



Conceptual problems of Ecological Continuity and its bioindicators

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Abstract. Very old, undisturbed forest stands may be important for biodiversity through their content of microhabitats or for the long periods available for colonisation, or for both. The term Ecological Continuity (EC) has been used to ascribe value to old forest stands. The relative importance of microhabitat and time for colonisation are usually not kept apart when EC is used as a conservation criterium. EC is broadly applied but poorly defined. Use of EC may lead to underestimation of the importance of forest dynamics and dispersal, and to overestimation of the importance of local land use history. If bioindicators of long-term habitat persistence are to be used, species with low dispersal capacity should be chosen. However, many lichens and other fungi, bryophytes and insects cited as indicators of EC, seem to have a patch-tracking lifestyle. They are 'colonists' according to life history strategy classification, and rather seem to indicate specific microhabitats. Terrestrial molluscs, some vascular forest plants, and those bryophytes and lichenized fungi classified as 'perennial stayers' in life history strategy classification, might be used to indicate long-term habitat persistence in forests, but more research is needed to evaluate such indicators.

Key words: bioindicators, dispersal capacity, Ecological Continuity, habitat persistence, lichenized fungi

Introduction

In community ecology and conservation biology, the earlier common assumption of 'balance of nature' has largely been replaced by a 'disturbance paradigm', in which patch dynamics is emphasized over equilibrium conditions (Wu and Loucks 1995). Although natural disturbance regimes should be valuable for biodiversity, many authors emphasize that forest age, and tree age are good indications of biodiversity values (Peterken 1996). Various forms of disturbance strongly influence forest ecosystems, but some forest types such as certain deciduous types, may become very old without being markedly affected by disturbance (Runkle 1985). Here we address the following questions which we think are essential in conservation biology and forestry:

- (1) Is an old natural forest stand, in which several tree-generations have lived, more or less important to biodiversity than a first-generation, but structurally similar, forest stand?
- (2) If a long history per se is important, how should such old and valuable forest sites be identified in the absence of archival data or old maps? Could indicator species be used?

(3) Which species are dependent on very old, undisturbed forest stands?

We consider these questions in the light of the dispersal capacity and life-history strategies of several forest species, especially lichens and other fungi, bryophytes, invertebrates and vascular plants. We discuss the concept of Ecological Continuity (EC), widely used to ascribe value to old forest stands, and the use of bioindicators of EC. The problems and proper use of indicator species have been discussed by several authors (Landres et al. 1988; Ehrlich 1996; Faith and Walker 1996a,b; Cranston and Trueman 1997; De Leo and Levin 1997; Flather et al. 1997; Prendergast and Eversham 1997; Caro and O'Doherty 1998; Jonsson and Jonsell 1999). We criticise the current use of indicators of EC and give some guidelines on how indicators of long habitat persistence could be used.

A forest stand is here used for a collection of trees present within a certain area with the size of about 1–30 ha. A habitat, such as a forest stand, may contain several microhabitats. Examples of relevant microhabitats are old snags, logs, and the rough bark of old trees. 'Microhabitat formation' is discussed in the caption of Figure 1.

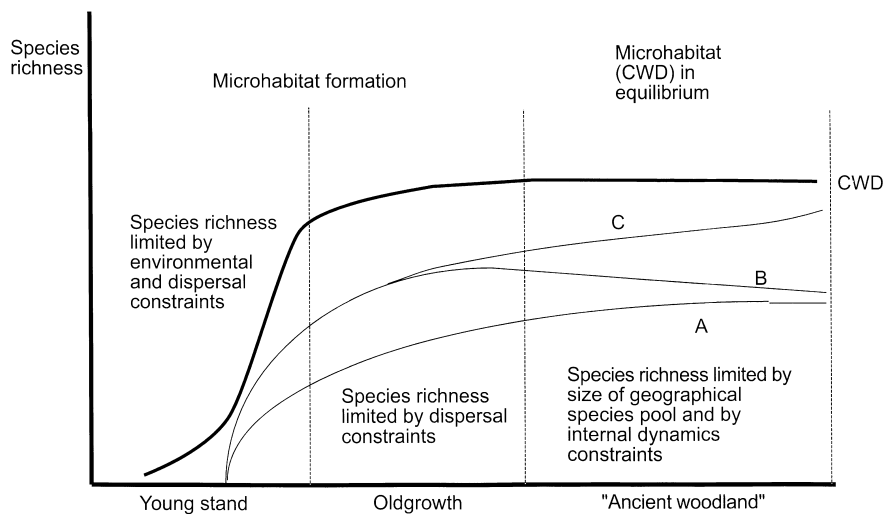


Figure 1. Tentative development of species richness of saproxylic biota dependent on Coarse Woody Debris (CWD) in a forest stand after initial colonisation of tree-less ground. Large amounts of dead wood is characteristic of old-growth forests (Kirby et al. 1991). Microhabitat formation here means the time needed to create 'equilibrium levels', at which input rate and decay rate of Coarse Woody Debris (CWD, bold line) are in balance in the stand. Several alternative scenarios are possible. (A) Possible scenario in which the geographical species pool is severely constrained by isolation or other factors, and the forest stand will have relatively few species. (B) Alternative scenario in a forest stand that is not isolated, but where diversity decreases in late succession due to competition, and local extinction (see text). (C) Scenario according to the EC-doctrine, where biodiversity is expected to increase slowly, but for a very long period. This scenario implies a very large geographical species pool. Note that this figure does not take forest succession or stochastic large-scale disturbance into account. The terminology follows Belyea and Lancaster (1999), see text.

Continuity and its indicators

The term Ecological Continuity (EC) is often applied to old-growth forests, or natural woodland. Alternative terms include ‘environmental continuity’ and ‘forest continuity’. Since the term EC was introduced by Rose (1974) it has been increasingly used to define areas with high protection value. Ecological continuity has many different connotations in the literature. The term has been used in connection with different spatial scales. The most commonly applied version is ‘stand continuity’ (or local continuity) and the second most common is ‘landscape continuity’ (or biological continuity) (Økland et al. 1996; Fritz and Larsson 1996; Ohlson and Tryterud 1999). ‘Stand continuity’ means that a forest stand has existed at a particular place for a long time. ‘Landscape continuity’ means that such habitat has been available in patches for a long time within the limits of a landscape, in which the juxtaposition of habitat patches is important for dispersal and metapopulation dynamics of species. The spatial scale of ‘landscape continuity’ is usually undefined and may be different for different organisms. Different time scales have been applied to different forest types. According to Gauslaa and Solhaug (1996), 200 years is sufficient for the establishment of lichenized fungi in forests, given the availability of vital source populations. EC is said by Hörnberg et al. (1998) to occur after 300 years in coniferous forests. In nemoral forests, periods of up to 1000 years have been proposed to be important (Nilsson and Baranowski 1994). Gauslaa and Ohlson (1997) discussed three spatio-temporal dimensions of EC in Norway: one European-Pleistocene, one Scandinavian-Holocene and a considerably shorter one, pertaining to forestry practices. Many forest organisms are assumed to be dependent on EC (Engelmark and Hytteborn 1999). Examples are wood-decay fungi (Karström 1993; Bredesen et al. 1997; Esseen et al. 1997), insects (Martin 1989; Økland 1994; Nilsson et al. 1995; Esseen et al. 1997; Jonsell and Nordlander 1999), lichenized fungi (Rose 1974, 1976, 1985, 1992; Seaward 1988; Tibell 1992; Goward 1994; Selva 1994, 1996; Anonby 1994; Kuusinen 1995; Arup et al. 1997; Esseen et al. 1997; Thor 1998), bryophytes (Söderström 1988; Hallingbäck and Weibull 1996), and vascular plants (Brunet 1993, 1994; Wulf 1997; Brunet and van Oheimb 1998; Lawesson et al. 1998; Diekmann 1999). Many indicator species are used in conservation evaluation and monitoring activities (Olsson 1993; Aronsson et al. 1995; Schwartz 1999), several of which are regarded as indicators of EC (Nilsson et al. 1995, and references therein).

The restriction of many valuable or rare species to old-growth forest fragments (Berg et al. 1994) has been explained by one or both of the following statements in the ‘EC-literature’: (1) Forest stands with long EC contain certain microhabitats, i.e. old-growth components, not found in younger forests (Rose 1974, 1976; Arvidsson et al. 1988; Nilsson et al. 1995), and (2) Organisms need a certain, prolonged time for colonisation by dispersal (Rose 1974, 1976; Arvidsson et al. 1988; Nilsson et al. 1995). The ‘dispersal theory of EC’ was elaborated by Goward (1994): “Diversity appears to be positively correlated with forest age or, more precisely, with environ-

mental continuity. In support of this, it is observed that successful long-distance dispersal by old-growth-dependent lichens occurs only rarely; older forests with long EC can therefore be expected to support a fuller complement of such species than younger forests with long EC." However, this process of accumulation may only continue until balanced by density-dependent mechanisms and local extinction (Figure 1).

Problems in studies dealing with the continuity concept

Below we list some examples of classes of problems pertinent in studies of forest continuity.

1. Differences in species richness and composition due to different forest histories can only be examined for areas in which similar microhabitats exist. In many studies, the microhabitats are not qualitatively identical in old and young forests. The observed differences in species composition may therefore not be a function of time directly, but of the lack in the young forest of some microhabitat which takes a long time to establish, for instance large hollow trees or big logs. It can also take a long time for soil chemistry in forests to return to normal after a period of field cultivation (Bossuyt et al. 1999; Honnay et al. 1999).

2. The structure and hence the microclimate may be different in old and young forests and species may thus be restricted by ecophysiological factors. For instance, Gauslaa and Solhaug (1996) found that differences in the susceptibility to light stress caused differences between the epiphytic community of lichenized fungi of ancient and young boreal forest stands.

3. Qualitatively identical microhabitats may exist in the compared forest stands, but in different proportions. For instance, a lower number of old trees in one type of stand may lead to greater extinction risk for epiphytic species or invertebrates.

4. Alternative microhabitats may be more overlooked in some forests. For instance, forests that are situated in hilly terrain may be wrongly regarded as ancient because they contain certain indicator species. However, these may have merely survived on cliffs or boulders when surrounding trees were felled (Willis 1993).

5. Old forests may be situated in a less fragmented landscape than young forests and therefore the differences in species composition may be a function of area and separation distance (Helliwell 1976; Connor and McCoy 1979; Ås et al. 1992), rather than of time.

6. Certain theoretical limitations to ongoing species richness increase with age of forest stands have been neglected. Belyea and Lancaster (1999) proposed that the actual species pool in an area, e.g. a forest stand, is limited by three types of constraints, viz. dispersal constraints, environmental constraints and internal dynamics constraints. It is the influence of the latter two that has often been neglected in the EC-literature (Figure 1). Species which have the ability to disperse to a stand and could potentially establish there (the geographical species pool), also need to be able

to exist in the range of microhabitats present in the forest stand. Colonisation can not take place in a forest stand if suitable microhabitat is not present (Grashof-Bokdam and Geertsema 1998). A certain time is needed for formation of microhabitats, e.g. coarse woody debris, but if this is neglected the absence of some species may instead be ascribed to low-dispersal capacity. Arriving species also need to be able to endure the internal dynamics (competition) of the community to establish and survive for a longer period. It is quite plausible that competition may increase with time and act to decrease total species richness and the number of red data species in the absence of disturbance (Figure 1). For example, 'EC-dependent' lichenized fungi have been observed to decrease in number in the oldest *Fagus*-forests (Arup et al. 1997), and the number of wood-decay fungi is negatively correlated with stand age in stands of hazel *Corylus avellana* in SE Sweden and (B. Nordén and H. Paltto, unpublished observations).

Some detailed examples from the literature

Rose (1974) produced an Index of Ecological Continuity (IEC), based on occurrence of lichenized fungi in different old-growth forests. Few data were given on the size of stands, surrounding landscape, forest structure, climate and sampling technique. Two non-equivalent groups of stands with different histories containing old oak trees, were compared. The first group had been clear-felled in the middle ages, but not the second. The first had a mean IEC of 30 whereas the second rated 57 (not tested). A third group of stands with trees less than 200 years old all had considerably lower mean IEC. It is important to note that oaks may survive considerably more than 200 years and probably had so in the first two groups of stands. The young and the old stands are therefore hardly comparable in terms of presence of suitable microhabitats. The IEC was changed by Rose (1976) to a 'Revised Index of Ecological Continuity' (RIEC) and more recently (Rose 1992) to a 'New Index of Ecological Continuity' (NIEC) – each change representing more refinements in the light of new knowledge.

Tibell (1992) compared the number of crustose lichenized fungi in 15 coniferous forests in Sweden. The stands in which sampling was made were of different size, and had different tree composition and structure. The aim was to find species indicative of EC, which was equated with the age of the oldest 5% of spruce trees in each area. The term EC could in this instance have been replaced by age, since no data were collected on forest history. Four classes were compared. Some species only occurred in the oldest stands, but since the two oldest stands were situated farthest to the north, some of the differences may be due to differences in climate or air pollution. It seems likely that there were systematic differences in the types and amounts of microhabitats between stands of different age and locality.

Kuusinen (1995) studied the occurrence of cyanobacterial lichenized fungi on trembling aspen *Populus tremula* in Finland and found a higher number of species

in old-growth forests than in managed stands. Differences in microhabitat, size, fragmentation or isolation may be responsible for this pattern and no role of absence of disturbance for long periods was unambiguously shown. Many lichenized fungi are dependent on old trees (Uliczka and Angelstam 1999), but it remains to be shown that many generations of this substratum in the same area are required for the occurrence of certain species.

Gustafsson et al. (1992) suggested that forest continuity was an important factor for occurrences of bryophyte species in Swedish broad-leaved forests, even more important than high mean age of the present tree layer, but no historic studies of the sites were performed. Of the analysed species, about half can be characterised as perennial stayers according to During (1992), and for these long-term habitat persistence may be important (see below), but others were typical colonists, probably with good capacity for long-distance dispersal, e.g. the moss *Ulota crispa*.

Nilsson et al. (1995) built on Rose (1976), and species lists were produced of beetles and lichenized fungi proposed to be dependent on EC. No tests of correlations between habitat persistence and species occurrences were presented, so the lists remain interesting hypotheses. Warren and Key (1991) cited several studies made on forest invertebrates in England and the majority of these seem to have used a similar explorative, rather than experimental methodology. Some of the lichenized fungi proposed by Nilsson et al. (1995) have later been found to occur also in forests that have not persisted for a long time at a particular place, viz. *Lecanora glabrata* and *Pyrenula nitida* (Fritz and Larsson 1996), *Bacidia biatorina*, *B. rosella*, *Biatorrella monasteriensis* and *Gyalecta ulmi* (B. Nordén, personal observation during field work in S Sweden). *Schismatomma decolorans* and *S. pericleum* have been shown to disperse to small habitat patches over distances of 1–2 km (Johannesson 1996), and not to show effects of isolation in an archipelago. In a similar study (Kruys and Jonsson 1997) lichenized fungi in the genera *Calicium* and *Chaenotheca*, congeneric to, and with the same type of dispersal as species proposed to be dependent on EC by Nilsson et al. (1995), were shown to have well developed dispersal capacity.

Studies dealing with problems of the EC concept

Some recent studies in boreal forests have questioned the value of the EC concept. Boreal swamp forests are thought to be the least dynamic forest type in the taiga biome and are often claimed to be important for 'EC-dependent' species. However, Ohlson et al. (1997) found that among several organism groups (bryophytes, lichenized fungi, wood-decay fungi and vascular plants), only vascular plants were dependent on long disturbance free periods in this forest type. Hörnberg et al. (1998) studied the same organism groups and concluded: "It is evident that extended fire-free periods and long stand continuity are not prerequisites for maintaining high species diversity in swamp forests." In another study, Linder et al. (1997) showed that the age of the forest

in boreal reserves important for biodiversity were shorter than presumed. From the observation that 100-year-old burned clear-cuts contained several red-listed species he concluded that the conservation value of forests disturbed by human impact has been underestimated.

Ahnlund (1996, 1997) studied saproxylic insects in clearcuts in SE Sweden and found that many red-listed species and ancient woodland indicator species occurred in microhabitats created on clearcuts (remnant dead wood of *Populus* and conifers). Many red-listed species appeared to be more favoured by disturbance than by long-lasting habitats. That many saproxylic species have a high mobility in the landscape was shown by Økland et al. (1996) who studied the species richness of saproxylic beetles at four different spatial scales (0.16, 1 ha, 1 and 4 km²). They found that total species richness and the number of red-listed species was strongly correlated to regional amount of suitable microhabitats (amount of decaying wood and wood-decay fungi) but only weakly or not at all to these factors in the local stands.

In England, studies have assigned great importance to EC in nemoral forests, but recently, it has been realised that using woodland history to help determine priorities for woodland conservation is a difficult task (Peterken 1996). Forest history is often very complex and it has been suggested that concepts, such as 'ancient woodland' should not be interpreted and used in a simplistic way (Kirby and Watkins 1998).

Which species are dependent on habitats with long-term persistence?

A major problem with the current use of EC indicators is that the groups of species proposed to indicate long habitat persistence also contain species that merely indicate the presence of suitable microhabitats. Little attention is given to the dispersal capacity and population dynamics of the different species. Dispersal capacity in natural conditions is difficult to study and our knowledge is still mostly fragmentary. Nevertheless, the existing knowledge of the relative dispersal capacity of different organism groups may provide guidelines for which groups that could be good bioindicators of long persistence in the absence of manipulative experiments, which are rare and time-consuming in forest habitats. Life history strategy classification (Rogers 1990; During 1992; Frey and Hensen 1995) and the habitat-template theory of Southwood (1977, 1988) could be used to evaluate which species have more or less well-developed dispersal capacity.

Some organism groups such as Aphyllophorales basidiomycetes that have been used as EC indicators (e.g. *Phlebia centrifuga*) have high dispersal capacity (Hallenberg 1995; Nordén and Larsson 2000). They have very small spores which are produced in prodigious numbers and may travel in the air for many kilometres (Kallio 1970; Nordén 1997). Many wood-decay fungi are therefore probably more favoured by a regionally rich supply of microhabitats than by long persistence of local forest stands. Epiphytic bryophytes and lichenized fungi again are in many cases

richly fertile and disperse widely by spores. For instance, Akiyama (1994) found that the low genetic divergence among populations of species of the epiphytic bryophyte genus *Leucodon* was probably related to effective spore dispersal by the wind.

Strategy classification predicts that species occurring in late successional stages usually have a longer life-span, higher competitive ability, lower or delayed reproductive allocation, and lower dispersal capacity. The theory of habitat-template holds that species in stable habitats, such as many ground-floor forest organisms, have fewer adaptations for long-distance dispersal than species of substrata with shorter persistence. Söderström & Herben (1997) used computer simulations to show the difference in metapopulation dynamics of bryophytes with different life history strategies. In this simulation, perennial stayers, colonists and shuttle species (categories according to During 1992), reacted differently to the fragmentation of habitat and the perennial stayers were the most vulnerable. This was not due to low production of diaspores per se, but rather to their delayed reproductive maturity.

Dispersal capacity is probably severely restricted (perhaps to a scale of meters per year) in groups such as terrestrial molluscs (Baur 1986; Baker 1988; Bengtsson et al. 1995), some beetles living in hollow trees (Nilsson and Baranowski 1994, 1997), myrmecochorous vascular forest plants (Bierzzychudek 1982; Peterken and Game 1984; Dzwonko 1993; Grashof-Bokdam and Geertsema 1998; Bossuyt et al. 1999; Edenhalm et al. 1999), some bryophytes, e.g. species dispersed by large gemmae (Kimmerer 1994; Longton 1997), and some lichenized fungi, e.g. pendant and terricolous species dispersed by thallus fragments (Renhorn 1997; Heinken 1999).

Several of these species should be possible to incorporate in methods of assessing long habitat persistence in forests. It is also important to specify the area in which the method is supposed to be useful, since a species' dispersal capacity may differ between regions. We will here briefly mention a few studies that we believe represent promising approaches of finding better indicators of old forests. Brunet (1994) proposed 11 vascular plant species as indicators of relatively undisturbed deciduous woodlands in south Sweden. On the basis of experiments of colonisation of secondary woodlands, Brunet and von Oheimb (1998) showed that several of the proposed indicator species colonised only slowly, or c. 0.3–0.5 m per year. Assmann (1999) investigated the ground beetle fauna in ancient and recent deciduous woodlands in north-west Germany. Four flightless species were predominantly found in ancient woodland, and the total number of species was higher in ancient stands, possibly due to dispersal limitation. Two species, *Abax parallelepipedus* and *Carabus glabratus* showed distinct focus in ancient woodlands and may be especially useful as bioindicators.

Conclusions and future research

The relative importance of old-growth microhabitats, dispersal ability, fragmentation and stand history needs to be addressed in conservation biology. The EC concept

is broadly applied but poorly defined and investigated, so its use may lead to risky decisions on conservation issues, and to too much effort being spent on the analysis of archival material and the reconstruction of old landscapes, rather than on inventory of the present situation. There has been a tendency to overestimate the importance of habitat persistence.

The proposed EC indicators should be revisited. The habitat requirements and life-history strategies of many saproxylic and epiphytic organisms are for example still poorly known. Species with low dispersal capacity are dependent on long habitat persistence, but easily dispersed organisms are not. For easily dispersed organisms it may be equally important to restore valuable habitats and microhabitats in the landscape as to protect old habitats.

On the basis of their high dispersal capacity many wood-decay fungi, epiphytic lichenized fungi, and saproxylic insects, should not be regarded as evidence for a long habitat persistence at a particular place (stand continuity). On the other hand, ground-floor-living organisms such as land-snails, certain vascular forest plants and bryophytes, may better indicators of long habitat persistence. Further studies of such indicators should be important.

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