of animal, aquatic, and air borne vectors (Nathan *et al.* 2008); commercial fisheries can be influenced by the connectivity of coastal marine ecosystems (Meynecke, Lee & Duke 2008); and recreation is influenced by our ability to move through landscapes (van der Zee 1990). For each ecosystem service, the patterns and rates of these important movements and flows are likely a function of landscape connectivity.

Here, we gather knowledge about landscapes, biodiversity, ecosystem function, and ecosystem services to evaluate the hypothesis that landscape connectivity has important effects on the provision of ecosystem services. We break this issue into three parts. First, we briefly define landscape connectivity and describe the theory that suggests that connectivity should affect the supply of ecosystem services. Second, we review the current landscape connectivity-ecosystem services literature and address three main questions: (1) How common are studies focusing on the links between landscape connectivity and ecosystem services? (2) Which ecosystem services and aspects of landscape connectivity are most studied in this context? (3) How does landscape connectivity change usually affect ecosystem service provision? Third, we identify some key gaps and promising paths for future research in this area. Our purpose here is to identify important areas for future research and spur advancement in ecosystem service science by providing a semi-quantitative review of the literature that links landscape connectivity with ecosystem services.

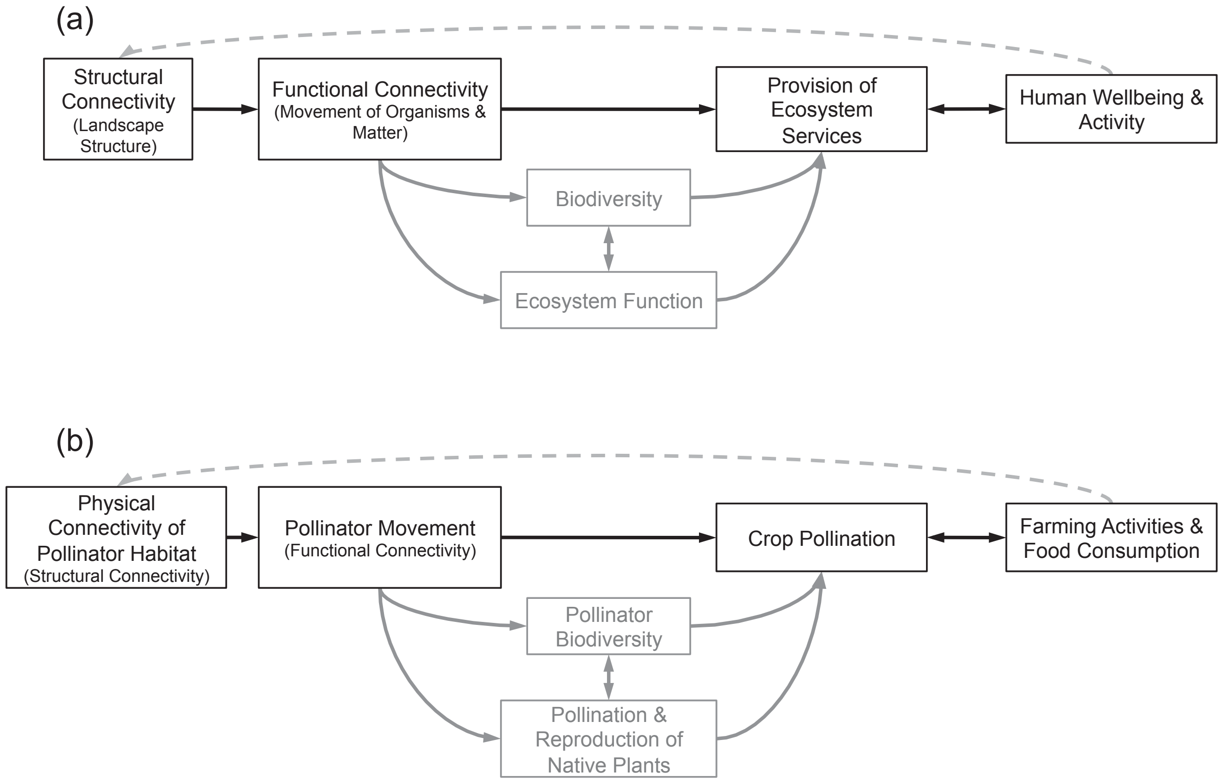


Figure 2.1: **Conceptual figure of the potential links between landscape connectivity and ecosystem service provision.** Both ecosystem service provision in general (**a**) and pollination service provision (**b**), as an example, will be influenced by landscape connectivity (*i.e.* the degree to which the landscape facilitates movement). Landscape connectivity can have direct effects on ecosystem service provision by influencing the magnitude of movement of organisms and matter (*black arrows*), and indirect effects by influencing the biodiversity and ecosystem functions that the landscape contains (*gray arrows*). Human activities influence landscape structure by changing land cover and land use (*dashed gray arrows*).

2.3 LINKS BETWEEN LANDSCAPE CONNECTIVITY AND ECOSYSTEM SERVICES

2.3.1 Landscape Connectivity

Landscape connectivity is the degree to which a landscape facilitates movement (Taylor *et al.* 1993). We use the term to include both biotic connectivity (movement of organisms) and abiotic connectivity (movement of water, nutrients, soil; Fischer & Lindenmayer 2007), each of which should influence the provision of different ecosystem services. Landscape connectivity is altered by changes in land cover and land use, including habitat fragmentation—the transformation of contiguous areas of habitat into numerous smaller patches. Fragmentation involves four unified processes: a reduction in habitat amount, an increase in the number of habitat patches, a decrease in habitat patch size, and an increase in patch isolation (Fahrig 2003). Each of these components affects landscape connectivity. Globally, habitat fragmentation is driven by human alteration of land cover, primarily to increase agricultural production, a key ecosystem service (Foley *et al.* 2005). However, the effects of fragmentation and changing connectivity on the provision of other ecosystem services are largely unknown.

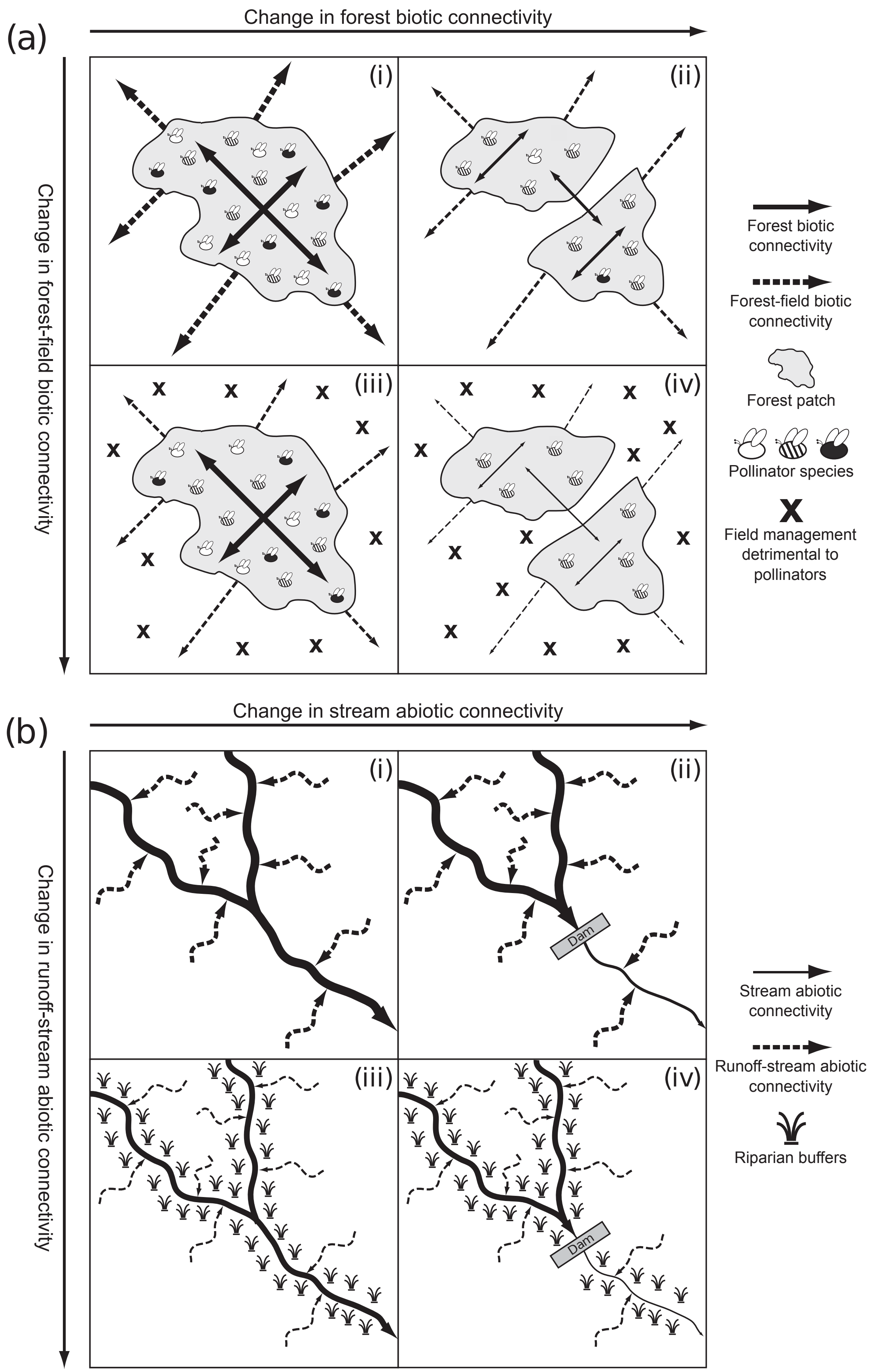
Landscape connectivity depends not only on landscape structure, including landscape composition and landscape configuration, but also on the responses of organisms and matter to this structure. Landscape composition and configuration define the structural connectivity of a landscape via its spatial structure, whereas the actual movement of organisms or materials in response to this structure defines the functional connectivity of the landscape (Brooks 2003). We place particular emphasis on the distinction between structural and functional connectivity because little is known about the relationship between the two for ecosystem service provision.

2.3.2 Direct Effects of Landscape Connectivity on Ecosystem Services

Landscape connectivity can directly affect the supply of ecosystem services by controlling the pattern and rate of the biotic and abiotic flows that are important for service provision (Figure 2.1). At the same time, connectivity can also influence population sizes and rates of resource uptake (Holt 1993; Gonzalez, Mouquet & Loreau 2009), both of which may affect ecosystem service provision. For many ecosystem services, the degree of functional connectivity across the landscape will contribute strongly to service supply. For example, insect pest regulation should increase as the movement of insect pest predators across a landscape increases. However, the direction of the relationships between connectivity and service provision (*i.e.* negative or positive) will depend on the service in question; a reduction in connectivity for a disease vector will likely increase disease regulation.

The movement of organisms across landscapes influences many important regulating services (*e.g.* pollination, pest regulation, seed dispersal, disease regulation; Kremen *et al.* 2007). For these services, we expect provision to increase when the movement of key organisms increases. For instance, insect pollinators often rely on non-crop habitat (*e.g.* meadows and forests) for nesting, and subsequently move into surrounding fields to pollinate crop species (Ricketts *et al.* 2008). The arrangement of non-crop areas with respect to agricultural fields and the ability of pollinators to move within each ecosystem should, therefore, influence the magnitude and distribution of pollination services across the landscape (Figure 2.2a). Human activities that alter landscape connectivity, including habitat fragmentation, habitat loss (Potts *et al.* 2010), and management (*e.g.* conventional vs. organic farming; Kremen, Williams & Thorp 2002), can have significant effects on pollinator movement. Similarly, the ways in which landscape connectivity influences the movement of seed dispersers, insect pest predators, and disease vectors should also be important for the provision of these services. For insect pest regulation, both the connectivity of non-crop habitat patches and cropland areas can affect movement and ecosystem service provision. Increased connectivity of cropland can facilitate the movement of crop pests across agricultural landscapes and lead to increased population sizes and pest pressure (Margosian *et al.* 2009). Adding non-crop habitat for insect predators to these landscapes, such as field margin strips, can facilitate predator movement into nearby fields and lead to increased pest regulation services (Tscharntke *et al.* 2005).

Provision of another set of services is strongly related to the movement of matter. This includes fresh water provision, and the regulation of air quality, water quality, erosion, and natural hazards. Here, a decrease in the rate of water flow through riparian buffers from upland areas



(a)
Change in forest biotic connectivity
Change in forest-field biotic connectivity
(i)
(ii)
(iii)
(iv)
Forest biotic connectivity
Forest-field biotic connectivity
Forest patch
Pollinator species
Field management detrimental to pollinators
(b)
Change in stream abiotic connectivity
Change in runoff-stream abiotic connectivity
Dam
Stream abiotic connectivity
Runoff-stream abiotic connectivity
Riparian buffers

Figure 2.2: **Hypothetical examples of the possible effects of changing landscape connectivity on ecosystem service provision.** Changes to landscape biotic and abiotic connectivity have the potential to affect the provision of many ecosystem services, including (**a**) pollination services and (**b**) water quantity/quality services. **a(*i*)** A diverse community of pollinators inhabit a forest patch within an agricultural landscape of pollinator-dependent crops and are able to move easily through the forest patch (*solid arrows*—forest biotic connectivity; width of *arrow* denotes strength of connectivity). The pollinators are also able to move from the forest into the surrounding fields (*dashed arrows*—forest-field connectivity) and provide pollination services. **a(*ii*)** When the forest patch is fragmented, pollinator habitat is lost and forest connectivity may be altered. This could result in a change in pollinator diversity or abundance (Winfree *et al.* 2009; Potts *et al.* 2010) and potentially change pollination services to surrounding fields (but see Hadley & Betts 2012). **a(*iii*)** Alternatively, the forest patch can remain intact, but a change in management of the surrounding fields (for example, application of insecticides or the loss of hedgerow habitat/corridors) can alter the ability of pollinators to move through the adjacent fields and provide pollination services. **a(*iv*)** When both forest and forest-field connectivity are disrupted and pollinator habitat is lost, there is a more significant change in the provision of pollination services. **b(*i*)** For a hypothetical freshwater stream system, flows of water and nutrients within the stream are high (*solid arrows*), as are flows from the surrounding landscape (*dashed arrows*). **b(*ii*)** When a dam is constructed, it disrupts stream connectivity, reducing the provision of water downstream. **b(*iii*)** Restoration of riparian buffers along the stream system reduces the flow of water and nutrients from surrounding areas, increasing water quality regulation but decreasing water quantity. **b(*iv*)** When both types of connectivity are altered, water quality is improved due to reduced inputs of nutrients and pollutants, but water provision downstream decreases.

might increase pollutant filtration and water quality regulation, but decrease water provision downstream (Figure 2.2b). Conversely, a decrease of water flow from a river to its surrounding riparian buffers might decrease water quality regulation and flood control, but increase water provision downstream (Brauman *et al.* 2007). Thus, the effective management of the landscape for these ecosystem services will depend to some degree on manipulating connectivity and the flows of water, nutrients, and pollutants.

2.3.3 Indirect Effects of Landscape Connectivity on Ecosystem Services

Landscape connectivity can indirectly affect ecosystem service provision by altering the important biodiversity and ecosystem functions that contribute to ecosystem services (Figure 2.1). Metacommunity theory predicts that connectivity between habitat patches is crucial to ensure the persistence of populations and diversity (Leibold *et al.* 2004). Building on this, the spatial insurance hypothesis predicts that moderate levels of connectivity between patches will maintain high levels of biodiversity, which in turn will increase the stability and mean level of ecosystem functions across habitat patches (Loreau, Mouquet & Gonzalez 2003; Gonzalez, Mouquet & Loreau 2009). We hypothesize that the provision of ecosystem services will in part depend on the metacommunity processes that mediate biodiversity and ecosystem function.

There is widespread evidence that ecosystem services are influenced by biodiversity and the ecosystem functions that biodiversity provides (Chapin *et al.* 2000; Balvanera *et al.* 2006; Cardinale *et al.* 2012); that the number of species required increases significantly as more and more services are considered (Duffy 2009); and that biodiversity provides insurance value to ecosystem services across time and space (Hooper *et al.* 2005). For example, the number of plant species contributing to ecosystem functions important for ecosystem services increases as more time and locations are considered (Isbell *et al.* 2011), whereas forest carbon sequestration over time is maximized in diverse plantings versus monocultures (Hooper *et al.* 2005). All services rely to some degree on biodiversity for their provision and some may be especially strongly related (for example, genetic resources, biochemicals, and natural medicines). Even food provision can be influenced by diversity. Crop genetic diversity can minimize vulnerability to pests and disease (Zhu *et al.* 2000) and diversity in commercial fish stocks can permit stability in the face of environmental change (Hilborn *et al.* 2003). Maintenance of this diversity in many cases relies on maintaining landscape connectivity, which in turn will affect ecosystem service supply and stability.

Examples of specific connectivity-biodiversity-ecosystem service links are known. For example, pollination services can be enhanced by a diverse pollinator community (Hoehn *et al.* 2008), which may depend on high levels of landscape connectivity (van Geert, van Rossum & Triest 2010; Holzschuh, Steffan-Dewenter & Tscharntke 2010). Similarly, regulation of insect pests such as aphids depends on a diversity of enemy species, each of which depends on the connectivity of non-crop habitats at different scales for their persistence in the landscape (Tscharntke *et al.* 2005). Because the important species and ecosystem functions for different ecosystem services are not well known (Kremen & Ostfeld 2005) it is uncertain if these indirect effects of connectivity on ecosystem service provision are common or important. To address the perceived knowledge gaps outlined above, we surveyed the literature to identify current knowledge.

2.4 LITERATURE SURVEY METHODS

We reviewed all indexed articles published up to the end of 2011 by searching ISI Web of Science, Scopus, Agricola, GeoRef and International Bibliography of the Social Sciences for articles that contained any of the terms "ecosystem service*/good*," "ecological service*/good*," and "environmental service*/good*," in combination with any of "connectivity," "corridor*," or "fragmentation" in the title, abstract, or keywords. We then classified papers based on the type and number of ecosystem services investigated, type of connectivity investigated, which ecosystems were studied, what connectivity metrics were used, and the type of paper (for example, experimental, modeling, review, and so on). Our goal was to understand where and how connectivity and fragmentation are being incorporated into the ecosystem services literature, so we did not limit our review to any specific paper types. We also relied on authors to identify that their study involved ecosystem services. Therefore, our search likely missed some papers with links to specific ecosystem services that were not labeled as such by their authors. It was beyond the scope of our study to perform a search for all of the studies with data relevant to the effects of changing connectivity for individual ecosystem services.

We initially identified 308 papers from 151 different sources (scientific journals, conference proceedings, and books). However, many of these papers did not explicitly investigate the effects of connectivity or fragmentation on the provision of a specific ecosystem service. Instead, they studied an ecosystem function, ecosystem property, or the abundance and diversity of specific species and would mention that these elements were important for ecosystem service provision. Yet it was often not obvious which ecosystem service was being specified or how the ecosystem function or species abundance linked to service provision. We, therefore, defined ecosystem services as the conditions and processes through which ecosystems, directly or indirectly, provide the benefits people require to sustain and fulfill human life (Daily *et al.* 1997; MA 2005), to identify a subset of articles that explicitly investigated the effects of landscape connectivity on the provision of at least one specific ecosystem service. Using this definition of an ecosystem service, we identified a subset of 69 papers from the original 308.

The majority of papers in this subset lacked quantitative empirical data (*i.e.* were reviews or modeling papers) and used a wide variety of methods and designs. Therefore, we could not perform a formal meta-analysis. Instead, we evaluated the observed or predicted changes in ecosystem service provision with landscape connectivity change across the 69 studies using a vote-counting methodology similar to Debinski & Holt (2000). Next, for a smaller set of 15 papers with empirical field data, we calculated average effect sizes of decreased landscape connectivity on ecosystem service provision using the log response ratio:

$$LRR = \ln\left(\frac{\textit{service provision with low connectivity}}{\textit{service provision with high connectivity}}\right)$$

For each of these 15 papers, ecosystem service provision data were extracted from digitized graphs using GraphClick (Arizona Software 2008) for the landscapes or plots at each end of the connectivity gradient used in that study. Across studies, the measurements of connectivity (see below) and the difference between low and high connectivity landscapes were inconsistent. Therefore, we calculated LRR separately for each paper. Many papers used multiple variables to quantify service provision (for example, species diversity, abundance, and ecosystem function); in these cases we averaged the LRR across all variables to calculate a single overall LRR value for the study.

2.5 QUANTITATIVE REVIEW OF CURRENT LITERATURE

2.5.1 *Effects of Connectivity Change on Ecosystem Service Provision*

Most studies observed or predicted negative effects of decreased landscape connectivity on ecosystem service provision (Figure 2.3a). Across the 69 papers in our detailed review, ecosystem service provision declined or was predicted to decline with decreased landscape connectivity 74 % of the time. Most of these papers focused on pollination, where service provision almost always declined with decreased connectivity. Other ecosystem services have not been investigated to the same extent, and for many services we only found one or two studies (for example, timber, climate regulation, soil erosion, and aesthetics).

Very few studies contained empirical data with which to test the effects of decreased connectivity on ecosystem service provision. Within the 15 field studies with extractable data, both pollination and pest regulation had negative mean LRR values, or loss of service provision with declining landscape connectivity (Figure 2.3b). Seed dispersal had varied responses in fragmented landscapes. Due to the small number of papers, only the pollination LRR was statistically different from zero (one sample *t* test; pollination: $p = 0.01$; seed dispersal: $p = 0.35$; pest regulation: $p = 0.07$).

2.5.2 *Types of Ecosystem Service-Connectivity Studies*

The 69 papers in our subset included reviews, observational field studies, modeling/GIS papers, and conceptual papers. Most were published within the last 3 years (61 %), and over 90 % were published since 2004. The majority of studies did not provide empirical evidence that ecosystem service provision is altered as landscape connectivity changes. Instead, they were either reviews of ecosystem function-connectivity papers that attempted to make links with ecosystem service provision (27 %; Figure 2.4a), or were modeling studies that predicted how ecosystem service provision might change as landscape connectivity declines (19 %). Given the logistical difficulty of manipulating connectivity at a landscape scale and measuring ecosystem services, this is not

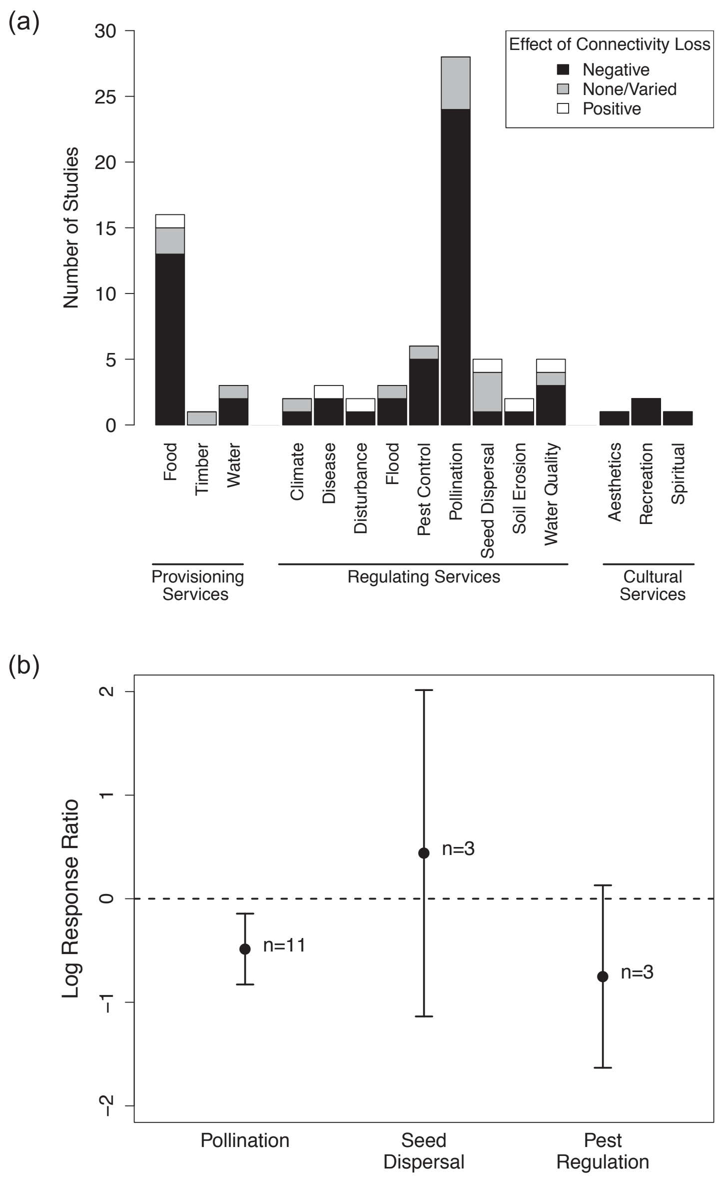


Figure 2.3: **Results of the effects of decreased landscape connectivity on ecosystem service provision.** (**a**) Number of studies showing negative, none/ varied, or positive effects of decreased landscape connectivity on ecosystem service provision. Some studies investigated multiple ecosystem services, in these cases each service measured was counted separately. (**b**) Average effect size (LRR) of landscape connectivity decline on pollination, seed dispersal, and pest regulation service provision. Negative values of LRR indicate loss of ecosystem service provision as landscape connectivity decreases. The dashed line indicates no difference between landscapes with high or low connectivity; error bars show 95 % confidence intervals.

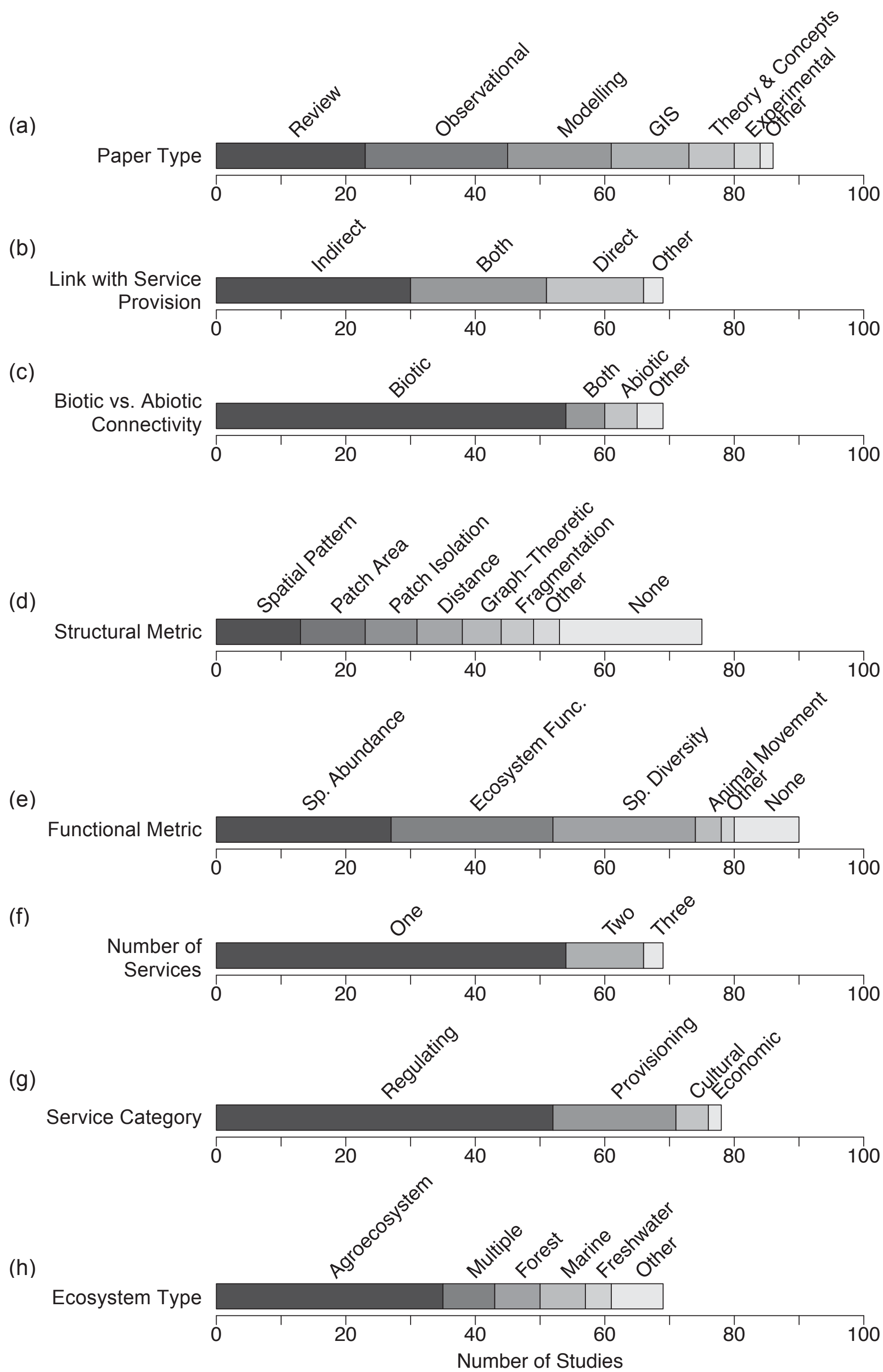


Figure 2.4: **Classification of landscape connectivity-ecosystem service studies.** Each graph shows the number of studies belonging to each specified factor level. The total number of studies in each graph differs as some studies met multiple criteria (for example, a study could investigate both a regulating and a provisioning service).

surprising. However, the small number of empirical studies currently limits our ability to understand how changing connectivity affects ecosystem service provision.

We also only found a handful of theory/concept papers (7 studies) that link connectivity with ecosystem service provision (Figure 2.4a), and the absence of this link is especially apparent for regulating services (Figure 2.5a). As the ecosystem services framework is relatively new and the conceptual links between biodiversity, ecosystem function, and ecosystem services have only recently been made (for example, Kremen & Ostfeld 2005; Mace, Norris & Fitter 2011; Cardinale *et al.* 2012), this gap is not entirely unexpected. Our review of the theory above suggests that multiple links should exist between landscape connectivity and ecosystem services; however, these links have not yet been systematically described in the literature.

2.5.3 Direct versus Indirect Effects of Connectivity

Both direct and indirect effects of connectivity on service provision have been investigated. The largest proportion of studies focused solely on indirect links (44 %; Figure 2.4b), namely for pollination, food provision in aquatic ecosystems, and pest regulation. This reflects a widespread emphasis in the ecosystem services literature on the importance of biodiversity for service provision. However, a substantial portion also addressed only direct links (22 %) or both direct and indirect links (30 %). A number of pollination and seed dispersal studies simultaneously investigated the effects of distance from forest patches on pollinator or disperser numbers and visitation rates (*i.e.* direct effects of connectivity) and pollinator or disperser species diversity (*i.e.* indirect effects). However, none of these studies quantified the relative importance of these different effects of connectivity on ecosystem service provision. Identifying the specific ecosystem services and situations where direct or indirect effects of connectivity are most important remains an important knowledge gap.

2.5.4 Biotic versus Abiotic Connectivity

Links between biotic connectivity and ecosystem service provision have been much more widely studied than for abiotic connectivity (78 % of papers vs. 7 %; Figure 2.4c), especially for regulating services (Figure 2.5b). Despite the fact that many regulating services, such as water

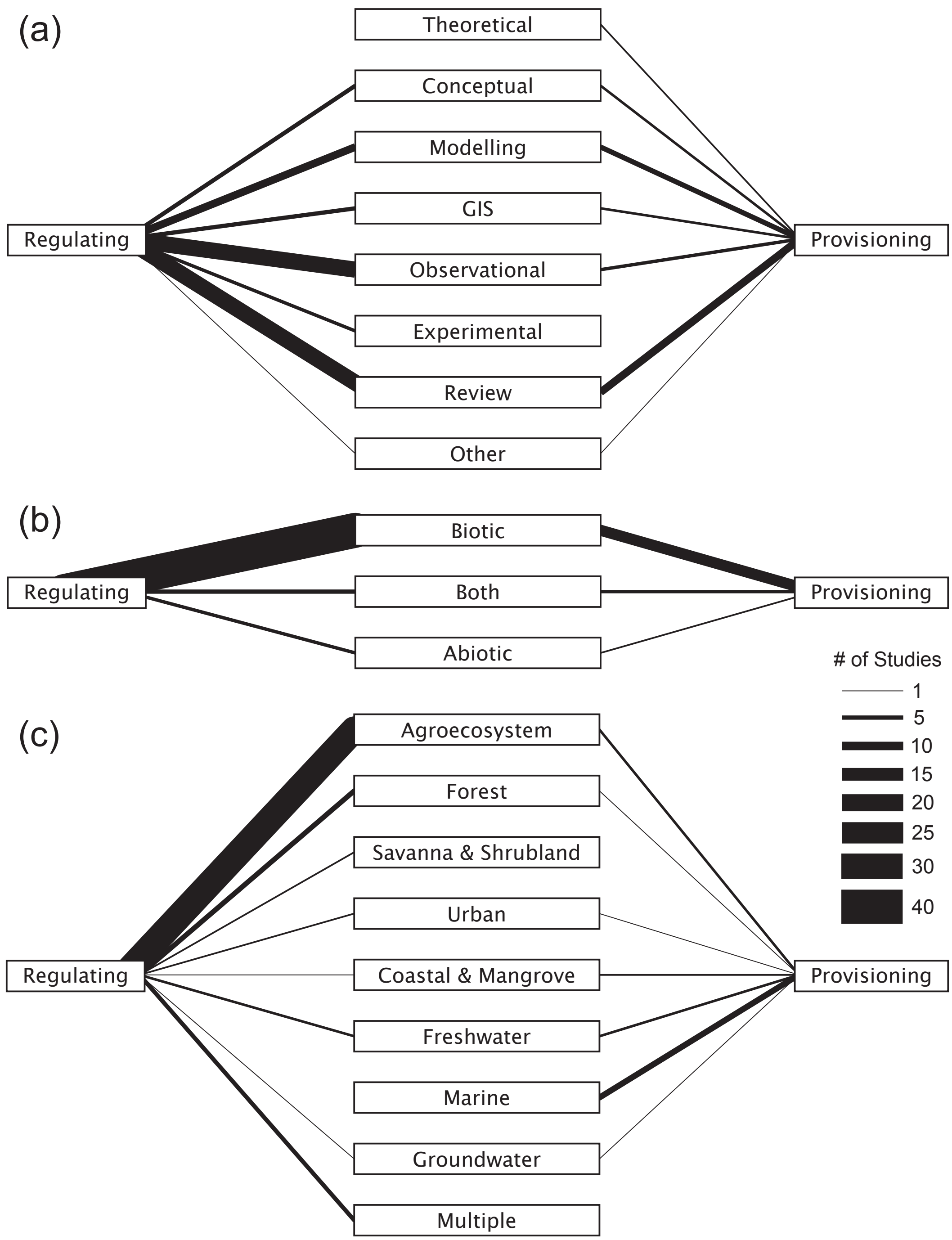


Figure 2.5: **Classification of regulating and provisioning landscape connectivity-ecosystem service studies.** Each graphs shows the number of studies of regulating and provisioning services (**a**) of different paper types, (**b**) which investigated biotic versus abiotic connectivity, and (**c**) of different ecosystem types. The width of the lines represents the number of studies that belong to each factor level.

quantity and quality, flood control, and erosion regulation, depend on the movement of matter through landscapes, these links have not been well described in the current ecosystem services literature. In many cases, water quantity depends on connectivity within freshwater systems (Steinman & Denning 2005; Brauman *et al.* 2007) and connectivity between surface and groundwater systems (Tomlinson & Boulton 2010); whereas water quality is, in part, determined by the connectivity between pollutant and nutrient sources and the wetland and riparian sinks that filter these substances (Gundersen *et al.* 2010; Opperman *et al.* 2010). It may be that many of these relationships have been explored in other subject areas, but have not been explicitly labeled as ecosystem service studies. Exploring how landscape connectivity can affect the movement of matter and service provision is an important link to make in the ecosystem services literature.

2.5.5 Measurements of Connectivity

A large variety of connectivity metrics have been used in the connectivity-ecosystem services literature. Structural connectivity metrics focused on spatial patterns (19 %; for example, metrics combining patch area, isolation and landscape pattern), the area of specific ecosystems in a landscape (13 %), isolation of habitat patches (11 %), and distances between habitat patches (9 %; Figure 2.4d). This variety of metrics makes it difficult to generalize about the effects of structural connectivity, but this is a general problem with connectivity studies (Kindlmann & Burel 2008). Measures of patch area or distances between patches (*i.e.* structural connectivity) are also difficult to relate to actual movement across a landscape (*i.e.* functional connectivity).

We found that functional connectivity is generally unmeasured in ecosystem service studies. Most studies indirectly measured functional connectivity using proxies such as species abundance (30 %), ecosystem function (28 %), or species diversity (24 %; Figure 2.4e). Although these metrics provide information about the role of different species in ecosystem service provision, and the importance of biodiversity to specific services, their ability to indicate actual movement across landscapes is limited. We found only three studies, all involving birds and seed dispersal services, which measured actual animal movement across landscapes and linked this to ecosystem service provision.

2.5.6 *Effects of Connectivity on Multiple Ecosystem Services*

We predicted above that different ecosystem services would respond in contrasting ways to landscape connectivity change, creating trade-offs and synergies. However, most papers investigated only one ecosystem service (78 %), although a few included two or three services (Figure 2.4f). Studies of single ecosystem services are common (Seppelt *et al.* 2011), but prevent the description of trade-offs and synergies as landscape connectivity is altered. Although none of the studies of multiple ecosystem services in our review found contrasting effects of decreased connectivity between services, our sample size was small (twelve papers) and included at most three services. How landscape connectivity simultaneously affects multiple ecosystem services, how biotic versus abiotic connectivity interact to affect different services, and how trade-offs between ecosystem services might change as connectivity is altered are not yet clear.

Most connectivity-ecosystem service studies also focused on food provision and pollination (Figures 2.3a, 2.4g), compounding the issues caused by the lack of multiple service studies. Ninety-one percent of the papers dealt with regulating and provisioning services, almost half (49 %) of the regulating service papers focused on pollination, and 80 % of the provisioning service papers focused on food provision. These trends also exist in the larger overall ecosystem services literature (Vihervaara, Ronka & Walls 2010). The prevalence of pollination studies is not unexpected; a large amount of research has linked the presence and pattern of natural ecosystems with pollination (for example, Ricketts *et al.* 2008) and complex landscapes with high connectivity often have higher levels of pollination (Tscharntke *et al.* 2005). However, it is surprising that links between connectivity and other regulating services, such as pest control, seed dispersal, and disease control, have not been made to the same extent. Links between cultural services (for example, aesthetics, recreation, spiritual, and education) and connectivity have also not been tested, although they might not be as strong as those for other types of services. Effective landscape management requires understanding how landscape connectivity affects all ecosystem services and their interactions.

2.5.7 *Links Across Ecosystems and Between Services*

Despite a current emphasis in the literature on agroecosystems and pollination (Figures 2.3a, 2.4h, 2.5c), there are many other combinations of ecosystems and services where the movements of organisms and substances are expected to be important. Ecosystems found at the boundaries of terrestrial and aquatic ecosystems (for example, estuaries, mangroves, and coastal zones) contribute to an inordinate number of ecosystem services (UNEP 2006) and links between terrestrial and freshwater or marine systems are also known to be important for many ecosystems (Barbier *et al.* 2011). Understanding how changes in connectivity between these systems affect multiple services, especially changes due to human activities, would be particularly valuable for landscape management.

There are also opportunities to investigate how landscape connectivity affects the links between regulating services and provisioning services within both terrestrial and marine ecosystems. In terrestrial ecosystems, most studies occurred in agroecosystems (66 %; Figures 2.4h, 2.5c) and reflect the dominance of pollination and pest regulation service studies. At the same time, food provisioning-connectivity studies in agroecosystems were rare (3 studies). In marine ecosystems, food provisioning studies were much more common, focusing on fish species and mangrove or seagrass connectivity (7 studies; Figure 2.5c). However, we did not find any papers that considered marine connectivity and regulating services. In agroecosystems, some of this apparent disconnect might stem from pollination service definitions that combine both regulating (*i.e.* pollination of crops) and provisioning services (*i.e.* crop yield). Yet the implications of changes in landscape connectivity for crops not dependent on animal pollinators are largely unstudied. In marine systems we found a contrasting result, with the majority of studies focused on provisioning instead of regulating services. However, there exist a large number of regulating services that help support marine provisioning services and human well-being (UNEP 2006). Effective ecosystem management depends on identifying the important regulating services in marine and terrestrial ecosystems that underlie provisioning services and understanding the relationships between these service categories as connectivity changes.

2.6 OPEN QUESTIONS FOR FUTURE RESEARCH

Overall, our review reveals a widely held view that change in landscape connectivity is likely to have important effects on ecosystem service provision; however, supporting empirical data are rare. Flows of matter and organisms are important for the provision of ecosystem services, but how biotic and abiotic landscape connectivity affects the strengths and patterns of these different flows has not been thoroughly quantified. What evidence exists suggests that decreased landscape connectivity usually has negative effects on regulating services such as pollination, pest control, and food provision. These effects occur through both direct and indirect pathways, with connectivity affecting both the movement of organisms and matter, and biodiversity and ecosystem function (Figure 2.1). Most studies of connectivity and ecosystem services focus on regulating services, whereas fewer studies have investigated provisioning or cultural services. There remain a large number of unexplored questions with respect to the specific ways that connectivity influences ecosystem service provision.

We propose a set of research questions within three broad categories that we feel would best address the uncertainties and gaps highlighted in our review (Table 2.1). Answering these questions will advance our understanding of the connectivity-ecosystem service provision relationship and the importance of this relationship across different landscapes.

2.6.1 What Aspects of Landscape Connectivity Most Influence the Provision of Ecosystem Services, and How Should they be Measured?

Few studies have developed conceptual or theoretical frameworks to link landscape connectivity with the provision of ecosystem services (Bagstad *et al.* 2012). We feel this has two main consequences. First, as there is little guidance for what types of connectivity might affect ecosystem service provision, a wide variety of structural connectivity metrics and proxies for functional connectivity have been used in the current literature, making it difficult to compare across studies or accurately assess the effects of biotic or abiotic movement on service provision. Newly developed metrics, including graph-theoretic measures (Rayfield, Fortin & Fall 2011), might help, but have not been widely used in connectivity-ecosystem service studies.

Second, the possible mechanisms by which connectivity might affect ecosystem service provision, both direct and indirect, have not been explicitly identified or measured. We predict that connectivity can affect ecosystem service provision not only directly through the movement of

Table 2.1: Research questions to advance understanding of the effects of landscape connectivity on ecosystem service provision.

What aspects of landscape connectivity most influence the provision of ecosystem services, and how should they be measured?

- What are the conceptual and theoretical ways that connectivity might influence ecosystem service provision?
- What are the important mechanisms by which connectivity can affect ecosystem services and what causes their relative importance to change?
- At what scales does connectivity affect the provision of ecosystem services?

How are different ecosystem services influenced by landscape connectivity?

- What ecosystem service categories or specific ecosystem services are most strongly influenced by landscape connectivity?
- How variable are ecosystem service responses to landscape connectivity change?
- What are the important directional flows for the provision of ecosystem services and how does connectivity influence these?
- Are there tradeoffs and synergies between different ecosystem services as landscape connectivity changes?

How does landscape connectivity influence our ability to access and benefit from ecosystem services?

- How do patterns of ecosystem service provision and landscape connectivity influence human activities, land use, and land management actions?
- How do patterns of human movement influence the ecosystem services that society can access and benefit from?
- Can patterns of ecosystem service provision and human activity be managed and restored by manipulating key parameters of landscape connectivity?

organisms and matter through a landscape, but also indirectly by altering levels of biodiversity and ecosystem function. However, the relative importance of these mechanisms is currently not known, and measuring the actual movement of organisms or matter across landscapes (*i.e.* functional connectivity) is difficult (Bélisle 2005) and is often not quantified in connectivity-service studies. Conceptual and theoretical frameworks built on meta-ecosystem (Loreau, Mouquet & Gonzalez 2003; Loreau, Mouquet & Holt 2003) and ecological network theories (for example, Gonzalez, Rayfield & Lindo 2011) are needed to develop a deeper understanding of the link between landscape connectivity and ecosystem services. This advance would allow for better empirical tests in the field and help identify the types of connectivity (*i.e.* biotic vs. abiotic) and spatial scales where connectivity is most likely to affect ecosystem service provision. For example, changes to connectivity and the provision of services such as pollination, pest regulation, or food from commercial fisheries can depend on the scale at which connectivity is altered, both spatially and temporally (Tscharntke *et al.* 2005; Deza & Anderson 2010). A theoretical framework could help identify these scales and the most effective ways to measure connectivity. Effective management of ecosystem services requires this understanding for multiple ecosystem services across multiple spatial scales within a variety of human-modified landscapes.

Understanding the relative importance of connectivity within and between ecosystems will also be important for predicting how land use will affect ecosystem services, and for designing landscape management techniques to maximize multiple ecosystem services. For instance, quantifying how the regulation of water quality is affected by the juxtaposition of terrestrial, riparian, and freshwater systems, versus how species diversity and ecological structure within each of these ecosystems mediates the flow of water and pollutants. Similarly, managing watersheds for potable water, navigation, recreation, flood control, waste processing, and hydroelectric power requires information about how various types of connectivity, including upstream-downstream, floodplain-river, hillslope-river, and surface water-groundwater connectivity, interact to influence each ecosystem service (Steinman & Denning 2005).

2.6.2 How are Different Ecosystem Services Influenced by Landscape Connectivity?

Our understanding of the effects of landscape connectivity on different ecosystem services is incomplete, as only a few services have been investigated to any significant extent. We also have little knowledge of the variability in ecosystem service response to connectivity change either within or across service categories (for example, provisioning, regulating, and cultural). Identifying if specific ecosystem services or categories of services are strongly influenced by landscape connectivity would be a powerful management tool when provision of specific ecosystem services is the goal. Additionally, our review only included studies that self-identified as ecosystem service studies. There remain many opportunities to perform comprehensive ecosystem service-specific reviews of all studies relevant to the effects of changing connectivity on service provision.

Currently, there is evidence that biotic connectivity is important for regulating ecosystem services that rely on mobile organisms (Kremen *et al.* 2007), such as insect pollination, seed dispersal, and pest regulation. However, a large number of other important services have not been investigated to the same extent, particularly timber and water provisioning services, regulating services that involve abiotic connectivity and flows of materials (for example, flood control, water quality regulation, and climate regulation), and cultural services. For a number of these services, the important flows of matter and organisms may be strongly directional and will involve specific ecosystem types. For example, insect pest regulation often relies on the movement of insects from native habitat fragments into adjacent crop fields (Tscharntke & Brandl 2004; Kremen *et al.* 2007) and many hydrology-based services such as water quality regulation and flood control depend on the flow of water through watersheds and the positioning of riparian and wetland ecosystems relative to agricultural, urban, and forested lands (Brauman *et al.* 2007). Additionally, food provision from commercial fisheries can depend on biotic connectivity between mangrove and seagrass nursery habitats and the coral reefs used by adult fish (Meynecke, Lee & Duke 2008; Barbier *et al.* 2011). Understanding the direction of the most important flows of organisms and matter for the provision of these services would provide valuable information for the design, management, and restoration of landscapes.

Different ecosystem services also respond differently to the variety of drivers and pressures that affect them, including connectivity. This creates a variety of positive and negative ecosystem service trade-offs as landscape structure and human land use are altered (Bennett, Peterson & Gordon 2009). For instance, in the Florida Everglades, during high water flow conditions (*i.e.* high hydraulic connectivity), nutrient runoff and loading increases, water quality decreases, and habitat quality is reduced (Steinman & Denning 2005). At the same time, boat recreation, irrigation, aquifer recharge, and water for human consumption are improved. These trade-offs may create bundles of ecosystem services (Raudsepp-Hearne, Peterson & Bennett 2010) that act in similar or dissimilar ways as landscape connectivity is changed. Ecosystem services can also directly influence each other. For example, increased pollination or pest regulation services can drive increased crop production, whereas erosion control and water purification by mangroves can enhance commercial fisheries and protect navigation corridors against siltation (Barbier *et al.*

2011). Yet, the interactions between connectivity and multiple ecosystem services are virtually unknown; our review identified very few studies that considered more than one ecosystem service at a time. One of the strengths of the ecosystem services framework for land management is the ability to consider the multi-functionality of landscapes. To properly understand and manage landscapes for connectivity with a goal to enhance ecosystem services requires that we understand the effects of connectivity on multiple ecosystem services.

2.6.3 How Does Landscape Connectivity Influence our Ability to Access and Benefit from Ecosystem Services?

Ecosystem services exist at the point of interaction between ecosystem function and human activity (de Groot, Wilson & Boumans 2002). Therefore, even with a constant biophysical supply of an ecosystem service, changes in human activity can alter service provision. It is likely that the patterns and ease of human movement across landscapes influence how people experience their environment (*i.e.* cultural services), and help determine the flows of all types of services from ecosystems to society (Bagstad *et al.* 2012). For example, increased transportation connectivity in the Amazon alters access to forest resources, fire damage to forests, and social-ecological resilience (Perz *et al.* 2012). However, we found very few studies that considered the effects of landscape connectivity on human activity and ecosystem service provision. Ultimately, human well-being and activities influence land use and landscape structure, feeding back to ecosystem provision through landscape connectivity (Figure 2.1). Understanding this cycle with respect to human actions and well-being is necessary to effectively manage landscapes for multiple ecosystem services, but requires interdisciplinary work between various fields, including ecology, economics, sociology, and geography.

2.7 CONCLUSIONS

Although landscape connectivity is expected to substantially influence the provision of ecosystem services across landscapes, it has not been widely investigated in the ecosystem services literature. What research has been done focuses on regulating services such as pollination and pest regulation in agricultural landscapes, and may not be applicable to other services or ecosystems.

The usefulness of the ecosystem services concept for ecosystem and landscape management depends on making the links between landscape structure, specifically landscape connectivity, and the provision of multiple ecosystem services. The research gaps we identified will only be filled by a concerted effort to incorporate landscape connectivity into the ecosystem services framework. This includes development of theory to link connectivity and the expected effects on provision of ecosystem services, as well as multi-disciplinary studies to quantify the effect of connectivity on multiple ecosystem services across a variety of landscapes. Incorporating flows of organisms and matter across landscapes into ecosystem service assessments necessarily involves a substantial increase in the complexity of theory, models, and understanding. However, the benefits of this understanding could be significant if it provides society with improved tools for the management of landscapes for ecosystem services.

2.8 ACKNOWLEDGMENTS

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2.10 SUPPORTING INFORMATION

2.10.1 Log Response Ratio Calculation Methods

We used the log response ratio (LRR) to calculate average effect sizes of decreased landscape connectivity on ecosystem service provision (pollination, pest regulation, and seed dispersal). Data was extracted from digitized graphs from 15 papers with empirical field data (Table 2.2) and LRR was calculated as:

$$LRR = \ln\left[\frac{service\ provision\ in\ low\ connectivity\ landscape}{service\ provision\ in\ high\ connectivity\ landscape}\right]$$

Landscapes with low and high landscape connectivity were selected from the ends of the connectivity gradient used in each paper. Some papers measured more than one ecosystem service. In these cases, each service was analyzed separately.

Across the 15 studies, the measurements of landscape connectivity and ecosystem service provision varied greatly, therefore we calculated LRR separately for each paper. Thus, the final LRR values for each ecosystem service represent average values from the wide range of landscape connectivities that have been measured up to this point in the current literature. Many of the papers used multiple variables to quantify the provision of a single service; for these papers we averaged the separate LRR values across all variables to calculate a single mean LRR value for each study.

Table 2.2: Connectivity and ecosystem service data for log response ratio calculations.

Paper	Ecosystem Service	Connectivity Gradient (connected vs. fragmented)	Ecosystem Service Measurement	Value in Connected Landscape	Value in Fragmented Landscape	Log Response Ratio	Mean Log Response Ratio
Albrecht *et al.* 2007	Pollination	0m vs. 200m from forest edge in ecological compensation areas (wildflower strips, hedges, hay meadows)	Abundance of solitary bees (# individuals/20 min)	3.30	0.23	-2.65	-1.59
			Species richness of solitary bees	2.98	0.23	-2.55	
			Abundance of hover flies (# individuals/20 min)	16.42	7.86	-0.74	
			Species richness of hover flies	9.43	5.94	-0.46	
			Abundance of large pollinators (# individuals/20 min)	5.24	1.03	-1.63	
			Species richness of large pollinators	3.35	0.76	-1.49	
Amorim & De Marco, 2011	Pollination	*B. coccolobifolia* plants 2m vs. 16m from each other	Proportion of fruits produced (calculated from regression line)	0.08	0.06	-0.22	-0.47
			Proportion of fruits produced (calculated from data points)	0.21	0.11	-0.71	
Breitbach *et al.* 2010	Seed Dispersal	Gradient of vertical vegetation heterogeneity in surrounding landscape, from high (connected) to low (fragmented)	Disperser species richness	8.49	2.18	-1.36	-0.13
			Disperser abundance (# individuals/5 min)	19.10	4.81	-1.38	
			Tree visitor species richness	6.82	4.83	-0.35	
			Total number of tree visitors (# individuals/8 h)	37.48	28.55	-0.27	
			Number of cherries removed	14.78	25.18	0.53	
			Flight distance of seed dispersers (m)	13.58	107.11	2.07	
Chacoff *et al.* 2006	Pollination	0m vs. 100m from forest in grapefruit plantations	Pollinator visitation rate (# visits/15 min/flower)	0.47	0.20	-0.88	-0.68
			Number of pollinator morphospecies (morphospecies/15 min.)	0.83	0.55	-0.41	
			Total number of pollinator morphospecies	32.10	15.08	-0.76	
Farwig *et al.* 2009	Pollination	Sites adjacent vs. 100m from woody habitat in agricultural landscape	Proportion of *Primula elatior* flowers setting seed	0.73	0.44	-0.51	-0.51

Table 2.2: Cont'd.

Paper	Ecosystem Service	Connectivity Gradient (connected vs. fragmented)	Ecosystem Service Measurement	Value in Connected Landscape	Value in Fragmented Landscape	Log Response Ratio	Mean Log Response Ratio
Farwig *et al.* 2006	Seed dispersal	Forest fragments vs. main forest landscape	Number of frugivorous species in forest	19.06	16.60	-0.14	0.32
			Number of frugivorous individuals in forest (# individuals/20 min)	97.72	89.13	-0.09	
			Number of frugivorous species in *P. africana* trees	4.18	5.01	0.18	
			Number of frugivorous individuals in *P. africana* trees (# individuals/ 3 h)	7.91	13.12	0.51	
			Number of seeds dispersed per tree	9.38	28.97	1.13	
Fazzino *et al.* 2011	Pollination	Fragmented vs. connected meadows	Potential germinants per inflorescence when naturally pollinated	4.30	2.81	-0.43	-0.43
Hadley & Betts, 2009	Pollination	Forested vs. agricultural landscape	Homing time for hummingbirds (min)	51.45	87.56	-0.53	-0.44
			Hummingbird movement path (m)	1141.17	1602.94	-0.34	
Holzschuh *et al.* 2010	Pollination	High edge density vs. low edge density agricultural landscape	Number of bee species (# species/4 trap nests)	1.81	1.06	-0.53	-0.52
			Number of bee brood cells	641.03	383.98	-0.51	
Klein *et al.* 2002	Pollination	Low land-use intensity vs high land-use intensity agroforestry landscapes	Number of bee brood cells (# brood cells/6 trap nets)	24.49	186.45	2.03	0.21
			Number of pollinator species	4.38	8.31	0.64	
			Abundance of solitary bees (# individuals/15 min/tree)	6.99	36.59	1.66	
			Diversity of solitary bees	4.78	7.27	0.42	
			Abundance of social bees (# individuals/15 min/tree)	63.15	5.98	-2.36	
			Diversity of social bees	4.77	1.51	-1.15	
Klein *et al.* 2006	Pollination	<100m from forest vs. >500m from forest in agroforestry landscape	Number of pollinator species	7.51	4.87	-0.44	-0.23
			Abundance of pollinators (# individuals/10 trap nests)	540.38	528.64	-0.02	
	Pest Regulation		Number of natural enemy species	7.69	4.03	-0.65	-0.86
			Abundance of natural enemy species (# individuals/10 trap nests)	9.41	3.19	-1.08	

Table 2.2: Cont'd.

Paper	Ecosystem Service	Connectivity Gradient (connected vs. fragmented)	Ecosystem Service Measurement	Value in Connected Landscape	Value in Fragmented Landscape	Log Response Ratio	Mean Log Response Ratio
Lenz *et al.* 2011	Seed dispersal	Forest vs. agricultural landscape	Modelled seed dispersal distance (m) from field data	86.0	265.0	1.13	1.13
Ricketts, 2004	Pollination	<50m from forest vs. >800m from forest in coffee agricultural landscape	2001 accumulated pollinator richness	11.58	2.29	-1.62	-0.96
			2001 pollinator visitation rate (# individuals/10 min)	7.93	3.99	-0.69	
			2002 accumulated bee richness	9.48	2.48	-1.34	
			2002 pollinator visitation rate (# individuals/10 min)	4.24	2.17	-0.67	
Schuepp *et al.* 2011	Pollination	Forest edge vs. isolated fields in agricultural landscape	Bee species richness	1.30	1.21	-0.08	0.27
			Bee abundance (# individuals/2 trap nests)	20.90	38.36	0.61	
	Pest Regulation		Enemy species richness	5.09	2.51	-0.71	-1.04
			Enemy species abundance (# individuals/2 trap nests)	32.84	8.40	-1.36	
Stutz & Entling, 2011	Pest Regulation	Adjacent to vs. 100-200m from forest habitat in agricultural landscape	Number of aphids on cherry trees without glue ring	80.86	200.61	-0.91	-0.35
			Syrphid abundance	1.34	0.64	-0.74	
			Coccinelid beetle abundance	0.06	0.11	0.58	

2.10.2 Paper distribution in journals

Papers from the subset of 69 articles that explicitly investigated the effects of landscape connectivity on a specific ecosystem service came from a variety of different journals (52 journals total; Table 2.3). Only 9 journals contributed more than one article, and most journals provided only a single paper.

Table 2.3: Distribution of connectivity-ecosystem service papers in academic journals.

	Journal	No. of papers	Cum. Distrib.
1	Journal of Applied Ecology	5	0.07
2	Biological Conservation	3	0.12
3	Conservation Biology	3	0.16
4	Ecological Applications	3	0.20
5	Ecology Letters	3	0.25
6	Oecologia	3	0.29
7	Journal of Animal Ecology	2	0.32
8	Landscape Ecology	2	0.35
9	Proceedings of the Royal Society of London Series B – Biological Sciences	2	0.38
10	Acta Ecologica Sinica	1	0.39
11	Ambio	1	0.41
12	American Midland Naturalist	1	0.42
13	Annals of the New York Academy of Sciences	1	0.43
14	Annual Review of Ecology and Systematics	1	0.45
15	Biological Control	1	0.46
16	Biology Letters	1	0.48
17	Bioscience	1	0.49
18	Bird Conservation International	1	0.51
19	Brazilian Journal of Biology	1	0.52
20	Chinese Geographical Science	1	0.54
21	Chinese Journal of Applied Ecology	1	0.55
22	Conservation Letters	1	0.57
23	Ecohydrology & Hydrobiology	1	0.58
24	Ecological Modelling	1	0.59
25	Ecological Monographs	1	0.61
26	Ecology	1	0.62
27	Ecosystem Function in Heterogeneous Landscapes[1]	1	0.64
28	Environment and Development Economics	1	0.65
29	Environmental & Resource Economics	1	0.67
30	Environmental Modeling and Assessment	1	0.68
31	Frontiers in Ecology and the Environment	1	0.70
32	Journal of the American Water Resources Association	1	0.71
33	Landscape and Urban Planning	1	0.72
34	Marine and Freshwater Research	1	0.74
35	Marine Ecology Progress Series	1	0.75
36	Marine Policy	1	0.77

Table 2.3: Cont'd.

	Journal	No. of papers	Cum. Distrib.
37	Modsim 2007 Conference Proceedings[2]	1	0.78
38	Nature	1	0.80
39	Northwest Science	1	0.81
40	Philosophical Transactions of the Royal Society B	1	0.83
41	PLoS Biology	1	0.84
42	Proceedings of the National Academy of Sciences of the USA	1	0.86
43	River Research and Applications	1	0.87
44	Society and Natural Resources	1	0.88
45	South African Journal of Botany	1	0.90
46	Sustainable Tourism III	1	0.91
47	Theoretical Ecology	1	0.93
48	Trends in Ecology & Evolution	1	0.94
49	Tropical Conservation Science	1	0.96
50	Wetlands	1	0.97
51	World Watch	1	0.99
52	2010 International Conference on Mechanic Automation and Control Engineering[2]	1	1.00

[1]Book chapter – see Steinman & Denning 2005 below.
[2]Conference proceedings

2.10.3 List of papers

1. Abramovitz. J. (1998) Putting a value on nature's 'free' services. *World Watch*, **11**, 10–19.

2. Agostinho, A.A., Bonecker, C.C. & Gomes, L.C. (2009) Effects of water quantity on connectivity: the case of the upper Paraná River floodplain. *Ecohydrology and Hydrobiology*, **9**, 99–113.

3. Albrecht, M., Duelli, P., Mueller, C., Kleijn, D. & Schmid, B. (2007) The Swiss agri-environment scheme enhances pollinator diversity and plant reproductive success in nearby intensively managed farmland. *Journal of Applied Ecology*, **44**, 813–822.

4. Allen-Wardell, G., Bernhardt, P., Bitner, R., Burquez, A., Buchmann, S., Cane, J., Cox, P., Dalton, V., Feinsinger, P., Ingram, M., Inouye, D., Jones, C., Kennedy, K., Kevan, P., Koopowitz, H., Medellin, R., Medellin-Morales, S., Nabhan, G., Pavlik, B., Tepedino, V., Torchio, P. & Walker, S. (1998) The potential consequences of pollinator declines on the conservation of biodiversity and stability of food crop yields. *Conservation Biology*, **12**, 8–17.

5. Amorim, M.E. & De Marco, P. (2011) Pollination of *Byrsonima coccolobifolia*: short-

distance isolation and possible causes for low fruit production. *Brazilian Journal of Biology*, **71**, 709–717.

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CONNECTING STATEMENT

In Chapter 2, I examined the theory that links landscape connectivity with ecosystem service provision and completed a review of the primary literature in this area. I found a common assumption that the loss of landscape connectivity will have negative effects on ecosystem service provision but an overall lack of empirical evidence. My review also identified a number of open questions to advance our understanding of the effects of landscape connectivity on ecosystem service provision.

In Chapter 3, I begin to address some of these gaps by empirically measuring the effects of changing landscape connectivity on ecosystem service provision. By means of a field study in the agricultural landscapes of the Montérégie of southern Québec, I investigate how forest fragments and landscape connectivity affect the provision of multiple ecosystem services in adjacent soybean fields.

The specific research questions emerging from the review in Chapter 2 that are addressed in this chapter are: (1) What aspects of landscape connectivity most influence the provision of ecosystem services? (2) What ecosystem service categories or specific ecosystem services are most strongly influenced by landscape connectivity? and (3) Are there tradeoffs and synergies between different ecosystem services as landscape connectivity changes?

FOREST FRAGMENTS MODULATE THE PROVISION OF MULTIPLE ECOSYSTEM SERVICES

3

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3.1 SUMMARY

1. Agricultural landscapes provide the essential ecosystem service of food to growing human populations; at the same time, agricultural expansion to increase crop production results in forest fragmentation, degrading many other forest-dependent ecosystem services. However, surprisingly little is known about the role that forest fragments play in the provision of ecosystem services and how fragmentation affects landscape multi-functionality at scales relevant to land management decisions.

2. We measured the provision of six ecosystem services (crop production, pest regulation, decomposition, carbon storage, soil fertility, and water quality regulation) in soybean fields at different distances from adjacent forest fragments that differed in isolation and size across an agricultural landscape in Quebec, Canada.

3. We observed significant effects of distance-from-forest, fragment isolation, and fragment size on crop production, insect pest regulation, and decomposition.

4. Distance-from-forest and fragment isolation had unique influences on service provision for each of the ecosystem services we measured. For example, pest regulation was maximized adjacent to forest fragments, while crop production was maximized at intermediate distances-from-forest. As a consequence, landscape multi- functionality depended on landscape heterogeneity: the range of field and forest fragment types present.

5. We also observed strong negative and positive relationships between ecosystem services that were more prevalent at greater distances-from-forest.

6. *Synthesis and applications*. Our study is one of the first to empirically measure and model the effects of forest fragments on the simultaneous provision of multiple ecosystem services in an agro-ecosystem at the landscape and field scales relevant to land owners and managers. Our results demonstrate that forest fragments, irrespective of their size, can affect the provision of multiple ecosystem services in surrounding fields, but that this effect is mediated by fragment isolation across the landscape. Our results also suggest that managing habitat fragmentation and landscape structure will improve our ability to optimize ecosystem service provision and create multi-functional agricultural landscapes.

3.2 INTRODUCTION

Maintaining the provision of multiple ecosystem services in agricultural landscapes while increasing crop production is a critical global challenge (Jordan & Warner 2010; Sachs *et al.* 2010). Agricultural landscapes provide numerous goods and services important for human well-being, including food, fiber, water quality regulation, soil formation, flood regulation, and recreation (Zhang *et al.* 2007; Power 2010). Yet management of agricultural landscapes generally focuses on crop production and the expansion of agricultural lands (Saunders, Hobbs & Margules 1991; Robinson & Sutherland 2002), typically leading to the loss of other ecosystems and their associated biodiversity (Green *et al.* 2005; Phalan *et al.* 2011), ecosystem services, and ultimately, loss of landscape multi-functionality (*i.e.* the ability to provide multiple ecosystem services) (Robertson & Swinton 2005; Tscharntke *et al.* 2012a).

There is considerable indirect evidence that forest fragments within agricultural landscapes affect many ecosystem services: they are habitat for insect species that provide pollination and pest regulation services in adjacent fields (Tscharntke *et al.* 2005; Bianchi, Booij & Tscharntke 2006; Ricketts *et al.* 2008; Holzschuh, Steffan-Dewenter & Tscharntke 2010) and plant species that provide climate regulation and water purification services (Foley *et al.* 2005); they can alter microclimate conditions that affect crop production (Kort 1988); change dispersal patterns for fungi and soil organisms that affect decomposition (Plantegenest, Le May & Fabre 2007); and alter water and nutrient flow through landscapes (Brauman *et al.* 2007). However, we have little direct empirical data that demonstrates how forest fragments influence sets of ecosystem services simultaneously, the distances over which this influence might occur, or how fragment size and connectivity can alter these patterns and the relationships between different ecosystem services.

One result of the expansion of agricultural lands is forest loss and fragmentation (Saunders, Hobbs & Margules 1991; Tscharntke *et al.* 2005). This, in turn, causes loss of connectivity and biodiversity, changes to ecosystem function, and may alter the supply and distribution of ecosystem services (Tscharntke *et al.* 2012b). Theory predicts that changes to landscape structure and forest connectivity should affect ecosystem service provision through two main mechanisms (Mitchell, Bennett & Gonzalez 2013). First, forest fragmentation can directly influence the movement of organisms and matter important for service provision. For example, fragmentation can alter the ability of pollinators, crop pests, pest predators (Tscharntke, Rand & Bianchi 2005; Kremen *et al.* 2007), water, and nutrients (Brauman *et al.* 2007; Power 2010) to move across a landscape, which might affect pollination, pest regulation, or nutrient cycling, among other services. Second, habitat loss and disruption of connectivity between fragments affects demography, leading to changes in biodiversity, and ecosystem functions that contribute to service provision (Loreau, Mouquet & Gonzalez 2003; Leibold *et al.* 2004). However, while current theory predicts that forest fragment size and connectivity should influence ecosystem service provision, the actual effects of forest fragments on multiple ecosystem services have rarely been measured or modeled (Mitchell, Bennett & Gonzalez 2013), especially at the scale of fields and forests relevant to land managers. Effective management of agricultural landscapes for multiple ecosystem services requires measurements of changes in service provision as forest cover varies, and an understanding of the processes that underlie these patterns.

Here, we describe how forest fragments in an agricultural landscape affect the patterns of six above- and belowground ecosystem services: crop production, pest regulation, decomposition, carbon storage, soil fertility, and water quality regulation. We hypothesized that forest fragments would influence the provision of multiple ecosystem services, that these effects would decay with distance-from-forest, and that this influence would depend on fragment size and isolation, as well as the service itself. We also hypothesized that because the overall influence of fragments would covary with forest fragment size and isolation, the presence of fragments would affect the relationships (synergies and tradeoffs) between ecosystem services.

3.3 MATERIALS AND METHODS

3.3.1 Study Site and Sampling Design

We measured ecosystem service indicators in soybean fields of the Richelieu River watershed east of Montréal, Québec (Figure 3.5 in the Supporting Information) in 2010 (n = 15 fields) and 2011 (n = 19 fields). New fields were chosen each year because soybean is grown in rotation with corn in this region. Soybean fields were selected adjacent to forest fragments that spanned the gradients of fragment size (range 0.5 to 4 880 ha; mean 530 ha) and fragment isolation present in this landscape. Using the Québec provincial Système d'information écoforestière dataset, we quantified forest fragment size, and calculated fragment isolation using proximity index for each fragment in Fragstats 3.3. Proximity index (PI) is the sum of fragment areas divided by the nearest edge-to-edge distance squared between each focal fragment and neighboring fragments within a specified distance. We used 2000 m, as it represents an intermediate scale to which arthropod groups respond (Chaplin-Kramer *et al.* 2011) and is larger than most fields in our system. Higher PI values indicate lower fragment isolation (*i.e.* a more connected forest landscape).

Within each soybean field, a transect perpendicular to the adjacent forest fragment edge was established. Agricultural fields in Québec follow the seigneurial system of land distribution, where fields are arranged in long narrow strips. This meant transects followed a gradient of distance-from-forest while other field and management variables were kept consistent. We expected that (1) forest fragments would affect belowground services at smaller distances than aboveground services due to differences in dispersal distances for above- and belowground organisms (van der Putten *et al.* 2001), and that (2) the effects of forest fragments on ecosystem services would decay with distance (*i.e.* the majority of variation in service provision would occur at small distances-to-forest). Therefore, belowground services were measured at 0, 5, 10 and 25 m from forest in 2010 and 0, 10, 25, 50, and 100 m in 2011. Aboveground services were measured at 0, 50, 100, 200, and 500 m from forest in both years. Additionally, the aboveground service of crop production was measured at 10 and 25 m in both years.

3.3.2 Ecosystem Service Indicators

We used eight indicators to quantify our six ecosystem services (Table 3.1). Each indicator was chosen because it 1) was expected to vary over the spatial scale of our transects, 2) was feasible to quantify during a single growing season, 3) matched metrics already used in the region (*e.g.* CRAAQ 2010; Raudsepp-Hearne, Peterson & Bennett 2010), and 4) was relevant to local landowners. We focused on using indicators that reflect some of the multiple processes underlying each ecosystem service; therefore, some services had multiple indicators. For example, we measured both litter and cotton decomposition to quantify total decomposition from both soil macro- and microorganisms. In addition, we chose to interpret each indicator only for the service each most strongly determined, although some indicators are involved in multiple services. For example, soil phosphorus saturation and nitrogen both contribute to water quality and soil fertility. However, in our system, water quality corresponds most strongly with soil P (Bochove *et al.* 2007), and soil fertility with soil N. Finally, some of our indicators correspond positively with service provision (*i.e.* soybean yield), others negatively (*i.e.* aphid numbers, herbivory). We present our results in terms of service provision, therefore in some cases, lower values of an indicator signal higher service provision.

Table 3.1: Ecosystem services and indicators analyzed.

Ecosystem service	Indicator	Relationship between indicator and service provision
Crop production		
Soybean yield	Kilograms of soybeans hectare^{-1}	Positive
Pest regulation		
Aphid regulation	Soybean aphids plant^{-1}	Negative
Herbivory regulation	Proportion of leaves damaged by insects	Negative
Decomposition		
Cotton decomposition	Proportion of buried cotton fabric decomposed	Positive
Litter decomposition	Proportion of buried litter decomposed	Positive
Carbon storage		
Soil organic matter	Percent carbon in soil by weight	Positive
Soil fertility		
Soil nitrogen	Percent nitrogen in soil by weight	Positive
Water quality regulation		
Soil phosphorus saturation	Phosphorus-sorption saturation (percent P binding sites occupied)	Negative

3.3.3 *Aboveground Ecosystem Service Indicators*

Crop Production: Soybean yield was measured as soybean dry weight. At each distance-from-forest, we collected soybean plants from two crop rows along a distance of 0.5 m just before harvest (22-24 September 2010; 27-30 September 2011). Plants were dried at 50°C for 48 hours, mechanically threshed, and the separated soybeans were then weighed. Yield (kg ha^{-1}) was calculated based on the area of field sampled.

Pest Regulation: We measured pest regulation through aphid abundance and herbivory levels. This definition incorporates both ecosystem services (*i.e.* predation or parasitism) and disservices (*i.e.* pest pressure or colonization), that may respond to forest fragments differently and at different scales, and measures net effects, the variable of greatest interest to farmers. Soybean aphids are an important pest of soybean crops in Québec, and economically harmful levels (> 250 aphids $plant^{-1}$) have increased pesticide use (Ragsdale *et al.* 2011). Aphid abundances were measured biweekly by counting all live individuals on the aboveground parts of five soybean plants at each distance-from-forest (Gardiner *et al.* 2009), twice in 2010 (27-30 July and 9-13 August) and three times in 2011 (19-22 July, 1-5 August, and 17-20 August). These sampling periods were timed to coincide with regional aphid population peaks (CRAAQ 2011). Because we used commercial soybean fields, destructive plant sampling was not possible. Instead, we estimated plant size by recording total leaf number (Sivakumar 1978), and insect herbivory by counting the number of leaves with obvious insect damage (*i.e.* holes).

3.3.4 *Belowground Ecosystem Service Indicators*

Water quality regulation, carbon storage and soil fertility were estimated using soil properties. At each distance-from-forest, a composite sample of five soil cores, 2 cm each in diameter and 0-15 cm deep, was collected in the middle of each growing season (7-12 July 2010; 4-16 July 2011). Each sample was air-dried for one week, ground to pass through a 1 mm mesh, and dried at 50°C for 48 hours.

Water Quality Regulation: We quantified soil phosphorus saturation index (*i.e.* the ratio of soil P to Al), which provides a measure of the ability of a soil to both release P and bind additional P

(Kleinman & Sharpley 2002). As the index increases, the potential for excess P to enter runoff and contribute to eutrophication rises; for our region, values > 12 % indicate excess P (Beauchemin & Simard 2000). We calculated P saturation using Mehlich-3 extractions: 2.5 g of soil and 25 ml of Mehlich-3 solution were shaken for 5 minutes, filtered and then analyzed colourimetrically for P and spectrophotometrically for Al.

Carbon Storage & Soil Fertility: Agricultural soils as carbon stores are important regulators of climate change, and soil carbon is vital to soil structure and fertility and is therefore often used as a proxy for soil ecosystem services (Bommarco, Kleijn & Potts 2013). Soil N is also critical for crop growth in our region, especially for corn (CPQ 2000), which in our region is grown in an annual rotation with soybean and requires high N input. Soil C and N were measured as percentage by weight using an elemental auto-analyzer on 60 μg of soil.

Decomposition: We quantified decomposition by measuring leaf litter decomposition and soil microbial/fungal activity, both important for decomposing organic matter in soils (Barrios 2007). For litter decomposition, 5 g of air-dried *Acer saccharum* Marsh. (sugar maple) litter was placed in 1 mm mesh 10 × 10 cm nylon bags (Harmon, Nadelhoffer & Blair 1999). Each bag had eight 5 mm holes to allow entry of soil macrofauna (Smith *et al.* 2009). Three litterbags were buried at a 45° angle and 15 cm depth at each distance-from-forest for approximately three months (24 June-23 September 2010; 22 June- 28 September 2011). Prior to soybean harvest and field tillage, litterbags were collected and frozen until processed. To process, remnant litter was removed from each bag, dried overnight at 55°C, and then ashed at 360°C to obtain the ash-free dry mass and correct for soil contamination (Smith *et al.* 2009). The percentage mass lost was calculated for each bag, representing total decomposition (physical breakdown and mineralization). Soil microbial activity was estimated using cotton fabric squares (Tiegs *et al.* 2007). Four 5 × 5 cm squares of unbleached, undyed cotton fabric were weighed and then buried vertically in the soil at 10 cm depth at each distance-from-forest. The fabric remained in the soil for approximately 3 weeks (23 June-16 July 2010; 27 June-22 July 2011). Each square was then removed and frozen until processing. Squares were hand-washed of all soil, air-dried, and weighed to determine mass loss from microbial/fungal decomposition.

3.3.5 *Statistical Modeling*

We used generalized additive mixed models (GAMMs; Wood 2006) to model each ecosystem service indicator as a function of distance-from-forest, forest fragment isolation (PI), and fragment size. We used GAMMs as opposed to generalized linear models as we had no *a priori* expectation that the relationships would be linear. GAMMs were fit using the '*gamm*' function in the 'mgcv' package of R version 3.0.2. We used cubic regression spline smoothers with 'shrinkage' for each explanatory variable in the GAMMs, with field as a random factor. 'Shrinkage' is a method to minimize the degree of smoothing in the model for each explanatory variable, reducing each relationship to a linear function where possible (Wood 2006). Forest fragment isolation and size were log_{10} transformed in every model. We analyzed data from each year separately as attempts to include year as a random or repeated measure prevented model convergence. For aphid abundance and herbivory, where multiple censuses were performed each year, we fit repeated measures GAMMs for each year separately. For these models, each census was nested within field as a random factor and we modeled compound symmetrical correlation between the censuses nested within distance-from-forest within field; other correlation types failed to improve model fit as evaluated using AICc values. For analyses of aphid abundance we also included plant size (*i.e.* number of leaves) as a covariate. For each ecosystem service indicator the appropriate distribution type (*i.e.* Gaussian, negative binomial, or binomial) and link function were used (see Table 3.2 in Supporting Information). Standard diagnostic plots were inspected to evaluate model fit.

To evaluate relationships between ecosystem service indicators at distances both relatively near- and far-from-forest fragments, we calculated Spearman-rank correlations between our indicators at each distance-from-forest. We split transects in half to define 'near' and 'far' locations: aboveground, values from 0, 50, and 100 m were considered near-to-forest, while 200 and 500 m were far; belowground, 0, 10, and 25 m were defined as near, and 50 and 100 m as far. Each indicator was transformed so that higher values corresponded to higher values of service provision (*e.g.* decreased herbivory or decreased soil phosphorus saturation equaled increased provision of pest regulation or water quality regulation, respectively); this same data was also used to evaluate landscape multi-functionality. We pooled data from 2010 and 2011 for the

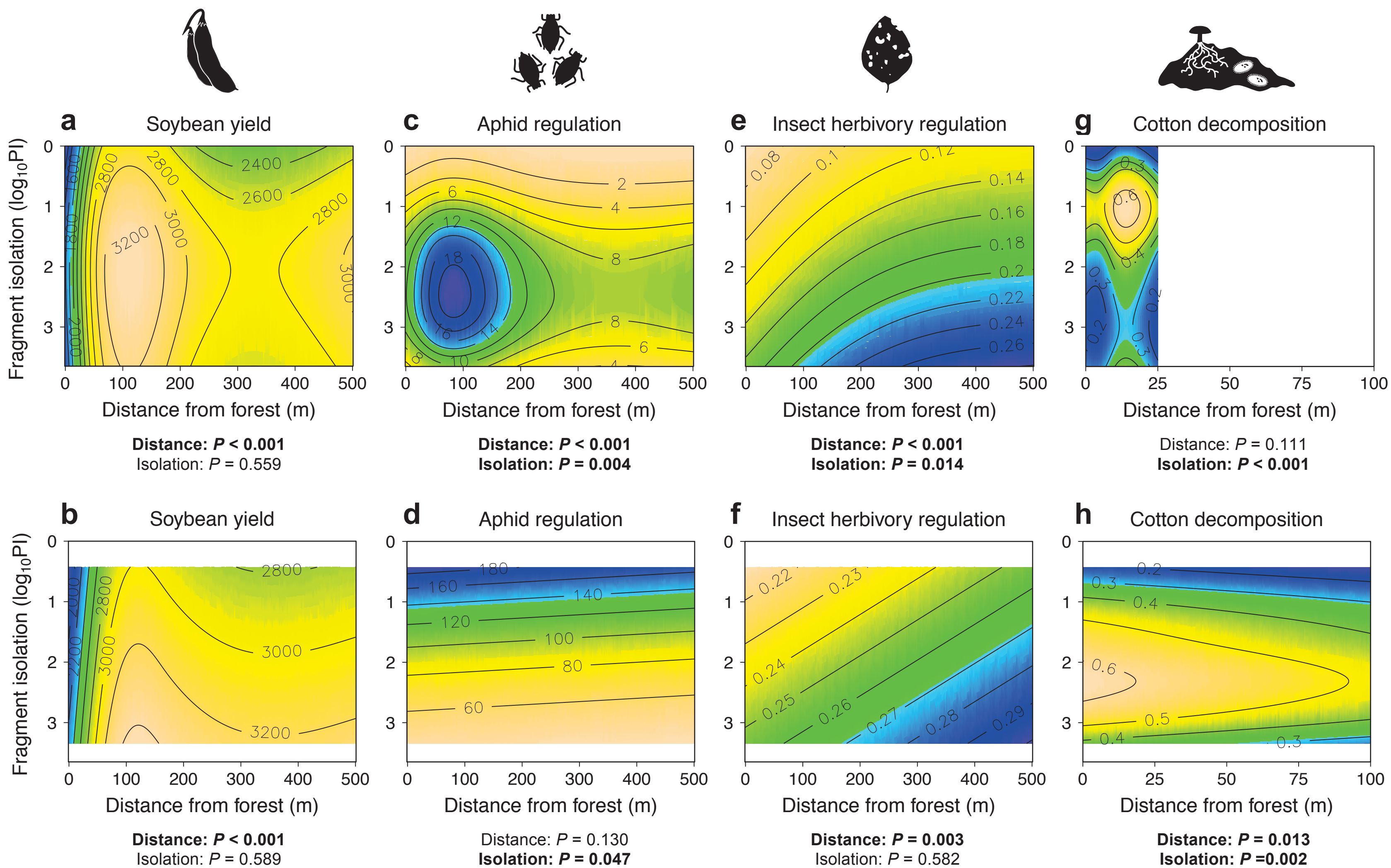
Spearman-rank and multi-functionality analyses, except for aphid abundance and herbivory as these showed distinct patterns between years. Despite this, relationships between these two indicators and all other service indicators were generally consistent between years. To evaluate correlations between belowground and aboveground service indicators, we used data from 2011 where measurements of both sets of services overlapped (*i.e.* 0 m for near- and 100 m for far-from-forest). Correlation values were tested as being different than zero (Spearman's *rho* $\alpha < 0.05$).

As a measure of landscape multi-functionality we calculated the inverse Simpson index in R using the 'vegan' package at each distance-from-forest for above- and belowground service indicators separately. Using the 'nlme' package in R, polynomial relationships for distance-from-forest, and field as a random factor, we fit nonlinear mixed-effects models to determine the effect of distance-from-forest, forest fragment isolation category (*i.e.* log_{10}(PI) < 1.16; 1.16 < log_{10}(PI) < 2.31; log_{10}(PI) > 2.31), and their interaction on the inverse Simpson index values. The three isolation categories equally divided the range of PI values present, and were used to simplify the presentation of the multi-functionality results. The appropriate n^{th}-order distance-from-forest polynomial term in each model was determined using AICc values.

3.4 RESULTS

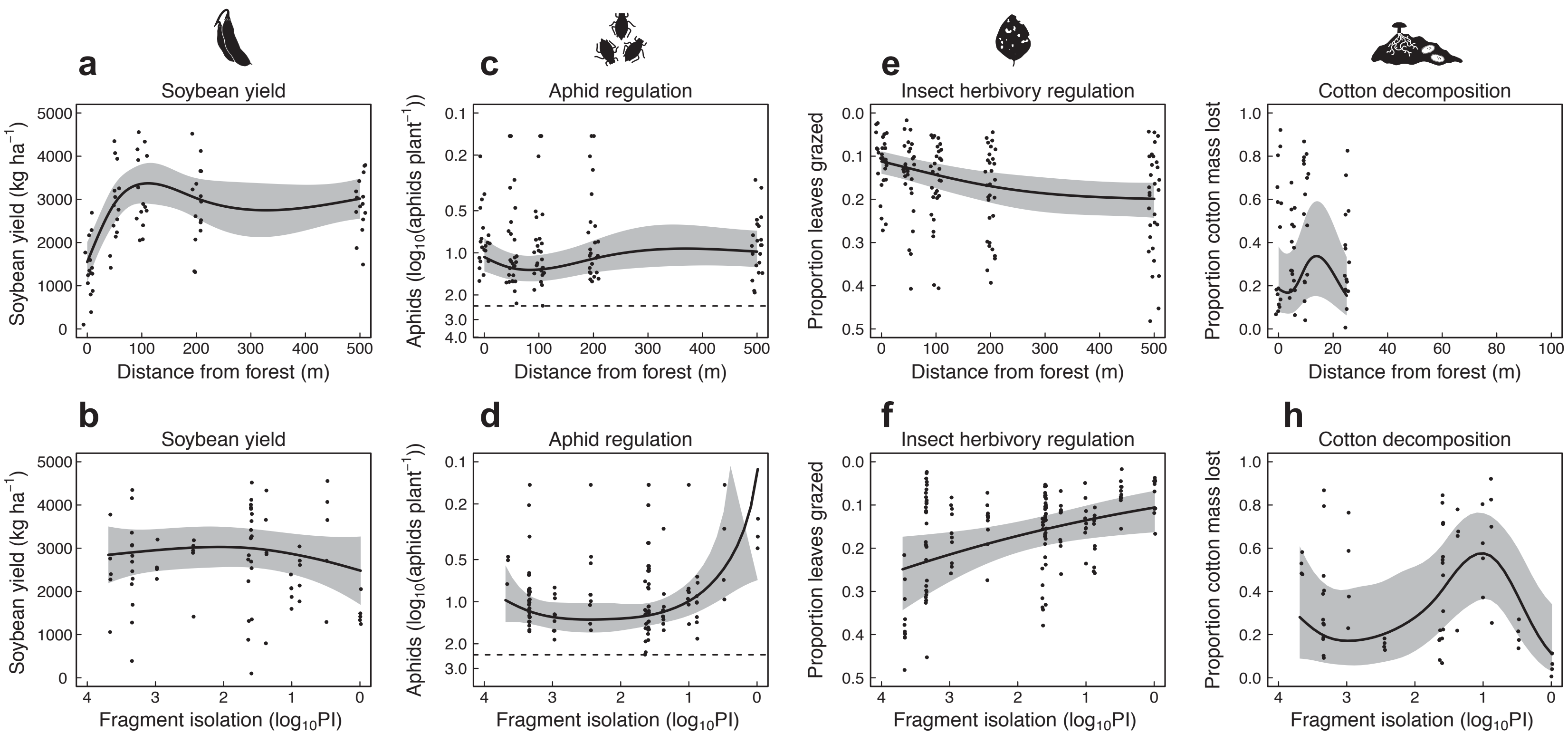
3.4.1 Effects of Distance-from-Forest

Distance-from-forest had strong effects on soybean yield, soybean aphids, and insect herbivory in adjacent soybean fields (see Table 3.2 & Figure 3.6 in the Supporting Information). Soybean yield peaked approximately 100 m from forest in both years (Figure 3.1ab), and was on average 117 % and 55 % greater at 100 m than directly adjacent to forest in 2010 (Figure 3.2a) and 2011, respectively. Aphid patterns were opposite those of soybean yield in 2010, with 75 % and 117 % less regulation at 100 m than at 0 m and 500 m, respectively, although aphid numbers in 2010 were very low and patchy, which could have affected our analysis (Figures 3.1c, 3.2c). Aphid numbers were on average 12 times higher in 2011, and the relationship between aphid numbers and distance-from-forest disappeared (Figure 3.1d); however, a pattern similar to 2010 was



a
Soybean yield
Distance: P < 0.001
Isolation: P = 0.559
b
Soybean yield
Distance: P < 0.001
Isolation: P = 0.589
c
Aphid regulation
Distance: P < 0.001
Isolation: P = 0.004
d
Aphid regulation
Distance: P = 0.130
Isolation: P = 0.047
e
Insect herbivory regulation
Distance: P < 0.001
Isolation: P = 0.014
f
Insect herbivory regulation
Distance: P = 0.003
Isolation: P = 0.582
g
Cotton decomposition
Distance: P = 0.111
Isolation: P < 0.001
h
Cotton decomposition
Distance: P = 0.013
Isolation: P =0.002
Fragment isolation (log10PI)
Distance from forest (m)

Figure 3.1: Relationships between forest fragment isolation and distance-from-forest for ecosystem service indicators in 2010 and 2011. (**a**,**b**) Soybean yield (kg ha^{-1}), (**c**,**d**) soybean aphid regulation (aphids $plant^{-1}$), (**e**,**f**) insect herbivory regulation (proportion of leaves grazed), (**g**,**h**) cotton fabric decomposition (proportion of cotton mass lost). We show mean relationships (*colored surfaces* and *contours*). From generalized additive mixed models with other explanatory variables (*i.e.* fragment size) kept at mean levels. Warmer colors (*orange and yellow*) represent higher levels of ecosystem service provision, cooler colors (*blue and purple*) lower levels. The y-axis is reverse in all graphs to run from connected forest fragments ($log_{10}PI = 4$) to isolated fragments ($log_{10}PI = 0$). *P*-values are from generalized additive mixed models. Field $n = 15$ in 2010 and $n = 19$ in 2011.



a
Soybean yield
Soybean yield (kg ha^{-1})
Distance from forest (m)
c
Aphid regulation
Aphids (log$_{10}$(aphids plant^{-1}))
Distance from forest (m)
e
Insect herbivory regulation
Proportion leaves grazed
Distance from forest (m)
Cotton decomposition
Proportion cotton mass lost
Distance from forest (m)
b
Soybean yield
Soybean yield (kg ha^{-1})
Fragment isolation (log$_{10}$PI)
d
Aphid regulation
Aphids (log$_{10}$(aphids plant^{-1}))
Fragment isolation (log$_{10}$PI)
f
Insect herbivory regulation
Proportion leaves grazed
Fragment isolation (log$_{10}$PI)
h
Cotton decomposition
Proportion cotton mass lost
Fragment isolation (log$_{10}$PI)

Figure 3.2: Examples of bivariate relationships between distance-from-forest or fragment isolation and ecosystem service indicators in 2010. (**a**,**b**) Soybean yield (kg ha^{-1}); (**c**,**d**) aphid regulation (aphids $plant^{-1}$); (**e**,**f**) insect herbivory regulation (proportion of leaves grazed); (**g**,**h**) cotton fabric decomposition (proportion of cotton mass lost). We show mean relationships (*black lines*) and 95 % confidence intervals (*grey areas*) from generalized additive mixed models with other model explanatory variables (*i.e.* fragment size) kept at mean levels. Y-axes are reversed for aphid and herbivory regulation (**c**-**f**) so that values higher on the axis represent higher levels of ecosystem service provision. The dashed horizontal line in (**c**) and (**d**) is the threshold at which a control action must be taken to prevent economic damage to soybeans from soybean aphids (250 aphids $plant^{-1}$). Note the log_{10} y-axes in (**c**) and (**d**). *P*-values are for the effect of distance-from-forest; n = 15 fields. Additional plots for other services, years, and for fragment size can be found in the Supporting Information.

present at the end of 2011 (see Figure 3.7 in the Supporting Information). Herbivory regulation was higher close to forest in both years (Figure 3.1ef), although herbivory was on average 38 % higher in 2011. Herbivory regulation was 77 % and 19 % lower at 500 m than at 0 m in 2010 (Figure 3.2e) and 2011, respectively. Belowground, distance-from-forest only affected decomposition in 2011, although the belowground transect in 2010 only spanned 25 m. In 2011 there was 20 % less cotton decomposition at 100 m than at 0 m from forest (Figure 3.1h). Relationships between distance-from-forest and other belowground service indicators were not statistically significant (see Table 3.2 in the Supporting Information).

3.4.2 *Effects of Forest Fragment Isolation*

Fragment isolation affected aphids, herbivory, and cotton decomposition (see Figure 3.8 in the Supporting Information). Average soybean yield was greater next to connected compared to isolated fragments by 15 % in both 2010 and 2011 (Figures 3.1ab, 3.2b), but these relationships were not statistically significant (see Table 3.2 in the Supporting Information). In 2010, aphid regulation increased with fragment isolation, and was 86 % higher in fields adjacent to the most isolated fragments (Figures 3.1c, 3.2d). A different pattern was observed in 2011, with aphid regulation on average 4.2 times lower in fields next to isolated fragments (Figure 3.1d). Herbivory regulation increased with fragment isolation (Figures 3.1ef, 3.2f); in 2010 it was 58 % greater in fields next to isolated fragments and 16 % greater in 2011. Cotton decomposition was greatest at intermediate levels of forest fragment isolation, but the position of this peak shifted between years (Figures 3.1gh, 3.2h). In both years, cotton decomposition was lowest in fields adjacent to the most isolated fragments (81 % less in 2010 and 72 % in 2011). Other relationships between ecosystem service indicators and forest fragment isolation were not statistically significant (see Table 3.2 in the Supporting Information).

3.4.3 *Effects of Forest Fragment Size on Ecosystem Service Indicators*

Only three indicators showed a relationship with forest fragment size: a negative relationship with aphid regulation in 2011, a concave-up relationship with cotton decomposition in 2010, and a concave-down relationship with soil nitrogen in 2010 (see Table 3.2, Figure 3.9 in the Supporting Information).

3.4.4 Effects of Forest Fragments on Ecosystem Service Indicator Relationships

We found both positive and negative correlations between service indicators, and typically the strength of these relationships varied with distance-from-forest (Figure 3.3; Figure 3.10 in the Supporting Information). Strong positive correlations were limited to belowground service indicators and varied in fields with distance-from-forest. Only the relationship between soil carbon and nitrogen was consistently positive. Negative correlations between indicators were more frequent far from the forest; only the tradeoffs between aphid regulation-soybean yield and 2011 herbivory regulation-soybean yield were statistically significant near-to-forest. While the strength of service indicator relationships varied with distance-from-forest, we did not observe any synergies changing to tradeoffs or vice versa as distance-from-forest varied.

3.4.5 Effects of Forest Fragments on Landscape Multi-Functionality

There was no single combination of forest fragment isolation and distance-from-forest where all above- or belowground service indicators were maximized as measured using the inverse Simpson index (Figure 3.4). Aboveground, multi-functionality was greatest directly adjacent to forest fragments and decreased significantly over 100 m, except for isolated forest fragments (see Figure 3.11 in the Supporting Information). There was little variation in belowground multi-functionality with distance-from-forest or fragment isolation, although connected fragments at 25 and 50 m did have slightly higher values.

3.5 DISCUSSION

We provide clear empirical evidence that forest fragments influence the provision of multiple ecosystem service indicators in adjacent agricultural fields. While some of these effects have been observed or modeled for a few services (Ricketts 2004; Bodin *et al.* 2006; Farwig *et al.* 2009), our results expand on these studies by simultaneously considering the effects of distance-from-forest, fragment isolation, and fragment size on multiple above- and belowground services.

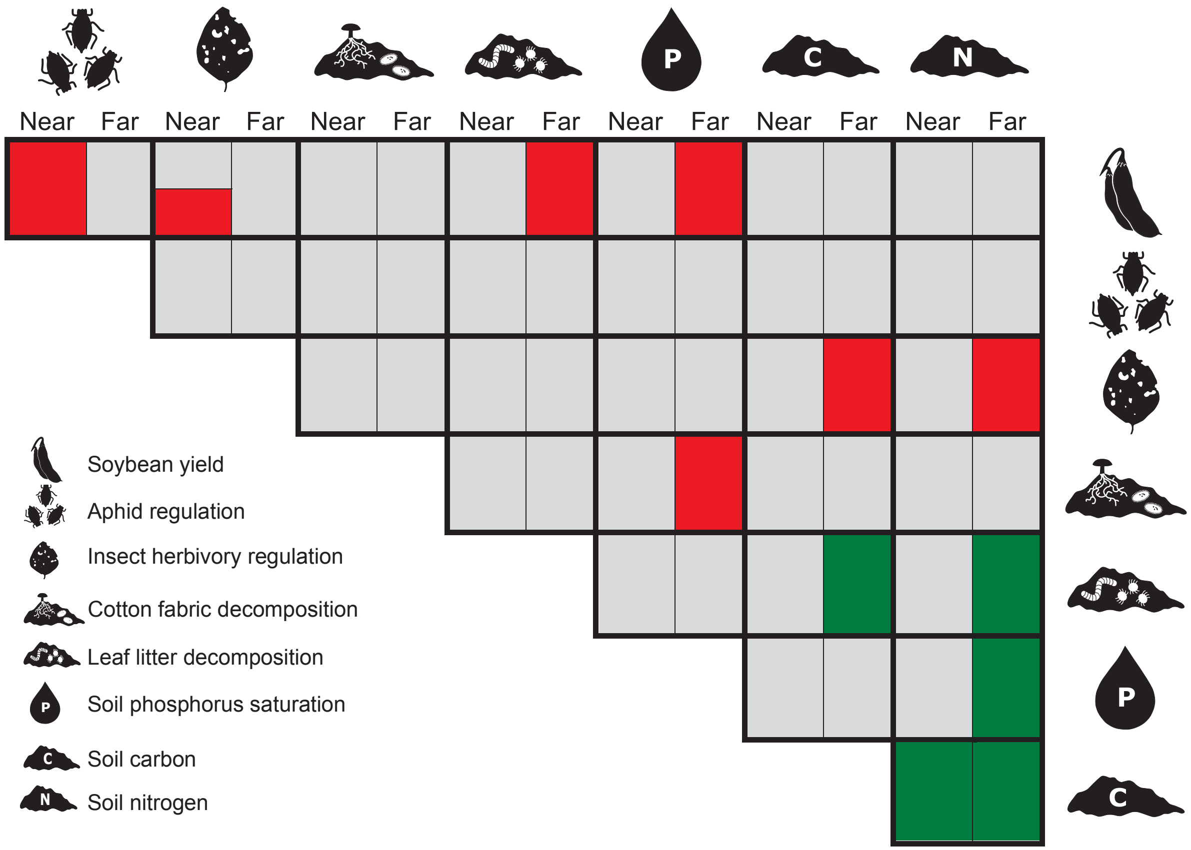


Figure 3.3: Effects of distance-from-forest on pair-wise Spearman-rank relationships between ecosystem service indicators. Green are positive relationships and red negative relationships, evaluated using Spearman's *rho* at an $\alpha < 0.05$ level. Grey reflects relationships not significantly different than zero. For each pair-wise relationship, squares on the left represent near-to-forest and those on the right far-from-forest relationships (*i.e.* aboveground service relationships: 0-100 vs. 200-500 m, belowground service relationship: 0-25 vs. 50-100 m, above-belowground service relationships: 0 vs. 100 m). For the near-to-forest relationship between insect herbivory and regulation and soybean yield, a negative relationships was only present in 2011.

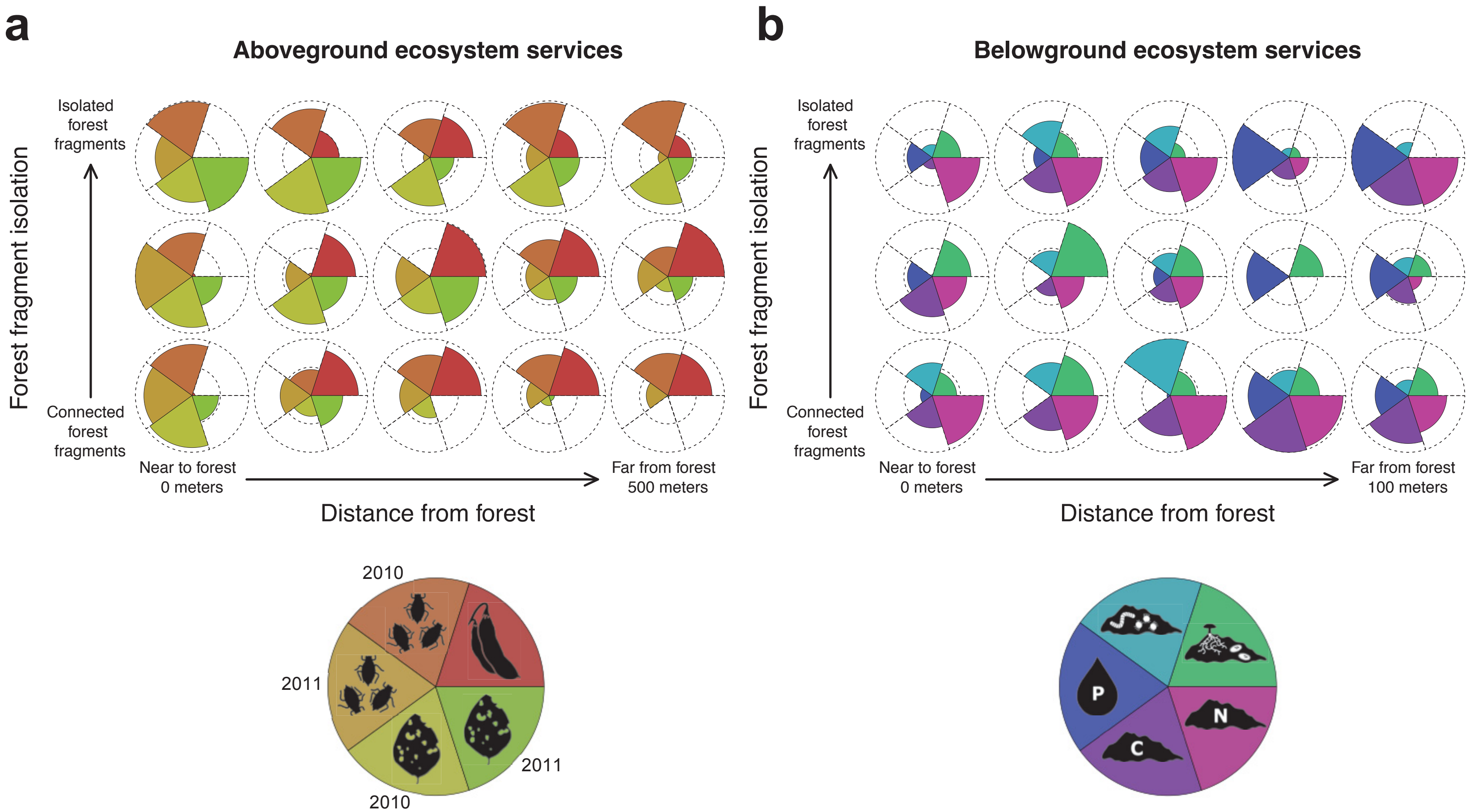

a
Aboveground ecosystem services
Isolated forest fragments
Forest fragment isolation
Connected forest fragments
Near to forest 0 meters
Far from forest 500 meters
Distance from forest
2010
2011
2011
2010
b
Belowground ecosystem services
Isolated forest fragments
Forest fragment isolation
Connected forest fragments
Near to forest 0 meters
Far from forest 100 meters
Distance from forest
P
N
C

Figure 3.4: Quantification of multiple ecosystem service indicators with respect to distance-from-forest and forest fragment isolation. The lengths of the petals in the flower diagrams represent ecosystem service indicator levels for each distance-from-forest and forest fragment isolation category (**a**) aboveground and (**b**) belowground. Ecosystem service indicator values were transformed to range between 0 and 1, so for each service indicator the location with the highest value equals 1. Increased provision of each ecosystem service (see Table 3.1) is indicated by larger values. Outer dashed circles represent the maximum values of 1, and inner dashed circles the values of 0.5.

3.5.1 *Effects of Forest Fragments on Ecosystem Services*

Each ecosystem service was maximized at a unique distance-from-forest and level of fragment isolation (Figures 3.1, 3.2). Key mechanisms for these patterns likely involve the effects of fragments on the movement of different service-providing organisms, matter, or energy (Mitchell, Bennett & Gonzalez 2013). For example, decreased crop production within 50 m of forest fragments was likely a consequence of competition for water and light from forest plants (Kort 1988), although soil compaction from farm machinery, which is often concentrated at field margins (Hamza & Anderson 2005), might have also contributed. The peak in soybean yield we observed between 75-200 m from forest could have resulted from decreased competition in combination with increased pollination near fragments (Ricketts *et al.* 2008); soybean is primarily self-pollinated, but insect pollination can increase yield (Chiari *et al.* 2005).

While crop production was affected primarily by distance-from-forest, aphid regulation appeared more tightly tied to forest fragment isolation, with specific effects dependent on overall aphid numbers. Aphid populations in North America undergo regular outbreak cycles, with long-distance dispersal occurring primarily via atmospheric movements (Ragsdale *et al.* 2011). Forest fragments can interrupt this long-distance dispersal and aphid landing is often concentrated next to movement barriers such as forest fragments (Irwin, Kampmeier & Weisser 2007). At the same time, aphid populations are affected by increased predator pressure near forest fragments (Chaplin-Kramer *et al.* 2011), and by resource levels (*i.e.* soybean growth). In 2010, aphid numbers were relatively low, and the peak at 100 m from forest was likely due to a combination of increased aphid dispersal, increased soybean growth, and relief from increased aphid predation closer to forest fragments. In 2011, aphid numbers were high enough that we suspect their short-distance dispersal within fields overwhelmed any effects of forest fragments on aphid landing patterns or soybean growth. Instead, we saw lower aphid numbers in more connected landscapes, suggesting that landscape connectivity benefited aphid predators (Thies, Roschewitz & Tscharntke 2005; Tscharntke *et al.* 2005).

Interestingly, herbivory regulation was greatest close to isolated forest fragments. While forest fragments in our system most likely provided habitat for insect predators that control soybean pests, forests and increased forest connectivity could have facilitated herbivore dispersal (Bianchi, Booij & Tscharntke 2006), especially far-from-forest where predator pressure is often reduced. Finally, for cotton decomposition, we observed the highest rates of decomposition near forest fragments with intermediate isolation. Forest fragments can act both as sources (Edman *et al.* 2004) and landscape barriers (Plantegenest, Le May & Fabre 2007) to the airborne dispersal of fungi and microorganisms, leading to increased decomposition near forest fragments. Why fragments with intermediate isolation might show increased decomposition remains unclear.

3.5.2 Ecosystem service tradeoffs and synergies.

Our results show that changes in field size and distance-from-forest could affect the presence and strength of tradeoffs between services in this system. While ecosystem service tradeoffs and synergies have been quantified elsewhere (Raudsepp-Hearne, Peterson & Bennett 2010; Gamfeldt *et al.* 2013), we currently know little about what drives these relationships (Bommarco, Kleijn & Potts 2013) or how they change across scales relevant to management. This lack of knowledge limits our ability to manage landscapes for multiple services, especially if tradeoffs identified at one scale (*i.e.* the watershed), are not present at the scale that the landscape is managed (*i.e.* the field).

We observed both positive (indicative of synergy) and negative (indicative of trade-off) relationships between service indicators whose strength changed with distance-from-forest (Figure 3.3; Bennett, Peterson & Gordon 2009). Strong positive or negative relationships were more common far from forest, suggesting that forest fragments can moderate ecosystem service relationships. This could occur through changes in environmental conditions, or if fragments affect the spatial subsidy of organisms to fields. For example, strong tradeoffs between soil carbon and herbivory and between soil nitrogen and herbivory, may not be present near forests because increased predator diversity and abundance decrease insect pest populations (Tscharntke, Rand & Bianchi 2005; Bianchi, Booij & Tscharntke 2006), weakening the link between plant quality and pest performance. Similarly, strong synergies between decomposition and soil carbon or soil nitrogen may be weaker near forest fragments because other drivers of decomposition, including temperature and moisture (Prescott 2010), may vary to a greater degree and obscure relationships between decomposition and soil nutrients.

3.5.3 *Effects of distance-from-forest and fragment isolation on multiple ecosystem services*

We observed that different ecosystem service indicators were maximized at different distances from forest fragments, and found no evidence that multi-functionality is maximized at a single distance-from-forest, degree of fragment isolation, or combination of the two (Figure 3.4). While the importance of species diversity for multiple ecosystem functions and services is now the focus of investigation (Isbell *et al.* 2011; Gamfeldt *et al.* 2013), landscape structure and heterogeneity have not been explored to the same extent (Symstad *et al.* 2003; Fahrig *et al.* 2011). Our results show that both distance-from-forest and forest fragment isolation are likely to be important for service provision. Ecological theory predicts this, because the key species and processes that mediate each service are expected to vary at different scales (Kremen 2005). Landscape heterogeneity may therefore be necessary to maintain biodiversity (Fahrig *et al.* 2011) and create multifunctional agricultural landscapes, but the combination and amount of different landscape elements is likely to depend on the agro-ecosystem in question, the biodiversity and ecosystem processes that it encompasses, and the needs and preferences of the landowners and policy-makers that manage it.

The distinct patterns of ecosystem service indicators we observed within fields, across forest fragments, and between years, highlight the difficulties of designing agricultural landscapes to optimize ecosystem service provision. Any change in landscape structure or heterogeneity is likely to have varying or even opposing effects on different services (de Groot *et al.* 2010). For example, clearing forests for fields may increase crop production but also jeopardize other functions upon which crop production relies, such as pest regulation or pollination (Power 2010). The effects of changing landscape structure or heterogeneity are also likely to depend on the spatial scale considered. For instance, forest fragments might act as movement barriers and increase aphid numbers in nearby fields, but simultaneously sustain aphid predators and aphid control across the wider landscape. Effective management for pest regulation may therefore require cross-scale cooperation between landowners and an understanding of the patterns of service provision at different scales (Bommarco, Kleijn & Potts 2013). Our results suggest that distance-from-forest (*i.e.* field size) and the configuration of forest fragments may be managed to influence landscape multi-functionality; however, improving the provision of all services is likely to be difficult. There is a pressing need to strongly link landscape structure at different scales with the provision of sets of ecosystem services and understand how landscape structure affects the species and processes underlying these patterns.

3.5.4 Conclusions

Agricultural expansion often leaves landscapes composed of small, isolated forest fragments while fields grow in size and connectivity (Robinson & Sutherland 2002). As global food demand increases, pressure to clear natural habitat and increase agricultural area will grow. Our results demonstrate that landscape structure, and specifically the characteristics of forest fragments, can affect multiple ecosystem services, and that these effects are mediated both by distance-from-forest in adjacent fields and forest fragment isolation across the landscape. Managing landscape structure to control forest fragment connectivity may therefore be a more effective tool to manage agricultural landscapes for multiple ecosystem services than simply limiting further forest loss. At the same time, the effects of distance-from-forest and fragment isolation on different ecosystem services vary widely. This emphasizes the importance of incorporating a variety of forest fragment types across agricultural landscapes to maximize multi-functionality. Knowledge of the effects of landscape structure and forest fragmentation on agricultural ecosystem services, and an enhanced understanding of how the movement of key organisms and matter affect service provision, has the potential to enhance the design and management of multi-functional agricultural landscapes in the future.

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3.8 SUPPORTING INFORMATION

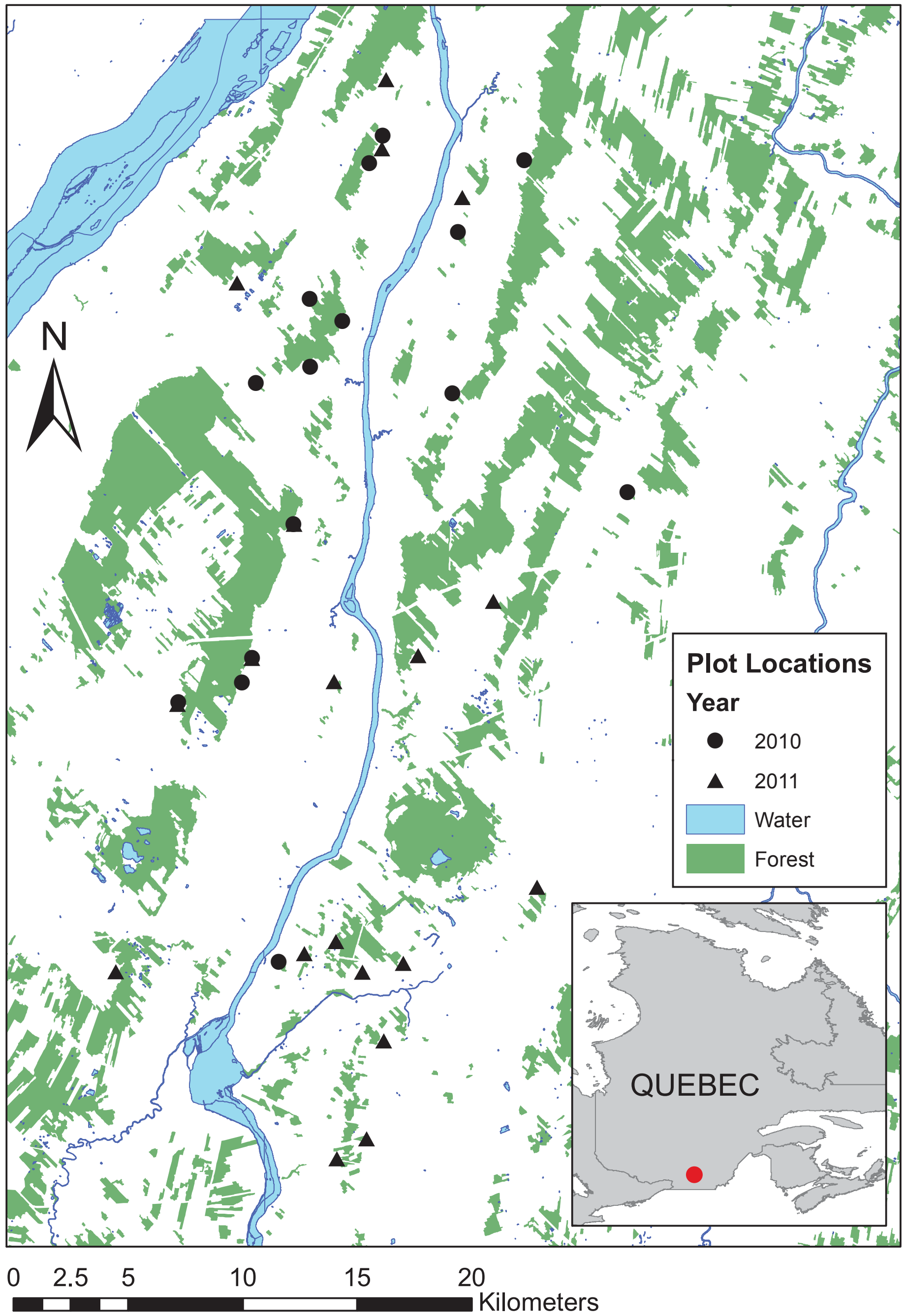


Figure 3.5: Location of field sampling locations in 2010 (circles; n = 15) and 2011 (triangles; n = 19). The region sampled lies in southern Québec (see inset map), just east of the city of Montréal, within the Richelieu River watershed. Each field was located adjacent to a forest fragment (denoted in green), although some fragments are too small to be visible on the figure. Three of the fields in 2011 were directly adjacent to fields selected in 2010, therefore their location markers overlap.

Table 3.2: **Results from generalized additive mixed models.** Each model fits the effect of distance-from-forest, forest fragment isolation, and forest fragment size on ecosystem service metrics for 2010 (n = 15 fields) and 2011 (n = 19 fields). Degrees of freedom (df) for each variable refer to the complexity of the additive curve; 1.00 denotes a straight line. For each variable, the appropriate data distribution was used: Gaussian for soybean yield, negative binomial corrected for overdispersion for soybean aphids; and binomial corrected for overdispersion for all other variables.

Ecosystem service variable	Year	Distance from Forest[1]		Forest Patch Isolation[1]		Forest Patch Size[1]	
		df	***F***	**df**	***F***	**df**	***F***
Crop production							
Soybean yield	2010	**3.51**	**21.86*****	1.72	0.54	1.00	0.17
	2011	**3.28**	**15.34*****	1.00	0.30	2.16	1.59
Pest regulation[2]							
Soybean aphids	2010	**3.23**	**8.62*****	**2.75**	**4.96****	1.00	0.47
	2011	1.00	2.31	**1.00**	**3.99***	**1.00**	**5.76***
Insect herbivory	2010	**2.06**	**22.68*****	**1.00**	**6.15***	1.00	0.12
	2011	**1.00**	**9.04****	1.00	0.30	1.00	0.62
Decomposition							
Cotton decomposition	2010	2.65	2.16	**4.12**	**5.95*****	**3.23**	**4.46****
	2011	**1.00**	**6.44***	**3.11**	**5.12****	1.00	0.04
Litter decomposition	2010	1.70	2.84	1.37	0.86	1.00	2.44
	2011	1.00	0.92	1.00	0.58	1.00	1.08
Water quality regulation							
Phosphorus saturation	2010	1.76	0.85	1.16	0.30	3.05	2.77
	2011	1.00	0.17	1.00	0.91	1.00	0.91
Carbon storage							
Soil carbon	2010	1.00	1.42	1.00	0.01	2.07	0.89
	2011	1.60	0.78	1.00	0.10	1.00	<0.01
Soil fertility							
Soil nitrogen	2010	1.00	0.58	1.00	<0.01	**3.24**	**3.85***
	2011	1.38	0.26	1.16	0.37	1.00	0.03

[1] *$p < 0.05$; **$p < 0.01$, ***$p < 0.001$

[2]For these variables, repeated measures generalized additive mixed models were used for each year (2 censuses in 2010, 3 censuses in 2011).

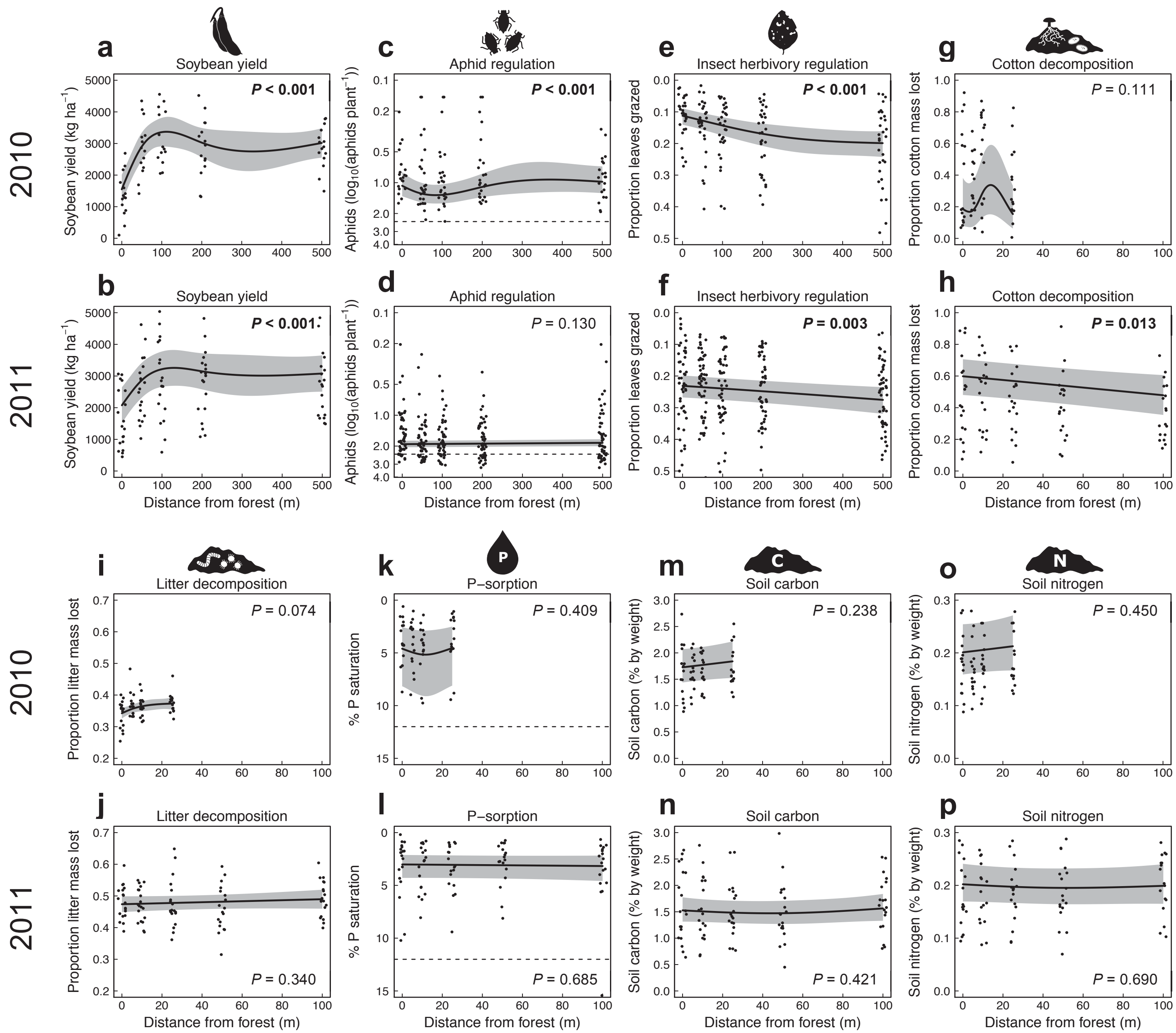

2010
2011
a
Soybean yield
P < 0.001
Soybean yield (kg ha−1)
b
Soybean yield
P < 0.001
c
Aphid regulation
P < 0.001
Aphids (log10(aphids plant−1))
d
Aphid regulation
P = 0.130
e
Insect herbivory regulation
P < 0.001
Proportion leaves grazed
f
Insect herbivory regulation
P = 0.003
g
Cotton decomposition
P = 0.111
Proportion cotton mass lost
h
Cotton decomposition
P = 0.013
Distance from forest (m)
i
Litter decomposition
P = 0.074
Proportion litter mass lost
j
Litter decomposition
P = 0.340
k
P−sorption
P = 0.409
% P saturation
l
P−sorption
P = 0.685
m
Soil carbon
P = 0.238
Soil carbon (% by weight)
n
Soil carbon
P = 0.421
o
Soil nitrogen
P = 0.450
Soil nitrogen (% by weight)
p
Soil nitrogen
P = 0.690

Figure 3.6: Relationships between distance-from-forest and ecosystem service indicators in 2010 and 2011. (**a**,**b**) soybean yield (kg ha^{-1}), (**c**,**d**) aphid regulation (aphids $plant^{-1}$), (**e**,**f**) insect herbivory regulation (proportion of leaves grazed), (**g**,**h**) cotton fabric decomposition (proportion mass lost), (**i,j**) leaf litter decomposition (proportion mass lost), (**k**,**l**) soil carbon (% by weight), (**m**,**n**) soil P saturation (% P saturation), and (**o**,**p**) soil nitrogen (% by weight). We show mean relationships (*black lines*), 95% confidence intervals (*grey areas*), and *p*-values for the effect of distance-from-forest from generalized additive mixed models with other model explanatory variables (*i.e.* fragment isolation and size) kept at mean levels. Y-axes are reversed for aphid and herbivory regulation (**c**-**f**) and P saturation (**k**-**l**) so that values higher on the axis represent higher levels of ecosystem service provision. The dashed horizontal line in (**c**) and (**d**) is the threshold at which a control action must be taken to prevent economic damage to soybeans from soybean aphids (250 aphids $plant^{-1}$) while that in (**k**) and (**l**) is a threshold for soil P saturation above which it can contribute to eutrophication. Note the log_{10} y-axes in (**c**) and (**d**) and different x-axes in (**a**-**f**) versus (**g**-**p**). n = 15 fields in 2010 and n = 19 fields in 2011.

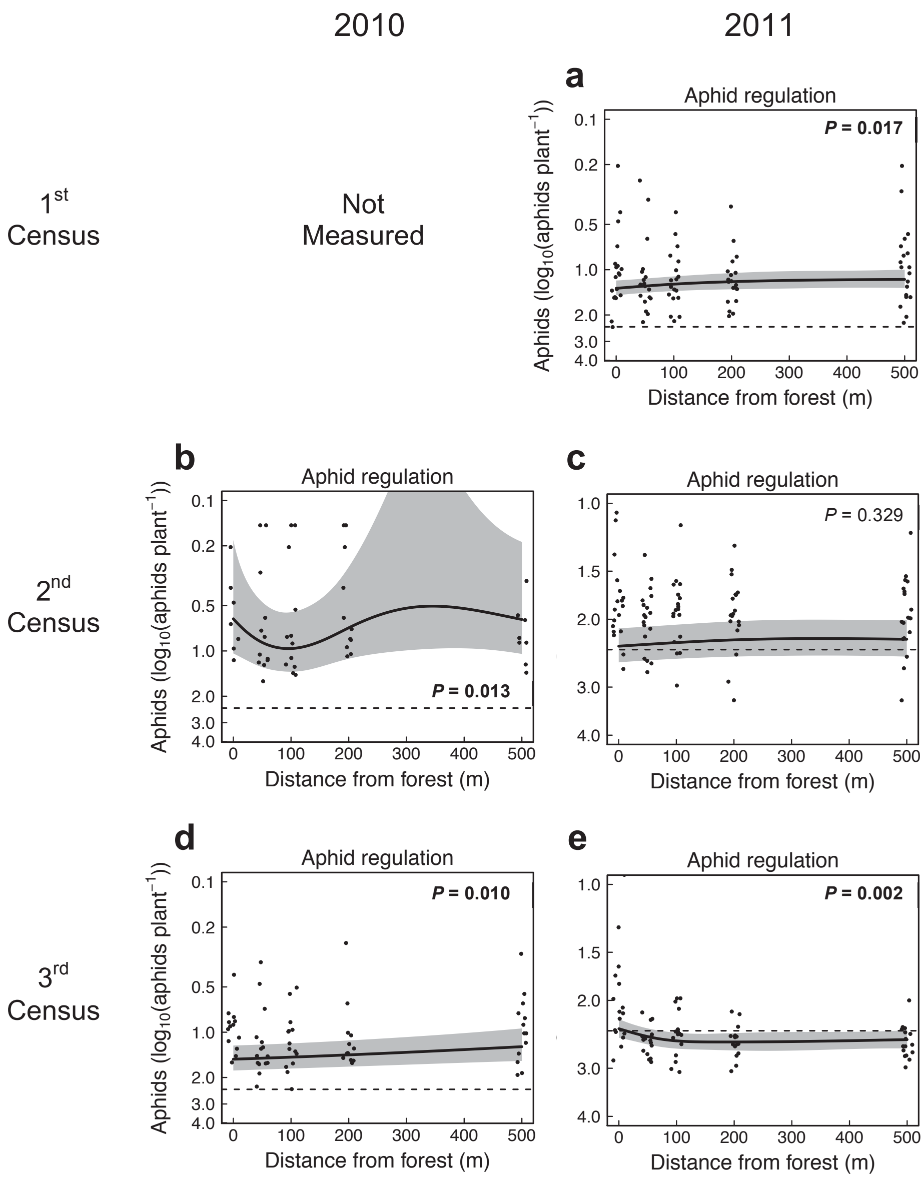


Figure 3.7: Relationships between distance-from-forest and aphid regulation in 2010 and 2011. (**a**) first census, (**b**,**c**) second census, (**d**,**e**) third census in each year. We show mean relationships (*black lines*), 95% confidence intervals (*grey areas*), and *p*-values for the effect of distance-from-forest from generalized additive mixed models with other model explanatory variables (*i.e.* fragment isolation and size) kept at mean levels. Y-axes are in $\log_{10}$ and are reversed so that values higher on the axis represent higher levels of ecosystem service provision. The dashed horizontal line is the threshold at which a control action must be taken to prevent economic damage to soybeans from soybean aphids (250 aphids plant^{-1}). Note the different x-axes in (**c**,**e**) versus (**a**,**b**,**d**). n = 15 fields in 2010 and n = 19 in 2011.

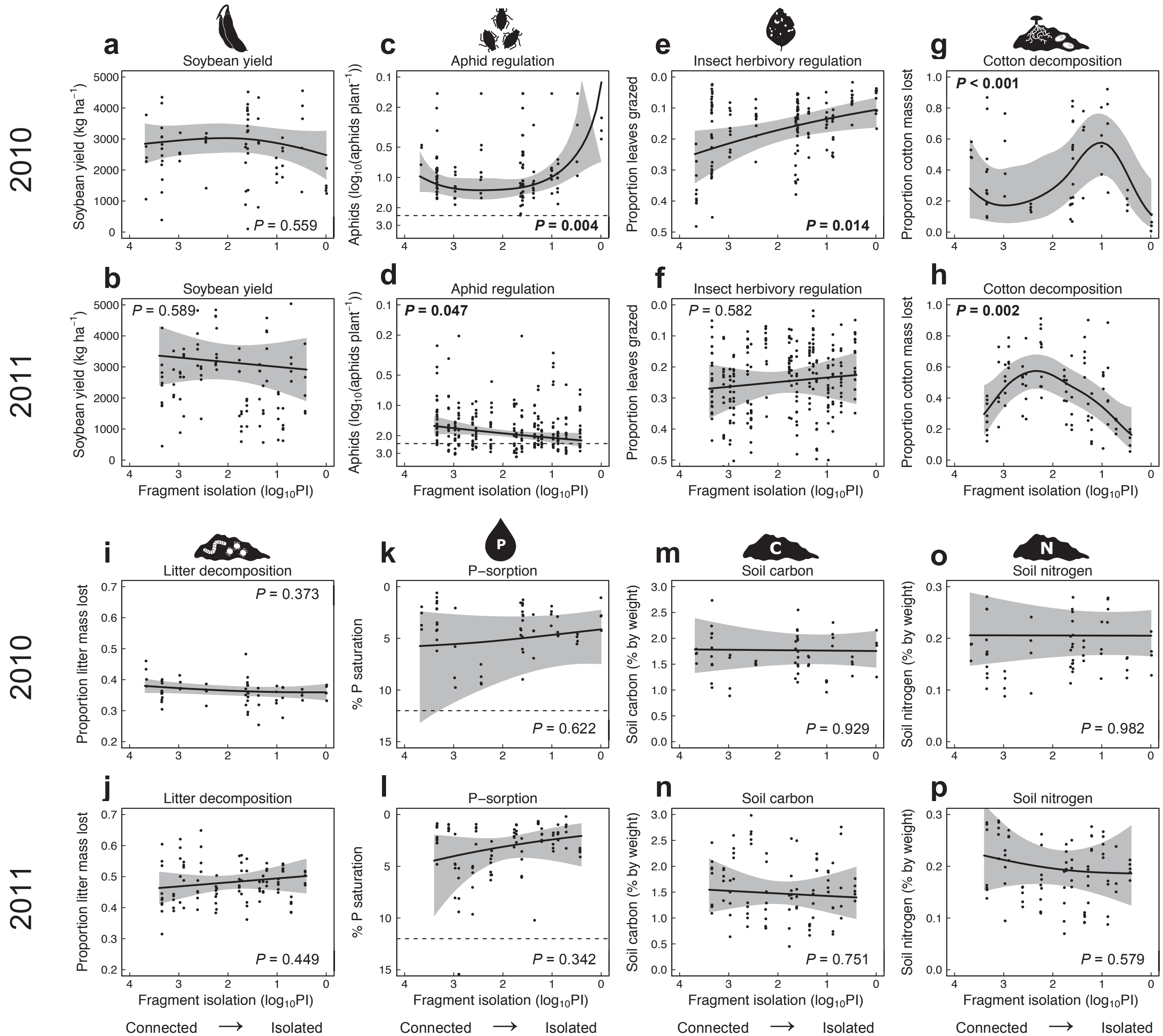
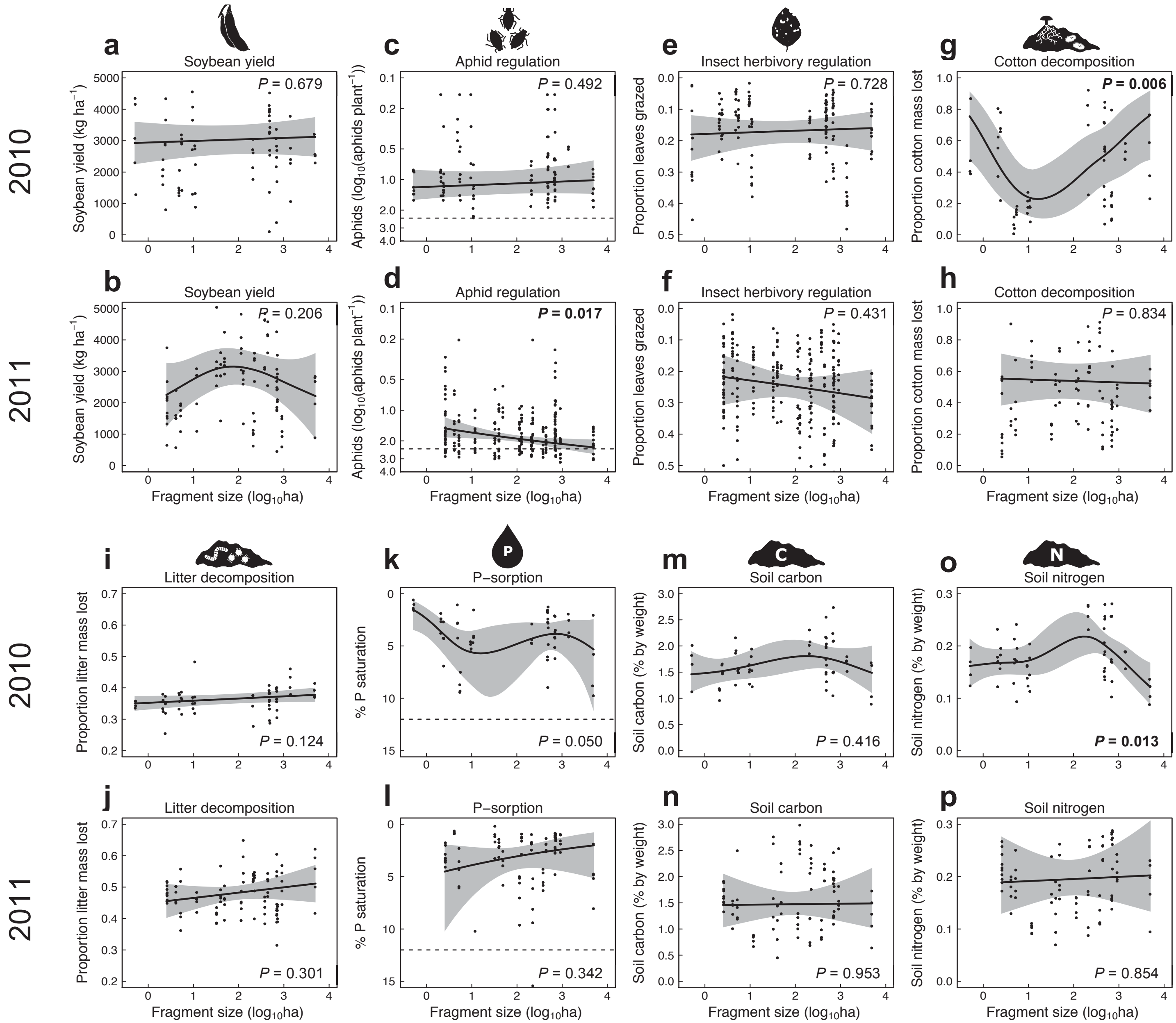

2010
2011
2010
2011
a
Soybean yield
P = 0.559
b
Soybean yield
P = 0.589
Soybean yield (kg ha−1)
c
Aphid regulation
P = 0.004
d
Aphid regulation
P = 0.047
Aphids (log10(aphids plant−1))
e
Insect herbivory regulation
P = 0.014
f
Insect herbivory regulation
P = 0.582
Proportion leaves grazed
g
Cotton decomposition
P < 0.001
h
Cotton decomposition
P = 0.002
Proportion cotton mass lost
i
Litter decomposition
P = 0.373
j
Litter decomposition
P = 0.449
Proportion litter mass lost
k
P–sorption
P = 0.622
l
P–sorption
P = 0.342
% P saturation
m
Soil carbon
P = 0.929
n
Soil carbon
P = 0.751
Soil carbon (% by weight)
o
Soil nitrogen
P = 0.982
p
Soil nitrogen
P = 0.579
Soil nitrogen (% by weight)
Fragment isolation (log10PI)
Connected → Isolated

Figure 3.8: Relationships between forest fragment isolation and ecosystem service indicators in 2010 and 2011. (**a**,**b**) soybean yield (kg ha^{-1}), (**c**,**d**) aphid regulation (aphids $plant^{-1}$), (**e**,**f**) insect herbivory regulation (proportion of leaves grazed), (**g**,**h**) cotton fabric decomposition (proportion mass lost), (**i**,**j**) leaf litter decomposition (proportion mass lost), (**k**,**l**) soil carbon (% by weight), (**m**,**n**) soil P saturation (% P saturation), and (**o**,**p**) soil nitrogen (% by weight). We show mean relationships (*black lines*), 95% confidence intervals (*grey areas*), and *p*-values for the effect of forest fragment isolation from generalized additive mixed models with other explanatory variables (*i.e.* distance-from-forest and fragment size) kept at mean levels. X-axes are reversed so that values run from connected forest fragments on the left to isolated fragments on the right of each graph. Y-axes are reversed for aphid and herbivory regulation (**c**-**f**) and P saturation (**k**-**l**) so that values higher on the axis represent higher levels of ecosystem service provision. The dashed horizontal line in (**c**) and (**d**) is the threshold at which a control action must be taken to prevent economic damage to soybeans from soybean aphids (250 aphids $plant^{-1}$) while that in (**k**) and (**l**) is the threshold for P saturation in soils above which it can contribute to eutrophication. Note the $\log_{10}$ y-axes in (**c**) and (**d**). n = 15 fields in 2010 and n = 19 fields in 2011.



2010
2011
a
Soybean yield
P = 0.679
b
Soybean yield
P = 0.206
Soybean yield (kg ha−1)
c
Aphid regulation
P = 0.492
d
Aphid regulation
P = 0.017
Aphids (log10(aphids plant−1))
e
Insect herbivory regulation
P = 0.728
f
Insect herbivory regulation
P = 0.431
Proportion leaves grazed
g
Cotton decomposition
P = 0.006
h
Cotton decomposition
P = 0.834
Proportion cotton mass lost
i
Litter decomposition
P = 0.124
j
Litter decomposition
P = 0.301
Proportion litter mass lost
k
P–sorption
P = 0.050
l
P–sorption
P = 0.342
% P saturation
m
Soil carbon
P = 0.416
n
Soil carbon
P = 0.953
Soil carbon (% by weight)
o
Soil nitrogen
P = 0.013
p
Soil nitrogen
P = 0.854
Soil nitrogen (% by weight)
Fragment size (log10ha)

Figure 3.9: Relationships between forest fragment size and ecosystem service indicators in 2010 and 2011. (**a**,**b**) soybean yield (kg ha^{-1}), (**c**,**d**) aphid regulation (aphids plant^{-1}), (**e**,**f**) insect herbivory regulation (proportion of leaves grazed), (**g**,**h**) cotton fabric decomposition (proportion mass lost), (**i**,**j**) leaf litter decomposition (proportion mass lost), (**k**,**l**) soil carbon (% by weight), (**m**,**n**) soil P saturation (% P saturation), and (**o**,**p**) soil nitrogen (% by weight). We show mean relationships (*black lines*), 95% confidence intervals (*grey areas*), and *p*-values for the effect of forest fragment isolation from generalized additive mixed models with other explanatory variables (*i.e.* distance-from-forest and fragment size) kept at mean levels. Y-axes are reversed for aphid and herbivory regulation (**c**-**f**) and P saturation (**k**-**l**) so that values higher on the axis represent higher levels of ecosystem service provision. The dashed horizontal line in (**c**) and (**d**) is the threshold at which a control action must be taken to prevent economic damage to soybeans from soybean aphids (250 aphids plant^{-1}) while that in (**k**) and (**l**) is the threshold for P saturation in soils above which it can contribute to eutrophication. Note the $\log_{10}$ y-axes in (**c**) and (**d**). n = 15 fields in 2010 and n = 19 fields in 2011.

Near	Far	Near	Far	Near	Far	Near	Far	Near	Far	Near	Far	Near	Far	
2010 r= -0.37 P= 0.01 **2011** r= -0.45 P=0.001	**2010** r= -0.13 P= 0.49 **2011** r= -0.02 P= 0.90	**2010** r= -0.20 P= 0.20 **2011** r= -0.32 P= 0.03	**2010** r= 0.08 P=0.69 **2011** r= -0.01 P= 0.94	r= 0.13 P= 0.21	r= 0.17 P= 0.33	r= -0.03 P= 0.80	r= -0.40 P= 0.01	r= -0.18 P= 0.07	r= -0.38 P= 0.02	r= 0.08 P= 0.42	r= -0.04 P= 0.80	r= 0.07 P= 0.49	r= -0.05 P= 0.75	
		2010 r= 0.15 P= 0.32 **2011** r= 0.02 P= 0.87	**2010** r= 0.21 P=0.28 **2011** r= -0.22 P=0.22	r= 0.02 P= 0.96	r= 0.22 P= 0.43	r= 0.28 P= 0.30	r= -0.39 P= 0.13	r= -0.19 P= 0.49	r= 0.07 P= 0.80	r= 0.18 P= 0.50	r= -0.13 P= 0.63	r= 0.14 P= 0.60	r= -0.16 P= 0.56	
				r= -0.02 P= 0.94	r <0.01 P= 0.99	r= -0.07 P= 0.79	r= -0.09 P= 0.75	r= -0.01 P= 0.97	r= -0.20 P= 0.46	r= -0.42 P= 0.10	r= -0.70 P <0.01	r= -0.43 P= 0.09	r= -0.73 P <0.01	
						r= 0.19 P= 0.06	r= -0.04 P= 0.81	r= -0.16 P= 0.10	r= -0.37 P= 0.03	r= -0.15 P= 0.13	r= -0.20 P= 0.24	r= -0.07 P= 0.48	r= -0.18 P= 0.29	
								r= 0.13 P= 0.19	r= 0.16 P= 0.33	r= -0.06 P= 0.52	r= 0.35 P= 0.03	r= 0.12 P= 0.24	r= 0.34 P= 0.04	
										r= 0.10 P= 0.34	r= 0.25 P= 0.13	r= 0.16 P= 0.12	r= 0.34 P= 0.04	
												r= 0.82 P<0.001	r= 0.95 P<0.001	

- Soybean yield
- Aphid regulation
- Insect herbivory regulation
- Cotton fabric decomposition
- Leaf litter decomposition
- Soil phosphorus saturation
- Soil carbon
- Soil nitrogen

Figure 3.10: Spearman's *rho* values and *p*-values from pair-wise Spearman-rank relationships between ecosystem service indicators. Green are positive relationships and red negative relationships, evaluated using Spearman's *rho* at an $\alpha < 0.05$ level. Grey reflects relationships not significantly different than zero. We also provide both the Spearman's *rho* value and statistical significance (*i.e. p*-value) of each relationship. For each pair-wise relationship, squares on the left represent near-to-forest and those on the right far-from-forest relationships (*i.e.* aboveground service relationships: 0-100 vs. 200-500 m, belowground service relationships: 0-25 vs. 50-100 m, above-belowground service relationships: 0 vs. 100 m). Note that the aboveground relationships between aphid regulation, herbivory regulation and crop production were evaluated separately for 2010 and 2011 as patterns of aphids and herbivory varied greatly between years. For the near-to-forest relationship between insect herbivory regulation and soybean yield, a negative relationship was only present in 2011.

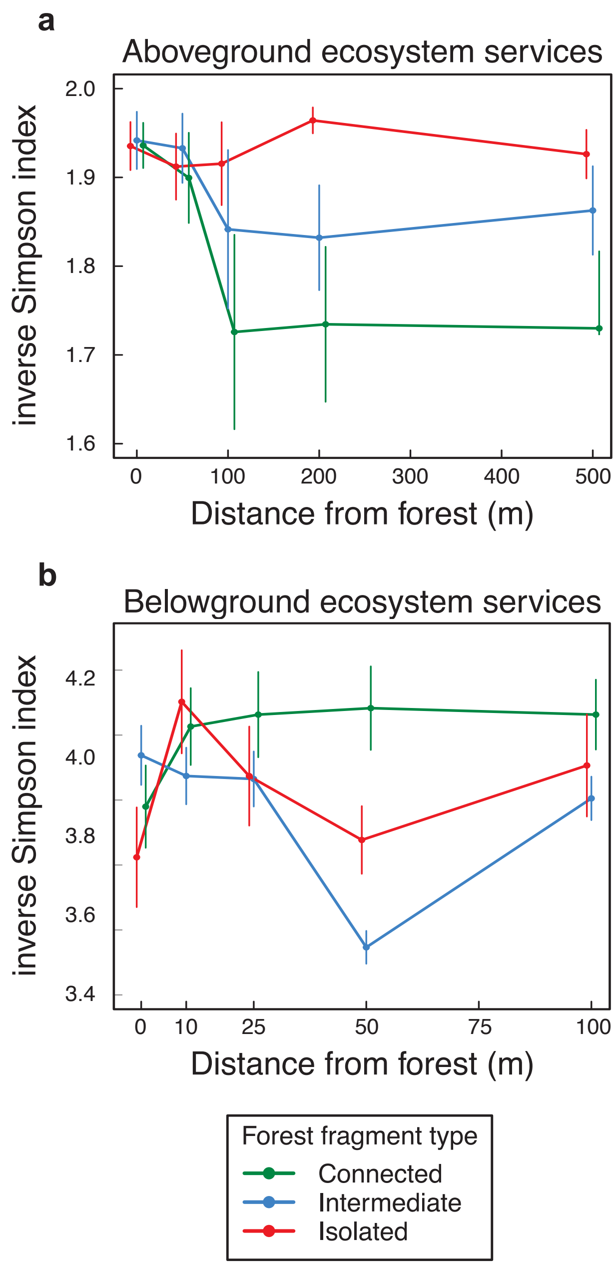


Figure 3.11: Relationships between distance-from-forest and landscape multi-functionality. (**a**) aboveground ecosystem services, (**b**) belowground ecosystem services. We show mean values of the inverse Simpson diversity index ± standard errors of the mean. For (**a**) multi-functionality was calculated using standardized values (*i.e.* between 0 and 1) for crop production, aphid regulation, and insect herbivory regulation; and for (**b**) using standardized values for cotton decomposition, litter decomposition, soil carbon, soil phosphorus saturation, and soil nitrogen. Note the difference in both x- and y-axes in the two figures.

Table 3.3: Results from nonlinear mixed models. Each model fits the effect of distance-from-forest (non-linear), and forest fragment isolation category on multi-functionality values (inverse Simpson diversity index) along our distance-from-forest transects for both 2010 and 2011 combined.

Variable	**Degrees of freedom *(num,den)***	***F*-value[1]**
Aboveground		
Distance from forest[2]	2,118	**6.19****
Isolation category	2,28	1.57
Distance x Isolation	4,118	1.99
Belowground		
Distance from forest[3]	3,94	1.64
Isolation category	2,31	0.34
Distance x Isolation	6,94	1.12

[1] $^{*}p < 0.05$; $^{**}p < 0.01$, $^{***}p < 0.001$
[2]For this variable a second-order polynomial for distance-from-forest was used.
[3]For this variable a third-order polynomial for distance-from-forest was used.

CONNECTING STATEMENT

Chapter 3 provides some of the first empirical evidence that landscape connectivity and fragments of natural habitat in an agricultural matrix can affect both the provision of ecosystem services and the relationships between services. I also discuss the potential importance of landscape heterogeneity for multi-functionality. However, the specific mechanisms by which landscape connectivity affects the different ecosystem services in Chapter 3 are uncertain. This includes possible effects of landscape connectivity on the biodiversity and ecosystem functions that are believed to underlie service provision.

In Chapter 4, I examine the role biodiversity plays in determining how landscape structure affects ecosystem services by delving into the effects of landscape structure on connectivity and pest regulation. Specifically, I focus on the diversity of aphid predators and soybean pests, as well as the abundance of aphids in order to determine how landscape structure influences these different arthropod groups and their interactions to affect final ecosystem service provision. I also investigate the potential effects of pest regulation on crop production in this system.

The research questions from Chapter 2 that are addressed in this chapter include: (1) What are the important mechanisms by which connectivity can affect ecosystem services and what causes their relative importance to change? and (2) At what scales does connectivity affect the provision of ecosystem services?

AGRICULTURAL LANDSCAPE STRUCTURE AFFECTS ARTHROPOD DIVERSITY & ARTHROPOD-DERIVED ECOSYSTEM SERVICES

4

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4.1 ABSTRACT

Knowledge of how landscape structure impacts the diversity and abundance of beneficial and pest arthropods, pest regulation, and ultimately crop yield has the potential to significantly improve management of agricultural landscapes. We examined how landscape structure in southern Québec affected soybean pests, predators of aphids, pest regulation including aphid and herbivory regulation, and crop production. Local-scale field characteristics and landscape structure at distances less than 2 km around each field were the most important predictors for these variables. Increasing field width consistently decreased arthropod diversity and abundance for both predators of aphids and soybean pests, but effects on pest regulation were inconsistent. Increased field width resulted in less damage to soybean plants from herbivore pests; but in contrast, aphid numbers were greatest in more complex landscapes where fields were generally narrower. Distance-from-forest within fields and no-till planting methods also decreased pest regulation. Despite these results, soybean yield was not strongly related to pest regulation and instead varied most with distance-from-forest. Thus, patterns of arthropod diversity and abundance may not necessarily coincide with those of pest regulation or crop yield. Understanding the relationships between landscape structure, species diversity, and service provision for multiple ecosystem services and the species groups that provide them could inform management of biodiversity, trophic interactions, and ecosystem services in agricultural landscapes.

4.2 INTRODUCTION

Management of agricultural landscape structure has the potential to improve arthropod-provided ecosystem services such as pest regulation and pollination. These services depend on the movement of arthropods across agricultural landscapes at different scales (Kremen *et al.* 2007; Mitchell, Bennett & Gonzalez 2013), as well as the abundance and diversity of the arthropods that provide them (Letourneau *et al.* 2009; Tscharntke *et al.* 2005). Agricultural landscape structure, the configuration and composition of crop and non-crop habitats, is expected to influence ecosystem service provision because it is known to affect arthropod movement, abundance, and diversity (Bianchi, Booij & Tscharntke 2006; Chaplin-Kramer *et al.* 2011). Forests, meadows, hedgerows, and field margins all provide resources and habitat connectivity for different arthropod groups, including natural enemies of crop pests. Thus, it is commonly predicted that pest regulation will be greater in landscapes that contain a greater proportion or diversity of these habitats (Bianchi, Booij & Tscharntke 2006; Chaplin-Kramer *et al.* 2011). However, we currently lack a detailed understanding of how different components of landscape structure simultaneously influence arthropod pests, their predators, and associated ecosystem services; the spatial scales at which this occurs; and the effects, if any, on crop production (Chaplin-Kramer *et al.* 2011).

Most studies of landscape structure and pest regulation focus on landscape complexity, measured as the proportion of non-crop habitat (*e.g.* Bailey *et al.* 2010; Batáry *et al.* 2011), the diversity of habitats present (*e.g.* Fabian *et al.* 2013; Gardiner *et al.* 2009), or the presence of linear elements such as hedgerows (*e.g.* Holzschuh, Steffan-Dewenter & Tscharntke 2010). The majority of these studies find positive effects of increased complexity on the diversity and abundance of beneficial arthropods (Bianchi, Booij & Tscharntke 2006; Chaplin-Kramer *et al.* 2011). Non-crop habitat provides foraging, nesting resources and overwintering habitat (Dennis, Fry & Anderson 2000); refuge from predators (Martin *et al.* 2013); and favorable environmental conditions for many arthropod species (see Bianchi, Booij & Tscharntke 2006 for a review). Additionally, linear elements such as hedgerows and field margins can provide critical landscape connectivity, both between non-crop habitat patches (van Geert, van Rossum & Triest 2010), and between non-crop and crop patches (Bianchi *et al.* 2010; Segoli & Rosenheim 2012). For example, increased edge density in wheat fields increases the abundance and diversity of herbivore-predating wasp species across the landscape (Holzschuh, Steffan-Dewenter & Tscharntke 2010). However, studies investigating how landscape structure or complexity affects both predator and pest species are rare (Bianchi, Booij & Tscharntke 2006; Martin *et al.* 2013). If a change in landscape structure increases both pest predation and pest abundance (Thies, Roschewitz & Tscharntke 2005), then there may be little net change in pest pressure, the variable of interest for farmers. Correctly measuring pest regulation means including measures of both predator and pest pressure on crops, and how landscape structure affects both variables (Chaplin-Kramer *et al.* 2011).

Changes to landscape structure can also affect arthropod predator diversity. However, the effects of changes in arthropod predator diversity on pest regulation vary widely, and examples of both positive and negative effects of increased diversity exist (Letourneau *et al.* 2009). Ecological theory predicts that more functionally diverse predator groups will show increased niche complementarity (Hooper *et al.* 2005); different species will attack pests in a greater diversity of ways through space and time, leading to increased pest regulation. There may also be a 'sampling effect,' where more diverse communities are increasingly likely to contain the most effective predator for a given pest species (Tscharntke *et al.* 2005). However, the importance of predator diversity for pest regulation can be altered by landscape structure and heterogeneity, pest abundance and patterns of distribution (Tylianakis & Romo 2010), negative interactions between predators (Letourneau *et al.* 2009), plant species diversity (Chaplin-Kramer & Kremen 2012), and human management (Rusch *et al.* 2013). In particular, there is evidence that predator diversity is increasingly important for biological control as landscape heterogeneity increases and pest populations become patchy (Tylianakis *et al.* 2008). Despite these results, the effects of landscape structure on the relationships between predator diversity and pest regulation are not well known. In addition, the importance of pest versus predator diversity is largely undetermined. Understanding how the diversity of these different arthropod groups interacts with landscape structure to alter pest regulation is important for the management of agricultural systems.

Effective management of landscape structure to maximize pest regulation also depends on identifying relevant ecological and management scales. Landscape structure effects operate at different scales for different arthropod groups, depending on their mobility and size (Tscharntke & Brandl 2004). In particular, pests, parasitoids, and specialized predators are thought to be influenced by landscape structure at smaller scales than generalized predators (Tscharntke & Brandl 2004). In many cases, the relationships between landscape structure and arthropod abundance or diversity are strongest at specific scales (Rusch *et al.* 2013; 2011) or are influenced by multiple scales (Chaplin-Kramer & Kremen 2012; Holzschuh, Steffan-Dewenter & Tscharntke 2010; O'Rourke, Rienzo-Stack & Power 2011). For example, both field size and the amount of non-crop habitat in the larger landscape affect the biocontrol of potato pests (Werling & Gratton 2010). Yet many studies of pest regulation and landscape structure only investigate a single scale. We currently do not have a good understanding of the specific spatial scales at which landscape structure could be altered to improve arthropod-produced ecosystem services.

Soybean fields (*Glycine max* L. Merr.) provide an ideal system to investigate the effects of landscape structure on arthropod diversity, abundance, and ecosystem service provision. The predominant pest of soybean crops in North America is the soybean aphid (*Aphis glycines* Matsumura), an introduced species from Asia. Soybean aphids were first discovered in Wisconsin in 2000, and arrived in Québec in 2002 (Ragsdale *et al.* 2011). In just over a decade, soybean aphids have become the most economically important soybean pest in North America, capable of reducing yield by up to 40 % (Ragsdale *et al.* 2011). Aphids overwinter on native shrubs (*Rhamnus* sp.) in forest fragments and hedgerows, and disperse locally into nearby fields (Ragsdale, Voegtlin & O'Neil 2004), as well as over longer distances via atmospheric movements (Ragsdale *et al.* 2011; Zhang & Swinton 2012). A diverse community of arthropod predators, including spiders (Costamagna & Landis 2007), is thought to be key in controlling soybean aphid populations (Costamagna & Landis 2006; Mignault *et al.* 2006; Rutledge *et al.* 2004). Soybean plants are also damaged by a diverse group of arthropod herbivores (Kogan & Turnipseed 1987). Yet the effects of landscape structure on the community of predators that control aphids, the aphids themselves, other generalist herbivores, and the resulting provision of pest regulation service and disservices, have been rarely studied in combination (Ragsdale *et al.* 2011).

Here, we evaluate the effects of both local and broad-scale landscape structure, as well as crop planting techniques and forest plant diversity, on the provision of pest regulation and crop production in soybean fields east of Montréal, Québec, Canada. Specifically, we asked: (1) How does landscape structure, and in particular field structure, affect the diversity and abundance of arthropods that provide key pest regulation services and disservices, (2) at what scales does this occur, and (3) how important are changes in landscape and field structure, and arthropod abundance and diversity, for pest regulation and crop production?

4.3 METHODS

4.3.1 Study system and design

We conducted our study in 34 commercial soybean fields (2010: $n = 15$, 2011: $n = 19$) within the Montérégie region east of Montréal (45°30' N, 73°35' W), Québec. This region consists of fragmented forests (21 % forest) surrounded by a matrix of agricultural fields (55 % agriculture) dominated by corn (48 % of cultivated area), soybean (26 %), and hay fields (8 %; M. Mitchell, *unpublished data*). Soybean in this region is planted using either conventional tillage or no-till practices in a yearly rotation with corn, therefore new fields were chosen each year. Agricultural fields in Québec follow the seigneurial system of land distribution, and are arranged in long narrow strips running from adjacent remnant forest fragments. Each field can therefore be seen as a transect where distance-to-forest varies but other landscape and management variables are uniform. Fields are generally oriented on a northwest-southeast bearing.

Our soybean fields spanned the range of crop-dominated to forest-dominated landscapes present in this region. Fields were originally chosen according to the size and isolation of their adjacent forest patch for a prior study (Mitchell et al. *submitted*). Around each field in circles of increasing radii (⊕ 0.5 km; ⊕ 0.75 km; ⊕ 1 km; ⊕ 1.5 km; ⊕ 2 km; ⊕ 3 km; ⊕ 4 km; ⊕ 5 km), we quantified the proportion of forest and the ratio of field perimeter to field area using available geospatial datasets (Système d'Information Écoforestière & Base de Données des Cultures Assurées) in ArcGIS 9.3.1. Field perimeter to area ratio is an indicator of landscape complexity; the relative length of field margins and hedgerows in each nested landscape. Using the same spatial datasets, we also measured field width and the orientation of each field from its adjacent forest fragment (*i.e.* NW or SE). Soybean planting method was assessed visually for each field. To determine plant diversity in each adjacent forest fragment, we established a 20 × 20 m square quadrat directly adjacent to each soybean field and identified each tree and shrub species present.

4.3.2 Measurement of arthropod diversity and abundance

Within each field, we established two sampling locations for arthropod diversity and abundance, pest regulation and crop production, one each at 0 m and 500 m from the adjacent forest fragment. Potential predators of aphids and soybean pests were collected at each distance-from-forest twice each growing season (2010: July 27-30 and Aug. 9-13; 2011: Aug. 1-5 and 17-20) using 100 figure-eight sweep net movements (Mignault *et al.* 2006) with a 30 cm diameter insect net along a transect parallel to the field-forest edge. Captured individuals were placed in 85% ethanol solution until identification. All individuals were sorted to morphospecies (Oliver & Beattie 1996) and then classified to family, except for Coccinellidae and Lepidoptera larvae, and Orthoptera (*i.e.* grasshoppers and crickets). For predators of aphids and soybean pests, individuals were classified to genus. Araneae (*i.e.* spider) individuals were also counted, but were not classified further.

4.3.3 Measurement of ecosystem services

At the same time as the sweep net collections we estimated two components of pest regulation: aphid regulation and herbivory regulation. Aphid numbers and arthropod herbivory (proportion of soybean leaves grazed) were quantified visually for five soybean plants at each distance-from-forest. We also recorded plant size (number of leaves; Sivakumar 1978) at the same time. Soybean yield was estimated by collecting soybean plants along 0.5 m of two crop rows just before harvest (2010: Sept. 22-24; 2011: Sept. 27-30). Plants were then dried at 50°C for 48 hours, mechanically threshed, and the separated soybeans were weighed and yield calculated based on the area of field sampled.

4.3.4 Statistical analyses

We used generalized linear mixed models (Zuur *et al.* 2009) and model averaging (Burnham & Anderson 2002) in R version 3.0.1 to determine how each of the predictor variables: 'proportion forest', 'landscape complexity', 'distance-from-forest', 'field width', 'tillage, 'field aspect', and 'forest plant diversity', affected arthropod diversity and abundance, spider abundance, aphid abundance, soybean herbivory and crop yield. In each model, 'field' and 'year' were included as random effects, and, since our two sampling locations were not located exactly in the middle of each field, 'distance to the nearest field edge' was included as a covariate. We also included 'plant size' as a covariate for our models of aphid abundance. Full models for aphid predator and soybean pest diversity and abundance included all of the above predictor variables; for aphid abundance and soybean herbivory all of the above predictor variables plus the appropriate arthropod group diversity and abundance; and for crop production all the predictor variables plus aphid abundance and soybean herbivory. Data from both years were pooled for analysis so that we could focus on the overall effects of the predictor variables. All predictor variables were standardized (Grueber *et al.* 2011) so that numeric variables had a mean of 0 and standard deviation of 0.5, and binary variables a mean of 0 and difference of 1 using the 'standardize' function of the 'arm' package in R. Each model was fit using the appropriate distribution type and link function: poisson for arthropod richness, abundance and aphid numbers; binomial for soybean herbivory; and gaussian for soybean yield. We tested for overdispersion in the dependent variables by calculating the sum of squared Pearson residuals and comparing it to the residual degrees of freedom. If present, overdispersion was corrected by adding an individual level random effect to the model (Elston *et al.* 2001).

For model averaging, full models at each landscape scale (*i.e.* $\oplus$ 0.5 km, $\oplus$ 0.75 km, $\oplus$ 1 km, etc.) were first fit using the 'lmer' function in the 'lme4' package in R, and the model with the lowest Akaike's Information Criteria corrected for small sample sizes (AICc; Hurvich & Tsai 1989) was chosen as the best scale. Next, variance inflation factors (VIFs), which indicate collinearity between variables, were calculated for each predictor variable and those with values > 2 were sequentially removed from the model (Zuur, Ieno & Elphick 2010). Next, a set of models consisting of all possible combinations and numbers of the predictor variables was created, and those models within < 2 AICc of the best model were used for model averaging (Burnham & Anderson 2002; Grueber *et al.* 2011) with the 'model.avg' function in the 'MuMIn' package. The final averaged models provided model-averaged coefficients for each retained predictor variable and variable importance (*i.e.* the sum of the model weights within the set that included that variable). The fit of each averaged model (*i.e.* R^2) was calculated for both the fixed effects portion and the fixed plus random effects portions of each model (Nakagawa & Schielzeth 2012).

4.4 RESULTS

4.4.1 Overall arthropod abundance and diversity

We collected 10 969 arthropods, of which 14.3 % were predators of aphids, 3.7 % spiders, and 27.8 % soybean pests. Soybean pest and spider relative abundances were similar between years (spiders: 3.5 % in 2010 vs. 3.8 % in 2011, ANOVA: $p = 0.25$; pests: 30.0 % vs. 26.2 %, ANOVA: $p = 0.24$), but aphid predator numbers increased slightly in 2011 (10.4 % vs. 16.8 %, ANOVA: $p = 0.08$). We identified 17 aphid predator genera in both 2010 and 2011 (Table 4.1 in the Supporting Information). *Orius* spp. dominated the aphid predator community in both years (2010: 53.0 % of all predators of aphids; 2011: 38.3 %). Coccinellidae larvae (2010: 5.9 %; 2011: 27.4 %) and adults (2010: 12.0 %; 2011: 11.7 %) were also common in both years; adults were dominated by *Harmonia axyridis* (2010: 6.8 %; 2011: 5.7 %) but also included *Coccinella septempunctata*, *Coleomegilla maculata*, *Hippodamia variegata*, and *Propylea quatuordecimpunctata*. Other common aphid predators included *Nabis americoferus* (7.2 %) and *Toxomerus* spp. (9.2 %) in 2010, and *Plagiognathus* spp. (11.3 %) in 2011. We collected 14 soybean pest genera in 2010 and 16 genera in 2011, plus Lepidoptera caterpillars (Table 4.2 in the Supporting Information). The majority of pest individuals were *Systena frontalis* (2010: 74.7 %; 2011: 73.8 %), but other common pests included *Empoasca fabae* (2010: 10.1 %; 2011: 3.1 %) and *Lygus lineolaris* (2010: 3.3 %; 2011: 4.3 %).

4.4.2 Landscape structure effects on arthropod diversity and abundance

Field width had the strongest relationship with both aphid predator richness and abundance (richness: $p < 0.001$; abundance: $p = 0.023$; Figure 4.1). As field width increased from 40 to 280 m, average aphid predator richness and abundance decreased by 80 % and 62 %, respectively (Figure 4.2). Predator richness and abundance also increased with distance-from-forest ($p < 0.001$) and the proportion of forest at $\oplus$ 0.75 km ($p = 0.057$), but the effects of surrounding forest were only marginally significant. As distance-from-forest increased from 0 to 500 m, average aphid predator abundance increased by 40% (Figure 4.3). Aphid predator abundance also decreased by 24 % in no-till fields (Figure 4.3). Neither landscape complexity at ⨁ 0.75 km, nor forest plant diversity was included in either averaged model. The fixed effects portions of the averaged models explained 46 % of the variance in aphid predator richness, and 29 % of the variance in predator abundance.

Spider abundance decreased with both field width and distance-from-forest (both $p < 0.001$; Figure 4.1); average spider abundance decreased by 90 % as fields widened and 79 % as distance-from-forest increased (Figure 4.2). Similar trends were also present for overall arthropod morphospecies richness (Table 4.3, Figure 4.4 in the Supporting Information). Landscape complexity (⨁ 2 km) and forest plant diversity were also included in the averaged model for spider abundance, but only the positive effect of forest diversity was statistically significant (p = 0.023). The fixed effects of our averaged model explained just over 70 % of the variance in spider abundance.

Soybean pest richness and abundance showed similar patterns to predators of aphids. Field width had the strongest effects, with negative relationships for both pest richness and abundance (both $p < 0.001$; Figure 4.1). Along our field width gradient, soybean pest richness decreased by 78 % and abundance by 86% (Figure 4.2). Pest abundance nearly tripled with distance-from-forest ($p <$ 0.001; Figure 4.3) but decreased by 37 % with no-till planting ($p = 0.061$; Figure 4.3). Landscape complexity at ⨁ 2 km was included in the averaged model for soybean pest richness, and the proportion of forest at ⨁ 0.5 km for abundance, but neither was statistically significant (Figure 4.1). The fixed effects portions of the averaged models explained 39 % and 42 % of the variance in soybean pest richness and abundance, respectively.

4.4.3 Landscape structure effects on pest regulation

Aphid densities in 2010 averaged 4.0 ± 1.1 individuals plant^{-1} at the first census and 15.1 ± 3.7 individuals plant^{-1} at the second. This increased to 148.8 ± 45.2 and 292.6 ± 37.7 individuals plant^{-1} in 2011. While aphid regulation wasn't strongly related to field width, it was related to landscape complexity at ⨁ 1 km (Figure 4.1). Average aphid numbers decreased by 86% in fields located within simple landscapes (Figure 4.2). Distance-from-forest wasn't included in the

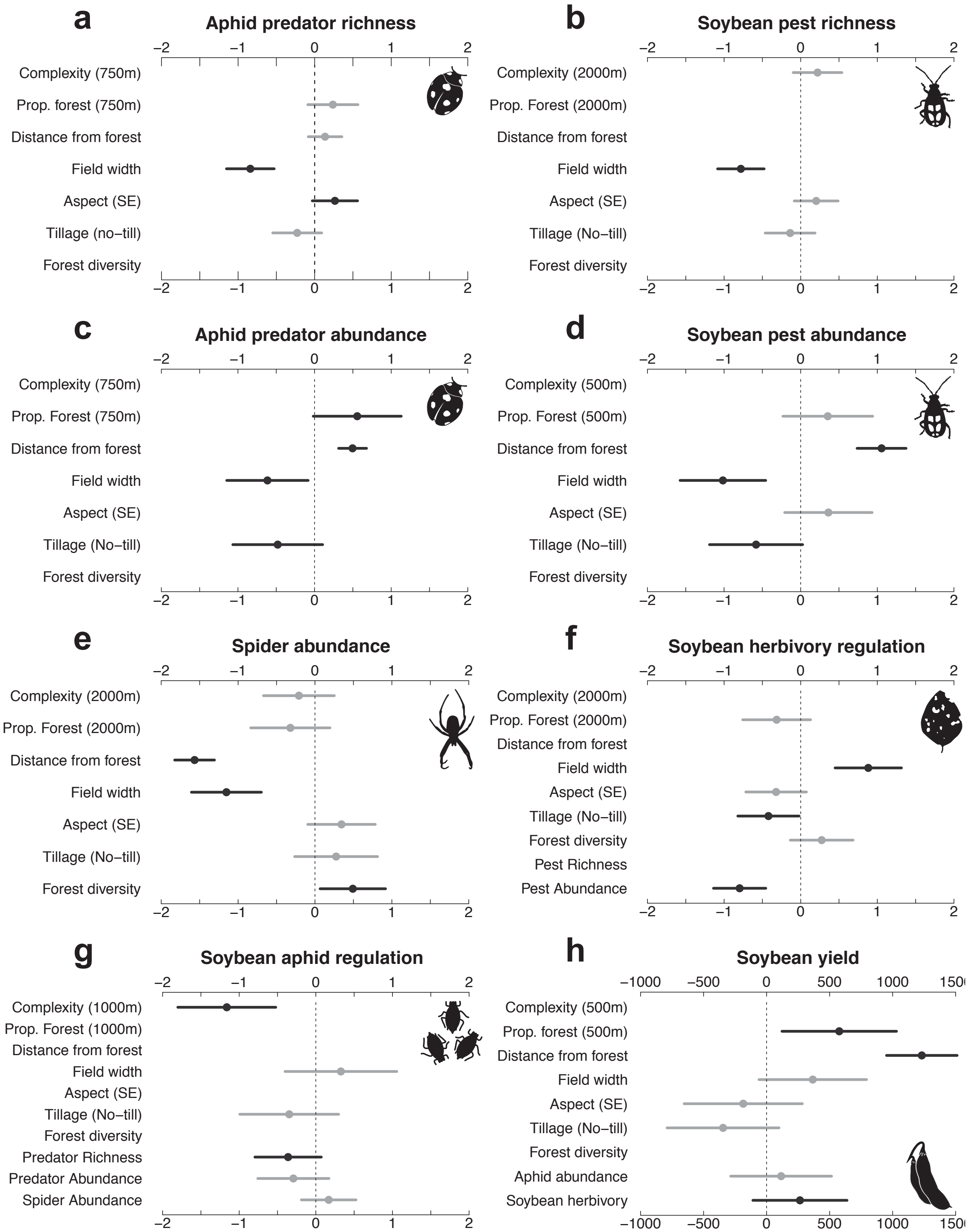
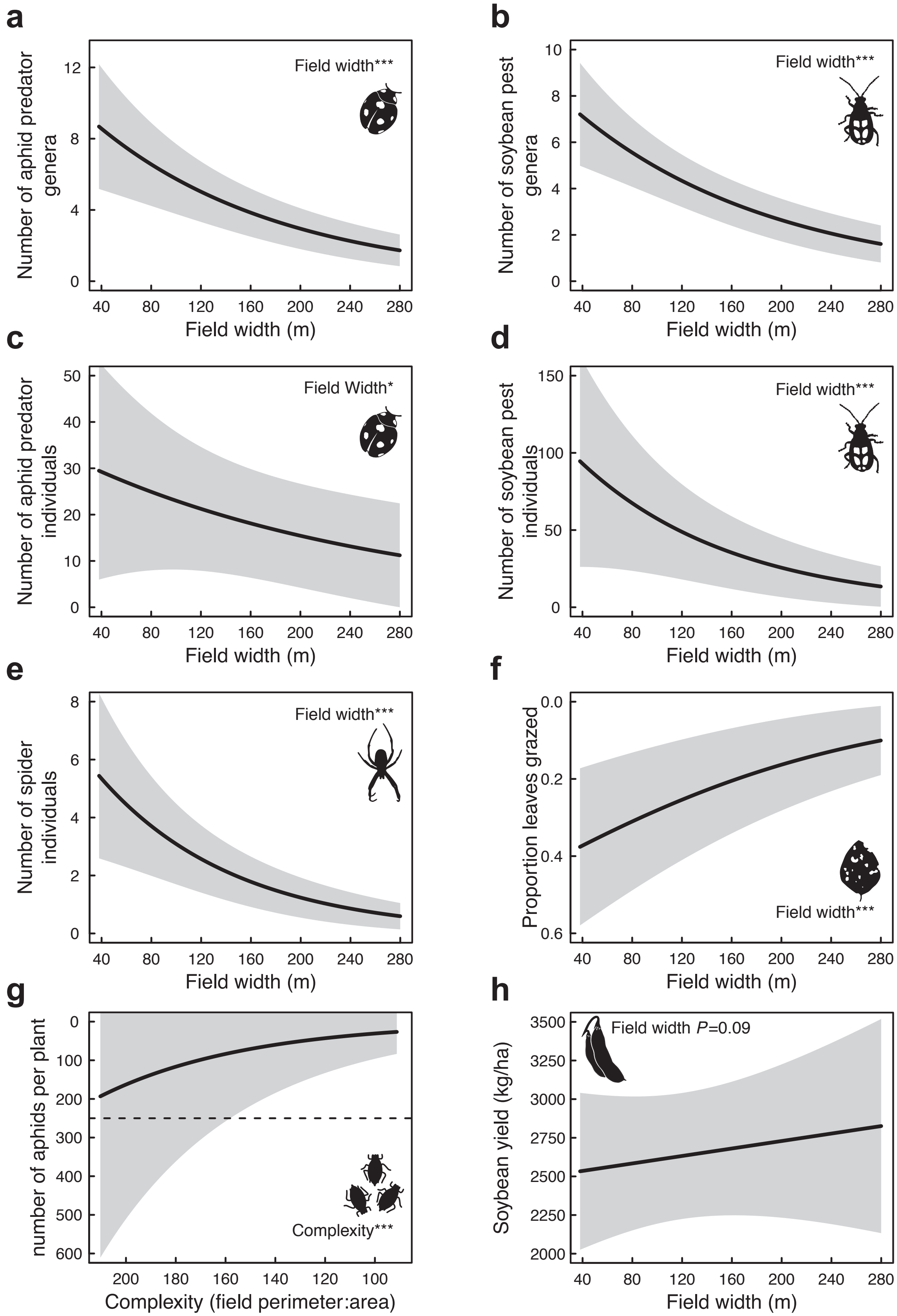

a
Aphid predator richness
−2 −1 0 1 2
Complexity (750m)
Prop. forest (750m)
Distance from forest
Field width
Aspect (SE)
Tillage (no−till)
Forest diversity
b
Soybean pest richness
−2 −1 0 1 2
Complexity (2000m)
Prop. Forest (2000m)
Distance from forest
Field width
Aspect (SE)
Tillage (No−till)
Forest diversity
c
Aphid predator abundance
−2 −1 0 1 2
Complexity (750m)
Prop. Forest (750m)
Distance from forest
Field width
Aspect (SE)
Tillage (No−till)
Forest diversity
d
Soybean pest abundance
−2 −1 0 1 2
Complexity (500m)
Prop. Forest (500m)
Distance from forest
Field width
Aspect (SE)
Tillage (No−till)
Forest diversity
e
Spider abundance
−2 −1 0 1 2
Complexity (2000m)
Prop. Forest (2000m)
Distance from forest
Field width
Aspect (SE)
Tillage (No−till)
Forest diversity
f
Soybean herbivory regulation
−2 −1 0 1 2
Complexity (2000m)
Prop. Forest (2000m)
Distance from forest
Field width
Aspect (SE)
Tillage (No−till)
Forest diversity
Pest Richness
Pest Abundance
g
Soybean aphid regulation
−2 −1 0 1 2
Complexity (1000m)
Prop. Forest (1000m)
Distance from forest
Field width
Aspect (SE)
Tillage (No−till)
Forest diversity
Predator Richness
Predator Abundance
Spider Abundance
h
Soybean yield
−1000 −500 0 500 1000 1500
Complexity (500m)
Prop. forest (500m)
Distance from forest
Field width
Aspect (SE)
Tillage (No−till)
Forest diversity
Aphid abundance
Soybean herbivory

Figure 4.1: Model-averaged coefficients of the effects of landscape and field variables on arthropod richness, arthropod abundance, and ecosystem services. Model-averaged coefficients for (**a**) aphid predator richness, (**b**) soybean pest richness, (**c**) aphid predator abundance, (**d**) soybean pest abundance, (**e**) spider abundance, (**f**) soybean herbivory regulation, (**g**) soybean aphid regulation, and (**h**) soybean yield. We show model-averaged coefficients (*points*) for each predictor variable that was included in the averaged set of best models (those models within 2 AICc of the best model) ± 95 % confidence intervals (*whiskers*). Points to the left of the dashed lines are negative relationships, to the right positive. Black points and whiskers indicate variables with importance values > 0.5, grey are those with importance values < 0.5.



a
Number of aphid predator genera
Field width***
Field width (m)
b
Number of soybean pest genera
Field width***
Field width (m)
c
Number of aphid predator individuals
Field Width*
Field width (m)
d
Number of soybean pest individuals
Field width***
Field width (m)
e
Number of spider individuals
Field width***
Field width (m)
f
Proportion leaves grazed
Field width***
Field width (m)
g
number of aphids per plant
Complexity***
Complexity (field perimeter:area)
h
Soybean yield (kg/ha)
Field width P=0.09
Field width (m)

Figure 4.2: Relationships between field width or landscape complexity and arthropod richness, arthropod abundance, and ecosystem services. (**a**) aphid predator richness, (**b**) soybean pest richness, (**c**) aphid predator abundance, (**d**) soybean pest abundance, (**e**) spider abundance, (**f**) soybean herbivory regulation, (**g**) soybean aphid regulation, and (**h**) soybean yield. We show mean relationships (*black lines*) and 95% confidence areas (*grey areas*) from model averaged generalized linear mixed models with the other model explanatory variables (*i.e.* distance-from-forest, tillage, proportion forest, etc.) kept at mean levels. Note that the x-axes of (**a**-**e**,**g**,**h**) are field width, and (**f**) is landscape complexity at ⨁ 1 km. Y-axes are reversed in (**f**) and (**g**) so that values higher on the axis represent higher levels of ecosystem service provision; the x-axis in (**g**) is reversed to run from complicated to simple landscapes. The dashed horizontal line in (**g**) is the threshold at which a control action must take place to prevent economic damage to soybeans from soybean aphids (250 aphids plant^{-1}). Statistically significant relationships are indicated with * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$. $n = 34$ fields.

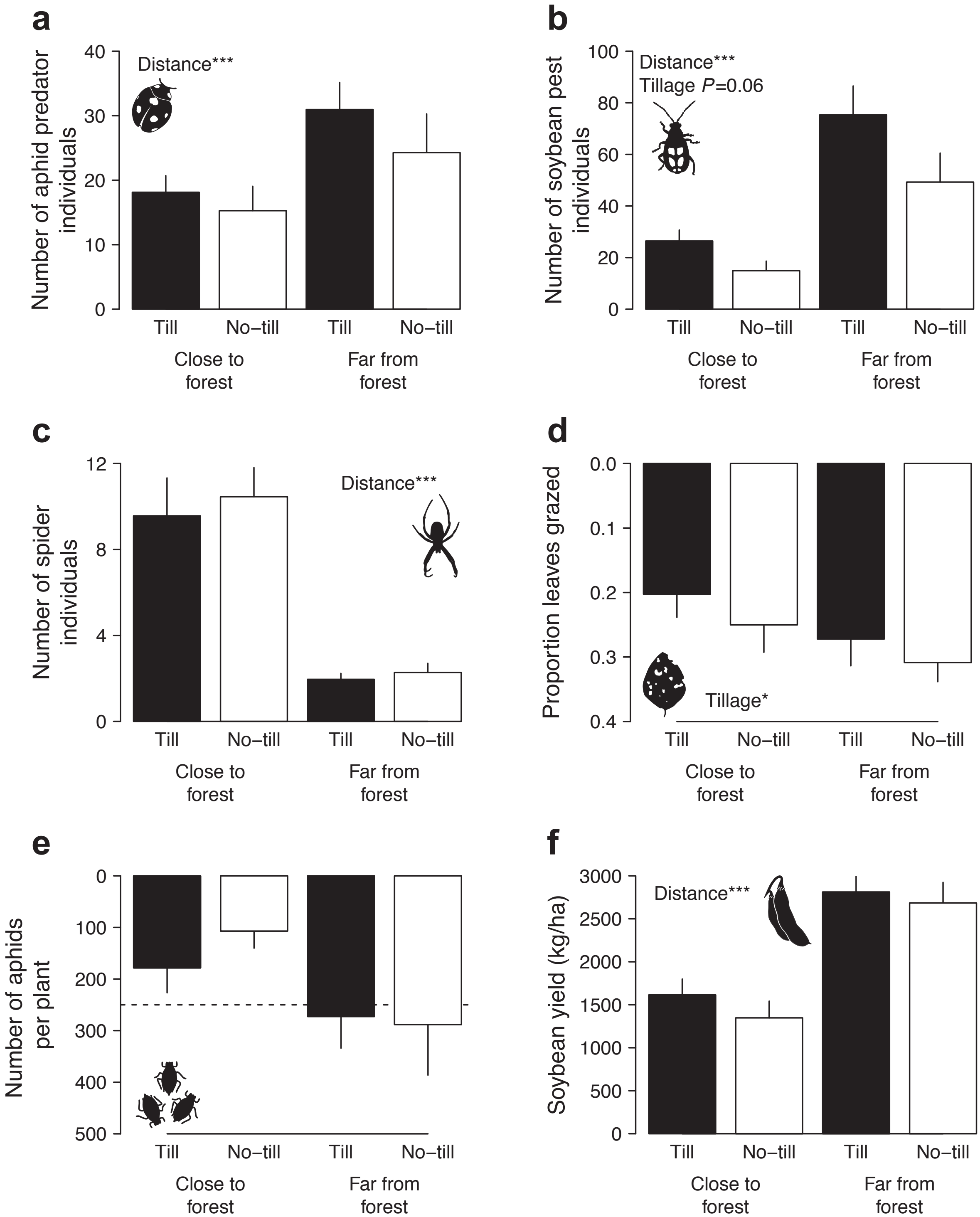

a
Number of aphid predator individuals
Distance***
40
30
20
10
0
Till
No–till
Till
No–till
Close to forest
Far from forest
b
Number of soybean pest individuals
Distance***
Tillage P=0.06
100
80
60
40
20
0
Till
No–till
Till
No–till
Close to forest
Far from forest
c
Number of spider individuals
Distance***
12
8
4
0
Till
No–till
Till
No–till
Close to forest
Far from forest
d
Proportion leaves grazed
0.0
0.1
0.2
0.3
0.4
Tillage*
Till
No–till
Till
No–till
Close to forest
Far from forest
e
Number of aphids per plant
0
100
200
300
400
500
Till
No–till
Till
No–till
Close to forest
Far from forest
f
Soybean yield (kg/ha)
Distance***
3000
2500
2000
1500
1000
500
0
Till
No–till
Till
No–till
Close to forest
Far from forest

Figure 4.3: **Effects of distance-from-forest and planting method on arthropod abundance and ecosystem services.** Abundance of (**a**) predators of aphids, (**b**) soybean pests, and (**c**) spiders; (**d**) soybean herbivory regulation, (**e**) soybean aphid regulation, and (**f**) soybean yield in conventionally tilled (*black bars*) and no-till fields (*white bars*) at 0 m from adjacent forest fragments (*close-to-forest*) and 500 m from forest fragments (*far-from-forest*). Data was averaged from the two years of the study. Bars indicate means ± standard errors. Y-axes are reversed in (**d**) and (**e**) so that values higher on the axis represent higher levels of ecosystem service provision; the dashed horizontal line in (**e**) is the threshold at which a control action must take place to prevent economic damage to soybeans from soybean aphids (250 aphids $plant^{-1}$). Statistically significant relationships from model averaged generalized linear mixed effects models are indicated with * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$. $n = 34$ fields.

averaged model due to collinearity with other variables, but aphid numbers were almost double at 500 m from forest (Figure 4.3). Aphid regulation decreased with both predator abundance and diversity but increased with spider abundance, although none of these relationships were statistically significant (Figure 4.1). Arthropod herbivory affected on average 16.2 ± 2.0 % of soybean leaves in 2010 and 29.6 ± 2.3 % of leaves in 2011. Herbivory regulation was positively related to field width (p < 0.001), but negatively to pest abundance and no-till planting (abundance: p < 0.001 ; tillage: p = 0.039; Figure 4.1). Soybean herbivory decreased by 73 % as field width increased from 40 m to 280 m (Figure 4.2) and 15 % with conventional tillage (Figure 4.3). Our averaged model for aphid regulation explained a substantial portion of the variance (R^2_{fixed} = 31 %), as opposed to our model for herbivory regulation (R^2_{fixed} = 12 %).

4.4.4 *Landscape structure effects on crop yield*

Soybean yield was positively related to distance-from-forest, the proportion of forest at ⊕ 0.5 km, and field width, although this last was relationship was only marginally significant (distance: p < 0.001; forest: p = 0.013; field width: p = 0.093; Figure 4.1). Distance from forest had the strongest effect, with yield increasing by 82 % (1 248 kg ha^{-1}) at 500 m from forest (Figure 4.3). Average soybean yield increased by approximately 300 kg ha^{-1} over the range of field widths in our study (Figure 4.2). The fixed effects portion of our average model explained almost half of the variation in soybean yield (R^2_{fixed} = 47 %).

4.5 DISCUSSION

We found consistent evidence that arthropod abundance and diversity are strongly affected by landscape structure, particularly by the presence of field margins and forest fragments. However, these patterns of arthropod diversity had variable effects on pest regulation and crop production, which instead were influenced more by the larger landscape and management contexts of each field. Aphid abundances in particular depended most on how landscape structure influenced aphids, rather than how it affected their predators. Similarly, crop production depended more on landscape structure than pest regulation. Our results demonstrate that patterns of arthropod diversity and abundance across agricultural landscapes are not necessarily correlated with pest regulation or crop production.

4.5.1 *Patterns of arthropod diversity and abundance*

We saw distinct effects of both forest fragments and field margins on the abundance and diversity of arthropods. Predators of aphids, spiders, and soybean pests all decreased significantly in abundance and richness as soybean fields widened (Figure 4.2), as did overall arthropod diversity (Figure 4.4 in the Supporting Information). Numerous natural enemy groups are more abundant and diverse near field margins, including Coccinellidae, Syrphidae, Chrysopidae, and Araneae predators of aphids (Dennis, Fry & Anderson 2000; Werling 2009). Field margins and hedgerows can also facilitate arthropod movement (Holzschuh, Steffan-Dewenter & Tscharntke 2009; van Geert, van Rossum & Triest 2010), and there is both empirical (Burel 1996; Dennis, Fry & Anderson 2000) and modeling evidence (Bianchi *et al.* 2010; Segoli & Rosenheim 2012) that their presence and arrangement, as well as field size, can be important for arthropod dispersal into fields. Our results emphasize the importance of field margins and field size for arthropod dispersal into fields in this region, as opposed to broader-scale landscape complexity, which had much weaker and more variable effects (Figure 4.1).

We expected forest fragments would have similar effects to field margins for arthropods, but found variable results. Aphid predator richness and abundance, and soybean pest abundance were greater far-from-forest (Figure 4.1, 4.3), while spider abundance and overall arthropod richness (Figure 4.4 in the Supporting Information) were significantly higher near-to-forest. While remnant forest fragments are important habitats for arthropods in similar ways to field margins (Bianchi, Booij & Tscharntke 2006), soybean growth was significantly reduced close-to-forest, and aphid numbers were much lower (Figure 4.3). Resource availability is important for arthropod herbivores and predators and can drive their population dynamics (Chaplin-Kramer *et al.* 2011). For example, Noma *et al.* (2010) found that many aphid predators respond positively to increased soybean aphid populations. Similarly, soybean growth and phenology can influence aphid population dynamics (Bahlai, Weiss & Hallett 2013). Thus, over our distance-from-forest transects, varying resource levels (*i.e.* soybean growth and aphid numbers) may have been important drivers of soybean pest and aphid predator abundances. At the same time, increased diversity and abundance of generalist predators near forests, such as spiders or other predators, may have also reduced aphid predators and soybean pests (Rand, Tylianakis & Tscharntke 2006).

Overall, our results show that both forest fragments and field margins can have strong effects on arthropod abundance in neighbouring fields, and that these effects can vary greatly for the different insect groups important for ecosystem services or disservices. Most studies of the effects of landscape structure on arthropods and ecosystem services do not distinguish between different non-crop habitats and field margins, but combine them into "landscape complexity." Our results highlight the importance of understanding how different components of landscape complexity affect distinct arthropod groups.

4.5.2 Patterns of pest regulation

Both of our components of pest regulation in our study - aphid and herbivory regulation - were greatest in simple landscapes, but the scale at which these effects occurred differed. These results run counter to the general consensus that simpler landscapes have fewer natural enemies and greater pest pressure (Bianchi, Booij & Tscharntke 2006), although recent analyses are challenging this (see Chaplin-Kramer *et al.* 2011). In our study, herbivory regulation increased as field width increased, while aphid regulation increased as the landscape was simplified (*i.e.* landscape complexity decreased) within 1 km of each field (Figure 4.2). Landscape complexity and field width are correlated in this landscape (2010: Pearson corr. = -0.68, p = 0.005; 2011: Pearson corr. = -0.50, p = 0.022); as fields widen, broader-scale landscape complexity decreases at 1 km, making it difficult to fully disentangle the independent effects of each variable.

The decrease in herbivory with increased field width was mainly a function of decreased soybean pest abundance. While landscape complexity and field margins are known to positively influence natural enemies, the effects of these variables on arthropod pests are much less certain. Our results suggest that despite significantly fewer natural enemies (*i.e.* spiders) in wide fields, this may not necessarily lead to increased pest pressure if pests respond in similar ways to changes in landscape structure. While we were unable to accurately determine the abundance of other arthropod predators that might be controlling soybean pests, our results highlight the need to measure patterns of both arthropod predators and pests across landscapes in pest regulation studies.

For aphid regulation, we saw an unexpected trend; aphid numbers were greater in complex landscapes and were positively related to aphid predator diversity (Figure 4.1). For the latter, we believe that aphid predators were likely responding to aphid abundance (see Section 4.5.1), but for the former, the mechanism is unclear as landscape effects on aphids are not well understood. Aphids are wind dispersed (Ragsdale *et al.* 2011), and the field margins, hedgerows, and forest fragments in our complex landscapes may have trapped aphids (Irwin, Kampmeier & Weisser 2007), increasing their abundance. There is some evidence that forest fragments acted this way early in each growing season (Mitchell, Bennett & Gonzalez *Submitted*). Alternatively, increased perennial habitat and hedgerows in more complex landscapes could have provided aphids shelter and overwintering host plant species (Thies, Roschewitz & Tscharntke 2005; Bahlai *et al.* 2010). However, we only found *Rhamnus* shrubs, a favored overwintering host plant, in five of the thirty-four forest fragments adjacent to our soybean fields and always at low abundance.

Our results highlight the fact that pest regulation across agricultural landscapes relies not only on beneficial arthropods, but also on pest movement. While landscape complexity can benefit both aphid parasitoids (Thies, Roschewitz & Tscharntke 2005) and other natural enemies (Taki *et al.* 2013) that provide ecosystem services, this can be counterbalanced by increased pest pressure, resulting in little change in pest regulation. Most studies use predator abundance to measure pest regulation, and very few quantify pest pressure or the actual reduction of pest populations by predators (Chaplin-Kramer *et al.* 2011). However, what matters most to farmers are the absolute levels of pests in fields. We therefore measured not only beneficial arthropods such as aphid predators and spiders, but also aphid abundances and herbivory levels. Our measures give a better indication of the service that the landscape and its constituent organisms provide, including both active (*e.g.* aphid predation by beneficial arthropods) and passive (*e.g.* landscape structure affecting pest dispersal patterns) mechanisms. While we couldn't distinguish between these two mechanisms or quantify actual levels of aphid predation in our study, our results nevertheless demonstrate that landscape patterns of pest abundance can counteract the potential control that beneficial arthropods provide (Chaplin-Kramer & Kremen 2012). To accurately quantify changes in pest regulation services and disservices across agricultural landscapes, future studies should measure actual pest suppression by arthropod predators (*e.g.* cage experiments), in combination with observations of pest pressure as landscape structure and complexity vary at different scales (Chaplin-Kramer *et al.* 2011).

4.5.3 Spatial scale and management for pest regulation

Our models suggest that management of landscape structure for arthropod diversity and abundance, and for pest regulation, will be most effective if focused within 2 km or less of soybean fields. Predators of aphids responded most strongly to landscape structure at 0.75 km, soybean pests at 0.5 and 2 km, and aphids at 1 km. While past studies suggest that larger-bodied insects experience the landscape at broader-scales (Tscharntke & Brandl 2004), as do aphids and their predators (Gardiner *et al.* 2009), this was not readily evident in our results. However, each of our arthropod groups included a diversity of species that varied widely in body sizes, which may have influenced our results. Irrespective of the best scale identified by our models, our results emphasize the importance of local-scale versus broader landscape-scale structure for pest regulation. For most of our arthropod and ecosystem service measures, field width or distance-from-forest had stronger effects than other broader landscape level variables. The relative importance of field versus landscape-level scales has not been well investigated and few studies include field-level measures (Chaplin-Kramer & Kremen 2012). Therefore, the broader importance of field versus landscape-level structure for pest regulation has yet to be established, despite the fact that field-level changes are likely easier and more practical to implement.

4.5.4 Patterns of crop production

Crop production, the most important metric for farmers and the service for which most of our landscape is managed, showed little relation to arthropod diversity/abundance or pest regulation (Figure 4.1). Similar to aphid regulation, soybean yield was positively related to soybean herbivory. We assume that the low levels of herbivory we observed did not affect soybean yield, and instead that soybean pests were responding to soybean growth. Soybean yield instead showed a strong relationship with distance-from-forest, likely an effect of competition and shading from the nearby forest (Kort 1988) or soil compaction by farm equipment at field margins (Hamza & Anderson 2005) as soybean yield also increased slightly with field width

(Figure 4.2). Soybean yield also increased with the proportion of forest in the surrounding landscape at 500 m. The mechanism for this effect is uncertain, but may be due to forest fragments providing pollinator habitat and increasing soybean pollination, which in some cases can improve soybean yield (Chiari *et al.* 2005).

Our results suggest that the landscape structure and management variables that drive soybean yield are independent of those for pest regulation in this system, at least over the period of our study. Therefore, by altering different landscape structure variables, land managers might be able to increase both services. For instance, by planting soybean in wider fields with high proportions of surrounding forest at 500 m to increase pest regulation and soybean yield simultaneously. Changes in landscape structure to maximize pest regulation and crop provision may also have negative effects on other ecosystem services. For example, conventional tillage increased pest regulation and soybean yield in our study. However, wide-scale implementation of this practice in our region would likely increase nutrient loss and soil erosion. Additional studies that investigate how landscape structure influences multiple ecosystem services simultaneously are needed to create effective landscape-level management plans.

4.5.5 Conclusions

We show that landscape structure can have significant effects on the arthropod groups that affect ecosystem services and disservices, but that these changes may not necessarily influence pest regulation and crop production. The effects of landscape structure are often unique for each arthropod group or ecosystem service, and sometimes, effects on one arthropod group can counteract those for another, leading to unexpected consequences for service provision. For example, increases in beneficial insects may be counterbalanced by increased pest pressure as landscape structure, in our case field width, varies. Our results also suggest that management of landscape structure at distances within 2 km of soybean fields will be most effective for these arthropod groups and ecosystem services. These results highlight the need to understand how the specific components of landscape structure and complexity affect multiple arthropod groups and how these effects, in turn, affect multiple ecosystem services. Increased knowledge in this area should lead to better management for both biodiversity and the set of ecosystem services that multifunctional agricultural landscapes provide.

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4.8 SUPPORTING INFORMATION

Table 4.1: Potential soybean aphid (*Aphis glycines* Matsumura) predators collected in 2010 and 2011 in soybean fields of the Montérégie, Québec.

Order		2010		2011	
Family	Species or Genus	Total	%	Total	%
Coleoptera					
Cantharidae	*Rhagonycha fulva* (Scopoli)	2	0.4	–	–
Coccinellidae	*Coccinella septempunctata* (L.)	5	1.1	21	1.9
	Coleomegilla maculata (DeG.)	2	0.4	–	–
	Harmonia axyridis (Pallas)	31	6.8	63	5.7
	Hippodamia variegata (Goeze)	–	–	8	0.7
	Propylea quatuordecimpunctata (L.)	17	3.7	38	3.4
	Coccinellidae spp. larvae	27	5.9	303	27.4
Lampyridae	*Ellychnia corrusca* (L.)	–	–	1	0.1
	Photinus scintillans (Say)	2	0.4	–	–
Diptera					
Dolichopodidae	*Condylostylus* sp.	6	1.3	7	0.6
Syrphidae	*Allograpta* sp.	5	1.1	2	0.2
	Chalcosyrphus sp.	–	–	1	0.1
	Eristalis sp.	–	–	1	0.1
	Melanostoma sp.	3	0.7	3	0.3
	Sphaerophoria sp.	10	2.2	1	0.1
	Syrphus sp.	–	–	3	0.3
	Toxomerus spp.	42	9.2	40	3.6
Heteroptera					
Anthocoridae	*Calliodis temnostethoides* (Reuter)	1	0.2	–	–
	Orius spp.	242	53.0	424	38.3
Miridae	*Phytocoris* sp.	1	0.2	–	–
	Plagiognathus sp.	6	1.3	125	11.3
Nabidae	*Nabis americoferus* (Carayon)	33	7.2	17	1.5
Neuroptera					
Chrysopidae	*Chrysopa oculata* (Say)	22	4.8	49	4.4
Total		**457**	**100.0**	**1107**	**100.0**

Table 4.2: Potential soybean (*Glycine max* L. Merr.) pests collected in 2010 and 2011 in soybean fields of the Montérégie, Québec.

Order		2010		2011	
Family	Species, Genus, or Subfamily	Total	%	Total	%
Coleoptera					
Chrysomelidae	*Cerotoma trifurcata* (Forster)	7	0.5	23	1.3
	Chrysomelinae sp.	1	0.1	–	–
	Diabrotica spp.	41	3.1	56	3.2
	Systena frontalis (Fabricius)	988	74.7	1272	73.8
	Popillia japonica (Newman)	–	–	1	0.1
Diptera					
Platystomatidae	*Riviella* sp.	39	3.0	58	3.4
Hemiptera					
Cicadellidae	*Empoasca fabae* (Uhler)	133	10.1	53	3.1
Miridae	*Adelphocoris lineolatus* (Goeze)	24	1.8	14	0.8
	Halticus bractatus (Say)	4	0.3	5	0.3
	Lygus lineolaris (PdeB.)	43	3.3	74	4.3
Pentatomidae	*Acrosternum hilare* (Say)	8	0.6	–	–
	Euschistus sp.	2	0.2	4	0.2
Lepidoptera	Lepidoptera caterpillars	24	1.8	131	7.6
Orthoptera					
Acrididae	Acridinae sp.	–	–	4	0.2
	Melanoplinae sp.	1	0.1	14	0.8
	Oedipodinae sp.	–	–	3	0.2
Gryllidae	Gryllidae sp.	1	0.1	7	0.4
	Oecanthinae sp.	–	–	3	0.2
Thysanoptera					
Thripidae	*Frankliniella* sp.	6	0.5	2	0.1
Total		**1322**	**100.0**	**1724**	**100.0**

Table 4.3: Model averaging results for aphid predator/soybean pest richness and abundance, aphid and herbivory regulation, soybean yield, spider abundance, and arthropod morphospecies richness as functions of landscape structure, forest diversity, and field management variables.

Model (variable)	**Estimate**	**z-value**	***p*-value**[a]	**Importance**[b]	R^2_{fixed}[c]	R^2_{full}[d]
Aphid predator richness					0.46	0.60
Field width	-0.840 ± 0.159	**5.290**	**<0.001**	1.00	–	–
Aspect	0.265 ± 0.151	1.757	0.079	0.57	–	–
Proportion $forest_{750m}$	0.238 ± 0.167	1.422	0.155	0.41	–	–
Tillage	-0.228 ± 0.163	1.404	0.160	0.34	–	–
Distance from forest	0.136 ± 0.112	1.214	0.225	0.30	–	–
Aphid predator abundance					0.29	0.82
Distance from forest	0.496 ± 0.093	**5.339**	**<0.001**	1.00	–	–
Field width	-0.615 ± 0.271	**2.267**	**0.023**	0.82	–	–
Proportion $forest_{750m}$	0.557 ± 0.293	1.901	0.057	0.65	–	–
Tillage	-0.481 ± 0.299	1.607	0.108	0.55	–	–
Soybean pest richness					0.39	0.52
Field width	-0.781 ± 0.155	**5.035**	**<0.001**	1.00	–	–
Aspect	0.202 ± 0.146	1.383	0.167	0.44	–	–
Landscape $complexity_{2000m}$	0.220 ± 0.162	1.361	0.173	0.35	–	–
Tillage	-0.138 ± 0.167	0.833	0.405	0.20	–	–
Soybean pest abundance					0.42	0.71
Distance from forest	1.056 ± 0.163	**6.498**	**<0.001**	1.00	–	–
Field width	-1.015 ± 0.285	**3.561**	**<0.001**	1.00	–	–
Tillage	-0.582 ± 0.310	1.876	0.061	0.67	–	–
Forest diversity	-0.369 ± 0.276	1.338	0.181	0.37	–	–
Aspect	0.362 ± 0.291	1.247	0.212	0.29	–	–
Proportion forest500m	0.354 ± 0.299	1.183	0.237	0.16	–	–
Soybean aphid regulation					0.31	0.74
Landscape $complexity_{1000m}$	-1.162 ± 0.326	**3.563**	**<0.001**	1.00	–	–
Aphid predator richness	-0.362 ± 0.221	1.638	0.101	0.65	–	–
Aphid predator abundance	-0.293 ± 0.237	1.235	0.217	0.20	–	–
Tillage	-0.347 ± 0.329	1.053	0.292	0.17	–	–
Spider abundance	0.168 ± 0.182	0.922	0.356	0.15	–	–
Field width	0.327 ± 0.372	0.879	0.379	0.14	–	–
Herbivory regulation					0.12	0.13
Soybean pest abundance	-0.797 ± 0.174	**4.576**	**<0.001**	1.00	–	–
Field width	0.882 ± 0.221	**3.984**	**<0.001**	1.00	–	–
Tillage	-0.421 ± 0.204	**2.068**	**0.039**	0.72	–	–
Aspect	-0.321 ± 0.202	1.585	0.113	0.48	–	–
Proportion $forest_{2000m}$	-0.314 ± 0.226	1.394	0.163	0.37	–	–
Forest diversity	0.274 ± 0.209	1.309	0.190	0.30	–	–
Soybean yield					0.47	0.70
Distance from forest	1231.5 ± 142.8	**8.622**	**<0.001**	1.00	–	–
Proportion $forest_{500m}$	576.3 ± 231.8	**2.486**	**0.013**	1.00	–	–
Soybean herbivory	264.6 ± 190.5	1.389	0.165	0.88	–	–
Field width	366.2 ± 217.7	1.682	0.093	0.42	–	–
Tillage	-345.5 ± 226.6	1.525	0.127	0.37	–	–
Aphid abundance	115.3 ± 204.1	0.565	0.572	0.12	–	–
Aspect	-185.4 ± 239.2	0.775	0.438	0.09	–	–

Table 4.3: Cont'd.

Model (variable)	Estimate	z-value	*p*-value[a]	Importance[b]	R^2_{fixed}[c]	R^2_{full}[d]
Spider abundance					0.70	0.88
Distance from forest	-1.566 ± 0.132	**11.866**	**<0.001**	1.00	–	–
Field width	-1.152 ± 0.232	**4.973**	**<0.001**	1.00	–	–
Forest diversity	0.492 ± 0.217	**2.269**	**0.023**	0.92	–	–
Aspect	0.345 ± 0.224	1.541	0.123	0.48	–	–
Tillage	0.275 ± 0.233	1.181	0.238	0.23	–	–
Proportion $forest_{2000m}$	-0.320 ± 0.263	1.220	0.222	0.11	–	–
Landscape $complexity_{2000m}$	-0.209 ± 0.235	0.889	0.374	0.17	–	–
Arthropod richness					0.55	0.92
Distance from forest	-0.303 ± 0.044	**6.915**	**<0.001**	1.00	–	–
Field width	-0.943 ± 0.158	**5.968**	**<0.001**	1.00	–	–
Proportion $forest_{3000m}$	-0.227 ± 0.156	1.461	0.144	0.37	–	–
Tillage	-0.120 ± 0.154	0.778	0.437	0.18	–	–

[a]Statistically significant *p*-values < 0.05 are indicated in bold.
[b]Variable importance values calculated as the sum of the model weights within the set that include that variable. Values > 0.5 are underlined.
[c]R-squared values for the fixed component of the model (i.e., with random effects excluded).
[d]R-squared values for the full model, including both fixed and random components.

Table 4.4: Component models (Λ_{AIC} < 2.0 from best model) **used in model averaging** for aphid predator and soybean pest richness and abundance, aphid and herbivory regulation, soybean yield, spider abundance, and arthropod morphospecies richness as functions of landscape structure, forest diversity, and field management variables.

Model (variable, coefficient ± SE)	**AIC**[a]	**Λ_{AIC}**[b]	**w_{AIC}**[c]
Aphid predator richness			
1. Field orientation (0.26 ± 0.14) + field width (-0.89 ± 0.14)	77.6	0.0	0.15
2. Field orientation (0.32 ± 0.14) + tillage (-0.21 ± 0.16) + field width (-0.86 ± 0.14)	78.3	0.7	0.11
3. Field width (-0.79 ± 0.16) + proportion $forest_{750m}$ (0.24 ± 0.15)	78.3	0.7	0.11
4. Field width (-0.88 ± 0.15)	78.4	0.8	0.10
5. Distance from forest (0.14 ± 0.11) + field orientation (0.26 ± 0.14) + field width (-0.89 ± 0.14)	78.5	0.9	0.10
6. Tillage (-0.23 ± 0.17) + field width (-0.74 ± 0.16) + proportion $forest_{750m}$ (0.32 ± 0.16)	78.8	1.2	0.08
7. Field orientation (0.24 ± 0.15) + tillage (-0.27 ± 0.16) + field width (-0.77 ± 0.15) + proportion $forest_{750m}$ (0.22 ± 0.16)	78.9	1.3	0.08
8. Field orientation (0.19 ± 0.16) + field width (-0.83 ± 0.16) + proportion $forest_{750m}$ (0.15 ± 0.16)	79.2	1.6	0.07
9. Distance from forest (0.14 ± 0.11) + field width (-0.79 ± 0.16) + proportion $forest_{750m}$ (0.24 ± 0.15)	79.2	1.6	0.07
10. Distance from forest (0.14 ± 0.11) + field width (-0.88 ± 0.15)	79.2	1.6	0.07
11. Distance from forest (0.14 ± 0.11) + field orientation (0.32 ± 0.14) + tillage (-0.21 ± 0.16) + field width (-0.86 ± 0.14)	79.3	1.7	0.07
Aphid predator abundance			
1. Distance from forest (0.50 ± 0.09) + tillage (-0.47 ± 0.27) + field width (-0.48 ± 0.25) + proportion $forest_{750m}$ (0.56 ± 0.26)	218.2	0.0	0.26
2. Distance from forest (0.50 ± 0.09) + field width (-0.73 ± 0.25)	218.4	0.2	0.24
3. Distance from forest (0.50 ± 0.09) + field width (-0.61 ± 0.25) + proportion $forest_{750m}$ 0.39 ± 0.25)	218.6	0.4	0.21
4. Distance from forest (0.50 ± 0.09) + tillage (-0.62 ± 0.28) + proportion $forest_{750m}$ (0.75 ± 0.26)	218.9	0.7	0.18
5. Distance from forest (0.50 ± 0.09) + tillage (-0.27 ± 0.27) + field width (-0.69 ± 0.25)	219.9	1.7	0.11
Soybean pest richness			
1. Field width (-0.81 ± 0.15)	72.1	0.0	0.26
2. Field width (-0.73 ± 0.16) + landscape $complexity_{2000m}$ (0.22 ± 0.16)	72.6	0.5	0.21
3. Field orientation (0.19 ± 0.14) + field width (-0.81 ± 0.15)	72.7	0.6	0.19
4. Field orientation (0.18 ± 0.14) + field width (-0.73 ± 0.15) + landscape $complexity_{2000m}$ (0.21 ± 0.16)	73.4	1.3	0.14
5. Field orientation (0.24 ± 0.15) + tillage (-0.18 ± 0.16) + field width (-0.80 ± 0.14)	73.9	1.8	0.10
6. Tillage (-0.10 ± 0.16) + field width (-0.80 ± 0.15)	74.1	2.0	0.10

[a]Akaike's information criterion.
[b]The difference between AIC values of the best ranked model and model *i*.
[c]Akaike weight.

Table 4.4: Cont'd.

Model (variable, coefficient ± SE)	AIC[a]	Λ_{AIC}[b]	w_{AIC}[c]
Soybean pest abundance			
1. Distance from forest (1.06 ± 0.16) + tillage (-0.48 ± 0.30) + field width (-1.0 ± 0.28)	294.1	0.0	0.17
2. Distance from forest (1.06 ± 0.16) + field width (-1.05 ± 0.29)	294.2	0.1	0.17
3. Distance from forest (1.06 ± 0.16) + field orientation (0.41 ± 0.28) + tillage (-0.62 ± 0.30) + field width (-1.00 ± 0.27)	294.7	0.6	0.13
4. Distance from forest (1.06 ± 0.16) + tillage (-0.54 ± 0.29) + field width (-1.05 ± 0.27) + forest diversity (-0.39 ± 0.27)	294.8	0.7	0.12
5. Distance from forest (1.06 ± 0.16) + tillage (-0.61 ± 0.31) + field width (-0.88 ± 0.29) + proportion $forest_{500m}$ (0.35 ± 0.30)	295.4	1.3	0.09
6. Distance from forest (1.06 ± 0.16) + field orientation (0.40 ± 0.28) + tillage (-0.67 ± 0.30) + field width (-1.04 ± 0.26) + forest diversity (-0.38 ± 0.27)	295.4	1.3	0.09
7. Distance from forest (1.05 ± 0.16) + field width (-1.09 ± 0.28) + forest diversity (-0.32 ± 0.29)	295.4	1.3	0.09
8. Distance from forest (1.05 ± 0.16) + field orientation (0.22 ± 0.29) + field width (-1.06 ± 0.29)	296.0	1.9	0.07
9. Distance from forest (1.06 ± 0.16) + tillage (-0.67 ± 0.31) + field width (-0.92 ± 0.28) + forest diversity (-0.39 ± 0.27) + proportion $forest_{500m}$ (0.35 ± 0.29)	296.0	1.9	0.07
Soybean aphid regulation			
1. Predator richness (-0.36 ± 0.22) + landscape $complexity_{1000m}$ (-1.18 ± 0.31)	422.6	0.0	0.34
2. Predator abundance (-0.29 ± 0.24) + landscape $complexity_{1000m}$ (-1.19 ± 0.30)	423.6	1.0	0.20
3. Tillage (-0.35 ± 0.33) + Predator richness (-0.37 ± 0.22) + landscape $complexity_{1000m}$ (-1.22 ± 0.31)	424.0	1.4	0.17
4. Spider abundance (0.17 ± 0.18) + landscape $complexity_{1000m}$ (-1.18 ± 0.31)	424.3	1.7	0.15
5. Predator richness (-0.35 ± 0.22) + field width (0.33 ± 0.37) + landscape $complexity_{1000m}$ (-0.99 ± 0.37)	424.4	1.8	0.14
Soybean herbivory regulation			
1. Tillage (-0.49 ± 0.20) + pest abundance (-0.85 ± 0.17) + field width (0.95 ± 0.18)	238.2	0.0	0.15
2. Tillage (-0.42 ± 0.20) + pest abundance (-0.83 ± 0.17) + field width (0.77 ± 0.21) + proportion $forest_{2000m}$ (-0.33 ± 0.21)	238.6	0.4	0.13
3. Field orientation (-0.29 ± 0.19) + tillage (-0.37 ± 0.20) + pest abundance (-0.84 ± 0.17) + field width (0.92 ± 0.18)	238.6	0.4	0.13
4. Tillage (-0.46 ± 0.19) + pest abundance (-0.80 ± 0.17) + field width (1.03 ± 0.18) + forest diversity (0.31 ± 0.21)	238.8	0.6	0.12
5. Field orientation (-0.43 ± 0.19) + pest abundance (-0.75 ± 0.17) + field width (0.88 ± 0.19)	239.0	0.8	0.10
6. Field orientation (-0.25 ± 0.19) + tillage (-0.36 ± 0.20) + pest abundance (-0.79 ± 0.17) + field width (0.99 ± 0.18) + forest diversity (0.26 ± 0.20)	239.8	1.6	0.07
7. Pest abundance (-0.73 ± 0.17) + field width (0.66 ± 0.22) + proportion $forest_{2000m}$ (-0.44 ± 0.22)	240.0	1.8	0.06
8. Tillage (-0.41 ± 0.19) + pest abundance (-0.79 ± 0.17) + field width (0.86 ± 0.22) + forest diversity (0.24 ± 0.21) + proportion $forest_{2000m}$ (-0.26 ± 0.21)	240.1	1.9	0.06

[a]Akaike's information criterion.
[b]The difference between AIC values of the best ranked model and model *i*.
[c]Akaike weight.

Table 4.4: Cont'd.

Model (variable, coefficient ± SE)	AIC[a]	Λ_{AIC}[b]	w_{AIC}[c]
Soybean herbivory regulation cont'd.			
9. Field orientation (-0.22 ± 0.20)+ tillage (-0.35 ± 0.20) + pest abundance (-0.83 ± 0.17) + field width (0.80 ± 0.21) + proportion forest$_{2000m}$ (-0.24 ± 0.22)	240.1	1.9	0.06
10. Field orientation (-0.32 ± 0.20) + pest abundance (-0.74 ± 0.16) + field width (0.73 ± 0.22) + proportion forest$_{2000m}$ (-0.29 ± 0.23)	240.1	1.9	0.06
11. Field orientation (-0.38 ± 0.18) + pest abundance (-0.71 ± 0.17) + field width (0.95 ± 0.19) + forest diversity (0.27 ± 0.21)	240.2	2.0	0.06
Soybean yield			
1. Distance from forest (1232.2 ± 142.1) + herbivory regulation (246.5 ± 192.5) + proportion forest$_{500m}$ (501.7 ± 219.0)	1065.6	0.0	0.23
2. Distance from forest (1223.2 ± 141.8) + tillage (-383.9 ± 219.3) + herbivory regulation (290.4 ± 185.5) + field width (405.9 ± 211.8) + proportion forest$_{500m}$ (689.9 ± 218.2)	1065.7	0.1	0.23
3. Distance from forest (1230.9 ± 141.9) + herbivory regulation (252.5 ± 189.1) + field width (319.3 ± 215.3) + proportion forest$_{500m}$ (583.9 ± 219.2)	1066.0	0.4	0.19
4. Distance from forest (1226.9 ± 142.0) + tillage (-285.6 ± 224.8) + herbivory regulation (272.1 ± 191.0) + proportion forest$_{500m}$ (564.0 ± 219.4)	1066.6	1.0	0.14
5. Distance from forest (1253.4 ± 146.8) + aphid regulation (115.3 ± 204.1) + proportion forest$_{500m}$ (506.5 ± 222.0)	1066.9	1.3	0.12
6. Distance from forest (1229.5 ± 142.1) + field orientation (-185.4 ± 239.2) + herbivory regulation (259.4 ± 192.3) + proportion forest$_{500m}$ (579.6 ± 239.2)	1067.5	1.9	0.09
Spider Abundance			
1. Distance from forest (-1.57 ± 0.13) + field width (-1.11 ± 0.22) + forest diversity (0.47 ± 0.22)	139.2	0.0	0.21
2. Distance from forest (-1.57 ± 0.13) + field orientation (0.32 ± 0.21) + field width (-1.11 ± 0.21) + forest diversity (0.51 ± 0.21)	139.3	0.1	0.20
3. Distance from forest (-1.57 ± 0.13) + tillage (0.31 ± 0.23) + field width (-1.14 ± 0.22) + forest diversity (0.52 ± 0.22)	139.9	0.7	0.15
4. Distance from forest (-1.57 ± 0.13) + field orientation (0.45 ± 0.23) + field width (-1.28 ± 0.25) + forest diversity (0.47 ± 0.21) + proportion forest$_{2000m}$ (-0.32 ± 0.26)	140.4	1.2	0.11
5. Distance from forest (-1.57 ± 0.13) + field width (-1.18 ± 0.24) + forest diversity (0.45 ± 0.22) + landscape complexity$_{2000m}$ (-0.20 ± 0.24)	140.9	1.7	0.09
6. Distance from forest (-1.57 ± 0.13) + field orientation (0.26 ± 0.22) + tillage (0.22 ± 0.23) + field width (-1.13 ± 0.21) + forest diversity (0.53 ± 0.21)	141.0	1.8	0.08
7. Distance from forest (-1.57 ± 0.13) + field orientation (0.33 ± 0.21) + field width (-1.19 ± 0.23) + forest diversity (0.48 ± 0.21) + landscape complexity$_{2000m}$ (-0.22 ± 0.23)	141.0	1.8	0.08
8. Distance from forest (-1.57 ± 0.13) + field width (-1.17 ± 0.23)	141.1	2.0	0.08
Arthropod Morphospecies Richness			
1. Distance from forest (-0.30 ± 0.04) + field width (-0.91 ± 0.14)	187.6	0.0	0.45
2. Distance from forest (-0.30 ± 0.04) + field width (-1.01 ± 0.16) + proportion forest$_{3000m}$ (-0.23 ± 0.16)	188.0	0.4	0.37
3. Distance from forest (-0.30 ± 0.04) + tillage (-0.12 ± 0.15) + field width (-0.89 ± 0.14)	189.4	1.8	0.18

[a]Akaike's information criterion.
[b]The difference between AIC values of the best ranked model and model *i*.
[c]Akaike weight.

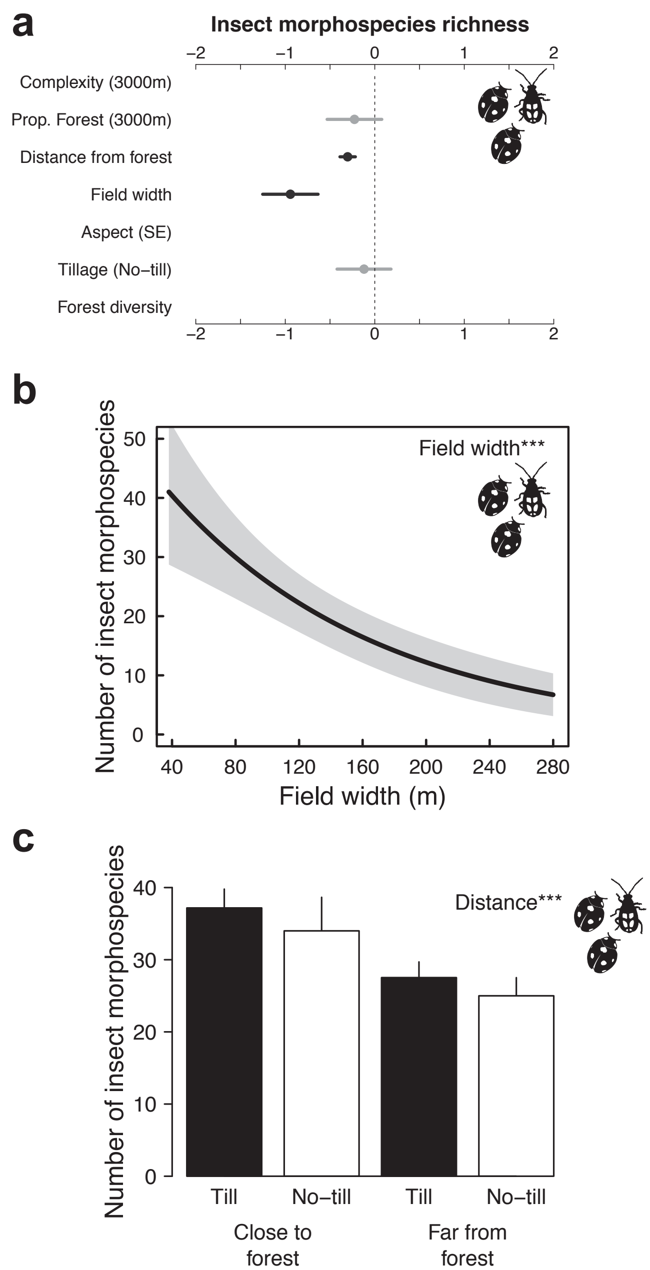

Figure 4.4: Patterns of landscape and field arthropod morphospecies richness. (**a**) Model averaged coefficients, (**b**) the relationship between field width and morphospecies richness, and (**c**) morphospecies richness in conventionally tilled (*black bars*) and no-till fields (*white bars*) at 0 m from adjacent forest fragments (*close-to-forest*) and 500 m from forest fragments (*far-from-forest*). Results and figures are as described for Figures 5.1, 5.2, and 5.3.

CONNECTING STATEMENT

In Chapters 3 and 4, I quantified the effects of landscape structure on patterns of ecosystem service provision in an agricultural landscape. While I found that landscape structure affects numerous ecosystem services, each in a unique way, and that some of these effects may be due to changes in the movement and populations of service-providing organisms, my results were limited to the field-scale. The implications of these results at broader scales are not fully known.

In Chapter 5, I scale up my results from Chapters 3 and 4 to further investigate how specific patterns of landscape structure and habitat fragmentation affect the provision of ecosystem services across whole landscapes. Using a simple modeling framework, I simulate the effects of habitat loss on ecosystem service provision in an agricultural landscape and ask how variation in the distance-dependent effects of habitat fragments on ecosystem service provision, along with patterns of habitat loss, will affect ecosystem service provision at different spatial scales.

While landscape connectivity is not directly modeled in this chapter, the research questions from Chapter 2 that this chapter begins to address are: (1) Theoretically, what are the ways that isolation might influence ecosystem service provision? (2) At what scales does habitat loss affect the provision of ecosystem services? and (3) How variable are ecosystem service responses to habitat loss and fragmentation change?

MODELING THE EFFECTS OF HABITAT LOSS AND LANDSCAPE STRUCTURE ON ECOSYSTEM SERVICES

5

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5.1 ABSTRACT

Globally, humans are altering landscapes by converting natural habitats to agricultural land for food production. The resulting loss and fragmentation of natural habitat has consequences for the ecosystem services provided by agricultural landscapes. However, our quantitative knowledge about precisely how different patterns of habitat fragmentation might affect ecosystem service provision is limited. We used a spatially explicit model to evaluate the impact of habitat loss and fragmentation on the supply of ecosystem services in a transformed landscape. We assumed that habitat fragments provide ecosystem services to the area surrounding them and modeled three distinct distance-dependent decay functions for ecosystem service provision in combination with seven patterns of habitat loss across the landscape. Habitat loss had strong and unimodal effects on ecosystem service supply, with clear thresholds indicating rapid loss of service provision beyond critical levels of habitat loss. In addition, we observed a tradeoff between ecosystem service provision and habitat conservation, and a mismatch between ecosystem service provision at landscape and field scales. Importantly, the pattern of habitat loss mitigated or intensified these tradeoffs and mismatches. Our model suggests that controlling patterns of habitat loss and fragmentation could be a powerful means to manage ecosystem service provision and create multi-functional landscapes.

5.2 INTRODUCTION

Human-altered landscapes such as agro-ecosystems provide numerous ecosystem services to people, including food, pest regulation, water purification, crop pollination, and opportunities for recreation (Zhang *et al.* 2007; Power 2010). Many of the ecosystem services provided by agricultural landscapes depend on fragments of natural habitat and the biodiversity that they contain (Tscharntke *et al.* 2005). There is also increasing evidence that landscape structure – the arrangement, size, and shape of different ecosystems across landscapes, has important effects on service provision (Bodin *et al.* 2006; Kremen *et al.* 2007; Termorshuizen & Opdam 2009; Syrbe & Walz 2012). Therefore, it may be possible to change landscape structure to alter the provision of various ecosystem services (Fisher, Turner & Morling 2009). However, at present, spatially explicit models formalizing how landscape structure mediates the supply of ecosystem services are rare (Brosi, Armsworth & Daily 2008; Keitt 2009; Bianchi *et al.* 2010).

The structure of agricultural landscapes is largely the result of the loss and fragmentation of natural habitats due to the expansion of croplands (Saunders, Hobbs & Margules 1991). This typically results in small, remnant fragments of natural habitat, typically forests, meadows, or wetlands, surrounded by a matrix of agricultural fields (Fahrig *et al.* 2011). Fragments of natural habitat can affect ecosystem service provision by influencing the magnitude and movement patterns of the organisms or matter important for service provision (Gonzalez, Rayfield & Lindo 2011; Mitchell, Bennett & Gonzalez 2013). For example, natural ecosystems such as meadows and forests often provide nesting and foraging habitat for bees and other pollinators who then disperse into surrounding fields, providing pollination services (Tscharntke *et al.* 2005; Ricketts *et al.* 2008). Similarly, natural habitat fragments can act as sources of crop pest predators, helping provide pest regulation across agricultural landscapes (Bianchi, Booij & Tscharntke 2006; Chaplin-Kramer *et al.* 2011). Forest fragments can also modify and moderate the microclimate in their immediate vicinity, improving conditions for crop growth (Kort 1988), and other ecosystem types, such as wetlands, can store water and retain sediments and nutrients across agricultural landscapes (Brauman *et al.* 2007; Fennessy & Craft 2011). Natural habitats are also important components of aesthetic beauty and viewscapes (Swinton *et al.* 2007). These effects of natural habitat fragments across agricultural landscapes are often distance-dependent – they vary most along distance-to-habitat gradients within the agricultural matrix (*e.g.* Mitchell, Bennett & Gonzalez, *In Review*). This raises the possibility that the distribution and supply of ecosystem services can be managed by controlling the spatial position and configuration of habitat fragments and fields in agro-ecosystems (Fahrig *et al.* 2011; Syrbe & Walz 2012).

Understanding how changing landscape structure might affect different ecosystem services requires knowledge about how ecosystem service provision varies across landscapes. In particular, the spatial functions that describe how a habitat fragment of a given size and form influences the supply of ecosystems services in its proximity (Dobson *et al.* 2006; de Groot *et al.* 2010). However, the spatial functions linking ecosystem service production by habitat fragments to the locations where the service benefits are realized are not known for most ecosystem services (Kremen & Ostfeld 2005; Fisher, Turner & Morling 2009; Syrbe & Walz 2012). Two exceptions are pollination and pest regulation. For pollination, there is generally an exponential decline in pollination services with distance from forest (Ricketts *et al.* 2008; Keitt 2009), while pest regulation often depends on 'landscape complexity' or the diversity of habitats present (Bianchi, Booij & Tscharntke 2006; Chaplin-Kramer *et al.* 2011) and can decline with increasing field size (Werling & Gratton 2010; Segoli & Rosenheim 2012). Recent studies have also started to describe the spatial effects of forest fragments on multiple ecosystem services in agricultural landscapes (Farwig *et al.* 2009); Mitchell, Bennett & Gonzalez, *In Review*).

The effects of changing the position and size of habitat fragments on their ability to provide ecosystem services to the surrounding agricultural matrix have not been widely investigated. Habitat loss and fragmentation are generally acknowledged to have negative effects on biodiversity (Ewers & Didham 2006; Ewers *et al.* 2013), and smaller habitat fragments usually support fewer species (Holt *et al.* 1999). However, commensurate effects of fragment size on service provision have not been widely explored, but may be important (*e.g.* (Ziter, Bennett & Gonzalez 2013)). This makes it difficult to predict how habitat loss and fragmentation will affect the provision of different ecosystem services, both at the landscape-scale and at smaller field-level scales.

Here, we present a spatially explicit model that we use to investigate how habitat loss affects the provision of ecosystem services. Our main questions were: (1) how do different degrees of habitat loss and patterns of habitat fragmentation affect ecosystem service provision, (2) how is ecosystem service provision mediated by the form of the spatial functions linking the effect of habitat fragments on ecosystem service provision, and (3) what degree of habitat loss and fragmentation maximizes ecosystem services at both landscape and field scales?

5.3 METHODS

We created a simple model to simulate ecosystem service provision as habitat loss occurs across agricultural landscapes. We model hypothetical ecosystem services that are provided by habitat fragments to the surrounding agricultural matrix, using anticipated functions instead of real data. We excluded agricultural production from our analysis in order to focus on the services most impacted by habitat fragments. As habitat is progressively lost from a landscape (*i.e.* from 100 % to 0 % habitat), we assume that the resulting fragments of natural habitat provide ecosystem services to surrounding agricultural fields, that the provision of these ecosystem services generally declines with distance-from-habitat (*i.e.* as one moves further from a habitat fragment into the agricultural matrix, service provision decreases), and that the form of this ecosystem service decay varies with fragment size (Figure 5.1a). We then model three different types of ecosystem service decay curves with seven different landscape-scale patterns of habitat loss (Figure 5.1b). By systematically altering how ecosystem services vary with distance-from-habitat and patterns of habitat loss, we identify conditions where changes to landscape structure can have significant effects on service provision.

5.3.1 Model Landscapes & Habitat Loss Simulation

We modeled landscapes consisting of a grid of 24 × 24 cells (576 total), where individual cells could be either native habitat (referred to below simply as *habitat*) or agriculture. Landscapes were bounded on each side and therefore incorporated landscape edge effects. We defined habitat 'fragments' within the landscape as groups of contiguous habitat cells that shared edges (*i.e.* Von Neumann neighborhood). Fragment area equaled the number of cells in that fragment, and distances between cells were calculated as the Euclidean distance between cell centers. We

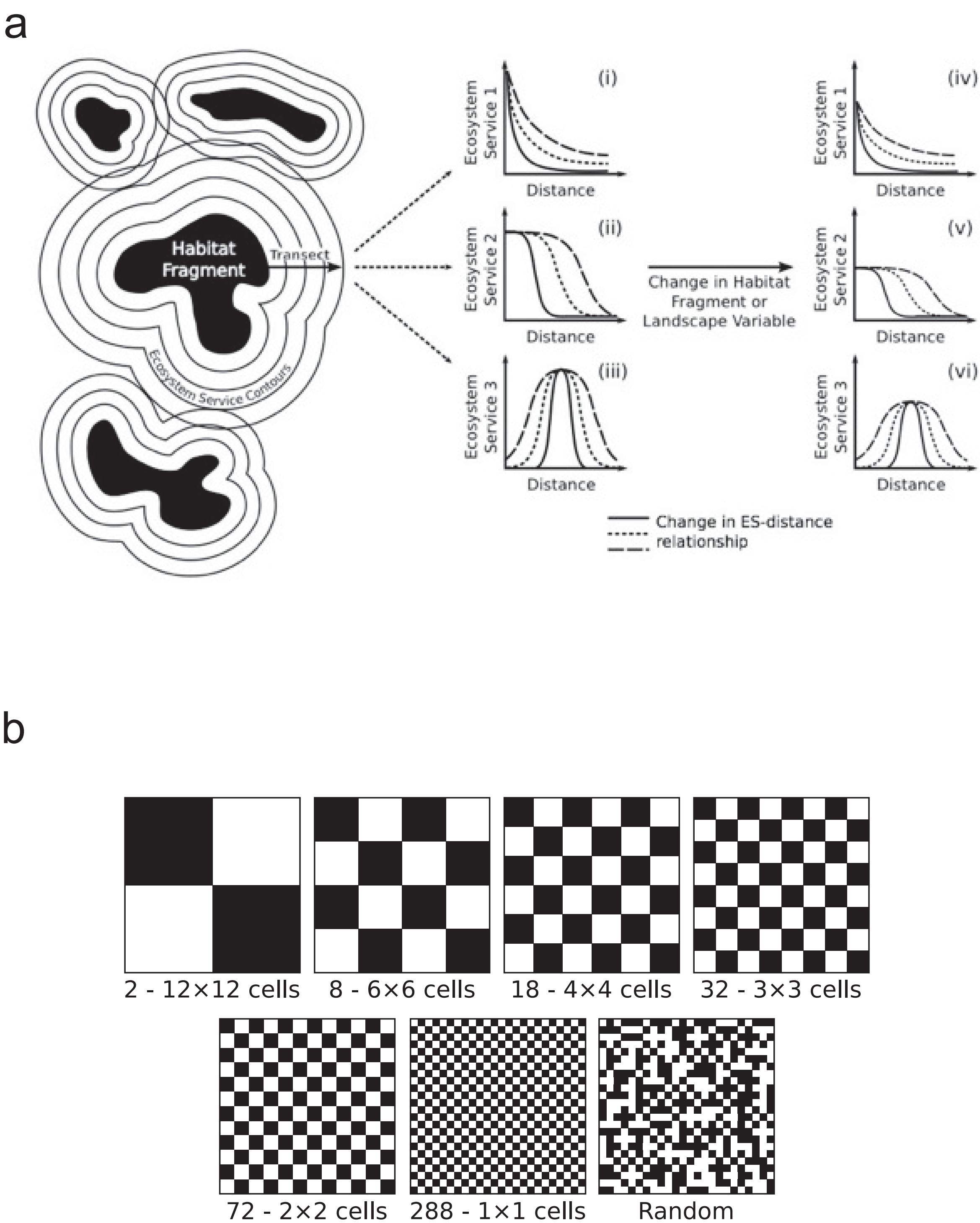

a
Habitat Fragment
Transect
Ecosystem Service Contours
Ecosystem Service 1
Ecosystem Service 2
Ecosystem Service 3
Distance
(i)
(ii)
(iii)
(iv)
(v)
(vi)
Change in Habitat Fragment or Landscape Variable
Change in ES-distance relationship
b
2 - 12×12 cells
8 - 6×6 cells
18 - 4×4 cells
32 - 3×3 cells
72 - 2×2 cells
288 - 1×1 cells
Random

Figure 5.1: Conceptual modeling framework and hypothetical landscape habitat loss patterns. In (**a**), ecosystem service provision (*contours*) will change with distance from habitat fragments (*black shapes*) according to hypothetical relationships, such as (***i***) exponential decay, (***ii***) logistic decay, or (***iii***) a Gaussian curve. The form of these curves could change depending on landscape management, the specific ecosystem services considered, or changes in societal values (*solid* and *dashed* lines). In our model, the maximum service provision that a habitat patch can provide to the surrounding landscape varies depending on its size (see (***iv***), (***v***), and (***vi***)), but this could also occur with changes in other fragment variables such as species or functional diversity. In (**b**) All landscapes are 50% natural habitat (*black squares*) and 50% cropland (*white squares*). Each landscape consists of 24 x 24 cells (576 cells total). These landscape defined the habitat loss patterns in our model runs (see text for description).

modeled our landscapes in Netlogo 5.0.4 (Wilensky 1999) to allow future inclusion of mobile agents. Each model run simulated the conversion of natural habitat to agriculture (*i.e.* agricultural expansion). At the start of each run, landscapes consisted entirely of habitat that was then progressively converted to agriculture until no habitat remained. We defined six hypothetical 'checkerboard' landscape patterns by which habitat loss occurred, plus a seventh pattern of completely random habitat loss (Figure 5.1b). These patterns specified the arrangement of habitat fragments and agricultural cells at the midpoint of each model run (*i.e.* 50% each habitat and agriculture). As such, they represent changes in landscape fragmentation *per se*, independent of habitat loss (Fahrig 2003) and are similar to those used in other studies that investigate the effects of changing landscape structure on ecosystems and services (Franklin & Forman 1987; Robinson, Brown & Currie 2009). They also vary systematically in landscape heterogeneity, area-to-edge ratio, average fragment size, and the average distance between agriculture and habitat cells (see Supplemental Information). In the first part of each model run, habitat cells were randomly converted to agriculture, but this was constrained by one of our landscape patterns (*i.e.* habitat cells were only converted within the *white areas* of Figure 5.1b). In the second part, the remaining habitat fragments were eroded by randomly converting habitat fragment edge cells to agriculture. At each model step, the area of each habitat fragment, the distance between each agriculture cell and the nearest cell of each habitat fragment, and total ecosystem service provision in each agriculture cell were calculated.

5.3.2 Ecosystem Service Provision Modeling

We selected three different functions governing the distance dependence of ES decay from habitat fragments, exponential decay, logistic decay, and Gaussian (Figure 5.1a), and varied the form of these curves by systematically changing specific model parameters. These functions match theoretical predictions (Ries *et al.* 2004) and observed responses of ecological flows and population movements (Duelli *et al.* 1990; Ricketts *et al.* 2008) to habitat edges that could potentially affect ecosystem service provision. They were also informed by the results of an empirical study of ecosystem services along distance-to-habitat gradients (Mitchell, Bennett & Gonzalez, *In Review*).

For exponential decay (Figure 5.1a(i)), we assumed that provision of ecosystem service Ɛ1 provided to agriculture cell *i* by habitat fragment *j* decays with increasing distance *d* according to:

$$\mathcal{E}1_{ij}(d) = N_j \cdot 2^{-\left(\frac{d}{d_{1/2}}\right)} \tag{1}$$

where N_j is the value of Ɛ1 adjacent to the habitat fragment (*i.e.* where $d = 0$), and $d_{1/2}$ is a constant that defines the distance-from-habitat where Ɛ1 equals one half its initial value. N_j is determined by habitat fragment size (see Equation 4). We varied $d_{1/2}$ between 0 and 10 to explore how changing the rate of ecosystem service decay affected model results.

For logistic decay (Figure 5.1a(ii)), we assumed that provision of ecosystem service $\mathcal{E}2_{ij}$ at distance *d* from a habitat fragment is specified by a modified logistic growth equation (Meyer, Yung & Ausubel 1999):

$$\mathcal{E}2_{ij}(d) = N_j \cdot \left(1 - \frac{1}{1+exp\left[-\frac{\ln(81)}{\Delta d}(d-d_m)\right]}\right) \tag{2}$$

where Δd defines the distance over which Ɛ2 decreases from 90 % to 10 % of its initial value N_j, and d_m defines the distance-from-habitat at which Ɛ2 equals one half of its initial value. Other variables are the same as in Equation 1. We varied d_m between 0 and 10 to investigate how altering the distance at which service provision declines affected results; variation in Δd had little effect.

To model a Gaussian relationship (Figure 5.1a(iii)), we assumed that provision of ecosystem service $\mathcal{E}3_{ij}$ at distance *d* is determined by:

$$\mathcal{E}3_{ij}(d) = N_j \cdot exp\left[-\frac{(d-\mu)^2}{2\sigma^2}\right] \tag{3}$$

where μ specifies the distance-from-habitat where maximum Ɛ3 provision occurs, and σ the variance of Ɛ3 around this peak. We varied σ between 0 and 10 to examine how changing the breadth of the service peak affected model results; changes to μ had much smaller effects, therefore we fixed it at 4 cells. N_j in this case determines the maximum value of Ɛ2 at the peak of service provision. All other variables are as in Equations 1 and 2.

We assumed that the most service provision a fragment could provide to any agriculture cell was 1, and that this maximum depended on fragment size (Figure 5.1a(iv-vi)). In other words, large fragments could provide full service provision, according to the ES-distance relationship being modeled, but smaller fragments could only provide a fraction of this. This effect is akin to larger fragments having greater numbers of ecosystem service-providing individuals (Connor, Courtney & Yoder 2000) or greater species or functional diversity (Holt *et al.* 1999) leading to increased service provision (Balvanera *et al.* 2006; Diaz *et al.* 2007). We modeled the maximum value of service provision a fragment j could provide (N_j) as a saturating curve:

$$N_j = 1 - exp\left[-(A_j \cdot p)\right] \tag{4}$$

where A_j is the fragment area and p is a constant defining the steepness of the curve. We used p = 0.008, defining a curve where 80% of decrease in N_j occurs for patches with A_j < 200 cells.

For any given agriculture cell i, multiple surrounding habitat fragments contribute to ecosystem service provision. We summed these contributions to give a total ecosystem service value $\mathcal{E}T_i$, assuming that service provision cannot increase above a maximum value of 1. Below this maximum, we assumed a logistic growth relationship, such that the contribution of any habitat fragment j to ecosystem service provision in agriculture cell i, decreases as $\mathcal{E}T_i$ approaches 0 or 1:

$$\mathcal{E}T_i = \left(\frac{1}{1+exp\left[-\frac{\ln(81)}{0.5}\left(\sum_{j=1}^{s}\mathcal{E}-0.5\right)\right]}\right) \tag{5}$$

where $\sum_{j=1}^{s}\mathcal{E}$ is the sum of ecosystem service provision contributions to that cell i from all surrounding habitat fragments.

5.3.3 *Model Runs & Statistical Analysis*

We performed two sets of simulations. In the first, we ran the model 20 times with each combination of four values of $d_{1/2}$, d_m and σ (*i.e.* 1, 2, 4, and 8) and the seven patterns of habitat loss. Running each parameter combination 20 times gave us an accurate estimate of the variation between model runs due to randomness in habitat loss. This variation was very small relative to ecosystem service levels (≤ 5 % for the standard deviation), therefore it is not presented in the results below. In the second set, we progressively changed the values of $d_{1/2}$, d_m and σ from 0 to 10 with an increment of 0.1 for each pattern of habitat loss, running each combination once since variation was so small between simulations.

We analyzed model results in terms of total landscape ecosystem service provision and average ecosystem service provision per individual cell of agriculture. For each, we were interested in peak values, maximum rates of service provision decline, and thresholds of habitat loss where ecosystem service provision changed rapidly. To determine rates of change, we fit a loess curve to each model run and then estimated the first derivative of this curve using the '*diff*' function in R 3.0.2. Differences for each point along each curve were calculated across 58 model steps (*i.e.* ~10% change in habitat). To identify thresholds in the ecosystem service provision as a function of habitat loss, we estimated the second derivative of each curve by adding an additional '*diff*' step to that described above. The second derivative measures how fast the rate of change of the ecosystem curve is itself changing, with maximum or minimum values indicating where the slope of the ecosystem service curve is rapidly changing. For our model results derived from varying the form of ecosystem service decay, we fit generalized additive model (GAM) curves to the results for each habitat loss pattern (Zuur *et al.* 2009) to account for variation between runs. GAMs were fit with 'smoothing splines' using the 'gam' package in R (Hastie 2013).

5.4 RESULTS

Both the form of the ecosystem service decay function and the pattern of habitat loss had strong effects on ecosystem service provision. The effects of the exponential and logistic decay functions on ecosystem service supply were qualitatively similar. Therefore, we only present results from the logistic decay and Gaussian relationships below. The results for exponential decay are given in the Supplemental Information.

5.4.1 Patterns of Ecosystem Service Provision with Habitat Loss

Total landscape ecosystem service provision reached its maximum at intermediate levels of habitat loss (Figure 5.2a,c), but the height of this maximum and the level of habitat loss at which it occurred depended on the form of ecosystem service decay. As d_m and σ increased from 1 to 8

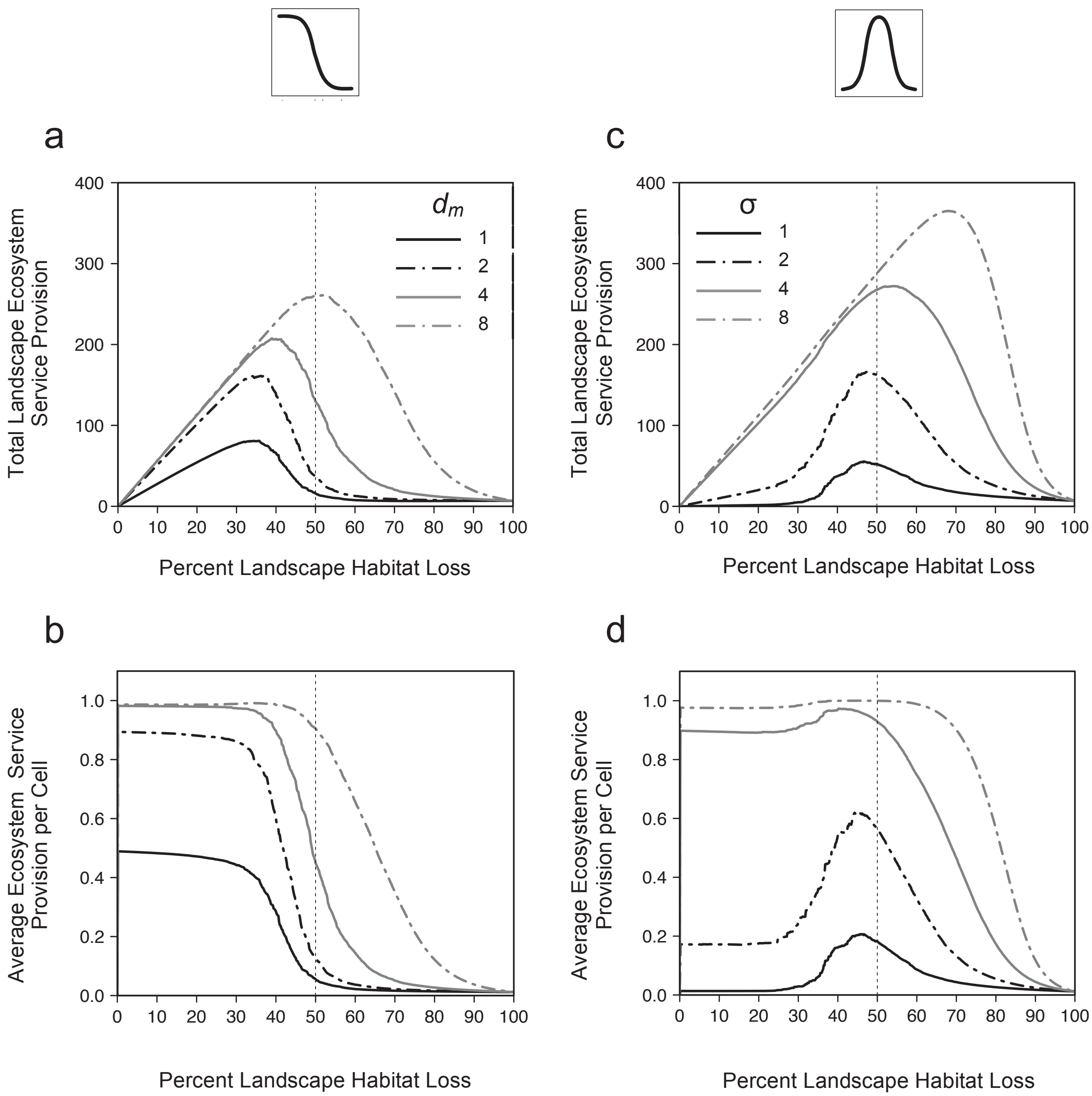

a
Total Landscape Ecosystem Service Provision
d_m
1
2
4
8
Percent Landscape Habitat Loss
b
Average Ecosystem Service Provision per Cell
Percent Landscape Habitat Loss
c
Total Landscape Ecosystem Service Provision
σ
1
2
4
8
Percent Landscape Habitat Loss
d
Average Ecosystem Service Provision per Cell
Percent Landscape Habitat Loss

Figure 5.2: Total landscape and average agricultural cell ecosystem service provision along habitat loss trajectories as distance-dependent ecosystem service provision functions are varied. Individual figures are for (**a**,**b**) logistic decay, and (**c**,**d**) Gaussian relationships; (**a**,**c**) show curves for ecosystem service provision over the entire landscape while (**b**,**d**) show average values of ecosystem service provision for individual agricultural cells. In all cases shown here, habitat loss occurred randomly across the landscape. For the logistic decay relationship, we altered the midpoint (d_m), while for the Gaussian relationship we altered the variance (σ) of the curve. The dashed line indicates 50 % habitat loss (*i.e.* when the model landscape matches the patterns in Figure 5.1); each line is the mean of 20 model runs.

with random habitat loss, maximum total landscape ecosystem service provision increased on average 3.2 and 6.6 times for the logistic and Gaussian relationships, respectively. At the same time, this peak occurred at progressively higher levels of habitat loss, changing from 35 to 52 % habitat loss for the logistic relationship and from 45 to 69 % for the Gaussian.

Average ecosystem service provision per cell generally began at its maximum level with low levels of habitat loss and then decreased rapidly beyond a threshold of intermediate habitat loss (Figure 5.2b,d). This threshold depended on the form of ecosystem service decay, changing from 32 to 48 % habitat loss for the logistic relationship and 45 to 70 % loss for the Gaussian, with d_m and σ increasing from 1 to 8 and random habitat loss. Similar to total landscape ecosystem service provision, as d_m and σ increased from 1 to 8, the maximum level of average ecosystem provision per cell also increased (logistic: from 0.5 to 1.0; Gaussian: from 0.2 to 1.0). A distinct pattern also emerged for the Gaussian function at small values of σ (Figure 5.2d). In these cases, average ecosystem service provision per cell peaked at intermediate levels of habitat loss (~ 45 % loss), showing a pattern similar to total landscape ecosystem service provision.

The specific pattern of habitat loss also affected ecosystem service provision at both the landscape and individual cell scales, but these effects were distinct from those of changes to the form of ecosystem service decay. Habitat loss into very small habitat fragments (*i.e.* 288 1×1 fragments) generally resulted in lower total landscape ecosystem service provision (logistic: 0.25 and 0.16 times less compared to the random or 18 fragment patterns; Gaussian: 0.17 and 0.1 times less compared to these patterns; d_m = 4 and σ = 2; Figure 5.3a,c). The 288-fragment pattern also shifted the peak of total landscape ecosystem service provision towards lower levels of habitat loss relative to other patterns of habitat loss (logistic: 30 % loss vs. 40 and 37 % loss with the random or 18-fragment patterns; Gaussian: 36 % loss vs. 48 and 44 % loss with these patterns; Figure 5.3b,d). A similar pattern also emerged for the threshold at which average ecosystem service provision per cell declined between the 288-fragment pattern and other patterns (logistic: 27 % loss vs. 38 or 33 %; Gaussian: 35 % loss vs. 46 or 42 %; Figure 5.3b,d). Habitat loss arranged into two fragments generally widened the peak of total landscape ecosystem service provision for both the logistic and Gaussian relationships, although the peak value was reduced between 0.11 to 0.33 times compared to other patterns (Figure 5.3a,c).

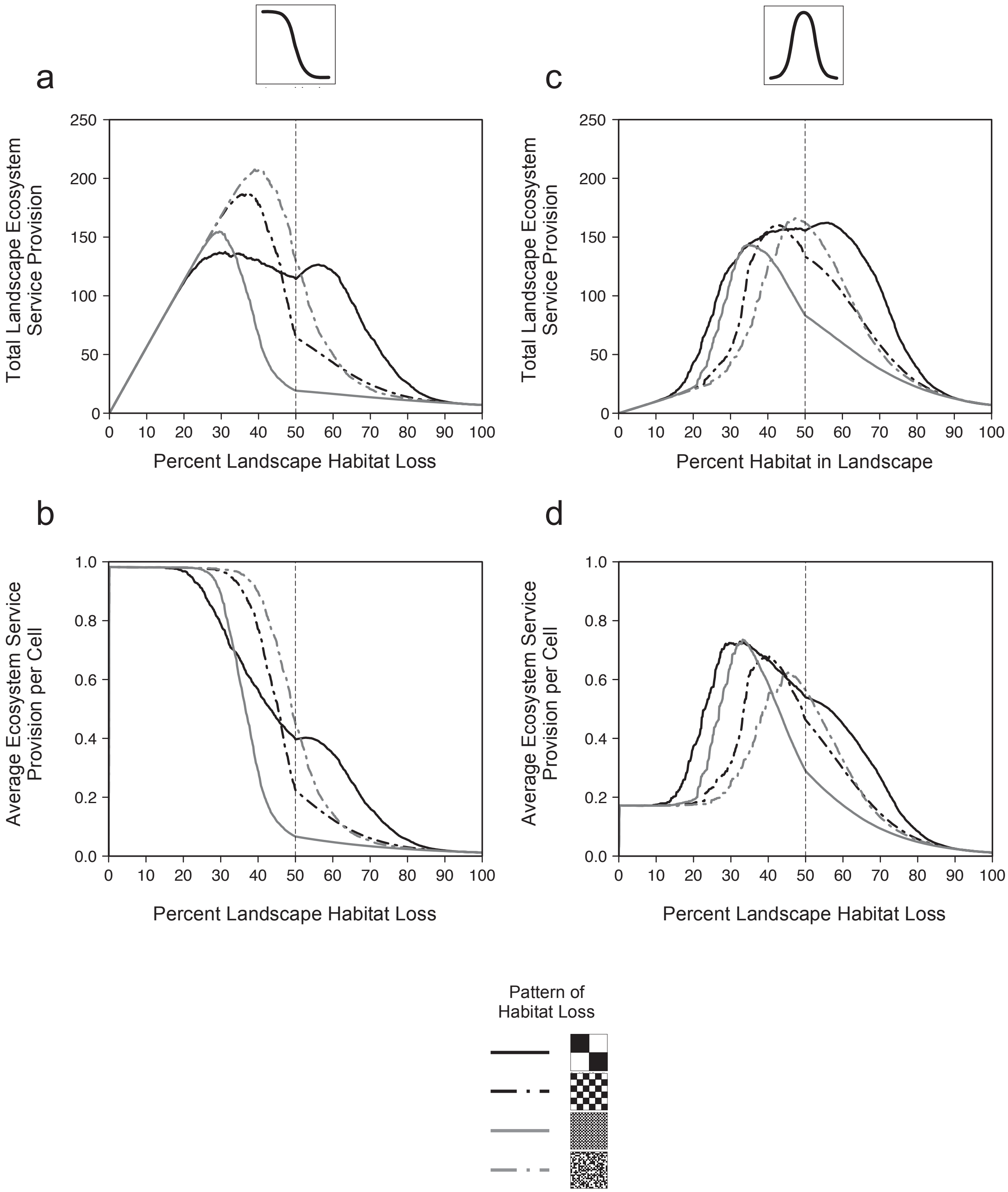
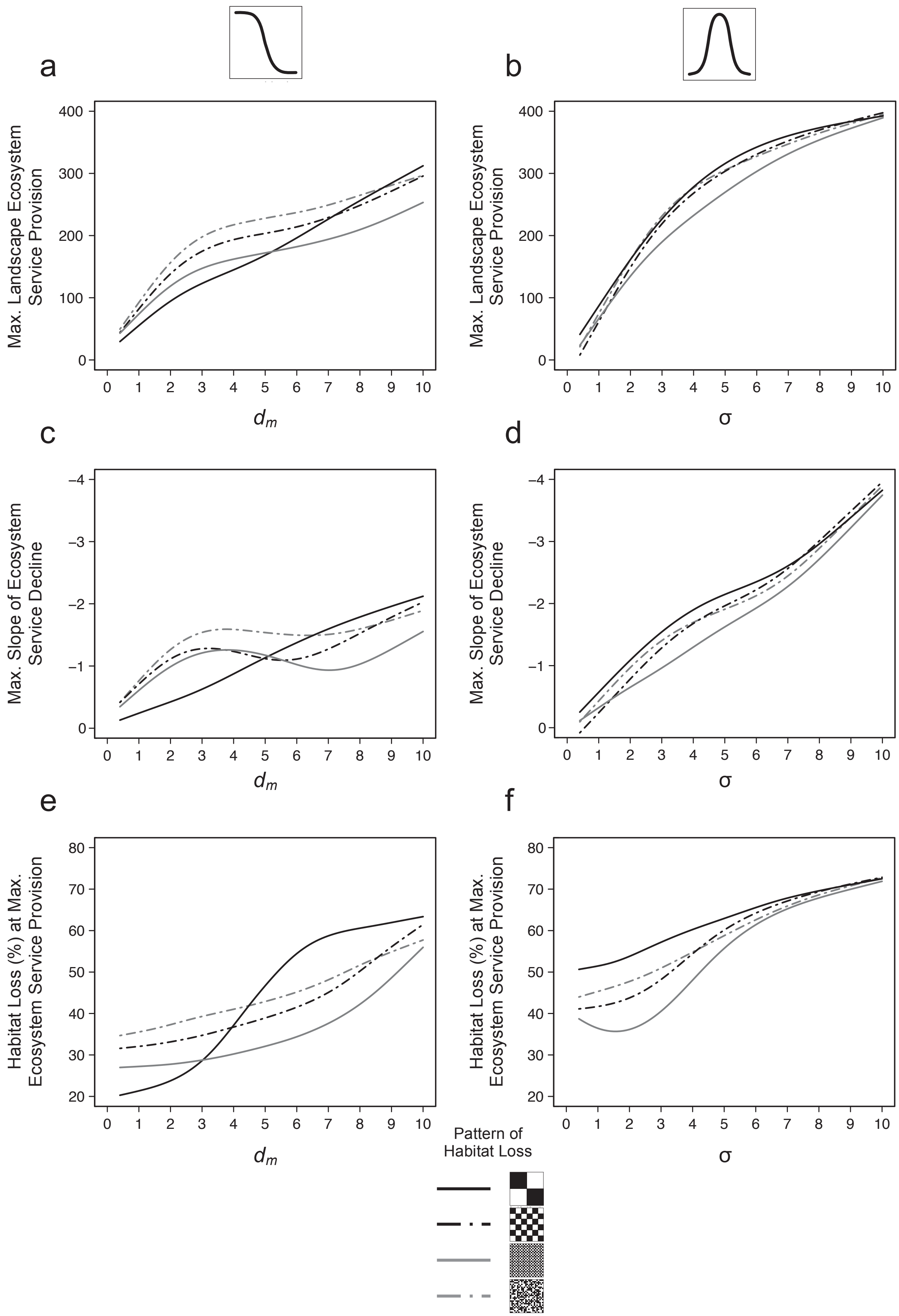

a
b
c
d
Total Landscape Ecosystem Service Provision
Average Ecosystem Service Provision per Cell
Percent Landscape Habitat Loss
Percent Habitat in Landscape
0
10
20
30
40
50
60
70
80
90
100
150
200
250
0.0
0.2
0.4
0.6
0.8
1.0
Pattern of Habitat Loss

Figure 5.3: Total landscape and average agricultural cell ecosystem service provision along habitat loss trajectories as habitat loss patterns are varied. Individual figures are for (**a**,**b**) logistic decay, and (**c**,**d**) Gaussian relationships; (**a**,**c**) show curves of ecosystem service provision for the entire landscape while (**b**,**d**) show average values of ecosystem provision for individual agricultural cells. For clarity, we show only forest loss patterns of 2, 18, and 288 fragments, along with random loss. For the logistic curve, we show results from a midpoint value (d_m) of 4 cells, while for the Gaussian relationship we show results for a variance (σ) of 2 cells. The dashed line indicates 50% forest loss (*i.e.* when the model landscape matches the patterns in Figure 5.1); each line is the mean of 20 model runs.

5.4.2 Effects of Changes in the Form of Ecosystem Service Decay

While overall patterns of ecosystem service provision at both scales were similar for the logistic and Gaussian functions as their forms varied (*i.e.* as d_m and σ varied from 0 to 10), even among different patterns of habitat loss, the magnitudes of change differed (Figure 5.4). As the form of ecosystem service decay varied, maximum total landscape ecosystem service values increased between approximately 6 to 11 times for the logistic relationship and 8 to 23 times for the Gaussian (Figure 5.4a,b), while the maximum rate of decline for total landscape ecosystem service provision increased between 4 to 16 times for the logistic and 13 to 1320 times for Gaussian (Figure 5.4c,d). At the same time, the level of habitat loss at which maximum total landscape ecosystem service provision occurred increased, changing from an average of 28 to 60 % loss for the logistic relationship and from 44 to 72 % for the Gaussian (Figure 5.4e,f). Our model also revealed a tradeoff among habitat loss patterns between maximum total landscape ecosystem service provision and the proportion of habitat on the landscape at this maximum. In most cases, the habitat loss pattern with the greatest maximum total landscape ecosystem service provision for a value of d_m or σ (Figure 5.4a,b) also had the greatest habitat loss at that point (Figure 5.4e,f). The 2-fragment pattern of habitat loss generally showed somewhat different trends than other patterns as the form of ecosystem service decay varied, especially for the logistic relationship (Figure 5.4a,c,e). For example, switching from the pattern with the least total landscape ecosystem service provision to the pattern with the most as d_m varied from 0 to 10.

Average ecosystem service provision per cell saturated for both the logistic and Gaussian relationships at values of d_m and σ of ~ 4 (Figure 5.5a,b). Maximum rates of decline for average ecosystem service provision per cell increased by only 1.4 to 3 times for the logistic relationship, although there was a pronounced peak at d_m values ~ 3, but by 7 to 18 times for the Gaussian as the form of ecosystem service decay varied (Figure 5.5c,d). Likewise, the level of habitat loss at which this decline occurred also increased, from an average of 23 to 61 % for the logistic and from 40 to 72 % for the Gaussian relationship (Figure 5.5e,f). Despite little effect of habitat loss patterns on the maximum value of average ecosystem service provision per cell, they did have strong effects on maximum rates of decline. This was especially true for the logistic function, where the two-fragment pattern had nearly half the rate of decline of the other patterns,



a
b
Max. Landscape Ecosystem Service Provision
d_m
σ
c
d
Max. Slope of Ecosystem Service Decline
e
f
Habitat Loss (%) at Max. Ecosystem Service Provision
Pattern of Habitat Loss

Figure 5.4: Effects of varying the distance-dependent ecosystem service functions on ecosystem service provision behaviour. (**a**,**b**) maximum landscape ecosystem service provision, (**c**,**d**) the maximum slope of ecosystem service decline as habitat is lost, and (**e**,**f**) the level of landscape habitat loss at maximum landscape ecosystem service provision. We show results of (**a**,**c**,**e**) logistic decay and (**b**,**d**,**f**) Gaussian functions with generalized additive model (GAM) curves fit to the data from models runs at each 0.1 increment of d_m and σ in combination with habitat loss patterns of 2, 18, and 288 patches, in addition to random habitat loss.

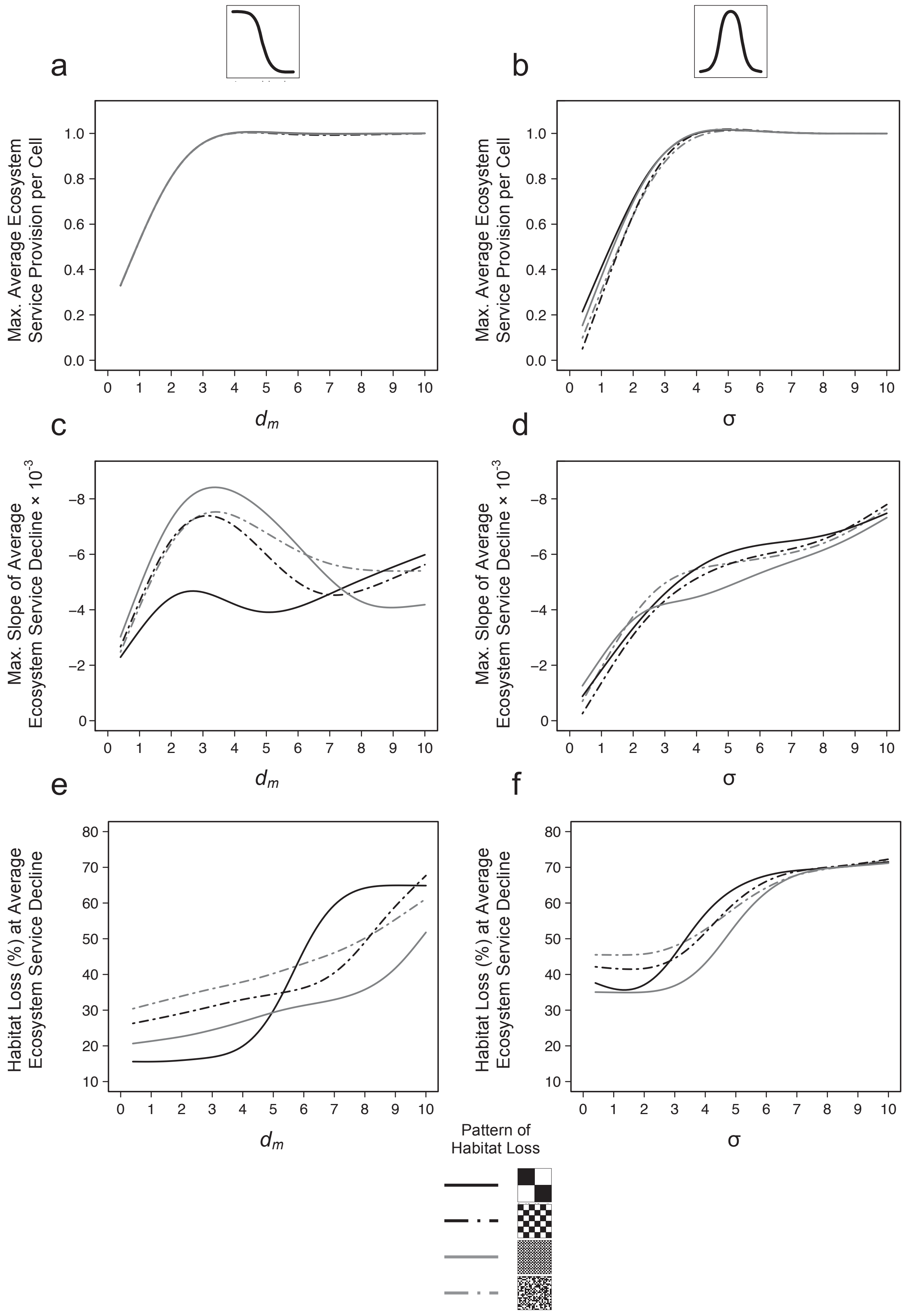

a
b
Max. Average Ecosystem Service Provision per Cell
d_m
σ
c
d
Max. Slope of Average Ecosystem Service Decline × 10^{-3}
e
f
Habitat Loss (%) at Average Ecosystem Service Decline
Pattern of Habitat Loss

Figure 5.5: Effects of varying the distance-dependent ecosystem service provision functions on ecosystem service behaviour. (**a**,**b**) maximum average ecosystem service provision per agricultural cell, (**c**,**d**) the maximum slope of decline of average ecosystem service per agricultural cell as habitat is lost, and (**e**,**f**) the level of landscape habitat loss when average ecosystem service provision per agricultural cell begins to decline. We show results of (**a**,**c**,**e**) logistic decay and (**b**,**d**,**f**) Gaussian functions with generalized additive model (GAM) curves fit to the data from models runs at each 0.1 increment of d_m and σ in combination with habitat loss patterns of 2, 18, and 288 patches, in addition to random habitat loss.

especially for values of d_m between 2 and 6 (Figure 5.5c). While the level of habitat loss at which average ecosystem service provision per cell began its decline increased with values of d_m and σ (Figure 5.5e,f), there was also significant variation between habitat loss patterns. This was especially true for the logistic relationship, where average ecosystem service provision per cell began its decline with the 2 fragment pattern at ~15 % habitat loss when d_m was small, but at ~65 % loss when d_m was large (Figure 5.5e). For the Gaussian relationship, differences between habitat loss patterns in the level of habitat loss where average ecosystem service provision per cell began its decline were evident at small values of σ, but these largely disappeared as σ increased (Figure 5.5f).

5.4.3 Landscape vs. Cell Ecosystem Service Provision

The level of habitat loss at which total landscape ecosystem service provision reached its maximum did not match the habitat loss levels where average ecosystem service provision per cell was maximized (Figure 5.6). Overall, maximizing total landscape ecosystem service provision meant an approximate 10 to 15 % loss in average ecosystem service provision per cell. For the logistic relationship, with habitat loss patterns other than the 2-fragment pattern, the match between landscape and cell ecosystem service provision was greatest at intermediate values of d_m between 3 and 8, where average ecosystem service provision per cell was ~ 0.9 times its maximum (Figure 5.6a). However, this was also where the two-fragment pattern showed the greatest mismatch between ecosystem service provision at the two model scales, with average ecosystem service provision per cell declining by almost 60 % (Figure 5.6a). For the Gaussian relationship, the opposite pattern was observed; the match between total landscape and average cell ecosystem service provision was greatest at either small or large values of σ (*i.e.* 3 > σ > 7; Figure 5.6b), and the 2-fragment pattern of habitat loss showed the greatest mismatch at σ values of 1 to 4, with average ecosystem service provision per cell declining by over 20 %.

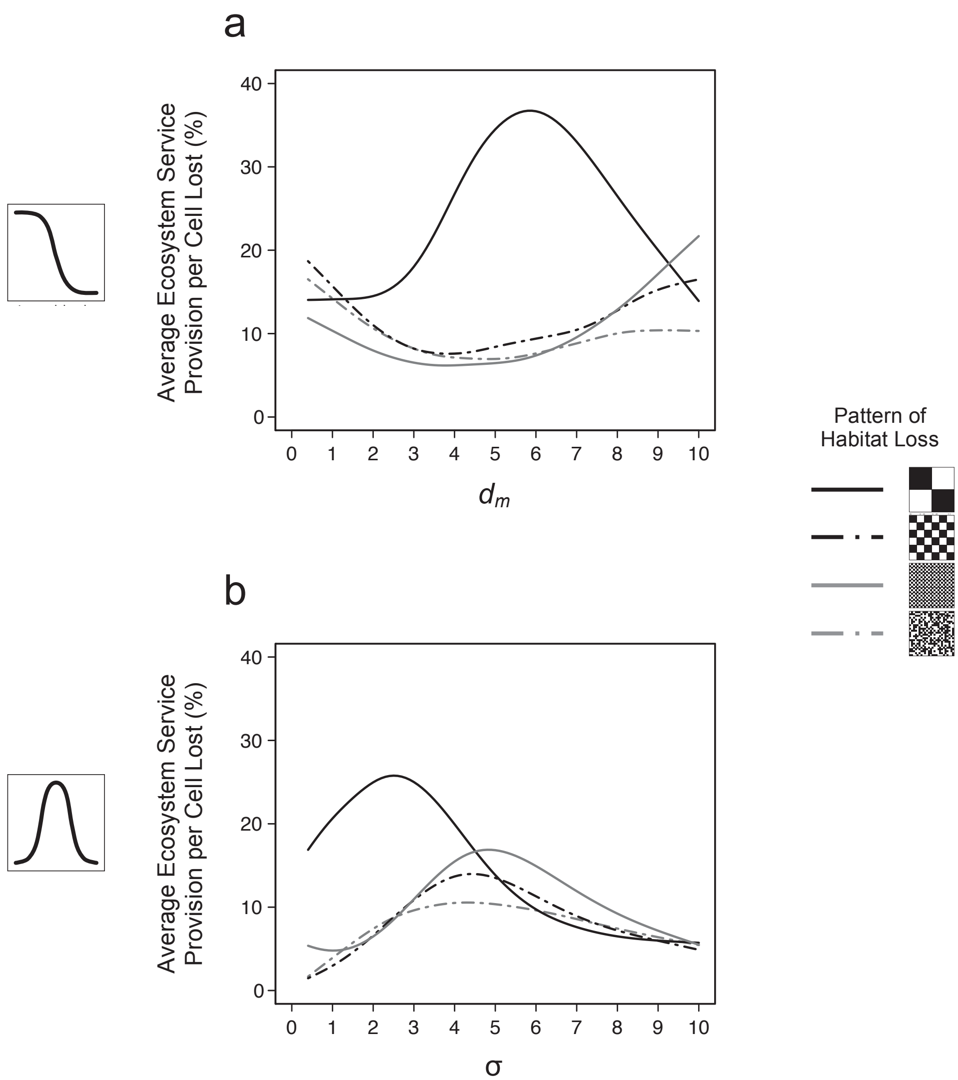


Figure 5.6: Effects of varying the distance-dependent ecosystem service provision functions on ecosystem service provision between scales. (**a**,**b**) the relative loss of average ecosystem service provision per agricultural cell from its maximum when total landscape ecosystem service provision is maximized. We show results of (**a**) logistic decay and (**b**) Gaussian functions with generalized additive model (GAM) curves fit to the data from models runs at each 0.1 increment of d_m and σ in combination with habitat loss patterns of 2, 18, and 288 patches, in addition to random habitat loss.

5.5 DISCUSSION

Our model predicts that the supply of ecosystem services provided by habitat fragments to surrounding agricultural areas will depend on the form of distance-dependent ecosystem service decay, along with the level and pattern of habitat loss. At the landscape-scale, provision of habitat-dependent ecosystem services will increase up to intermediate levels of habitat loss and then decline rapidly. Contrastingly, at the cell or field-scale, these services will be at their maximum at low levels of habitat loss, declining quickly as habitat loss passes these same intermediate levels. Specifically, our results suggest that: (1) levels of ecosystem service provision across landscapes will be determined by the interactions between the distance-dependent effects of habitat fragments on ecosystem services, and the landscape-scale amounts and patterns of habitat loss; (2) that there is a tradeoff between maximizing ecosystem services provided by habitat fragments to surrounding agricultural areas and conserving that same habitat; and (3) a tradeoff exists between landscape and field level ES provision that can be strongly affected by patterns of habitat loss.

5.5.1 Maximizing Ecosystem Services Across Landscapes

Peaks in ecosystem service provision increased the most at both the landscape and field scales when the decay of ecosystem services with distance-from-habitat was minimized (Figures 5.4a,c, 5.5a,c). Thus, decreasing the distance-dependent ecosystem service decay of these types of services may be important to increase service provision in agricultural landscapes. For services provided by mobile organisms like pollination and pest regulation (Kremen *et al.* 2007), decreasing the resistance of the agricultural matrix to the movement of these organisms might therefore improve service provision at multiple scales. Indeed, the few studies that investigate how to optimize ecosystem service provision by modifying landscape structure have found similar results. For example, Brosi, Armsworth & Daily (2008) predict that pollination services and crop yield will increase as bees forage over greater distances. Similarly, Bianchi *et al.* (2010) found that the most mobile predators provide the highest and most uniform pest control across landscapes as landscape structure varies. However, translating these various model results into management tools requires empirical understanding of the actual patterns of ecosystem service provision across landscapes as distance-from-habitat and landscape structure changes. Currently, our understanding in this area is incomplete and these patterns are only well known for a few ecosystem services like pollination (*e.g.* Ricketts *et al.* 2008).

While minimizing the decay of ecosystem services with distance-from-habitat might help maximize overall service provision across landscapes, our model also suggests that it could increase rates of service decline as habitat loss progresses (Figures 5.4c,d, 5.5c,d), resulting in a more sudden loss of ecosystem services. This is a function both of the increased height of the ecosystem service peak, as well as the fact that this peak usually occurred at higher levels of habitat loss. In real landscapes habitat loss is a function of many drivers, including the provision of different ecosystem services, competing land uses, urban development, social variables, and economic globalization, among others (Lambin *et al.* 2001; Veldkamp & Lambin 2001; Lambin & Meyfroidt 2011). Therefore there is the potential that habitat loss will progress beyond that solely needed to maximize ecosystem service provision, leading to service decline. Our model suggests that these declines will be more sudden and steep when ecosystem services provided by habitat fragments show decreased variation with distance-from-habitat or when management practices have been put in place to increase service provision provided by habitat fragments. However, we know of no studies that have empirically tested this in real landscapes.

5.5.2 Tradeoffs Between Ecosystem Service Provision and Habitat Conservation

Increasing the distances at which habitat fragments affected ecosystem service provision resulted in increased maximum levels of service provision at both landscape and cell scales, but these maximum levels occurred at progressively higher levels of habitat loss (Figures 5.4e,f, 5.5e,f). These relationships were also altered by the pattern of habitat loss. Thus, in landscapes where ecosystem service provision from natural habitat drives land use change, our model predicts that management actions to alter ecosystem service relationships with distance-from-habitat might result in increased loss of natural habitat. At the same time, it might be possible to mitigate or compound these effects by changing patterns of habitat loss. In other words, we may be able to optimize both ecosystem service provision and habitat conservation at a given level of habitat loss by altering landscape structure.

The loss of natural habitat could affect other ecosystem services provided exclusively by fragments of natural habitat that aren't currently included in our model. For example, carbon storage and timber provision by forest fragments (Ziter, Bennett & Gonzalez 2013); recreational opportunities provided by fragments of forest, grassland, or wetland (Chan *et al.* 2006); or the genetic resources and biochemical products provided by a variety of habitat types. Our current model purposely only considered ecosystem services provided by habitat fragments to the surrounding agricultural matrix and thus misses some of the complexity of real landscapes that land managers must balance. There are likely thresholds of habitat loss where the gain in service provision to the agricultural matrix as habitat is lost fails to compensate for the reduction in services that are provided directly by the natural habitat. These thresholds will depend on the system in question and the valuation of these services by society, but studies of multiple ecosystem services across landscapes and their trade-offs are relatively rare, especially between different habitat or ecosystem types (de Groot *et al.* 2010; Raudsepp-Hearne, Peterson & Bennett 2010).

Habitat loss and fragmentation might also have effects on biodiversity and ecosystem function that our model does not incorporate. Including the effects of biodiversity and ecosystem function in our model might change how habitat fragments affect ecosystem service provision around themselves. For example, habitat fragmentation can prevent the dispersal and movement of organisms and matter important for ecosystem service provision (Mitchell, Bennett & Gonzalez 2013) altering population demography and viability. This in turn can alter levels of biodiversity across the landscape and the ecosystem functions that underlie ecosystem services (Dobson *et al.* 2006). While our model includes a fragment size effect on service provision, we did not include any additional effects of fragmentation or landscape connectivity on ecosystem services. At present, these effects have not been well quantified and the specific landscape structure variables that affect them are relatively unknown (Mitchell, Bennett & Gonzalez 2013). However they could have important effects on the ability of habitat fragments to provide ecosystem services to the surrounding landscape. This gap currently prevents us from more accurately modeling the effects of habitat fragmentation on ecosystem service provision.

5.5.3 *Trade-offs in Ecosystem Service Provision Between Scales*

Our model predicts that maximum ecosystem service provision at the landscape scale will not occur at the same level of habitat loss as maximum service provision at the field scale. In each case in our model, average service provision at the cell scale began to decline before the maximum landscape level of service provision was reached (Figure 5.6). Our model, therefore, reveals a potential trade-off in ecosystem service management at different scales, such that actions to maximize provision at either small or large scales can result in a sub-optimal result for the other scale. In real landscapes, the presence of a similar mismatch might have important consequences for policy and land management (de Groot *et al.* 2010). While regional land managers might seek to maximize ecosystem service provision at the landscape scale, especially for services that have an easily measured economic value, individual landowners might seek to maximize service provision for their individual farms or fields. Therefore a tension could exist between stakeholders who operate at different scales across the landscape. Issues of scale are known to be of importance for both ecological and economic processes (de Groot *et al.* 2010) but have not been well integrated into our understanding of ecosystem services.

If these types of trade-offs do exist in real landscapes, our model predicts that altering the pattern of habitat loss across landscapes could help minimize them. In particular, creating large areas of protected habitat may result in a disproportionate loss at the individual agricultural cell-scale of the ecosystem services provided by natural habitat to agricultural areas (*e.g.* pollination, pest regulation; Figure 5.6). Therefore, maintenance of smaller habitat patches throughout the landscape or landscape heterogeneity (Fahrig *et al.* 2011) may be the best strategy for maximizing ecosystem services at multiple scales. Our results also suggest that understanding the scales at which ecosystem services vary will be important for predicting what the best scales of habitat loss and fragmentation will be to maximize service provision across landscapes. While our knowledge of these relationships is increasing, at present we only have knowledge in this area for a few single ecosystem services. Determining these patterns for multiple services as landscape structure and fragmentation varies is a pressing research need.

5.5.4 *Future Directions*

A number of additions to our model could help explore the importance and applicability of our results. First, modeling multiple services simultaneously across landscape would be a valuable avenue of research to help develop policy tools whose objective is multi-functional agricultural landscapes. In particular, ecosystem services are not independent and interact with each other in a variety of ways (Bennett, Peterson & Gordon 2009) and adding relationships between services would help explore how landscape structure affects the provision of multiple ecosystem services in a more realistic modeling environment. Understanding the effects of landscape structure on biodiversity, and how this can affect provision of ecosystem services would also be beneficial, although this might only be possible for certain services (*e.g.* pollination) where empirical data is available. Adding additional landscape heterogeneity, either with respect to the ability of habitat fragments to provide ecosystem services, human management actions across the landscape via mobile actors, or alternatively by including different crop types or farm productivity might help increase the generality of our results. Finally, incorporating human valuation of different services into our modeling framework could be a useful approach to help develop effective management tools.

5.5.5 *Conclusions*

Our simple model reveals the importance of understanding how habitat loss and fragmentation mediate ecosystem service provision. We observed trade-offs between service provision and habitat conservation, as well as between ecosystem service provision at two spatial scales. As demand for multiple ecosystem services from agricultural landscapes increases, understanding how to structure these landscapes and the implications of different land management policies, will become increasingly important. At the same time, we require tools that can predict patterns of service provision across landscapes in order to balance human needs with ecological consequences when making land use decisions (DeFries, Foley & Asner 2004). Our model is a first step towards understanding the ways in which landscape structure might affect the provision of ecosystem services. Future development of the modeling principles here will help advance our ability to manage agricultural landscapes for multiple ecosystem services.

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5.8 SUPPORTING INFORMATION

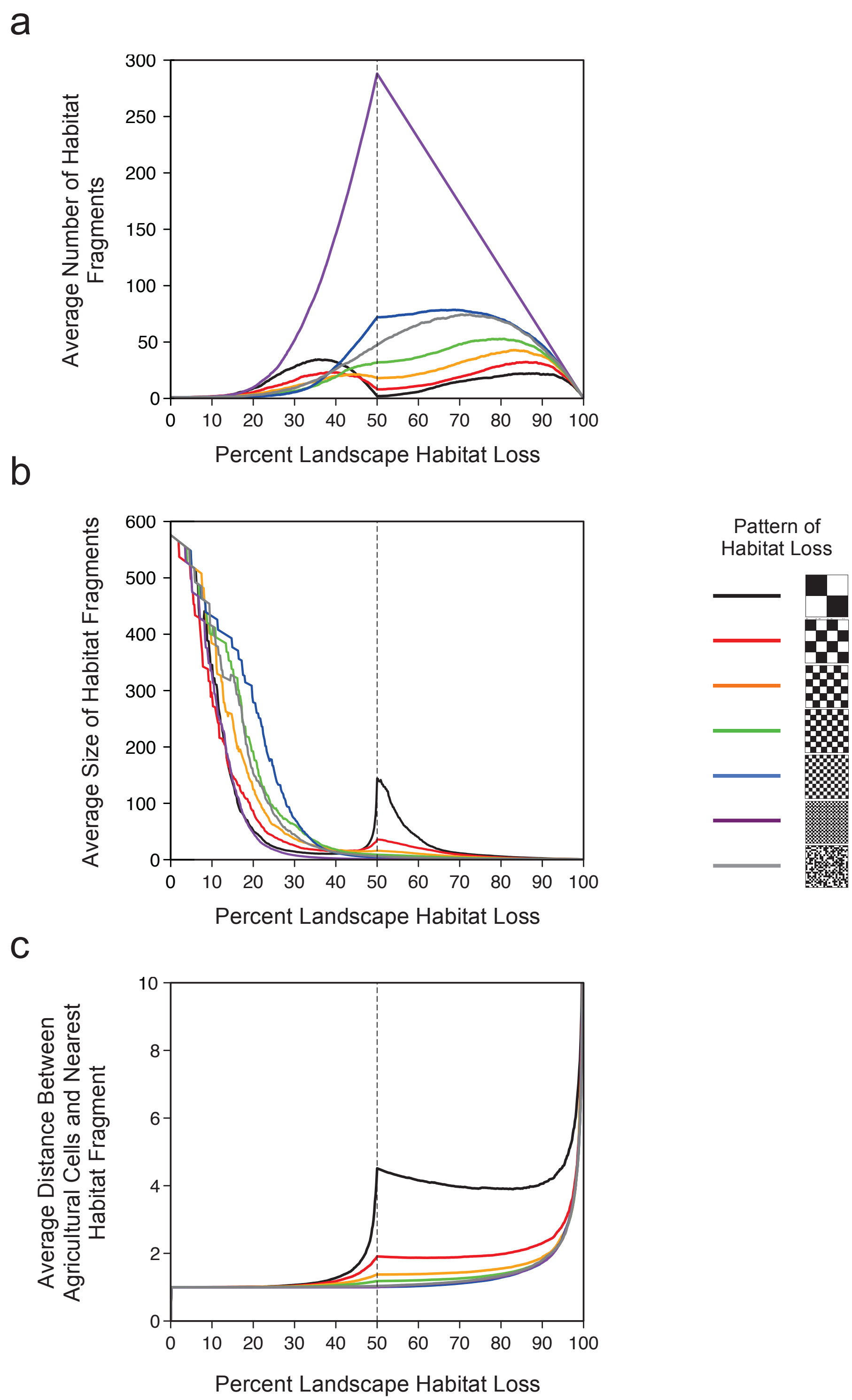

Figure 5.7: Model simulation characteristics as habitat is lost from the landscape. (**a**) the average number of habitat fragments, (**b**) average size of habitat fragments, and (**c**) average distance between individual agricultural cells and the nearest habitat fragment. The dashed line indicates 50% habitat loss; each line is the mean of 20 model runs.

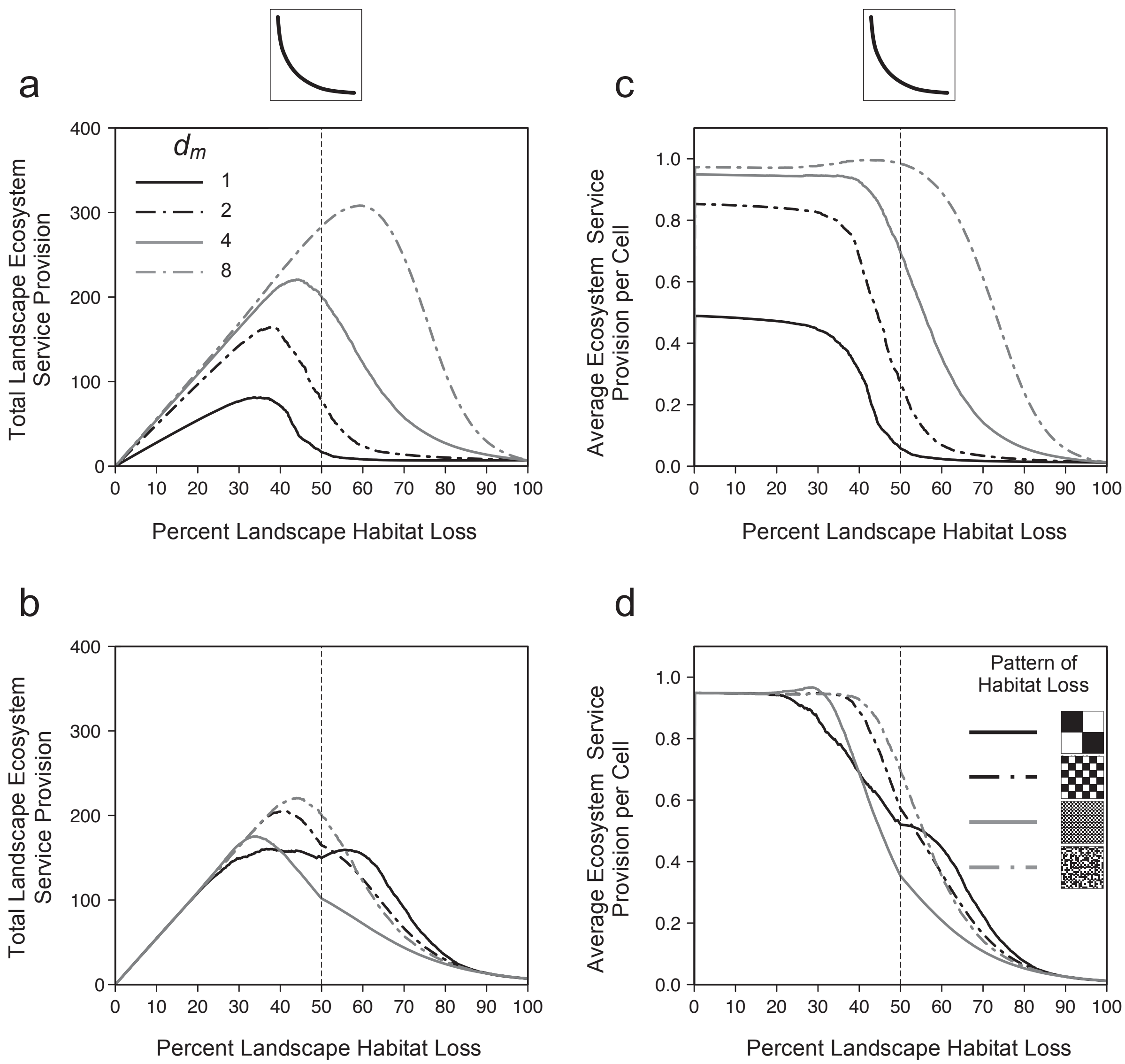
a
b
c
d
d_m
1
2
4
8
Total Landscape Ecosystem Service Provision
Average Ecosystem Service Provision per Cell
Percent Landscape Habitat Loss
Pattern of Habitat Loss
0
10
20
30
40
50
60
70
80
90
100
0.0
0.2
0.4
0.6
0.8
1.0
200
300
400

Figure 5.8: Total landscape and average agricultural cell ecosystem service provision along habitat loss trajectories for the exponential decay distance-dependent ecosystem service function. Individual figures are for (**a**,**b**) total landscape ecosystem service provision, and (**c**,**d**) average ecosystem service provision per agricultural cell. (**a**,**c**) Show curves that differ in the form of the distance-dependent functions vary. (**b**,**d**) Show curves that differ in the pattern of habitat loss, for clarity we show only forest loss patterns of 2, 18, and 288 fragments along with random loss. For (**b**,**d**) we used a half-life value of $d_{1/2} = 4$. In (**a**,**c**) habitat loss occurred randomly across the landscape and we altered the half-life ($d_{1/2}$) of the curve. The dashed line indicates 50% habitat loss; each line is the mean of 20 model runs.

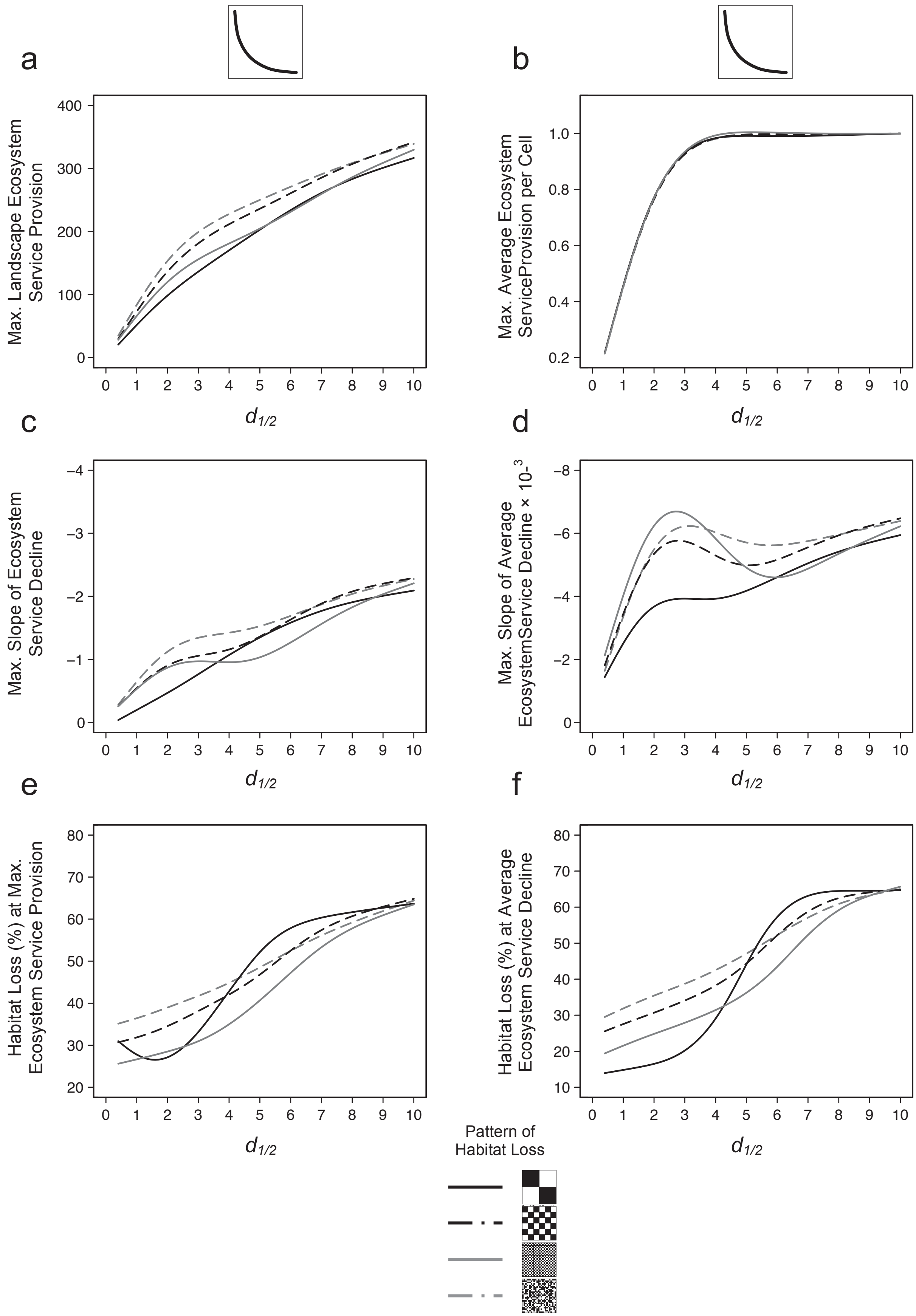
a
b
Max. Landscape Ecosystem Service Provision
Max. Average Ecosystem ServiceProvision per Cell
c
d
Max. Slope of Ecosystem Service Decline
Max. Slope of Average EcosystemService Decline × 10^-3
e
f
Habitat Loss (%) at Max. Ecosystem Service Provision
Habitat Loss (%) at Average Ecosystem Service Decline
d1/2
Pattern of Habitat Loss

Figure 5.9: Effects of varying the distance-dependent exponential decay function on ecosystem service behavior. (**a**) maximum landscape ecosystem service provision, (**b**) maximum average ecosystem service provision per agricultural cell, (**c**) the maximum slope of ecosystem service decline as habitat is lost, (**d**) the maximum slope of decline for average ecosystem service per agricultural cell as habitat is lost, (**e**) the level of landscape habitat loss at maximum landscape ecosystem service provision, (**f**) the level of landscape habitat loss when average ecosystem service provision per agricultural cell begins to decline. We show curves from generalized additive models (GAMs) fit to the data from model runs at each 0.1 increment of $d_{1/2}$ in combination with habitat loss patterns of 2, 18, and 288 patches, in addition to random habitat loss.

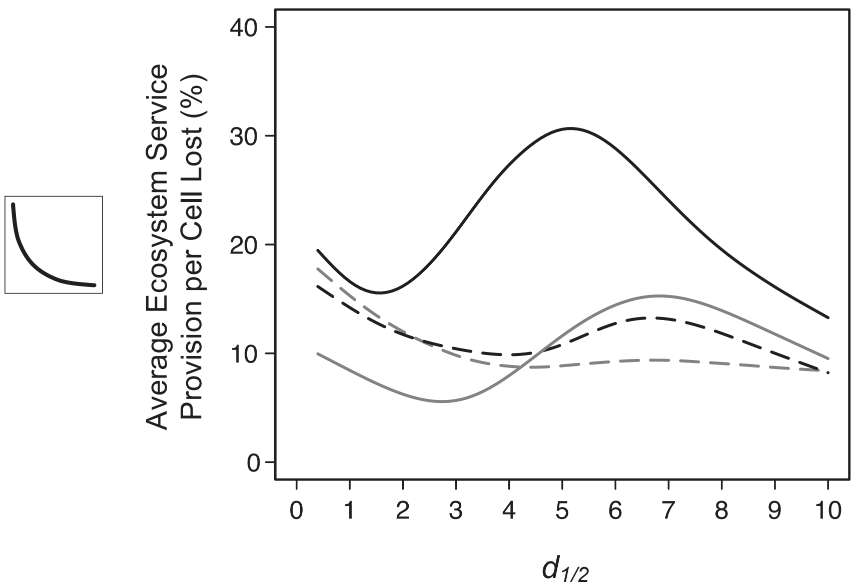

Figure 5.10: Effects of varying the exponential distance-dependent ecosystem service provision function on ecosystem service provision between scales. We show the relative loss of average ecosystem service provision per agricultural cell from its maximum when total landscape ecosystem service provision is maximized. Curves are from generalized additive models (GAMs) fit to the data from models runs at each 0.1 increment of $d_{1/2}$ in combination with habitat loss patterns of 2, 18, and 288 patches, in addition to random habitat loss.

SYNTHESIS, CONCLUSIONS & FUTURE DIRECTIONS

6

6.1 OVERALL CONCLUSIONS & CONTRIBUTIONS TO KNOWLEDGE

Understanding how changes to landscape structure affect the provision of ecosystem services is a critical gap in our knowledge (Kremen & Ostfeld 2005; Kremen *et al.* 2007; Biggs *et al.* 2012). Significant anthropogenic changes to landscapes and ecosystems are likely to continue in the future (Tilman *et al.* 2002), driving changes in landscape structure, and leading to loss of biodiversity (Rands *et al.* 2010). At the same time, demand for food from agricultural systems in addition to other services will most likely continue to increase (Tilman *et al.* 2011). This creates a vital need for scientific understanding of the links between landscape structure, biodiversity, and ecosystem services in order to develop management tools that can produce multi-functional agricultural landscapes. To fill this gap effectively, both theoretical and empirical approaches are needed to describe the patterns of ecosystem service provision as landscape structure varies.

As a first step toward filling this gap, I developed a conceptual framework that links landscape connectivity with ecosystem service provision (Chapter 2). This is an essential step for improving our understanding and effectively investigating the links among landscapes, biodiversity, ecosystem services. While numerous conceptual frameworks have been put forward for understanding ecosystem services and implementing this knowledge to improve management (Kremen & Ostfeld 2005; Carpenter *et al.* 2009; Daily *et al.* 2009; Nicholson *et al.* 2009; de Groot *et al.* 2010), none have explicitly linked landscape structure with service provision (*but see* (Kremen *et al.* 2007). Indeed, most existing models of ecosystem service provision tend to assume that landscape structure is of little impact overall in determining the level of service provision (Polasky *et al.* 2008; Lautenbach *et al.* 2011). Thus, it is not surprising that the scientific literature is currently incomplete and a number of significant research gaps exist. I found that while there is a widespread assumption that loss of connectivity across landscapes will negatively affect the biodiversity and ecosystem processes that contribute to ecosystem services, there is also a widespread lack of empirical data about these effects. This is particularly the case for services other than food or pollination, and to a lesser extent, pest regulation.

To understand how landscape structure affects the provision of different ecosystem services, we need empirical data that describes the patterns of multiple ecosystem services across landscapes as their structure varies. In Chapter 3, I measured the provision of six different ecosystem services as distance-from-forest, forest fragment size, and forest fragment isolation varied in an agricultural landscape in the Montérégie of southern Québec. This is one of the first case studies to empirically measure multiple ecosystem services as landscape structure varies at the spatial scales relevant to land managers. While each of distance-from-forest, fragment isolation, and fragment size had significant effects on at least one ecosystem service, distance-from-forest and fragment isolation affected many more ecosystem services that fragment size. Additionally, the response of each ecosystem service to these variables was unique, and I saw no common patterns in service provision as landscape structure varied. Consequently, landscape multi-functionality depended on landscape heterogeneity – the presence of a variety of forest fragment and field types across the landscape. This corresponds somewhat with my modeling results (Chapter 5), where random habitat loss maximized ecosystem service provision across the landscape in many cases. Finally, I observed that strong negative and positive tradeoffs between services were less common adjacent to forest fragments, suggesting that the presence of forest fragments might moderate relationships between ecosystem services.

Taken together, these results strongly suggest that controlling the presence and isolation of forest fragments across this landscape could be used both to change the provision of specific ecosystem services, but also to enhance landscape multi-functionality. At the same time, my results also demonstrate the complexity of these relationships and how difficult it will be to optimize ecosystem service provision across landscapes. Instead, landscape managers may need to embrace 'ecosystem service heterogeneity', maximizing particular services in different areas of the landscape in order to provide multiple ecosystem services at the landscape scale. However, our limited understanding of the interactions between services and the specific groups of species and ecosystem processes that underlie service provision undermines our ability to design landscapes effectively for different ecosystem services.

Fully understanding the effects of landscape structure on ecosystem service provision depends on understanding how landscape structure affects biodiversity and the related ecosystem functions that ultimately drive the provision of services. In Chapter 4, I focused on pest regulation in the Montérégie, and showed that understanding the effects of landscape structure on this service depends on quantifying the patterns of diversity and abundance for both beneficial and pest arthropods. In particular in my study, field width was a key landscape structure variable for controlling both the diversity and abundance of aphid predators and soybean pests, but also for determining soybean aphid numbers. Therefore, despite strong effects of landscape structure on the biodiversity and abundance of one set of species important for service provision (*i.e.* aphid predators), contrasting effects on soybean aphids meant that the overall effects of landscape structure on pest regulation were inconsistent across the landscape. Currently, the majority of pest regulation studies focus only on pest predators (Chaplin-Kramer *et al.* 2011), missing a key part of the story and possibly misconstruing how landscape structure affects this ecosystem service. Additionally, levels of pest regulation did not, in the years that we gathered data, affect crop provision. Thus, determining the importance of landscape structure for multiple ecosystem services is not a simple endeavor. It depends on understanding how landscape structure affects all of the different functional groups important for service provision, and how different ecosystem services are linked across the landscape.

In part, our incomplete understanding of how landscape structure links with ecosystem services is due to the difficulty in gathering data about these variables at landscape scales (Eigenbrod *et al.* 2010a; b). Experimentally varying landscape structure is often unfeasible, and data to quantify service provision at these scales is typically unavailable. Landscape modeling of ecosystem services is therefore an important tool to explore these relationships and create hypotheses that can be tested in real landscapes. However, at present, very few studies have attempted to model the effects of landscape structure on ecosystem services, although this is slowly changing (Bodin *et al.* 2006; Brosi, Armsworth & Daily 2008; Keitt 2009; Bianchi *et al.* 2010). In Chapter 5, I developed one of the first spatially explicit landscape-scale models of the effects of landscape structure on ecosystem services. Using this simple modeling framework, I found that both the distance over which habitat fragments affect ecosystem services in the surrounding landscape, as well as patterns of habitat loss across landscapes, have important effects on ecosystem service provision. At the same time, I observed a tradeoff between preserving fragments of natural habitat on landscapes and maximizing the ecosystem services that these fragments provide to the surrounding matrix, as well as a mismatch between ecosystem service provision at different spatial scales. However, these tradeoffs and mismatches could be either mitigated or intensified by altering the pattern of habitat loss across the landscape. The results of this model suggest that altering landscape structure could help optimize ecosystem services across spatial scales, and balance habitat and biodiversity conservation with our need to maximize agricultural output.

Overall, my results indicate that landscape structure is critically important for the provision of ecosystem services in the Montérégie and could be used as a tool to manage agricultural landscapes for multi-functionality. However, the creation of effective tools to manage landscape structure and ecosystem services depends on a significant increase in our understanding of the complexity behind these relationships. In particular, we need improved understanding of how landscape structure affects the interactions between multiple ecosystem services, how much variation exists in the effects of landscape structure on ecosystem services, how these effects change across spatial scales, and how socioeconomic drivers and social factors might alter or be altered by these relationships.

6.2 FUTURE DIRECTIONS

6.2.1 Multi-functional Agricultural Landscapes

Realizing ecosystem service science's potential to create multi-functional agricultural landscapes means understanding how landscape structure affects multiple services. This includes not just those within the agricultural matrix, as in this thesis, but also on the important services produced by fragments of natural habitat. For example, carbon storage for climate regulation, disease regulation, flood regulation, provision of high quality water, recreation, and timber production, among others. Each of these services will most likely be affected by landscape structure differently and at different scales, although some may covary (Raudsepp-Hearne, Peterson & Bennett 2010). In addition to describing the patterns of service provision across landscapes, we need to understand the relationships among services and how this creates synergies or tradeoffs between them (Bennett, Peterson & Gordon 2009). My thesis focused on ecosystem services in agricultural fields, neglecting the services provided in the forest fragments (*e.g.* carbon storage, maple syrup production, timber) or by aquatic ecosystems (*e.g.* water quality regulation, flood regulation). How landscape structure in the Montérégie affects these services and how they interact with the services that I measured remains an open area for investigation. Measuring multiple services is a challenging endeavor and one that is currently a weakness in the field (Seppelt *et al.* 2011). Studies that include two or more ecosystem services are increasing, but there is a need for more of these types of studies that also incorporate the effects of landscape structure on service provision.

In addition, simply measuring multiple services across landscapes is likely not enough. We need to better understand the important processes, including ecological, social and economic, that link ecosystem services to each other and create interactions between them (Bennett, Peterson & Gordon 2009; Carpenter *et al.* 2009; Nicholson *et al.* 2009). For example, while I found negative interactions between decomposition in the soil, phosphorus saturation, and aphid regulation with soybean production (Chapter 4), predicting under what conditions and in what types of landscapes these tradeoffs might occur would require investigating the specific species and ecosystem functions that underlie these relationships. Thus, there is a need, both in the Montérégie and in agricultural landscapes in general, to identify which specific species groups and ecosystem processes underlie the provision of particular ecosystem services and then determine how landscape structure affects them. This will be a challenging undertaking, but is required to move beyond simply cataloging ecosystem service patterns across landscape to develop a functional and predictive understanding of how ecosystem services are provided as landscape structure varies.

6.2.2 Linking Landscape Models with Empirical Results

To effectively move our understanding of landscape structure and ecosystem service provision forward, better coupling of landscape models and empirical results will be needed. As models to explore these relationships are created, the predictions and hypotheses they generate will need to be tested in real landscape with empirical data. Vice versa, this data should be used to inform the next generation of models. Ideally, the predictions from Chapter 5 of my thesis will be tested in real agricultural landscapes like the Montérégie and this data will be used to adjust and improve future models. At present, landscape models of ecosystem services have not been extensively tested using empirical data (Eigenbrod *et al.* 2010a). This is a function both of a lack of models, and the difficulty in gathering data on both landscape structure and ecosystem services at landscape scales (Holland *et al.* 2011). Closely coupling modeling and empirical efforts should lead to a more rapid understanding of the effects of landscape structure on ecosystem service provision.

6.2.3 Variation in the Effects of Landscape Structure

While my thesis shows that landscape structure can have important effects on ecosystem service provision, additional studies are needed to understand the variability in these effects. The effects of landscape structure on service provision will likely vary depending on the specific landscape structure variable that is altered, the scale considered, and the types of ecosystems and biodiversity present. At present, this variation has not been explored to any great degree, but is important to understand to create effective management tools (Nicholson *et al.* 2009). Do the patterns that I observed at the field scale with respect to forest fragment isolation and size hold at broader spatial scales? Are there general patterns between landscape structure and ecosystem services that are common across agricultural landscapes globally? My modeling results from Chapter 5 suggest that there will be contrasting effects of landscape structure on ecosystem service provision at different scales, and that there may be common relationships between service provision and patterns of habitat loss, but these differences have only been investigated for a few regions and services (Anderson *et al.* 2009). Understanding how specifically to alter landscape structure for service provision, for which ecosystem services or landscapes this will be effective, requires replication of studies similar to those presented here across space and time and at different spatial scales.

6.2.4 Understanding the Effects of Landscape Structure on People

Ecosystem services are the result of interactions between ecosystems and human activities.

Creating policy and management tools to alter landscape structure in order to change the provision of ecosystem services requires understanding how landscape structure will affect both the biodiversity and ecosystem functions that underlie services, but also how changing landscape structure will affect human actions. For example, a change in landscape structure that leads to increased pollination or pest regulation may lead to farmers planting specific crops to take advantage of this change in ecosystem service. This in turn could affect other ecosystem services like water quality regulation or erosion regulation, or it could lead to changes in landscape structure if field structure or connectivity changes. In addition, realization of ecosystem services also depends on flows from areas of supply to the regions where beneficiaries are located (Bagstad *et al.* 2012), and this flow may depend on landscape structure. Finally, landscape structure doesn't only affect the movement of organisms and matter, but also of humans, with potential effects on how we interact with ecosystems and receive benefits (*e.g.* recreation, cultural services). However, these specific patterns and how they might influence ecosystem services remains unexplored. There are numerous opportunities to unite our current natural science understanding of ecosystem services with the social sciences (Carpenter *et al.* 2009). This should lead to more effective management of landscapes for multiple ecosystem services.

6.3 OVERALL CONCLUSIONS

My thesis indicates that the structure of landscapes has important effects on the provision of ecosystem services, and that these effects can arise both from changes in the movement of organisms as well as changes to patterns of biodiversity. Support for this conceptual framework comes from a variety of sources, including our current scientific understanding (Chapter 2), empirical studies (Chapters 3 & 4), and modeling exercises (Chapter 5). However, the generality of these results; how consistent they are across space, time, and for different services; and how they can be translated into effective management tools for multiple ecosystem services remain open questions. These are promising areas for future research.

Landscape structure in human-dominated systems like agricultural landscapes is, to a large degree, controlled by human activities. In turn, the goal of these activities is the provision of specific sets of ecosystem services. By affecting the movement of organisms and matter across landscapes, and the biodiversity and ecosystem functions present, landscape structure connects human activities with the provision of ecosystem services. As such, it is a critical component for understanding our influence on ecosystems, and the benefits we receive from them. Increased attention of and research into the effects of landscape structure on ecosystem service provision will ensure that we move towards the creation of truly multi-functional landscapes.

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