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2015 Environ. Res. Lett. 10 094014

(http://iopscience.iop.org/1748-9326/10/9/094014)

Environmental Research Letters

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OPEN ACCESS

RECEIVED
21 April 2015

REVISED
21 August 2015

ACCEPTED FOR PUBLICATION
21 August 2015

PUBLISHED
10 September 2015

LETTER

Strong and nonlinear effects of fragmentation on ecosystem service provision at multiple scales

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Keywords: landscape structure, landscape fragmentation, spatially explicit model, ecosystem service supply, ecosystem service flow

Supplementary material for this article is available online

Abstract

Human actions, such as converting natural land cover to agricultural or urban land, result in the loss and fragmentation of natural habitat, with important consequences for the provision of ecosystem services. Such habitat loss is especially important for services that are supplied by fragments of natural land cover and that depend on flows of organisms, matter, or people across the landscape to produce benefits, such as pollination, pest regulation, recreation and cultural services. However, our quantitative knowledge about precisely how different patterns of landscape fragmentation might affect the provision of these types of services is limited. We used a simple, spatially explicit model to evaluate the potential impact of natural land cover loss and fragmentation on the provision of hypothetical ecosystem services. Based on current literature, we assumed that fragments of natural land cover provide ecosystem services to the area surrounding them in a distance-dependent manner such that ecosystem service flow depended on proximity to fragments. We modeled seven different patterns of natural land cover loss across landscapes that varied in the overall level of landscape fragmentation. Our model predicts that natural land cover loss will have strong and unimodal effects on ecosystem service provision, with clear thresholds indicating rapid loss of service provision beyond critical levels of natural land cover loss. It also predicts the presence of a tradeoff between maximizing ecosystem service provision and conserving natural land cover, and a mismatch between ecosystem service provision at landscape versus finer spatial scales. Importantly, the pattern of landscape fragmentation mitigated or intensified these tradeoffs and mismatches. Our model suggests that managing patterns of natural land cover loss and fragmentation could help influence the provision of multiple ecosystem services and manage tradeoffs and synergies between services across different human-dominated landscapes.

Introduction

Human dominated landscapes around the world are characterized by the loss and fragmentation of natural land cover (DeFries *et al* 2004, Foley *et al* 2005). Human activities, especially agricultural and urban expansion, often result in landscapes consisting of fragments of natural land cover interspersed with agricultural fields or residential areas (Cardille and Lambois 2010). For example, more than 70% of the world's forests are now within one kilometer of an edge—often in close proximity to human modified spaces (Haddad *et al* 2015). This loss and fragmentation has widely acknowledged negative effects on many types of biodiversity and many ecosystem functions (Ewers and Didham 2006, Haddad *et al* 2015). Despite this, fragments of natural land cover continue to supply important ecosystem services such as pollination, pest regulation, water quality regulation, recreation, and cultural services to people (Mitchell *et al* 2015), and in some cases increased fragmentation could increase service provision. For example, fragmentation of pollinator habitat by agricultural fields to increase the interspersion of these two habitats could maximize pollination services (Brosi *et al* 2008). While there is increasing evidence that landscape structure—the arrangement, size, and shape of habitat fragments—has important effects on ecosystem service provision (Bodin *et al* 2006, Kremen *et al* 2007, Syrbe and Walz 2012), our understanding of the effects of fragmentation on service provision remains rudimentary. For most services we do not currently understand how different patterns of fragmentation across landscapes affect how ecosystem services are supplied by fragments of natural land cover and then subsequently flow to people. This limits our capacity to manage ecosystem service provision in human-dominated landscapes.

Fragments of natural land cover often supply ecosystem services that then flow across the landscape to people in the surrounding area via the movement of organisms, or materials such as nutrients or soil, that are important for service provision (Ries *et al* 2004, Mitchell *et al* 2013, 2015). For example, meadows and forests often provide nesting and foraging habitat for pollinators or predators that disperse into surrounding fields, providing pollination and pest regulation services that can ultimately improve crop production (Tscharntke *et al* 2005, Ricketts *et al* 2008). Similarly, fragmentation can also affect the movements of people that are important for service flow. In urban areas, more evenly distributed parks across a city can increase use of green spaces and the recreational and health benefits they provide (Takano *et al* 2002, Wolch *et al* 2011). Thus, in both urban and agricultural landscapes, increased amounts of natural-anthropogenic edge and closer proximity to fragments of natural land cover can increase the flow of ecosystem services to people. Because of this, while natural land cover loss and fragmentation often have negative effects on biodiversity and service supply, they can simultaneously place people and ecosystems in closer proximity, potentially increasing service flows (Bagstad *et al* 2013, Mitchell *et al* 2015). Recognition of these contrasting effects of natural land cover loss and fragmentation on service provision has only recently occurred.

While the effects of edges and fragmentation on species population dynamics are relatively well known (Ries *et al* 2004, Rand *et al* 2006, Blitzer *et al* 2012), their importance for ecosystem service provision is only just now becoming evident. Often termed 'spillover' effects, the ecological effects of edges and fragmentation arise from increases in ecological flows, increased access to resources (e.g., landscape complementation and supplementation; Tscharntke *et al* 2012), altered resource or abiotic conditions, or changes in species interactions relative to distance from edge (Ries *et al* 2004). A potentially important consequence of these effects is decay in ecosystem service provision as one moves away from fragments of natural land cover (Mitchell *et al* 2015). These distance-dependent patterns are increasingly being observed in human-dominated landscapes (Farwig *et al* 2009, Koch *et al* 2009, Mitchell *et al* 2014). For example, pollination services decline exponentially with distance from forest (Ricketts *et al* 2008, Keitt 2009, Martins *et al* 2015) and pest regulation often declines with increasing field size as distances from habitat fragments and hedgerows increase (Werling and Gratton 2010, Segoli and Rosenheim 2012). The distance urban residents will travel to neighborhood parks, as well as property values around urban green spaces, also vary in similar distance-dependent ways (Tajima 2003, Nielsen and Hansen 2007). However, tests of the consequences of these distance-dependent effects on ecosystem service provision as landscape structure varies are rare and are often focused on specific services or case studies (e.g. Brosi *et al* 2008, Keitt 2009, Bianchi *et al* 2010, Ricketts and Lonsdorf 2013).

Thus, there is currently a lack of understanding around how changes to landscape structure and fragmentation might affect the provision of multiple ecosystem services when distance-dependent effects are present. Past work has modeled services in spatially-explicit ways (e.g. Naidoo and Ricketts 2006, Nelson *et al* 2009), incorporated distance-dependent effects on service provision (e.g. Chan *et al* 2006, Koch *et al* 2009, Barbier 2012), and included nonlinear effects of habitat area on ecosystem service provision (e.g. Barbier *et al* 2008). However, none of these models have combined these approaches to model how simple changes in the structure of human-dominated landscapes might affect ecosystem service provision as patterns of distance-dependent service flow vary.

To address this gap, we created a spatially explicit model to investigate how loss and fragmentation of natural land cover affect the provision of ecosystem services when service supply and, in particular, variation in service flow, are considered. Our main questions were: (1) how do the loss of natural land cover, patterns of fragmentation, and the form of distance-dependent service flow interact to affect final service provision, and (2) how do these effects differ depending on the spatial scale considered?

Methods

We created a simple model using Netlogo 5.0.4 (Wilensky 1999) to simulate change in ecosystem service provision as natural land cover is lost across a human-dominated landscape. We modeled a hypothetical ecosystem service supplied by fragments of natural land cover that flows to the surrounding human-dominated lands. In our model, a fragment's

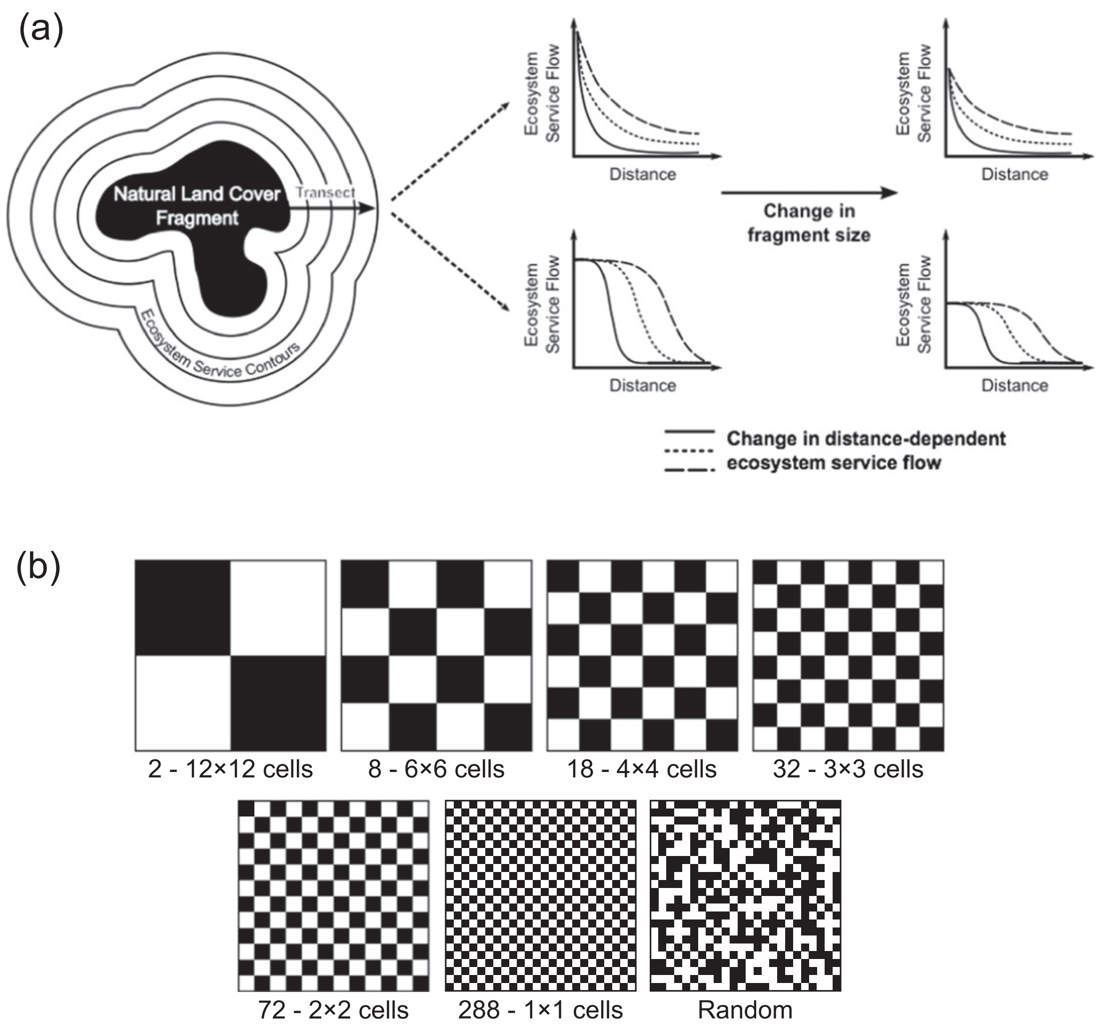

Figure 1. (a) Modeling framework and (b) landscape patterns of natural land cover loss. In (a), ecosystem service provision (*contours*) varies with distance from a natural land cover fragment (*black shape*) according to different distance-dependent relationships, each of which can vary in form (*solid* and *dashed lines*). The maximum service provision a fragment can provide varies depending on its size. In (b), each pattern specifies the arrangement of natural land cover fragments (*black squares*) and anthropogenic cells (*white squares*) at the midpoint of each model run (i.e. 50% natural and 50% anthropogenic land cover). Each landscape consists of 24 × 24 cells (576 cells total).

ability to supply the service varies with fragment size, while the flow of the service depends on proximity to the fragment (figure 1).

Model landscapes and natural land cover loss simulation

Landscapes consisted of a 24 × 24 cell grid (576 total cells), where individual cells could be either natural or anthropogenic land cover. Landscapes were bounded on each side and therefore incorporated landscape edge effects. We defined natural land cover 'fragments' as groups of contiguous cells that shared edges. Fragment area equaled the number of cells in that fragment, and distances between individual cells were calculated as the Euclidean distance between cell centers. We modeled ecosystem service provision exclusively within our model landscapes, acknowledging that large fragments in reality would provide services outside this study area.

Each model run simulated the conversion of natural land cover to anthropogenic, with landscapes initially consisting entirely of natural land cover that was progressively converted to anthropogenic. We modeled a set of six hypothetical, 'checkerboard' patterns of natural land cover loss, plus a seventh random pattern (figure 1). These represent a gradient in landscape fragmentation, varying systematically in area: edge ratio, average fragment size, and average distance between anthropogenic and natural land cover cells (see appendix figure A.2). These patterns are similar to those used previously to investigate how landscape structure affects ecosystem services (e.g. Robinson *et al* 2009). The checkerboard patterns specified a two-stage process of natural land cover conversion: first, random loss of natural land cover cells until the specified checkerboard pattern was obtained at the model run midpoint (i.e., 50% each natural and anthropogenic land cover), and then erosion of the remaining natural land cover fragments via the conversion of fragment edge cells.

Ecosystem service provision modeling

We modeled potential ecosystem service supply from each fragment of natural land cover as a function of fragment size. Large fragments could provide maximum service provision, but smaller fragments provided only a fraction of this. This effect is akin to larger fragments having greater numbers of ecosystem service-providing individuals (Sisk *et al* 1997, Connor *et al* 2000), or greater species or functional diversity (Holt *et al* 1999), leading to increased service provision (Balvanera *et al* 2006). We modeled the relative maximum ecosystem service supply (between 0 and 1) that a fragment of natural land cover j could provide (N_j) as a saturating curve (Barbier *et al* 2008):

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

where A_j is fragment area and p is a constant defining the steepness of the curve. We used $p = 0.008$, defining a curve where 80% of the decrease in N_j occurs for fragments with $A_j < 200$ cells for the main analysis. We also examined how varying p from 0.008 to 0.161 (to make ecosystem service supply less dependent on fragment size) affected model results (i.e., defining curves where 80% of the decrease in N_j occurs for fragments with $A_j < 100, 50, 25$, or 10 cells, respectively).

For ecosystem service flow, we modeled two different distance-dependent decay functions: exponential and logistic. These functions match theoretical predictions of the effects of edges on wildlife populations (Ries *et al* 2004, Rand *et al* 2006) and observed responses of ecological flows and population movements to habitat edges (Duelli *et al* 1990, Ricketts *et al* 2008) that could affect ecosystem service provision, as well as empirical data of ecosystem service provision along distance-to-fragment gradients (Farwig *et al* 2009, Mitchell *et al* 2014, Martins *et al* 2015). We describe the logistic decay function below, details about the exponential decay function can be found in the appendix.

For logistic decay, we assumed that flow of ecosystem service $\mathcal{E}_{ij}$ at distance d from a fragment edge is specified by a modified logistic growth equation (Meyer *et al* 1999):

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

where Δd defines the distance over which $\mathcal{E}$ decreases from 90% to 10% of its initial value N_j, and d_m the distance-from-fragment edge at which $\mathcal{E}$ equals one half its initial value. This equation for logistic decay uses 'characteristic duration' (i.e., $\ln(81)/\Delta d$) instead of growth rate. This enabled us to specify a precise distance over which the majority of ecosystem service flow declined. We varied d_m between 0 and 10 to investigate the effects of altering the distance-from-fragment where service flow declines; variation in Δd had little effect on model results and was kept at 4 cells.

For any given anthropogenic land cover cell i, ecosystem services can flow from multiple surrounding fragments. We summed these contributions to give a total ecosystem service provision value $\mathcal{E}T_i$, assuming that service provision saturates at a maximum value of 1. Below this maximum, we assumed a logistic function, where the contribution of any fragment j to service provision in anthropogenic cell i, decreases as $\mathcal{E}T_i$ approaches 0 or 1:

$$\mathcal{E}T_i = \left(\frac{1}{1 + \exp\left[-\frac{\ln(81)}{0.5}\left(\sum_{j=1}^{s}\mathcal{E} - 0.5\right)\right]}\right) \tag{3}$$

where $\sum_{j=1}^{s}\mathcal{E}$ is the sum of ecosystem service provision contributions to that anthropogenic cell i from all surrounding fragments. We tested the sensitivity of our results to this assumption by alternatively using a linear relationship for the summed contributions of multiple fragments; results were very similar (see appendix figure).

Model runs and statistical analysis

We performed two sets of simulations. In the first, the model was run 20 times with each of four values of $d_{1/2}$ and d_m (i.e. 1, 2, 4, and 8) and the seven patterns of natural land cover loss. This showed that variation between runs due to randomness in the exact pattern of natural land cover loss was very small relative to ecosystem service provision (±5% for the standard deviation). In the second set, we progressively changed the values of $d_{1/2}$ and d_m from 0 to 10 at an increment of 0.1 for each pattern of natural land cover loss, running each combination only once since between-run variation was so small.

We analyzed model results at two spatial scales: across the entire landscape and at the scale of individual anthropogenic cells (i.e., average service provision across all of the anthropogenic cells present at each model step). For each scale, we were interested in peak service provision values, maximum rates of service provision decline, and thresholds of natural land cover loss where ecosystem service provision changed rapidly. We fit simple 'smoothing splines' to model results using the 'gam' package in R to account for variation between multiple runs (Hastie 2013). To determine rates of change (i.e., slopes) in our second set of simulations, we fit a loess curve to each run and estimated the first derivative of the curve using the '*diff*' function in R 3.0.2. Instantaneous rates of change for each point along each curve were calculated across 58 model steps (i.e. ∼10% change in natural land cover amount). To identify thresholds in ecosystem service provision as a function of natural land cover 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 a curve is itself changing, with maximum or minimum values indicating where the slope changes the most rapidly (i.e., inflection points). An example of how this method was used is provided in the appendix (figure A.1).

Results

Ecosystem service provision at both the landscape and cell scale in our model showed nonlinear responses to natural land cover loss. These relationships were strongly affected by interactions between the pattern of landscape fragmentation and the form of distance-dependent service flow decay as well as the capacity of small fragments to supply services. Here, we highlight the common trends and range of results that emerged, focusing on the effects of the pattern of natural land cover loss. Results from the logistic decay and exponential functions were qualitatively similar, therefore only those from the logistic relationship are presented below. Exponential decay results can be found in the appendix. For clarity, we only present results from four of the seven landscape fragmentation patterns modeled that capture the full range of outcomes produced by the model. Also, we only evaluated service provision within our model landscapes, but acknowledge that fragments could, in reality, provide services outside this boundary. Thus, ecosystem service provision is artificially zero when the landscape is 100% natural land cover.

Changing the pattern of landscape fragmentation significantly altered the spatial pattern of service provision (figure 2). At both spatial scales, the maximum values of service provision, the level of natural land cover loss at which these maxima occurred, and rates of service decline were affected by the pattern of landscape fragmentation (figure 3). Fragmenting the landscape into many small fragments (i.e. 1 × 1 cell fragments) resulted in lower and narrower peaks of landscape-scale service provision across all values of d_m (figure 3(a)). These peaks also occurred at lower levels of natural land cover loss. Conversely, fragmenting the landscape into two large fragments broadened the landscape-scale ecosystem service peak, although maximum provision values were in some cases reduced. At the cell-scale, landscape fragmentation into many small fragments meant an earlier decrease in average service provision (figure 3(b)). Interestingly, random loss of natural land cover prolonged maximum cell-scale service provision.

Increasing the rates of distance-dependent ecosystem service flow rapidly increased service provision maxima at both spatial scales. It also shifted the location of these maxima at the landscape-scale, and the location where cell-scale service began to decline, towards increased levels of natural land cover loss (figure 4). Increasing the capacity of smaller fragments of natural land cover to supply ecosystem services to the surrounding landscape had similar effects (figure 5), but more rapidly shifted the landscape-scale maxima, and the locations where cell-scale service began to decline, towards levels of higher natural land cover loss. It also reduced differences in ecosystem service provision between the different patterns of landscape fragmentation at both scales, except for the pattern of fragmentation resulting in two large fragments (see appendix figures A.8–A.12). For this pattern of fragmentation, because it reduces the presence of small fragments of natural land cover and no small fragments are present at 50% natural land cover loss, overall service provision is reduced and a local minimum in landscape- and cell-scale service provision is present at the midway point of each model run.

Altering the pattern of landscape fragmentation in our model interacted nonlinearly with the form of distance-dependent service flow to influence patterns of ecosystem service provision. We focus here on measures most relevant to landscape planning and ecosystem service management; other effects are presented in the appendix. At the landscape-scale, maximum values of service provision occurred at progressively higher levels of natural land cover loss as d_m increased from 0 to 10 (figure 6(a)). Similarly, the thresholds of natural land cover loss at which cell-scale ecosystem service values began to decline increased as d_m increased (figure 6(b)). These relationships were nonlinear, especially for specific patterns of natural land cover loss. For example, at low values of d_m with the 2-fragment pattern of loss, maximum service provision occurred at much lower levels of natural land cover loss than other patterns. However, at large values of d_m this reversed, and maximum service provision for the 2-fragment pattern occurred at the highest levels of natural land cover loss. Similar patterns were also present for cell-scale service decline.

There was a substantial mismatch between the levels of natural land cover loss needed to maximize landscape-scale versus cell-scale ecosystem service provision. Landscape-scale service provision was maximized at levels of natural land cover loss that on average corresponded to a 10% to 40% loss in average cell-scale service provision (figure 7). This mismatch was generally smallest at intermediate values of d_m, except for the 2-fragment pattern, where cell-scale ecosystem service loss reached its maximum. The 2-fragment loss pattern showed the most nonlinear pattern and greatest discrepancy between the levels of natural land cover loss needed to maximize landscape versus cell-scale service provision as d_m varied.

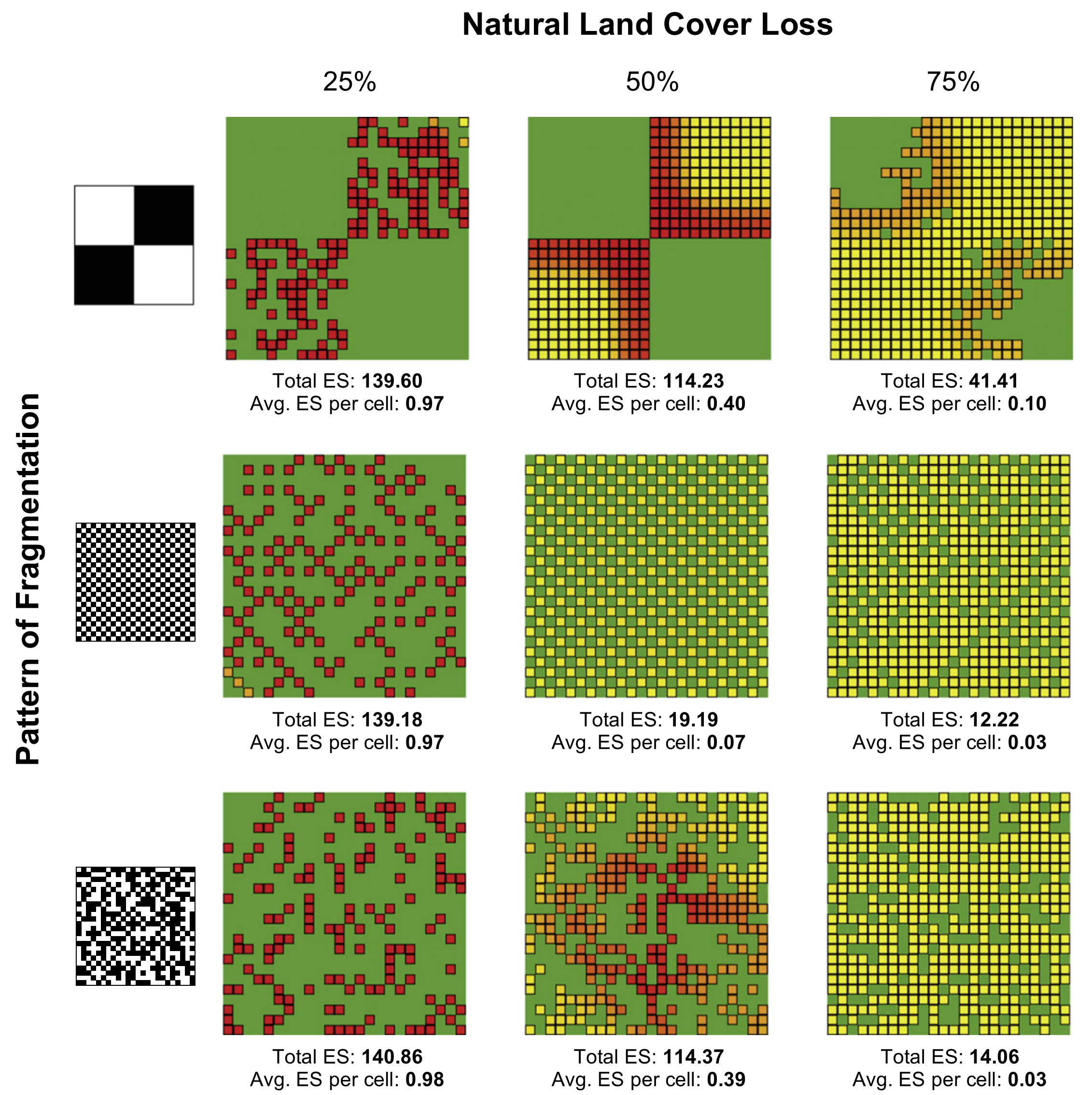

Figure 2. Spatial patterns of ecosystem service (ES) provision at different levels of natural land cover loss as landscape patterns of fragmentation are altered. We show results of logistic distance-dependent ecosystem service decay with a halving distance (d_m) of 4. *Green* cells represent natural land cover, while ecosystem service provision in anthropogenic cells varies from high (*red* cells) to low (*yellow* cells).

Discussion

Our model predicts, for hypothetical ecosystem services, that (1) service provision peaks at intermediate levels of natural land cover loss; (2) managing ecosystem service provision in human-dominated landscapes in part depends on understanding the interaction between the flow of services from fragments of natural land cover and patterns of landscape fragmentation; and (3) the tradeoff between landscape and cell-scale ecosystem service provision has the potential to be strongly affected by the pattern of natural land cover loss. Each of these has important implications for ecosystem service based landscape management. Our modeling framework provides a first step to understand how changes to landscape structure can affect ecosystem service provision while emphasizing the need to quantify these relationships and the processes that underlie them in real landscapes.

Maximizing ecosystem service provision

Ecosystem service provision in our modeled landscapes peaked at intermediate levels of natural land cover loss, depending on the form of distance-dependent service flow, pattern of landscape fragmentation, and capacity of small fragments to supply services (figures 2–5). This highlights that loss and fragmentation of natural land cover in human-dominated landscapes might not always be detrimental to the provision of every ecosystem service. Instead, heterogeneous landscapes that intersperse fragments of different types of natural land cover within the agricultural or urban landscape will likely enhance service flow and provision by increasing average proximity to natural land cover across the landscape.

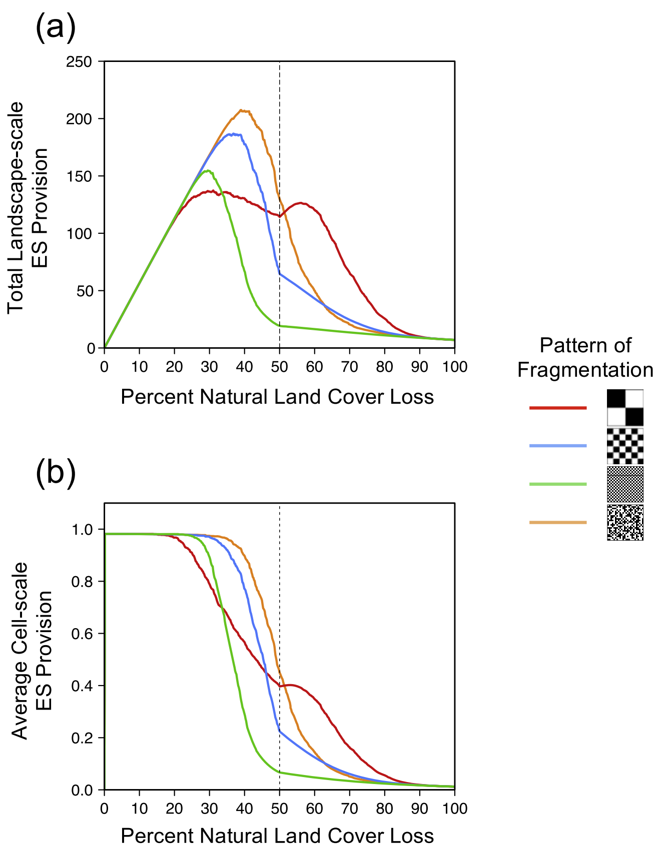

Figure 3. (a) Total landscape-scale and (b) average cell-scale ecosystem service (ES) provision as patterns of fragmentation are varied. We show results of logistic distance-dependent ecosystem service decay with $d_m = 4$. The dashed line indicates 50% natural land cover loss; each line is the mean of 20 model runs.

This effect has been predicted conceptually (Mitchell *et al* 2015) and modeled for pollination in linear landscapes (Brosi *et al* 2008). Our model expands on these results by explicitly modeling the effects of landscape fragmentation on both the supply and flow of services in a two-dimensional landscape. Our results underscore the prediction that for services that depend on movement across landscape to and from areas of natural land cover (e.g., pollination, recreation, waste treatment, pest regulation, cultural services), provision depends on some level of fragmentation.

Importance of landscape fragmentation

The pattern of landscape fragmentation in our model strongly affected the size and location of the ecosystem service provision peak as natural land cover was lost, especially when the capacity of small fragments to provide ecosystem services was decreased. These results suggest that taking into account not just the amount of natural land cover present, but also its spatial pattern across the landscape and how this might impact levels of biodiversity and the supply of different ecosystem services are important for managing ecosystem services at landscape scales.

Landscape management is increasingly incorporating spatial planning for ecosystem services (Bateman *et al* 2013, McKenzie *et al* 2014). For example, agro-ecological schemes often seek to maximize pollination, pest regulation, biodiversity, and crop production across agricultural landscapes via changes to landscape structure (e.g., preservation of hedgerows), agricultural management, and farming intensity (Ekroos *et al* 2014). Similarly, urban planning often focuses on maintaining or increasing access to green space and the ecosystem services these areas provide (Barbosa *et al* 2007). Our results suggest that managing the spatial pattern of different types of land cover, at different scales, across these types of landscapes could help optimize the provision of multiple ecosystem services. In addition, controlling landscape fragmentation of different land cover types at different scales could be an important tool to simultaneously conserve biodiversity (Tscharntke *et al* 2005, Fahrig *et al* 2011) and sustain ecosystem services.

While the patterns of natural land cover loss used in our model, and the sharp distinction between natural and anthropogenic land cover, are simplifications, they do reflect real-world landscape patterns. For example, over the last fifty years, the loss and fragmentation of natural land cover is a common trend in agricultural areas as cropland extent and farm-size have increased (Ihse 1995, Robinson and Sutherland 2002, Lunt and Spooner 2005). Similarly, rectangular arrangements of fields and farmlands

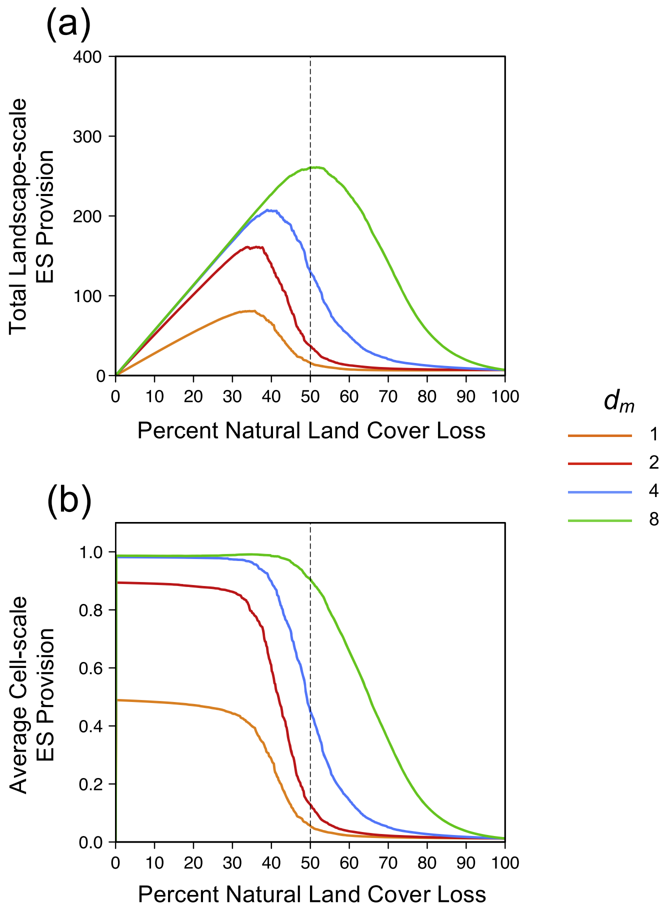

Figure 4. (a) Total landscape-scale and (b) average cell-scale ecosystem service (ES) provision as rates of logistic distance-dependent ecosystem service flow decay are varied. We show results from random natural land cover loss across the model landscape in all cases. The dashed line indicates 50% natural land cover loss; each line is the mean of 20 model runs.

interspersed with forests are ubiquitous across the continental US (Cardille and Lambois 2010). There remain many opportunities to adapt our modeling framework using more realistic landscapes that contain a mosaic of land use and land cover types, combined with empirical information on the supply and flow of specific ecosystem services.

Importance of distance-dependent ecosystem service flow

Modeled ecosystem service provision depended not only on the pattern of landscape fragmentation, but also on how rapidly ecosystem service flow declined with distance-to-fragment. In our model, service provision maxima were greatest at both spatial scales when this distance-dependent decay in service flow was minimized (figures 4 and 5), either by altering the distance-dependent decay in service provision, or changing the capacity of small fragments to provide ecosystem services.

Decreasing the rate of decline in ecosystem service flow as one moves away from fragments of natural land cover could be one way to influence ecosystem service provision in human-dominated landscapes. This requires research to identify the important mechanisms driving these distance-dependent effects relative to edges (Ries *et al* 2004) and their positive and negative ecological and economic effects (Tscharntke *et al* 2012). For example, services provided by mobile organisms such as pollination and pest regulation (e.g. Brosi *et al* 2008, Bianchi *et al* 2010), might be increased by improving the ability of service-providing organisms to move across an agricultural matrix via changes to field management such as increasing floral resources in fields (Kremen *et al* 2007). Similarly, policies that increase the distances urban residents will travel to visit city green spaces should improve recreational and cultural services.

Additionally, our model suggests that efforts to reduce biodiversity loss from fragmentation, if this increases the capacity of small fragments to supply ecosystem services, could also be important. However, while fragmentation has well-known effects on biodiversity and ecosystem function (e.g., extinction and function debts; Haddad *et al* 2015), how these affect relationships between fragment size and levels of ecosystem service supply is largely unknown. Thus, while our model results emphasize the potential importance of managing not just landscape fragmentation, but

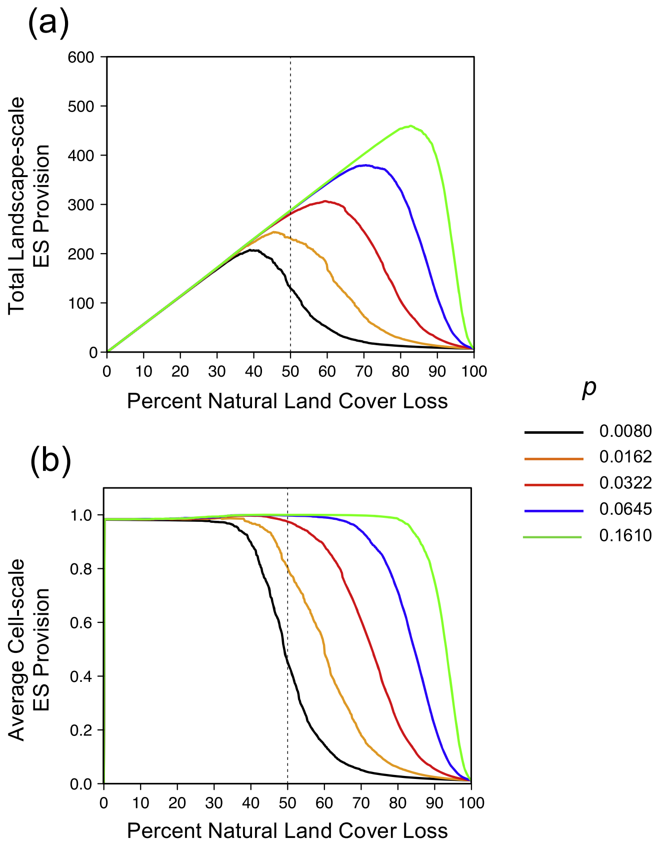

Figure 5. (a) Total landscape-scale and (b) average cell-scale ecosystem service (ES) provision as the strength of area-dependent effects of fragment size on the ability of fragments to supply ES are varied. As p increases, smaller fragments of natural land cover are able to supply increasing amounts of ES. We show results from logistic distance-dependent ES flow with $d_m = 4$ and random natural land cover loss across the model landscape in all cases. The dashed line indicates 50% natural land cover loss; each line is the mean of 20 model runs.

also the landscape matrix within which fragments of natural land cover exist, and how these influence biodiversity and the movement of species and people, improved understanding of the mechanisms behind these effects in real landscapes is needed.

Furthermore, minimizing the distance-dependent decay of service flow or increasing the capacity of small fragments to provide services in our model also resulted in more sudden losses of ecosystem services. In part, this is because these changes in model parameters drove larger ecosystem service peaks that occurred at higher levels of natural land cover loss. In real landscapes, where natural land cover loss is a function of multiple social and economic drivers (Lambin and Meyfroidt 2011), there is the potential that the loss of natural land cover could progress to levels that result in substantial and rapid ecosystem service decline. Our model suggests that these declines will be more sudden when there is little decay in ecosystem service flow across distances from fragments of natural land cover or where area-dependent effects on the capacity of fragments to supply services are small. This could lead to unforeseen and less predictable changes in service provision at higher levels of natural land cover loss.

Ecosystem service provision between scales

Our modeling results predict that optimizing a landscape for service provision at the cell scale requires different management than for the entire landscape. In every case, average cell-scale service provision began to decline before the landscape-level service provision maximum was reached (figure 7). If this holds for real landscapes, it means that actions to maximize provision at one scale might result in a sub-optimal result at another scale; a mismatch that would have important consequences for policy and land management in real landscapes (de Groot *et al* 2010). While land managers might seek to maximize ecosystem service provision at the landscape scale, individual landowners will likely want to maximize service provision for their individual properties. If these two goals conflict, as in our model, it could result in a tension between actors who operate at different scales across the landscape.

Managing patterns of natural land cover loss across landscapes could help minimize these types of ecosystem service tradeoffs. For example, maintaining smaller fragments of natural land cover throughout the landscape (Fahrig *et al* 2011), may be a better strategy for optimizing ecosystem services at multiple scales than maintaining large

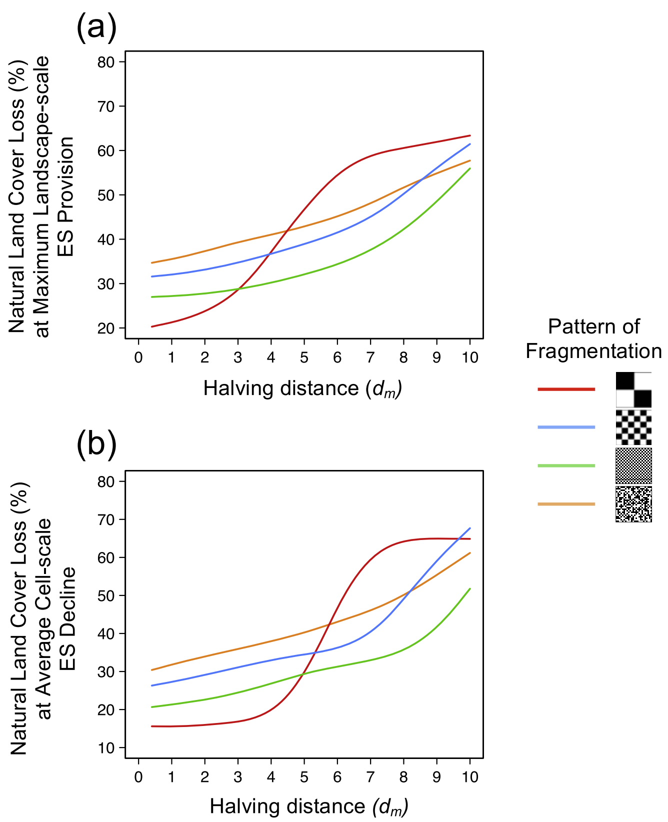

Figure 6. Effects of varying the form of the logistic distance-dependent ecosystem service (ES) flow decay on (a) the level of natural land cover loss at maximum landscape-scale ecosystem service provision, and (b) the level of natural land cover loss where average cell-scale ecosystem service provision begins its decline. We show generalized additive model (GAM) curves fit to the model results.

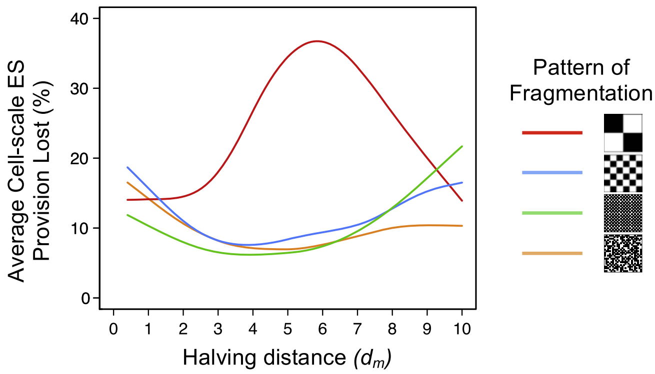

Figure 7. Effects of varying the form of the logistic distance-dependent ecosystem service (ES) flow decay on the relative loss of average cell-scale ecosystem service provision when landscape-scale ecosystem service provision is maximized. We show generalized additive model (GAM) curves fit to the model results.

contiguous areas of conserved natural land, which our model predicts could lead to disproportionate loss of services at the cell-scale (figures 2 and 7). Our results suggest that understanding the scales over which provision of ecosystem services vary will be important for predicting the scales at which natural land cover loss and fragmentation should be managed to influence and optimize service provision. Currently, we only have this knowledge for a few ecosystem services in real landscapes (e.g. Mitchell *et al* 2014).

Model extensions

A future extension to our model will be to incorporate effects of natural land cover loss and fragmentation that can reduce the movement of organisms important for ecosystem service provision (Mitchell *et al* 2013). Incorporating these types of landscape connectivity and metapopulation dynamics (Dubois *et al* 2015) could help us understand how changes in landscape structure might affect biodiversity levels and the ecosystem functions that underlie ecosystem service supply (Dobson *et al* 2006, Mitchell *et al* 2015). We also plan to include more realistic patterns of landscape fragmentation to help assess the generality of the results presented here. Additionally, we hope to incorporate ecosystem services that don't require flows between areas of natural land cover and people for their provision (e.g., carbon storage) that may be affected negatively by natural land cover loss and fragmentation, and consider multiple services at the same time, each with different distance-dependent decay functions. These improvements will be useful to explore how to manage landscape structure for multiple services. Finally, we would like to parameterize our model using data from real landscapes for real ecosystem services to test the applicability of the results presented here. However, this type of data is currently not available for many ecosystem services. This highlights the need to better understand the processes that underlie the effects of landscape structure on service provision.

Conclusions

Our results emphasize the importance of understanding how patterns of natural land cover loss and fragmentation mediate ecosystem service provision in real landscapes. Using a simple model, we predict tradeoffs between maximizing ecosystem service provision at the cell versus landscape scales, and between service provision and the maintenance of natural land cover. As demand for multiple ecosystem services from human-dominated landscapes increases, understanding how to structure these landscapes to optimize service provision will be increasingly important. This requires increased understanding of the actual mechanisms behind these relationships, their spatial patterns across real and complex landscapes, and tools that can predict the consequences of different land use decisions on flows of service provision across landscapes. Our model is a first step towards understanding the ways in which patterns of landscape fragmentation might affect the provision of ecosystem services. Future development of the modeling principles here, in concert with increased efforts to understand the processes that link landscape structure to ecosystem service provision, will help advance our ability to manage human-dominated landscapes for multiple ecosystem services.

Acknowledgments

We thank S Delmotte for conceptual input and NetLogo programming support. This work was supported by an NSERC PGS-D scholarship to MGEM, an NSERC Strategic Projects Grant to EMB and AG, and a grant from the Ouranos Consortium to AG and EMB; AG is supported by the Canada Research Chair Program.

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