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Influence of habitat quantity, quality and isolation on the distribution and abundance of two epiphytic lichens

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Summary

1 We assessed the relative importance of habitat quantity, quality and isolation for the distribution and local abundance of two epiphytic lichens, *Parmelina tiliacea*, which is red-listed in Sweden, and the common *Pleurosticta acetabulum*. We predicted that habitat isolation should constrain the distribution of the mainly vegetatively dispersed *P. tiliacea* more than the sexually dispersed *P. acetabulum*.

2 All patches of habitat containing suitable host trees for the study species were mapped from aerial, infra-red photographs. Presence and abundance of the lichens were recorded for a total of 3237 trees in 94 patches.

3 Patch identity had strong influence on presence of both species on individual trees. Within patches, presence was positively correlated with tree size and was also influenced by tree species.

4 At patch-level, species presence was positively correlated with tree number and negatively correlated with the proportion of the boundary that bordered coniferous forest and with isolation. Abundance was mostly correlated with tree size or with the number of large trees at tree- and patch-levels, respectively. For *P. acetabulum*, within-patch abundance was also influenced by isolation from other patches.

5 Presence at patch-level was affected by isolation for both species, but this effect differed between the three isolation measures used. There was no clear evidence that the distribution of *P. tiliacea* was more constrained by isolation than that of *P. acetabulum*.

6 Whilst this study emphasizes the importance of habitat quantity for species occupancy and local abundance, it shows that explanations of species occurrence in fragmented landscapes must also involve variables describing habitat quality and spatial configuration. Moreover it illustrates the difficulties in predicting species' occupancy from general knowledge about their dispersal traits.

Key-words: connectivity, dispersal ability, landscape configuration, *Parmelina tiliacea*, *Pleurosticta acetabulum*

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Introduction

Although a common cause of variation in species local abundance and regional distribution may be resource or habitat availability (e.g. Venier & Fahrig 1996; Gregory & Gaston 2000), species may not be able to colonize all suitable habitat because their dispersal cannot reach isolated fragments. According to metapopulation theory, both local habitat availability (often measured as patch size) and habitat isolation are important in determining species' distributions (Hanski 1999). Patch size determines local population size, which in turn affects extinction rates, while patch isolation affects colonization rates. There is empirical evidence from several systems that both patch size and isolation influence patch occupancy patterns (e.g. Hanski 1994; Hokit *et al.* 1999; Hames *et al.* 2001). In addition, patch quality may affect species occupancy and turnover rates (Summerville & Crist 2001; Fleishman *et al.* 2002).

The response to habitat quantity and isolation differs between species (e.g. McGarigal & McComb 1995; Villard *et al.* 1999), with their relative importance likely to depend on species traits such as habitat requirements and dispersal ability (e.g. Quintana-Ascencio &

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Menges 1996; Hokit *et al.* 1999; Marshall *et al.* 2000). For mosses and higher plants there is a general relationship between vegetative dispersal and rarity (Longton 1992; Gaston & Kunin 1997), suggesting that vegetatively dispersed species are more constrained by their dispersal capacity than sexually dispersed species. Lichens have several different mechanisms for dispersal, including sexually derived spores as well as vegetative propagules such as soredia and isidia (Hale 1983). Besides a functional difference between these propagules, their size varies considerably, in general with spores being smaller than soredia, which are smaller than isidia.

A few recent studies have examined the influence of patch size, quality and isolation on lichen species incidence, abundance, richness or composition (Kruys & Jonsson 1997; Peck & McCune 1997; Dettki & Esseen 1998; Berglund & Jonsson 2001; Gu *et al.* 2001). Isolation has generally been measured as habitat cover in the landscape, and no study has examined how patch size, quality, connectivity or isolation measures influence both species occupancy patterns and local abundance.

The aim of this study was to assess the relative importance of habitat quantity, quality and isolation for the distribution and abundance of two epiphytic lichens in a mesoscale landscape with a low proportion (< 10%) of suitable habitat. We chose to compare *Parmelina tiliacea* (Hoffm.) Hale and *Pleurosticta acetabulum* (Neck.) Elix & Lumbsch, which are both large, foliose lichens within the family Parmeliaceae, and have similar habitat requirements but differ in rarity and dispersal attributes. In Sweden *P. tiliacea* is rare and red-listed as 'near threatened' (Gärdenfors 2000), while *P. acetabulum* is fairly common (Hallingbäck 1995). We asked: (i) how species presence and abundance on trees are influenced by the tree-level variables tree size, exposure and tree species; (ii) how species presence at patch-level is affected by patch size, quality and isolation; (iii) how species abundance at patch-level is influenced by patch size, quality and isolation; and (iv) whether the relative importance of patch size, quality and isolation for species presence and abundance at patch-level differs between the two species. We predicted that patch isolation should constrain patch occupancy more for *P. tiliacea* than for *P. acetabulum*, because the former produces few spores but develops large, vegetative dispersal propagules, whereas the latter lacks vegetative propagules, but produces numerous small, and presumably more easily dispersed, spores.

Materials and methods

THE STUDY SPECIES

Parmelina tiliacea and *Pleurosticta acetabulum* are mainly found in exposed habitats on nutrient-rich broad-leaved trees such as *Acer*, *Fraxinus*, *Quercus*, *Tilia* and *Ulmus* (Hale 1976; Moberg & Holmåsen 1982; Purvis *et al.* 1992). *P. tiliacea* is also found on nutrient-enriched rocks, especially in coastal areas. The global distribution of both species is limited to Europe, apart from an extension of the range of *P. tiliacea* to western India (Hale 1976). In Sweden both species are mainly confined to the large agricultural districts in the south (Sernander 1923; Sernander-Du Rietz 1926; Moberg & Holmåsen 1982; Thor & Arvidsson 1999).

The formation of apothecia is rare in *P. tiliacea*, while the formation of isidia, which act as vegetative propagules, is common (Hale 1976, 1983). Apothecia are common in *P. acetabulum* but this species is not known to produce vegetative propagules (Moberg & Holmåsen 1982; Purvis *et al.* 1992). Consequently, the dispersal of *P. tiliacea* is mainly vegetative and that of *P. acetabulum* exclusively sexual. The isidia of *P. tiliacea* (up to 0.1 mm in diameter) are several orders of magnitude larger than the spores of *P. acetabulum* (typically 17 × 8.5 μm) (Purvis *et al.* 1992).

THE STUDY AREA

The study area comprises *c.* 940 hectares (Fig. 1) and is located in the hemiboreal zone (Ahti *et al.* 1968), in the province of Uppland, south Sweden (59°43′ N, 17°30′ E). The area was selected to represent a landscape suitable for *P. tiliacea* and *P. acetabulum*, i.e. an agricultural landscape with a high proportion of exposed broad-leaved, deciduous trees, in which the spatial pattern of the patches that contained these trees was variable. The study area consists mainly of arable and pasture land, with some mixed coniferous forest (*Picea abies* and *Pinus sylvestris*). Deciduous trees are found in alleys, gardens, parks, forest edges' pastures and as deciduous groves. The area borders the freshwater Lake Mälaren in the north and east and coniferous forest or large arable fields from the south to the north-west (Fig. 1).

HABITAT MAPPING

The major substrates for *P. tiliacea* and *P. acetabulum* in the study area were considered to be the broad-leaved,

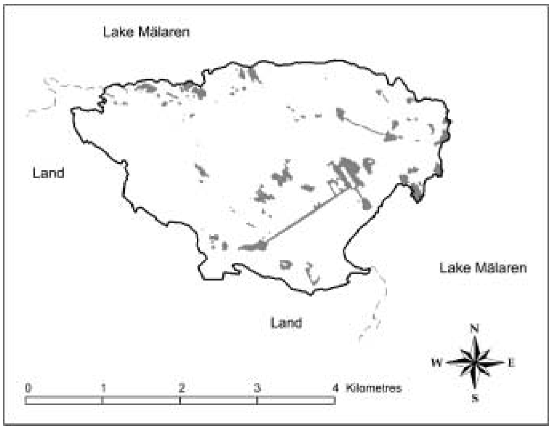

Fig. 1 Study area and location of all patches (shaded areas) where broad-leaved trees were searched for the epiphytic lichens *Parmelina tiliacea* and *Pleurosticta acetabulum*.

deciduous trees *Acer platanoides*, *Aesculus hippocastanum*, *Fraxinus excelsior*, *Quercus robur*, *Tilia cordata* and *Ulmus glabra*. All patches with these tree species were mapped from infra-red aerial photographs and delimited into patches consisting of one to several hundred trees. All patches were visited and the number of trees that were at least 10 cm in diameter at breast height was estimated by visual inspection. Both lichen species prefer larger trees (Moberg & Holmåsen 1982; Purvis *et al.* 1992; P. Johansson, personal observation), and including smaller trees would have added little extra information. Trees were sampled by walking along adjoining transects through each patch surveying every tree (in patches with less than 100 trees according to the estimation), every second tree (in patches with 100–200 trees), every third tree (200–300 trees) and so on, until the whole patch had been surveyed. Every sampled tree was described by species and diameter at breast height (d.b.h.) in centimetres. The light conditions close to the tree trunk were described by estimating the tree exposure in a coarse four-grade scale (1 = less than 20% tree crown cover; 2 = between 20 and 50% crown cover; 3 = more than 50% crown cover but no closed understorey vegetation layer; 4 = more than 50% crown cover with closed understorey vegetation). Crown cover was estimated by visual inspection of the tree crown projection to the sky in a 5-m radius around the focal tree crown edges. The understorey vegetation included young trees and bushes up to *c*. 5 m in height and a closed understorey layer was defined as where the ground cover of this layer was more than 70%.

To test the validity of the assumption that *A. platanoides*, *A. hippocastanum*, *F. excelsior*, *Q. robur*, *T. cordata* and *U. glabra* were the major substrates for the surveyed lichen species in the study area, all deciduous trees except *Betula* spp. were included in some patches. Our own field experience and the published literature, suggest that *Betula* spp. and siliceous rocks were of minor importance.

LICHEN SPECIES MAPPING

Every sampled tree was searched for presence of the two lichen species. Both species are easy to detect, even at a distance, and binoculars (8×) were therefore used to search as much of the tree trunks and crowns as possible. The mean height of the highest recorded specimen on each tree with presence was 3.0 m (SD 2.4) for *P. tiliacea* and 4.2 m (2.9) for *P. acetabulum*. Where either species was encountered, its abundance was recorded as total cover on the whole tree to the nearest whole dm^2. Cover was estimated visually, and the accuracy of these estimations was calibrated repeatedly by using a 1-dm^2 frame. When present, but with cover less than 1 dm^2 found, abundance was set to 0.25 dm^2, a value that roughly corresponded to the modal value in this category. This allowed us to separate very low cover from zero values despite using estimates of cover that had relatively low precision. For *P. tiliacea*, presence of fertile specimens was noted.

PATCH VARIABLES

In the analyses of presence and abundance at patch-level we estimated habitat quantity, quality and isolation for each patch. Species incidence was recorded as presence or absence and total abundance for each lichen species was determined by adding up the cover of the recorded occurrences, corrected, as appropriate, for the proportion of trees surveyed (see Habitat mapping). Total number of trees, number of large trees and patch area were used to measure habitat quantity (Table 1). Patch quality was described by patch shape and the nature of the patch edge, as well as a tree quality index accounting for differences in host tree composition between patches (Table 1). Patch shape and patch edge were included because of the natural history of the study species, which are both mainly found on exposed trees in agricultural landscapes. Patches whose shape was described by a high edge ratio should therefore be of high quality and patches with a large proportion of edge adjacent to coniferous forest should be of low quality. Finally, three variables describing patch isolation were used (cf. Hanski *et al.* 1994): distance to nearest patch with occupancy, species isolation index (S-species), based on distances to all other patches occupied by the species, and habitat isolation index (S-habitat), based on distances to all other patches irrespective of occupancy (Table 1).

Patch area, perimeter, proximity to forest and distances between patches were measured on digital maps in ArcView. Distance to nearest patch increases with increasing isolation, whereas values for the species and habitat isolation indices decrease, and they are therefore better described as connectivity measures (cf. Moilanen & Nieminen 2002). The dispersal capacity was unknown for either study species and we therefore tried different values of α (0.5, 1, 2, 3, 5, 10) for both (cf. Bastin & Thomas 1999). It has been suggested that connectivity measures should also be scaled by a parameter b that takes into account the fact that the relationship between the number of propagules leaving a patch and patch size is not linear, and also that measures should include the area of the focal patch (Moilanen & Nieminen 2002). We used only the linear relationship ($b = 1$) because b was unknown for the study species, and did not include area in the connectivity measure as we used several separate variables to describe patch size or habitat quantity.

DATA ANALYSIS

The influence of d.b.h., tree species, exposure and patch identity on the presence of the lichen species at tree-level was examined by multiple logistic regressions performed in the GENMOD procedure in SAS (SAS Institute 2000). Tree species and patch identity were

Table 1 Description of the variables of patch habitat quantity, quality and isolation used to model species presence and abundance at patch-level

Variable	Variable description
1. Estimated total number of trees	1. Given by multiplying the number of sampled trees by 1, 2, 3, etc., depending on the proportion of trees sampled
2. Estimated number of large trees: trees ≥ 50 cm d.b.h.	2. Number of large trees corrected for proportion sampled
3. Area	
4. Patch shape	4. The ratio between the patch perimeter and the perimeter of a circle with the same area as the patch, cf. Bastin & Thomas (1999)
5. Patch edge	5. The proportion of the patch perimeter adjoining coniferous forest. If not coniferous forest the adjacent habitats were open farmland or water
6. Tree quality index	6. The probability of a tree supporting each lichen species, averaged over all trees within the patch. The probability was given by the parameter estimates for d.b.h., exposure and tree species from logistic regressions for each lichen species with all trees within the study area pooled This variable was included because it takes into account the effects of the quality of the trees found in the analyses of presence at tree level
7. Distance to nearest patch	7. The distance to the nearest patch occupied by each of the lichen species
8. Species isolation index, S-species	8. Calculated for each lichen species as $\text{S-species}_i = \Sigma A_j e^{(-\alpha d_{ij})}$ where d_{ij} is the distance from the edge of the focal patch i to the centre of each other patch j occupied by the focal lichen species, A is the total abundance of the lichen species in the corresponding patch j. α is a constant describing the species' distance-dependent dispersal rate (Hanski 1999)
9. Habitat isolation index, S-habitat	9. This index gives the connectivity of the focal patch without regard to species presence or absence in the other patches. Calculated in the same way as S-species, but area replaced abundance as an estimate of A and d_{ij} is the distance from the focal patch i to each other patch j in the study area

included as nominal variables. We had to exclude patches with fewer than 40 trees for *P. tiliacea* and < 16 trees for *P. acetabulum* in order to get the algorithms to converge. For the same reason interaction terms were excluded. Because of the nested structure in this data (trees within patches) we also used a mixed model using the GLIMMIX macro in SAS. However, we had to exclude even more patches to get these mixed models to converge, and, as the results of the mixed models were very similar to those of non-mixed, present only the results of the latter.

The influence of d.b.h., tree species, exposure and patch identity on the abundance of the lichen species at tree-level was examined by multiple linear regressions, including only trees with presence of respective lichen species. For this analysis we used the same patches as for the logistic regressions, but accordingly, excluded those without presence of either study species. The residuals were checked for independence and normality. *A. hippocastaneum* was excluded both from the logistic and linear regressions because of the low number of sampled trees (10). The aim with the analyses of presence and abundance at tree-level was to examine the relative effects of tree conditions and patch identity. Therefore, removing patches from these analyses should not affect the main patterns of these relationships as we still included a large number of trees.

The influence of the patch variables (see Table 1) on lichen species presence at patch-level was analysed by multiple logistic regression performed in the GENMOD and LOGISTIC procedures in SAS. Our aim was to use the best-fitting models that included one variable of habitat quantity (patch area, number of trees or number of large trees, see Table 1), one descriptor of isolation (see Table 1) and all three variables of patch quality (shape, forest edge and tree quality index, Table 1) and we tried all possible models that fulfilled these criteria. The effect of one isolation measure (S-species, Table 1) was examined for different values of α, whereas we used only $\alpha = 1$ for the other (S-habitat) because the habitat configuration will often be used when modelling species occupancy, if species actual occurrences and dispersal abilities are unknown. We also included all two-way interaction terms in the candidate models. Both the model deviances and the Akaike's information criteria (AIC) of these candidate models were compared in order to find the model with the best fit.

The influence of the patch variables on total lichen abundance was examined by multiple linear regressions with the same predictors as in the final models for patch occupancy, but also with the other measures of isolation. In these regressions we only included patches where the focal species were present. The values of abundance and number of large trees were log-transformed before analyses. The residuals were checked for independence and normality.

Table 2 The influence of patch identity, diameter at breast height (d.b.h.), tree species and exposure on presence and abundance of *Parmelina tiliacea* and *Pleurosticta acetabulum* at tree-level. Chi-square values from logistic regressions and *F*-values from linear regressions are for each variable when entered last in multiple regression models. For *P. tiliacea*, 2570 trees in 26 patches were used in the logistic regression analysis and 515 trees in 24 patches in the linear regression. Corresponding figures for *P. acetabulum* were 2991 trees in 42 patches and 623 trees in 38 patches. Linear regression adjusted r-square values are given for each species

		Species presence			Species abundance		
	Variables	DF	χ^2	$P > \chi^2$	DF	*F*-value	$P > F$
P. tiliacea	Patch identity	25	398.16	< 0.0001	23	2.14	0.0017
	d.b.h.	1	+55.85	< 0.0001	1	37.57	< 0.0001
	Tree species	4	25.04	< 0.0001	4	0.89	0.4684
	Exposure	1	−2.69	0.1007	1	1.19	0.2762
					$n = 515$, Adj $R^2 = 0.19$		
P. acetabulum	Patch identity	41	360.47	< 0.0001	37	2.31	< 0.0001
	d.b.h.	1	+55.55	< 0.0001	1	106.28	< 0.0001
	Tree species	4	32.25	< 0.0001	4	6.41	< 0.0001
	Exposure	1	−5.39	0.0202	1	0.47	0.4926
					$n = 623$, Adj $R^2 = 0.22$		

+/– sign denotes the direction of the relationship.

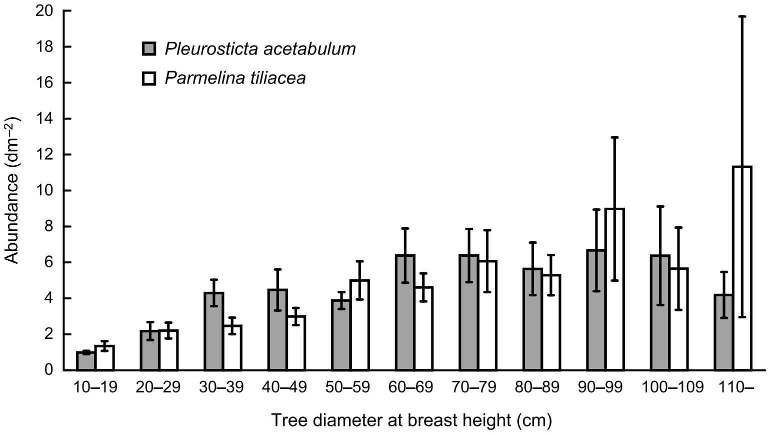

Fig. 2 Mean abundance (cover in dm^2) of *Parmelina tiliacea* and *Pleurosticta acetabulum* on trees arranged in size classes according to diameter at breast height (d.b.h.). The diagram includes all examined trees with presence of respective lichen species. Bars indicate standard errors.

Results

A total of 94 broad-leaved tree patches in the study area were mapped and surveyed (Fig. 1), covering *c.* 6% of the total area. The number of trees > 10 cm d.b.h. ranged from 1 to 1057 in individual patches (1 to 198 of which were surveyed), and totalled 7239 (3237 of which were surveyed). *P. acetabulum* occurred in more patches than *P. tiliacea*, 62 vs. 47 ($\chi^2 = 4.92$, $P < 0.05$), and was also found on a higher number of trees (692 (21%) vs. 563 (17%)). Fertile *P. tiliacea* was recorded on only seven individual trees (1.2% of all trees occupied) and then only for a few specimens per tree.

SPECIES PRESENCE AND ABUNDANCE AT TREE-LEVEL

The presence of *P. tiliacea* and *P. acetabulum* on tree species other than *A. platanoides*, *A. hippocastanum*, *F. excelsior*, *Q. robur*, *T. cordata* and *U. glabra* was low. Other substrates were recorded almost exclusively within patches where the lichens were abundant on the major species.

For both species, patch identity had strong influence on the probability of presence on individual trees (Table 2), and within patches, presence increased with increasing tree size and differed between tree species. Exposure had no effect, or relatively weak effect, on species presence (Table 2).

The abundance of both species also differed between patches and, within patches, abundance was strongly correlated with tree size (Table 2, Fig. 2). For *P. acetabulum* the abundance was influenced by tree species, while exposure had no significant effect for either species.

SPECIES PRESENCE AND ABUNDANCE AT PATCH-LEVEL

For *P. tiliacea* inclusion of the number of large trees as a measure of habitat quantity consistently gave better models than did the total number of trees or patch area. For *P. acetabulum* the number of large trees gave better

Table 3 The influence of patch variables on presence of *Parmelina tiliacea* and *Pleurosticta acetabulum* at patch-level. S-species with $\alpha = 5$ was used for *P. tiliacea*, and S- species with $\alpha = 3$ for *P. acetabulum*. Parameter estimates with Wald chi-square significance levels and type 3 likelihood ratio chi-square values for the multiple logistic regression models. n (number of patches) = 94, d.f. = 88

	Parmelina tiliacea		*Pleurosticta acetabulum*	
	Estimate	χ^2	Estimate	χ^2
Number of large trees	0.414**	16.43***	1.126*	21.21***
Proportion of adjacent coniferous forest	−0.058**	15.58***	−0.031*	7.62**
Patch shape	3.131*	7.40**	1.536	1.89
Tree quality index	5.189	2.68	−0.344	0.02
S-species	1.891**	19.58***	0.439*	6.85**

$^*P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$.

Table 4 The influence of patch variables on the within-patch abundance of *Parmelina tiliacea* and *Pleurosticta acetabulum*. α – values for S-species as in Table 3. Parameter estimates and F-values from type 3 sum of squares in the multiple regression models

	Parmelina tiliacea $F = 27.32$, d.f = 46, adj $R^2 = 0.74$		*Pleurosticta acetabulum* $F = 21.29$, d.f. = 61, adj $R^2 = 0.64$	
	Estimate	F-value	Estimate	F-value
Log number of large trees	1.130	69.57***	0.827	41.57***
Proportion of adjacent coniferous forest	−0.007	2.77	0.003	0.87
Patch shape	−0.038	0.07	−0.056	0.17
Tree quality index	−0.093	0.04	−0.158	0.06
S-species	0.060	2.18	0.061	12.71***

$^*P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$.

models than area and slightly, but not significantly, better models than did the total tree number. We therefore used the number of large trees as our quantity measure in all subsequent models. The presence of both species was significantly positively related to the number of large trees (Table 3). A high proportion of coniferous forest adjacent to the patches had a negative influence on the presence of both species. For *P. tiliacea*, but not *P. acetabulum*, patch shape influenced presence, occurring more frequently in patches with a high proportion of edges than in more circular patches. For both species, presence increased with increasing connectivity to con-specific patches (Table 3). For *P. tiliacea*, S-species using $\alpha = 5$ gave the best model fit, compared with $\alpha = 3$ for *P. acetabulum*. Interaction terms did not significantly improve the models.

When S-habitat with $\alpha = 1$ was used instead of S-species the model fit did not change significantly for *P. acetabulum* (model deviance decreased by 1.23, $P = 0.28$, S-habitat $\chi^2 = 8.08$, $P = 0.0045$). However, for *P. tiliacea* the model fit became significantly worse and S-habitat had no significant effect (model deviance increased by 17.46, $P < 0.001$, S-habitat $\chi^2 = 2.12$, $P = 0.14$). When distance to nearest patch was used instead of S-species, the model fit for *P. tiliacea* decreased (model deviance increased by 3.60, $P = 0.06$, distance to nearest patch $\chi^2 = 15.98$, $P < 0.001$), whereas for *P. acetabulum* the fit was significantly worse (model deviance increased by 5.86, $P = 0.01$) and distance to nearest patch had no effect ($\chi^2 = 0.99$, $P = 0.33$).

For both species, the total within-patch abundance increased with increasing number of large trees and, for *P. acetabulum*, connectivity (as S-species) showed a positive relationship with abundance (Table 4). Replacing S-species with S-habitat gave a better model fit for the abundance of *P. acetabulum* (model $F = 25.21$, adj $R^2 = 0.66$, cf Table 4) and the effect of S-habitat was significant ($F = 21.00$, $P < 0.001$). For *P. tiliacea* the model fit did not change and S-habitat was not significantly related to total abundance ($F = 2.28$, $P = 0.139$). Distance to nearest patch slightly improved the model for *P. tiliacea* ($F = 32.41$, adj $R^2 = 0.77$), and its effect was significant ($F = 8.36$, $P = 0.0061$). In contrast, distance to nearest patch decreased model fit for *P. acetabulum* ($F = 16.52$, adj $R^2 = 0.56$, cf Table 4), and had no significant effect on abundance ($F = 2.61$, $P = 0.112$).

Discussion

We found that the distribution of *Parmelina tiliacea* and *Pleurosticta acetabulum* was influenced by both habitat quantity and quality at patch-level as well as by patch isolation, while the abundance of both species, at tree- and patch-level, was mainly correlated with tree size and tree number, respectively. Relationships between patch size or area and local population size, and between patch isolation and colonization are well established for many organisms (e.g. MacArthur & Wilson 1967; Hanski 1999). However, no previous study has demonstrated both these relationships for lichens.

Presence at tree level showed a similar pattern for both species. Tree size and tree species influenced species presence, but the strongest effect was due to differences between patches. There may be at least three reasons why tree size is important. First, large, old trees have been exposed to colonization for longer, increasing the probability of propagule arrival (cf. Gu *et al.* 2001). Secondly, dispersing propagules are more likely to get caught in the cracks and crevices of larger trees with rough bark than on young trees with smooth bark (Armstrong 1990). Thirdly, larger and older trees may have properties that make them more suitable for lichen establishment, such as different bark chemistry (Gustafsson & Eriksson 1995). These factors may also vary between tree species and, for epiphytic lichens, the importance of tree age, tree species and bark chemistry is often stressed (e.g. Gauslaa *et al.* 1998; Uliczka & Angelstam 1999). In this study, the strong influence of patch identity on species presence at tree-level emphasizes the importance of factors acting over larger spatial scales.

In both species patch occupancy was affected by patch isolation. Isolation and landscape configuration are common predictors of species incidence although there are still few examples of this for lichens (but see Quintana-Ascencio & Menges 1996; Gu *et al.* 2001). Isolation implies dispersal constraints, and there are strong indications of limited dispersal abilities among epiphytic lichens (Sillet *et al.* 2000; Dettki *et al.* 2000; Hilmo & Såstad 2001). Patch occupancy by both study species was also positively correlated with the number of large, deciduous trees, which can be interpreted as an effect of patch size. An increasing proportion of adjacent coniferous forest, at the expense of open farmland, had a negative influence on both species, in agreement with descriptions of their natural histories, i.e. that both occur primarily in open, agricultural landscapes (e.g. Hallingbäck 1995). Coniferous forest may affect colonization and persistence by acting as a filter for dispersing propagules and by influencing the local climate. Similarly, a higher edge ratio, which had a significant effect on the presence of *P. tiliacea*, may enhance both colonization and growth because a larger proportion of trees is exposed. The influence of coniferous forest and patch shape demonstrates the importance of quality-related variables for species occurrence (cf. Summerville & Crist 2001; Fleishman *et al.* 2002).

In addition to the factors considered in this study, stand age is an important factor for epiphytic lichen occurrence (e.g. Dettki & Esseen 1998). We did not include any variables describing past land-use or patch age. However, there are no differences in the landscape configuration today and that on a 50-year-old-map. Further, we found both species on a relatively high number of young trees (*P. tiliacea* on 66 trees below 20 cm in d.b.h and *P. acetabulum* on 134 such trees), which indicates a dynamic system with continuous dispersal and colonization.

Compared with species presence, abundance was affected mainly by a single variable, namely tree size and the number of large, broad-leaved deciduous trees, at tree- and patch-level, respectively. There were strong relationships between within-patch abundance and the number of large trees, suggesting that dispersal within the patches is efficient. The strong influence of tree size and tree number may be interpreted as effects of both habitat quantity and time. Most corticolous lichens are long-lived and, once established, growth is limited only by habitat area, habitat persistence or competition, assuming a constant environment. Habitat area increases with increasing tree size and tree number, and habitat persistence may also be correlated with tree age. Besides the influence of tree number, there was an effect of isolation on total patch abundance, especially for *P. acetabulum*, that may indicate an effect of continuous dispersal from surrounding patches on local population size, i.e. a rescue effect (Brown & Kodric-Brown 1977).

Overall, the responses to the tree- and patch-level variables were similar for the two study species. Both were affected by isolation measured as the S-species index but, contrary to our prediction, increased isolation from all other patches negatively influenced both the presence and within-patch abundance for *P. acetabulum* but not for *P. tiliacea*. However, the best-fitting model for *P. tiliacea* included an S-species index with a higher α-value than the corresponding model for *P. acetabulum*, indicating a stronger effect of the distance to other patches occupied by conspecifics. The S-species index also explained more of the variation in occupancy for *P. tiliacea*. This index and the simple distance to nearest patch, which was significant for *P. tiliacea* but not *P. acetabulum*, describe species' spatial autocorrelation, and the strong effect of these measures on *P. tiliacea* indicates a stronger degree of aggregation than for *P. acetabulum*. Further, the positive influence of connectivity on within-patch abundance of *P. acetabulum* suggests that this species has more efficient and continuous dispersal between patches than *P. tiliacea*.

The different effects of isolation indicated by models using different isolation indices demonstrate the difficulties in finding a relevant measure of isolation or connectivity. There are both practical and theoretical considerations involved in deriving such measures. The distance to nearest patch is very easy to measure and was found to be the best predictor, in most cases, of isolation for plant species in urban vegetation (Bastin & Thomas 1999). In contrast, Moilanen & Nieminen (2002) found more complex measures to be better at predicting species occurrence than the nearest neighbour distance. They stressed that the latter measure ignores patches within the migration from a focal patch. For applied purposes, when the species' actual distributions are unknown, the S-habitat index is appealing for predicting species responses to habitat fragmentation, because it is relatively easy to obtain. One problem with such an index is the definition of suitable habitat, where errors may lead to under- or overestimations of the influence of isolation. The S-species index takes all occurrences into account and may therefore be better at predicting species colonizations (cf. Hanski *et al.* 1994), but this index requires good knowledge of species distribution and local abundance, and could only be used in well-known systems.

This study emphasizes the importance of habitat quantity for species occupancy and local abundance, but also that explanations of species occurrences in fragmented landscapes must involve variables describing both quality and spatial configuration of suitable habitat patches. We did not find any clear differences between the rare and vegetatively dispersed *P. tiliacea* and the fairly common and sexually dispersed *Pleurosticta acetabulum*. Our results thus suggest that general conclusions about species occupancy patterns in fragmented landscapes are difficult to make based on considerations of natural history traits, such as dispersal mechanisms, alone.

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