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# Evaluation of bioindicators and structural attributes as indicators of old-growth forests

**Meghan Anderson**

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## Abstract

There is a lack of practical and accurate tools for identifying old-growth forests that are of important conservation value. In order to achieve more accurate methods for identifying old-growth forests, species and structural attributes of forests have been suggested as indicators. To assess which indicators among those commonly used for old-growth may be most practical and applicable a system of evaluating the indicators based on biological traits and current research was done. Species evaluated were saproxylic beetles, wood-inhabiting fungi, bryophytes and lichen. Structural attributes evaluated were dead wood measured, wildlife values, diameter at breast height (DBH), tree density and basal area. Indicators were evaluated on the basis of 15 criteria. None of the indicators were able to fulfill all criteria. The indicators that were able to fulfill most criteria were saproxylic beetles and lichen (67%) followed by structural indicators (64%). Evaluation of indicators suggests that saproxylic beetles and lichen used in concert may more suitable indicators for indicating old-growth forests, where as structural indicators may be less suitable but a more practical method. However, species indicators are unreliable and more research is required to determine their accuracy and improve their reliability.

**Key Words:** species indicators, ecological indicators, old-growth index, ecological continuity.

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# 1. Introduction

## 1.1 Problem Statement

Currently forest managers and landowners lack practical tools for identifying old-growth forests and forests that are of high-conservation value (Whitman and Hagan 2006). Identification of old-growth forest can be challenging (Whitman and Hagan 2006). The ability to identify old-growth forests may be of particular importance to some foresters as the major certification systems for sustainable forestry in the western hemisphere (the Forest Stewardship Council and Sustainable Forestry Initiative) require the conservation of rare natural communities and forest structure, which includes late successional forests (Whitman and Hagan 2006). Current methods of identifying old-growth forests are typically based on a definition of tree age, however, this is usually subject to high levels of error and may not capture functional attributes of the forest important for conservation. In a study by DeLong et al. (2004), 40% of the stands were misclassified based on the mean age of the largest trees. In another study by Harrison et al. (2001) 33% of stands were misclassified based on age. Thus there is a need to a more accurate tool for identifying old-growth forests.

In response to this inability to correctly identify old-growth forests, researchers and land managers have suggested the use of bioindicators or the measurement of a set of structural attributes of the forest. Research in this area is new and little has been done to evaluate and compare these different methods for identifying old-growth forests. Of the new methods developed for identifying old-growth forests it remains unknown which are the most appropriate for conservation use. Several schemes of criteria have been developed but only rarely are these criteria considered when using indicators. This paper uses a mixture of criteria that have been suggested in order to evaluate some of the most commonly suggested bioindicators and structural attributes for old-growth forests. This may help to identify which indicators or structural attributes are best for reaching biodiversity and management goals concerning old-growth and prevent the use of indicators that are inappropriate.

It is important to identify old-growth forests that have a high conservation value as wildlife communities of old-growth forests are generally (but not always) richer than younger forests (Peterken

1983). On a global scale the amount of old-growth forest is declining (Freedman et al. 1996, Recher 1996) and many species that require old-growth forests are expected to become extinct (Recher 1996, Berg et al. 2002). Old-growth forests tend to contain a high proportion of rare and vulnerable species (Goldberg et al. 2005). Many species depend on attributes of old-growth forests such as saproxylic beetles, mosses, liverworts, lichens and fungi that depend on large live and dead trees (Selva 1994, Ruggeiro et al. 1991, Berg et al. 2002). There are also processes in old-growth forests that are absent from younger stands such as soil churning by wind throw (Lindenmayer and Franklin 2003). Old-growth forests contain a special community of species, structural attribute and process that are important to identify and protect.

## 1.2 The Definition of Old-Growth

The first step in a decision-making framework for selecting indicator taxa requires a definition of what the indicator should reflect (Hilty and Merenlender 2000). This requires a robust definition of old-growth. Development of a robust definition of old-growth can be quite a challenge though. There are many definitions of old-growth (see Hilbert and Wiensczyk 2007, Mosseler et al. 2003, Wells et al. 1998, Spies and Franklin 1988) but there is currently no internationally compatible definition for old-growth. This is due to the variability in forest types and climates. The different types of old-growth definitions include structural definition, process based definition, conceptual/ecology based definitions and silviculture or economics based definitions.

Process based definitions tend to focus on how old-growth forests develop and are useful when trying to manage a forest to achieve old-growth status or to maintain a certain level of old-growth (Spies 1997). Process based definitions lend themselves better to the idea that old-growth is a dynamic entity rather than a static one (Spies 1997). The idea of gap-phase dynamics can be applied to a wide range of forest (with the exception of naturally open forest types such as found in xeric climates) (Wells et al. 1998, Spies 1997). However, it is difficult to incorporate process based definitions into inventories of old-growth (Spies 1997). Gap-phase dynamics is the successional stage at which regeneration in the forest canopy occurs from small disturbances such as windfall, which create openings in the canopy for the understory to be released and grow into the overstory layer. Large scale disturbances do not dominate the structure and composition of the forest. Definitions based on gap-phase dynamics are useful conceptually to understand old-growth, however, it is difficult to directly measure gap-phase dynamics in a forest both structurally and with the use of bioindicators.

Franklin and Spies (1991a) find that the most practical definition of old-growth forests is a structural one because functional characteristics of a forest are too difficult to measure. A structural definition describes attributes of old-growth that can be easily measured and are biologically important (Wells et al. 1998, Spies 1997) such as tree density or the abundance of dead wood. Examples of a structural definition are: the presence of dead fallen wood in various stages of decay (Mosseler et al. 2003), decay features in large trees, large snags, large trees relative to species and climate, wide range of tree sizes and spacing (Franklin and Spies 1991a). It is important to note that the abundance and density of these structural characteristics will vary with forest type. Also the presence of a wide range of tree sizes and spacing may not apply to all forest types (e.g. the boreal pine-spruce forests of northern Canada) (Wells et al. 1998). These structural attributes are important to ecosystem function and provide important habitat. A structural definition of old-growth is best for inventory, wildlife habitat, recreation and timber management (Spies 1997). Structural attributes of a forest in old-growth definitions are often the focus of management concerns and can easily be made the target of management actions (Wells et al. 1998). The drawback of a structural definition is that it does not provide information on the processes that created the structural attributes (Spies 1997). This is important since some structural attributes such as dead wood could be achieved through processes other than natural succession. For example logging can leave behind large amounts of dead woody debris that has no lumber value. Also it is difficult to apply structure based definitions to different kinds of forests, since differences in climate and species will create different levels at which structural attributes indicate old-growth (Spies 1997). Thus for the purpose of bioindicators of old-growth a structural definition is not useful.

For the purpose of bioindicators of old-growth it is important that a definition of old-growth consider concepts of ecological integrity and ecosystem health. These are other ecological states that indicators have been used for (e.g. Carignan and Villard 2002, Hilty and Merenlender 2000). Ecological integrity can be defined as a whole system that includes the presence of certain species, populations and communities as well as ecological processes that progress at appropriate rates and scales (Angermeier and Karr 1994, Karr 1991). Ecosystem health can be defined as the absence of signs of ecosystem distress, an ecosystem's ability to recover with speed and completeness (resilience), and/or a lack of risks or threats pressuring the ecosystem composition, structure, and/or function (Rapport 1995 a,b). The goal of using indicators for old-growth is to identify old-growth areas that lack human disturbance and represent an area of biological importance as it houses a suite of species that can not be found in other states of succession or ecosystem health. In areas such as Europe where the landscape has been highly modified by both large scale and small scale human disturbances it is necessary to separate the old-growth forests that are entire and healthy from ones that may not be as healthy. For example, in Britain varying degrees of naturalness in forests aged back to 1600 complicated an inventory of ancient woodlands (Goldberg et al. 2005). Due to varying degrees in the integrity and health of old-growth forests it is important that an indicator is able to signify higher states of ecosystem integrity and health.

Considering the concepts of ecosystem integrity and health and process and structural definition of old-growth forest a definition that can be used for the purpose of this paper is a relatively old forest, relatively undisturbed by human activity, a climax or shifting steady state, the average tree has reached the life expectancy of the species (Wells et al. 1998), and presence of complex food webs and associated animals (Burton and Kneeshaw 1998). This definition has been developed in order to attempt to encompass most forest types and thus characteristics of old-growth that do not apply to some forest types, such as high understory productivity (Wells et al. 1998), have been excluded. The goal is to identify old-growth forests with conservation value. This requires that the stand have landscape continuity (defined by species dispersal ability) and to some extent ecological continuity.

Ecological continuity as it applies to forests is a stand that has existed for a long time and remains unaffected by human disturbances. However, for the purposes of this paper it is not necessary to choose a definition of ecological continuity that extends back to European-Pleistocene or Scandinavian-Holocene (Gauslaa and Ohlson 1997). It is unlikely that forests exist today that have not been disturbed by humans to some extent. However, small disturbances such as bark stripping by First Nations people will have a much smaller effect on the biodiversity of a forest than logging. It is also possible that forest stands have recovered from such small disturbances since their occurrence. It is important nonetheless to distinguish between forests that may have old-growth type characteristics but have not recovered yet from human disturbances that occurred at a scale large enough to affect biodiversity and those that have recovered from human disturbances or remain unaffected. Thus the task an indicator of old-growth forests is charged with is quite a large one: ability to identify continuous sections old-growth forests that are relatively undisturbed by humans and maintain their ecological continuity, ecosystem integrity and ecosystem health.

# 2. Indicators (Literature Review)

A range of different types of species have been suggested as indicators of old-growth as well as multiple system of indexes based on structural attributes of forest. Some of the more common bioindicators of old-growth, e.g. saproxylic beetles, wood-rotting fungi, bryophytes and lichen, are evaluated here. Some more common structural attributes used to identify old-growth forests are measurements based on dead wood such as abundance, decay classes, density of snags; density of live trees; diameter at breast height (DBH); and basal area are also evaluated. Another type of structural index that was evaluated was one based on functionality of attributes for wildlife (e.g. DeLong et al. 2004). This type of index was included despite it being new and relatively unused because it has the potential to address shortcomings in more common indices.

## 2.1 Bioindicators

<u>Saproxylic beetles</u>

Saproxylic beetles depend on dead wood at some point in their life cycle. Saproxylic insects use a range of microhabitats associated with old-growth forests such as well decayed fallen wood, brokenoff-branches, fissured bark and rot-holes in living trees (Grove 2002a). Saproxylic beetles require a range of microhabitats associated with old-growth forests and because of this, a richness in saproxylic beetles can be considered as related to the functional integrity of a forest (Grove 2002a). Saproxylic insect are particularly sensitive to any form of forest management that causes a break in the continuity of a mature forest (Grove 2002a). Examples of breaks in continuity are the loss of dead wood through anything from firewood collection (Speight 1989) to intensive forestry operations (Grove 2002a). Due to this sensitivity saproxylic species are used as indicators of continuity in many European countries (Speight 1986, Good 1997).

Use of saproxylic insects as indicators can be research and skill intensive. It requires a species inventory of the area in question, that compatible inventories exist for other areas within the bio-region against which the inventory can be compared, that the inventories cover areas that are known to differ in their ecological continuity or successional stage and finally it is necessary that the inventories are able to recognize the key indicator species within the samples collected (Grove 2002a). Unfortunately such inventories of saproxylic species are rare or non existent outside of Europe (Grove 2002a). Furthermore, in tropical forests the taxonomic diversity of insect fauna may preclude saproxylic insects from being used as indicators (Grove 2002a). In areas that are less suitable to use saproxylic insects Grove (2002a) suggests the use of surrogate indicators such as dead wood, upon which saproxylic insects depend.

Despite the questionable use of saproxylic species as indicators outside of Europe, there are several characteristics of saproxylic beetles that could make them good indicators. First, some families, such as carabids (ground beetles), are widely distributed over broad geographic ranges and inhabit all major habitats except for dry desert regions (Raino and Niemelä 2003). In general, saproxylic insects respond to differences in the abundance (Økland et al. 1996, Martikainen et al. 2000) and quality (Irmler et al. 1996, Schiegg 2001) of dead wood. Some saproxylic species have narrow micro-habitat requirements and are poor dispersers (Grove 2002a) which makes it difficult for them to avoid disturbances. However, Økland et al. (1996) found that many species of saproxylic insects were in fact highly mobile. Ground beetles, flightless beetles and beetles living in hollow trees may be very dispersal limited though and may still be good indicators of old-growth (Nordén and Appelqvist 2001).

Within the order Coleoptera, carabids have shown the ability to respond to forest fragmentation. Davies and Margules (1998) found that Carabidae beetles in a Eucalyptus forest of Australia increased or decreased in abundance with forest fragmentation but species composition did not change. Halme and Niemelä (1993) found that there was a high species richness of Carabidae in small forest patches versus medium and large forest patches but that no forest specialists were found in the small forest fragments. Spence et al. (1996) found that only a few species of Carabidae beetles were sensitive to forest edge in the Boreal forest of Canada. Not all carabids respond to forest fragmentation, but most do respond with a change in species assemblage (Raino and Niemelä 2001). However, Rykken et al. (1997) felt that carabids were not suitable indicators due to their lack in habitat specialization and their response to a gradient in moisture versus a response to different landscape types. This makes it questionable how reliable of an indicator saproxylic beetles are.

Saproxylic species may not be dependable indicators. Ahnlund (1996, 1997) found many red-listed and old-growth indicator saproxylic insects using microhabitats in clearcuts (left behind dead wood). In this study it appeared as if many red-listed species were favored by disturbance rather than by long lasting habitats. While saproxylic species do possess attributes that have the potential to make them good indicators, studies are unclear as to their reliability.

Fungi

In Scandinavia certain wood-rotting fungi are used to indicate old-growth forests based on the hypothesis that they require an unbroken input of dead wood for 200-300 years (Karström 1993, Bredesen et al. 1997, From and Delin 1995, Haugset et al. 1996). Only a few studies have been done though, to test the association of fungi with old-growth forests. The number of wood decay fungi is negatively correlated with stand age in stands of hazel (*Corylus avellana*) in Sweden possibly due to an increase in competition with stand age (Nordén and Appelqvist 2001). Sverdrup-Thygeson and

Lindenmayer (2003) found that presence of the wood-inhabiting fungus *Phellinus nigrolimitatus* was positively correlated with an absence of disturbances such as forest fires, stormfellings and clearcutting over the past 240 years. However, the study also found that presence of *Cystostereum murraii*, also an indicator species frequently used, was not explained by ecological continuity of a stand. The difference may be explained by the fact that *C. murraii* is not dependent on logs as large as *P. nigrolimitatus*. The species composition is dependent on both the decay class of a log and the size of the log (Jönsson et al. 2008).

Due to a high dispersal ability in fungi, in groups such as the *Aphyllophorales* and *basidiomycetes,* which have very small spores, produced in high numbers, (Kallio 1970) fungi maybe poor indicators. Organisms in the group have been used as indicators of ancient forests, however, species with high dispersal abilities should not be used as indicators (Nordén and Appelqvist 2001). Many wood decaying species of fungi thus are probably more related to an abundant supply of microhabitat than to ecological continuity (Nordén and Appelqvist 2001).

While wood-inhabiting fungi may not be related to ecological continuity, they may be related to landscape continuity. Jönsson et al. (2008) found *Asterodon ferruginosus, Phellinus ferrugineofuscuc, P. viticola* and *Phlebia centrifugia* responded positively to landscape continuity, in terms of supply of logs to colonize. The authors assumed this indicated a limited dispersal ability. However, they noted that surprisingly little was known about the population dynamics of fungi in relation to their host substrates. However, it is difficult to detect spatial patterns in fungi because by the time a species that has colonized a new area forms fruiting bodies, the source point of dispersal may have decomposed fully (Jönsson et al. 2008). While Scandinavian forest managers actively use wood-inhabiting fungi, their ability to indicate old-growth forests remains questionable and they also have attributes that make them difficult to study.

<u>Bryophytes</u>

Bryophytes, on the other hand, have attributes that suggests that they may be good indicators. Some bryophytes that are dispersed by large gemmae are likely dispersal limited and thus may be good indicators of old-growth (Nordén and Appelqvist 2001). Bryohpyte distribution can be strongly influenced by stand age and habitat heterogeneity (Newmaster et al. 2003). Newmaster et al. (2003) found that there was a unique set of species between young and old forests in the interior cedar hemlock (ICH) forests and the coastal western hemlock (CWH) forests of British Columbia. The old-growth forests of the ICH and CWH supported a rich flora of rare and endemic hepatics (Newmaster et al. 2003). Newmaster et al. (2003) also found high bryophyte diversity was associated with the continuity of the old-growth forests in terms of large scale disturbances.

Bryophytes are not always reliable indicators though. For example, in Wales a forest was misclassified as ancient (meaning it had not suffered any anthropogenic disturbances for a very long time) using a desiccation-sensitive bryophyte. However, a palaeoecological study revealed that the forest had actually been disturbed by actions such as coppicing, clear felling and grazing during the past 300 years (Willis 1993). Richness and abundance of Atlantic bryophyte communities has been shown to be more related with the availability of rock with permanent moisture, shelter and a favorable substrate rather than old-growth or ancient forests (Ratcliffe 1968). Another, downfall is a lack of knowledge on the effects of logging on bryophytes and this area requires further research (Jonsson and Esseen 1990, Söderström 1995). Studies have indicated, however, that clearcutting reduces stand age, the number of habitats and thus the cryptogam diversity (Gustafsson and Hallingbäck 1988, Lesica et al. 1991). Also sensitive bryophyte species will disappear from an area that is logged (Newmaster et al. 2003). The species can recolonize the area once regeneration of the forest has started but this is dependent on the gap size created and the dispersal range of the species (Söderström 1988). Certain attributes of bryophytes suggests that they could be used as indicators, like other species they lack reliability though.

Lichen

Several studies suggest that certain genera of lichen (e.g. *Alectoria* and cyanolichens) can be used to differentiate old-growth from second growth forests (Stevenson 1988, Lesica et al. 1991, McCune 1993, Neitlich 1993, Esseen et al. 1996). An abundance of aboreal lichen is a common characteristic of old-growth coniferous forests of the circumboreal zone (Edwards et al. 1960, Lesica et al. 1991, Goward 1993). Many studies have also found higher lichen abundance in old-growth than in managed second-growth forests (Lesica et al. 1991, Hyvärinen 1992 Esseen et al. 1996). In particular, *Alectoria*, *Bryoria* (Stevenson 1988. Neitlich 1993, Essen et al. 1996), trunk epiphyte species (Lesica et al. 1991), fruticose lichen (Esseen et al. 1996) and nitrogen-fixing "cyanolichens" (McCune 1993, Neitlich 1993) have been found in higher abundance in old-growth forests. However, the relationship between old-growth forests and a higher abundance of lichen is not consistent. Arup et al. (1997) observed lichen that were old-growth forest dependent decline in abundance in the oldest oak forests, possibly due to competition for a limited number of microclimate habitat areas (Nordén and Appelqvist 2001).

Reasons for the association of certain groups of lichen with old-growth forests is related to the character of the substrate they grow on. Aboreal lichen biomass is related to tree size (height and DBH), however, these characteristics are not always related to tree age (Arseneau et al. 1997, Esseen et al. 1996). For shade tolerant species, such as balsam-fir, lichen biomass is independent of tree age but is related to branch age (Arseneau et al. 1998). Esseen et al. (1996) identified four reasons for a lower biomass of lichen in logged forests: low substrate availability, slow growth rate of lichens, unfavorable microclimate and dispersal limitations (Stevenson 1990, Neitlich 1993). This suggests that lichen is able to respond to disturbances beyond that of just loss of branch mass (Esseen et al. 1996), an important characteristic.

There are many other characteristics of lichens that make them good indicators. Lichens are responsive to environmental factors (McCune et al. 1997, Oksanen et al. 1990, Richardson 1992), have slow growth rates, inefficient dispersal, require particular microclimates or substrates, are sensitive to disturbances (Kershaw 1985, Esseen et al. 1996) and the biomass of lichens is a steady state in mature forests (Pike et al. 1972). Within the group of crustose lichens, diaspore-producing species appear to be more area sensitive (Ellis and Coppins 2007). Species which are both specialist and rare, such as some micro-lichens, will be particularly sensitive to isolation (Ellis and Coppins 2007).

Unfortunately, there is a limited amount of information available on the dispersal, establishment, growth of lichen and the influence of microclimate and forest structure on lichen (Esseen et al. 1996). Many species of lichen are likely widely dispersed by spores, for example *Leucodon* (Akiyama 1994), which makes them poor indicators. However, *Alectoria* spp. are a poor dispersers and have been proven to be lower in abundance the further away a mature forest is (Stevenson 1988). *Bryoria* spp. are also poor dispersers but they are able to disperse slightly better than *Alectoria* spp. (Esseen 1985). Also Lichens that disperse by thallus fragments are likely severely dispersal limited and may provide good indicators (Nordén and Appelqvist 2001).

Some drawback in the use of lichens are that lichens cannot be used reliably as indicators in areas that have been exposed to high atmospheric pollution (Rose and Coppins 2002) and their measurement is not easy. Estimates of epiphytic lichen biomass at the branch, tree and stand level are difficult and time-consuming (Esseen et al. 1996). Also some lichen have been identified as potential indicators but were later found to occur in young successional forests or have larger than previously believed dispersal abilities (table 1). There exists a vast amount of literature available on lichens as indicators, in particular as indicators of atmospheric pollution. However, the full causal relationship of lichen to forestry is not fully understood (Esseen et al. 1996) and more research is required on ecological processes of lichen.

It remains questionable if lichens are indicators of ecological continuity. Tidbell (1992) demonstrated that a set of crustose lichens were highly correlated with an increase in ecological continuity, which was measured as time since disturbance. However, Esseen et al. (1996) did not find a significant difference in species richness of macrolichens between old-growth stands and managed stands. Essen et al. (1996) contributed this to differences in forest type and climate and that crustose lichens had not been included in their survey. Thus lichens that serve as indicators of ecological continuity or old-growth in one location may not be useful in another. On a further note, Nordén and Appelqvist (2001) criticize studies such as that by Tidbell (1992), arguing that these studies have shown that lichens depend on old trees but have yet to prove that lichen depend on ecological continuity. Nordén and Appelqvist (2001) argue that no study has been able to isolate the effect of ecological continuity by demonstrating a change in species composition with a change in ecological continuity on the same substratum in the same forest type and use of historic data records were not used to backup claims that stands were ancient forests, exhibiting ecological continuity. Despite this criticism Rose and Coppins (2002) created a New Index of Ecological Continuity (NIEC) that uses lichens to create an index of ecological continuity of a forest that is based off of original index Nordén and Appelqvist (2001) criticize. They also ranked species by their ability to correctly identify old-growth forests. The problem, however, is that Rose and Coppins (2002) did not change the base of the index and continued to suggest species as indicators without the methods Nordén and Appelqvist (2001) suggest are necessary in order to indicate ecological continuity. Surprisingly, two studies have used the NIEC to test lichens as indicators of ecological continuity (Plata et al 2008, Zedda 2002). This is interesting since in a study Rolstad et al. (2001) cautioned against the use of certain red-listed macrolichen species as indicators of ecological continuity or canopy continuity since they were found in forests that had been selectively logged in the past 100 years. Furthermore, a study by Humphrey (2002) they found species on the NIEC list by Rose and Coppins (2002) that were supposed to indicate ecological continuity in native semi-natural stands of lowland oak and stands of planted Scots pine. Humphrey et al. (2002) guessed that in the case of the planted stand the lichen were relics from the ancient woodland that covered the site previously.

An interesting study by Ellis and Coppins (2007) supports Humphrey's (2002) guess. The study by Ellis and Coppins (2007) indicates that lichen species diversity is more strongly related to historic woodland extent and fragmentation than the current woodland extent and fragmentation. They predicted that small species rich areas that were surrounded by an unsuitable matrix would eventually lose species richness, but that there was a lag in the response of lichen to spatial changes. This study was successful in also comparing the response of lichens across variations in microclimate in aspen woodlands and was able to detect a significant response to habitat extent and fragmentation despite environmental variables. Thus, while the study was able to verify that lichens are useful indicators of habitat fragmentation and may require landscape continuity, their results indicate that the lag in response to spatial changes may mean that the response is more related to historical conditions rather than present conditions. What the study fails to do is quantify a time frame required for a detectable response in lichens. Without this knowledge it becomes difficult to know how reliable lichens are as indicators of current forest conditions. It will be necessary to weigh the negative and positive aspects of lichens as indicators to determine if they are beneficial as indicators of old-growth forests. A number of studies have indicated though that lichens are unable to indicate ecological continuity.

**Table 1: List of lichen species that have been suggested as bioindicators but have been proven ineffective.**

| Family | Species | Reason | Source |
|---|---|---|---|
| Lecanoraceae | *Lecanora glabrata,* | Found in young forests | Frtiz and Larsson 1996 |
| Pyrenulales | *Pyrenula nitida* | Found in young forests | Frtiz and Larsson 1996 |
| Ramalinaceae | *Bacidia biatorina, B. rosella* | Found in young forests | Nordén and Appelqvist 2001 |
| Biatorellaceae | *Biatorella monasteriensis* | Found in young forests | Nordén and Appelqvist 2001 |
| Gyalectaceae | *Gyalecta ulmi* | Found in young forests | Nordén and Appelqvist 2001 |
| Roccellaceae | *Schismatomma decolorans, S. pericleum* | Dispersal rate of 1-2 km No response to isolation | Johannesson 1996 |
| Lecanorales | *Calicium* | Good dispersal ability | Kruys and Jonsson 1997 |
| Coniocybaceae | *Chaenotheca* | Good dispersal ability | Kruys and Jonsson 1997 |
| Cladoniaceae | *Cladonia parasitica* | Found in clear-cut forests, not only old-growth. Used in the NIEC. | Lõhmus and Lõhmus 2009 |

## 2.2 Structural Attributes

Old-growth indices based on structural attributes of old-growth forests have been successfully demonstrated to identify old-growth forests but have some limitations. Indices are based on only a small subset of possible old-growth attributes which makes it difficult for them to account for all natural variability in stands and at the same time exclude the old-growth stands from mature forests. This excludes some characteristics of old-growth forests that are important for ecosystem function or habitat (Wells et al. 1998). Also the line drawn between what is old-growth and what is not is somewhat arbitrary in many cases (Wells et al. 1998). This relates to different definitions of old-growth and the different number of successional classes used in a study. As mentioned above, there is rarely a reliable definition for old-growth and this can lead to some arbitrary decisions on what is old-growth or not.

In a study by Franklin and Spies (1991b) structural criterion for old-growth forests did not do a good job of capturing all the old-growth forests. Only 52% to 70% of the forests over 200 years old that would have normally been considered old-growth were classified as old-growth using the U.S. Forest Service's interim definition of old-growth based on structural characteristics. This was because many stands met some criteria but did not meet all of them and some stands were missed because they had lower than average values because some stands used in the index had influenced the average to be high with extremely high values in some attributes. Since then the index has been revised and now 80% of forests over 200 years old have successfully been identified (Franklin and Spies 1991b). An index such as that by Franklin and Spies can be used in other forests, however, site specific criteria may have to be developed for forests outside of Western United States, where this index was developed (Hamilton and Nicholson 1991). Unfortunately, the use of structural indices requires that an initial reference data set is established to develop threshold values of old-growth characteristics (Whitman and Hagan 2006). However, the databases used in establishing indices can be used in other management activities such as evaluating wildlife habitat (Wells et al. 1998). The variability in stand structural attributes in old-growth forests between different climatic and geographical units is the reason characteristics chosen to identify old-growth will need to be selected for each individual forest type, climatic and geographical zone (DeLong 2004). As an example of the level of variability, in a study of the density in three different size classes of large trees by Quesnel (1996), he found that only 6 of the 26 stands were within one standard deviation of the mean value for all attributes. Thus there is a high variability in structural attributes between forests.

Nonetheless, many studies have successfully established indices locally. Franklin and Spies (1991b) established and index for Oregon and Washington that gives a score based on the abundance, density or biomass of an attribute. This system effectively accounted for the variability in stands but still relied on an abstract threshold to define limits between different successional stages.

An index developed by Whitman and Hagan (2006) for northern hardwood and upland spruce-fir forests based on structural attributes found that large live and dead tree density accounted for the largest percentage of difference between economically mature and late successional stands. Unfortunately, the index still misclassified 15% of economically mature and late-successional stands.

DeLong et al. (2004) developed a new type of index that is based on functional attributed of old-growth forest structure to identify old-growth forests. The index was based on density of trees with attributes such as trees with large concealed spaces at the base or trees that are soft on the inside, but hard on the outside. The goal was to establish a better system to indentify old-growth forests that provide habitat value for wildlife in an easy way that could be used by forest practitioners and had a lower error rate than 40% for identification based on tree age. Their index based on functionality provides an easy method for identifying old-growth forests, however, its error rate is still 20% and it is also sensitive to small climatic differences, meaning it requires indexes to be adapted locally (DeLong et al. 2004).

Other studies have simply used a particular abundance over some threshold of structural attributes to indicate old-growth forests. In the Australian tropics, Grove (2002a) found that basal area and fallen dead wood were better measures of saproxylic species richness than the number of dead standing trees. Of these two he found basal area acted as a more reliable indicator. Grove (2002a) suggested that basal area in combination with a system of classifying a tree's rot class (e.g. Carpenter et al. 1989) could be used to indicate long-term sustainable forest management. A study by Sverdrup-Thygeson (2001) suggests that structural attributes could also be used in the place of indicators. The study found that indicator fungi and beetle species richness were not correlated, but that dead wood best explained species richness and presence of red-listed beetles. An exception to this was that singles species of beetles, such as *Atomaria alpina*, were positively associated with the indicator fungi.

In Douglas-fir and western hemlock forests the strongest structural characteristics for identifying old-growth forests was overstorey features, a decline in tree density, and an increase in tree size (Spies and Franklin 1991).

Also the density of large trees and/or snags has been used an identifier of old-growth forests in a number of different areas (Harrison et al. 2001, Quesnel 1996, Holt et al. 1999, Burton and Coates 1996, Kneeshaw and Butron 1998, Franklin and Spies 1991b). However, the distribution of snags will only vary between age classes if they are sub-divided into size classes (Holt et al. 1999). Thus there is a lot of variability as to what the best attributes are for indicating old-growth and there is a lot of variability in the threshold levels for these attributes.

# 3. Methods

To evaluate bioindicators and structural attributes of forests as indicators of old-growth forests a set of criteria based on a collection of previously published articles (see: The National Academy of Sciences 2000, Dale and Beyeler 2001, Hilty and Merenlender 2000, Andreasen et al. 2001, Rolstad et al. 2001) was developed. The criteria chosen were based on whether or not they applied to old the definition of old-growth as some of the suggested criteria by the above mention authors are meant for indicators in general, not just old-growth. The criteria used are normally used for bioindicators but should be applicable as criteria to structural attributes as well as measurement of their ability to indicate old-growth forests. In some cases, however, the criteria did not apply to the structural attributes. In this case the criteria was only used to compare bioindicators. The ability of an indicator to fulfill criteria was scaled to the number of criteria for which an answer was available for each individual criterion. Of the criteria used some are much more important than others. Three very important criteria used were respond to disturbance at the stand scale, know response to disturbances and a limited mobility. Failing to fulfill one of these three criteria would make that organism or structural attribute a very poor indicator. The criteria are listed and explained below.

## 3.1 Criteria for Evaluation

A long description of the criteria used in this study follows bellow, for a short summary see Table 2.

**Respond to disturbances at the stand scale**

Respond to disturbances at stand scale was a criteria developed to ensure that disturbances indicated are at the appropriate scale. If the bioindicator can respond to a disturbance that affect an entire stand it fulfills this requirement, all structural indicators fulfill this requirement since they represent levels of a structural attribute across a stand.

**Known response to disturbance (human and natural)**

The responses of an indicator to disturbance, both natural and human are known (Dale and Beyeler 2001) can not be detected or predicted unless it is known. The requirement for this was that there was a study or studies that quantified the response of the bioindicator or structural attribute to disturbances affecting forests.

**Limited Mobility**

An organism should have limited mobility (Hilty and Merenlender 2000) so that the indicator has a limited ability to avoid the disturbance (Landres et al. 1988, Johnson et al. 1993). For example, if a forest stand is subjected to logging, the indicator used should have a limited ability to leave the forest stand and avoid the disturbance or to re-colonize new areas. For all structural indicators this was assessed as true since structural indicators are based on trees. An exception to this would be disturbances that increase the amount of dead wood. However, the abundance across all different decay classes will not be affected, only one decay class of wood will be affected by events such as logging.

**Sensitive to forest fragmentation/ Requires continuity**

Sensitivity to forest fragmentation or requires continuity was a criteria added that did not come from another list of criteria from other author's. Since the goal is for indicators to represent old-growth forest, it is important a patch of old-growth in a stand of second growth forest does not falsely cause the entire stand to be identified as old-growth. This helps to indicate the quality of a forest stand, since the edge effect from forest fragmentation can penetrate into the stand and affect the structure and ecological processes such as nutrient cycling (Harper et al. 2005). This is related to an organism's dispersal ability but more directly takes into account spatial disturbances in the landscape that structural attributes may not be sensitive to. It is important to take into account effects of fragmentation on old-growth stands because edge effects can penetrate into a stand and affect the microclimate and increase predation rates and blow down of trees.

Bioindicators were considered sensitive to fragmentation if previous research indicated this. However, structural indicators were not considered sensitive to fragmentation since there is no direct response from structural attributes to the surrounding matrix. In an old-growth forest inventory in Orgeon, excluding strips of forests within 120m of a road or clearcut and stands smaller than 30 hectares from an inventory of old-growth forests resulted in 38% less total area defined as old-growth (Morrison 1988).

**Low variability in response**

The criteria low variability in response was modified from Dale and Beyeler (2001) to signify if the indicator had a consistent response in studies across different forest types. This is a measure of how well the indicator can be depended upon to give a response and respond to changes in different climatic gradient. All structural characteristics of old-growth based on an abundance of the characteristic were given a zero in this category since their levels are highly variable within a forest type and between two different locals (Wells et al. 1998, Grove 2002b). While natural variability in structural characteristics of one forest type can be adjusted for using Spies and Franklin's method (1991b) based on abundance, biomass or density of an attribute, site specific criteria would have to be developed (Wells et al. 1998). For bioindicators this was assessed based on fluctuations in the population level. Species that are temporally unpredictable (Rolstad et al. 2001) or have high population fluctuations (Hilty and Merenlender 2000), will make it difficult to detect a response from the background variation.

In researching bryophytes and fungus nothing could be found to indicate that their populations had high fluctuation or were not temporally predictable thus they were given a score of 1.

Saproxylic beetles have life cycles and population cycles that can be highly variable and respond to changes in the weather (Kimberling et al. 2001). Furthermore, the emergence and peak in populations varies between species thus, it is necessary to know the life cycle of the indicator species that are being used and sample at an appropriate time of the day and an appropriate time of the season. Due to this saproxylic beetles receive a zero for this criterion. However, Kimberling et al. (2001) in their study on the use of beetles as indicators of anthropogenic disturbances, suggest using an index to help single out a response to a disturbance from natural variation. They suggest also that the overall direction of the response may still be identifiable as well. While lichens have stable populations (Ellis and Coppins 2007, Rose and Coppins 2002, Pike et al. 1972), their reliability as indicators is questionable as shown in Table 1. Due to their being unreliable as indicators they received a zero for this criteria.

**Knowledge of natural history of organism, habitat affiliation and interactions with other organisms and role in the ecosystem**

It is important to have knowledge of natural history of organism, habitat affiliations and interactions with other organisms and the role in the ecosystem (Andreasen et al. 2001, Hilty and Merenlender 2000). Following Hilty and Merenlender (2000), an indicator was considered to have sufficient background information if more than 30 articles had been published on the organism or the structural attribute. However, to refine results to old-growth forests, old-growth forests or mature forests or ancient forests had to be a topic in the article. These results were further verified with literature where available. Lichen was given a value of 1 for this criteria, despite the fact that Esseen et al. (1996) felt that there was insufficient knowledge of lichens baseline information and an understanding of their response to management regimes in forests. This is because 33 new articles on lichens were found to have been published since Esseen et al. (1996) published their article. However, the search did not indicate if new research on lichen was in areas Esseen et al. (1996) saw as deficient such as dispersal. Furthermore, though, as Nimis et al. (2002) states there is a large amount of research available on the use of lichens as bioindicators.

For bryophytes there was a low number of search results returned and Esseen et al. (1996) also felt information was lacking on baseline information of bryophytes thus they were assigned a value of zero for this category.

For fungi a search in biosis on old-growth and fungi returned 236 results (167 excluding articles with animals), many of these publications provided little information on the natural history, habitat affiliation and interaction with other organisms. Jönsson et al. (2008) found that little information was known about the population dynamics of fungi or some were alternatively about lichen. Furthermore the lack of information present here is indicative of a lack of knowledge in the area of wood-inhabiting fungi. Due to this and the resent publication by Jönsson et al. (2008) fungi were assigned a value of zero, despite high search results.

**Clear Taxonomy**

Clear taxonomy evaluates how clear the taxonomy of the indicator has been established (Hilty and Merenlender 2000). If literature reviewed indicated taxonomy in the indicator group was unclear it was assigned a zero in this category, otherwise it was considered established.

In temperate regions taxonomy and ecology of cararbid beetles has clearly been established (Lövei and Sunderland 1996, Niemelä 1996, New 1998), however, it is unknown if this applies to other regions and other families. The shear abundance of species in the coleopteran family might indicate that the taxonomy at this point remains unclear, in particular in tropical regions with higher abundance. However, a value of 1 was granted to saproxylic species since this was the method used for other categories when literature reviewed did not indicate a problem in taxonomy.

**Low tolerance levels**

An indicator with low tolerance levels is more sensitive to disturbances (Hilty and Merenlender 2000, Dale and Beyeler 2001). An indicator was considered to have low tolerance levels if articles reviewed stated this.

**High reproductive rate**

Species with higher reproductive rates will be able to provide early responses to disturbances (Hilty and Merenlender 2000). For disturbances that do not directly effect the stand structure it may take a long time before a response is measurable in the stand structure.

Bryophytes and lichen were both assigned a value of zero for this category. While Bryophytes are capable of producing a high number of spores when they do reproduce sexually, a lot of evidence suggests that successful sexual reproduction in bryophytes is rare. Successful sexual reproduction is also thought to be rare in lichens (During 1992). A time lag in the response to changes in spatial continuity of a forest has also been noted in lichen (Ellis and Coppins 2007). Structural attributes were all assigned a zero in this a category since structural attributes of old-growth forests, by definition take a long time to produce.

**Food/habitat specialist**

Generalist will not adequately represent the system and may be able to avoid disturbances (Hilty and Merenlender 2000). Species were defined as habitat specialists if they required specific attributes in their habitat. For example saproxylic beetles are habitat specialists because they require abundant amounts of dead wood. The structural attributes of a forest cannot be evaluated on this criterion.

**International compatibility**

International compatibility is how the indicator compares to indicators being used elsewhere in the world (The National Academy of Sciences 2000). In this study the international compatibility of the bioindicators was assessed on whether or not that community or taxonomic group or structural attribute could be used temperate and tropical forests. This did not consider whether the indicator was still valid across all types of forests possible since data at this scale is not available.

As an example for saproxylic beetles no studies were found that directly stated the successful use of saproxylic species as indicators in the southern hemisphere. However, Grove (2002) suggests that saproxylic species could be used as indicators in the Australian tropics if it was not for the lack of surveys on saproxylic species and the over abundance of saproxylic beetles in comparison to Europe where they are used as bioindicators. A study by Lachat et al. (2006) also suggests that saproxylic species could also be used in the tropical forests in Africa as indicator species.

**Easy to find**

Some species may be difficult to find and thus present a challenge in their use as an indicator (Hilty and Merenlender 2000). Although saproxylic species can be cryptic in their nature, field sampling methods based on alcohol traps allow for them to be easily collected thus they were still assigned a value of 1. Fungi received a score of zero because identification of fungi requires the presence of fruiting bodies to be present.

**Data requirements low**

In order for an indicator to be used feasibly it should have low data requirements The National Academy of Sciences 2000). If no prior research is required for the use of an indicator in a stand, it was considered to have low data requirements. Saproxylic species do not fulfill this requirement because there is a lack of species inventories outside of Europe (Grove 2002b). Laaksonen et al.

(2008) suggest that use of fungi and saproxylic species to study fragmentation would need to be calibrated to the level of fragmentation. Thus, this would require surveys of species presences and establishment of an index of sensitivity to fragmentation. As such, the data requirements for saproxylic beetles and fungi is not low.

Bryophytes were assigned a value of zero since lists of bryophyte indicator species is not well established outside of Europe, and even within Europe the lists are small and uncertain (Rose 1992).

Lists of lichens to be used as indicators are also not well established outside of Europe (Rose 1992) and those that are established are questionable. However, there are more and more studies that are beginning to use lichens as indicators of old-growth and methods are being developed to reduce the cost of and skills required to use lichens as indicators of air quality (see Nimis et al. 2002), which may make it easier to use lichens as indicators of old-growth.

The structural characteristics do not fulfill this criteria either because use of structural characteristics would have to be adapted to each new forest type or site (Wells et al. 1998). Thus, all of the indicators fail to meet this requirement. However, both bioindicators and structural attributes may have low data requirements in specific areas where surveys have previously been carried out.

**Skill required low**

An indicator is more practical to use if the skill requirements are low (The National Academy of Sciences 2000). This allows for a diversity of land manager to use the indicator. Saproxylic beetles, lichen, bryophytes and fungi all received a score of zero because it requires a highly trained individual to identify species in these groups.

**Low Cost**

If research indicated it would be expensive to use a particular indicator, then it did not fulfill this criterion and received a value of zero. As for Bryophytes and Lichen because they are not well developed as indicators outside boreal forests, it would be expensive to use them as indicators outside of Boreal forests.

**Table 2: Summary of criteria used to evaluate indicators of old-growth forests.**

| **Criteria** | **Short Description** |
|---|---|
| International compatibility | Potentially useful in temperate and tropical forests. |
| Limited mobility | Low dispersal ability |
| Sensitive to forest fragmentation/ requires continuity | Response to fragmentation in the forest landscape |
| Respond to disturbances at the stand scale | Responds to disturbances happening in forest stands |
| Known response to disturbances | Studies document response of organisms to disturbances within forests |
| Low variability in response | Low population fluctuations, reliability of organism as an indicator |
| Knowledge of natural history of organism, habitat affiliation and interactions with other organisms and role in the ecosystem | Sufficient studies provide required information about the ecology of the organism |
| Clear taxonomy | Taxonomy well documented and established |
| Low tolerance levels | Respond to small changes in forest environment |
| High reproductive rate | Progeny generated on a regular basis relative to other organisms |
| Food habitat specialists | Requires specific resources for presence in habitat |
| Easy to find | Not a cryptic organism |
| Data requirements low | Does not require preliminary field research |
| Skills required low | Does not require expert |
| Low cost | Low cost to data collection |

## 3.2 Other Criteria

Some studies have suggested that species should be able to indicate biodiversity and ecological continuity as well. These citeria were not directly used in the evaluation of indicators in this study. Biodiversity, or the ability of species to indicate presence of other taxa was not evaluated in this paper since congruence among rare species has been found to be low (Grenyer et al. 2006). Furthermore, other studies have falsely suggested species, such as Tiger beetles can represent the presence of other species such as butterflies and birds (McGeoch 1998).

Also it is also important to consider a species or the ability of a structural attribute to represent ecological continuity since this directly related to old-growth forests and a lack of disturbances. Ecological continuity, or more simply put is the dependence of an organism on an undisturbed old-growth forest (Nordén and Appelqvist 2001). However, the scale and definition of ecological continuity is highly variable between studies. Other terms that are the same or similar are environmental continuity and forest continuity. It is important not to confuse this with landscape continuity which is the absence of fragmentation in the landscape. The two are related but not the same since there is no historical scale related with landscape continuity often. Nordén and Appelqvist (2001) also highly criticized studies that indicated that a species was dependent of ecological continuity since often the methods used were insufficient in being able to prove ecological continuity. In consideration of this and the variability in the definition of ecological continuity, this concept has been excluded as a criterion for evaluating indicators. Instead a comparison of available studies of species and structural attributes on ecological continuity was done.

# 4. Results

There were more studies available on species such as lichen, which made their evaluation easier. However, for other species such as fungi or new concepts such as wildlife trees, evaluation was much more difficult due to a great dearth in research. The ability of bioindicators or structural attributes to fulfill the criteria can be seen in Table 3. The bioindicator that was able to fulfill the highest percentage of attributes was lichen and saproxylic beetles. There was not much difference between the ability of structural attributes as indicators. As far as an organism's ability to indicate ecological continuity studies have suggested certain species may be suitable but none are conclusive (Table 4).

**Table 3: Table of criteria for evaluating groups of organisms and structural attributes of old-growth forests as indicators of old-growth forests. 1= a species or structural attribute fulfills the criteria, 0= a species or structural attribute fails to fulfill the criteria. Citations in brackets are studies from which evaluation was based on for that species and criteria.**

| **Criteria** | **Species Indicators** | | | | **Structural Indicators** | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | Saproxylic Beetles | Wood-inhabiting Fungi | Bryophytes | Lichen | Dead wood measurements (density, size, number of snags, DBH of snags, decay classes) | Dead wood and Wildlife trees (functionality measurement) | DBH (density above x threshold) of live trees and shade tolerant associates | Tree density | Basal Area |
| Respond to disturbances at the stand scale | 1 (Grove 2002a) | 1 (Sverdrup-Thygeson and Lindenmayer 2003) | 0 (Willis 1993) | 1 (Plata et al. 2008) | 1 (Burrascano et al. 2008) | 1 (DeLong et al. 2004) | 1 (Grove 2002a) | 1(Burrascano et al. 2008) | 1 (Grove 2002a) |
| Known response to disturbances (natural and human) | 1 (Laaksonen et al. 2008, Bouget and Gosselin 2005, Grove 2002a) | 1 (Sverdrup-Thygeson and Lindenmayer 2003) | 1 (Bates and Farmer 1992) | 1 (Bates and Farmer 1992, Plata et al. 2008) | 1 (Burrascano et al. 2008, Quesnel 1996) | 1 (Burrascano et al. 2008, Quesnel 1996) | 1 (Burrascano et al. 2008, Quesnel 1996) | 1 (Quesnel 1996) | 1 (Quesnel 1996) |
| Limited mobility | 1 (Hilty and Merenlender 2000) | 0 (Nordén and Appelqvist 2001 (Aphyllophorales))<br>1 (Jönsson et al. 2008 (for *Asterodon ferruginosus, Phellinus ferrugineofuscuc, P. viticola,* | 1 (Nordén and Appelqvist 2001 (spp dispersed by large gemmae), During 1992) | 1 (Kershaw 1985, Esseen et al. 1996) | 1 | 1 | 1 | 1 | 1 |

| | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | *Phlebia centrifugia*)) | | | | | | | |
| Sensitive to Forest fragmentation/ requires continuity | 1 (Halme and Niemelä 1993, Siitonen and Martikainen 1994, Davies and Margules 1998, Grove 2002a,b, Bouget and Gosselin 2005, Laaksonen et al. 2008, Nilsson 1995) | 1 (Laaksonen et al. 2008, Snäll and Jonsson 2001(polyporous fungi), Komonen et al. 2000) | 1 (Newmaster et al. 2003)<br>0 (Willis 1993) | 1 (Esseen and Renhorn 1998, Esseen et al. 1996) | 0 (Morrison 1988) | 0 (Morrison 1988) | 0 (Morrison 1988) | 0 (Morrison 1988) | 0 (Morrison 1988) |
| Low variability in response | 0 (Kimberling et al. 2001) | 1 | 1 | 0 | 0 (Harrison et al. 2001, Wells and et al. 1998) | NA | 0 (Harrison et al. 2001, Wells and et al. 1998) | 0 (Harrison et al. 2001, Wells and et al. 1998, Quesnel 1996) | 0 (Harrison et al. 2001, Wells and et al. 1998) |
| Knowledge of natural history of organism, habitat affiliation and interactions with other | 0 (Nordén and Appelqvist 2001) | 0 (Jönsson et al. 2008) | 0 Esseen et al. (1996) | 1 (Nimis et al. 2002) | 1 (Quesnel 1996) | 1 (Quesnel 1996) | 1 (Quesnel 1996) | 1 (Quesnel 1996) | 1 (Quesnel 1996) |

| | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| organisms and role in the ecosystem | | | | | | | | | |
| Clear taxonomy | 1 | 0 (Webster 1970, Watling 2003) | 1 | 1 | ________ | ________ | 1 | 1 | 1 |
| Low tolerance levels | 1 (Laaksonen et al. 2008) | 1 (Toljander et al. 2006, Sverdrup-Thygeson and Lindenmayer 2003) (inferred) | 1 (Newmaster et al. 2003) | 1 (Kricke and Loppi 2002). | 0 (Steen et al. 2008, Burton et al. 1999) | 0 (Steen et al. 2008, Burton et al. 1999) | 0 (Steen et al. 2008, Burton et al. 1999) | 0 (Steen et al. 2008, Burton et al. 1999) | 0 (Steen et al. 2008, Burton et al. 1999) |
| High reproductive rate | 1 (Murdoch 1966) | 1 (Kallio 1970) | 0 (During 1992) | 0 (Ellis and Coppins 2007, Kershaw 1985, During 1992, Esseen et al. 1996) | 0 | 0 | 0 | 0 | 0 |
| Food/habitat specialist | 1 (Hilty and Merenlender 2000) | 1 (Toljander et al. 2006, Sverdrup-Thygeson and Lindenmayer 2003, Snäll and Jonsson 2001) | 1 (Watson 1964) | 1 (Kershaw 1985, Esseen et al. 1996, Plata et al. 2008) | ______ | ______ | ______ | ______ | ______ |
| International compatibility | 1 (Grove 2002a, Lachat et al. 2006) | NA | NA | 1 (Rose 1992, Plata et al. 2008) | 1 (Grove 2002a) | NA | 1 (Grove 2002a) | 1 (Grove 2002a) | 1 (Grove 2002a) |
| Easy to find and measure | 1 (Hilty and Merenlender 2000) | 0 | 1 | 1 (Plata et al. 2008) | 1 (Grove 2002a, Holt et al. 1999) | 1 (DeLong et al. 2004) | 1 (Holt et al. 1999) | 1 Holt et al. 1999 | 1 (Grove 2002) |
| Data Requirements | 0 (Grove 2002) | 0 (Laaksonen et al. 2008) | 0 | 0 | 0 (Wells et al. 1998) | 0 (DeLong et al. 2004) | 0 (Wells et al. 1998) | 0 (Wells et al. 1998) | 0 (Wells et al. |

| | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| low | | | | | | | | | 1998) |
| Skills Required low | 0 | 0 | 0 | 0 | 1 (Wells et al. 1998) | 1 (DeLong et al. 2004) | 1 (Wells et al. 1998) | 1 (Wells et al. 1998) | 1 |
| Low cost | 0 (Grove 2002) | 0 | 0 | 0 | 1 | 1 (DeLong et al. 2004) | 1 | 1 | 1 |
| **Total** | 10/15 | 8/14* | 8/14** | 10/15 | 8/13 | 7/11 | 9/14 | 9/14 | 9/14 |
| **Percent** | 67% | 57% | 57% | 67% | 62% | 64% | 64% | 64% | 64% |

*Used Jönsson et al. (2008) value for limited mobility since some species are able to fulfill this requirement

**Used Newmaster et al. (2003) for value of sensitivity to forest fragmentation, if Willis (1993) value was used score would be 50%

**Table 4: List of studies that associate an organism or structural attribute of old-growth with ecological continuity.**

| **Indicator** | **Definition of Ecological Continuity** | **Ecological Continuity** | **Comments** | **Source** |
|---|---|---|---|---|
| Wood-inhabiting fungi | Lack of large scale disturbances in the last 250 years. Study did not require complete absence of human disturbance (e.g. single tree removal). | Presence of *Phellinus nirgolimitatus* depended more on the continuity of the landscape than continuity of the stand scale. | Possibility *P. nirgolimitatus* could be used as an indicator of landscape continuity but this requires further testing. *P. nirgolimitatus* appears to be unsuitable as an indicator of ecological continuity at the stand scale. | Sverdrup-Thygeson and Lindenmayer 2003 |
| Wood-inhabiting fungi | Lack of large scale disturbances in the last 250 years. Study did not require complete absence of human disturbance (e.g. single tree removal). | Continuous presence of old-growth forest did not explain occurrence of *Cystostereum murraii*. | *C. murraii* is not a suitable indicator of ecological continuity | Sverdrup-Thygeson and Lindenmayer 2003 |
| Saproxylic Beetles | NA | Higher abundance of rare species in Russian Karelia versus Finish Karelia assumed to be due to differences in management history. In Russia leaving of non-marketable trees has probably increased the diversity of beetles. | Doesn't isolate the effect of differences in historic management or ecological continuity | Siitonen and Martikainen 1994 |
| Saproxylic Beetles | Following that of (Nordén and Appelqvist 2001) | Observed difference in the biodiversity of rare or interesting saproxylic beetles in the forests of Boulogne and Vincennes in Paris, | Only observations, hypothesis remains untested | Bouget and Brustel 2008 |

| | | | | |
|---|---|---|---|---|
| | | France and in the Pyrenean Forests of southern France. Differences assumed to be due to difference in the major disturbances to break the continuity in the forest in the Parisian forests or in the naturalness of the forests in the Pyrenees | | |
| Bryophytes | Environmental continuity- directly affect by size and number of large disturbances | Largest stand with the highest environmental continuity in the coastal western hemlock (CWH) had highest bryophyte diversity | Disturbances considered were forest fire and logging- only the history of logging was considered. | Newmaster et al. 2003 |
| Decay classes | NA | Supply of dead wood in all decay classes related to length of time with no human disturbance. Unmanaged stand had a continuous supply of dead wood in all decay classes but managed stand lacked wood in some decay classes. | Study used an old-growth forest that was subject to dead wood removal to compare it to a managed forest of the same type. | Burrascano et al. 2008 |
| Dead wood (different decay classes) | Lack of large scale disturbances in the last 250 years. Study did not require complete absence of human disturbance (e.g. single tree removal). | Very weak correlation (R-0.15) between dead wood in all decay classes and 140 years continuous old-growth forest. Plots lacking continuity still supported logs in the last 3 decay classes. | Dead wood decay classes unsuitable as ecological continuity indicators | Sverdrup-Thygeson and Lindenmayer 2003 |

## 5. Discussion

Of the indicators evaluated in this study, Lichen and saproxylic beetles appear to be the two better indicators of old-growth forest when evaluated on their suitability to be an indicator. Several authors have also suggested the use of multiple indicators to strengthen the ability of species to indicate an ecological state (Hilty and Merenlender 2000). The use of lichen and saproxylic species could complement each other well. Saproxylic species have high reproductive rate, where as lichens have a low reproductive rate and lichens have been better researched as an indicator than saproxylic species have. Lichens are less reliable as indicators of old-growth forest since they have a slower response rate to disturbances (Ellis and Coppins 2007). In fact, the long time lag in the response of lichen creates quite a problem for their use. If the time lag in the response of lichen can be quantified, this would make their use more reliable. Until this is done, lichen should not be used without species that are able to respond more immediately to disturbances. Saproxylic species that have a high reproductive rate may be faster to respond to disturbances than lichen. It would be important, however, to choose saproxylic beetles that have predictable population fluctuations. In some situation it may be possible to counter fluctuations in the population of beetles with the use of an index (Kimberling et al. 2001). For simple presence/ absence studies fluctuation in the population of beetles may create a difference in the ability of beetles to be detected. Thus, it would be important to compare results across years and times of the year that would be expected to have similar levels of population. When using ecological indicators it is important to be aware of their abilities and their deficiencies and attempts to correct for any deficiencies.

Another problem with the use of lichens is that a number of lichen suggested as indicators have proven ineffective. It may be possible for lichens as ecological indicators more reliable, though, since lichens are currently well established as an indicator of air quality (environmental indicator) (e.g. Skye 1979, Kovalchuk et al. 1998). Since lichens are well established as environmental indicators, this adds a benefit to using lichens because there have been many studies published on the use of lichen as indicators. The level of research available is a weakness in saproxylic species, thus the use of lichen and saproxylic beetles may complement each other well.

Bryophytes and fungi appear to be less valuable indicators of old-growth forests than lichen and saproxylic beetles. What contributed to the low score of wood-inhabiting fungi was a lack of information on the natural history, the taxonomy was not clear and they are not easy to find and measure. These criteria do not mean that functionally wood-inhabiting fungi are not associated with old-growth forests, simply they are not practical to use as bioindicators. More research will not make wood-inhabiting fungi better indicators of old-growth forests since they are not easy to find and measure, making it difficult to assess the presence or absence of species. On the other hand, what contributed to the low score of bryophytes was their inability to respond to disturbances at the stand scale, insufficient information on their natural history, and their low reproductive rate. Failure of these criteria does signify that bryophytes are unsuitable to indicate old-growth forest. An important criterion was the ability to respond to disturbances at the stand scale and failure of this criteria means that bryophytes should not be used as indicators at the stand scale. In addition to this, bryophytes do not have a high reproductive rate and thus there will be a delay in the response of bryophytes to disturbance. Thus, wood-inhabiting fungi are not practical indicators of old-growth forests and bryophytes are inappropriate indicators.

None of the species indicators evaluated here provide a quick, easy and low cost method for indicating old-growth forests. Thus it is unlikely that they will ever be used on a broad scale as a management tool. Lichen does have the possibility, however, of being used on a more broad scale if the NIEC developed by Rose and Coppins (2002) is revised once again and tested for its reliability. The NIEC could potentially help reduced the time and skill required for sampling lichen as a bioindicator. The NIEC also shows potential for being used as an indicator of old-growth forests across a diversity of forests since it has been used in the United Kingdom, northern hardwoods and spruce-fir forests of New Brunswick and New England in North America (Selva 1994), in Sardinia, Italy (Zedda 2002, the tropical forests of Costa Rica (Plata et al. 2008). However, until the NIEC is completely revised and tested it is not a reliable tool of ecological continuity.

Structural indicators of old-growth do provide a fast, low skill and low cost method for identifying forests. The use of DBH, density and basal area is not necessarily better than dead wood measurements which received a slightly lower score (64% versus 62%). What contributed to the higher score for DBH, density and basal area is that they had a clear taxonomy, where as dead wood measurement were not dependent on the identification of the species and thus this criteria was irrelevant in evaluating dead wood. Discounting the criteria clear taxonomy, dead wood measurements, DBH, density and basal area all have the same score (62%). A major barrier in the use of structural measurements as indicators of old-growth forests is the requirement to calibrate the use of the structural indicator to different forest types, where climate and species dominance differ. This would require field research in every forest type to establish threshold levels that indicate different successional stages. A further problem with structural indicators is their inability to respond to fragmentation and small scale disturbances. Discounting a particular distance of forest from the edge (e.g. Morrison 1988) could be used as a method to exclude areas influenced by edge effects. However, once the area disturbed begins to recover there may be no easy way to measure the area considered edge habitat but edge effects may still be persistent and have a lasting effect on sensitive flora and fauna. For example Matlack (1993) found that microhabitat in edge habitat had recovered only partially from forest fragmentation after 20-40 years in eastern United States forests. Using structural indicators may also fail to detect small scale disturbances such as coppicing. Or, if only DBH, density or basal area are used they may not detect the impacts of firewood collection. Thus, it would be important that structural indicators be used together (e.g. DBH measurement, tree density and dead wood measurements). The method of using wildlife trees as suggested by (DeLong 2004) has potential to be useful but still suffers from the same problems as the other structural indicators except it is more subjective and less quantitative than the use of other structural indicators. In theory the use of wildlife trees may be a better surrogate measurement for ecological indicators since it should be more closely related to habitat availability, however, this remains untested. Nonetheless, use of structural indicators provides a more accurate way of indicating old-growth forest than methods based on tree age (Whitman and Hagan 2007, DeLong 2004, Franklin and Spies 1991b).

Choosing a bioindicator versus a structural indicator may depend on the accuracy required and budget available. In situations where a high level of accuracy and ecological continuity are not important, then it may be appropriate to use structural indicators. However, the accuracy of lichen and saproxylic species versus structural attributes remains untested in many forest types. In theory, for identifying high priority conservation areas due to a lack of human disturbance it may be more appropriate to use species indicators since they are able to response to small scale disturbances and forest fragmentation. All indicators face a tradeoff between simplicity and accuracy (Failing and Gregory 2003).

As for indicating ecological continuity, studies indicate that wood-inhabiting fungi, saproxylic beetles, bryophytes and dead wood measurements are able to represent ecological continuity. It is important, however, to pay attention to the definition of ecological continuity used and the methods used in the study as seen in Table 2. After evaluating definitions and methods used in studies regarding ecological continuity it is still unclear which species or structural attribute is a better indicator of ecological continuity as defined by Nordén and Appelqvist (2001). The study by Sverdrup-Thygeson and Lindenmayer (2003) on wood-inhabiting fungi was one of the better studies on ecological continuity and concluded that the species of wood-inhabiting fungi that they studied were inappropriate as indicators of ecological continuity at the forest stand scale. Sverdrup-Thygeson and Lindenmayer (2003) also concluded that dead wood provided a good indicator of important habitat structure but is not a good indicator of absence of disturbance within a stand. The other studies on ecological continuity were not as useful in being able to conclude if a species is useful as an indicator of ecological continuity or not. It is important that studies attempt to isolate the effect of ecological continuity on species presence. These studies are merely suggestions that the species may require ecological continuity. For example, for saproxylic beetles another study indicates that a relationship with ecological continuity may depend on the forest type. However, in regions with higher natural disturbance frequencies the abundance of dead-wood may have a greater effect on saproxylic species presence than ecological continuity as is the case in boreal forests of Fennoscandia (Kouki et al. 2001). Also a few studies have suggested lichen can be used as indicators of ecological continuity (e.g. Rose and Coppins 2002), however, the study by Ellis and Coppins (2007) indicates that lichens are not suitable indicators of ecological continuity. Due to the lack of consistency in studies on ecological continuity and methods that do not allow for definitive conclusions, it is still unclear which species may be better indicators of ecological continuity. Future studies of ecological continuity should attempt to use a definition of ecological continuity compatible to that of (Nordén and Appelqvist 2001) rather than creating confusion by the use of multiple forms of ecological continuity.

However, the concept of ecological continuity may only be useful for areas with low natural disturbance frequencies. Areas that naturally have high fires frequencies may be excluded based on the concept of ecological continuity. In more xeric landscapes that lack disturbance from fire due to fire suppression, this can be considered a type of anthropogenic disturbance. The concept of ecological continuity though, does not account for these types of natural disturbances. Thus, ecological continuity is not a useful concept to apply in all ecosystems and traditional ecological indicators will be unable to indicate ecological continuity in areas of high natural disturbance.

Unfortunately, the use of indicators species may not be as simple as previous thought and change may be required in how indicators are used. In a study by Laaksonen et al. (2008) on generalist and specialist species of beetles and fungi in old-growth forests in Finland and Russia they suggested which species will demonstrate a response to habitat fragmentation will vary with the stage of fragmentation and will vary with the forest location. This implies that for each stage of forest fragmentation different indicators will be required and that different indicators may be needed in different locations. For example *Pytho kolwensis*, the most sensitive species in the study by Laaksonen et al. (2008) was too rare in Finland to be used as an indicator species and the other specialist species they studied (*Olisthaerus substriatus, Harminius undulatus, Fomitopsis rosea and Phellinus ferrugineofuscus*) were still too common and abundant in eastern Finland that habitat fragmentation has still not affected their population densities. To improve the use of ecological indicators it is necessary that effectiveness of a species is tested in an area before use and that response of the species to disturbance is quantified along a gradient.

None of the indicators evaluated in this study were able to fulfill all criteria for indicators. It is important to consider that it is not possible for indicators to capture the full complexity of the system though (Dale and Beyeler 2001). In order to capture the full complexity of the system complete surveys of the forest structure, processes and species would be necessary (e.g. Ruiz-Jaen and Aide 2005). It is, however, important to identify which indicators will be able to capture a higher level of complexity and which one are more appropriate for use as indicators. Lichen and saproxylic beetles relative to the other indicators evaluated in this study appear to be more appropriate indicators of old-growth forests.

Unfortunately, the use of ecological indicators is still fraught with uncertainty and lacks reliable conclusions. To clarify the situation more research is need. What is crucial is that indicators are evaluated and tested before they are used and applied. There are many examples where indicators have been incorrectly used because testing was not done before their use. These kinds of studies only propagate confusion and the inappropriate use of indicators. There is also the need for consistency in testing methods and terms used. Differences in definitions of ecological continuity and methods used make results from studies incomparable and difficult to apply in management. Before an indicator is used it is important that it is tested in the forest type before hand. Overall, a large amount of research is still required on the use of bioindicators and structural attributes. By evaluating indicators for a particular system though, it is possible to identify more appropriate indicators and thus focus research on these species. In the case of old-growth forests, research should focus on lichens and saproxylic beetles. Alternatively, structural indicators provide a method of indicating old-growth forests that may not capture the full complexity of the system like species indicators but is a more accurate method than those currently used.

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