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Forest Ecology and Management 174 (2003) 353–363
Forest Ecology and Management
www.elsevier.com/locate/foreco

Ecological continuity and assumed indicator fungi in boreal forest: the importance of the landscape matrix

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Received 2 May 2001; accepted 23 January 2002

Abstract

In a boreal forest in southeast Norway, we evaluated the relative importance of stand-level structures versus historical data on forest age and absence of logging (at two spatial scales; stand and surrounding landscape), on the presence and abundance of the wood-rotting fungi *Phellinus nigrolimitatus* and *Cystostereum murraii*. Both species are often considered to be indicators of long-time continuous presence of downed logs in Scandinavian forest stands.

Of the stand-level variables, number of logs in late stages of decay was positively related to *P. nigrolimitatus* presence, while diversity of coarse woody debris was positively related to the abundance of the species. Both the presence and abundance of *P. nigrolimitatus* was strongly and positively correlated with the area of forest uninterrupted by major disturbance the past 240 years (equalling 140 years of "old growth continuity") in the surrounding landscape (80 ha). For *C. murraii*, consistent results was not found.

We conclude that the causal relationships between ecological continuity and possible indicator species must be investigated on a larger scale than the stand-level as the condition of the forest surrounding a stand can have a large influence on these relationships.

Keywords: Conservation; *Cystostereum murraii*; Forest management; Fragmentation; Old growth; *Phellinus nigrolimitatus*

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1. Introduction

There has been an increasing concern over the past 10 years about how to harvest timber from Scandinavian boreal forests while at the same time minimising negative impacts on forest biodiversity (Angelstam and Pettersson, 1997; Fries et al., 1998). The need for simple and rapid assessment methods has received particular attention and the use of indicator species to identify areas of high conservation value has been suggested as one such method (Tibell, 1992; Nilsson et al., 1995; Kuusinen, 1996). The indicator species concept is not new (Lindenmayer et al., 2000) and it has been applied in many different contexts (Landres et al., 1988; Spellerberg, 1994). In Scandinavia, wood-inhabiting fungi have attracted particular interest as potential indicators of coniferous forest with "long ecological continuity"; that is, the continuous long-term (200–300 years) presence of logs on the floor of a given stand (Høiland and Bendiksen, 1996; Lindblad,

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PII: S0378-1127(02)00043-9

1998). Two species widely used for this purpose are the wood-rotting *Phellinus nigrolimitatus* (Romell) Bourdot and Galzin and *Cystostereum murraii* (Berk and Curtis) Pouzar that both occur in old spruce forest (Nitare and Norén, 1994; Bredesen et al., 1997). Both species are listed as "in need of care" on the Norwegian Red List (Anonymous, 1999b).

The concept of ecological continuity recently has become popular in Scandinavia where it is now widely used in connection with forest management (Angelstam and Pettersson, 1997). Indeed, together with the presence of rare and threatened species (hereafter called red-listed species), the notion of "ecological continuity" is currently one of the prime criteria for the selection of forest sites for conservation in Scandinavia (Nilsson et al., 1995; Esseen et al., 1997). Ecological continuity has been defined as "an ecological attribute that is maintained within an area over time" (Gundersen and Rolstad, 1998; p. 21). Many authors consider ecological continuity to relate best at the stand-level, although several workers emphasise the importance of landscape-level considerations (Kuusinen, 1996; Økland, 1996; Ohlson et al., 1997). In boreal forest management, 200–300 years—the natural generation time for dominant tree species—is considered to be the most relevant time-scale for ecological continuity (Gauslaa and Ohlson, 1997).

According to the definition given above, ecological continuity can be described for different attributes that persist in a stand over a prolonged period (e.g. forest floor conditions, the quantity and condition of dead wood or large hollow trees). Ecological continuity in old growth attributes is considered to occur in boreal forest only if such attributes are unaffected by: (1) large-scale natural disturbance (e.g. forest fire) in the past 200–300 years; and/or (2) human disturbance regimes such as logging (with the possible exception of single tree removal harvesting methods) (Bredesen et al., 1997). An old growth specialist species may be dependent on 200 or even 300 years of ecological continuity because of dependence on certain micro-habitat structures which need hundreds of years to develop (e.g. dead wood from trees of high age in an advanced decay stage) or because of dependence on continuous presence over the last 200–300 years of certain structures and conditions. Possible explanations for dependence on ecological continuity could be: (1) "poor" dispersal abilities; (2) slow rates of establishment, development or growth; or (3) a combination of these factors. If some species may depend on ecological continuity for either of the above reasons, the species assemblage can reflect differences in the forest history that are no longer discernible in the forest structures as they can be measured at present.

Several authors have emphasised the importance of the matrix surrounding biodiversity study sites, both in general terms (Franklin, 1993; Sisk et al., 1997; Lindenmayer and Franklin, 1999) and in species-specific studies in boreal forest (Ås, 1993; Økland, 1996; Gustafsson et al., 1999). The quality of this matrix, from the perspective of the species in interest, can significantly influence the future occurrence of the species in a landscape of habitat patches embedded in less suitable forest (Lindenmayer and Franklin, in press).

Obtaining reliable information on disturbance that occurred in a boreal forest more than 100 years ago demands reliable historical information or the use of independent, labour-intensive methods like dendrochronology or analyses of coal in soil samples (Lorimer and Frelich, 1989; Dynesius and Johnsson, 1991; Ohlson and Tryterud, 1999). These methods are not operationally practical for widespread use in boreal forest management. However, the presence of particular species of organisms (e.g. fungi) might be a useful indicator that a form of ecological continuity has occurred in a given stand. For example, Bader et al. (1995) found that selective logging approximately 100 years ago decreased the present abundance of large and highly decayed logs and that fungal species characteristic of forest with old growth conditions became rarer with increased past logging activity. However, Ohlson et al. (1997) argued that the concept of ecological continuity was based on correlative assumptions and it had become established without knowledge of the causal relationships with forest history. Given this, in the present paper, we explore the relationships between forest history (such as the absence of past logging operations) and the occurrence of particular fungal species thought to be indicative of ecological continuity of dead wood in a forest stand. We address the following questions: (1) To what extent can stand-scale structures alone explain the presence of *P. nigrolimitatus* and *C. murraii*, both suggested as indicators of 200–300 years of ecological continuity of old growth forest? (2) How do changes in the state of the forest surrounding a given stand over the past 140 years influence the presence and abundance of *P. nigrolimitatus* and *C. murraii* in that stand? (3) Finally, what are the consequences of our results in a conservation management context, both for the use of *P. nigrolimitatus* and *C. murraii* as indicator species of continuity of old growth forest and for the conservation of these red-listed species themselves?

2. Study species

P. nigrolimitatus is a polypore fungus with perennial, tough fruit bodies located underneath large, downed conifer logs (notably Norway spruce *Picea abies* (L.) Karst.) in late stages of decay (Kotlaba, 1972; Bader et al., 1995; Lindblad, 1998). After their death, the fruit bodies decay slowly and can persist on logs for several years. This species has a circumboreal distribution and in North America and Asia it grows on *Picea*, *Abies* and *Pinus* (Ryvarden and Gilbertson, 1993–1994).

C. murraii is a perennial, resupinate corticoid fungus species with fruit bodies that occur underneath or on the side of logs in intermediate stages of decay where the bark is still present (Eriksson et al., 1976–1988; Ryvarden and Gilbertson, 1993–1994; Bader et al., 1995). The species is known from continental and alpine Europe, Asia and North America. In Europe, the species grows on logs and stumps of Norway spruce and in North America it is mostly found on hardwoods, such as *Acer* (Eriksson et al., 1976–1988).

3. Study region

The study was completed in boreal forest on a 35 000 ha forested area in the boreal zone in south-eastern Norway, approximately 100 km north of Oslo (latitudes: 60°15′–60°30′N, longitudes: 10°43′–11°05′E) (Fig. 1). The altitude varied between 400 and 750 m above sea level. Norwegian spruce (*P. abies*) is the dominant tree species in the old forest and the vegetation is either mesic and *Vaccinium*-dominated or more moist vegetation types that are dominated by ferns.

The forest in the study area is privately owned and the property has a well-documented history of extensive logging throughout the 20th century. Information on local forest age and the likely application of selective cutting was recorded as early as 1906, but mapping of stand age and condition was not completed for the entire area until 1954. After this time, all management operations were recorded in all stands (average stand size ∼5 ha) and an inventory of forest age and condition was repeated every 10 years.

4. Materials and methods

4.1. Placement of plots

The field study was undertaken in the summer of 1997. The present study is part of a larger investigation that included comparison of so-called "key habitats"

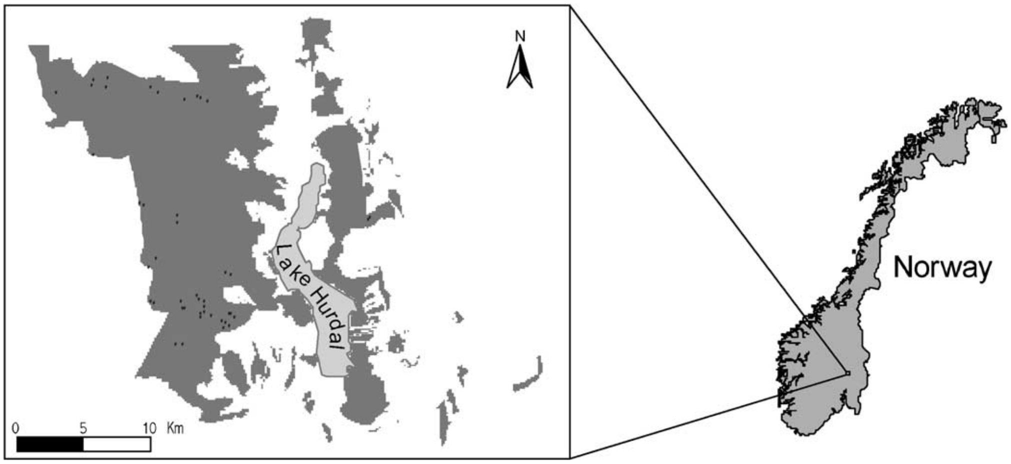


Fig. 1. Map showing the study area, with the 45 study plots marked as dark dots. The geographic position of the study area is also indicated.

and production forest, both within old (>100 years), spruce-dominated forest. In the main study, there were 60 study plots, one plot in each of the 30 old forest key habitats listed in the forest owners inventory and one plot outside each of these key habitats in nearby production forest. The distances between the WKH sites and their corresponding production forest sites were between 300 and 500 m. This paper focuses only on the 45 plots for which information on forest age and stand conditions dating back to at least 1954 was available (22 plots in key habitats and 23 in production forest) (Fig. 1). For further details of the sampling method, see Sverdrup-Thygeson (in press).

The main study also included sampling for beetles attracted to fungi and therefore, the plots were placed around a randomly chosen log hosting the common wood-rotting fungus *Fomitopsis pinicola* (Sw.:Fr.) Karst. according to the following procedure. Within the key habitats, all occurrences of *F. pinicola* were mapped and then one of the occurrences was chosen randomly. Because of the much greater area of production forest, a different approach had to be used there—a random walk was undertaken through the stands of old production forest situated 300–500 m outside the key habitats and the first sighted *F. pinicola* was chosen as the midpoint of the plot. Sverdrup-Thygeson (in press) found that the "key habitats versus production forest" parameter could not explain differences in habitat or presence of suggested indicator species of fungus as a group in the study area. Therefore, the data from the two forest types have been pooled in the present study.

4.2. Recording of indicator fungus occurrences

The number of logs hosting fruiting bodies of *P. nigrolimitatus* and *C. murraii* was recorded in 45 plots, each measuring 40 m × 40 m, within spruce-dominated forest aged about 100 years and older.

4.3. Recording of explanatory variables at the stand scale

Plots were considered to be representative of the forest stands in which they were located and therefore, the term stand-level was used also for recordings made within a plot. Information on productivity (measured as standing volume per ha), altitude, forest age and condition was gathered from the forest management plan and maps of the study region. We considered plots classified as >100 years in 1954, 1974 and 1994 and with no record of thinning operations, to have a minimum of 140 years stand-level continuity of old growth forest.

Dead logs were classified into one of four decay stages and two diameter classes. The following definition was used for decay stages (modified from Dynesius and Johnsson (1991)): (1) wood hard, bark mostly intact; (2) wood starting to soften, bark falling off, texture smooth; (3) wood soft, with crevices, pieces of wood lost so the outline of the log was deformed; and (4) wood soft, possibly with a hard core, log often covered by bryophytes, outer surface of the log hard to define. Logs were also classified as small (those between 15 and 30 cm in diameter) or large (those exceeding 30 cm in diameter). Diameter was measured 1.3 m from the thickest end of a log.

The 45 sample plots were categorised according to the occurrence of logs in the different decay classes: plots lacking logs in at least one of the decay stages 2–4; plots supporting small logs in decay stages 2–4; and plots with large logs in decay stages 2–4. The number of cut stumps, snags and standing dead trees was also recorded in each plot (Table 1).

4.4. Recording of explanatory variables at the 80 ha scale

We scanned the maps from 1954 and 1974 into a computer and adjusted them to the 1994 digital map using the "rubbersheeting" technique in the Arc View extension called Image Analysis (Anonymous, 1999a). We then digitised all stands belonging to the oldest age class (>100 years) close to the survey plots. The proportion of old forest in 1954, 1974 and 1994 within a 500 m zone of each plot was then calculated.

Using ArcView (Anonymous, 1998) scripts, we further calculated the proportion of overlapping old forest, i.e. the forest that was recorded as older than 100 years both in 1954, 1974 and 1994 (Fig. 2). This approach enabled us to identify areas that had been old growth forest for at least 140 years, in 80 ha area surrounding each plot. This was considered the maximum spatial scale of the buffer zones around the plots, as the buffer zones of closely spaced plots increasingly overlapped.

Table 1
Description of variables

Variable	Description
Habitat variables	
Productivity	Productivity measured as standing cubic volume per area
Altitude	Height above sea level, recorded from maps
Vegtype	Vegetation type; mesic or moist
LaLog1	Number of large logs (>30 cm diameter) in first decay stage
LaLog2	Number of large logs (>30 cm diameter) in second decay stage
LaLog3	Number of large logs (>30 cm diameter) in third decay stage
LaLog4	Number of large logs (>30 cm diameter) in fourth decay stage
SumLaLogs	Total number of large logs
SmLog1	Number of small logs (<30 cm diameter) in first decay stage
SmLog2	Number of small logs (<30 cm diameter) in second decay stage
SmLog3	Number of small logs (<30 cm diameter) in third decay stage
SmLog4	Number of small logs (<30 cm diameter) in fourth decay stage
SumSmLogs	Total number of small logs
Standing	Number of standing dead spruces
Snag	Number of spruce snags, defined as upright basal part of dead spruce >60 cm high and lacking more than upper 200 cm of the original tree
DWCont	Degree of perceived continuity in plot judged from the presence of different decay stages: (1) logs in at least one of the three last decay stages was lacking; (2) small logs in the three last decay stages was present; and (3) large logs in the three last decay stages was present
Forest history	
CutStump	Number of cut stumps, 0–10 or more than 10
140yr_stand	Forest age in stand recorded as >100 years in 1954 and not thinned since, i.e. forest continuity is at least 140 years today, 0 or 1
Old54_matrix	Proportion of forest >100 years in 1954 in the 80 ha surrounding the plot
Old74_matrix	Proportion of forest >100 years in 1974 in the 80 ha surrounding the plot
Old94_matrix	Proportion of forest >100 years in 1994 in the 80 ha surrounding the plot
140yr_matrix	Proportion of forest with at least 140 years continuity in the surrounding 80 ha of a site, measured as the overlapping area of Old54_matrix, Old74_matrix and Old94_matrix

4.5. Statistical analysis

Three types of statistical analyses were used. First, univariate logistic regression analyses (Hosmer and Lemeshow, 1989) were performed for the occurrence (presence/absence) of *P. nigrolimitatus* and *C. murraii*. Univariate analyses were run for all explanatory variables. For multiple comparisons, there is a probability that some tests will be statistically significant purely by chance (type I error). Therefore, we corrected the *P*-values of multiple univariate comparisons with Bonferroni correction (Weisberg, 1985). Because the occurrence of *C. murraii* had a highly skewed bimodal distribution with many zero values and few occurrences per plot when present (Fig. 3), further analyses on this species could not be justified.

Second, stepwise forward logistic regression was used to select a model explaining *P. nigrolimitatus* occurrence. Stepwise logistic regression procedure is an effective analysis tool to screen a large number of variables for significant associations with the outcome (Hosmer and Lemeshow, 1989).

Finally, a stepwise forward log-linear procedure (Agresti, 1990) was used to select a model explaining the abundance of *P. nigrolimitatus* (number of logs with fruiting bodies).

Odds ratios for a continuous variable gives the change in the log odds for an increase of one unit in that factor. The exception is for variables relating to the proportion of old forest surrounding the survey plots. For these variables, the odds ratio corresponds to an increase of 10 units (Hosmer and Lemeshow, 1989; p. 56). In the case of categorical variables, the first category was set to zero as a reference class and the odds ratios corresponded to the changes in the log odds between a preceding category and the level

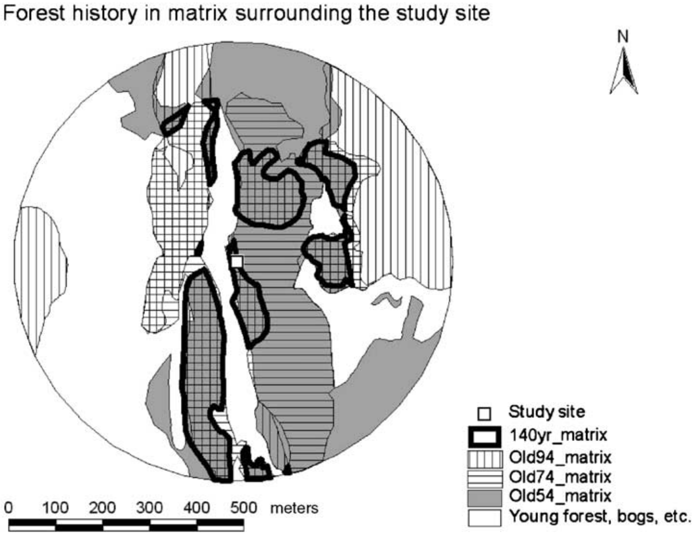
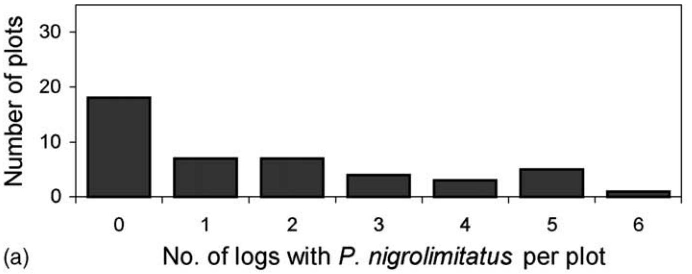


Fig. 2. Map showing how the variable 140yr_matrix was constructed by calculating overlap between forest that was >100 years in 1954, 1974 and 1994 within a 500 m zone around the study sites.



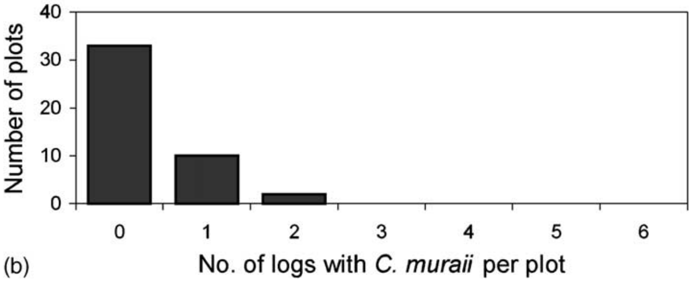


Fig. 3. Distribution of number of logs with (a) *P. nigrolimitatus* and (b) *C. murraii*.

i. In the log-linear analyses, parameter estimates refer to a logarithmic scale. For all multiple models, we tested for biologically relevant interactions between explanatory variables and included them in the final model if they were statistically significant ($P < 0.05$).

5. Results

5.1. *P. nigrolimitatus*

P. nigrolimitatus was present in 60% (27/45) of the plots, the distribution varying between 0 and 6 logs per

Table 2
Multiple models for incidence and abundance of *P. nigrolimitatus* on complete sample ($n = 45$) and on a sub-sample of non-overlapping zones ($n = 21$)

Step	Variable	Odds ratio	95% CI	*P*-value	Step	Variable	Odds ratio	95% CI	*P*-value
Logistic model ($n = 45$)					Logistic model ($n = 21$)				
	Intercept	0.001	(0.0, 0.02)	0.0136		Intercept	0.03	(0.0, 0.05)	0.02
1	LaLog4	36.5	(1.3, 1023.1)	<0.0001	1	LaLog4	9.2	(0.7, 123.0)	0.004
2	140yr_matrix	5.5	(1.2, 25.6)	0.0001	2	140yr_matrix	2.9	(1.1, 7.6)	0.0005
3	SmLog4	6.7	(1.0, 47.1)	0.0086					
Step	Variable	Ratio	95% CI	*P*-value	Step	Variable	Ratio	95% CI	*P*-value
Log-linear model ($n = 45$)					Log-linear model ($n = 21$)				
	Intercept	0.5	(0.2, 1.3)	0.15		Intercept	0.1	(0.0, 0.3)	0.0009
1	140yr_matrix	1.2	(1.1, 1.4)	0.0002	1	140yr_matrix	1.6	(1.3, 2.0)	0.0001
2	LaLog3	1.3	(1.1, 1.5)	0.003	2	LaLog3	1.6	(1.3, 2.0)	0.0001
3	SmLog3	1.2	(1.0, 1.3)	0.05	3	SmLog3	1.3	(1.1, 1.6)	0.0024
4	DWCont1–2	4.0	(1.4, 11.3)	0.01					
	DWCont2–3	1.1	(0.7, 1.8)	0.7					

plot (Fig. 3). Analysis of the incidence pattern of *P. nigrolimitatus* showed that the most significant variable was the abundance of large logs in the latest decay stage, followed by the proportion of the forest surrounding a plot with 140 years of old growth continuity. These two variables explained 68% of the variation in the incidence pattern. A third variable, the abundance of small logs in the last decay stage, further improved the model. Together, these three variables explained 80% of the variation in the occurrence of *P. nigrolimitatus* on measured logs (Table 2).

We used univariate analyses to assess relationships between the probability of occurrence of *P. nigrolimitatus* and the proportion of old (>100 years) forest in the landscape at different points in time. The historical variables showed increasingly better explanatory power with increasing time from the present (Table 3). While the data from the present forest management plan explained only 15% of the incidence pattern of *P. nigrolimitatus*, the 1954 data explained 28%. The highest R^2 value (42%) was achieved when using the variable 140yr_matrix, i.e. the proportion of forest that was old in 1954 and had not been managed (logged) since that time (Table 3). This means that historical information on the landscape conditions adds significantly to the understanding of the species' present occurrence patterns. Around plots where *P. nigrolimitatus* was present, an average of 36% of the surrounding 80 ha forest had 140 years continuity of old growth forest, while around plots lacking *P. nigrolimitatus*, there was an average of only 11% forest with patterns of ecological continuity (Fig. 4). Local (stand-level) continuity of old growth (140yr_stand) also was significant in a univariate analysis (Table 3), but was not an explanatory variable in the final model (Table 2). The correlation coefficient between 140yr_matrix and 140yr_stand was 0.62, indicating that these two variables were not strongly correlated.

The 500 m buffer zones around some of the plots partly overlapped. This was because several of the plots were located less than 1000 m apart. Therefore, it was possible that the plots were not spatially independent. To assess this possible source of error, the analyses were re-run on a sub-sample of the 21 plots with non-overlapping zones. These analyses revealed similar results as outlined above, except that the variable describing the abundance of small logs in the last decay stage was no longer statistically significant

Table 3
Univariate analyses of the incidence of *P. nigrolimitatus* by the forest history variables

Variable	Odds ratio	95% CI	*P*-value	R^2
Old94_matrix	1.8	(1.2, 2.7)	0.003	0.15
Old74_matrix	1.8	(1.2, 2.7)	0.0003	0.22
Old54_matrix	2.1	(1.3, 3.3)	<0.0001	0.28
140yr_matrix	3.9	(1.7, 9.1)	<0.0001	0.42
140yr_stand	7.0	(3.5, 14.1)	0.003	0.15

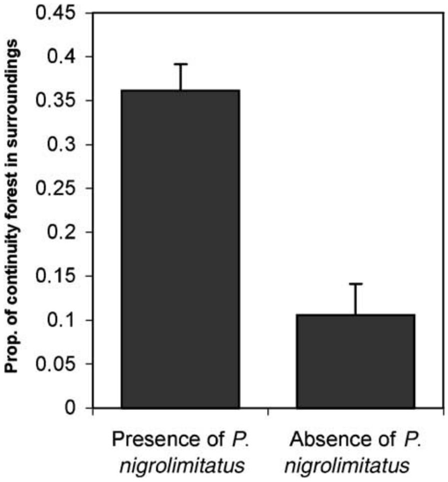


Fig. 4. Mean proportion of forest with at least 140 years of old growth continuity within a 80 ha area surrounding the plots, compared for plots where *P. nigrolimitatus* was present and plots where *P. nigrolimitatus* was absent (ANOVA: $P < 0.0001$, $R^2 = 0.41$). Standard errors are indicated by vertical bars.

(Table 2), indicating that spatial dependency was a minor problem.

The analysis of the number of logs supporting *P. nigrolimitatus* showed that the proportion of surrounding forest with 140 years of ecological continuity was the most significant explanatory variable, followed by the abundance of logs in the third stage of decay and the simultaneous presence of logs in medium and late decay stages (Table 2). The final model explained 20% of the variation in abundance of *P. nigrolimitatus*-infected logs. An analysis on the sub-sample of non-overlapping buffer zones gave identical results, except that the last variable (simultaneous presence of logs in medium and late decay stages) was no longer statistically significant (Table 2).

5.2. *C. murraii*

C. murraii was present in 27% (12/45) of the plots, and always occurred on logs. The probability of recording *C. murraii* increased significantly ($P < 0.05$) with the total abundance of small logs, with the abundance of small logs in early stages of decay, with an increasing number of snags and when vegetation was moist rather than mesic (Table 4). However, none of these variables remained statistically significant after Bonferroni corrections and no multiple model could be constructed. None of the variables relating to ecological continuity, either on the stand-level or in the surrounding 80 ha, were statistically significant for this species.

Table 4
Univariate analyses of the incidence of *C. murraii* by the habitat and forest history variables

Variable	Odds ratio	95% CI	*P*-value	R^2
SumSmLogs	1.2	(1.0, 1.4)	0.007	0.14
Snag	1.3	(1.0, 1.6)	0.01	0.12
SmLog1	1.4	(1.0, 1.9)	0.02	0.10
Vegtype	4.5	(1.1, 18.9)	0.04	0.08

Only variables that were statistically significant ($P > 0.05$) before a Bonferroni correction for multiple testing are shown. None of the variables were significant after such correction.

6. Discussion

We compared the presence and abundance of fungal species in plots with and without old growth continuity on a time-scale dating back at least 140 years and at two spatial scales (the stand-level and the level of the surrounding landscape (80 ha)). We found that the number of logs in decay stages 3 and 4 were the stand-level structures that best explained the incidence and abundance of *P. nigrolimitatus* (Table 2). However, forest conditions in the surrounding landscape also was important in explaining both the presence and the abundance of the species. Especially when we extended both the spatial scale (from forest stand to surrounding 80 ha) and the temporal scale (from present day to 240 years back in time), we found that the absence of forest fires, stormfellings, clearcuttings and thinnings in the matrix the past 240 years increased the chance of present occurrence of *P. nigrolimitatus* within a stand.

Notably, the definition of old growth continuity used in this present study did not require the complete absence of human disturbance (such as single tree removal). However, as clearcutting was not used before the turn of the century, it is reasonable to assume that the forest assigned to the oldest age class in 1954 had never been clearcut. We were not able to detect major disturbances further back in time than 1850. We have also focused on only two of the many suggested indicator species of old growth continuity.

Therefore, this study is a substantial but still preliminary attempt to explain the causal relationships between potential indicator species and the entities for which they are thought to be indicative.

The incidence pattern of *C. murraii* fruiting bodies differed from that observed for *P. nigrolimitatus*, and no statistically significant model could be constructed. Notably, the lower sampling rate for this species and the skewed distribution (Fig. 3) may have made it more difficult to detect factors influencing its distribution pattern. Continuous presence of old forest surrounding the survey plots did not explain the occurrence of *C. murraii*. This species is often found on small and intermediate diameter logs (Bader et al., 1995; Bredesen et al., 1997) and is not as dependent on large logs as *P. nigrolimitatus*. This may explain why the total number of small logs was a significant factor in statistical modelling (before Bonferroni corrections) (Table 4).

6.1. Stand-level structures

The statistical relationship for *P. nigrolimitatus* differed depending on whether the presence of the species or the abundance of the species was the response variable. Logs in the final decay stage (especially large diameter logs) were important for the presence of *P. nigrolimitatus* in a stand. In contrast, the abundance of logs with *P. nigrolimitatus* was significantly related to the number of logs in the third stage of decay (Table 2). If logs in the late stages of decay are the preferred substratum for *P. nigrolimitatus* (Kotlaba, 1972; Bader et al., 1995; Lindblad, 1998), our findings indicate that large, viable local populations also inhabit less than optimal logs.

The simultaneous presence of logs in all decay stages has been used to assess the continuity of supply of logs in a forest stand during the past 200 years (Økland, 1996; Bredesen et al., 1997). However, in this study, there was only a very weak correlation between the variable DWCont and 140 years of continuity of old growth forest in the stand ($R = 0.15$). Many plots lacking 140 years of stand-level continuity still supported logs in the three last decay stages. As DWCont still significantly improved the model explaining abundance of *P. nigrolimitatus* (Table 2), it is reasonable to hypothesise that the variable is important because it describes important habitat structures (i.e. diverse dead wood habitats) rather than it being a reliable indicator of absence of major disturbances within a stand.

There was no significant effect of the number of cut stumps on the presence or abundance of *P. nigrolimitatus*. When studying threatened species of fungi (the majority of which have been suggested to be indicator species), Bader et al. (1995) identified significant correlations with the number of cut stumps per area. The differences between the two studies could be attributed to our focus on a single species rather than on an assemblage of threatened species of fungi. It could also be related to differences in the amount of old growth forest surrounding the survey plots.

6.2. Management consequences

Our findings weaken the potential value of *P. nigrolimitatus* as an ‘‘indicator’’ of ecological continuity of old growth on a local (stand-level) scale, because the presence of *P. nigrolimitatus* in a forest stand depended on the landscape context of the stand. If we assume that this is because a high proportion of old growth in the surrounding landscape correlates with a high probability of *P. nigrolimitatus* presence outside the stand, this finding is in line with general dispersal theory as well as metapopulation theory, which suggests that isolation is an important factor influencing species distribution patterns (Hanski and Simberloff, 1997). Our data showed that presence of *P. nigrolimitatus* in a stand was dependent on the conditions in the surrounding matrix over a time-scale of more than 200 years. This means it can be potentially misleading to use *P. nigrolimitatus* as an indicator species of continuity on the stand-level without knowing the history of the forest on a much broader spatial scale.

Can *P. nigrolimitatus* instead be used as an indicator of continuity at a larger scale, as its presence and abundance was clearly associated with the ratio in the surrounding landscape of forest with 140 years of continuity? This question must be further tested in different landscapes and at several spatial and temporal scales. However, our results emphasise the need to include the matrix when studying the relationship between the occurrence of this species and ecological continuity. Further testing of these relationships is important to establish causal links between the occurrence of *P. nigrolimitatus* and significant explanatory variables like the presence of logs in various decay classes and the extent of continuity of old growth forest in the surrounding landscape.

Apart from being used as an indicator species, *P. nigrolimitatus* is also listed as a species “in need of care” on the Norwegian Red List. Few large areas of old growth remain in Scandinavia (Esseen et al., 1997). Even though there have been reports of rare occurrences of *P. nigrolimitatus* on logs in managed stands (Haugan, 1996; Bredesen et al., 1997), the question of whether viable populations of *P. nigrolimitatus* can survive on isolated suitable logs or logs in isolated woodland key habitats is unresolved. The fact that the landscape ratio of forest unaffected by major disturbances the past 240 years had such a large influence on the presence of *P. nigrolimitatus* (Table 2; Fig. 4) is discouraging in that respect. If our findings are confirmed in further studies, it means that conservation efforts for *P. nigrolimitatus* should focus on retaining or restoring substantial areas of old growth forest within managed forest landscapes.

As we have only compared a limited span of spatial and temporal scales, we are not able to draw general conclusions on the causal relationships between the occurrence of *P. nigrolimitatus* and *C. murraii* and old growth continuity. This, however, does not weaken our main conclusion: that, the questions of continuity and potential indicator species must be considered on a larger scale than the forest stand, as the condition of the forest surrounding a stand can strongly influence the incidence and abundance pattern of species.

Acknowledgements

We would like to thank Mathiesen Eidsvold Værk ANS for giving access to study sites as well as to maps and management plans. Jan Løvlie and Erik Toverud have kindly supplied local information and practical assistance. We also want to thank Liv Dervo and Randi Sverdrup-Thygeson for assistance in the field. Rolf Ims, Irene Lindblad, Leif Ryvarden and two anonymous referees made valuable comments on earlier versions of the manuscript. Thanks also to Centre for Resource and Environmental Studies, at the Australian National University in Canberra, where Sverdrup-Thygeson spent 3 months as a research fellow in 1998. This study is part of a co-operation project between Norwegian Forestry Association NORSKOG and University of Oslo, Department of Zoology and received financial support from The Norwegian Research Council.

References

Agresti, A., 1990. Categorical Data Analysis. Wiley, New York.

Angelstam, P., Pettersson, B., 1997. Principles of present Swedish forest biodiversity management. Ecol. Bull. 46, 191–203.

Anonymous, 1998. ArcView GIS version 3.1 for Windows. ESRI Inc., California.

Anonymous, 1999a. Image Analysis version 1.0. ESRI Inc., California.

Anonymous, 1999b. Norwegian Red List 1998. Direktoratet for Naturforvaltning, Trondheim.

Ås, S., 1993. Are habitat islands islands—woodliving beetles (*Coleoptera*) in deciduous forest fragments in boreal forest. Ecography 16, 219–228.

Bader, P., Jansson, S., Jonsson, B.G., 1995. Wood-inhabiting fungi and substratum decline in selectively logged boreal forest. Biol. Conserv. 72, 355–362.

Bredesen, B., Haugan, R., Aanderaa, R., Lindblad, I., Økland, B., Røsok, Ø., 1997. Wood-inhabiting fungi as indicators on ecological continuity within spruce forest of southeastern Norway. Blyttia 3, 131–141.

Dynesius, M., Johnsson, B.G., 1991. Dating uprooted trees: comparison and application of eight methods in a boreal forest. Can. J. For. Res. 21, 655–665.

Eriksson, J., Hjortstam, K., Larsson, K.H., Ryvarden, L., 1976–1988. The *Corticiaceae* of North Europe. Fungiflora, Oslo.

Esseen, P.A., Ehnström, B., Ericson, L., Sjöberg, K., 1997. Boreal forest. Ecol. Bull. 46, 16–47.

Franklin, J.F., 1993. Preserving biodiversity—species, ecosystems or landscapes. Ecol. Appl. 3, 202–205.

Fries, C., Carlsson, M., Dahlin, B., Lämås, T., Sallnäs, O., 1998. A review of conceptual landscape planning models for multi-objective forestry in Sweden. Can. J. For. Res. 28, 159–167.

Gauslaa, Y., Ohlson, M., 1997. Continuity and epiphytic lichens in Norwegian forests—a historical perspective. Blyttia 55, 15–27.

Gundersen, V., Rolstad, J., 1998. Nøkkelbiotoper i skog. En vurdering av nøkkelbiotoper som forvaltningstiltak for bevaring av biologisk mangfold i skog. NISK, Ås.

Gustafsson, L., DeJong, J., Norén, M., 1999. Evaluation of Swedish woodland key habitats using red-listed bryophytes and lichens. Biodivers. Conserv. 8, 1101–1114.

Hanski, I., Simberloff, D., 1997. The metapopulation approach, its history, conceptual domain and application to conservation. In: Hanski, I., Gilpin, M. (Eds.), Metapopulation Biology. Ecology, Genetics and Evolution. Academic Press, San Diego, pp. 5–26.

Haugan, R., 1996. Arealandel av kontinuitetspregete granskoger rundt Oslo. Naturvernforbundet i Oslo og Akershus, Oslo.

Høiland, K., Bendiksen, E., 1996. Biodiversity of wood-inhabiting fungi in a boreal coniferous forest in Sor-Trondelag County, Central Norway. Nord. J. Bot. 16, 643–659.

Hosmer, D.W.J., Lemeshow, S., 1989. Applied Logistic Regression. Wiley, New York.

Kotlaba, F., 1972. Ecology and distribution of *Phellinus nigrolimitatus* (Romell) Bourd. et Galz. in Czechoslovakia. Ceská Mycol. 26, 91–102.

Kuusinen, M., 1996. Cyanobacterial macrolichens on *Populus tremula* as indicators of forest continuity in Finland. Biol. Conserv. 75, 43–49.

Landres, P.B., Verner, J., Thomas, J.W., 1988. Ecological use of vertebrate indicator species: a critique. Conserv. Biol. 2, 316–328.

Lindblad, I., 1998. Wood-inhabiting fungi on fallen logs of Norway spruce: relations to forest management and substrate quality. Nord. J. Bot. 18, 243–255.

Lindenmayer, D.B., Franklin, J., 1999. Managing unreserved forest land for biodiversity conservation: the importance of the matrix. In: Craig, J.L., Mitchell, N., Saunders, D.A. (Eds.), Nature Conservation in Production Environments: Managing the Matrix. Surrey Beatty & Sons, Chipping Norton, pp. 13–25.

Lindenmayer, D.B., Franklin, J.F., Conserving forest biodiversity: from logs to landscapes. Island Press, Washington, DC, in press.

Lindenmayer, D.B., Margules, C.R., Botkin, D.B., 2000. Indicators of biodiversity for ecologically sustainable forest management. Conserv. Biol. 14, 941–950.

Lorimer, C.G., Frelich, L.E., 1989. A methodology for estimating canopy disturbance frequency and intensity in dense temperate forest. Can. J. For. Res. 19, 651–663.

Nilsson, S.G., Arup, U., Baranowski, R., Ekman, S., 1995. Tree-dependent lichens and beetles as indicators in conservation forests. Conserv. Biol. 9, 1208–1215.

Nitare, J., Norén, M., 1994. Signalarter i projekt nyckelbiotoper. National Board of Forestry, Stockholm.

Ohlson, M., Tryterud, E., 1999. Long-term spruce forest continuity—a challenge for a sustainable Scandinavian forestry. For. Ecol. Manage. 124, 27–34.

Ohlson, M., Söderström, L., Hornberg, G., Zackrisson, O., Hermansson, J., 1997. Habitat qualities versus long-term continuity as determinants of biodiversity in boreal old growth swamp forests. Biol. Conserv. 81, 221–231.

Økland, B., 1996. Unlogged forest: important sites for preserving the diversity of *Mycetophilids* (Diptera: Sciaroidea). Biol. Conserv. 76, 297–310.

Ryvarden, L., Gilbertson, R.L., 1993–1994. European Polypores. Fungiflora, Oslo.

Sisk, T., Haddad, N.M., Ehrlich, P.R., 1997. Bird assemblages in patchy woodlands: modelling the effects of edge and matrix habitats. Ecol. Appl. 7, 1170–1180.

Spellerberg, I.F., 1994. Monitoring Ecological Change. Cambridge University Press, Cambridge.

Sverdrup-Thygeson, A. Key habitats in the Norwegian production forest: a case study. Scand. J. For. Res., in press.

Tibell, L., 1992. Crustose lichens as indicators of forest continuity in boreal coniferous forest. Nord. J. Bot. 12, 427–450.

Weisberg, S., 1985. Applied Linear Regression. Wiley, New York.