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PERSPECTIVE

Six key steps for functional landscape analyses of habitat change

Federico Riva · **Scott E. Nielsen**

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Abstract

Context An important part of landscape ecology is to identify relationships between landscape characteristics and ecological processes. One common approach to this is relating raster surfaces to ecological responses, assuming that the characteristics emphasized by rasters are representative of the processes determining changes in the ecological responses being assessed. Consequently, choices made in the design and assessment of rasters affect our understanding of the relationship between landscape characteristics and ecological responses.

Objectives We propose a six-step framework for informing the choices made in creating and measuring rasters for landscape analyses: (i) acknowledge ecological theory and conceptual paradigms, (ii) evaluate the fit of available data, (iii) assess the three facets of scale, (iv) recognize different sampling designs, (v) use proper conceptual models, and (vi) measure meaningful raster characteristics.

Conclusions We discuss how each step can benefit from a "functional" perspective, i.e., an explicit focus on the ecological processes under investigation. This is especially important for landscape analyses of habitat change, which are highly complex due to the many processes potentially involved. A functional perspective draws attention to common pitfalls in landscape ecology, while promoting more process-oriented research in the study of habitat change.

Keywords Habitat heterogeneity · Habitat connectivity · Habitat loss · Habitat fragmentation per se · Anthropogenic disturbance · Functional landscapes

Introduction

Landscape ecology focuses on the relationships between environmental heterogeneity and ecological patterns and processes (Turner 1989). In practice, patterns of landscape heterogeneity are often defined through spatially-aggregated geospatial data, usually as categorical or continuous rasters processed in a Geographic Information System (GIS; McGarigal et al. 2009; Cushman and Huettmann 2010; Wang et al. 2014). These "abstract landscapes" are used to assess relationships between landscape characteristics and ecological responses (Fletcher and Fortin 2018), and thus testing hypotheses and processes in a study (Lechner et al. 2012a, b; Wang et al. 2014). Yet, researchers face several arbitrary choices when creating and measuring raster surfaces. Although rarely acknowledged by ecologists (Lechner et al. 2012a),

F. Riva (✉) · S. E. Nielsen
Department of Renewable Resources, University of Alberta, 751 GSB, 9007 - 116 St NW, Edmonton, AB T6G 2H1, Canada
e-mail: friva@ualberta.ca

these choices determine “the lenses” through which we observe natural processes (Cushman and Huettmann 2010).

Despite being widely discussed in the literature (e.g., Cushman and Huettmann 2010; Lechner et al. 2012b; Fletcher and Fortin 2018), there has been little synthesis of the relations between ecological processes, landscape properties, and how landscapes are characterized and measured. Here, we summarize these broad themes into a six-step framework aimed at bolstering the ecological rationale of landscape analyses (Fig. 1), especially for analyses of habitat change (Fig. 2). Specifically, we first outline how landscape ecology benefits from a focus on processes, explaining why a sound understanding of theories and conceptual paradigms is important for designing meaningful analyses. We then discuss how geospatial data quality, the three facets of the scale concept, sampling designs, and different methods of representing and measuring landscape heterogeneity in GIS implicitly determine the processes evaluated. We conclude by summarizing how a focus on ecological processes in each step can improve our understanding of mechanisms in landscape ecology, and why this is a priority for ecology and conservation. Each step begins with a recapitulatory question (Table 1), encouraging the reader to

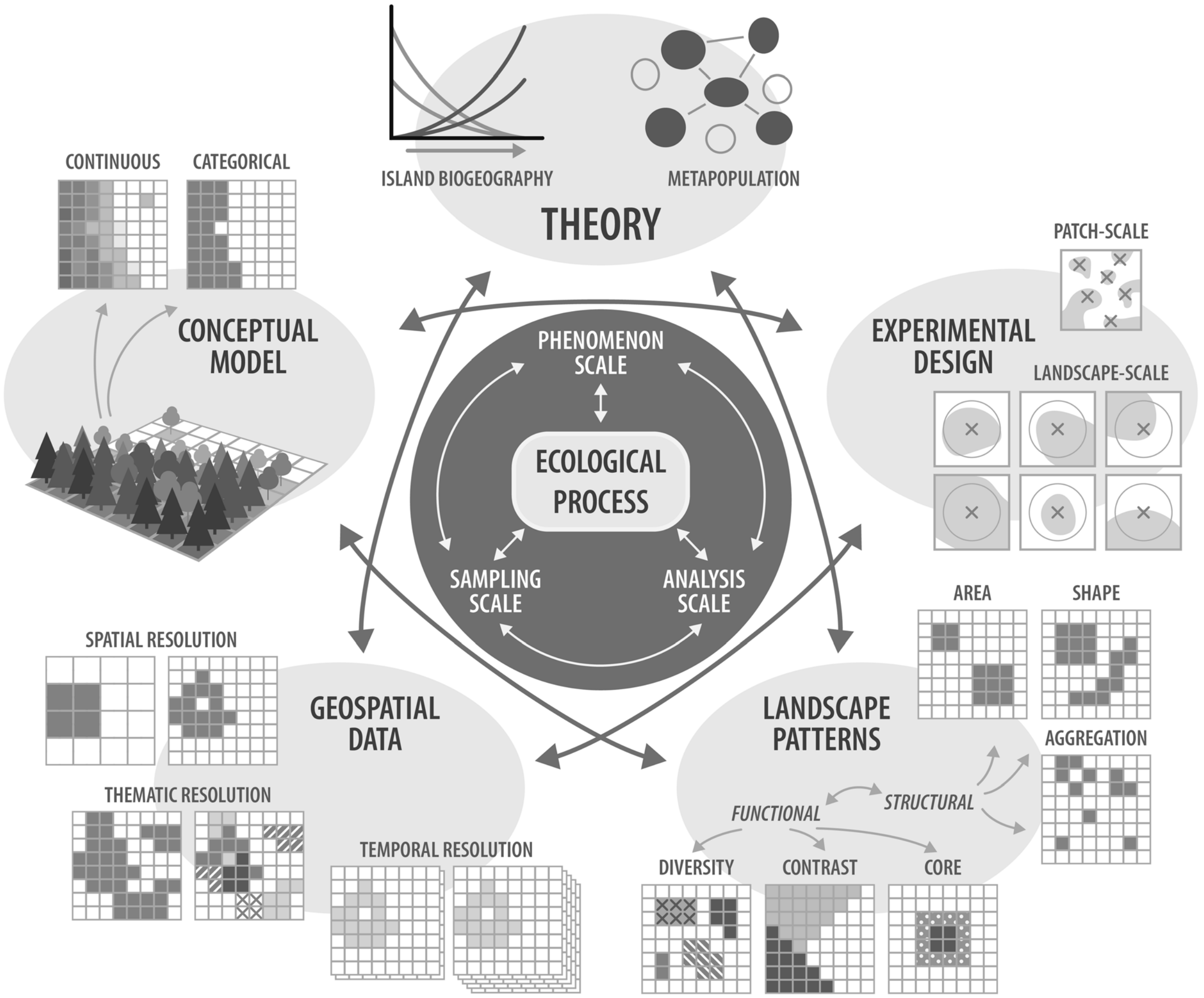

Fig. 1 Relations between ecological processes and the six domains affecting the outcome of landscape analysis. Every ecological process is latent, i.e., observed through the lenses of the scales of observation and analysis, and should inform the experimental design of a study while determining an appropriate conceptual model, the necessary quality of geospatial data, and which landscape pattern should be measured

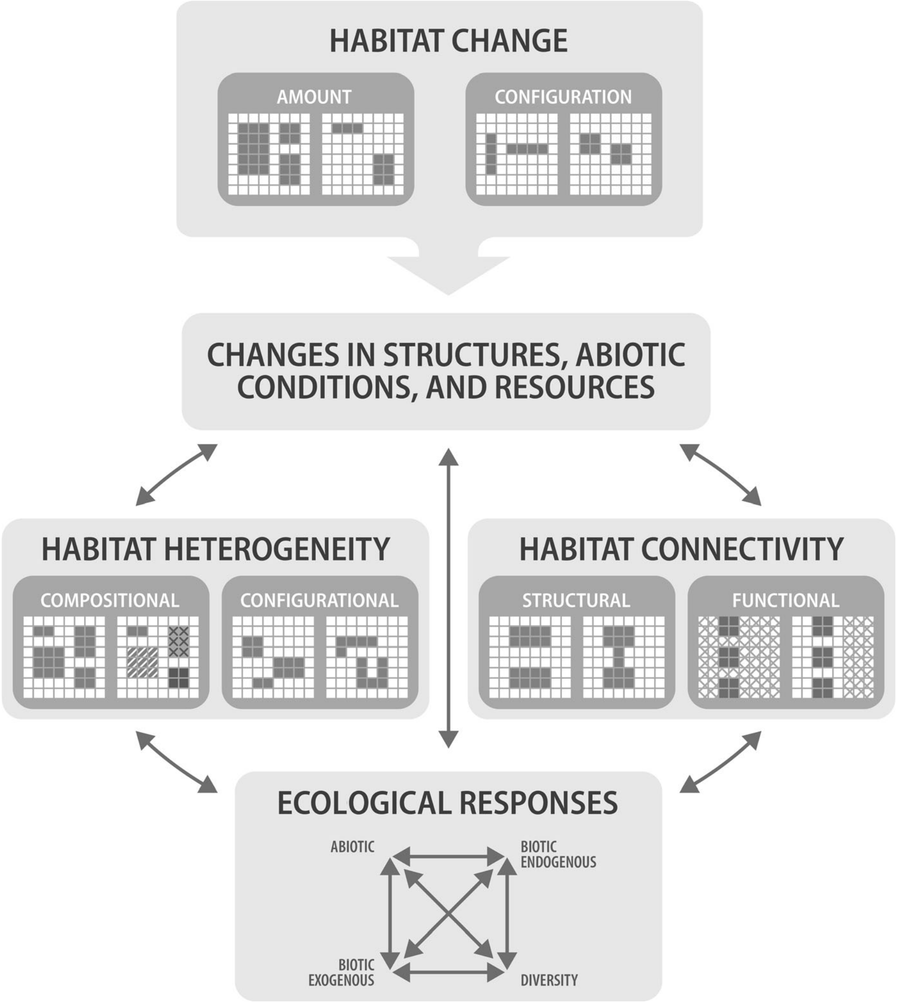

Fig. 2 Pathways through which changes in habitat at the landscape scale influence ecological responses

Table 1 Questions to address for the six steps of conducting functional landscape analyses of habitat change

Acknowledge ecological theory and conceptual paradigms	Does the process of interest fit traditional conceptual paradigms? If not, which alternative mechanisms or hypotheses are proposed in the study?
Evaluate the fit of available data	Are spatial, thematic and temporal resolution of available data adequate to represent the ecological process under investigation?
Assess the three facets of the scale concept	Is there information available on the phenomenon scale of the process of interest, and how is this related to the sampling and analysis scales in the study?
Recognize different sampling designs	Is the sampling design appropriate to evaluate the process of interest? Which spatial units are assessed (e.g., pixels, patches, landscapes), and why?
Use proper conceptual models	Which conceptual model better represents the process of interest? Is the study characterized by contrasting land cover types, or better represented by environmental gradients?
Measure meaningful raster characteristics	Which landscape characteristics are hypothesized to influence changes in the ecological response, and is it possible to measure them through appropriate data, conceptual models, and landscape metrics?

critically assess the appropriateness of different approaches based on the objective of their study. Overall, our objective is to raise awareness around the importance of the many arbitrary choices that researchers make in landscape analyses, explaining why a focus on ecological process can facilitate decisions on those choices, particularly for landscape analyses of habitat change.

Prelude: patterns and processes in landscape ecology

Ecology is broadly divided between studies of patterns and studies of processes. On the one hand, empirical observations of a pattern can inspire new hypotheses (Fahrig 2017), as well as pursuit of generalities (McGill 2019). On the other hand, a mechanistic understanding of the processes behind a pattern is needed for better prediction and extrapolation (Ries et al. 2004). In landscape ecology it has been historically difficult to identify relationships between landscape patterns and the processes that condition a response of interest (Tscharntke et al. 2012; Lausch et al. 2015; Fahrig 2017), especially when one landscape pattern can be linked to multiple processes. For instance, we know that several small patches usually harbor more species than a few larger ones for a given amount of habitat, but why this is remains only partially understood (Fahrig 2020).

We contend that assessing properties of landscapes linked to ecological processes—a "functional" perspective sensu Tischendorf and Fahrig (2000)—allows one to focus on one or a few processes at a time, and thus increases our understanding of relationships between pattern and process. This is especially important in studies of habitat change, one of the most pressing issues in ecology and conservation (Haddad et al. 2015). Indeed, because the "habitat change" paradigm encompasses several phenomena across scales and biological hierarchies (Fig. 2), misinterpretations and debates have been historically common (e.g., definition and effects of "habitat fragmentation"; Hayla 2002; Fahrig 2003). Understanding the mechanisms through which changes in landscapes determine changes in ecological responses will be necessary to address these inconsistencies, requiring a focus on processes rather than patterns (Didham et al. 2012; Fletcher et al. 2018; Fahrig et al. 2019).

Acknowledge ecological theory and conceptual paradigms

Does the process of interest fit traditional conceptual paradigms? If not, which alternative mechanisms or hypotheses are proposed in the study?

Much work has been done to assess how changes in habitat affect ecological processes (e.g., Hayla 2002; Didham et al. 2012; Haddad et al. 2015, 2017; Wilson et al. 2016; Fahrig 2017), delineating several relevant patterns and processes in the context of landscape studies of habitat change (Fig. 2). Notably, because changes in habitat are widespread across the Earth (Haddad et al. 2015), understanding them requires a landscape perspective in many cases (Fahrig 2017). Changes in native habitat usually result in variation in amount and configuration of habitat (Fahrig 2003; Didham et al. 2012; Haddad et al. 2015), with the effects of configuration (e.g., edge and isolation effects) while holding amount of habitat constant defined as habitat fragmentation per se (Fahrig 2003, 2017). In turn, landscapes structure, abiotic conditions, and resources vary (Ries et al. 2004; Didham et al. 2012; Haddad et al. 2015), altering structural and functional connectivity (Tischendorf and Fahrig 2000; Baguette and Van Dyck 2007; Fletcher et al. 2016), as well as compositional and configurational heterogeneity of landscapes (Fahrig et al. 2011; Perović et al. 2015). Ecological processes respond idiosyncratically to these changes, determining feedbacks across space and time (Turner 1989; Didham et al. 2012). The conceptual framework illustrated in Fig. 2 has its origins with the application of island biogeography and metapopulation theories (Fig. 1, top domain) to fragmented terrestrial ecosystems (MacArthur and Wilson 1967; Levins 1969; Laurance 2008; Didham et al. 2012), but tests of the original theories evolved towards more mechanistic approaches. Acknowledging historical connections should not limit researchers in established paradigms, but rather inform knowledge gaps, suggest relevant processes, and identify common issues and pitfalls (Laurance 2008; Haddad et al. 2017).

Evaluate the fit of available data

Are spatial, thematic, and temporal resolution of available data adequate to represent the ecological process under investigation?

Because geospatial data are an abstraction of real-world phenomena, they have unavoidable limitations in processing. It is therefore important to understand the characteristics of available data in relation to the ecological rationale of a study, i.e., assessing data "fitness for use" (Wu et al. 2006; Lechner et al. 2012a, 2014; Fig. 1, bottom-left domain). The quality of geospatial data is evaluated in the spatial, temporal, and thematic domains based on accuracy (absence of errors in attributes), resolution (level of detail), consistency (absence of discrepancies between observations), and completeness (relationship between data and reality) (Wu et al. 2006; Cushman and Huettmann 2010). Outdated, missing, or incorrect observations are obviously problematic, but more subtle errors are associated with capturing, processing, and classifying data (Wu et al. 2006). For instance, the spatial resolution of a raster based on remote sensing depends on the capability of the sensors employed to sample a landscape, which determines pixel size, but also on the imposition of a minimum mappable unit or other filters that reduce detail. Furthermore, spatial data is characterized by uncertainties associated with classification schemes, spatial scales, and classification errors (Lechner et al. 2012a), and different sources of uncertainties can interact resulting in undesirable synergistic effects (Lechner et al. 2014). Although some degree of uncertainty is inherent to spatial data, different spatial representations and error can be evaluated through sensitivity analyses (Lechner et al. 2012b). Finally, making inferences on the characteristics of a system represented at one spatial scale from its characteristics as observed at another scale (the "ecological fallacy"), and the effects of aggregation/spatial resolution of remote sensing data on statistical analyses (the "modifiable areal unit problem"), are a common concern for spatially-aggregated data (Jelinski and Wu 1996). If ignored, all these issues can result in spurious inferences.

Assess the three facets of the scale concept

Is there information available on the phenomenon scale of the process of interest, and how is this related to the sampling and analysis scales in the study?

Scale-dependencies are a prominent theme in ecology because the spatiotemporal domain of a study determines ecological inference (Wiens 1989; Levin 1992). Nevertheless, "scale" is an elusive term used to describe multiple properties of data. Dungan et al. (2002) proposed three dimensions of the scale concept (Fig. 1, central domain): (i) *phenomenon scale*, the extents at which an ecological process is structured and interacts with the environment; (ii) *sampling scale*, the units used to acquire information about the phenomenon; and (iii) *analysis scale*, how the sampling units are summarized in the analysis. In landscape ecology, this framework encompasses both the representation in GIS and analytical choices (Lechner et al. 2012a).

Phenomenon scale

The phenomenon scale represents the dimension at which organisms or processes respond to environmental heterogeneity, a "functional grain" that should determine the resolution of geospatial data (Levin 1992; Baguette and Van Dyck 2007). However, since the phenomenon scale is always evaluated through analysis and sampling scales (Dungan et al. 2002; Lechner et al. 2012a), revealing generalities in how organisms interact with their environment has been historically difficult (Dungan et al. 2002; Jackson and Fahrig 2015; Miguet et al. 2016). Because intuitive predictions are generally supported (e.g., bigger and long-lived taxa tend to respond to larger spatial and temporal scales), defining categories of ecological responses that share similar characteristics can inform appropriate phenomenon scales (Fletcher and Fortin 2018). We suggest four categories of phenomenon scale: (i) changes in the abiotic environment; (ii) endogenous biotic responses, e.g., behavioral responses; (iii) exogenous biotic responses, e.g., species' occurrence/abundance; and (iv) changes in diversity patterns. However, we also note that there can be important differences within these categories, and the choice of an appropriate phenomenon scale is context-dependent. For instance, microclimatic conditions can depend on both local and landscape properties (Latimer and Zuckerberg 2017), while habitat heterogeneity can affect biodiversity across scales, in a hierarchical fashion (Fahrig et al. 2011). A functional perspective will help navigate these complexities.

Sampling scale

Sampling scales depend on the resolution of geospatial data, which sets the spatial, qualitative, and temporal limits of analysis. While technological constraints and author's choices determine sampling scales (e.g., pixel size, processing operations, classification schemes, sampling period, and frequency of time-series; Lechner et al. 2012a, b; Coops and Wulder 2019), the appropriate level of detail in these domains depends on the ecological process being investigated (Wiens 1989; Levin 1992). Therefore, researchers must critically evaluate if the available data match the process. Data quality and availability were historically limited (Jelinski and Wu 1996), but recent technological developments open exciting new venues for the assessment of scaling rules and ecological processes at extraordinary levels of detail (Coops and Wulder 2019; Wickham and Riitters 2019).

Analysis scale

Contrary to the phenomenon and sampling scale, researchers can define the analysis scale through three factors. First, while the spatial resolution of a raster depends on the sampling scale, and higher resolutions are usually preferred, an excessively-high resolution relative to the phenomenon scale can add noise (Wiens 1989; Fletcher and Fortin 2018). Researchers should therefore consider aggregating data to better represent the ecological process investigated (Lechner et al. 2012b; Fletcher and Fortin 2018).

Second, "characteristic scales" or "scales of effect" refer to the spatial extent at which an ecological phenomenon interacts with landscapes (Jackson and Fahrig 2012; Fletcher and Fortin 2018). Characteristic scales are usually evaluated empirically, measuring landscapes around sampling locations at multiple spatial extents, and evaluating at which scale(s) landscape characteristics explain the ecological response. Because assessing an insufficient range of scales bears the risk of overlooking scale-dependent relationships and the modifiable areal unit problem (Wiens 1989; Levin 1992; Miguet et al. 2016), areas $\sim$ 10 times greater than the phenomenon scale have been recommended as appropriate (Jackson and Fahrig 2015). However, species can respond to different environmental factors at different characteristic scales, to one environmental factor at multiple characteristic scales, and across different hierarchical levels of biological organization (Stuber et al. 2017; Wright et al. 2020). Therefore, identifying generalities has proved to be difficult (e.g., Moraga et al. 2019). For instance, while species mobility must play a role in determining characteristic scales, other factors seem to confound this relationship (Jackson and Fahrig 2012, 2015; Miguet et al. 2016; Moraga et al. 2019).

Third, inferences on scale-dependency vary with the "size" of the study area. Indeed, assessing larger areas increases the probability of sampling rare/new environments (Wiens 1989), and characteristic scales might vary between regions (Miguet et al. 2016).

Recognize different sampling designs

Is the sampling design appropriate to evaluate the process of interest? Which spatial units are assessed (e.g., pixels, patches, landscapes), and why?

Designing landscape studies requires explicit consideration of the phenomenon, sampling, and analysis scales. For instance, while it is recommended that one select multiple non-overlapping landscapes to avoid spatial autocorrelation and ensure independence of observations (Fahrig 2003; but see Zuckerberg et al. 2012), characteristic scales are estimated a posteriori, and thus only previous studies and knowledge of the system evaluated can inform this.

Additionally, there are different approaches to conducting landscape analyses (Fig. 1, top-right domain). First, "patch-scale" studies evaluate ecological responses that are summarized among patches within one landscape, whereas "landscape-scale" studies compare observational units across different landscapes (Fahrig 2003, 2017). These approaches differ in objectives and applications, e.g., disentangling the effects of habitat amount and configuration is possible only when comparing different landscapes, and thus patch-scale studies cannot assess the effects of habitat fragmentation per se (Fahrig 2017). Second, there are differences in study design between traditional experiments (Resasco et al. 2017) and mensurative experiments, i.e., pseudo-experiments with sampling locations selected across landscape gradients of environmental heterogeneity (Cushman and Huettmann 2010). Last, it is possible to assess different observational units, from pixels to patches and landscapes (Cushman and Huettmann 2010; Fletcher and Fortin 2018). For instance, generally speaking, species distribution models adopt pixels as observational units, studies of metapopulation dynamics adopt patches, and tests of the habitat amount hypothesis compare equal sampling units across landscapes varying in amount of habitat (Fahrig 2013; Fletcher and Fortin 2018).

Use proper conceptual models

Which conceptual model better represents the process of interest? Is the study characterized by contrasting land cover types, or better represented by environmental gradients?

Conceptual models bridge landscape analyses and ecological theory (Brudvig et al. 2017; Pulsford et al. 2017; Fig. 1, top-left domain). Two dominant paradigms—the island biogeographic model and the dynamic landscape mosaic—have been applied using categorical, continuous, gradient, and hybrid conceptual models (McGarigal and Cushman 2005; Lausch et al. 2015; Brudvig et al. 2017; Fletcher and Fortin 2018).

Categorical models have been the most common approach to landscape analyses (Lechner et al. 2012a; Lausch et al. 2015). Specifically, the island model divides landscapes in suitable habitat vs. unsuitable matrix (e.g., natural vs. anthropogenic habitats), whereas the landscape mosaic model incorporates different land cover types (e.g., coniferous, broadleaf, and mixed forests). Conversely, continuous models describe landscapes as gradients (e.g., canopy height or elevation). When a process is well-known, it is possible to implement models based on "multivariate, multi-scale gradient representations" of the environment (e.g., habitat suitability surfaces; McGarigal and Cushman 2005; Cushman and Huettmann 2010). Hybrid models incorporate different aspects of these conceptual models (e.g., Brudvig et al. 2017).

Categorical models have been extensively used in the past because land cover data have been readily available (Lechner et al. 2012a; Lausch et al. 2015), but these models are limited by arbitrary definitions of land cover, discrepancies between real environmental conditions and geospatial data, species perception of ecological gradients that differ from defined categories, and loss of variability within and between land cover types (Lausch et al. 2015; Brudvig et al. 2017; Pulsford et al. 2017). Most generally, categorical models are only appropriate when assessing land cover types that are contrasting the ecological process of interest. Because continuous models make fewer assumptions on how ecological processes respond to environmental variation, they can be biologically more accurate and relevant than categorical models (Lausch et al. 2015; Brudvig et al. 2017; Pulsford et al. 2017), particularly in places characterized by smooth environmental transitions (e.g., successional stages within a forest).

Measure meaningful raster characteristics

Which landscape characteristics are hypothesized to influence changes in the ecological response, and is it possible to measure them through appropriate data, conceptual models, and landscape metrics?

There is no universal metric of landscape pattern, and understanding how each metric works is thus crucial to informing effective analyses. Landscape metrics are designed to assess composition of habitat (i.e., attributes independent of spatial references), configuration of habitat (i.e., attributes dependent on spatial reference), or some aspect of both (McGarigal et al. 2009; Wang et al. 2014). Some metrics are "functional" in that they vary with the process investigated (e.g., core area), while others are purely "structural" (e.g., edge density) (Fig. 1, bottom-right domain). Each level of a spatial hierarchy—pixels, patches, classes, and landscapes—should be measured specific to the study objective (Cushman and Huettmann 2010; Fletcher and Fortin 2018).

Because categorical models provided a basic framework for landscape ecologists, measures of land cover characteristics have been used and scrutinized for decades (Gustafson 1998; Cushman et al. 2008; Wang et al. 2014). Conversely, surface metrics for continuous surfaces have been less appreciated (e.g., autocorrelation structure functions, surface metrology, fractal analysis, and spectral and wavelet analysis; McGarigal et al. 2009; Cushman and Huettmann 2010; Kedron et al. 2018). Notably, measures of landscape pattern differ depending on the conceptual model employed; analogs between the two categories are sporadic, and researchers should explore how different conceptual models allow one to represent uniquely the characteristics of landscapes in relation to the process assessed, rather than searching for generalities (McGarigal et al. 2009; Kedron et al. 2018). For instance, continuous surfaces lack the division of patches typical of categorical models, but are more appropriate to evaluate variation in environmental conditions within patches (Kedron et al. 2018).

Concluding remarks: functional landscape analyses, moving forward

In this perspective we advocate that a process-oriented research approach to landscape ecology allows one to better evaluate the effects of changes in habitat on species and ecosystems. Structural properties of landscapes moderate important mechanisms (Tscharntke et al. 2012), but organisms' attributes and ecological processes ultimately interact with landscape characteristics in idiosyncratic ways, determining among other things what is habitat (Dennis et al. 2003) and landscape connectivity (Tischendorf and Fahrig 2000; Baguette and Van Dyck 2007). While relating landscape patterns to ecological patterns is important (Fahrig et al. 2011; McGill 2019), too often we lack an understanding of the mechanisms through which patterns in landscape heterogeneity affect ecological responses (Fahrig 2020). This reduces our ability to predict, and thus mitigate, the effects of changes in habitat (Didham et al. 2012; Haddad et al. 2017). Therefore, pursuing a "functional" perspective centered on ecological processes (Table 1) is a priority in ecology and conservation, especially when the objective is to understand why a certain landscape pattern results in different patterns in ecological responses (Ries et al. 2004). Furthermore, because landscape analyses require choosing between hundreds of combinations of sampling approaches, data types, conceptual models, and landscape metrics, focusing on ecological processes first avoids "fishing expeditions" (Gustafson 2018). Despite these advantages, one caveat of this framework is the need to establish which processes are hypothesized to affect the ecological response of interest. This choice can be arbitrary, even when informed by previous studies, but this is true for most studies in ecology (Diamond 1983). Like in many other disciplines, a balance between different approaches will be fundamental to further understanding landscape ecology, with studies on patterns and processes complementing each other.

Ultimately, landscape ecologists routinely deal with the themes discussed in this perspective. Indeed, recent papers from Tarr (2019), Stuber et al. (2017) and Wright et al. (2020) share many considerations with our six key steps (e.g., on scale-dependencies, on the importance of focusing on processes, and on idiosyncrasies in species responses to landscape gradients). However, researchers are often inconsistent in defining and acknowledging these concepts, usually choosing to do so implicitly. We suggest that the synthetic framework presented here will aid landscape ecologists—particularly early career researchers or interdisciplinary scientists—in explicitly considering the six, intertwined domains that underlie functional landscape analyses (Fig. 1; Table 1). We believe that this will be especially important for process-oriented research: fundamentally, every landscape analysis is based on the assumption that the abstract landscape created for analysis is representative of relevant natural processes, an assumption valid only when all the themes discussed here are evaluated critically.

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