

## Distribution pattern of the epiphyte *Neckera pennata* on three spatial scales – importance of past landscape structure, connectivity and local conditions

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We tested which factors explain the distribution pattern of the epiphytic moss *Neckera pennata* on three spatial scales using the framework of generalized linear models. First, we tested which factors explained its occurrence in forest stands in a 2500 ha landscape. At this scale, we also tested the effect of the historic landscape structure. We recorded its occurrence in all suitable stands. The occurrence probability increased with increasing present quantity of *Acer platanoides*, and with increasing present and past quantity of *Fraxinus excelsior*. The probability also increased with increasing connectivity to occupied stands. However, the connectivity to stands present in 1977 (recorded from infra-red aerial photographs) explained more of the variation. This suggests that the regional metapopulation size of *N. pennata* has decreased during the past decades, and that its present distribution pattern reflects the age of the remaining stands, and the distribution of past dispersal sources in the landscape. Second, we tested which factors explained the occurrence and abundance on individual trees in three forest stands. *Neckera pennata* mainly occurred on *Acer* and *Fraxinus* stems. The most important variable in explaining occurrence probability was connectivity to surrounding occupied trees, which probably reflects the restricted dispersal range in this species. The abundance on occupied trees was also explained by this variable. The occurrence probability and abundance also increased with increasing tree diameter, probably reflecting the time that a tree has been available for colonization and the time since colonization, respectively. The occurrence probability and abundance furthermore decreased on strongly leaning (and deteriorating) trees. The occurrence probability increased with increasing bark roughness, probably reflecting increasing suitability regarding bark chemistry and moisture. Third, we tested its vertical distribution on occupied trees. The main distribution was below 1.6 m.

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Habitat loss and fragmentation are the primary causes for species declines and extinctions worldwide (Heywood 1995). Species forming metapopulations naturally go extinct and re-colonize their habitat patches in the landscape (Hanski and Gaggiotti 2004), but they too experience declines as the area of suitable habitat

decreases and the spatial distance between habitat patches increases. The metapopulation capacity of a landscape depends on the amount of suitable habitat and its spatial configuration, and, together with the species-specific colonization and extinction rates, defines the equilibrium fraction of patches occupied by a species in

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the landscape (Hanski and Ovaskainen 2000). As the metapopulation capacity of a landscape decreases, some species will pass their extinction thresholds. These will constitute the extinction debt, i.e. species which are doomed to extinction unless the landscape structure is improved (Tilman et al. 1994, Hanski 2000).

It has been suggested that many metapopulation species only very rarely go extinct from their habitat patches (Snäll et al. 2003). In these species with inertia to local extinctions, it has been theoretically shown that the time lag between passing the extinction threshold and regional extinction is particularly long (Ovaskainen and Hanski 2002). These patch-tracking species should show distribution patterns that reflect the past landscape structure for long periods after landscape change. More specifically, their occurrences in habitat patches should be largely explained by the age of the patches, and by the connectivity (sensu Hanski 1999a) to the dispersal sources occurring in the landscape in the past.

The importance of the landscape history for species occurrences has earlier been shown. Variables related to patch age increase occurrence probability of old-growth species (Rose 1992, Penttilä et al. 2004). Lately, the historic surrounding landscape has been accounted for in metapopulation theory (Hanski 1999b), but empirical studies are scarce. It has been shown that the present distribution of a beetle species was better explained by the past than by the present landscape structure (Petit and Burel 1998). A simulation study by Gu et al. (2002) suggested that occurrences of some fungi were better predicted by variables related to the earlier surrounding landscape than by connectivity to occupied patches, or by variables related to patch age.

Trees are patches for a large number of organisms in forest landscapes (Lowman and Nadkarni 1995). They are dynamic patches that emerge, grow and fall. Epiphytes must track their patches for long-term metapopulation persistence. We study the red-listed epiphytic moss, *Neckera pennata*. Its colonizations of trees are mainly explained by the connectivity to other trees occupied by the moss (Snäll et al. 2005). This finding, which reflects its restricted dispersal range, has been found also in other epiphytes (Snäll et al. 2003, Snäll et al. in press). The restricted dispersal is reflected in the spatial genetic structure of the epiphytes in the landscape (Snäll et al. 2004). The risk for a local extinction of *N. pennata* from an occupied tree which remains standing is negligible (Snäll et al. 2005). This inertia to local extinctions suggests that its occurrence and abundance is largely explained by the age of the patches, and by the connectivity to past dispersal sources.

In this study, we test the importance of present and past factors in explaining the distribution pattern of *N. pennata* on different spatial scales. First, we

investigate which factors explain the occurrence pattern of *N. pennata* among stands in the landscape. We test the importance of present stand conditions, of past stand conditions, of connectivity to stands presently occupied by *N. pennata*, and of connectivity to stands suitable for *N. pennata* in the past. Second, within forest stands, we investigate which factors explain the occurrence and abundance pattern of *N. pennata* among trees. We test the importance of the characteristics of the trees, of nearby environmental conditions, and of connectivity to trees presently occupied. Third, we investigate the vertical distribution of *N. pennata* on the tree stem.

## Materials and methods

### Study species and study areas

We studied *Neckera pennata*, an autoicous, epiphytic moss dispersed by spores (sized 24 µm) from frequently encountered sporophytes, or by stoloniform branches (Nyholm 1960). After our study was initiated, Appelgren and Cronberg (1999) suggested that *N. pennata* consists of two sibling species differing at the genome level, in morphology and in tree species preference. We did not consider this differentiation since the possible sibling species cannot be separated in the field. The species is red-listed in Sweden (Vulnerable), mostly found in old forest (Gärdenfors 2000). Its host trees are the broad-leaved trees, ash *Fraxinus excelsior*, elm *Ulmus glabra*, maple *Acer platanoides*, aspen *Populus tremula*, rowan *Sorbus aucuparia*, lime *Tilia cordata*, oak *Quercus robur*, and bird-cherry *Prunus padus*. The moss is considered a good indicator of occurrence of other red-listed species (Nitare 2000).

The study was conducted in the boreo-nemoral zone (Rydin et al. 1999) in Uppland, Sweden. The stand level survey was conducted in a landscape where the local conservation authorities conducted a mapping study of stands where the tree species suitable for *N. pennata* occurred (Eriksson 1997; 60°05'N, 18°20'E). During the 16th–18th centuries this landscape was colonized and inhabited by crofters. Some of the wetlands were turned into arable land after ditching. The forest was utilized for producing charcoal used in the blast furnaces in ironworks. At the end of this era, many of the fields were abandoned and turned into forests through natural succession. The forestry was extensive until it was very much intensified during the mid-1970s. Since then, modern forestry has prevailed (Eriksson 1997). Several stands suitable for *N. pennata* have been cut (Fig. 1), and they are now replaced by young forest successions with trees that are not yet suitable for *N. pennata*, or with tree species that are unsuitable for *N. pennata*, e.g. Norway spruce *Picea abies*. Many of these stands might have been occupied by *N. pennata* prior to cutting. The



Fig. 1. The study landscape where *Neckera pennata* was surveyed in forest stands.

proportion of broad-leaved trees is higher than in other parts of Uppland (Anon. 1997a).

For the study of *N. pennata* occurrence on individual trees, we selected three forest stands located up to 25 km south of the studied landscape. The sites were Erken1 (0.6 ha; 59°52'4"N, 18°30'16"E), Erken2 (1.1 ha; 59°52'4"N, 18°30'14"E), and Valkrör (2.4 ha; 60°3'25"N, 18°26'8"E). At all sites, the host trees for *N. pennata* were intermingled with other broad-leaved trees, and with Norway spruce. *Fraxinus* was most common. The field layer indicated productive soil conditions. They were all old-growth stands. Valkrör is protected as a nature reserve, and the Erken stands are protected as woodland key habitats.

### Occurrence in forest stands

In the year 2000, we recorded the occurrence of *N. pennata* (0, 1) in all 128 potentially suitable stands

in a 2565 ha landscape (Fig. 1). The selection of the stands was based on a survey of biodiversity values related to broad-leaved trees, conducted by the local conservation authorities (Eriksson 1997). Minimum distance between stands was 20 m, and their area ranged 0.01–15 ha.

For each stand we recorded predictor variables, summarized in Table 1. The data were collected as follows: In stands with an area <0.5 ha, or with <100 suitable trees, we counted all suitable trees, and recorded tree species and diameter at breast height (dbh). Minimum dbh to include a tree was 15 cm. In other stands, trees were measured in circular plots with a radius of 7 m. The circular plots were placed in the intersections of a square grid randomly placed across each stand. The length (L) of the edges in the grid was calculated as

$$L = (A/4)^{1/2},$$

where A is stand area in m<sup>2</sup> (Anon. 1999). This leads to approximately constant sampling effort (four plots) in all large stands. Stand area and perimeter were calculated using a geographic information system (ArcView 3.2). We estimated soil moisture on a four-level ordinal scale (Anon. 1997b), where 1 was dry (ground water level >2 m below soil surface), 2 was mesic (ground water level 1–2 m below soil surface), 3 was mesic-moist (ground water level <1 m below soil surface, flat ground), and 4 was moist (ground water level <1 m below soil surface, visible in hollows). In stands where plots were used, soil moisture was recorded for each plot and the mean of the recorded values was used in the analysis.

The local abundance of *N. pennata* (cm<sup>2</sup>) was recorded on each surveyed tree. The abundance data were used for estimating connectivity (see below). The local abundance in each stand was calculated as the sum of the recorded abundances on all trees. In stands where trees had been surveyed in plots, the local abundance (Abund) was calculated as

Table 1. Independent variables recorded for each tree and each stand, respectively.

Tree level analysis	Stand level analysis
Study stand (3 stands)	Number of trees <sup>2</sup>
Tree species (8 species)	Density of trees <sup>2</sup> (ha <sup>-1</sup> )
Diameter (cm)	Mean diameter <sup>2</sup> (cm)
Depth of bark crevices <sup>1</sup> (mm)	Maximum diameter <sup>2</sup> (cm)
Tree inclination (in degrees)	Sum of tree diameters <sup>2</sup> (cm)
Spruce branch (0, 1)	Area (ha)
Soil moisture (4 classes)	Stand perimeter (m)
Relative bryophyte cover	Soil moisture (4 classes)
	Total volume <sup>3</sup> in 1977 (m <sup>3</sup> )
	Volume per ha in 1977 (m <sup>3</sup> ha <sup>-1</sup> )
	Area in 1977 (ha)

<sup>1</sup>Measured 50 cm above the ground. <sup>2</sup>For each tree species separately, and for all trees irrespectively of tree species. <sup>3</sup>Calculated as volume per ha in 1977 × area in 1977.

$$\text{Abund} = \text{Abund}_{\text{plot}} (\text{Area}_{\text{stand}} / \text{Area}_{\text{plot}})$$

where Abund is the summed *N. pennata* abundance recorded on the surveyed plots, Area<sub>stand</sub> is stand area, and Area<sub>plot</sub> is the summed plot area surveyed.

### Landscape state in 1977

Preliminary analysis suggested that *Fraxinus* and *Acer* were the most suitable host trees for *N. pennata*. As *Fraxinus* trees can be distinguished in infra-red aerial photographs (IR photo henceforth), we mapped the past spatial distribution of forest stands with *Fraxinus* trees using IR photos from 1977 (Fig. 1). For each stand, we recorded average *Fraxinus* crown diameter, *Fraxinus* crown cover and average *Fraxinus* tree height. Based on those variables we roughly estimated the volume per ha of *Fraxinus*. As no data from Fennoscandia exist on the relation between these variables and stand volume of broad-leaved trees, we used tabular data for Kentucky hardwoods (Table 8 in Avery 1978).

### Occurrence, abundance and vertical distribution on trees

In each of the three stands, we mapped all potential *N. pennata* host trees with a minimum dbh of 5 cm in 1997. For each tree, we recorded occurrence, total abundance (in cm<sup>2</sup>), and abundance of *N. pennata* in four height zones above the ground (0–80, 80–160, 160–240, >240 cm).

For each tree, we recorded predictor variables summarized in Table 1. As a proxy for chemical environment for *N. pennata*, we noted if a branch from a spruce touched the host tree, since rainwater percolating through coniferous tree branches might affect host tree bark chemistry and bryophyte viability (Gustafsson and Eriksson 1995). We estimated soil moisture for a zone with a 2 m radius around each host tree according to the above scale.

At Valkrör and Erken1, we recorded the summed abundance (in cm<sup>2</sup>) of other epiphytic bryophytes up to 2.4 m above the ground. This measure was used to calculate the relative bryophyte cover (%). As we only measure this at two sites, the variable was not used in the multiple regression models (see below).

### Statistical modelling strategy

To analyze the effect of local variables (Table 1) and connectivity on the abundance and occurrence of *N. pennata*, we applied the framework of generalized linear models (McCullagh and Nelder 1989). When modelling the abundance of *N. pennata*, we assumed

normally distributed residuals and used an identity link function, typical for regression models with a continuous response variable. The initial exploratory analysis showed that the assumption of normality was not fulfilled unless we ln-transformed the abundance variable prior to fitting the model. When modelling the occurrence probability of *N. pennata*, we assumed binomially distributed residuals and a logit link function (logistic regression). The tree and stand levels were analyzed separately following the modelling strategy in Snäll et al. (2003).

We first tested single environmental variables for present local conditions (Table 1) one by one, and selected those with p-values <0.40 in likelihood ratio tests (McCullagh and Nelder 1989). Next, we built a multiple start model with these selected variables, and included biologically reasonable two-way interactions, and squared variables. The multiple model was simplified using stepwise variable selection minimizing AIC (Akaike's information criterion, Akaike 1974) defined by:  $AIC = -2(\text{maximized model log-likelihood}) + \kappa(\text{number of model parameters})$ . The aim of the modelling was to test for significance. We therefore set  $\kappa = 4$ , which is equivalent to the use of  $p = 0.05$  (McCullagh and Nelder 1989).

We then extended the models. At the landscape level analysis, we tested three different model extensions. Firstly, we tested whether connectivity (similar to Hanski 1999a; see detailed definition below) to stands occupied by *N. pennata* improved model fit. Secondly, we tested whether connectivity to suitable stands, irrespectively of whether they were occupied or not occupied, improved model fit. In the third model extension, we tested which local variables for the state in 1977 (Table 1) gave best model fit, and whether this model was improved by adding connectivity to suitable stands in 1977. At the tree level analysis, we tested if connectivity to trees occupied by *N. pennata* improved model fit.

Connectivity ( $S_i$ ) is defined as:

$$S_i = \sum_{j \neq i} p_j \exp(-\alpha(\ln(d_{ij}))^2) Q_j^y$$

Trees and stands are collectively referred to as "units". The indices  $i$  and  $j$  refer to the focal and surrounding units, respectively. In the analysis of connectivity to *N. pennata*, the variable  $p_j = 1$  if *N. pennata* occurred on unit  $j$ , otherwise  $p_j = 0$ . In the analysis of connectivity to stands, irrespectively if *N. pennata* occurred or not,  $p_j = 1$ . The influence of each surrounding unit,  $j$ , is quantified by the log-normal function of the distance  $d_{ij}$  in meters between the units  $i$  and  $j$ . We do not have information about *N. pennata* occurrence beyond 100 m of the periphery of the trees, and beyond 500 m of the periphery of the stands. Therefore, in the analysis of trees maximum  $d_{ij}$  was 100 m, and in the analysis of stands maximum  $d_{ij}$  was 500 m (between the centroids of the stands). The rate of decay is controlled by  $\alpha$ , a parameter

to be estimated from the data.  $Q_j$  denotes different variables in different analyses. In tests of connectivity to *N. pennata*,  $Q_j$  denotes local abundance of *N. pennata* on the units,  $j$ . In the test of connectivity to surrounding suitable stands, irrespectively of whether they were occupied or not,  $Q_j$  denotes the area of the stands,  $j$ . Finally, in the test of effect of connectivity to surrounding suitable stands present in 1977,  $Q_j$  denotes area of the stands,  $j$ , present in 1977.  $\gamma$  is a scaling parameter.

We judged the significance of the connectivity variables and parameters based on likelihood ratio tests (Azzalini 1996), which is appropriate for nested models (McCullagh and Nelder 1989). However, because of their non-linearity, the  $\chi^2$ -distribution approximation is rough, and exact p-value would require computer intensive bootstrap estimation. Therefore, we do not report p for these variables.

We tested if the abundance of *N. pennata* on occupied trees differed among height zones using pairwise t-tests. We report Bonferroni corrected p-values.

The statistical analyses were performed using the software R version 1.8.1 (R Development Core Team 2003), with the add-on libraries geoR version 1.4–4 (Ribeiro and Diggle 2001), and MASS version 7.1–14 (Venables and Ripley 1999), all freely available at <<http://www.r-project.org>>. We wrote our own functions to fit the connectivity variable.

## Results

*Neckera pennata* occupied 50 of the 128 suitable stands. At Erken1, it occupied 36 of the 111 trees, at Erken2 it occupied 148 of the 444 trees, and at Valkrör, it occupied 131 of the 495 trees. Both local variables and connectivity explained abundance and occurrence probability as shown in the first tests of the effect of single variables (Table 2).

### Occurrence in forest stands

The initial analysis showed that the probability of occurrence of *N. pennata* in a forest stand was mainly explained by quantity of *Acer*, but also of *Fraxinus* (Table 2). For each stand the following quantity measures for *Acer* and *Fraxinus* had a positive effect in order of decreasing explanatory power: mean tree diameter, maximum tree diameter, tree density (number  $\text{ha}^{-1}$ ), sum of the tree diameter, and number of trees.

The multiple model for the probability of occurrence of *N. pennata* in a forest stand (null deviance = 172.3, residual deviance = 118.5,  $n = 128$ ; Table 3) showed that the probability increased with increasing density of *Acer*, and with increasing mean diameter of *Fraxinus* trees. The probability furthermore increased with increasing

connectivity to *N. pennata* in the landscape. Best fit was given by  $\alpha = 0.37$ , and  $\gamma = 0.91$ , which implies that the spatial scale of the aggregated structure was  $< 100$  m. We found no spatial structure of *Acer* density or mean tree diameter of *Fraxinus* trees (analyses not shown) within the analyzed spatial scale (500 m). The probability of occurrence was not related to connectivity to suitable stands in general, i.e. irrespectively if they were occupied or not.

The multiple model for probability of occurrence of *N. pennata* in a forest stand was further improved when the past landscape was accounted for (null deviance = 172.3, residual deviance = 93.5,  $n = 128$ ; Table 3). The positive effects of *Acer* tree density and diameter of *Fraxinus* trees remained. The probability also increased with increasing local *Fraxinus* volume  $\text{ha}^{-1}$  in 1977, and furthermore with increasing connectivity to stands present in 1977. Best fit was given by  $\alpha = 0.10$ , and  $\gamma = 0.84$ .

### Occurrence on trees

The probability of occurrence of *N. pennata* on a tree increased with increasing relative cover of other bryophytes, as shown by a single regression model (null deviance = 676.9, residual deviance = 661.0,  $\chi^2 = 15.9$ ,  $n = 556$ ,  $DF = 1$ ,  $p < 0.001$ ).

The multiple model for probability of occurrence of *N. pennata* on a tree (null deviance = 1162.1, residual deviance = 868.6,  $n = 994$ ; Table 3) showed that the probability differed between trees species. *Acer* had higher occupancy than *Fraxinus*. Conversely, aspen had lower occupancy, but there where only 10 aspens in the stands studied. The probability of occurrence increased with increasing dbh, and with increasing depth of bark crevices. The probability was unimodally related to tree inclination, with a positive parameter value for inclination, and a negative parameter value for its square. Finally, there was a clear aggregated pattern in occurrence, as judged by increasing probability of occurrence with increasing connectivity to *N. pennata*. Best fit was given by  $\alpha = 0.36$ , and  $\gamma = 0.62$ .

### Abundance on trees

The abundance of *N. pennata* (ln-transformed) on occupied trees was unrelated to the relative cover of other bryophytes, as shown by a single regression model (null deviance = 572.4, residual deviance = 572.3,  $F = 0.06$ ,  $n = 163$ ,  $DF = 1$ ,  $p = 0.81$ ).

The multiple model (null deviance = 1239.1, residual deviance = 908.2,  $n = 288$ ; Table 3) showed that the abundance of *N. pennata* (ln-transformed) on occupied trees differed among sites. It was highest in Erken2, and lowest in Valkrör. The abundance increased with increasing dbh. As for occurrences, it was unimodally

Table 2. Likelihood ratio tests of the effect of single variables on abundance and occurrence probability of *Neckera pennata*. The p-value for models for occurrence is based on the assumption that deviance reduction follows the  $\chi^2$ -distribution. The p-value for connectivity ( $S_i$ ) was not calculated (see Statistical analysis for explanation). The models with squared variables also included the variables untransformed, and the model with the interaction also included the two single variables.

Variable	N	Sum of square	F	DF	p
<b>Abundance of <i>N. pennata</i> on a tree (ln-transformed)</b>					
Stand	313	1320.4	5.7	2	0.004
Tree species	312	1315.4	2.5	7	0.017
Tree diameter (dbh)	313	1320.4	33.5	1	<0.001
Bark crevice depth	310	1308.4	19.8	1	<0.001
Tree inclination	288	1239.1	0.4	1	0.506
Soil moisture	313	1320.4	3.2	3	0.025
$S_i$ (trees occupied by <i>N. pennata</i> )	313	1320.4	36.6	3	–
Tree inclination, squared	288	1239.1	4.4	1	0.036
Tree species $\times$ bark	309	1303.4	1.1	6	0.388
<b>Probability of <i>N. pennata</i> occurrence on a tree</b>					
	N	Null deviance	$\chi^2$	DF	p
Stand	1049	1282.8	5.6	2	0.060
Tree species	1048	1280.4	41.8	7	<0.001
Tree diameter (dbh)	1049	1282.8	57.7	1	<0.001
Bark crevice depth	999	1241.4	62.3	1	<0.001
Tree inclination	975	1187.6	0.4	1	0.530
Soil moisture	1030	1269.1	4.2	4	0.370
$S_i$ (trees occupied by <i>N. pennata</i> )	1049	1282.8	191.9	3	–
Tree inclination, squared	975	1187.6	5.7	1	0.020
<b>Probability of <i>N. pennata</i> occurrence in a stand</b>					
	N	Null deviance	$\chi^2$	DF	p
Number of <i>Acer</i>	128	172.3	7.0	1	0.008
Number of <i>Acer</i> + <i>Fraxinus</i>	128	172.3	4.8	1	0.029
<i>Fraxinus</i> density	128	172.3	5.4	1	0.020
<i>Acer</i> density	128	172.3	22.9	1	<0.001
Mean <i>Fraxinus</i> diameter	128	172.3	23.8	1	<0.001
Mean <i>Tilia</i> diameter	128	172.3	13.2	1	<0.001
Maximum <i>Tilia</i> diameter	128	172.3	27.7	1	<0.001
Sum of <i>Fraxinus</i> diameters	128	172.3	5.3	1	0.022
Sum of <i>Acer</i> diameters	128	172.3	7.7	1	0.006
Stand area	128	172.3	0.1	1	0.80
Stand perimeters	128	172.3	0.1	1	0.71
Soil moisture	128	172.3	2.1	1	0.146
$S_i$ (stands occupied by <i>N. pennata</i> )	128	172.3	31.9	3	–
<i>Fraxinus excelsior</i> volume ha <sup>-1</sup> in 1977	128	172.3	32.3	1	<0.001
$S_i$ (stands present in 1977)	128	172.3	31.0	3	–

related to the inclination of the tree, and increased with increasing connectivity to *N. pennata*. Best fit was given by  $\alpha=0.58$ , and  $\gamma=1.17$ .

### Vertical distribution on trees

The abundance of *N. pennata* decreased with increasing height above the ground (Table 4). The abundance was higher in both the lowest and second zone compared to the two highest zones (highest  $p=0.03$ ). There were no differences in abundance between the two lowest ( $p=1.00$ ), or the two highest ( $p=1.00$ ) zones.

## Discussion

Our study shows that the distribution pattern of *Neckera pennata* on different spatial scales is explained by local

habitat factors, and by connectivity. Both connectivity to present occurrences of the epiphyte, and connectivity to past suitable stands in the landscape explain today's distribution pattern in this species. We even found that the *N. pennata* occurrence in the landscape was better explained by connectivity to stands suitable in 1977, irrespectively if they were occupied or not, than by connectivity to stands that were presently occupied by *N. pennata*. Connectivity to presently suitable stands, irrespectively if they were occupied or not, did not even significantly explain the current occupancy pattern.

### Occurrence in forest stands

The local properties of a stand clearly affect the probability of *N. pennata* occurrence (Table 3). The probability increased with increasing present density of

Table 3. Variables, with coefficient signs, of multiple generalized linear models for abundance and occurrence of *Neckera pennata* on trees, and in stands. The p-value for connectivity ( $S_i$ ) was not calculated. See Statistical analysis for explanation.

Variable	Sign	F	DF	p
<b>Abundance of <i>N. pennata</i> on a tree (ln-transformed)</b>				
Stand		6.6	2	0.002
Tree diameter (dbh)	+	46.7	1	<0.001
Tree inclination	+	17.3	1	<0.001
Tree inclination, squared	-	12.6	1	<0.001
$S_i$ (trees occupied by <i>N. pennata</i> )	+	30.7	3	-
<b>Probability of <i>N. pennata</i> occurrence on a tree</b>				
	Sign	$\chi^2$	DF	p
Tree species		33.9	7	<0.001
Tree diameter	+	6.1	1	0.01
Bark crevice depth	+	27.0	1	<0.001
Tree inclination	+	4.9	1	0.03
Tree inclination, squared	-	3.7	1	0.05
$S_i$ (trees occupied by <i>N. pennata</i> )	+	161.3	3	-
<b>Probability of <i>N. pennata</i> occurrence in a stand</b>				
	Sign	$\chi^2$	DF	p
<i>Acer</i> density	+	11.7	1	<0.001
Mean <i>Fraxinus</i> diameter	+	9.2	1	0.002
$S_i$ (stands occupied by <i>N. pennata</i> )	+	13.8	3	-
<b>Probability of <i>N. pennata</i> occurrence in a stand, Including landscape history</b>				
	Sign	$\chi^2$	DF	p
<i>Acer</i> density	+	14.6	1	<0.001
Mean <i>Fraxinus</i> diameter	+	11.8	1	<0.001
<i>Fraxinus</i> volume ha <sup>-1</sup> in 1977	+	10.1	1	0.001
$S_i$ (stands present in 1977)	+	20.8	3	-

*Acer* and mean diameter of *Fraxinus*. Similar positive effects have been found in other epiphytes (Hazell et al. 1998, Ojala et al. 2000, Gu et al. 2001). The occurrence probability furthermore increased with increasing volume ha<sup>-1</sup> of *Fraxinus* in 1977. There may be several explanations why both variables had a positive effect in the model. The volume of a stand in 1977 may reflect the time length, prior to 1977, that the stands have been available for colonization. With increasing time length, the probability of a successful establishment having occurred is increased (Rose 1992, Gu et al. 2001, Snäll et al. 2003). The variables describing the present stand conditions may reflect their suitability for colonization between 1977 and present. Alternatively, as these variables measure different forest stand properties, they may reflect different properties which affect the colonization probability of *N. pennata*. The increasing density or volume may also lead to less sun exposure, thereby increasing bark moisture, which may increase the estab-

Table 4. Abundance of *Neckera pennata* in different height zones above the ground. The values refer to mean and standard deviation (in parenthesis) for occupied trees (n = 315).

	0–80 cm	80–160 cm	160–240 cm	>240 cm
Abundance (cm <sup>2</sup> )	137 (364)	150 (424)	55 (207)	63 (280)

lishment probability. Spore germination in *N. pennata* increase with increasing moisture (Wiklund and Rydin 2004a). The relative importance of moisture is, however, uncertain since soil moisture was not significant in the model. The coupling between our variable and bark moisture may though be weak.

The spatial scale of the aggregated *N. pennata* pattern among stands was small, as judged by the high  $\alpha$  in the connectivity variable. The small scale implies that a stand was more likely to be occupied if the nearest surrounding stands were occupied. The same scale of *N. pennata* aggregation was found among trees within stands. These findings support the conclusion of restricted dispersal range in this species by Snäll et al. (in press). They studied *N. pennata* colonizations of trees and found the 95% confidence interval for  $\alpha$  to be 0.13–0.47. The agreement is interesting, and suggests that some of the *N. pennata* occurrences in stands are recent colonizations by short range dispersal from a nearby stand. These conclusions of restricted dispersal are not in agreement with Kuusinen and Penttinen (1999) who found a random distribution pattern, but they had a low statistical power. Snäll et al. (2004) studied spatial genetic structuring of two epiphytic moss species at the landscape scale using amplified fragment length polymorphism (AFLP) markers. They could verify the restricted dispersal range in *Orthotrichum*

*speciosum*, as suggested by the demographic study by Snäll et al. (2003), and they could detect a restricted dispersal range in *O. obtusifolium* that was not revealed by Snäll et al. (2003). Colonizations from mainly nearby dispersal sources have also been found in vascular plants (Verheyen et al. 2003).

In the model where the past connectivity was included, the  $\alpha$  estimate (0.10) defines a spatial scale with a radius of ca 200–500 m. This suggests that *N. pennata* presently mainly occurs in stands that used to be surrounded by *Fraxinus* stands located up to 500 m away. We believe that the dispersal sources for many of today's occurrences were situated in these past surrounding stands.

### Occurrence and abundance on trees

We found that the occurrence probability of *N. pennata* differed between tree species (Table 3), as shown for other epiphytes (Kuusinen 1996, Heegaard and Hangelbroek 1999). This explains why variables related to *Fraxinus* and *Acer* turned out to be significant in the stand level analysis. Different tree species have different bark chemistry (Kuusinen 1996), and this affect the germination of bryophyte spores (Wiklund and Rydin 2004a). The increasing occurrence probability with increasing stem diameter has earlier been found in *N. pennata* (Kuusinen and Penttinen 1999), and several other epiphytes (Rose 1992, Gu et al. 2001, Snäll et al. 2003). The positive effect is likely to mainly reflect time available for colonization, in accordance with the above reasoning, since stem diameter does not affect current colonization probability of *N. pennata* (Snäll et al. 2005). A similar reasoning may hold for the positive effect of increasing bark crevice depth – bark roughness increase with increasing tree age. However, also bark chemistry or moisture may improve with increasing bark roughness, but this effect is probably smaller since the variable does not affect the colonization probability of *N. pennata* (Snäll et al. 2005). Finally, the risk that diaspores are flushed off the bark should decrease with increasing bark roughness. Decreasing risk for diaspore flush-off may also explain the higher occurrence probability on slightly leaning trees. This positive effect may decrease with increasing inclination, which agrees with the study of *N. pennata* colonizations (Snäll et al. 2005). They hypothesized that leaning trees had less suitable bark chemistry and moisture conditions, assumed to change with decreasing tree vitality, or that colonizations may be hindered on such trees because of high abundance of other bryophytes. The present study indicates that the latter effect is negligible, as we instead found a positive effect of the relative cover of other epiphytic bryophytes.

The abundance of *N. pennata* on occupied trees was explained by similar variables that explained its

occurrence probability. We believe that the same underlying mechanisms explain the importance of stem diameter and inclination. The importance of connectivity on abundance may reflect an aggregated suitable environment (Heegaard and Hangelbroek 1999), but it may also reflect that well connected trees were colonized longer ago than isolated trees, allowing longer time for local abundance growth. Well connected trees may also have multiple establishments of colonies arising from diaspores that originate from surrounding trees. This corresponds to increased local population size due to immigration.

It has been suggested that the radial growth of single colonies below 1.7 m may be restricted by interference competition (Wiklund and Rydin 2004b). We believe that this competition is low because we found no effect of relative cover of other epiphytic bryophytes on *N. pennata* abundance, and its main distribution is on the lower part of the stem (Table 4) where the relative cover of potential bryophyte competitors is highest (unpubl.).

### Concluding remarks and implications for conservation

The large importance of the past landscape structure reflects an inertia in *N. pennata* in responding to landscape change. This is typical for patch-tracking metapopulation species (Snäll et al. 2003). In a changing landscape, the distribution pattern will reflect the age of the patches and the distribution pattern of the dispersal sources in earlier times. In contrast, classic metapopulations, characterized by high turnover among their patches, quickly reach a new metapopulation equilibrium after a landscape change (Hanski 1998).

The large importance of the past landscape structure also suggests that *N. pennata* used to occupy more stands in the past. Habitat destruction and fragmentation has probably rapidly decreased its metapopulation size during the past decades. The distribution pattern of *N. pennata* is typical for species that constitute the extinction debt – their distribution pattern reflects the past landscape structure, and they are more frequent than expected by the present landscape structure. With time, they decrease in frequency, and are eventually doomed (Tilman et al. 1994, Hanski 2000). We do not know whether the metapopulation capacity (Hanski and Ovaskainen 2000) of the present landscape permits for a viable *N. pennata* metapopulation at the stand level, but we do believe that its size may decrease further. However, since *N. pennata* only very rarely go extinct from occupied patches (Snäll et al. 2005), the time to a regional extinction in this species is likely to be long. This implies that the chance of successful landscape restoration is high. By retaining the presently occupied



stands, and by increasing the amount of suitable stands in the landscape, there is a great chance for increasing the *N. pennata* metapopulation size as new stands become colonized by diaspores dispersed from the presently occupied stands. The most cost efficient strategy should be evaluated using population viability analysis (PVA) that includes the dynamic nature of forest landscapes (Akçakaya et al. 2004, Snäll et al. in press). The general strategy should, however, be to establish the new stands in the vicinity of presently occupied stands (Hanski 2000).

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