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PERSPECTIVE

A functional perspective on the analysis of land use and land cover data in ecology

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Abstract Assessments of large-scale changes in habitat are a priority for management and conservation. Traditional approaches use land use and land cover data (LULC) that focus mostly on "structural" properties of landscapes, rather than "functional" properties related to specific ecological processes. Here, we contend that designing functional analyses of LULC can provide important and complementary information to traditional, structural analyses. We substantiate this perspective with an example of functional changes in habitat due to industrial anthropogenic footprints in Alberta's boreal forest, where there has been little overall forest loss ($\sim$ 6% structural change), but high levels of functional change (up to 93% functional change) for species' habitat, biodiversity, and wildfire ignition. We discuss the methods needed to achieve functional LULC analyses, when they are most appropriate to add to structural assessments, and conclude by providing recommendations for analyses of LULC in a future of increasingly high-resolution, dynamic remote sensing data.

Keywords Functional landscape analyses · Geographic information systems · Remote sensing · Scale of analysis · Scale of phenomenon · Scale of sampling

INTRODUCTION

Understanding the consequences of human activities is one of the most pressing challenges to protecting and managing natural resources in the twenty-first century (Soulé 1985; Kareiva and Marvier 2012). Today, anthropogenic disturbances dominate ecosystems, eroding biodiversity and affecting several other ecosystem services (Newbold et al. 2015; Crooks et al. 2017; Daskalova et al. 2020). As a result, ecologists, managers, and policy makers are often required to evaluate changes in habitat across large regions of the Earth. This has been traditionally achieved by assessing changes in land use and land cover data (LULC), using remote sensing tools (O'Neill et al. 1988; Riitters et al. 2004).

Owing to technological and statistical developments, LULC are now available at unprecedented broad scales (e.g., global; Tuanmu and Jetz 2014) and high resolutions (e.g., 1-m resolution; Wickham and Riitters 2019). Use of these products has revealed important patterns and trends: for instance, deforestation occurs consistently across the tropics (Taubert et al. 2018), taxa inhabiting fragmented regions suffer increased extinction risks (Crooks et al. 2017), and most of the world's forests are proximal to edges (Haddad et al. 2015). While increasing availability and quality of LULC data contributed to the establishment of landscape ecology, macroecology, and conservation planning as cornerstones in the environmental sciences (Gustafson 2018), developing meaningful analyses of LULC can be complex, and these analyses are not exempt from those limitations (Coops and Wulder 2019; Riva and Nielsen 2020).

Assessments of LULC generally evaluate "structural" properties of landscapes, i.e., properties that are not representative of specific ecological processes (Tischendorf and Fahrig 2000). Indeed, while landscape properties sampled with remote sensing usually bear broad ecological relevance, not all ecological processes respond to the same landscape characteristics (Tischendorf and Fahrig 2000).

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Access to finished products where different LULC categories are defined prior to the analysis also limit their application for ecologists (e.g., satellite images classified based upon spectral signatures, Borra et al. 2019). Therefore, structural properties of LULC might not be representative of the "functional" changes in habitat of interest in different regions or studies.

Analyses of LULC have become common in management and conservation given widespread availability of these data and their intuitiveness (Riva and Nielsen 2020). For instance, Ambio published within the past 5 years 600 articles related to "land use" and 132 articles related to "land use AND geographic information system", or 434 and 98 related to "land cover" and "land cover AND geographic information system" (search conducted June 19th 2020). Since these analyses are often structural (e.g., Cousins et al. 2015; Mendoza-Ponce et al. 2019), it is important to recognize the benefits and limitations of this approach. Essentially, structural analyses of LULC assess coarse-filter, top-down patterns of changes in habitat across landscapes, thereby broadly evaluating a variety of processes. Yet, these analyses miss fine-filter, bottom-up responses to changes in habitat, overlooking specific ecological processes or species that typically respond to changes in habitat idiosyncratically, and in a context- and scale-dependent fashion. Appropriate management and conservation actions require an understanding of both facets, and understanding these nuances is especially important when the goal is to protect landscapes in a holistic fashion, e.g., to manage biodiversity and ecosystem services (Nielsen et al. 2007; Tingley et al. 2014).

In this perspective, we advocate that functional LULC analyses can provide important and complementary information to traditional, structural analyses of LULC. We discuss the benefits and framework for adapting LULC to represent functional responses to changes in habitat based on relationships between geospatial data and ecological phenomena, suggesting a formal distinction between structural and functional analyses of LULC data. We show how a functional perspective can influence our understanding of changes in habitat using a case study of international relevance—the anthropogenic industrial footprint of Alberta's boreal forest in western Canada. Contrasting structural and functional quantifications of habitat change in Alberta's forests, we demonstrate how the information provided by functional and structural assessments is distinct and complementary. We conclude by discussing when and how it will be appropriate to conduct functional analyses of LULC in the future of high-resolution, continuous, and dynamic data.

WHAT IS A FUNCTIONAL PERSPECTIVE, AND WHY IS IT IMPORTANT TO PURSUE IT?

The idea of contrasting "structural" and "functional" approaches is recurring in the ecological literature. For instance, Tischendorf and Fahrig (2000) defined structural vs. functional landscape connectivity, whereas McGarigal (2014) defined structural vs. functional landscape metrics. Defining a more general paradigm, Riva and Nielsen (2020) proposed that functional landscape analyses be defined as assessments of patterns in spatial heterogeneity that are explicitly related to ecological processes, as opposed to structural assessments where there is an implicit link between geospatial data and ecological processes. A "functional perspective" is therefore the upfront and explicit evaluation of all the characteristics of geospatial analyses in relation to ecological process of interest in a study (e.g., spatial, thematic, and temporal resolution, conceptual model employed, or metrics used to assess the geospatial data). This framework applies to the analysis of LULC, where functional analyses are those that evaluate how LULC represent specific ecological processes, whereas structural analyses are those that explore general patterns assuming that LULC represent broad ecological processes. While both approaches have their merits, a focus on ecological processes might be the key to tackle long-term, unsolved questions in ecology and conservation (Fahrig 2020; Riva and Nielsen 2020).

One could argue that all LULC analyses are functional, because all LULC assume that geospatial data are appropriate to describe ecologically relevant patterns in environmental heterogeneity. However, many concepts related to species' habitats are dependent on life history traits, are inherently idiosyncratic, and are scale-dependent, yet structural LULC analyses do not usually account for these differences. For instance, the simple question of 'what is habitat' depends on the resources necessary for a species to persist (Dennis et al. 2003), while the question of 'how diverse is a landscape' depends on the taxa examined (Fahrig et al. 2011), and the question of 'how connected is a landscape' depends on the characteristics of the ecological process assessed, as well as countless context-dependent factors (Tischendorf and Fahrig 2000). There is, therefore, value in explicitly defining how LULC relate to the processes of interest. A functional perspective is important because it forces the authors to define clear study objectives and to measure relevant landscape properties, thereby reducing the risk of making spurious inferences (Lechner et al. 2012; Riva and Nielsen 2020), and because it strengthens the application of "day science", the systematic process of testing hypotheses through structured and rational studies (Jacob 1988). Since original values of LULC data can rarely represent all the ecological process of interest in a study, evaluating if a functional perspective is needed should be a critical and explicit step when evaluating patterns of landscape change using LULC.

LINKING LULC AND ECOLOGICAL PROCESSES TO PROMOTE A FUNCTIONAL PERSPECTIVE

To achieve a functional perspective in the context of LULC analyses, it is necessary to assess LULC that appropriately represent landscape properties hypothesized to condition an ecological process of interest. Different phenomena are structured and interact with the environment at different scales (*phenomenon scale*), which should define appropriate units to acquire information about ecological processes (*sampling scale*) and units to analyze them (*analysis scale*) (Dungan et al. 2002; Riva and Nielsen 2020; Fig. 1). Furthermore, even when affected by similar phenomenon, sampling, and analysis scales, different ecological processes can respond to different landscape patterns, and measuring different patterns can further exacerbate discrepancies between structural and functional assessments (Riva and Nielsen 2020).

A functional perspective often requires manipulating the original LULC data to match the characteristic of a given ecological phenomenon (e.g., thematic resolution, spatial resolution, or temporal resolution). In the past, limited availability of high-resolution remote sensing data has been an important limitation because the resolution of LULC was often coarser than the scales necessary to represent many natural phenomena (Fig. 1). Indeed, scales of analysis and sampling tend to be inversely correlated, with large-scale analyses typically conducted at coarser resolutions. However, since we are entering a new era of large-scale, high-resolution remote sensing and biodiversity data (Jetz et al. 2019; Wickham and Riitters 2019), this trend is bound to change and the time is ripe to recognize the benefits of a functional perspective when assessing LULC. In the coming years, a focus on integrating biodiversity and remote sensing data will allow for a greater understanding of the human impacts on natural habitats (Jetz et al. 2019). This revolution will benefit the analysis of LULC especially in relation to functional analyses (e.g., allowing the

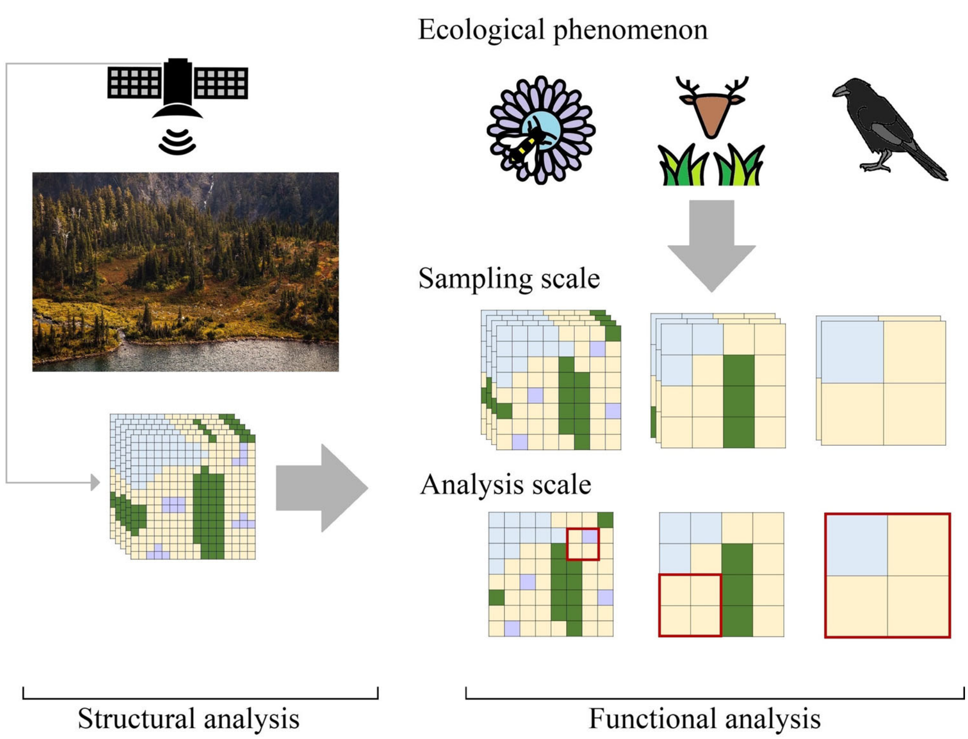

Fig. 1 Using land use/land cover maps (LULC) to represent natural processes and functional changes in habitat (a "*functional*" perspective) requires evaluating spatial, temporal, and thematic resolution (*sampling scales*), and the spatio-temporal extents considered (*analysis scales*) to match the phenomenon assessed. We illustrate this with three hypothetical processes occurring in the same landscape: (i) pollination of smooth blue aster (*Symphyotrichum leave*) from yellow bumblebee (*Bombus fervidus*), (ii) resource selection in white-tailed deer (*Odocoileus virginianus*), and (iii) dispersal in raven (*Corvus corax*). Pollination of yellow bumblebee can occur only in grassland patches that contain smooth blue asters, whereas all grassland patches are homogeneous for white tail deer, and ravens use any terrestrial land cover, but not water bodies. These differences justify different thematic resolutions between different scenarios, but similar considerations apply to all the facets of the sampling and analysis scales. Structural analyses assess LULC as sampled by remote sensing, whereas functional analyses evaluate LULC designed to explicitly match ecological processes

exploration of scaling patterns (Wickham and Riitters 2019), or fine-scale requirements of different species in determining what is habitat (Dennis et al. 2003)). Notably, as technology progresses, continuous geospatial data are also becoming increasingly available and relevant (Coops and Wulder 2019). We describe in the discussion below how categorical and continuous surfaces are complementary, and lead to advances and integration in the fields of ecology and remote sensing.

COMPARING STRUCTURAL AND FUNCTIONAL ANTHROPOGENIC CHANGES IN THE ALBERTA BOREAL BIOME

Quantifying the degree to which an area is disturbed by anthropogenic activities is a standard practice and first step in environmental management, e.g., to inform species distribution models, conservation prioritization, or restoration activities. To highlight the importance of a functional approach to LULC analyses, we use a case study that assesses structural and functional changes associated with anthropogenic footprints in the Alberta boreal forest. A detailed description of the case study is provided in Electronic Supplementary Material (ESM1).

Human activities in the Alberta boreal forest

Understanding the consequences of anthropogenic footprints in Alberta is of global significance, because resource extraction here affects more than 100 000 km^2 of one of the largest and most intact forest biomes in the world (Rosa et al. 2017; Fisher and Burton 2018) (Fig. 2). The focus within the Alberta boreal biome has historically been on species or biodiversity responses to forestry (e.g., Nielsen et al. 2004), and on the effects of habitat loss associated with open-pit mining of oil sands (e.g., Rooney et al. 2012). However, there has been increasing attention to the more localized, but widespread (i.e., more than 1.8 million km of linear features), footprint of in situ oil sands developments (Fisher and Burton 2018; Riva et al. 2018a; Fig. 2).

Most Canadian oil sands are subterranean and thus extracted with wells (in situ extraction), not open-pit mining, which is limited to the area around Fort McMurray to Fort MacKay. Consequently, hundreds of thousands of kilometers of seismic lines have been cleared of trees and shrubs to map oil sands deposits (Dabros et al. 2018). Seismic lines represent only one footprint with additional disturbances associated with well pads, pipelines, cutblocks, and other industrial features (Fisher and Burton 2018). Add to that an active natural wildfire regime (Flannigan et al. 2009) and the successional dynamics and structural patterns of these forests are being substantially altered, resulting in long-lasting and complex interactive responses (van Rensen et al. 2015; Mahon et al. 2019; Riva et al. 2020).

Habitat loss is, however, quite limited in these landscapes compared to many regions of the world (i.e., estimates to date suggest less than 15% of the native forest cover; Rosa et al. 2017; Mahon et al. 2019), but it is widespread in extent because of the exploration nature of the linear features. This affects a variety of ecological processes due to hyper-connected patches of early seral forests and unprecedented amounts of forest edges (e.g., 80 km of edges per km^2 of forest; Stern et al. 2018), including movements of species, alterations to the abiotic environments, and more broadly the distribution of resources in these forests (Fisher and Burton 2018; Riva et al. 2018b; Roberts et al. 2018; Stern et al. 2018). Changes in resources determine idiosyncratic responses between taxa, with "winners or losers" depending on species' ecology and context, and key to these responses are biotic interactions (Fisher and Burton 2018; Dickie et al. 2019; Mahon et al. 2019; Riva et al. 2020). Despite awareness of these phenomena, assessments of anthropogenic footprints in Alberta's boreal forest have been primarily structural (Jordaan 2012; Rosa et al. 2017), not functional. Furthermore, the resolution of common LULC ($\geq$ 30 m) underestimates the effect of thousands of kilometers of narrow (< 10 m) seismic lines in the area (Rosa et al. 2017).

Analysis overview

We used high-resolution (5 m) baseline LULC data to assess 11 anthropogenic footprint categories and a "boreal forest" category (see Table S1 in Electronic Supplementary Material). Specifically, a baseline disturbance raster was created by rasterizing a series of polygon and polyline layers from the Alberta Biodiversity Monitoring Institute ("Wall-to-Wall Human Footprint Inventory", available at https://www.abmi.ca/). Based on this raster, we first measured the total surface of the study area affected by different anthropogenic LULC categories, providing a structural quantification of anthropogenic changes (i.e., loss of forest cover). Then, we manipulated the thematic and spatial resolution of the baseline LULC to create functional LULCs that match six ecological processes of interest—diversity of woody plants, diversity of butterflies, occurrence of American marten (*Martes americana*), habitat suitability for ovenbird (*Seiurus aurocapilla*), habitat use for woodland caribou (*Rangifer tarandus caribou*), and wildfire ignition (Table 1). We chose these six processes (five taxa and wildfire) because Environmental Impact Assessments in northern Alberta generally assess between ~ 5 and 15 taxa (Campbell et al. 2019),

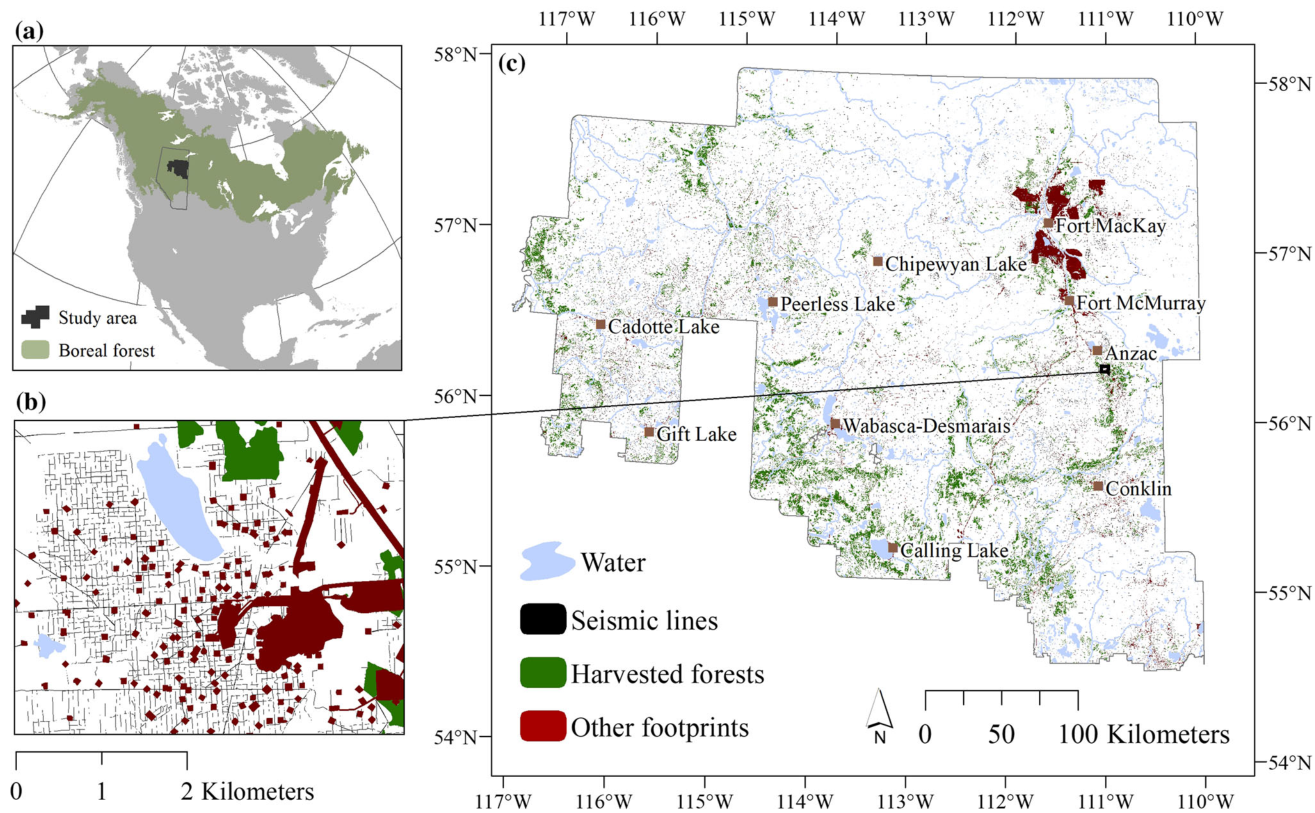

Fig. 2 Boreal forest of North America **a** is one of the largest and most intact biomes in the planet. In Alberta, these forests are characterized by widespread anthropogenic footprints associated with the extraction of timber and petroleum products (**b**). In situ extraction of oil sands is especially prevalent in this region, dissecting thousands of km^2 of forests (**b**, **c**), primarily due to linear features necessary to locate the underground oil sands reserve

Table 1 Phenomena informing the sampling and analysis scales for six functional LULC evaluated in this case study

Phenomenon	Sampling scale (spatial resolution) (m)	Analysis scale (moving window size) (m)	References
Woody plant diversity decreases at sites closer than 20 m from forest edges	5	20	Dabros et al. (2017)
Butterfly diversity increases at sites surrounded from more disturbed landscapes in 250 m radii	10	250	Riva et al. (2018a)
Occurrence of American marten decreases with high densities of anthropogenic linear features in their home range	5	1250	Tigner et al. (2015)
Abundance of ovenbird declines at line densities higher than 15 km of lines per km^2	10	2000	Bayne et al. (2005)
Woodland caribou avoid forests in a radius of 500 m from anthropogenic footprints	10	500	Environment Canada (2011)
Wildfire ignition increases in areas with higher road densities at 5000 m radii	1000	5000	Arienti et al. (2009)

but certainly more species and processes can be added for a more detailed assessment. We assessed patterns of functional change for the six functional LULCs by measuring: (i) presence of anthropogenic footprints, and (ii) proportion of anthropogenic footprints within a moving window of sizes representing ecologically meaningful "scale of effects". We then measured these responses around 1173 systematically spaced points at distances of 10 km (distance between points selected to avoid overlapping between moving windows at the largest analysis scale, 5 km) where values for each ecological measure were queried. The moving window analysis summarized the

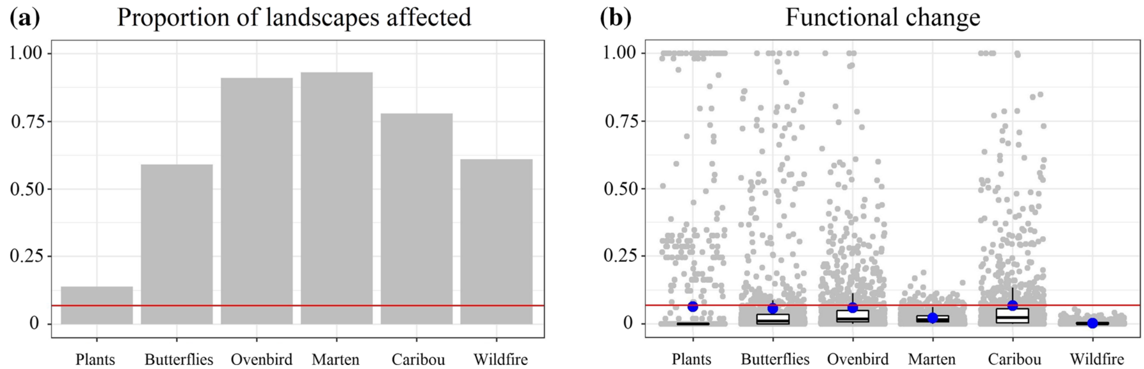

Fig. 3 Proportion of landscapes affected by anthropogenic footprints (**a**), and relative amount of functional change (**b**) for the six ecological processes described in Table 1. In **b**, each of the gray points represents one of 1173 landscape sampled, boxplots summarize the distribution of the samples (i.e., box delimiting 25%, 50% (median) and 75% percentiles), and blue dots represent the mean proportion of functional change in each scenario. Horizontal red lines in each graph represent the total amount of anthropogenic cover in the study area (~ 6%), a measure of structural forest changes

proportion of footprint defined for that ecological measure based on a binary disturbance grid (i.e., 0, boreal forest; 1, anthropogenic footprint) at radii specific for each measure (Table 1) by calculating their mean value. Finally, to evaluate if patterns of functional change were similar across the six processes evaluated, we calculated pairwise Pearson correlation coefficients between the measures from each scenario at each point. Low correlation coefficients would suggest that, despite originating from the same structural change, functional changes related to the anthropogenic footprint differ substantially.

Functional changes largely exceed structural changes

We documented limited structural changes, with ~ 94% of the area covered by natural forests. Among different anthropogenic LULC categories, ~ 3% of the study area was affected by forestry, ~ 1% was affected by open-pit mining, and ~ 2% was affected by energy exploration due to seismic lines (Table S1). On the other hand, between 14% (for woody plants) and 93% (for American marten) of the landscape was affected by anthropogenic footprints as determined by their process scale (Fig. 3a). The proportion of anthropogenic footprints varied substantially between different processes (Fig. 3b; Pearson correlation coefficient varying between 0.2 and 0.9; Appendix S1) and across space (Fig. 4). While similar scales of sampling (spatial resolutions) and analysis (moving window size) tended to result in higher correlations between scenarios, the characteristics of different ecological processes mediated important differences. For instance, woody plants and American marten respond to the same sampling scale (5 m), but patterns in functional change between these two processes showed the lowest Pearson correlation coefficient ($r = 0.2$; ESM 1, and insets “a” vs. “d” in Figs. 4, 5).

Management implications

This analysis demonstrates how structural and functional assessments of LULC can differ substantially due to the characteristics of different ecological processes, e.g., here due to responses to edges in behavior, microclimate or resources. Environmental impact assessments in Canada focus on valued ecosystem components (e.g., species of conservation interest or culturally important, such as woodland caribou), and the impact to wildlife are measured indirectly through predicted changes in habitat amount (Campbell et al. 2019). It has been argued that these environmental assessments need to be improved in their efficiency and rigor (Campbell et al. 2019), requiring an integrative management plan that explicitly defines which processes ought to be prioritized, and which effects are desirable or undesirable. These objectives require a functional perspective: integrating structural and functional assessments of habitat change could therefore complement other approaches (e.g., habitat suitability surfaces, research selection functions) in informing areas of priority for regional development plans, as well as management, conservation, and restoration practices.

More broadly, when ecologists and practitioner are required to quantify habitat change, they need to be aware of the limitations of structural LULC analyses, and acknowledge that it is not possible to describe the myriad of effects of habitat changes with a single structural measure. This is especially important in areas where the effects of habitat configuration (e.g., edge effects or connectivity/isolation effects) play an important role in determining species responses, such as in the dissected forests of Alberta that we show here. Similar patterns in habitat configuration occur worldwide, with 70% of the world forests being within 1 km from forest edges (Haddad et al. 2015), and over 21 million km of roads on the Earth

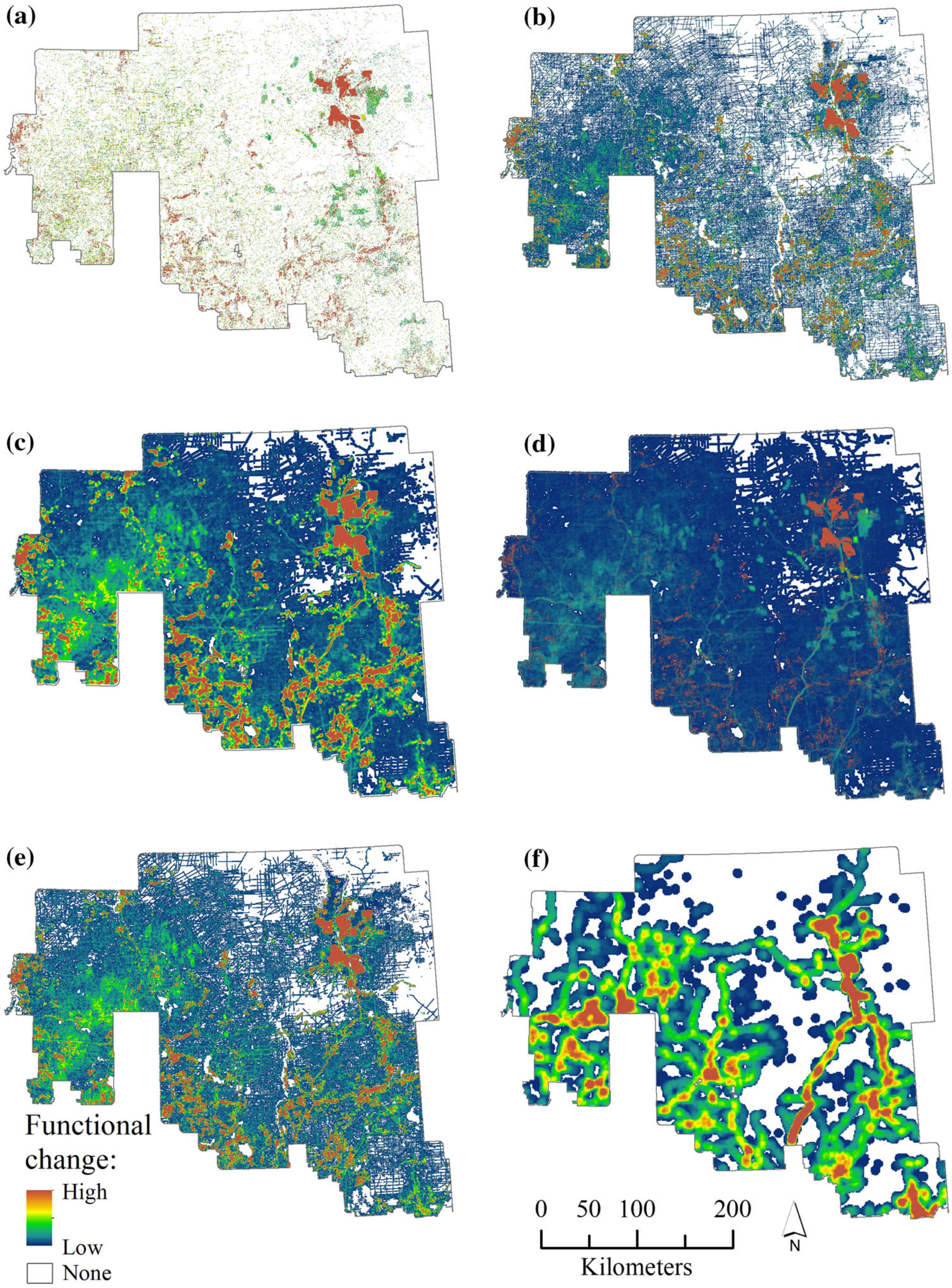

Fig. 4 Spatial distribution of functional changes associated with anthropogenic footprints in the Alberta boreal forest, for six processes of interest: **a** diversity of woody plants, **b** diversity of butterflies, **c** habitat suitability for ovenbird, **d** occurrence of American marten, **e** habitat use for woodland caribou, and **f** wildfire ignition

(Meijer et al. 2018). Notably, an increase of $\sim$ 3–5 million km of roads is expected by 2050, especially within the world's last remaining wilderness areas (e.g., Amazon, the Congo basin and New Guinea; Meijer et al. 2018). Here, structural LULC assessments alone will fail to capture the full effect of road edges on biodiversity and ecosystem processes.

DISCUSSION

In this perspective, we discuss the benefits of taking a functional perspective in designing and analyzing LULC. The premise of functional analyses is to explicitly link the characteristics of geospatial data to an ecological phenomenon of interest (Riva and Nielsen 2020) and, in a future of high-resolution remote sensing data (Jetz et al.

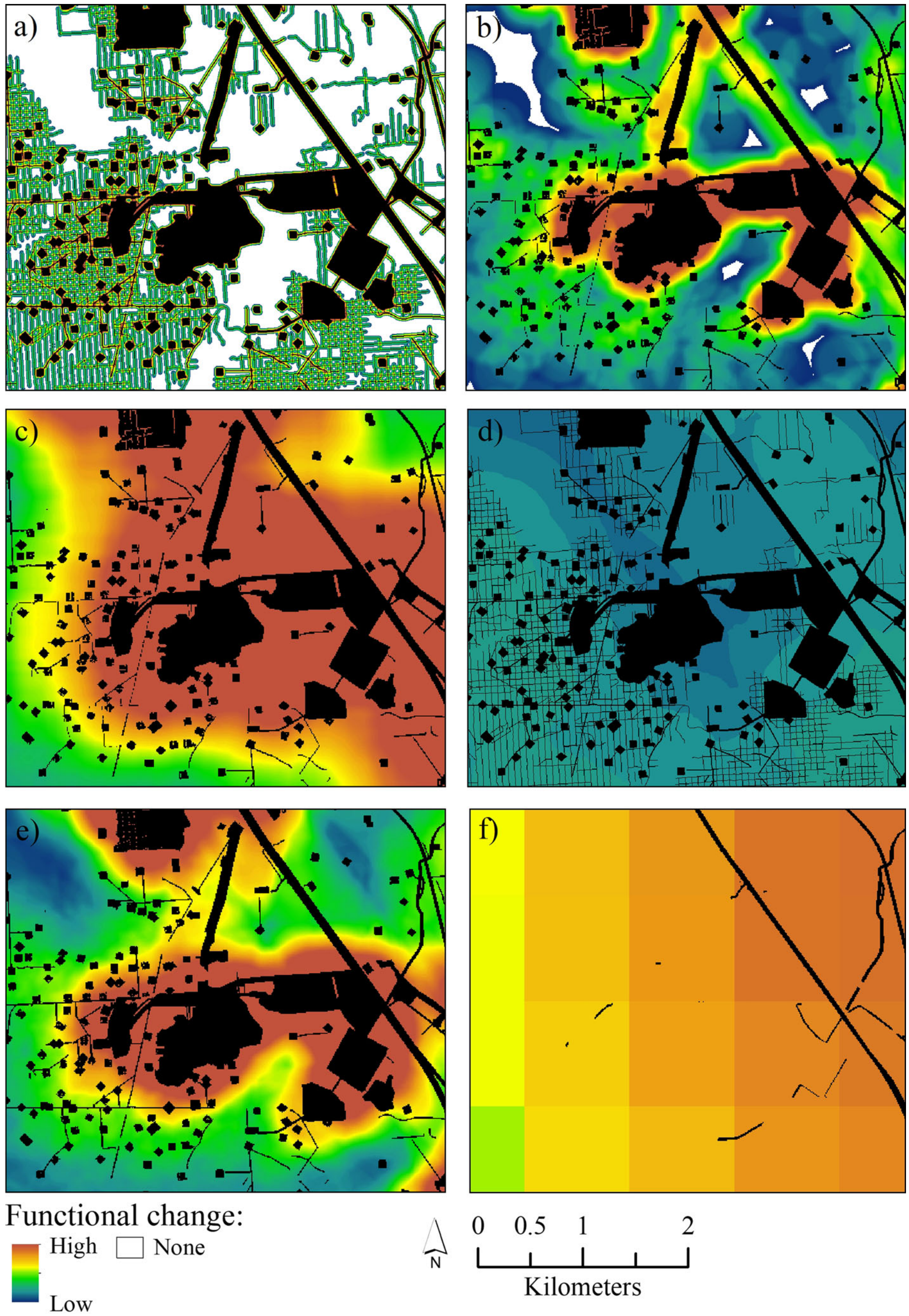

Fig. 5 Functional changes associated to anthropogenic footprints (black mask) across the same landscape in relation to six ecological processes: **a** diversity of woody plants, **b** diversity of butterflies, **c** habitat suitability for ovenbird, **d** occurrence of American marten, **e** habitat use for woodland caribou, and **f** wildfire ignition. Color surfaces indicate functional change measured as proportion of anthropogenic footprint within moving windows. Thematic resolution (i.e., which anthropogenic footprints where included in the black mask), spatial resolution (i.e., pixel size), and moving window extent were tailored to the characteristics of the different phenomena as described in Table 1 and ESM1

2019; Wickham and Riitters 2019), opportunities to conduct these assessments will be increasingly common. Therefore, a clear and explicit focus on ecological processes have high potential to enhance our understanding of changes in habitat via analyses of LULC. We demonstrated this by measuring environmental change within the Alberta boreal biome, where localized anthropogenic footprints affect many ecological processes and in different ways (Fig. 2). As one pattern of structural change often results in multiple patterns of functional changes, functional analyses can provide complementary insights to structural analyses: in our example, the functional changes associated with anthropogenic footprints vary by nearly one order of magnitude (Fig. 3) and in geographic space (Figs. 4, 5). How human activities affect the Canadian boreal biome is a case of international relevance (Fisher and Burton 2018), with ecological responses to anthropogenic footprints being relatively well known (Dabros et al. 2018), but for areas where information is scarce our results suggest that relying solely on a structural assessment may underestimate the effect of human activities on ecological processes.

Categorical or continuous models in functional analyses?

LULC are one of the most commonly used sources of geospatial information in analyses of habitat loss and change, including analyses of habitat amount (Watling et al. 2020), heterogeneity (Riva et al. 2018a), and connectivity (Tischendorf and Fahrig 2000). Yet, LULC are abstractions of continuous gradients in environmental heterogeneity, and are therefore affected by well-known limitations. For instance, LULC can be defined arbitrarily, can differ from real environmental conditions, can be ecologically irrelevant, and can lose variability within and between categories (Coops and Wulder 2019; Riva and Nielsen 2020). Furthermore, LULC may not describe accurately temporal dynamics and landscape changes (Coops and Wulder 2019). Given these limitations, it has even been argued that discrete geospatial data should be abandoned altogether, "breaking the habit" of relying on LULC (Coops and Wulder 2019).

One factor that is catalyzing a transition from use of categorical to continuous data is the increasing availability of geospatial information at high resolutions and for the entire planet. For instance, Sentinel-2 satellites provide 10-m resolution, multispectral images every 10 days since 2015, and the Global Ecosystem Dynamics Investigation (GEDI) provides information on vegetation structure at a 25-m resolution. These remote sensing products may relate to ecological processes more strongly than traditional LULC, as demonstrated by studies relating indices of vegetation structure and species richness in birds (Farwell et al. 2020) or spectral–temporal metrics and species' habitat for mammals (Oeser et al. 2020). In the light of these facts, we agree with Coops and Wulder (2019) that continuous maps can be biologically more meaningful, and have significant potential in aiding studies at the interface between ecology and remote sensing. However, it is also true that LULC remain widely used, and have the potential to remain a valuable tool in ecology.

We stress that we are not recommending using LULC in every assessment of habitat change, but rather are proposing a framework that facilitates integrating ecological theory in their analysis. Approaches to increase the ecological relevance of LULC have been common in the literature, including analyses that combine LULC and continuous data (e.g., Abdi 2013), and metrics that evaluate specific landscape properties (e.g., habitat amount and connectivity; Sadoti et al. 2017) or are designed to incorporate ecological processes (e.g., core habitat; McGarigal 2014). A functional perspective does not exclude these approaches; rather, it is a necessary precondition to ensure that they are applied in meaningful ways.

Ultimately, we believe that LULC will remain useful for both applied and basic research, but the objective of a study should dictate whether continuous or categorical surfaces (or their combination) are the most appropriate tool to address the question of interest. In some cases, LULC may be the only product available for assessing changes in habitat. For instance, defining patches can be problematic with continuous geospatial data, and some fields in ecology rely on the definition of patches as part of their framework (e.g., metapopulation ecology; Hanski 1998). Additionally, historical maps have even been digitized to compare changes in LULC across centuries (Cousins et al. 2015; Pindozzi et al. 2016), and there is a tradition of studies evaluating temporal changes in land cover (e.g., the seminal work of Curtis 1956). Yet, it is also true that we have accumulated decades of continuous spectral data (e.g., Landsat imagery since 1972) and thus the potential to describe more subtle dynamics in space and time, e.g., the physiognomy of plants (Kattenborn et al. 2020). Therefore, we stress that the focus of a study, technical limits (e.g., classification accuracy and sources of uncertainty in geospatial data), and the scales of phenomenon, sampling, and analyses should inform when LULC are adequate to address a specific question (Lechner et al. 2014; Riva and Nielsen 2020).

Enhancing the ecological rationale of the analysis of LULC

Moving forward, it is crucial that scientists and practitioners interested in geospatial analyses begin their study by critically evaluating what properties of landscapes they are interested in representing, if these properties can be meaningfully represented with LULC and/or continuous data, and whether a functional perspective is required. To facilitate this task, we provide a series of questions that will help to assess the appropriateness of LULC for a given project:

- Are the environmental gradients of interest better represented by continuous or categorical LULC data for assessments of habitat change?
  Continuous data better represent smooth gradients (e.g., canopy height), whereas categorical, LULC data better

represent abrupt environmental changes (e.g., forest vs. grassland).

- What is the scope of the study?
  Structural LULC analyses are coarse-filter, top-down assessments that focus on broad classifications of environmental gradients based solely on spectral properties, whereas functional LULC analyses provide fine-filter, bottom-up assessments that focus on species or specific ecological processes. The information provided by the two approaches are complementary and distinct.
- What is the extent of the study area?
  Structural analyses are the most reasonable approach to larger study extents (e.g., continents), because the ecological implications of changes in LULC often change across biomes. Conversely, functional analyses of LULC are appropriate at regional scales, where ecological processes can more reasonably be assumed to be stationary.
- Are geospatial data appropriate for conducting functional LULC analyses?
  LULC at resolutions coarser than the scale of phenomenon are not appropriate to conduct functional analyses. The fit of available data (e.g., resolution, minimum mappable unit, filters, and uncertainties associated with classification schemes, spatial scales, and classification errors) is crucial in determining the appropriateness of LULC for an analysis.
- Are the authors interested in testing specific hypotheses?
  Studies based on rigorous test of hypotheses (the "day science" sphere) benefit from a functional perspective, whereas studies that are inherently exploratory (the "night science" sphere) by definition do not require a functional perspective (Jacob 1988).
- Is there reliable information to the phenomenon of interest?
  When the phenomenon of interest is poorly understood, exploratory structural analyses may be the only viable approach to evaluating changes in habitat.

Increasing availability and quality of geospatial data will provide ecologists and practitioners with endless opportunities in the twenty-first century. LULC have been traditionally used to evaluate changes in habitat, and we believe that in the future there will be opportunities to use LULC in novel, exciting ways. We hope this perspective will stimulate a constructive debate around the benefits and limitations of the analysis of LULC, while inspiring future work in the use of functional analyses.

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