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RESEARCH ARTICLE

Detecting human-driven deviations from trajectories in landscape composition and configuration

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Abstract While landscape trajectories are increasingly used for tracking change in processes such as agricultural intensification and urbanization, analyses that combine environmental and human disturbances remain scarce. The aim of this study was to investigate the relationship between Shannon evenness, a measure of landscape composition, and spatial contagion, a measure of landscape configuration, within sixteen Canadian regions covering a gradient of land-uses and human disturbances: natural, semi-natural, urban, and agricultural. The agricultural regions showed generally lower variation in contagion and evenness and overall lower contagion values (smaller patches), leading to steeper contagion-evenness slopes than in the other region categories. In addition, the sampled agricultural regions were much more similar to each other than were the sampled regions within each of the other three region categories. These results indicate that the process of agricultural development (at least in western Canada) leads to a reduction in pattern variation and an alteration of the expected relationships among pattern metrics in agricultural regions. This possibility is supported by a neutral model of patch dynamics, suggesting that the characteristic scale of disturbances is a generic structuring process of landscape trajectories.

Keywords Landscape composition · Landscape configuration · Contagion · Landscape development · Disturbance · Spatial scale · Agriculture · Urbanization · Neutral model

Introduction

Sustainable landscape management addresses the question of how to ensure that ecosystem functions are maintained in the face of land-use intensification resulting from increasing economic demands (Kessler et al. 1992; Noble and Dirzo 1997). Trade-offs between ecosystem productivity and land-use intensification led Antrop (1998) to ask: is a landscape trajectory the result of planned human actions or environmental constraints? While landscape trajectories are increasingly used for tracking change in processes (e.g., urbanization, agriculture intensification, climate change; Cushman and McGarigal 2007; Hulse et al. 2009; Ruiz and Domon 2009), models capturing both environmental constraints and human impacts remain scarce.

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Huston (2005) introduced a simple conceptual model of the development of human-dominated landscapes that captures the interaction between ecosystem productivity and land-use distribution. He hypothesized that agricultural land-uses develop first in the locally most productive areas of the rural landscape. Next, during the industrial phase, urban land-uses are created around transportation nodes connecting primary production areas to industrialized ones. Ultimately, the communication phase involves exploitation of the whole landscape by human population freed from constraints associated with transportation of food, energy, and other resources (Huston 2005). Human-dominated landscapes are therefore predicted to gradually change through four main human disturbance phases (McIntyre and Hobbs 1999; Wood and Handley 2001; Huston 2005): (i) intact: protection, (ii) variegated: agricultural, (iii) fragmented: industrial, and (iv) relictual: communication. A central aspect of Huston's conceptual model is that progressive development of landscapes results in a decoupling of economic and environmental disturbances. As new land-uses are created on a natural landscape, the resulting pattern is dynamically modified in the direction of increased land-use evenness and fragmentation.

A more general understanding of how disturbance processes determine landscape patterns was formalized under the "hierarchical patch dynamics" concept (Wu and Loucks 1995). This concept recognizes that local disturbances give rise to emergent structural, spatial, and temporal patterns which may span multiple levels of spatial organization (e.g., populations, communities, ecoregions). In other words, the landscape pattern is dynamically constrained by the scale at which local disturbances take place. Hulse et al. (2009) similarly defined a landscape trajectory as the change in land-uses emerging from interactions among environmental and human processes over space and time. The landscape trajectory of a region will depend on the scale and rate at which land-use patches are created and modified through the main disturbance phases of economic development (Cushman and McGarigal 2007; Ruiz and Domon 2009).

Irrespective of whether landscapes are primarily natural or human-dominated, measures of landscape composition (e.g., diversity or evenness of cover types) and landscape configuration (e.g., contagion or fragmentation of cover types) are correlated across a range of real (Riitters et al. 1995; Griffith et al. 2000) and simulated landscapes (Hargis et al. 1998; Fortin et al. 2003). Although the correlation of landscape composition and configuration is usually perceived as a matter of statistical confounding (Smith et al. 2009), their inter-relationship nevertheless suggests that the environmental and human processes that shape landscape development limit the range of realized landscape patterns. To better understand the constraints and drivers of landscape trajectories, we need to better understand why composition and configuration patterns are so strongly correlated in real landscapes.

In addition, we expect the relationship between composition and configuration to change with increasing human activity in the landscape for two reasons. First, human activities insert novel land covers into landscapes, thus affecting landscape composition. Second, humans tend to introduce patches into landscapes (e.g., crop fields, clear-cuts) that are scaled to human activities; this constrains the scale of pattern development and the resulting landscape configuration. The aim of this article is to investigate how the relationship between Shannon evenness, a measure of landscape composition, and spatial contagion, a measure of configuration, varies across a gradient of increasing economic activity.

Methods

We used Landsat 5 TM images to investigate the relationship between composition (evenness) and configuration (contagion) within regions. Images in this dataset are centered on 16 Canadian cities, each covering an area of approximately 185 km × 185 km at a resolution of 30 m. Clear sky images were collected between mid-July and mid-September from 1984 to 1989 and geo-referenced to UTM83. This dataset was pre-packaged by the Canadian Center for Remote Sensing (CCRS) that freely distributes the visible bands through its GeoGratis portal. The images collectively represent major Canadian ecoregions. Some of the original images were cropped to reduce the proportion of large water zones near the margins; i.e., areas always returning evenness of zero and contagion of one. These large water zones are either large lakes or oceans.

The 16 regions were selected to represent four categories (with four representative regions for each) of economic activity: Agriculture (former grassland prairie now dominated by croplands and ranches), Urban (former mixed temperate–deciduous forest now dominated by dense urban–suburban settlements of more than 1,000,000 habitants, including farmlands in the periphery), semi-natural (former Acadian forest dominated by large patches of now exploited forest), and natural (nearly undisturbed taiga dominated by topographic elements like bogs, rocky hilltops and forested valleys). Our classification scheme was supported by information from the Canada Land Inventory (AAFC 1998) and population censuses. Each region in the Canada Land Inventory is rated depending on its potential to grow commercial timber, its capability for agricultural production and for high intensity recreational activities (AAFC 1998). In that respect, Agriculture and Urban regions presented a high capability for economic activity, while semi-natural and natural regions received intermediate and low ratings ,respectively. The same coarse classification could be obtained by using the actual gradient in human population density as a proxy for economic activity. However, while a high population density suggests high level of economic activity, the reverse is not necessarily true.

For each region independently, we used the reflectance in the visible spectrum to extract intensity values in a raster form, by computing the average across bands one to three. We linearly rescaled intensity values in each region to an integer between one and fifteen. Pixels in each of these integer bins represent different classes of landscape elements, ranging from dark to bright intensity. Although intensity-level measures of texture cannot easily distinguish between specific ecological habitats (e.g., young tree plantation vs. fallow field), their ability to capture land-use diversity in satellite images has been previously confirmed (Rao et al. 2002). Our analysis focuses on how evenly distributed and spatially contagious are the land-use patches of a landscape based on their similarity in reflectance intensities.

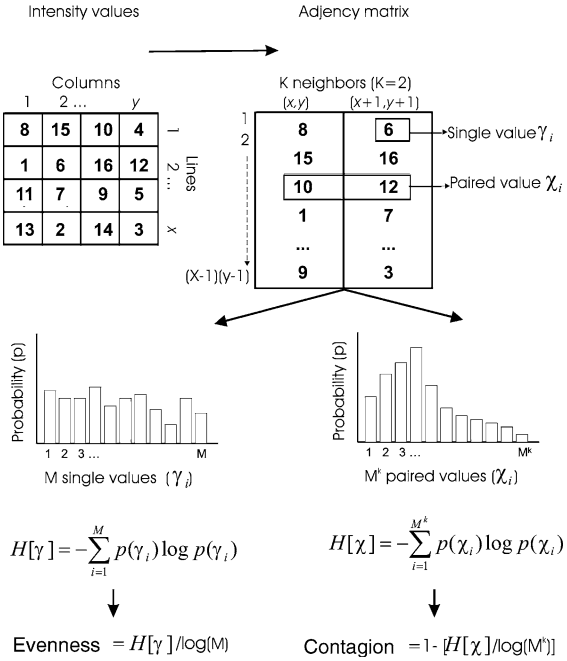

Fig. 1 Schematic representation of the calculation steps of the Shannon evenness (composition) and contagion (configuration) measures in a raster landscape. *1*) start with a landscape containing the grid of binned intensity values from a Landsat image; *2*) construct the co-occurrence matrix of intensity values by finding the neighbor in diagonal of each pixel; *3*) build two histograms; a first one of the probabilities $p(\gamma_i)$ of observing a pixel's intensity value γ_i independently of its location, and a second one of the probabilities $p(\chi_i)$ of observing a pair of neighbour intensity values χ_i in the matrix; *4*) apply the normalized Shannon entropy formula on these probability distributions to obtain evenness and contagion values (Li and Reynolds 1995). Evenness is maximal and contagion minimal when the landscape pattern is completely random. We used $M = 15$ bins and $k = 2$ neighbors in our analyses

Analyses

We used a moving-window algorithm to extract Shannon evenness and contagion values for landscapes within each region; their calculation is summarized in Fig. 1. Each window can be perceived as an individual landscape within the larger region. It is well established that both evenness and contagion measures are sensitive to the effect of grain size and window extent (Turner et al. 1989). To distinguish these effects, we performed the moving window algorithm on each region using two grain sizes (30 m and 60 m) and two window extents (100 × 100 pixels and 400 × 400 pixels). The 60 m grain size was obtained by re-sampling and interpolating intensity values at every 2 pixels using the imresize function in Matlab. The four grain-extent combinations were selected to cover different landscape dimensions in ground distance units: Small Grain-Small Extent (S-S; 9 ha.), Small Grain-Large Extent (S-L; 144 ha.), Large Grain-Small Extent (L-S; 36 ha.), and Large

Grain-Large Extent (L-L; 576 ha.). Windows did not overlap at the smaller extent, but overlapped two-thirds with each other at the larger extent.

For each region and grain-extent combination we calculated the major axis slope β and R^2, for the type II regression of evenness versus contagion measures across landscapes. To allow slope comparison between regions, we calculated β and R^2 over the evenness range (0.2–0.8) where all regions overlapped, but our conclusions are independent of this choice. Within each region we plotted the relationship between evenness and contagion for individual landscapes of 9 ha (Small Grain-Small Extent). We inspected the frequency histograms to determine if landscapes with higher evenness values are more frequently observed in regions subjected to increased economic activity, such as the Agriculture and Urban categories.

We implemented an exact permutation test for a two-way nested design (Anderson and ter Braak 2003) to test for the main effect of region category (REGION; agriculture, urban, semi-natural, natural) on β, while including the grain-extent combination (SCALE; S-S, S-L, L-S, L-L) as a nested factor. The exact permutation test for the region category compares the pivotal statistics $F_{REGION} = MS_{REGION}/MS_{SCALE(REGION)}$ to the null F-distribution obtained by randomly permuting blocks of four replicates, where MS stands for the mean square error. The exact permutation test for the grain-extent combination compares the pivotal statistics $F_{SCALE} = MS_{SCALE}/MS_{RESIDUALS}$ to the F-distribution obtained by randomly permuting replicates within each region category (Anderson and ter Braak 2003). To test the statistical significance of each effect, we compared the observed F statistics to its null F-distribution obtained from 1,000 random permutations. The probability of accepting the null hypothesis of no effect was set to 0.05. All simulations and analyses were performed in Matlab version 7.0.1 (MathWorks, Natick, MA, USA).

Results

The evenness-contagion relationships for the sixteen regions are shown in Fig. 2. All R^2 were above 0.9. An inspection of evenness frequency histograms (Fig. 2) reveals that evenness and contagion values for landscapes in the Agriculture regions tended to be normally distributed, covering smaller gradients (less platykurtic) than for the other three region categories. In addition, the evenness values in the Agriculture regions were consistently higher than in the other region categories. For the Urban, Semi-Natural, and Natural region categories, differences in the distributions of contagion and evenness values were at least as large among regions within categories as among region categories (Fig. 2).

Both the region category and the grain-extent combination significantly affected the slope β (two-way nested design, $P < 0.01$; Table 1). The mean slope (±SE) for the different region categories decreased in steepness as follows: agriculture, −0.908 (0.019); urban, −0.837 (0.019); semi-natural, −0.835 (0.018); natural, −0.780 (0.018). Slopes were also negatively steeper in the L-L and S-L grain-extent combinations than in the L-S and S-S combinations, suggesting an effect of the landscape dimension (Table 1). The mean slope (±SE) for the different grain-extent combinations decreased in steepness as follows: L-L, −0.892 (0.019); S-L, −0.879 (0.018); L-S, −0.795 (0.018); S-S −0.794 (0.018). Note that a steeper negative slope reflects a region where landscape patterns are characterized by smaller patch sizes.

Discussion

What is the reason for our observed strong relationship between composition (evenness) and configuration (contagion) across a wide range of landscapes containing widely varying dominant processes from geomorphic to natural disturbances to anthropogenic development? One possibility is that the different landscapes within a region represent different stages of landscape development for that region, and that historic constraints during any (generic) process of landscape development results in decreasing contagion and increasing evenness over time. We confirmed this possibility using a neutral “dead-leaves” model of patch dynamics (Ruderman 1997; Lee et al. 2001) in which no particular processes were assumed. Landscape structure was developed by simply placing square patches sequentially on a landscape in randomly selected locations (allowing a later-placed patch to replace part or all of an earlier-placed patch) until the whole landscape was full. The type of each

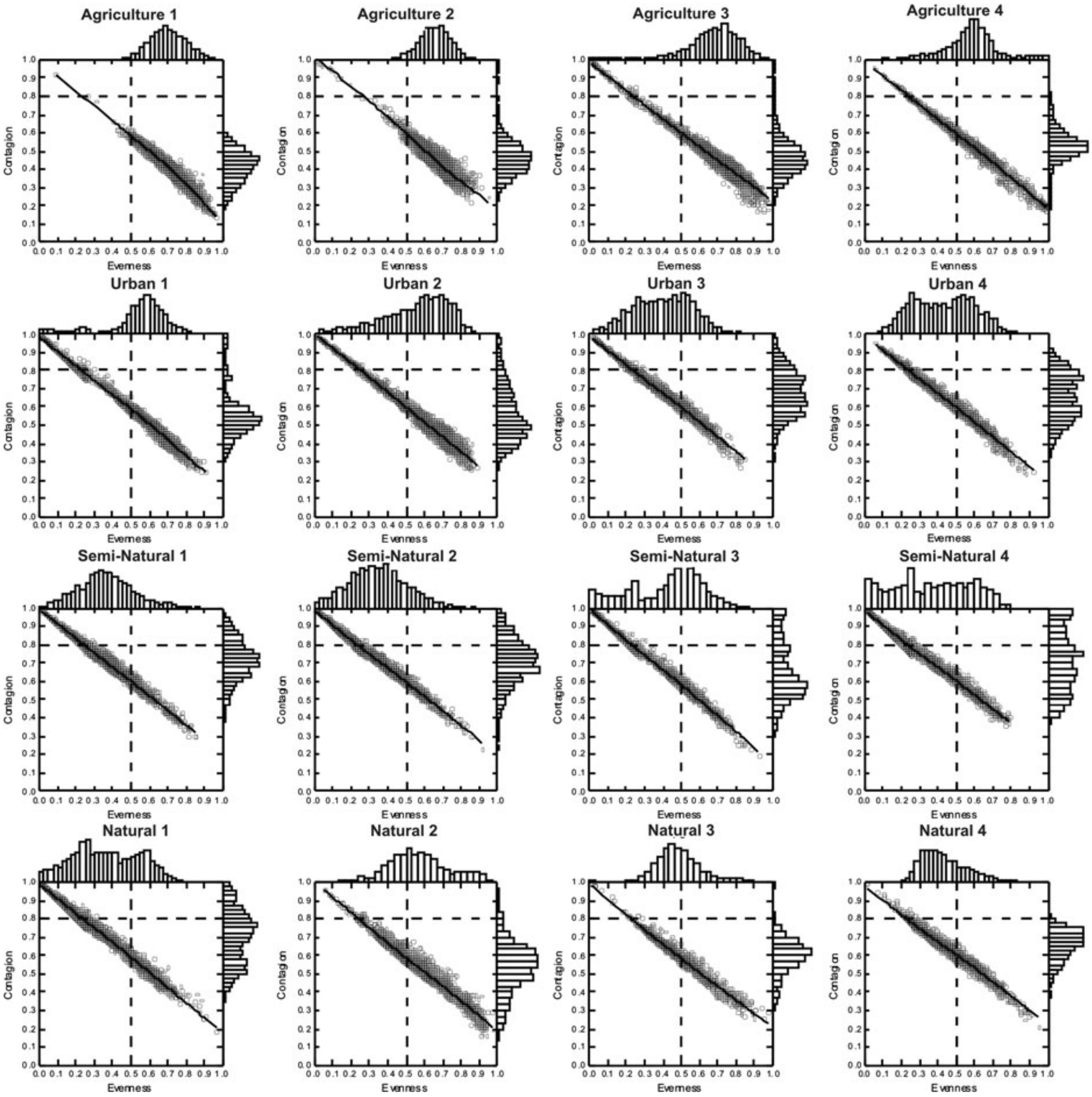

Fig. 2 Relationship between land-use Shannon evenness and contagion for 16 Canadian regions classified into four categories (agriculture, urban, semi-natural, natural). The relationships are shown for the Small-Small (S-S) grain-extent combination. The R^2 values are all above 0.9

patch was randomly selected from a uniform distribution of possible types, and its size was randomly chosen from a declining power function. Over time, contagion decreased and evenness increased in this simple model. This can be seen by plotting contagion and evenness of each time iteration in the landscape development as a point (Fig. 3); the resulting curve is then a strong negative relationship between contagion and evenness as we observed for the real landscapes.

We propose that landscape trajectories along a gradient of increasing economic activity (Natural, Agricultural, Urban, and Communication; Huston 2005) produce patterns similar to the dead-leaves model through constraints and processes that are

Table 1 Two-way nested design testing for the effect of the region category (agriculture, urban, semi-natural, natural) and grain-extent combination (Large-Large, Small-Large, Large-Small, Small-Small) on the linear slope β of the relationship between land-use evenness and contagion. The sample size was 64 treatments (16 regions × 4 grain-extent combinations)

Effect	β ($\pm$ 1SE)	MS	F-ratio	*P*	Steeper negative slope in
Region category		0.032	2.91	<0.01	Agriculture regions
Agriculture	−0.908 (0.019)				
Urban	−0.837 (0.019)				
Semi-Natural	−0.835 (0.018)				
Natural	−0.780 (0.018)				
Grain-Extent combination		0.038	12.67	<0.01	Larger landscapes
Large-Large	−0.892 (0.019)				
Small-Large	−0.879 (0.018)				
Large-Small	−0.795 (0.018)				
Small-Small	−0.794 (0.018)				
Residual error		0.003			

consistent with the underlying assumptions of the model: (i) each economic disturbance phase increases patch diversity by creating new land-uses (e.g., new crop types, new development types); (ii) small sized patches have a greater chance of being formed than larger ones (e.g., small farm ponds vs. large wetlands), so the frequency and magnitude of disturbances are inversely related; (iii) whenever larger land-use patches are formed, smaller ones may hierarchically form within them (e.g., small housing developments within large farm fields) thus modifying the land-use patch. Therefore it seems reasonable to propose that the contagion–evenness relationships we observed within each region were due to different portions of the region (different landscapes) representing different stages in the development of that region.

Landscape trajectories are one instance of the wide applicability of stochastic geometry models, to which the dead-leaves model belongs. Such models have been proposed as a unifying framework for explaining how macro-ecological patterns (e.g., the species-area relationship, the species-abundance distribution) emerge from the spatial distribution of species home-ranges (McGill and Collins 2003). In vision research, the dead-leaves model has been proposed as a unifying framework for representing natural image properties (e.g., scale invariance of the power spectrum distribution, long range 2 pixel covariance; Lee et al. 2001). We know that species interactions, natural image properties, and landscape trajectories do not depend on random processes, but it seems that the large scale behavior of these systems may be captured by ignoring the local details.

Despite the consistently strong ($R^2 > 0.9$) relationships between composition (evenness) and configuration (contagion) across the widely varying regions in our study, a more detailed look indicates marked differences between the patterns in the agricultural regions compared to the other region categories. The agricultural regions showed generally lower variation in both contagion and evenness and overall lower contagion values (smaller patches), leading to steeper contagion-evenness slopes than in the other region categories. In addition, the four agricultural regions were much more similar to each other than were the sampled regions within each of the other three region categories. These results indicate that the process of agricultural development (at least in western Canada) leads to a reduction in pattern variation and an alteration of the expected relationships among pattern metrics in agricultural regions.

The results for agricultural regions lead to a hypothesis for these regions that is analogous to a prevailing hypothesis for forested areas, namely that the impacts of forest harvesting on biodiversity are lower if the cutting pattern is similar to the disturbance patterns (from fire, hurricanes, insect outbreaks) with which forest-dwelling species have evolved (Franklin et al. 2002). Perhaps the same logic could be applied to agricultural landscapes. If

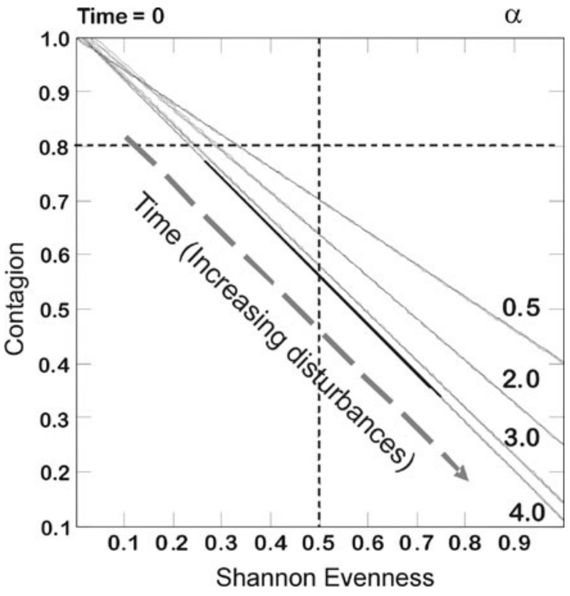

Fig. 3 Predicted relationship between evenness and contagion based on the "dead-leaves" model. Different points are data at different points in time. Evenness increases and contagion decreases over time, resulting in a strong evenness-contagion relationship. The 95% confidence interval around the linear least-square fit is too narrow to be visible. Each model's run proceeds as follows: *1*) generate a uniform landscape of a prescribed size (100 × 100 pixels); *2*) randomly pick the dimension of a landscape object (here a square patch of length *r*) from a power function *f(r)* of exponent α: $f(r) = r^{-\alpha}$, where $r_{min} = 1$ pixel $\leq r \leq r_{max} = 100$ pixels; *3*) choose at random a land-use integer value (patch color or intensity) from a uniform distribution; *4*) choose at random from a uniform distribution of coordinates a geographic position on the landscape, and place the patch there; *5*) repeat steps 2-4 iteratively until the landscape is completely covered by a set of hierarchically scaled patches such that previously-placed patches occlude the newly created ones (Lee et al. 2001)

the pattern of agricultural activity were structured to mimic disturbance patterns in natural prairie landscapes, it is possible that the impacts of agriculture on biodiversity (Tscharntke et al. 2005) would be lessened. This hypothesis remains to be tested. It is clear that implementation of altered patterns of agriculture would be more difficult than altering forestry patterns due to the highly distributed land ownership patterns in agricultural regions. Moreover, a landscape that is set on a trajectory of increasing agricultural intensity may be hard to reverse (e.g., Ruiz and Domon 2009). That is, the deep cultural and economical footprint left on agricultural landscapes may not allow them to recover to historical conditions even if restoration practices are initiated.

We emphasize that, despite the apparent ubiquity of the contagion-evenness relationship, in the context of biodiversity conservation it is still important to understand the independent effects of changes to composition and configuration. Human activities that change landscape composition in a particular way can occur in a variety of spatial patterns, resulting in different configurations. For example, the same amount of forest can be harvested in various patterns, resulting in different changes to forest configuration for the same change in composition. The same is true for agricultural conversion and urban development. For example, 20% of a region could be converted to a particular crop, but this could occur in a few large fields or many small fields distributed throughout the region, and this difference in pattern could affect biodiversity. Likewise, the same overall increase in urban development can be accomplished by distributing housing evenly over a region or in concentrated clumps, with large consequences to biodiversity (S.A. Gagné and L. Fahrig, unpublished data).

Environmental and human disturbances maintain landscape patterns or constrain the creation of new land-use patches across a range of spatial and temporal scales (Bolliger et al. 2003). The observed effect of landscape dimension (combination of grain size and window extent) on the evenness-contagion relationship provides additional clues on the role of the disturbance scale, as slopes were negatively steeper among larger landscapes (144 and 576 ha.) than among smaller ones (9 and 36 ha). This result indicates that choosing the landscape dimension smaller, the contagion-evenness slopes in agricultural regions were more similar to those observed in the other regions. In other words, region categories were best discriminated on the basis of their contagion-evenness slopes (landscape trajectories) when analyzing larger (114 and 576 ha) landscapes. The landscape trajectory of a region depends on the spatial scale at which land-use patches are created and modified through the main disturbance phases of environmental (e.g., historic bio-geo-climatic conditions) and economic development (e.g., zoning policy, resource proximity, land availability, management incentives). This suggests that our approach may allow identifying the characteristic development scale of a region. The characteristic scale of a region would be represented by an abrupt decrease in the contagion-evenness slope with increasing landscape dimension. Slope deviations from trajectories in landscape composition and configuration are captured by the parameter α in our “dead-leaves” model of patch dynamics (Fig. 3).

Conclusions

In the words of Antrop (1998), landscape change is neither planned human actions nor environmental disturbances but emerges from the dynamical trade-offs between ecosystem productivity (driven by environmental inputs) and land-use distribution (driven by economic activity). Recent theoretical and empirical studies have shown that local dynamical trade-offs in growth-inhibition and disturbance-recovery may be sufficient conditions for self-organization to develop in real ecosystems (Solé and Bascompte 2006; Rietkerk and van de Koppel 2008). Some authors furthermore suggested that landscapes may spontaneously evolve close to a critical self-organized state (Phillips 1999; With and King 2004). Criticality occurs when complex systems are poised in an intermediate state between pure determinism and complete stochasticity. Systems pushed beyond this-state are sensitive to threshold behaviors creating sudden shifts to alternative stable states and, as such, may not be long-term sustainable. It remains to be elucidated whether natural landscape dynamics conform to such critical patterns and whether human-dominated landscapes are more susceptible to threshold behaviors. In the meantime, identifying how the characteristic spatial scale of disturbances constrains landscape trajectories in composition and configuration metrics could provide a common framework for side-by-side comparisons of different regions of the world functioning under different environmental and economical regimes.

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