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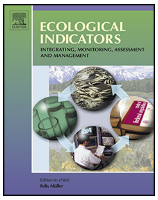

Assessing ecological integrity: A multi-scale structural and functional approach using Structural Equation Modeling

Virginia Capmourteres*, Madhur Anand

School of Environmental Sciences, University of Guelph, 50 Stone Road East, Guelph, Ontario, N1G 2W1, Canada

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ABSTRACT

Facing increasing levels of ecosystem degradation, scientists and practitioners aim to preserve ecological integrity — to maintain structures and functions expected of ecosystems in a region. This requires an understanding of the relationship between structural components and functional integrity. In this paper we focused on the study forests of the Credit River Watershed (Southern Ontario, Canada). For this ecosystem we consider one of the major contributors to functional integrity: habitat functions which are defined as the capacity of the ecosystem to provide refuge and reproduction habitat to wild species of plants and animals. We define these 'habitat functions' as a latent variable in Structural Equation Modeling, which allows us to examine its relationship with a number of candidate indicators. We first determined two community-level structural indicators to represent the latent variable: native plant cover and forest bird abundance. We then found underlying causal relationships between multi-scale structural components of the ecosystem and the provision of habitat functions. Three variables at the local scale explain native plant cover — soil nitrogen, soil organic matter, and soil pH. A significant landscape-level variable, patch area, explained native plant cover. Percent natural land cover in a 500 m radius explained forest bird abundance. From a theoretical point of view, this modeling technique allows us to explore complex and simultaneous interactions between structures and functions of ecosystems. As for its practical applications, it can be used to improve ecological integrity monitoring programs by contributing to the selection of meaningful indicators.

1. Introduction

The conversion of natural lands to agricultural and urban landscapes, and its consequent fragmentation processes, have led to habitat degradation and destruction and are main drivers of biodiversity loss (Millennium Ecosystem Assessment, 2005a,b; Barnosky et al., 2012; Jantz et al., 2015). Genetic diversity and population sizes and ranges have declined (Mooney, 2010), while extinction rates have increased 1000 times (Pimm et al., 2014). Changes in community assemblages and loss of interaction among species have been observed as well (Dornelas et al., 2014; Valiente-Banuet et al., 2015). Lack of interactions can diminish ecological processes (e.g., pollination, climate regulation, seed dispersal, pest control, erosion regulation), deriving in shortages of ecosystem services (Millennium Ecosystem Assessment, 2005b,c). Given this scenario, the integrity of our ecosystems is clearly under threat.

Integrity has been defined as "the capacity of the ecosystem to support and maintain a balanced, integrated, adaptive biological system having the full range of elements and processes expected in the natural habitat of a region" (Karr and Dudley, 1981). Integrity can be further subdivided into structural components — related to structures of the system such as organisms, resources, and physical conditions (Odum, 1962; Sutton-Grier et al., 2010) — and functional components — related to processes that move energy through the ecosystem, biogeochemical cycles, regulation processes (Odum, 1962; Kandziora et al., 2013), or ecological processes that can provide ecosystem services (De Groot et al., 2002). To monitor ecological integrity, the elucidation of the relationship and interdependence of structural components and functions — which structures are significantly involved in the provision of functions — and the selection of relevant indicators to measure these functions are essential. However, explaining structure-function relationships and selecting indicators can be challenging.

There has been extensive literature regarding the multiple criteria used in the selection of indicators, including how well they represent structure and function, how easy they are to measure, how sensitive they are to environmental stress, and how they inte-

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* Corresponding author.
E-mail address: vcapmour@uoguelph.ca (V. Capmourteres).

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grate scales and gradients (Dale and Beyeler, 2001). Additional criteria include cost-effectiveness and meaningfulness to the public and decision makers (Jones et al., 2011), applicability to distinct ecosystems, and their independence with sampling size, among others (Noss, 1990). This issue is even trickier to tackle given that ecosystems behave as complex systems. They: (a) involve several agents that interact locally and give rise to emergent patterns and behaviours; (b) are usually difficult to predict due to uncertainty and non-linear dynamics; (c) are characterized by feedbacks and hierarchical scales; (d) have a capacity for self-organization but are not always predictable; (e) are open in terms of energy, matter, information, species, people, and capital; and, (f) possess memory, meaning the past history of the system affects its present and future structure, composition, and behaviour (Hendry and McGlade, 1995; Parrott and Kok, 2000; Anand et al., 2010; Newman, 2011; Filotas et al., 2014). As of yet, indicators tend to fail in comprising the complexity of the systems, do not represent specific conservation goals, lack a defined protocol for their selection (Dale and Beyeler, 2001), and underrepresent structures and functions that are linked in a hierarchical fashion.

Recently, modeling techniques such as Structural Equation Modeling (SEM) have gained momentum to pose hypotheses on how systems work and to test ecosystem structure and function using field data (Grace and Kelley, 2006; Sutton-Grier et al., 2010). SEM has been applied to evaluate the effect of grazing on ecosystem processes (Laliberté and Tylianakis, 2012; Chen et al., 2013), the relationships between fire and edaphic factors and woody vegetation structure and composition (Diouf et al., 2012), the impacts of biological invasions in ecosystem structure and function (Eldridge et al., 2011; Hermoso et al., 2011), the sensitivity of soil respiration to environmental factors (Matías et al., 2012), the impacts of land uses on stream integrity (Riseng et al., 2011), the way wildlife tourism moves visitor's experiences (Ballantyne et al., 2011), and the factors that affect plant richness in recovering forests (Leithead et al., 2012).

In this paper we focused on habitat functions, defined as the capacity of the ecosystem to provide refuge and reproduction habitat to wild species of plants and animals (De Groot et al., 2002). Habitat functions include a refugium function — suitable living space for wild plants and animals — and nursery a function — suitable reproduction habitat. These habitat functions were defined in terms of processes that naturally occur in the system, but can provide a potential ecosystem service to humans (De Groot et al., 2002). Habitat functions are not only critical for the provision of regulation, production, and information functions, but also key in the implementation of nature protection policies (Bunce et al., 2013).

In particular, this paper had a methodological focus and aimed to answer the following questions: (a) What are the structures of the ecosystem (organisms, resources, physical conditions) that are mainly involved in the provision of habitat functions? (b) Which structural components can be used to represent the concept of habitat functions? (c) Is it possible to test hypotheses on the interdependence between structures and habitat functions and, thus, structure and functional integrity? and, (d) What structural components of the ecosystem should be preserved if the provision of habitat functions is to be ensured? For this, we applied SEM and proposed a conceptual model that represents the underlying causal relationships between structural components of the ecosystem and the provision of habitat functions in complex systems. We used forest habitats of the Credit River Watershed (CRW), in Southern Ontario, as our case study. We empirically defined the concept of habitat functions and tested potential indicators to represent them. Furthermore, we tested hypotheses about the relationship between habitat functions and multi-scale structural components. We also aimed to gain insight into the relative importance of various variables that may influence functions by partitioning covariances among variables into pathways. Finally, we discussed how this methodology could be applied to improve integrity monitoring in complex systems.

2. Methodology

2.1. Study area

The Credit River Watershed extends over 1000 km^2 of land, drained by the Credit River and its 1500 km of tributaries. It is part of the Great Lakes Basin that drains into the St. Lawrence River and eventually the Atlantic Ocean (CVC, 2012; Fig. 1). Forested ecosystems include upland (deciduous, coniferous, and mixed forests), lowland (deciduous, coniferous, and mixed swamps), and cultural forested habitats (deciduous, coniferous, and mixed plantation). Non-forested habitats encompass cultural meadows, savannahs and woodlands, non-intensive and intensive agriculture, marshes, bog/fen habitats, thicket swamps, and aquatic environments. The watershed can be divided in upper, middle, and lower sectors. The upper watershed is dominated by sugar maple forests and white cedar swamps, and agriculture has been the main land use in the area, lately changing to rural estate development. The middle watershed includes the Niagara Escarpment and is dominated by a mixture of deciduous stands in upland areas and coniferous swamps in lowland areas. The lower section of the watershed is highly urbanized, with over 80% of the total 750,000 residents of the watershed living there (CVC 2009, 2011). Broadly, natural areas are dominant in the middle watershed (35%), agricultural lands are the main use in the upper sector (35%), and urban sprawl is the dominant land cover in the south region of the watershed (30%).

2.2. Structural Equation Modeling

SEM is related to statistical analysis such as regression, principal components analysis, and path analysis. In SEM, an *a priori* theoretical model is contrasted against data. This model can include observed variables and theoretical constructs for which we do not have direct measurements (Pugesek and von Eye, 2003; Grace et al., 2010). The model is expressed in terms of structural equations, which represent statistical dependencies or associations between the variables. In order to infer causation, theoretical knowledge is needed to propose causal links in the conceptual model and to interpret results. Causality here is defined as "Y is a cause of Z if we can change Z by manipulating Y" (Grace, 2006). After equations are proposed, an expected covariance matrix is generated (based on the specified model) and compared to the observed covariance matrix (based on real data). A model fit test is then used to establish whether the difference between matrices is significant or not (Grace et al., 2010; Bizzi et al., 2013). SEM tests not only the general model fit, but also all individual pathways proposed in the conceptual model. SEM allows for both confirmatory and exploratory modeling, and thus is suited to theory testing and development (Bizzi et al., 2013).

We first proposed a Structural Equation Metamodel as a generalization of the modeling problem. Habitat functions was depicted as a latent variable, a complex and multi-dimensional construct that has no direct measure, as it represents the capacity of the ecosystem to provide refuge and reproduction habitat to wild species of plants and animals (De Groot et al., 2002). Given that habitat functions are related to the maintenance of biodiversity, we proposed these functions could be represented through biotic variables at the community scale. Furthermore, we hypothesized that these ecological communities can be affected both by abiotic variables at local (e.g., soil nutrients, soil physico-chemical properties) and landscape lev-