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Species indicators of ecosystem recovery after reducing large herbivore density: Comparing taxa and testing species combinations

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Indicator species have been used successfully for estimating ecosystem integrity, but comparative studies for defining optimal taxonomic group remain scarce. Furthermore, species combinations may constitute more integrative tools than single species indicators, but case studies are needed to test their efficiency. We used Indicator Species Analysis, which statistically determines the association of species to one or several groups of sites, to obtain indicators of ecosystem recovery after various deer density reductions. We used five taxonomic groups: plants, carabid beetles, bees, moths and songbirds. To test whether species combinations could complement single indicator species, we used plants as a model taxon and examined the indicator value of joint occurrence of two or three plant species. Our study relies on experimental controlled browsing enclosures established for six years on Anticosti Island (Quebec). Four levels of deer density (0, 7.5 and 15 deer km^{-2} and natural densities between 27 and 56 deer km^{-2}) were studied in two vegetation cover types (uncut forests and cut-over areas), in a full factorial design for a total of eight experimental treatments. For all taxa but bees, we tested 54 treatment groups consisting in one specific density or in a sequence of two or more consecutive deer densities in one or both cover types (ten groups for bees, sampled only in cut-over areas). We found 12 plants, 11 moths and one songbird to be single species indicators of ecosystem conditions obtained under 12 different treatment groups. Six treatment groups were indicated by plants and six different ones by moths, of which one group was also identified by a songbird species. Moths were thus worth the extra sampling effort, especially since the groups they indicated were more treatment-specific (mainly one or two deer density treatments). We tested the same 54 treatment groups for plant species combinations represented by two or three co-occurring species. Plant combinations efficiently complemented plant singletons for detecting ecosystem conditions obtained under various deer densities. In fact, although singletons were highly predictive, 17 additional treatment groups were identified exclusively with two- and three-species combinations, some being more treatment-specific. Our findings show that plants and moths provide complementary indicators of ecosystem conditions under various deer densities, and that computing species combinations increases our capacity to monitor ecosystem recovery after reducing herbivore densities.

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1. Introduction

Overabundant populations of large herbivores represent a threat to ecosystem integrity since they may overexploit their habitat to the point of compromising plant regeneration and the maintenance of associated fauna (Côté et al., 2004). Under certain conditions, large herbivore populations can be controlled by hunting to meet specific management goals (Conover, 2001; Lebel et al., 2012) such as reducing ungulate-human conflict (Gill, 1992) or maintaining/restoring biological diversity (Gaultier et al., 2008). To manage large herbivore populations efficiently, reliable estimates of their density are required (Morellet et al., 2007). Most estimates of herbivore density rely on direct or indirect information on the animal population itself, as for example the kilometric index (Maillard et al., 2001), pellet counts (Marques et al., 2001), harvest data or aerial counts (Pettorelli et al., 2007). Other indices focus on the browsing pressure on selected plants of the ecosystem (Anderson, 1994; Koh et al., 2010).

These indices are adapted to regional management of large herbivore populations and are implemented over several hundreds of km^2. However, to determine if we meet management goals, we also need to survey ecosystem recovery after implementing any management plan of large herbivore population. It is impossible to measure all ecosystem processes or the full array of species, but the identification of indicator species that could be tracked in long-term monitoring sites would be useful to determine whether ecosystem recovery is successful (Carignan and Villard, 2002). Because they focus on the impact of browsers on ecosystem integrity and have low application costs, such indicator species have high potential for monitoring and comparing sustainability of various management plans.

Indicator species have been used successfully in applied ecology for evaluating ecosystem integrity (Brooks et al., 1998; Laroche et al., 2012) or estimating ecosystem responses to disturbances like fire (Moretti et al., 2010). However, such approach has never been used to monitor ecosystem recovery after reducing large herbivore density in strongly overbrowsed ecosystems. From a management point of view, indicator species must be easy to identify and measure, sensitive to disturbances, respond to disturbances in a predictable manner, and have a narrow and constant ecological niche (Carignan and Villard, 2002; Dale and Beyeler, 2001; Reza and Abdullah, 2011). Most studies adopting the indicator species approach have focused on a single species or higher taxonomic group (e.g., Laroche et al., 2012) even though it has been established that considering multiple taxonomic groups is likely to capture the complex responses of an ecosystem to disturbances or management practices more precisely (Carignan and Villard, 2002; Reza and Abdullah, 2011; Sattler et al., 2010). While multi-taxa surveys may be costly, the choice of the appropriate taxonomic group or species to monitor must be based on sound comparative studies, which remain surprisingly scarce in the literature (Kotze and Samways, 1999; Rooney and Bayley, 2012).

Indicator Species Analysis (ISA) is being applied increasingly in population management (e.g., Pöyry et al., 2005; Rainio and Niemelä, 2003). Recently, methods for this type of analysis have been improved in two complementary ways. First, indicator species can now be identified for groups of sites (De Cáceres et al., 2010), an approach more adapted to an experimental design with multiple treatments. In the context of reducing herbivore population density, this allows a given species to serve as an indicator of ecosystem recovery along a range of herbivore densities. Second, De Cáceres et al. (2012) recently developed a method that considers species combinations, and demonstrated that the *joint* occurrences of two or more species can have a higher predictive value than data on two species evaluated independently, but not strongly correlated. While these two methodological innovations have substantially increased the potential of indicator species analyses, case studies that test the benefits of applying them in particular contexts are still lacking. Consequently, the objectives of this study are (a) to assess the complementary value of plants, insects and songbirds as potential indicator species for monitoring ecosystem recovery after reducing deer densities and (b) to verify, using plants as a model taxon, whether species combinations can be more efficient indicators of ecosystem recovery than single species. Due to their low mobility, plants generally have site-specific requirements (soil, topography, etc.) and are more subject to browsing pressure from herbivores than other guilds. For this reason, we hypothesize that plant species will provide more and better indicators of ecosystem recovery than insects and birds. We also hypothesize that, within insects, bees and moths will be better indicators than carabid beetles since they are strongly associated with plants due to specific habitat or dietary requirements. Finally, species combinations should complement the single species approach for indicating particular ecosystem recovery resulting from specific reductions of deer density or from a range of deer densities.

2. Materials and methods

2.1. Study area

Our study was carried out on Anticosti Island (7943 km^2) in the Gulf of St. Lawrence (Quebec, Canada; 49° 28′ N and 63° 00′ W). Climate is maritime and characterized by cool summers and long but relatively mild winters (for more details on climate see Beguin et al., 2009). In 1896–97, approximately 220 white-tailed deer were introduced on this island, which is located at ca. 70 km north of the north-eastern limit of the species' distribution range. Theoretical model suggests that the deer population has increased rapidly, reaching a peak about 30 years after its establishment and then gradually stabilized at its current level (Potvin et al., 2003), which is estimated at >20 deer km^{-2}. Population fluctuations are mostly related to winter severity (Potvin and Breton, 2005) as the island is presently void of predator. The indigenous black bear (*Ursus americanus*) was abundant on the island at the introduction time, but rapidly became rare (1950s) and then extinct (1998) likely due to the disappearance of wild berries due to deer overbrowsing (Côté, 2005). Ecological conditions of Anticosti Island have not been as favorable for other introduced large herbivores that have disappeared (bison, wapiti, caribou) or remained at low density, like moose (*Alces alces*; 0.04 moose km^{-2}; Beaupré et al., 2004).

The forests of Anticosti belong to the boreal zone. They are naturally dominated by *Abies balsamea*, *Picea glauca* and *P. mariana*, while deciduous tree species (*Betula papyrifera*, *Populus tremuloides*, *P. balsamifera*) occur sporadically. Despite the short history of deer herbivory on the island, the impacts of deer browsing on the structure, composition and dynamics of forest ecosystems have been extensive (Potvin et al., 2003; Tremblay et al., 2006). For instance, the surface covered by *A. balsamea* stands, a key habitat for winter survival of deer, has been reduced by half over the last century and replaced by *P. glauca* stands (Potvin et al., 2003; Tremblay et al., 2007). Furthermore, the shrub layer has been almost entirely eliminated and the most palatable ubiquitous woody plant species such as *Acer spicatum*, *Cornus sericea* subsp. *sericea*, *Corylus cornuta*, and *Taxus canadensis*, have almost been extirpated (Pimlott, 1963; Potvin et al., 2003). A recent study also showed that the community composition of bees and moths, two groups of insects strongly associated with vegetation, has been modified by deer overabundance, while the abundance and community composition of carabid beetles, most of which have no direct trophic relations with plants, do not vary with deer density (Brousseau et al., 2013). Deer over-browsing on the island has also changed the community