Use of Indicator Species to Assess Forest Continuity: a Critique

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Introduction

Conservation biologists often must apply novel approaches to address critical issues before they have been thoroughly validated by scientific studies. One technique of particular interest is the use of indicator species as a shortcut to assess ecological conditions or species assemblages too difficult to measure directly (e.g., Landres et al. 1988; McGeoch 1998; Caro & O'Doherty 1999). It is necessary to acknowledge the inherent complexity of natural ecosystems and the need for reliable indicators or surrogate measures.

Whereas the spatial aspects of forest fragmentation have received much attention, less focus has been put on the temporal dimension, on what has been called forest continuity, or the uninterrupted, site-specific presence in time of a forest stand or components thereof (Nilsson et al. 1995). Concern has risen that many forest-dwelling organisms are strongly dependent on continuously present forest stands or structural components, partly because these organisms are poor dispersers and therefore unable to recolonize secondary stands that emerge after logging (Duffy & Meier 1992). Thus, a break in continuity is the temporal counterpart of fragmentation in space. If assemblages of forest organisms are not replaceable within reasonable time, it has been suggested that forest continuity should be the prime criterion for the selection of forest reserves (Nilsson et al. 1995). During the last decade, it has been proposed that indicator species be used to identify forest stands with long-term continuity of structural components, especially old-growth or old-growth-resembling stands (e.g., Tibell 1992; Økland 1996; Selva 1996; Bredesen et al. 1997; Lindblad 1998). Recently, the indicator-species concept has been applied in forest survey programs, mostly in northern Europe, but also in North America (Kirby et al. 1998; Marcot et al. 1998; Hansson 2001).

Despite criticisms of the concept, indicator species continue to be used within many fields of conservation biology. The purpose of our comment is to take a critical look at the use of indicator species to assess the temporal continuity of forest stands and stand structures. (A similar critique has recently been put forward by Nordén & Appelqvist 2001). First, we briefly review the origin and use of the term continuity, pinpointing difficulties in defining it consistently. Second, we discuss the appropriateness of species as indicators of temporal continuity, questioning their indicative precision. Finally, we propose retrospective studies (e.g., dendro- and paleoecology) to improve the reliability of methods for discerning components of forest continuity, thereby aiding in identifying dispersal-limited species that subsequently may be screened for possible indicator values. Although we focus on temperate forest ecosystems in general, and old-growth stands in particular, the issue may be relevant to other ecosystems as well.

We define indicator species, following Landres et al. (1988) and McGeoch (1998), as organisms whose presence is used to mirror environmental conditions or biological phenomena too difficult, inconvenient, or expensive to measure directly. According to Lindenmayer et al. (2000), indicator species of forest continuity most appropriately fall into the category that indicates environmental conditions (category 5), as opposed to those that indicate co-occurring species assemblages, or biological diversity. Ideally, indicator species should meet the following criteria: They should be sensitive to changes in the real phenomena of interest and should be used only when direct measurement is impossible or infeasible. In addition, their biology should be fairly well known, and they should be spatially and temporally predictable. If not otherwise stated, we use *continuity* in a temporal context to describe the continuous presence of forest

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stands (0.1–10 ha) or forest-stand structures (e.g., snags, logs, and closed canopy) through time.

The Concept of Forest Continuity

The term *continuity*, as applied in conservation biology, originated in Britain in the early 1970s. Studying deciduous woodlands, Peterken (1974) and Rose (1974) suggested that the occurrences of certain vascular plants and epiphytic lichens could distinguish ancient woods (defined as being continuously wooded since 1600 A.D.) from more recent woods. The list of indicator taxa has been expanded to include invertebrates, bryophytes, and fungi (Edwards 1986; Nilsson et al. 1995; Bredesen et al. 1997). The apparent success of the indicator-species concept in identifying woodlands with a long continuity of tree cover in Britain has led other biologists to adopt the indicator-species methods. During the last decade, *ancient forest* (Whitney & Foster 1988; Selva 1996; Honnay et al. 1998), *antique forest* (Goward 1994), and *continuity forest* (Røsok 1998) have been used synonymously in North America and northern Europe to label old-growth stands that presumably have escaped large-scale disturbances for long time periods.

According to Rose (1976) and Selva (1996), the basic idea behind the method is to use selected species as evidence that a forest "that looks old really is old." Thus, indicator species of forest continuity are supposed to distinguish apparently similarly structured stands that differ in forest history. But if continuity is to be judged more precisely than as a general aspect of temporal processes, three parameters should be explicitly dealt with: (1) ecological factors, (2) spatial scale, and (3) temporal scale.

First, forest ecosystems are complex, and there is a need to address ecological factors, such as coarse woody debris, closed tree canopy, and microclimatic conditions, on which the indicator species depend and that consequently can serve as a substitute surrogate measure (Karström 1992; Nilsson et al. 2001). For example, clearcut logging breaks the canopy continuity and wipes out the epiphytic lichen flora, whereas wood-dwelling fungi and beetles may survive on the remaining dead wood. Epiphytic lichens and saproxylic beetles may survive on remnant trees despite frequent disturbances of the field layer by livestock grazing (Nilsson et al. 1995).

Old-growth stands are characterized by small-scale disturbances such as windthrows and death of canopy dominants (gap-phase dynamics). Coarse woody debris and snags may be continuously present on 1 ha, albeit highly dynamic at the scale of 100 m^2. At the scale of a single tree, a wood-dwelling fungus or insect is dependent on a disturbance event that creates dead wood. At the scale of a forest stand, the same organisms may depend on a moist microclimate maintained by the absence of stand-replacing disturbances such as fire. Thus, continuity has to be related to spatial scale. Although any scale, in principle, could be used as reference, it has often been applied to ecological conditions at the scale of forest stands 0.1–10 ha in size (Nilsson et al. 1995; Kuusinen 1996; Bredesen et al. 1997; Ohlson et al. 1997; Lindblad 1998).

Finally, the time scale should be considered. Although this is what the indicator species are supposed to indicate, the scale may vary tremendously. For example, is the question whether a British woodland has been continuously wooded since the last glaciation more than 10,000 years ago (Day 1993; Peterken 1993), or is it whether a boreal forest stand has had a closed canopy for more than 100 years (Goward 1994; Bredesen et al. 1997). To summarize, as with the term *fragmentation*, the term *continuity* is practically useful only when a specified ecological feature or condition is defined within an explicitly spatiotemporal context. Many researchers fail to recognize this and use the term in a general sense as it applies to forest stands with no or slight human impact based on visual appearance (e.g., Kuusinen 1996).

Use of Indicator Species

According to the selection criteria we have listed, indicator species should be spatially and temporally predictable and easier to recognize than the phenomena of interest. Ideally, one would browse a checklist of indicator species and taxa, each having a score according to their indicator precision, and translate it to time since break of continuity.

Many researchers do not explicitly define the ecological factor with which they are dealing. Kuusinen (1996) used cyanobacterial macrolichens on aspen (*Populus tremula*) as indicators of forest continuity in Finland. One of his best indicator candidates was *Lobaria pulmonaria*, a species now known to survive on single remnant aspen trees on clearcuts (Hazell & Gustafsson 1999). Ambiguous use of indicator species can be seen in official field guides of Nordic countries (e.g., The Swedish National Board of Forestry). For example *Phellinus nigrolimitatus* (a saproxylix fungi) is listed as a good indicator species of old forests with dead-wood continuity. When the species is found on dead wood in managed young forests, its indicator value is said to be lower (Nitare 2000).

To successfully identify structurally diverse old-growth forests, it appears that one needs a whole suite of indicator species, each applying to different ecological features. Honnay et al. (1998) needed 25–27 plant species to discriminate, with 75% certainty, between deciduous old-growth stands with long (prior to 1775 A.D.) and short continuity in tree cover. Much effort has been devoted to constructing lists of indicator species to be used in calculating various indices of forest continuity (Peterken 1974; Rose 1976; Tibell 1992; Nilsson et al. 1995; Selva 1996). A weakness of species lists, however, is that they tend to apply only to local regions (Peterken 1993) (i.e., they are scale dependent [Watt 1998; Hamer & Hill 2000]).

Studying vascular plants in Britain, Gibson (1988) wrote: "Most individual species were 'indicators' only in the sense that they were commoner in ancient woodland than outside it." When secondary stands adjacent to ancient ones harbor many of the same indicator species (Whitney & Foster 1988), their spatial precision is diminished. For most ecological factors one can find a spatial scale at which they become continuously present. Fritz and Larsson (1997), for example, described fire continuity as frequently occurring forest fires within a larger landscape context. Unfortunately, as the spatial scale is increased the predictive power of the indicator species is gradually eroded. The spatial precision of indicator species depends on their dispersal ability: the more restricted their dispersal ability, the better they indicate continuity (Nilsson & Baranowski 1997; Nilsson et al. 2001; Nordén & Appelqvist 2001).

Few studies have critically compared the use of indicator species with historical data. Ohlson et al. (1997) studied epiphytic lichens and saproxylic fungi that were supposed to indicate old-growth spruce forests (1–6 ha) with long stand continuity. Paleoecological records indicated no relationship between the occurrence of 33 indicator species and the actual time since fire (300–2000 years). Unexpectedly, the tendency was that the stands most affected by earlier natural or human-caused fires harbored more indicator species than stands less affected by fire disturbance. The most important indicator of the presence of the indicator species was the amount of coarse woody debris originating from gap-phase dynamics during the previous 100 years. They concluded that a more critical and careful use of the concept of forest continuity is needed.

In our opinion, indicator species of forest continuity fail to fulfill all the criteria of a suitable indicator. In most cases the dispersal ability of the species is based on intuition and the forest history is based on anecdote. The continuity concept is based on correlative assumptions and has become established without knowledge of the causal relationships. There is a remarkable lack of clear definition, goal directedness, and hypothesis testing in studies in the field (e.g., Tibell 1992; Kuusinen 1996; Økland 1996; Selva 1996; Bredesen et al. 1997; Lindblad 1998). To echo Spencer (1991), "At worst [the indicator species approach] can lead to a risk of falling into the pitfall of circular logic: those woods that contain 'ancient woodland indicators' are by definition ancient woodland." This brings us to our final critical question: are we looking for forests that have been around for a while, or are we looking for species that do not move around easily?

Retrospective Studies

At present, indicator species can only hint at the likely history of a forest stand. Thus, to identify old-growth forests with the long-term continuity of structural components, we argue that stand structures themselves (structure-based indicators, sensu Lindenmayer et al. 2000) provide more reliable evidence than indicator species (see also Spies & Franklin 1988; Whitbread 1990; Watt 1998). If long time scales are at work, dendroecological techniques (using tree rings; Storaunet et al. 2000; Groven et al. 2002; Rolstad et al. 2001) and paleoecological techniques (e.g., using pollen and charcoal in soil layers; Day 1993; Segerström et al. 1996; Ohlson et al. 1997) would be useful. Good reviews of these methods are provided by Fritts & Swetnam (1989), Foster et al. (1996), and Swetnam et al. (1999).

Ultimately, the goal is to conserve biodiversity associated with old-growth forests, both the species that depend on structural components per se and those that are hampered by poor dispersal ability. In conservation practice this distinction is important. Species that are limited by stand structures alone should be expected to colonize secondary stands, and therefore should be able to persist in managed forest landscapes allowing old-growth structures to develop and be restored. Strictly dispersal-limited species, in contrast, strongly depend on the presence of appropriate stands (or stand structures) continuously over long time periods (for a discussion of possible dispersal-limited taxa, see Nordén and Appelqvist (2001). Care should be taken to preserve these stands within a matrix of favorably managed forests aimed at enhancing the dispersal of these species.

Thus, in questioning the scientific validity and necessity of species that indicate continuity, we do not want to throw the species approach overboard. Many species associated with old growth are rare and highly threatened. But hitherto their presence or absence has often been seen as calling for an explanation based on history (how long they have been present) rather than ecology (whether or not they are dispersal-limited). Herein lies the crux of our critique. Instead of using presumably slow-dispersing species to indicate the likely history of a forest stand, we should use forest stands of known history to help us understand the dispersal ecology of their threatened inhabitants (Bratton 1994; Matlack 1994).

We have argued that the most appropriate first step is to use structure-based indicators and dendro- and paleoecological methods to discern how long forest stands or structures have been continuously present. The second step involves species inventories to test for possible nested patterns that might reveal dispersal-limited candidates, species that repeatedly occur in the oldest stands only, despite suitable habitats being present in younger stands. The conclusive step would be to test their dispersal ability in controlled experiments (Hazell & Gustafsson 1999; Sillett et al. 2000). This way, true dispersal-limited species might be identified and their dispersal capacity determined, so they can subsequently serve as a guide to preserving suitable forest stands spatially arranged to promote the dispersal of the species.

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