Environmental Research Letters

LETTER

Landscape structure affects the provision of multiple ecosystem services

T Lamy1,3, K N Liss2,5, A Gonzalez3 and E M Bennett2,4
1 Département de sciences biologiques, Université de Montréal, C.P. 6128, Succursale Centre-ville, Montréal, Québec, Canada H3C 3T7
2 Department of Natural Resource Sciences, McGill University, 2111 Lakeshore Road, Ste Anne de Bellevue, Quebec, Canada, H9X 3V9
3 Department of Biology, McGill University, 1205 Docteur Penfield, Montreal, Quebec, Canada, H3A 1B7
4 McGill School of Environment, McGill University, 3534 University, Montreal, Quebec, Canada, H3A 2A7
5 These authors contributed equally to the manuscript.

E-mail: Elena.bennett@mcgill.ca

Abstract
Understanding how landscape structure, the composition and configuration of land use/land cover (LULC) types, affects the relative supply of ecosystem services (ES), is critical to improving landscape management. While there is a long history of studies on landscape composition, the importance of landscape configuration has only recently become apparent. To understand the role of landscape structure in the provision of multiple ES, we must understand how ES respond to different measures of both composition and configuration of LULC. We used a multivariate framework to quantify the role of landscape configuration and composition in the provision of ten ES in 130 municipalities in an agricultural region in Southern Québec. We identified the relative influence of composition and configuration in the provision of these ES using multiple regression, and on bundles of ES using canonical redundancy analysis. We found that both configuration and composition play a role in explaining variation in the supply of ES, but the relative contribution of composition and configuration varies significantly among ES. We also identified three distinct ES bundles (sets of ES that regularly appear together on the landscape) and found that each bundle was associated with a unique area in the landscape, that mapped to a gradient in the configuration and composition of forest and agricultural LULC. These results show that the distribution of ES on the landscape depends upon both the overall composition of LULC types and their configuration on the landscape. As ES become more widely used to steer land use decision-making, quantifying the roles of configuration and composition in the provision of ES bundles can improve landscape management by helping us understand when and where the spatial pattern of land cover is important for multiple services.

Introduction

The field of ecosystem service (ES) science is rapidly maturing; increasingly, we are able to predict the provision of ecosystem services under a variety of different conditions and in a variety of different locations. While many ES models once assumed a benefits-transfer approach in which landscape composition, the amount of each land use/land cover (LULC) type, dominated the prediction of ES provision, landscape configuration, the spatial characteristics including the shape and connectivity of patches of different LULC types relative to one another (Gustafson 1998), is now understood to have an important effect on many ES. Indeed, recent meta-analysis (Mitchell et al 2013), theory (Mitchell et al 2015a), conceptual frameworks (Mitchell et al 2015b), and some empirical studies (Laterra et al 2012, Kennedy et al 2013, Chaplin-Kramer et al 2015, Qiu and Turner 2015), suggest that both LULC composition and configuration affect how ES are supplied across landscapes especially in landscapes
Table 1. List of the ten ecosystem services used in this study. For more information, see Raudsepp-Hearne et al (2010).

| Ecosystem service               | Description                                      |
|--------------------------------|--------------------------------------------------|
| Pork production                | Number of pigs produced per km²                  |
| Water quality                  | IQBP quality index (1-5) used by the provincial government to assess the raw water supply intended for consumption |
| Maple syrup production         | Number of maple-syrup taps per km²               |
|                                |                                                  |
| Carbon sequestration           | Kilograms of carbon per km² and per year         |
| Soil phosphorus retention      | Percent of saturation index measured from soil samples |
| Soil organic matter            | Percent organic matter measured from soil samples |
|                                |                                                  |
| Deer hunting                   | Number of deer killed per km²                    |
| Tourism                        | Number of tourist attractions per km²            |
| Nature appreciation            | Number of reported sightings of rare species per km² |
| Summer home value              | Tax value of summer homes per km²                |

where spatial heterogeneity is high and land cover is changing (Petrosillo et al 2010, Laterra et al 2012, Turner et al 2013, Mitchell et al 2015a). For example, proximity to native forest fragments and size of forest fragments have been linked to changes in pollination (Steffan-Dewenter and Tscharntke 1999, Aguirre and Dirzo 2008, Martins et al 2015), carbon storage (Smithwick et al 2003, Ziter et al 2013, Chapin-Kramer et al 2015), insect pests (Mitchell et al 2014a, Maguire et al 2015) and biodiversity (Mitchell et al 2014b). Disease control has been shown to be vulnerable to landscape structure (Ostfeld and LoGiudice 2003), for example when spatial configuration enhances or suppresses the coexistence of elements facilitating circulation of the West Nile Virus (Pradier et al 2008). Movement and habitat selection of roe deer vary with habitat availability and distance to buildings and roads, which affect vulnerability to hunting (Coulon et al 2008, Morellet et al 2011). In cities, the urban heat island effect has been mitigated by altered configuration of green space (Li et al 2012).

Taken together, these studies suggest that landscape structure, which includes both composition (amount of each LULC type) and configuration (the spatial arrangement of LULC types), impacts the provision of ES. However, most studies of ES provision incorporate only one or a few facets of the landscape structure, or examine only a single ES. Yet we know that landscapes are multifunctional, providing many services (Raudsepp-Hearne et al 2010, Qiu and Turner 2015) and varying in many aspects of their structure. In particular, despite evidence of the importance of configuration, empirical studies of exactly which aspects of configuration affect the provision of multiple services, remain rare (Andrieu et al 2015, Bennett et al 2015, Mitchell et al 2015a). Ultimately, this leaves a gap in our understanding of exactly how and when composition and configuration contribute the provision of multiple ES (Laterra et al 2012, Syrbe and Walz 2012), limiting our ability to use these factors to ensure optimal provision of services across landscapes.

Here, we examined the role of landscape composition and configuration in the provision of bundles of ES, where bundles are sets of services that appear together on the landscape in similar relative proportions (Raudsepp-Hearne et al 2010). We use multivariate statistical modelling to quantify the influence of landscape composition and configuration in the provision and distribution of ten ecosystem services in the Montérégie region outside Montreal, Canada.

Methods

Study site
We assessed the relationship between landscape structure, measured as both landscape composition and landscape configuration, and ES provision for municipalities (n = 130) in an agricultural, peri-urban region in Southern Quebec, Canada. The study site covers two adjacent watersheds spanning 7288 km² close to metropolitan Montreal with mean municipality area of 74 km², and includes agricultural land dominated by corn-soy rotation and pork production, urban settlements, recreational areas, and nature reserves.

ES in this region were quantified by Raudsepp-Hearne et al (2010; table 1). These measurements used publicly available datasets collected by the MDDEP (Ministry for Sustainable Development, Environment and Parks) and the MRNF (Ministry for Natural Resources and Fauna) from 1988 to 2007 at the scale of the municipality, reflecting a common unit for landscape planning and decision-making. The ES assessed included provisioning (maple syrup production, pork production, water quality), regulating (soil organic matter, soil phosphorus retention, carbon
Landscape composition-based metrics were applied to two LULC types representing various aspects of the landscape structure. See Table 2 for their variation across the studied region.

| Percentage | Percentage of the landscape cover by each LULC type |
| Density    | Patch density of each LULC type measured as the number of patches of each LULC type divided by the total landscape area |

Landscape configuration-based metrics include:

- Shape: Average shape of patches of each LULC type measured as the complexity of patch shape of each LULC type with the landscape, as compared to a standard square shape of the same size.
- Connectance: Connectance among patches of each LULC type measured as the number of functional connections between patches of the corresponding LULC type, where a pair of patches is connected if the distance between them is less than 300 m. Connectance is reported as the percentage of the maximum possible Connectance given the total number of patches.

Sequestration, and cultural services (nature appreciation, tourism, deer hunting and summer home value). All service measurements were normalized to a range between 0 and 1, where 1 represented the maximum value measured for the service across all study sites. We removed forest recreation and crop production from our analysis because their provision was calculated based on land use in the original Raudsepp-Hearne et al. (2010) paper.

### Composition and configuration-based metrics of landscape structure

We used four metrics to quantify the landscape structure within each municipality (Table 2). The four metrics were divided into two categories, based on whether they quantified the composition of the landscape without reference to the spatial distribution of patches of each LULC type, or the configuration of the landscape (Figure 2). Each metric was applied to two LULC types (forest and agriculture) to produce a total of eight final variables (i.e., 4 metrics by 2 LULC types).

Landscape composition-based metrics captured features associated with the overall prevalence and the number of patches of each LULC type within the landscape. Specifically, we computed the percentage (the amount of the landscape comprised of each LULC type) and density (the number of patches of each LULC type per unit area) of each LULC type. These two metrics addressed the most fundamental aspects of the landscape composition. Metrics of landscape configuration took into account information on the spatial distribution of each LULC in the landscape. We computed the shape and connectance of patches for each LULC type. The shape metric characterized each LULC type based on the averaged complexity of their patch boundaries and size. Connectance characterized, for each LULC type, the degree of patch isolation and fragmentation in the landscape.

Each of the four metrics (landscape composition-based metrics: percentage and density; landscape configuration-based metrics: shape and connectance) were calculated for each LULC type and for each municipality using FRAGSTATS (McGarigal and Cushman 2002). To map LULC, we generated a two-class raster (5 m resolution) LULC map, classifying forest and agriculture, using data from the Système d’Information Écoforêté (SIEF) 2001. For comparison with the normalized ES measurements, and with an interest in specifying the relative influences rather than absolute relationships, the eight landscape structure variables were also normalized to a range between 0 and 1, with 1 representing the maximum value measured across all municipalities.

### Contribution of landscape composition and configuration to the provision of each ES

We assessed how each landscape metric contributed to explaining variability in the provision of the ten ES individually. We first quantified the contribution of each of the four types of landscape metrics. Then, quantified the overall contribution of landscape composition-based metrics (percentage and density) versus landscape configuration-based metrics (shape and connectance).

For the first goal, we used multiple regressions. In a multiple regression, the proportion of the variance in the provision of an ES explained by the eight landscape variables corresponds to its coefficient of multiple determination ($R^2$), which can be further decomposed into the contribution of each of the eight variables as follows:

$$R^2 = \sum_{j=1}^{N} a_j^2 r_{ES,x_j}$$

where $a_j'$ is the standardized regression coefficient of the $j$th landscape variable and $r_{ES,x_j}$ is the correlation coefficient between an ES and the $j$th landscape variable. The contributions of each of the four landscape metrics were computed by summing contributions over LULC types. Note that a contribution can be either positive or negative.
We then quantified the relative importance of landscape composition and landscape configuration in explaining the provision of each ES using variation partitioning (Borcard et al. 1992). Variation partitioning uses redundancy analysis (RDA) to partition the variation in the provision of each ES into different fractions that are calculated based on adjusted $R^2$ ($R^2_{adj}$). Unlike $R^2$, $R^2_{adj}$ provides unbiased estimates of each component (Peres-Neto et al. 2006). This approach is particularly relevant in our case as each ES can be influenced (a) only by landscape composition, (b) only by landscape configuration or (c) by both. In statistical terms, it means that the total importance of landscape composition is (a) + (c), while the total importance of configuration is (b) + (c). Based on partial RDA we estimated the unique contribution of landscape composition to the provision of each ES while controlling for landscape configuration (a) and vice versa (b), and tested their significance based on 999 permutations. The joint contribution of both composition and configuration (c) was calculated by subtracting the individual components (a) and (b) from the total variance explained, and hence its significance cannot be tested (Borcard et al. 1992, Legendre and Legendre 2012).

**Multivariate perspective on the contribution of landscape composition and configuration to the provision of multiple ES**

In addition to treating each ES independently, we also modeled the ES data as a multivariate object, which has the advantage of directly taking into account relationships among ES. To investigate the relationship between the provision of multiple ES and landscape structure (represented by the eight landscape variables), we computed a RDA on the multivariable ES data. RDA allowed us to represent this relationship in a correlation biplot, in which the angles between ES and landscape metrics, and between ES themselves or landscape metrics themselves, reflects their correlations. The significance of both the canonical relationship between ES provision and landscape variables and the individual canonical axes was tested based on 999 permutations. As above, we partitioned the total variation in the provision of all ES into three components: the two unique contributions (a and b) and the joint contribution of landscape composition and landscape configuration (c) following the same method as above but applied to multivariate response variables (Borcard et al. 1992).

**Constraint clustering of municipalities**

We used multivariate regression tree (MRT) as a form of multivariate clustering (Legendre and Legendre 2012) on the ES data. We used the eight landscape variables as a constraint in the analysis. Cross-validation within the MRT analysis resulted in the delineation of groups of municipalities that were fairly homogenous with respect to ES provision. Following the splitting of the data into statistically similar clusters of municipalities, we produced bundles of ES within each of these clusters (i.e. a given branch of the resulting MRT). These bundles represent the difference between the mean values of each ES within each cluster of municipalities compared with the mean of that ES over all municipalities. In addition, because MRT partitions the ES multivariate data set according to the eight landscape variables, it can be used to define clusters of municipalities that are explained by a reduced set of landscape features. The tree with the lowest cross-validation error was chosen as the best predictive tree. All statistical analyses were conducted using R 3.0.1 (R Core Team 2014). Variation partitioning of single ES provision and multiple ES provision was performed using the ‘varpart’ function of the ‘vegan’ package (Oksanen et al. 2016). The RDA was performed using the ‘rda’ function within the ‘vegan’ and the MRT was performed using the ‘mvpart’.

**Results**

Composition and configuration of both agriculture and forest vary across our study region (figure 1). There is an east-west trend of high forest cover to the east of the region and greater agricultural land use to the west. Forest patches are numerous, more structurally complex and better connected to the east and smaller, and more isolated in the west, while the opposite is true for agriculture.

Landscape structure explains different amounts of the variation across the ten ES among municipalities (figure 2 and supporting information [SI] table 1). For instance, landscape structure explains 66%, 41% and 32% of the variation in carbon sequestration, deer hunting, and soil organic matter respectively but only 5%, 4% and 3% of the variation in water quality, tourism, and summer home value. With the exception of the latter three services, the provision of ES is significantly explained by landscape structure (SI table 1).

Overall, landscape composition contributed more than landscape configuration to variation in ES, though their relative importance varies from service to service (figure 2(b)). The fraction of the variation in each ES due only to landscape composition varies from 1% for soil phosphorus retention to 26% for carbon sequestration, while the fractions due only to the spatial configuration of the landscape is significantly higher than 3% only for pork production (figure 2(b) and SI table 1). Although landscape composition has a large unique contribution to the provision of most ES as compared to landscape configuration, the effect of configuration on ES is to a large extent confounded with the effect of composition (figure 2(b)). Indeed, the joint contribution of composition and configuration on the variation of each ES was strong.
For instance, the joint effect of composition and configuration explained 40.5%, 13.1% and 13.7% of the variation in carbon sequestration, deer hunting and soil organic matter.

The multivariate test of the relationship between the provision of multiple ES and landscape variables allows us to further tease apart the joint effects of composition and configuration. The relationship between the provision of multiple ES and landscape structure was highly significant ($F_{8,119} = 6.360, P < 0.001$) explaining 30% of the provision of multiple ES ($R^2_{adj} = 25.2\%$). The first two canonical axes were significant ($P < 0.001$) accounting for 21.8% and 5.1% of the variation of multiple ES, respectively (figure 3(a)). The unique contribution of landscape composition ($R^2_{adj} = 13.4\%, P = 0.001$) accounted for most of the total variation in the provision of multiple ES. The unique contribution of configuration was low and non-significant ($R^2_{adj} = 0.5\%, P = 0.162$).

However, the joint contribution of both composition and configuration explained half of the total variation in the provision of multiple ES ($R^2_{adj} = 12\%$), hence both aspects of landscape structure are implicated in a larger fraction of variation that cannot be partitioned into either configuration or composition alone. The RDA biplot (figure 3(a)) suggests that ES exhibit contrasting relationships with landscape variables. Pork production is tightly related to two variables, related both to the spatial configuration (shape of agricultural fragments) and composition (density of forest fragments) of the landscape in agreement with our univariate analysis (figure 2(b)). Deer hunting, maple syrup production and soil organic matter are tightly related to the composition of forest fragments, while nature appreciation is located in the opposite direction in the canonical space. Carbon sequestration, soil phosphorus retention, summer home value, water quality and tourism form a group of ES for which the

![Figure 1. Landscape structure across a peri-urban region in Southern Quebec, Canada. Each cell represents one of the 130 municipalities. Landscape structure was assessed based on four landscape metrics (percentage, density, connectance, and shape) applied to two land-cover types, forest fragments (maps in the left-hand column) and agricultural patches (maps in the right hand column). Landscape metrics are based on either the composition (red maps) or the spatial configuration (blue maps) of land-cover types. Darker polygons indicate higher values of landscape structure. Thus, darker coloured polygons for shape indicate more complexity of patch shape; darker coloured polygons for connectance indicate more connection between patches of this land-cover type in this municipality; darker colors for density indicate more interspersion with different types of land cover; and darker colors for percentage indicate more overall area in that type of land use in that polygon.](image)
influence of composition (percentage of forest fragments and density of agricultural fragments) is lower relative to variables of the spatial configuration of the landscape (shape and connectance of forest fragments).

Three clusters of municipalities emerged; these clusters reveal the primary contribution of landscape composition in the provision of ES bundles (figure 3(b)). The location of these clusters reflects both social and ecological features of the landscape, such as the distribution of forest cover from east (more forest) to west (less forest) and primary land use (more agricultural to the west, and more recreational to the east, with pork production featuring in the middle). The first cluster of municipalities provides more nature appreciation (figure 3(c)) than other municipalities and is characterized by a lower proportion (≤0.565) and density (≤0.645) of forest fragments.

Pork production is higher in the second cluster of municipalities. This second cluster of municipalities exhibit a low proportion of forest (≤0.565) but higher density of forest fragments (>0.645) than the first cluster. The provision of seven ES (summer home value, maple syrup production, carbon sequestration, deer hunting, soil organic matter, water quality and soil phosphorus retention) is higher in cluster 3, which is characterized by municipalities displaying a higher proportion of forest fragments (>0.565).

**Discussion**

Theory and meta-analyses have pointed to the likely importance of both landscape composition and configuration in the relationship between LULC and ES, but no study has quantitatively addressed the role both factors plays in determining provision of multiple
services (Petrosillo et al 2010, Laterra et al 2012). We find an influence of both landscape composition and configuration on ES alone and in bundles. Although the overall contribution of landscape composition was higher than landscape configuration, a large fraction of the spatial variation was jointly explained by configuration and composition. The configuration of forest cover to the east was a particularly important determinant in the provision of pork, summer home value, water quality, and tourism, and played a key role in the provision of soil phosphorus retention.

In this region, there is an east-west gradient in the provision of multiple ES. The western part of the region is mainly dominated by agriculture and influenced by its proximity to Montreal, providing primarily nature appreciation. This may be because nature appreciation was assessed based on the number of rare species that happen to have been seen in a given area, which likely reflects areas that have been frequented by nature enthusiasts. Many people in this region go to ecotone habitats at the edge of forests and agriculture to appreciate nature, which might explain this somewhat paradoxical result. The central region of the landscape is a mix of agricultural patches and higher density of smaller forest patches in a part of the region focused agriculturally on pork production. Finally, the eastern part of the Montérégie is dominated by forest cover. In this part of the landscape, there is greater provision of those ES directly related to ecological processes, such as carbon sequestration, soil phosphorus retention, and provision of high quality water. The greater abundance of forest here provides additional social benefits such as summer home value, maple syrup production, and deer hunting.

This work brings into focus the fundamental contribution of both composition and configuration to the relationship between LULC and ES, and develops a statistical approach for unraveling the complex relationship between composition, configuration, and ES provision. While correlation does not imply causation, one can hypothesize about the processes that may be at work behind the finding that both aspects of landscape structure—configuration and composition—are related to the provision of individual and bundles of services. For example, clearly, part of what determines the overall level of carbon sequestration is LULC—whether a municipality is dominated by forest, agriculture, suburbs, or water will necessarily
change the amount of carbon able to be sequestered. But another part of what determines carbon storage in forests might be the size, shape, and position of each individual forest patch (Ziter et al. 2013, Ziter et al. 2014). Ultimately, while there is growing evidence in the literature that configuration matters to the provision of services, there remain important questions still to answer about the mechanisms and processes behind this role, including key questions about when and where configuration is likely to matter most.

Our work expands upon investigations that established the role of configuration in the provision of single ES, such as the influence of edge effects on the magnitude of carbon storage (Robinson et al. 2009, Ziter et al. 2013, Chaplin-Kramer et al. 2015), and distance from natural habitat on pollination services (Ricketts et al. 2008, Martins et al. 2015) among other services (e.g. De Marco and Coelho 2004, Pradier et al. 2008, Mitchell et al. 2014a, 2014b).

While models of single ES have emphasized the role of landscape composition, our work extends recent efforts to also incorporate specific aspects of landscape configuration into these models, and also offer an approach to understand the role of landscape structure on multiple services. Existing models are generally restricted to the position dimension of landscape structure, in the form of downslope flow in hydrological models (Eigenbrod et al. 2011), or relationships between nesting and foraging habitat for pollinators (Tallis and Polasky 2009). Expanding these valuable developments by incorporating additional dimensions of landscape configuration into models of multiple services is a critical next step for ES modeling.

ES modelling tools based on multivariate LULC datasets are indispensable for evaluating the effects of LULC change and projecting ES provision under alternative management scenarios. As temporal data become available, our approach can be extended to multivariate time series models to capture the spatio-temporal trends in multiple ES as landscape composition and configuration change (Zuur et al. 2003). The next generation of ES models will support more effective landscape planning that considers the outcomes for multiple ES and aligns with both ecological and economic goals for ecosystem management (Polasky et al. 2008, Mendenhall et al. 2014).

Conclusion

We found that configuration and composition of LULC together explain the supply of ecosystem services in landscapes spanning a transition from forest to agriculture. Indeed, our results indicate that models of ES provision that fully incorporate information about landscape configuration, will likely provide better estimates of the supply of many services, and improve our understanding of the apparent trade-offs and synergies among ES (Bennett et al. 2009). These results show that the supply of ES in any given location depends upon juxtaposition with other ecosystems and on the overall mosaic of ecosystems across a region. This in turn means that management for bundles of ES must take into account changes in landscape configuration and composition at multiple spatial scales. As ES become more widely used to steer land use decision-making, accurate quantification of the roles of configuration and composition in the provision of multiple ES and ES bundles is needed to improve the accuracy of ES-based landscape management tools.

Acknowledgments

This project was made possible by an NSERC Strategic Projects Grant to EMB and AG, NSERC Discovery Grants to EMB and AG, a Julie-Payette Research Scholarship and McGill Schulich Fellowship to KNL. AG was supported by the Canada Research Chair. TL was supported by a post-doctoral scholarship from NSERC grant no. 7738. We thank Ciara Raudsepp-Hearne for generously providing the ecosystem service measurement data used in our analysis and Delphine Renard for help with GIS. AG is supported by the Canada Research Chair program and a Killam Fellowship. EMB is supported by an EWR Steacie Fellowship. We acknowledge the support of the Quebec Centre for Biodiversity Science. We thank Maria Dumitru for her help in providing maps of the region, and two anonymous reviewers for their comments, which significantly improved the manuscript.

References

Aguirre A and Dirzo R 2008 Effects of fragmentation on pollinator abundance and fruit set of an abundant understory palm in a Mexican tropical forest Biol. Conserv. 141 375–84
Andrieu E, Vialatte A and Sirami C 2015 Misconceptions of fragmentation’s effects on ecosystem services: a response to Mitchell et al Trends Ecol. Evol. 30 633–4
Bennett E M, Peterson G D and Gordon L J 2009 Understanding relationships among multiple ecosystem services Ecol. Lett. 12 1394–404
Bennett E M, Cramer W, Begossi A, Cundill G, Diaz S, Ego B N, Geijzendorffer I R, Krug C B, Lavorel S and Luoto E 2015 Linking biodiversity, ecosystem services, and human well-being: three challenges for designing research for sustainability Curr. Opin. Environ. Sustain. 14 76–85
Borcard D, Legendre P and Drapeau P 1992 Partialling out the spatial component of ecological variation Ecology 73 1045–55
Chaplin-Kramer R et al. 2015 Spatial patterns of agricultural expansion determine impacts on biodiversity and carbon storage Proc. Natl Acad. Sci. 112 7402–7
Coulon A, Morell et N, Goulard M, Cargnelutti B, Angibault J-M and Hewison A J M 2008 Inferring the effects of landscape structure on roe deer (Capreolus capreolus) movements using a step selection function Landsc. Ecol. 23 603–14
De Marco P Jr and Coelho F 2004 Services performed by the ecosystem: forest remnants influence agricultural cultures’ pollination and production Biodivers. Conserv. 13 1245–55
Eigenbrod F, Bell V A, Davies H N, Heinemeyer A, Armstead P R and Gaston K J 2011 The impact of projected
increases in urbanization on ecosystem services Proc. R. Soc. London B Biol. Sci. 278 3201–8
Gustafson E J 1998 Quantifying landscape spatial pattern: what is the state of the art? Ecosyst. 1 143–56
Kennedy C M et al 2013 A global quantitative synthesis of local and landscape effects on wild bee pollinators in agroecosystems Ecol. Lett. 16 584–99
Laterra P, Oruè M E and Booman G C 2012 Spatial complexity and ecosystem services in rural landscapes Agric. Ecosyst. Environ. 154 56–67
Legendre P and Legendre L 2012 Numerical Ecology. (Amsterdam, The Netherlands: Elsevier)
Li X, Zhou W, Ouyang Z, Xu W and Zheng H 2012 Spatial pattern of greenspace affects land surface temperature: evidence from the heavily urbanized Beijing metropolitan area, China Landsc. Ecol. 27 887–88
Maguire D Y, James P M A, Buddle C M and Bennett E M 2015 Landscape connectivity and insect herbivory: A framework for understanding tradeoffs among ecosystem services Glob. Ecol. Conserv. 4 73–84
Martins K T, Gonzalez A and Lechowicz M J 2015 Pollination services are mediated by bee functional diversity and landscape context Agric. Ecosyst. Environ. 200 12–20
McGarigal K and Cushman S A 2002 Comparative evaluation of experimental approaches to the study of habitat fragmentation effects Ecol. Appl. 12 335–45
Mendenhall C D, Karp D S, Meyer C F J, Hadly E A and Daily G C 2013 Predicting biodiversity change and averting collapse in agricultural landscapes Nature 499 213–7
Mitchell M E, Bennett E and Gonzalez A 2013 Linking landscape connectivity and ecosystem service provision: current knowledge and research gaps Ecosystems 16 894–908
Mitchell M G E, Bennett E M and Gonzalez A 2014a Agricultural landscape structure affects arthropod diversity and arthropod-derived ecosystem services Agric. Ecosyst. Environ. 192 144–51
Mitchell M G E, Bennett E M and Gonzalez A 2014b Forest fragments modulate the provision of multiple ecosystem services J. Appl. Ecol. 51 909–18
Mitchell M G E, Bennett E M and Gonzalez A 2015a Strong and nonlinear effects of fragmentation on ecosystem service provision at multiple scales Environ. Res. Lett. 10 094014
Mitchell M G E, Suarez-Castro A F, Martinez-Harms M, Maron M, McAlpine C, Gaston K J, Johansen K and Rhodes J R 2015b Reframing landscape fragmentation’s effects on ecosystem services Trends Ecol. Evol. 30 190–8
Morellet N, Van Moorter B, Cargnelutti B, Angibault J-M, Loutet B, Merlet J, Ladei S and Hewison A J M 2011 Landscape composition influences roe deer habitat selection at both home range and landscape scales Landsc. Ecol. 26 999–1010
Oksanen J et al 2016 vegan: Community Ecology Package. R package version 2.4-1(http://CRAN.R-project.org/package=vegan)
Ostfeld R S and LoGiudice K 2003 Community disassembly, biodiversity loss, and the erosion of an ecosystem service Ecology 84 1421–7
Peres-Neto P R, Legendre P, Dray S and Borcard D 2006 Variation partitioning of species data matrices: estimation and comparison of fractions Ecology 87 2614–25
Petrosillo I, Zaccarelli N and Zurlini G 2010 Multi-scale vulnerability of natural capital in a panarchy of social–ecological landscapes Ecol. Complex. 7 359–67
Polasky S et al 2008 Where to put things? Spatial land management to sustain biodiversity and economic returns Biol. Cons. 141 1305–24
Pradier S, Leblond A and Durand B 2008 Land cover, landscape structure, and west Nile virus circulation in southern France Vector-Borne Zoonotic Dis. 8 253–64
Qiu J and Turner M G 2013 Importance of landscape heterogeneity in sustaining hydrologic ecosystem services in an agricultural watershed Ecosphere 4 art229
R Core Team 2014 R: A Language and Environment for Statistical Computing (Vienna, Austria: R Foundation for Statistical Computing)
Raudsepp-Hearne C, Peterson G D and Bennett E M 2010 Ecosystem service bundles for analyzing tradeoffs in diverse landscapes Proc. Natl Acad. Sci. 107 5242–7
Ricketts T H et al 2008 Landscape effects on crop pollination services: are there general patterns? Ecol. Lett. 11 499–515
Robinson D T, Brown D G and Currie W S 2009 Modelling carbon storage in highly fragmented and human-dominated landscapes: Linking land-cover patterns and ecosystem models Ecol. Modell. 220 1325–38
SIEF 2001 1:20 000, Système d’information écoforestière. Feuille 21L/02-NE, 4e programme d’inventaire forestier (Québec: Resources naturelles et Faune)
Smithwick E H, Harmon M and Domingo J 2003 Modeling multiscale effects of light limitations and edge-induced mortality on carbon stores in forest landscapes Landsc. Ecol. 18 701–21
Steffan-Dewenter I and Tscharntke T 1999 Effects of habitat isolation on pollinator communities and seed set Oecologia 121 432–40
Sybre R-U and Walz U 2012 Spatial indicators for the assessment of ecosystem services: Providing, benefiting and connecting areas and landscape metrics Ecol. Indic. 21 80–8
Tallis H and Polasky S 2009 Mapping and valuing ecosystem services as an approach for conservation and natural-resource management Ann. N. Y. Acad. Sci. 1162 265–83
Turner M, Donato D and Romme W 2013 Consequences of spatial heterogeneity for ecosystem services in changing forest landscapes: priorities for future research Landsc. Ecol. 28 1081–97
Ziter C, Bennett E M and Gonzalez A 2013 Functional diversity and management mediate aboveground carbon stocks in small forest fragments Ecosphere 4 art85
Ziter C, Bennett E M and Gonzalez A 2014 Temperature forest fragments maintain aboveground carbon stocks out to the forest edge despite changes in community composition Oecologia 176 893–902
Zuur A F, Fryer R J, Jolliffe I T, Dekker R and Beukema J J 2003 Estimating common trends in multivariate time series using dynamic factor analysis Environmetrics 14 665–85