Landscape Ecol (2021) 36:3097–3104
https://doi.org/10.1007/s10980-021-01312-9

PERSPECTIVE

How the relationship between vegetation cover and land-cover variance constrains biodiversity in a human dominated world

Charles A. Martin · Raphaël Proulx · Mark Vellend · Lenore Fahrig

Received: 14 March 2021 / Accepted: 3 August 2021 / Published online: 13 August 2021

Abstract
Context Alteration of natural vegetation cover across the landscape drives biodiversity changes. Although several studies have explored the relationships between vegetation cover and species richness, as well as between land-cover variance and species richness, few have considered the non-independence of these two biodiversity drivers.

Objectives The goal of this perspective paper is to present theoretical and empirical relationships linking vegetation cover to land-cover variance at the landscape scale, and the implication of these relationships for species richness change along a gradient of increasing anthropization.

Methods and results We used simulated and empirical Normalized Difference Vegetation Index data to examine the generality of the relationship between vegetation cover and land-cover variance. Using the province of Québec (Canada) as a case study, our results show that decreasing vegetation cover captures the transition from landscapes with low land-cover variance (non-anthropized landscapes), to intermediate variance (agricultural landscapes), to high variance (urban landscapes).

Conclusion Based on this relationship between vegetation cover and land-cover variance, and assuming independent positive monotonic relationships between biodiversity and both of these drivers, we predict a unimodal relationship between species richness and anthropization. This suggests a threshold of anthropization beyond which the positive effects of land-cover variance no longer compensate for the negative effects of vegetation cover loss. Identifying these thresholds could be key to setting conservation targets at a landscape scale.

Keywords Biodiversity · Species richness · Vegetation cover · Environmental heterogeneity · Landscape composition · Landscape structure

---

C. A. Martin · R. Proulx (✉)
Chaire de Recherche du Canada en Intégrité Écologique,
Centre de Recherche sur les Interactions Bassins
Versants-Écosystèmes Aquatiques (RIVE), Université du
Québec à Trois-Rivières, C.P. 500, Trois-Rivières,
QC G9A 5H7, Canada
e-mail: raphael.proulx@uqtr.ca

M. Vellend
Département de Biologie, Université de Sherbrooke, 2500
Boulevard de l'Université, Sherbrooke,
QC J1K 2R1, Canada

L. Fahrig
Department of Biology, Carleton University, 1125
Colonel By Drive, Ottawa, ON K1S 5B6, Canada

Introduction

A central goal of conservation ecology is to understand how organisms respond to our increasing human footprint. Organisms' responses to habitat alteration are highly complex, multifaceted, and variable among species and across contexts (Bender et al. 1998; Connor et al. 2000; Debinski and Holt 2000; Prugh et al. 2008). Nevertheless, at a landscape scale, the net effect of anthropization is driven in large part by the response of species to changes in vegetation cover and/or changes in spatial land-cover variance. Early conceptual models in landscape ecology expressed the anthropization gradient as follows (Forman 1995; McIntyre and Hobbs 1999): (1) start with a uniform natural landscape with relatively high vegetation cover and low land-cover variance; (2) progress to a heterogeneous semi-natural landscape with an intermediate vegetation cover and increased land-cover variance; (3) end with an impacted landscape with relatively low vegetation cover and low land-cover variance. This trajectory suggests a decreasing relationship between the anthropization gradient (i.e., transitioning from stages 1 to 3 above) and vegetation cover, and a hump-shaped relationship between the anthropization gradient and land-cover variance.

We define *vegetation cover* as the average leaf area per unit of land area, typically known as the Leaf Area Index. Vegetation cover changes over space in relation to the proportion of land occupied by plants, but also how tall or densely packed plants are. In practice, vegetation cover can be quantified using surrogate measures like the normalized difference vegetation index (NDVI) or the enhanced vegetation index (EVI). Mean vegetation cover decreases along an anthropization gradient if newly created land-cover patches, such as roads, abandoned fields, or crops, do not contain as much leaf area as the original vegetation. Likewise, we define land-cover variance as the magnitude of contrast (in terms of vegetation cover) among different areas within the landscape. Land-cover variance thus measures only compositional heterogeneity, and ignores its configurational component (*sensu* Fahrig et al. 2011). For present purposes, we quantified vegetation cover as the mean of NDVI values across a landscape and land-cover variance as the mathematical variance of these NDVI values.

Although vegetation cover and land-cover variance are well-studied variables, few authors have investigated how the two are interrelated. We expect they are related, as this is often the case for the mean and variance of measured variables (here, NDVI) (e.g., Tokeshi 1995). Possible relations for vegetation cover and land-cover variance have been postulated in conceptual models (Tilman and Pacala 1993; Abrams 1995), but the relationship between them remains unexplored. In this perspective paper, we present both theoretical and empirical arguments for the presence of a non-linear hump-shaped relationship between vegetation cover and land-cover variance at landscape scales. We discuss the ecological and conservation implications of this relationship, providing a new perspective on productivity-biodiversity and heterogeneity-biodiversity relationships observed in nature.

How are vegetation cover and land-cover variance related?

A mathematical example

Let us imagine a landscape in which vegetation cover is measured on a continuous scale, for example, as NDVI on the bounded interval [− 1,1]. Each portion (pixel) of the landscape has a value of NDVI. Let us now assume that the distribution of vegetation cover values over the landscape is described statistically by the Beta distribution:

$$P(x) = \frac{\Gamma(\alpha+\beta)}{\Gamma(\alpha)\Gamma(\beta)} x^{\alpha-1}(1-x)^{\beta-1},$$

which is often the case for ecological variables with bounded distributions (Stoy et al. 2009). Following our definitions of vegetation cover and land-cover variance, the mean is directly related to the α and β parameters of the Beta distribution as follows:

$$E[X] = \frac{\alpha}{\alpha+\beta},$$

and its variance depends on the same two parameters:

$$var[X] = \frac{\alpha\beta}{(\alpha+\beta)^2(\alpha+\beta+1)}$$

Hence, the mean vegetation cover of a landscape will directly affect the land-cover variance that can be observed (Remmel 2009). The intuition behind such mathematical statements is that, in the context of a bounded distribution, large deviations around the mean can only exist when the mean is towards the middle of the range of possible values. Any distribution with a mean near the upper or lower bound of the range implies small deviations around that mean. This relationship can be visualized by sampling evenly spaced intervals of α and β parameters and calculating the mean and variance of each combination. Technically, the procedure is equivalent to simulating landscapes over a large range of NDVI spatial patterns and calculating the mean and variance of these values. Plotting the mean vs. variance of NDVI values in these landscapes reveals a clear hump-shaped envelope between them (Fig. 1A). Each combination of mean and variance in Fig. 1A translates into a different type of landscape pattern.

Empirical illustration

To characterize the predicted mean-variance relationship in real landscapes, we calculated vegetation cover and land-cover variance using Sentinel-2 radiometric data (Drusch et al. 2012). We selected 10 000 random longitude and latitude coordinates from a gaussian distribution centered around Montréal, QC (Latitude 45.50, Longitude − 73.56, standard deviation 2.5°) covering the whole gradient of ecosystems found throughout the province of Québec (Canada), including tundra, boreal, mixed, and deciduous forests, as well as urban and agricultural areas. A land-cover classification conducted using 2015 data from the Operational Land Imager (OLI) Landsat sensor (Government of Canada et al. 2019) was associated with each pair of coordinates. We removed coordinates falling outside the boundaries of Québec or directly on water, ice, snow or wetland land-cover categories, leaving 8970 landscapes.

Gradients in vegetation cover and land-cover variance in this dataset stem from a combination of natural (e.g., across biomes) and anthropized areas. For each pair of coordinates, we used Google Earth Engine (Gorelick et al. 2017) to create circular 100 m radius and 564 m radius (i.e., 1 km^2) landscapes centred on the coordinates on Sentinel-2 images (10 m ground resolution). These sizes correspond respectively to the radius around which bird songs can typically be heard in point count surveys and the home range size of most passerine birds (Brown and Sullivan 2005). We refer to these arbitrarily-selected scales as small and large landscapes hereafter. We selected all Sentinel-2 images taken between 1 Jun and 1 Sep 2018, to ensure that they are representative of summertime vegetation cover. For each band and each pixel forming the image, we calculated the median value of the time series to remove the influence of

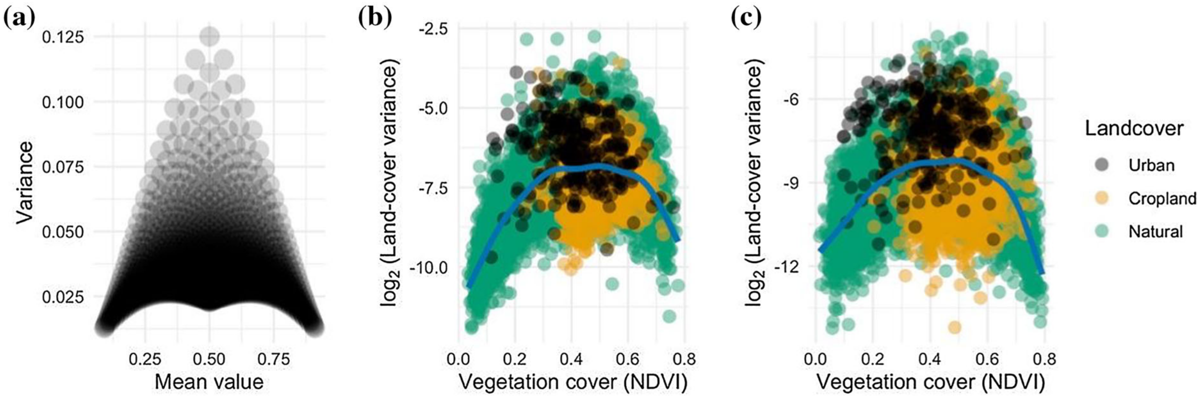

Fig. 1 Mathematical and empirical relationship between vegetation cover and land-cover variance. Each point on a plot represents a prediction (**A**) or observation (**B** and **C**) for an individual landscape. **A** Predicted relationship between vegetation cover and land-cover variance based on the mathematical parameterization of a Beta distribution. Each pair of mean and variance values notionally represents the mean and variance of vegetation cover for a hypothetical landscape. They are sampled from the Beta distribution, using an evenly spaced grid of α and β parameters, both ranging from 0.5 to 5.0. **B** and **C** Relationship between vegetation cover and land-cover variance measured in 8970 landscapes across the province of Quebec, Canada, at two different scales (**B** 564-m-radius landscapes, **C** 100-m-radius landscapes) with corresponding land-use category. Vegetation cover and land-cover variance were calculated for NDVI values across each landscape. Land-cover variance was log-2 transformed to better visualize the hump-shaped pattern

cloud cover and cloud shadows (Namikawa 2017). We then calculated the Normalized Difference Vegetation Index (NDVI; Rouse et al. 1974) for each pixel, using bands B8 (near infrared) and B4 (red). In a subsequent step, we extracted NDVI mean and variance across pixels, which we interpreted as vegetation cover and land-cover variance values for each landscape. Graphically representing these variables together revealed a hump shape, which we illustrated using a thin-plate spline with penalized regression coefficients (Wood 2003). Spline functions fitted to small (100 m radius) and large landscapes (564 m radius) explained respectively 28 and 41% of land-cover variance using only vegetation cover as the explanatory variable (Fig. 1B, C).

The vegetation cover gradient captures the transition from natural landscapes with a high vegetation cover (low land-cover variance), to croplands (moderate variance), to urban lands (high variance), and finally to landscapes with a naturally low vegetation cover (low variance) (Fig. 1). In particular, several urban landscapes in southern Québec show very high levels of land-cover variance; i.e., black points in the upper left of the envelope (Fig. 1B, C). Considering the proximity of these landscapes to the upper boundary of the relationship, further losses of vegetation cover are likely to translate into decreasing land-cover variance. In other words, the land-cover variance of urban landscapes at the boundary will start decreasing if they are pushed farther to the left on the vegetation cover axis (Fig. 1).

The extent of the landscape influences some aspects of the cover-variance relationship. Although the overall shape of the data envelope did not change, the strength of the relationship increased with increasing spatial extent. Indeed, at a large spatial extent it is hard to find landscapes with either very high or very low land-cover variance, thus decreasing the variation of observed values on that axis. Spatial extent also influences the relative position of landscapes along the vegetation cover axis. For instance, the same urban area could reveal a low vegetation cover at a small spatial extent (e.g., a parking lot), but a much higher vegetation cover if observed at a larger extent that incorporates green spaces such as residential yards or municipal parks. The effect of extent will be especially marked if the landscape overlays different land-cover classifications (e.g., urban and cropland areas).

Implications for biodiversity conservation

The relationships between vegetation cover and land-cover variance described above have implications for our understanding of how species richness changes along an anthropization gradient. To highlight these implications, let us consider circumstances where species richness increases monotonically with both vegetation cover and land-cover variance. Such a scenario is supported by an extensive literature on the productivity-species diversity hypothesis (Cusens et al. 2012; Gillman et al. 2015) and the heterogeneity-species diversity hypothesis (Tews et al. 2004; Stein et al. 2014). The above hypotheses are represented by positive monotonic relationships between vegetation cover and species richness, as well as between land-cover variance (i.e., spatial heterogeneity) and species richness (Fig. 2).

Conceptually, the anthropization gradient captures how landscapes change as they move along the non-linear relationship between vegetation cover and land-cover variance, and combines their joint effects. These gradients are represented by a decreasing relationship between anthropization and vegetation cover, and a hump-shaped relationship between anthropization and land-cover variance (Fig. 2). Assuming for our purposes that vegetation cover and land-cover variance have independent and additive effects on the species richness of a landscape, a concave relationship is then obtained between species richness and the level of anthropization (Fig. 2).

From our investigation, we speculate that confusion may arise when studying the bivariate empirical relationship between biodiversity variables and vegetation cover at the landscape scale. Although many species might respond monotonically to vegetation cover (Gilroy et al. 2014), our results above reveal that vegetation cover and land-cover variance are in fact interrelated in a non-linear fashion (Fig. 1). Thus, the observed bivariate relationship between vegetation cover and species richness could appear hump-shaped; although this would be the net result of the two factors acting at one on species richness (see Evans et al. 2005).

Our conceptual model predicts a concave response of species richness to anthropization whenever vegetation cover and land-cover variance are respectively a monotonic decreasing and a unimodal function of

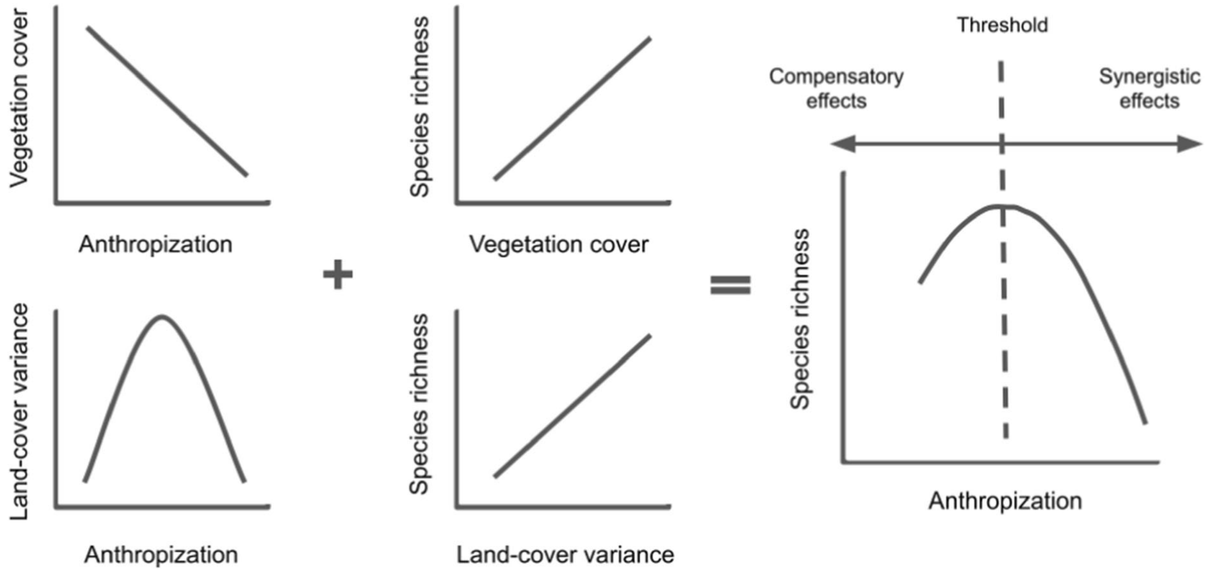

Fig. 2 Conceptual representation of the net effect of vegetation cover and land-cover variance on species richness along the anthropization gradient. The framework assumes positive monotonous relationships between vegetation cover and species richness, as well as between land-cover variance (i.e., spatial heterogeneity) and species richness. Conceptually, the anthropization gradient captures how landscapes change as they move along the non-linear relationship between vegetation cover and land-cover variance, and combines their joint effects. These gradients are represented by a decreasing relationship between anthropization and vegetation cover, and a hump-shaped relationship between anthropization and land-cover variance. Assuming that vegetation cover and land-cover variance have independent and additive effects on the species richness of a landscape, a concave relationship is obtained between species richness and the level of anthropization

landscape anthropization. Other studies support the idea that species richness varies unimodally with anthropization. The PREDICTS project, for Projecting Responses of Ecological Diversity In Changing Terrestrial Systems, is a large concerted effort to better understand the influence of land-use change on species richness and composition. The database consists of 320,924 records at 11,525 sites, from 284 publications, including 26,953 species from 13 terrestrial biomes (Newbold et al. 2015). The main results of PREDICTS show that intensive land-use of plantation, cropland, or urbanization is associated with a steep decline of species richness based on rarefied estimates (ca. − 40 %). In contrast, areas of lower human population density, as well as extensive land cover of primary and secondary natural vegetation, are associated with a slight increase in species richness (ca. + 5 %). While there exists considerable spatial variation in the data, the overall inference would be that species richness should increase, on average, with increasing human population from low to moderate density (up to 20–40 persons/km^2), then decrease steadily at higher human density (Newbold et al. 2015). In particular, the relationship between species richness and human population density (extended data Fig. 2 in Newbold et al. 2015) bears striking similarities with the conceptual ones presented herein (Fig. 2).

Another global analysis of 375 studies distributed worldwide evaluated the effect of land-use intensity on plant diversity (Gerstner et al. 2014). The study found negative effects of intensive land-use practices, like nutrient-input farming and tree plantations, on plant diversity (correlation of ca. − 0.46). Yet, the study also reports positive, although weak, effects on plant diversity of extensive management practices, such as mowing/grazing of grasslands and logging/thinning of forests (correlation of ca. + 0.14). Remarkably, abandonment of extensively managed landscapes (e.g., meadow or pasture) decreased plant diversity, while abandonment of intensively managed landscapes (e.g., conventional farming or tree plantation) increased diversity (Gerstner et al. 2014).

We emphasize that the relationship we describe here is not equivalent to other conceptual models that have predicted a hump-shaped response of species richness to increasing temporal disturbance (the intermediate disturbance hypothesis; Connell 1978) or more recently to spatial heterogeneity; i.e. the intermediate heterogeneity hypothesis (Fahrig et al. 2011) also called the area-heterogeneity trade-off (Allouche et al. 2012). While the intermediate disturbance hypothesis was criticized on both empirical and theoretical grounds (see Fox 2013), the area-heterogeneity trade-off has received some support (Yang et al. 2015; Schuler et al. 2017; but see Ben-Hur and Kadmon 2020). These two hypotheses suggest that “environmental variation”, either in time or space, drives species coexistence. In contrast, we herein propose that this environmental variation is a (non-linear) function of vegetation cover change, and that both factors affect species richness at the landscape scale. We also note that our framework has the advantage of clearly defining landscape properties in terms of mean and variance of the vegetation cover. This last point is particularly important as concepts like “disturbance” or “heterogeneity” have received multiple interpretation in the literature (e.g., Stein and Kreft 2015). Even the term “area” in the area-heterogeneity trade-off can be challenging in practice because it implies that species habitats are discrete, measurable quantities. However, the generality of the framework we propose also has its downsides, as it makes no prediction about which species should be favoured or disfavoured with increasing anthropization. For example, species richness may increase mostly through the addition of cosmopolitan exotic species as well as a few disturbance-tolerant native species (McKinney and Lockwood 1999; McCune and Vellend 2013).

Future directions

In a metapopulation-based model describing species coexistence in patches of fragmented habitats, Tilman et al. (1994) showed that the relationship between the proportion of habitat destroyed and the proportion of species driven extinct should be relatively flat in the early stages of anthropization and rapidly accelerate with further habitat loss. Syntheses of biodiversity changes at landscape scales in the Anthropocene point to a flat response, or even a slight increase with anthropization of species richness in plants (Vellend et al. 2017) and vertebrates (Pautasso 2007). Such compensatory effects could precede the steeper and more consequential part of Tilman et al.’s (1994) prediction, where species extirpation rapidly increases following further habitat losses. However, Tilman’s model assumes that no species can survive in habitats with a vegetation cover below some level. The conceptual model we propose here offers a simple, yet realistic, explanation for the observed increase in biodiversity with landscape anthropization. Increasing land-cover variance in the early stages of anthropization might compensate for natural habitat loss (Fig. 1). It suggests that each landscape has a threshold beyond which the loss of vegetation cover will switch from increasing to decreasing variance, with synergistic negative effects on the persistence of species. Identifying where this shift occurs along various anthropization gradients and environmental contexts could be key in setting conservation targets at a landscape scale. Future work on this topic should explore the influence of spatial scale (Fig. 1), as well as assumptions of a linear mapping of species richness on vegetation cover and land-cover variance (Fig. 2).

In summary, our framework implies that species richness responses to land-use intensification result from the opposing effects of decreasing vegetation cover and increasing land-cover variance at low to moderate anthropization levels, and from synergistic negative effects of these two factors at high anthropization levels. Results from two global syntheses so far corroborate these general predictions across many species and environmental contexts (Gerstner et al. 2014; Newbold et al. 2015).

Acknowledgements This work was partly funded from a Natural Sciences and Engineering Research Council (NSERC) Canada Research Chair Program and Discovery Grant to RP (RGPIN-2016-04519). CM was supported by a graduate NSERC fellowship for doctoral studies. We would like to thank two anonymous reviewers and editor who provided thoughtful comments on a previous version of the paper.

Author contributions All authors contributed to the writing and conceptual framing of the paper. CM and RP conceived and managed the study. CM compiled the data, conducted analyses and made the figures.

Funding This research was supported by grants from the Natural Sciences and Engineering Research Council of Canada and the Canada Research Chair Program to R. Proulx.

Data availability The data are available on Figshare: https://doi.org/10.6084/m9.figshare.12937241.

Code availability The code is available on Figshare: https://doi.org/10.6084/m9.figshare.12937241.

Declarations

Conflict of interest The authors declare that they have no known competing financial interest or personal relationships that could have influences the work reported in this paper.

Consent for publication All authors consent to publication.

References

Abrams PA (1995) Monotonic or unimodal diversity-productivity gradients: what does competition theory predict?. Ecology 76:2019–2027.

Allouche O, Kalyuzhny M, Moreno-Rueda G, Pizarro M, Kadmon R (2012) Area–heterogeneity tradeoff and the diversity of ecological communities. Proc Natl Acad Sci 109:17495–17500

Bender DJ, Contreras TA, Fahrig L (1998) Habitat loss and population decline: a meta-analysis of the patch size effect. Ecology 79:517–533.

Ben-Hur E, Kadmon R (2020) An experimental test of the area–heterogeneity tradeoff. Proc Natl Acad Sci USA 117:4815–4822.

Brown WP, Sullivan PJ (2005) Avian community composition in isolated forest fragments: a conceptual revision. Oikos 111:1–8.

Connell JH (1978) Diversity in tropical rain forests and coral reefs. Science 199:1302–1310

Connor EF, Courtney AC, Yoder JM (2000) Individuals–area relationships: the relationship between animal population density and area. Ecology 81:734–748.

Cusens J, Wright SD, McBride PD, Gillman LN (2012) What is the form of the productivity–animal-species-richness relationship? A critical review and meta-analysis. Ecology 93:2241–2252.

Debinski DM, Holt RD (2000) Review: a survey and overview of habitat fragmentation experiments. Conserv Biol 14:342–355.

Drusch M, Del Bello U, Carlier S, Colin O, Fernandez V, Gascon F, Hoersch B, Isola C, Laberinti P, Martimort P, Meygret A (2012) Sentinel-2: ESA's optical high-resolution mission for GMES operational services. Remote Sens Environ 120:25–36

Evans KL, Greenwood JJD, Gaston KJ (2005) Dissecting the species–energy relationship. Proc R Soc B 272:2155–2163.

Fahrig L, Baudry J, Brotons L, Burel FG, Crist TO, Fuller RJ, Sirami C, Siriwardena GM, Martin JL (2011) Functional landscape heterogeneity and animal biodiversity in agricultural landscapes: heterogeneity and biodiversity. Ecol Lett 14:101–112

Forman RT (1995) Land mosaics: the ecology of landscapes and regions. Cambridge University Press, Cambridge

Fox JW (2013) The intermediate disturbance hypothesis should be abandoned. Trends Ecol Evol 28:86–92.

Gerstner K, Dormann CF, Stein A, Manceur AM, Seppelt R (2014) Effects of land use on plant diversity—a global meta-analysis. J Appl Ecol 51:1690–1700

Gillman LN, Wright SD, Cusens J, McBride PD, Malhi Y, Whittaker RJ (2015) Latitude, productivity and species richness. Glob Ecol Biogeogr 24:107–117

Gilroy JJ, Edwards FA, Medina Uribe CA, Haugaasen T, Edwards DP (2014) Surrounding habitats mediate the trade-off between land-sharing and land-sparing agriculture in the tropics. J Appl Ecol 51:1337–1346

Gorelick N, Hancher M, Dixon M, Ilyushchenko S, Thau D, Moore R (2017) Google earth engine: planetary-scale geospatial analysis for everyone. Remote Sens Environ. https://doi.org/10.1016/j.rse.2017.06.031

Government of Canada, Natural Resources Canada, Canada Centre for Remote Sensing (2019) 2015 Land cover of Canada

McCune JL, Vellend M (2013) Gains in native species promote biotic homogenization over four decades in a human-dominated landscape. J Ecol 101:1542–1551.

McIntyre S, Hobbs R (1999) A framework for conceptualizing human effects on landscapes and its relevance to management and research models. Conserv Biol 13:1282–1292.

McKinney ML, Lockwood JL (1999) Biotic homogenization: a few winners replacing many losers in the next mass extinction. TREE 14:450–453.

Namikawa LM (2017) A method to build cloud free images from CBERS-4 AWFI sensor using median filtering. GEOINFO XVIII:52–61

Newbold T, Bentley LF, Hill SL, Edgar MJ, Horton M, Su G, Şekercioğlu ÇH, Collen B, Purvis A (2015) Global effects of land use on local terrestrial biodiversity. Nature 520:45–50

Pautasso M (2007) Scale dependence of the correlation between human population presence and vertebrate and plant species richness. Ecol Lett 10:16–24.

Prugh LR, Hodges KE, Sinclair ARE, Brashares JS (2008) Effect of habitat area and isolation on fragmented animal populations. Proc Natl Acad Sci 105:20770–20775.

Remmel TK (2009) Investigating global and local categorical map configuration comparisons based on coincidence matrices. Geogr Anal 41:144–157.

Rouse J Jr, Haas RH, Schell JA, Deering DW (1974) Monitoring vegetation systems in the Great Plains with ERTS. NASA, Washington, DC

Schuler MS, Chase JM, Knight TM (2017) Habitat size modulates the influence of heterogeneity on species richness patterns in a model zooplankton community. Ecology 98:1651–1659.

Stein A, Gerstner K, Kreft H (2014) Environmental heterogeneity as a universal driver of species richness across taxa, biomes and spatial scales. Ecol Lett 17:866–880.

Stein A, Kreft H (2015) Terminology and quantification of environmental heterogeneity in species-richness research. Biol Rev 90:815–836.

Stoy PC, Williams M, Disney M, Prieto-Blanco A, Huntley B, Baxter R, Lewis P (2009) Upscaling as ecological information transfer: a simple framework with application to Arctic ecosystem carbon exchange. Landsc Ecol 24:971–986

Tews J, Brose U, Grimm V, Tielbörger K, Wichmann MC, Schwager M, Jeltsch F (2004) Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures. J Biogeogr 31:79–92

Tilman D, May RM, Lehman CL, Nowak MA (1994) Habitat destruction and the extinction debt. Nature 371:65.

Tilman D, Pacala S (1993) The maintenance of species richness in plant communities. In: Ricklefs RE, Schluter D (eds) Species diversity in ecological communities. Chicago Press, Chicago, pp 13–25

Tokeshi M (1995) On the mathematical basis of the variance–mean power relationship. Res Popul Ecol 37:43–48.

Vellend M, Baeten L, Becker-Scarpitta A, Boucher-Lalonde V, McCune JL, Messier J, Myers-Smith IH, Sax DF (2017) Plant biodiversity change across scales during the Anthropocene. Annu Rev Plant Biol 68:563–586

Wood SN (2003) Thin plate regression splines. J R Stat Soc 65:95–114.

Yang Z, Liu X, Zhou M, Ai D, Wang G, Wang Y, Chu C, Lundholm JT (2015) The effect of environmental heterogeneity on species richness depends on community position along the environmental gradient. Sci Rep 5:15723