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# The effects of habitat connectivity on cryptogam richness in boulder metacommunity

Risto Virtanen<sup>a,\*</sup>, Jari Oksanen<sup>b</sup>

<sup>a</sup>Department of Biology, Botanical Museum, University of Oulu, P.O. Box 3000, FI-90014, Finland

<sup>b</sup>Department of Biology, University of Oulu, FI-90014, Finland

## ARTICLE INFO

### Article history:

Received 22 December 2005

Received in revised form

22 August 2006

Accepted 10 October 2006

### Keywords:

Species–area relationship

Community ecology

Threatened bryophytes

Conservation

Life history strategies

Dispersal limitation

## ABSTRACT

We investigated the effects of habitat patch size and connectivity on cryptogam richness on 288 calcareous boulders. The studied boulders were found to be a particularly suitable ‘metacommunity model system’ and allowed comparison of species richness among cryptogams with differing substrate specificity, life history and red list status. The dependence of species richness on boulder surface area was modelled using Arrhenius power model, and contrasts were analysed between connected and isolated boulders. Species richness was clearly related to boulder size, but the rates of increase of species richness with increasing boulder area ( $z$ -values) were highly variable among species groups. Highest value of  $z$  (1.17) was found for species with large propagules, and values around 0.5 were obtained for calciphilous and regionally red-listed species and  $z=0.42$  for perennials. The lowest value of  $z$  (0.27) occurred in calcicolous species while for all species, colonists, and species with small propagules the values were 0.3–0.4. The richness of all species was 11% higher on connected than isolated boulders, while connected boulders had 31% more of both calcicolous and regionally red-listed species and 19% more of colonists. The result suggests that in the investigated system that boulder size is a crucial determinant of cryptogam richness, and their spatial configuration in terms of connectivity may further contribute to cryptogam richness. The latter result lends support to the importance of metacommunity processes for the maintenance of cryptogam richness.

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## 1. Introduction

The effects of habitat patch size and the spatial distribution of habitat patches have been regarded as important in conservation biology (Fahrig and Merriam, 1994), and the inclusion of these measures in ecological research can give more applicable management or conservation recommendations (Kareiva, 1990; Tilman and Kareiva, 1997). An important step in this research has been the development of metapopulation theory forming the core for many model based approaches (Hanski, 1999). These approaches best apply to systems where populations are spatially subdivided into local populations and

where migration among the local populations affect local dynamics, with a possibility of a local extinction (Hanski and Simberloff, 1997). A key prediction from metapopulation theory (Hanski, 1991; Söderström and Herben, 1997) is that increasing connectivity [or decreasing degree of isolation] among habitat patches increases colonization probability, and therefore connected patches should contain more species than isolated ones. Moreover, increasing habitat patch or population size decreases the extinction probability, and contributes to species richness in local communities. Therefore, connectivity and patch size can be expected to have measurable effects on species richness of isolated local com-

\* Corresponding author. Tel.: +358 8 553 1555; fax: +358 8 553 1584.

E-mail address: [risto.virtanen@oulu.fi](mailto:risto.virtanen@oulu.fi) (R. Virtanen).

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doi:10.1016/j.biocon.2006.10.013

munities (richness of the metacommunity; Hanski and Gilpin, 1991; Ovaskainen and Hanski, 2003).

The effects of habitat size and connectivity on species richness have been known for long, and particularly since the formulation of the dynamic theory of island biogeography (MacArthur and Wilson, 1963; see also Rosenzweig, 1995). These processes have been investigated in various subdivided systems (e.g. Quinn and Harrison, 1988), and their consequences for local species richness are discussed in many recent studies on isolated rock boulders (e.g. Kimmerer and Driscoll, 2000; Hunter, 2003; Weibull and Rydin, 2005). While there is some evidence that habitat size has significant effects on species richness on cryptogams growing on rock boulders (Weibull and Rydin, 2005), the effect of connectivity on local richness is poorly known (but see Kimmerer and Driscoll, 2000).

We sampled species data from a erratic boulder system filling most of the assumptions of a metacommunity: boulders form discrete habitat patches being occupied or unoccupied by several individual species. There can be local extinctions and colonizations, and species are potentially limited by dispersal. The system comprises specifically of calcareous boulders suitable for specialized calcicolous epilithic cryptogams, and these are virtually exclusively dependent on the presence of boulders (not growing in the matrix area). Our approach is to model species richness on each boulder (richness of metacommunity on a particular patch) in relation to boulder area and connectivity. We found it fruitful to test how richness of species groups differing ecological requirements and life histories because they will likely have strong effects (Söderström and Herben, 1997; Leibold et al., 2004). We also wanted to see whether regionally red-listed species and non-vulnerable (“least concern”) species have different relation to habitat size and connectivity.

## 2. Material and methods

### 2.1. Study system

We sampled cryptogam species on calcareous boulders distributed in boreal forest and mire landscape in Kiiminki (Obo, Central Finland, Kaakinen and Kukko-oja, 1981). The studied boulder formation is a result of the latest glaciation that distributed dolomite rock boulders as a 14 km long and 3 km wide strip over an area of siliceous bedrock. The rock boulders emerged from the Baltic Sea c. 4000–5000 y ago following isostatic uplift (Eronen, 1990). In total, 288 boulders were surveyed. The boulders were mapped at an accuracy of 1 m using a GPS (global positioning system). The survey was thorough enough for us to be confident that most boulders were found. For each boulder we recorded width, length and height of boulders. The surface area of the boulder ( $A$ ) was defined as  $A = lw + 2lh + 2wh$ , where  $l$  = length,  $h$  = height and  $w$  = width. The occurrences of cryptogams exclusive or preferential to calcareous boulders were recorded. The focal pool of species included bryophytes (42 taxa), lichens (8) and ferns (1) (Appendix). We assigned the studied 51 species into categories depending on their substrate preference (Hallingbäck, 1996; Dierßen, 2001), life history (Dierßen, 2001; During, 1979, 1992), propagule size (various literature sources), and re-

gional red list status (Ulvinen et al., 2002), strictly following these publications. Pioneer colonists were assigned into ‘colonists’, and perennials, competitive perennials, stress tolerant perennials and long-lived shuttle species were assigned into ‘perennials’ based on their dominant life history strategy (see Dierßen, 2001). Species with propagule diameter  $<20\ \mu\text{m}$  were assigned into ‘small propagule species’ and species with propagules (spore or gemmae)  $>20\ \mu\text{m}$  assigned into ‘large propagule species’ (see During, 1992; Moberg and Holmåsén, 1990). The propagule size of the moss *Pseudoleskeella papillosa* was unknown. Altogether, 22 of the taxa (43%) were regarded as regionally threatened (RT) or near threatened (NT) in the middle boreal Ostrobothnia subarea (Ulvinen et al., 2002). The remaining species were assessed as non-threatened “least concern” (LC) taxa.

### 2.2. Data analysis and modelling

We used generalized linear modelling to analyse the effects of the boulder area and connectivity on cryptogam species richness (all species or a subset of species). In all models boulder area and connectivity were used as explanatory variables and species richness (number of taxa) was the response variable. We examined only the main effects and no interaction terms were used in the models. In the modelling we used the following Arrhenius type power function to examine the relationship between expected species richness ( $E(S)$ ) and boulder area ( $A$ ):

$$E(S) = kA^z,$$

where  $k$  and  $z$  are estimated model parameters. The fitting was made using log link and Poisson error and log-transformed area so that the fitted model was  $\log(E(S)) = \log k + z \log A$ . Connectivity was treated as categorical variable taking two levels “connected” and “non-connected” boulders. This solution was motivated by need to make simple contrast to see how the degree of connectivity affects species richness. We estimated connectivity ( $\Gamma_i$ , gamma) using one of the commonly used measures

$$\Gamma_i = \sum_j \exp(-\alpha d_{ij}) A_j,$$

where  $\alpha$  is the inverse of average dispersal distance (Hanski, 1999, p. 83, Eq. (5.5); see also Lindborg and Eriksson, 2004; Verheyen et al., 2004) and  $d_{ij}$  is distance between boulders. This connectivity measure describes the overall connectivity among rock boulders. We estimated  $\alpha$  values separately for a representative set of species (21 taxa) using non-linear optimization and using only those boulders where the species was present (Hanski, 1999, Eq. (5.11)). The estimates of  $\alpha$  varied among species, and we selected  $\alpha = 0.8$  ( $1/\alpha$  meaning average dispersal distance 1.25 km) which was typical of species showing some degree of spatial aggregation, and this value was used to estimate  $\Gamma$  in the present data. The observed  $\Gamma$  values had a bimodal density distribution (not shown), and this supported the division of boulders into isolated and connected ones. The threshold value was obtained from a density plot of  $\Gamma$  values and this showed a discontinuity at values smaller or greater than 60. The exact value of  $\alpha$  was not critical since it only was used for dividing data into connected

and non-connected categories, and other values would produce nearly identical classification.

### 3. Results

The species richness of cryptogams growing on calcareous boulders clearly increased with boulder area ( $\log(A)$ ) (Figs. 1 and 2, Table 1) and the fitted Arrhenius power model of the species–area relationship yielded a wide range of exponents ( $z$ ) from 0.27 to 1.17. The inclusion of connectivity had significant effects in most cases, and the inclusion of both  $\log(A)$  and connectivity in the models caused a reduction 45–71% in deviance. This shows that boulder area and connectivity explain a relatively large proportion of the variation in cryptogam richness. The correlation between connectivity and boulder area was negative though weak (correlation coefficient  $-0.133$ ,  $p = 0.07$  after Welch's  $t$ -test). The exponents of the power equation were variable among species groups. The maximum value ( $z = 1.17$ ) was found for species with large propagules and the shape of the fitted power regression lines differed remarkably from other cases. Relatively large  $z$ -values of ca. 0.5 were found for calciphilous and regionally red-listed species. The lowest value of  $z$  occurred in calcicolous species (0.27), while for all species, colonists, species with small propagules the  $z$ -values ranged from 0.3 to 0.4. A relatively high value 0.42 was obtained for perennials.

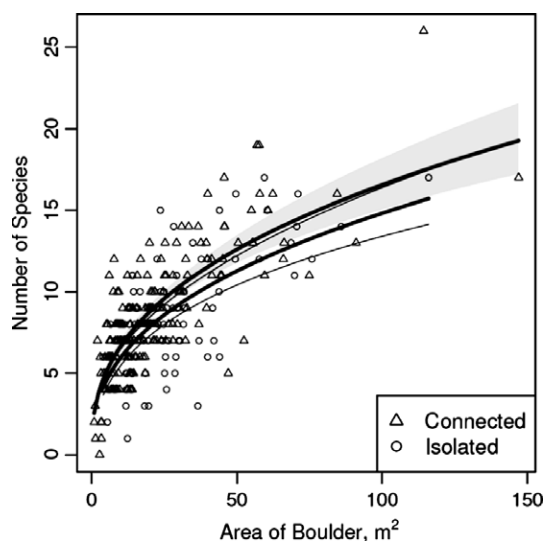
The contrasts made between isolated and connected boulders showed that connected boulders have higher species richness, but the strength of connectivity depends on the species group (Figs. 1 and 2, Table 1). Connectivity had highly significant effect on richness of calcicolous species and regionally red-listed species. Connected boulders had 31% more of both calcicolous and regionally red-listed species. Cryptogam richness of all species, colonists, species with

small propagules species was also higher on connected boulders. There were 11% more cryptogams on connected than isolated boulders, and there were 19% more colonists and 9.5% more species with small propagules on connected boulders. There was no significant effect of connectivity on calciphilous, perennial or species with large propagules. However, calciphilous species were the only group where isolated boulders tended to have higher richness than connected ones.

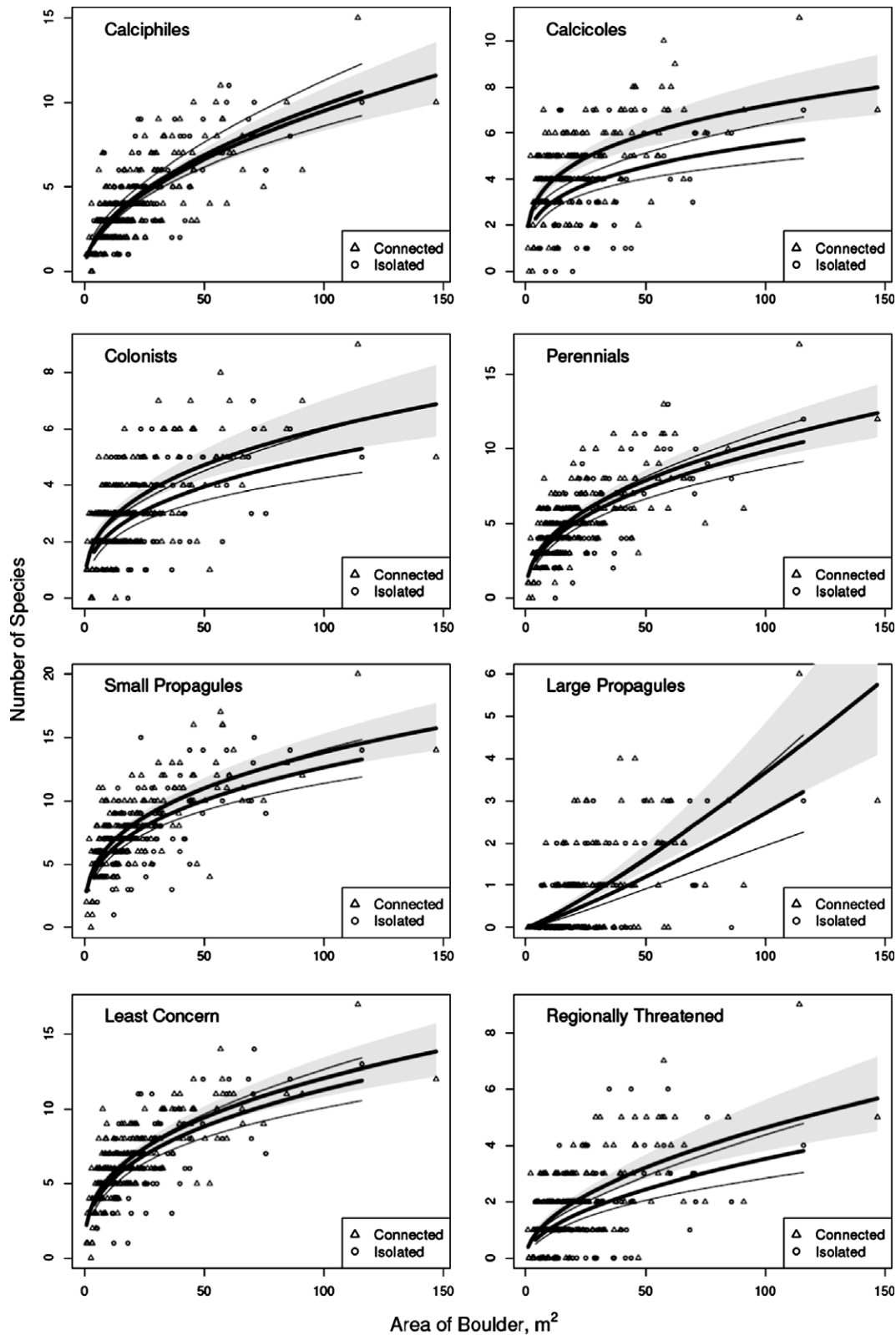
### 4. Discussion

Although the questions about the effects of habitat patch size and spatial configuration have been regarded as important in conservation biology (Fahrig and Merriam, 1994; Fahrig, 2003), their effects on species richness are difficult to demonstrate. A reason for this is that in many natural systems, these effects are confounded by environmental heterogeneity and temporal stochasticity. These factors may override effects of metapopulation dynamics and thus the chances to detect the effects of area or connectivity on species richness remain low (Désilets and Houle, 2005; Kubešová and Chytrý, 2005; Pharo et al., 2005; see also Leibold et al., 2004). In many cases, inferences about metapopulation processes can be made in experimental model systems where at least some of the confounding effects have been minimized (Gilbert et al., 1998; Gonzalez et al., 1998), or in systems where long term data are available (Lindborg and Eriksson, 2004; Verheyen et al., 2004; Helm et al., 2006). Alternatively, one can examine these in natural model systems, such as rock boulders, where most of the necessary assumptions of metacommunities are fulfilled (Armesto and Contreras, 1981). In boulder systems, habitat patches are discrete, relatively permanent and dispersal occurs among habitat patches. The boulder system studied by us is also fairly “closed”, because it results from a discrete geological formation with definable boundaries. In addition, we have been able to conduct fairly complete survey of species occurrences and their habitat patches.

Our primary aim was to find out the effects of spatial arrangement (isolation) and boulder area on cryptogam richness on boulders. We applied modelling to identify parameter estimates for their effects. The area effects were always strong and this suggests that boulder area is one of the primary factors determining species richness. This finding agrees well with most other relevant studies from insular systems (e.g. Rosenzweig, 1995), and also suggests that boulder size is important for species richness. This agrees with findings of Weibull and Rydin (2005) who found significant boulder area effects on bryophyte richness, and Kubešová and Chytrý (2005) who found positive effect of cliff area on bryophyte richness. Haig et al. (2000) found no effects of cliff area on bryophyte richness and only weak effects on lichen richness, and they attributed this to the stability of the habitats and proposed that even smallest cliffs in their system are able to support most of the species in the area. This obviously contrasts with the boulder system studied by us where smallest boulders have only a few species, probably owing to high extinction rates. Kimmerer and Driscoll (2000) attributed the lack of species–area relationship in their study system to dispersal from multiple source populations and from matrix



**Fig. 1** – The species–area relationship for cryptogam species on connected and isolated boulders. The fitted lines after Arrhenius power model. The 95% confidence intervals indicated. The confidence limits for connected sites are shown in grey and for more isolated sites by lines. For parameter estimates and their significance, see Table 1.



**Fig. 2** – The species–area relationship for different groups of cryptogam species on connected and isolated boulders. The fitted lines and their 95% confidence intervals after Arrhenius power model. The confidence limits for connected sites are shown in grey and for more isolated sites by lines. For parameter estimates and their significance, see [Table 1](#).

area (see also Cook et al., 2002). We only included species being largely restricted to calcareous boulders and excluded matrix species, e.g. species of forest floors, in the analyses.

The area effects on cryptogams richness in the boulder metacommunity system was very clear and the rates of increase (parameter  $z$ ) values tended to be high ( $z = 0.39$  for all

**Table 1 – Parameter estimates from generalized linear models**

Response variable	Explanatory variable	Parameter estimate	Standard error	z-Value (t-value)	p-Value	Null deviance	Residual deviance	Change of deviance %
Species richness (all)	Intercept	0.879	0.091	9.712	<0.0001			
	Boulder area (z)	0.394	0.026	15.303	<0.0001			
	Connectivity	0.111	0.044	2.531	0.011	437.7	198.6	45.4
Calciphilous	Intercept	−0.112	0.131	−0.856	0.057			
	Boulder area (z)	0.521	0.037	14.077	<0.0001			
	Connectivity	−0.037	0.060	−0.617	0.537	391.0	180.7	46.2
Calcicolous	Intercept	0.446	0.126	3.541	0.0004			
	Boulder area (z)	0.273	0.036	7.605	<0.0001			
	Connectivity	0.268	0.064	4.176	<0.0001	238.5	170.0	71.3
Colonists	Intercept	0.0007	0.146	0.005	0.996			
	Boulder area (z)	0.351	0.042	8.439	<0.0001			
	Connectivity	0.178	0.0720	2.472	0.0134	217.6	143.5	65.9
Perennials	Intercept	0.344	0.115	2.976	0.003			
	Boulder area (z)	0.422	0.033	12.832	<0.0001			
	Connectivity	0.07	0.055	1.278	0.2	348.6	180.1	51.7
Propagules small	Intercept	0.999	0.093	10.73	<0.0001			
	Boulder area (z)	0.334	0.027	12.494	<0.0001			
	Connectivity	0.09	0.046	1.994	0.046	343.0	184.2	53.7
Propagules large	Intercept	−4.396	0.381	−11.536	<0.0001			
	Boulder area	1.17	0.099	11.78	<0.0001			
	Connectivity	0.305	0.159	1.913	0.056	395.4	245.54	62.1
Least Concern	Intercept	0.778	0.102	7.663	<0.0001			
	Boulder area (z)	0.357	0.029	12.277	<0.0001			
	Connectivity	0.066	0.049	1.346	0.178	300.0	146.3	48.8
Regionally red-listed	Intercept	−1.176	0.2	−5.884	<0.0001			
	Boulder area (z)	0.528	0.056	9.507	<0.0001			
	Connectivity	0.273	0.096	2.841	0.0045	332.7	237.3	71.3

Species richness modeled as function of boulder area and connectivity. Connectivity treated as categorical variable (connected or not connected, see Section 2 for details).

species). It may be that such high values are typical to true metacommunity systems where extinction risk is high and dispersal limitation strong (Hanski, 1999). The z-values found by us tended to be higher than those reported from cryptogams occupying forest islands (Berglund and Jonsson, 2001). The latter authors found variability in z-values among different species groups. This is supported by our data and this implies that species extinction and colonization dynamics can be highly affected by biological characteristics of species (Söderström and Herben, 1997; Jonsson and Essén, 1998; Berglund and Jonsson, 2001). Berglund and Jonsson (2001) found that red-listed or rare species had comparatively high z-values. This trend prevails also in our study system. The exception is that for some cases z-values exceed unity (1.17 in species with large propagules). Such an extreme value obviously results from the species-area relationship distribution conforming not solely to extinction-colonization dynamics. Indeed, a possible reason for the high z-value can be that there is a threshold of minimal boulder size for the occurrence of species with large propagules, and their richness depends non-linearly on boulder size. The z-value was also high for regionally red-listed species (mostly rare species with large propagules) being of the same order of magnitude as the values reported by Berglund and Jonsson (2001). Overall, our results demonstrate that boulder size is a good predictor of species richness, and in this system its effect is not strongly confounded by degree of isolation (low correlation between boulder area and connectivity).

Our analyses seem to demonstrate a rather clear positive effect of connectivity on cryptogam richness. Connected boulders had higher overall species richness of cryptogams than isolated ones, and this can be attributed to dispersal limitation. The effects of connectivity have been demonstrated only in very few boulder systems (Kimmerer and Driscoll, 2000), and in cliff systems these effects are often unclear (Kubešová and Chytrý, 2005) as well as in epiphytes (Löbel et al., 2006). In the Kiiminki system, the effect of confounding factors is relatively small and therefore the detection of connectivity is possible. An interesting feature of the present analyses is that the effects of connectivity seem to depend on species group. The richness of calcicoles was clearly increased by connectivity whereas no such effect was found in calciphilous species. It seems possible that the latter group of species may gain immigrants from source populations in the surroundings. Some calciphilous species, such as *Amblystegium serpens*, *Brachythecium erythrorhizon* and *Homalia trichomanoides*, are known to occur on non-dolomitic schistose boulders occurring in the study area. Connectivity effects were also linked to life history characteristics of the focal species group. Based on some earlier studies we could have expected that the effects of connectivity are low in species with high dispersal ability, i.e. colonist species (Strong and Levin, 1975). Contrary to this expectation, connectivity had stronger impact on richness of colonists than of perennial species. This is also supported by comparison of species with small propagules (mostly colonists) and those with large

propagules (usually perennials). This can be due to the fact that dispersal limitation among most cryptogam species in this system is strong. In perennials, dispersal limitation may be strong or even stronger than in colonists, but their longevity or some other life history traits (establishment, competitive ability) may reduce the effects of connectivity. Our results agree with Johansson and Ehrlén (2003) who found that spatial configuration affects species distributions, but from the evidence from Kiiminki system we can infer that species life history and dispersal traits may have predictive value.

It seems that largest boulders are important for maintenance of high cryptogam richness and are of high priority in conservation planning and management. However, it is also evident that spatial configuration has clear effects on the richness of ecologically specialized, colonists species, and even

on regionally red-listed species. For maintenance of high cryptogam richness, one needs to consider insular boulder networks as a metacommunity instead of focusing on single boulders. Increased losses of local populations (e.g. owing to deterioration of environmental conditions in the boulder surroundings) may affect the species persistence in the entire boulder system.

### Acknowledgements

We thank M. Ohenoja and T. Ulvinen for useful information in the initial phase of the cryptogam inventory, I. Hanski for advice in adopting metapopulation approach, and A. Eskelinen for assistance in field work. The Finnish Ministry of Environment supported field work financially.

### Appendix

**Cryptogam species of the dolomitic rock boulders (n = 288) of Kiiminki schist area and their characteristics.**

Taxon	Substrate after Dierssen	Substrate after Hallingbäck	Substrate own judgement	Life history	Propagule size ( $\mu\text{m}$ )	Regional red-list status	Frequency
<i>Abietinella abietina</i>	Neutral	Neutral	Calciphilous	p	14	LC	3
<i>Amblystegium serpens</i>	Neutral	Neutral	Calciphilous	p	13	LC	14
<i>Anomodon longifolius</i>	Basic	Neutral	Calcicolous	p	17	RT	80
<i>Anomodon viticulosus</i>	Neutral	Neutral	Calciphilous	p	16.5	RT	50
<i>Barbula convoluta</i>	Neutral	Neutral	Calciphilous	c	8	LC	18
<i>Brachythecium erythrorhizon</i>	Neutral	Neutral	Calciphilous	p	17	LC	34
<i>Brachythecium glareosum</i>	Neutral	Basic	Calcicolous	pc	16.5	RT	60
<i>Bryoerythrophyllum recurvirostre</i>	Neutral	Neutral	Calciphilous	c	15.5	LC	5
<i>Bryum flaccidum</i>	Subneutral	Subneutral	Calciphilous	c	12.5	LC	110
<i>Camphylophyllum calcareum</i>	Basic	Basic	Calcicolous	p	13	RT	6
<i>Campyliadelphus chrysophyllus</i>	Neutral	Neutral	Calciphilous	p	14	RT	15
<i>Dicranum brevifolium</i>	Subneutral	Subneutral	Calciphilous	pc	20	RT	1
<i>Distichium capillaceum</i>	Subneutral	Subneutral	Calciphilous	cp	18.5	LC	143
<i>Ditrichum flexicaule</i>	Basic	Basic	Calcicolous	c	10	LC	222
<i>Encalypta rhaptocarpa</i>	Basic	Neutral	Calcicolous	l	42	RT	1
<i>Encalypta streptocarpa</i>	Basic	Basic	Calcicolous	p	10.5	LC	248
<i>Eurhynchium pulchellum</i>	Subneutral	subneutral	Calciphilous	ps	13	LC	184
<i>Homalia trichomanoides</i>	Subneutral	Subneutral	Calciphilous	ps	16	LC	12
<i>Homalothecium sericeum</i>	Basic	Neutral	Calcicolous	p	16.5	RT	6
<i>Hypnum recurvatum</i>	Basic	Basic	Calcicolous	p	13.5	RT	210
<i>Isopterygiopsis pulchella</i>	Subneutral	Subneutral	Calciphilous	ps	12	LC	9
<i>Leicolea heterocolpos</i>	Neutral	Neutral	Calciphilous	p	23	LC	30
<i>Myurella julacea</i>	Neutral	Subneutral	Calcicolous	c	10	RT	2
<i>Neckera complanata</i>	Neutral	Neutral	Calciphilous	p	22	LC	31
<i>Neckera crispa</i>	Neutral	Neutral	Calciphilous	l	27	RT	4
<i>Orthotrichum alpestre</i>	Subneutral	Basic	Calciphilous	c	11.5	RT	2
<i>Plagiochila porelloides</i>	Subneutral	Subneutral	Calciphilous	ps	16	LC	73
<i>Plagiomnium rostratum</i>	Basic	Basic	Calcicolous	pc	25	RT	1
<i>Plagiopus oederiana</i>	Basic	Neutral	Calcicolous	l	21.5	RT	3
<i>Platydictya jungermannioides</i>	Basic	Basic	Calcicolous	ps	14	RT	15
<i>Porella platyphylla</i>	Neutral	Subneutral	Calciphilous	ps	42.5	RT	1
<i>Pseudoleskeella papillosa</i>	Subneutral	Subneutral	Calciphilous	ps		RT	2

## Appendix - continued

Taxon	Substrate after Dierssen	Substrate after Hallingbäck	Substrate own judgement	Life history	Propagule size ( $\mu\text{m}$ )	Regional red-list status	Frequency
<i>Pseudoleskeella nervosa</i>	Neutral	Neutral	Calciphilous	ps	15	LC	68
<i>Scapania calcicola</i>	Basic	Basic	Calcicolous	cp	33	RT	9
<i>Scapania gymnostomophila</i>	Basic	Basic	Calcicolous	c	26	RT	49
<i>Schistidium boreale</i>	Subneutral	Basic	Calciphilous	c	11	LC	39
<i>Schistidium papillosum</i>	Subneutral	Neutral	Calciphilous	c	11.5	LC	230
<i>Schistidium pulchrum</i>	Neutral	Neutral	Calciphilous	c	11.5	LC	3
<i>Seligeria diversifolia</i>	Basic	Basic	Calcicolous	c	10	RT	2
<i>Syntrichia ruralis</i>	Subneutral	Subneutral	Calciphilous	c	11	LC	21
<i>Timmia austriaca</i>	Subneutral	Subneutral	Calcicolous	pc	15	RT	3
<i>Tortella tortuosa</i>	Basic	Basic	Calcicolous	ps	11	LC	213
<i>Cystopteris fragilis</i>	Neutral	Neutral	Calciphilous	l	44	LC	35
<i>Acarospora glaucocarpa</i>	Basic	Basic	Calcicolous	cp	5	LC	58
<i>Caloplaca</i> spp.			Calciphilous	c	8.5	LC	2
<i>Cladonia pocillum</i>			Calciphilous	ps	5	LC	25
<i>Cladonia symphyocarpa</i>			Calciphilous	ps	5	LC	33
<i>Collema fuscovirens</i>			Calcicolous	ps	10	LC	4
<i>Gyalecta ulmi</i>			Calcicolous	ps	21	RT	2
<i>Peltigera lepidophora</i>			Calciphilous	s	25	LC	8
<i>Solorina saccata</i>			Calcicolous	l	46	LC	8

## REFERENCES

- Armesto, J.J., Contreras, L.C., 1981. Saxicolous lichen communities: nonequilibrium systems? *American Naturalist* 118, 597–604.
- Berglund, H., Jonsson, B.G., 2001. Predictability of plant and fungal species richness of old-growth boreal forest islands. *Journal of Vegetation Science* 12, 857–866.
- Cook, W.M., Lane, K.T., Foster, B.L., Holt, R.D., 2002. Island theory, matrix effects and species richness patterns in habitat fragments. *Ecology Letters* 5, 619–623.
- Désilets, P., Houle, G., 2005. Effects of resource availability and heterogeneity on the slope of the species–area curve along a floodplain-upland gradient. *Journal of Vegetation Science* 16, 487–496.
- Dierßen, K., 2001. Distribution, ecological amplitude and phytosociological characterization of European bryophytes. *Bryophytorum Bibliotheca* 56, 289.
- During, H.J., 1979. Life strategies of bryophytes: a preliminary review. *Lindbergia* 5, 2–18.
- During, H.J., 1992. Ecological classifications of bryophytes and lichens. In: Bates, J.W., Farmer, A.M. (Eds.), *Bryophytes and Lichens in a Changing Environment*. Clarendon Press, London, pp. 1–31.
- Eronen, M., 1990. The post-glacial development of the Baltic Sea. *The Atlas of Finland Geology – Sheets*, 123–126 (in Finnish).
- Fahrig, L., 2003. Effects of habitat fragmentation on biodiversity. *Annual Review of Ecology Evolution and Systematics* 34, 487–515.
- Fahrig, L., Merriam, G., 1994. Conservation of fragmented populations. *Conservation Biology* 8, 50–59.
- Gilbert, F., Gonzalez, A., Evans-Freke, I., 1998. Corridors maintain species richness in the fragmented landscapes of a microecosystem. *Proceedings of the Royal Society of London Series B – Biological Sciences* 265, 577–582.
- Gonzalez, A., Lawton, J.H., Gilbert, F.S., et al., 1998. Metapopulation dynamics, abundance, and distribution in a microecosystem. *Science* 281, 2045–2047.
- Haig, A.R., Matthes, U., Larson, D.W., 2000. Effects of natural habitat fragmentation on the species richness, diversity, and composition of cliff vegetation. *Canadian Journal of Botany* 78, 786–797.
- Hallingbäck, T., 1996. *Ekologisk katalog över mossor*. ArtDatabanken, SLU, Uppsala.
- Hanski, I., 1991. Single-species metapopulation dynamics: concepts, models and observations. *Biological Journal of the Linnean Society* 42, 17–38.
- Hanski, I., 1999. *Metapopulation Ecology*. Oxford University Press, Oxford.
- Hanski, I., Gilpin, M., 1991. Metapopulation dynamics: brief history and conceptual domain. *Biological Journal of the Linnean Society* 42, 3–16.
- Hanski, I., Simberloff, D., 1997. The metapopulation approach, its history, conceptual domain, and application to conservation. In: Hanski, I., Gilpin, M.E. (Eds.), *Metapopulation Biology: Ecology, Genetics, and Evolution*. Academic Press, San Diego, pp. 5–26.
- Helm, A., Hanski, I., Pärtel, M., 2006. Slow response of plant species richness to habitat loss and fragmentation. *Ecology Letters* 9, 72–77.
- Hunter, J.T., 2003. Factors affecting range size differences for plant species on rock outcrops in eastern Australia. *Diversity and Distributions* 9, 211–220.
- Johansson, P., Ehrlén, J., 2003. Influence of habitat quantity, quality and isolation on the distribution and abundance of two epiphytic lichens. *Journal of Ecology* 91, 213–221.
- Jonsson, B.G., Essén, P.A., 1998. Plant colonisation in small forest-floor patches: importance of plant group and disturbance traits. *Ecography* 21, 518–526.
- Kaakinen, E., Kukko-oja, K., 1981. Kiiminki rich fen area: an example of an mire conservation area and its conservation values. *Papers of the Department of Botany, University of Oulu* 15, pp. 58 (in Finnish).
- Kareiva, P., 1990. Population dynamics in spatially complex environments: theory and data. *Philosophical Transactions of the Royal Society of London – Biological Sciences* 330, 175–190.

- Kimmerer, R.W., Driscoll, M.J.L., 2000. Bryophyte species richness on insular boulder habitats: the effect of area, isolation, and microsite diversity. *Bryologist* 103, 748–756.
- Kubešová, S., Chytrý, M., 2005. Diversity of bryophytes on treeless cliffs and talus slopes in a forested central European landscape. *Journal of Bryology* 27, 35–46.
- Leibold, M.A., Holyoak, M., Mouquet, N., Amarasekare, P., Chase, J.M., Hoopes, M.F., et al, 2004. The metacommunity concept: a framework for multi-scale community ecology. *Ecology Letters* 7, 601–613.
- Lindborg, R., Eriksson, O., 2004. Historical landscape connectivity affects present plant species diversity. *Ecology* 85, 1840–1845.
- Löbel, S., Snäll, T., Rydin, H., 2006. Species richness patterns and metapopulation processes – evidence from epiphyte communities in boreo-nemoral forests. *Ecography* 29, 169–182.
- MacArthur, R.H., Wilson, E.O., 1963. An equilibrium theory of insular zoogeography. *Evolution* 17, 373–387.
- Moberg, R., Holmåsén, I., 1990. *Lavar - en fälthandbok*. Interpublishing, Stockholm.
- Ovaskainen, O., Hanski, I., 2003. The species–area relationship derived from species-specific incidence functions. *Ecology Letters* 6, 903–909.
- Pharo, E.J., Kirkpatrick, J.B., Gilfedder, L., Mendel, L., Turner, P.A.M., 2005. Predicting bryophyte diversity in grassland and eucalypt-dominated remnants in subhumid Tasmania. *Journal of Biogeography* 32, 2015–2024.
- Quinn, J.F., Harrison, S.P., 1988. Effects of habitat fragmentation and isolation on species richness: evidence from biogeographic patterns. *Oecologia* 75, 132–140.
- Rosenzweig, M.L., 1995. *Species Diversity in Space and Time*. Cambridge University Press, New York, NY.
- Söderström, L., Herben, T., 1997. Dynamics of bryophyte metapopulations. *Advances in Bryology* 6, 205–240.
- Strong Jr., D.R., Levin, D.A., 1975. Species richness of the parasitic fungi on British trees. *Proceedings of National Academy of Sciences* 72, 2116–2119.
- Tilman, D., Kareiva, P., 1997. *Spatial Ecology*. Princeton University Press, Princeton.
- Ulvinen, T., Syrjänen, K., Anttila, S. (Eds.), 2002. The bryophytes of Finland: distribution, ecology, threats. *The Finnish Environment* 560, 1–354 (in Finnish).
- Verheyen, K., Vellend, M., Van Calster, H., Peterken, G., Hermy, M., 2004. Metapopulation dynamics in changing landscapes: a new spatially realistic model for forest plants. *Ecology* 85, 3302–3312.
- Weibull, H., Rydin, H., 2005. Bryophyte species richness on boulders: relationship to area, habitat diversity and canopy tree species. *Biological Conservation* 122, 71–79.