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Landscape structure affects the provision of multiple ecosystem services

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Supplementary material for this article is available [online](#)

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 composition and configuration 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 (Lattera *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
Provisioning	
Pork production	Number of pigs produced per km ²
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 km ²
Regulation	
Carbon sequestration	Kilograms of carbon per km ² and per year
Soil phosphorus retention	Percent of saturation index measured from soil samples
Soil organic matter	Percent organic matter measured from soil samples
Cultural	
Deer hunting	Number of deer killed per km ²
Tourism	Number of tourist attractions per km ²
Nature appreciation	Number of reported sightings of rare species per km ²
Summer home value	Tax value of summer homes per km ²

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, Chaplin-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

Table 2. List of the four landscape metrics used to assess landscape structure within each municipality. Metrics differ based on whether they quantified two major aspects of the landscape structure, namely the landscape composition or the landscape configuration. These four metrics were applied to two LULC types (forest and agriculture at 5 m resolution) to produce a total of eight variables used in our analysis to represent various aspect of the landscape structure. See figure 1 for their variation across the studied region.

Landscape composition-based metrics	
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	
Shape	Average shape of patches of each LULC types 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 Écoforestière ([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:

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

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 multivariate 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

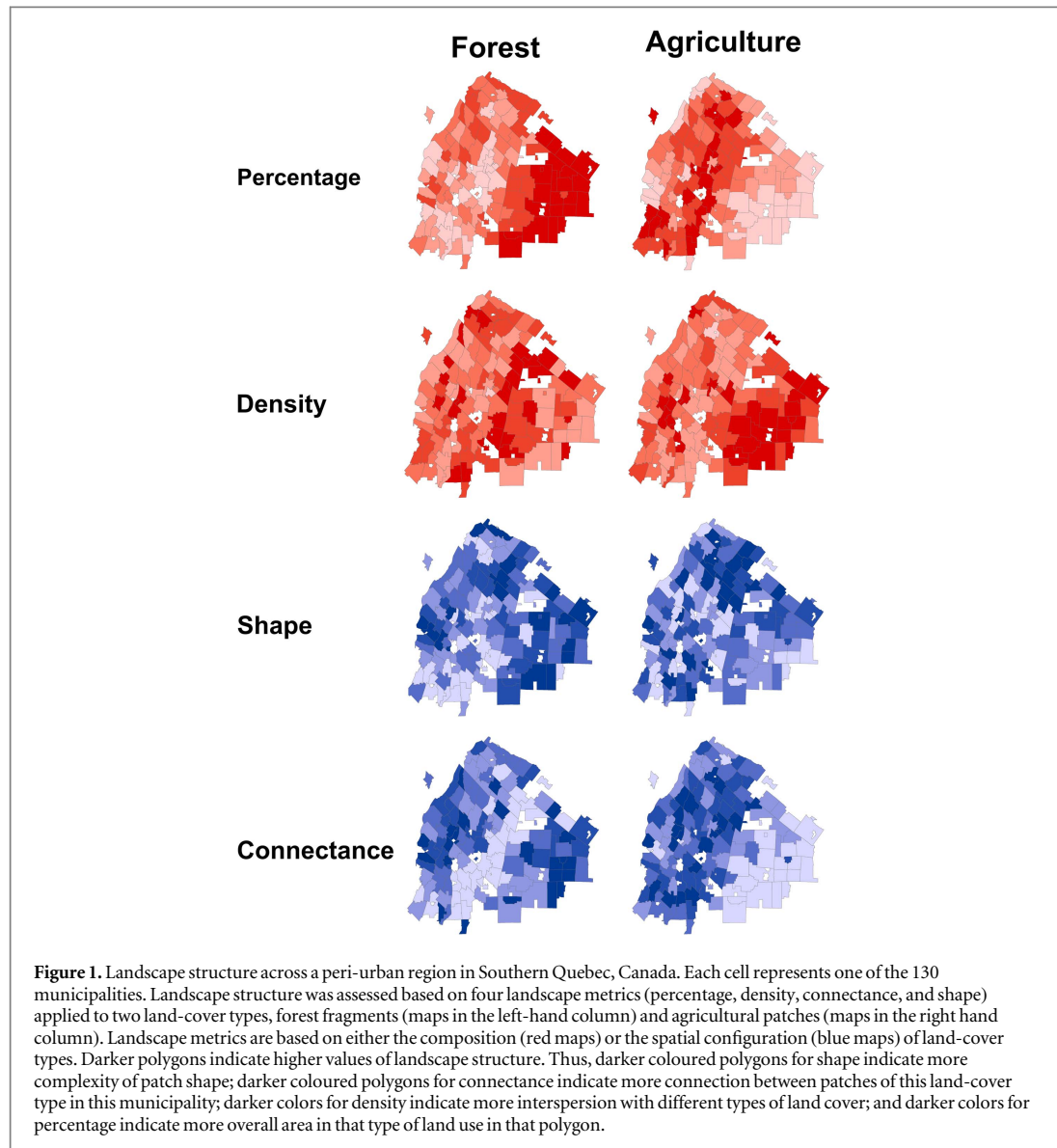
fairly homogenous with respect to ES provision. Following the splitting of the data into statistically similar clusters of municipalities, we produced bundles of ES within each of these clusters (i.e. a given branch of the resulting MRT). These bundles represent the difference between the mean values 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 'mvpert'.

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).

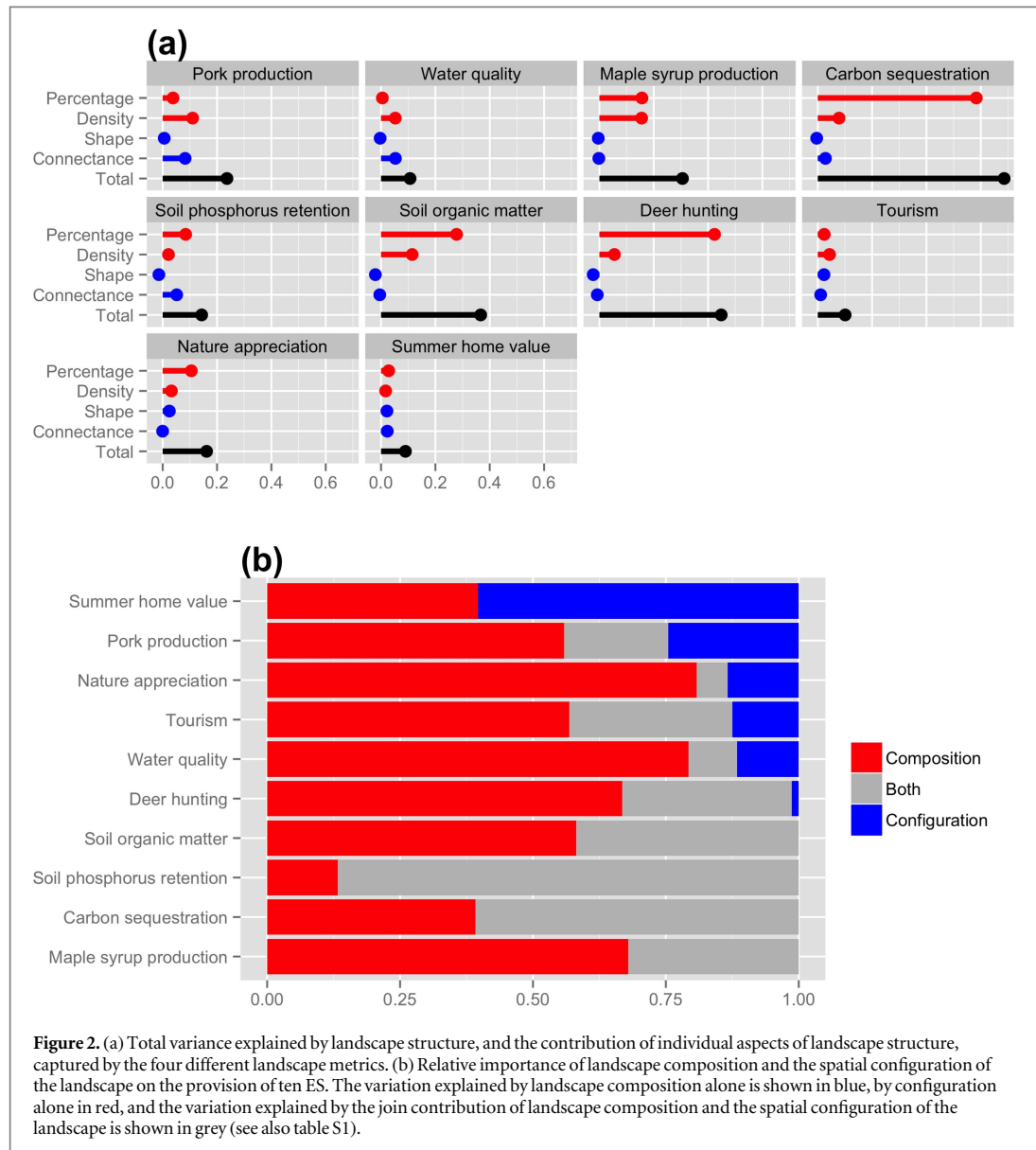
Overall, landscape composition contributed more than landscape configuration to variation in ES, though their relative importance varies from service to service (figure 2(b)). The fraction of the variation in each ES due only to landscape composition varies from 1% for soil phosphorus retention to 26% 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



(figure 2(b)). For instance, 40.5%, 13.1% and 13.7% of the variation in carbon sequestration, deer hunting and soil organic matter is explained by the joint effect of composition and configuration.

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 ($R^2_{\text{adj}} = 25.2\%$). 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 ($R^2_{\text{adj}} = 13.4\%$, $P = 0.001$) accounted for most of the total variation in the provision of multiple ES. The unique contribution of configuration was low and non-significant ($R^2_{\text{adj}} = 0.5\%$, $P = 0.162$).

However, the joint contribution of both composition and configuration explained half of the total variation in the provision of multiple ES ($R^2_{\text{adj}} = 12\%$), 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



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

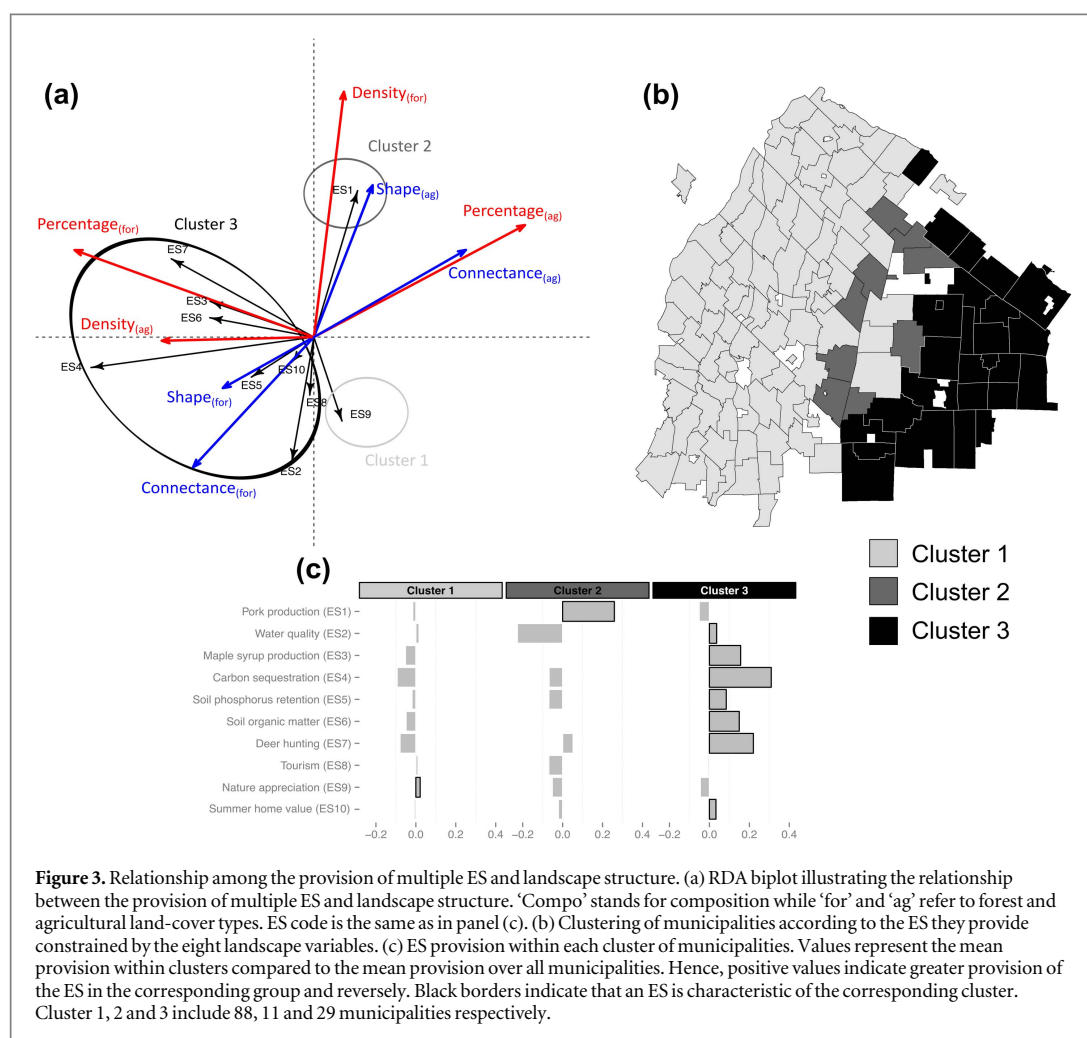


Figure 3. Relationship among the provision of multiple ES and landscape structure. (a) RDA biplot illustrating the relationship between the provision of multiple ES and landscape structure. ‘Compo’ stands for composition while ‘for’ and ‘ag’ refer to forest and agricultural land-cover types. ES code is the same as in panel (c). (b) Clustering of municipalities according to the ES they provide constrained by the eight landscape variables. (c) ES provision within each cluster of municipalities. Values represent the mean provision within clusters compared to the mean provision over all municipalities. Hence, positive values indicate greater provision of the ES in the corresponding group and reversely. Black borders indicate that an ES is characteristic of the corresponding cluster. Cluster 1, 2 and 3 include 88, 11 and 29 municipalities respectively.

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.

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