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# Rarity patterns in members of the Lophoziaceae/Scapaniaceae complex occurring North of the Tropics – Implications for conservation

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ABSTRACT

Rarity along two of the three parameters of rarity of Rabinowitz (habitat specificity and distribution range) is investigated for the members of the Lophoziaceae/Scapaniaceae complex occurring north of the Tropic of Cancer (174 species).

Using a rarity index built on the Shannon–Wiener diversity index, 31 species (18%) are rare on both parameters (most urgent in need of evaluation of threat status and conservation actions), 16 species (9%) are range restricted habitat generalists and 9 species (5%) widespread habitat specialists.

The species are most frequently growing on soil, rocks and decaying wood, but no habitat have an exceptional high number of habitat specialists. Four areas do have more habitat specialists than expected from their number of species.

The species are most abundant in arctic and boreal areas but also in alpine and oceanic areas. Nepal, East Himalaya (Bhutan and Sikkim) and south-central China (Yunnan and Sichuan) are hot spots both for range restricted species and for habitat specialists.



## 1. Introduction

Rare species are not necessary threatened by extinction and many rare species are able to persist without declining distribution areas or population sizes. However, the rarer a species becomes, the more vulnerable it will be for stochastic events affecting its populations or environment. Thus, identifying rare species also identifies species potentially in need for conservation or at least in need for monitoring for future negative changes. But what is rare? Most of us probably see rarity as “difficult to find” in one way or another but there are several types of rarity and the conservation methods and needs differs for different types of rarity.

There are several different treatments of rarity. One of the most well-known classifications is that by Rabinowitz (1981). She used three variables along which species may be common or rare. A species distribution range may be large or small, their local populations may be large or small, or they may be habitat specialists or generalists, and all combinations of them exist. This gives eight possible combinations, out of which seven can be regarded as rare in one way or another. Only the species with wide distribution range occurring in large populations on a wide range of habitats are common. Most species are rare in only a part of its distribution range. This type of rarity was termed pseudo-rarity by Rabinowitz (1981), extraneous elements by Hedderson (1992) and diffusive rarity by Schoener (1987; as opposite to suffusive rarity).

Rarity in bryophytes (and other organisms) is often connected with some life history characteristics (cf. Söderström

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and During, 2005) and production of small, easily dispersed diaspores often means that a species is widespread. Many of these characteristics are phylogenetically dependent. *Riccia* spp., e.g. all produces large spores without any mean of distance dispersal. To understand rarity and the threat to species it is thus also important to look at the constraints that the phylogeny have on characteristics of the species.

We are interested in rarity patterns among related species to reduce the effect of phylogeny and like to compare closely related species within, ideally, a monophyletic group. We have looked at rarity from three angles, types of rarity, where do range restricted species (rare on distribution variable) occur and where do habitat specialists (rare on habitat variable) occur. Thus we concentrate on two of the three variables of Rabinowitz, geographical distribution and habitat specificity. The 3rd variable, population size, was originally included but we have not been able to obtain enough reliable data.

The more specific questions we put forward in this paper are: (1) which species show the most restricted distribution ranges, (2) which areas are most species rich and which areas include most range restricted species, (3) is there a correlation between species richness and number of range restricted species, (4) which species are most habitat specific, (5) which habitats are most species rich and which habitats have most habitat specialists, (6) is there a correlation between species richness and number of specialists among habitats, (7) what is the relation between habitat specificity and distribution ranges, (8) do some habitats have more range restricted species than expected, and (9) do some areas have more habitat specialists than expected.

## 2. Methods

### 2.1. Species and study area

We choose to study the liverwort family Lophoziaceae. This family has variably been treated as a family of its own or as a subfamily of Jungermanniaceae. At the time this project started, a couple of papers were published showing that also the family Scapaniaceae should be included in Lophoziaceae (Schill et al., 2004; Davis, 2004; Yatsentyuk et al., 2004; De Roo et al., unpubl.). In addition, these investigations show that *Leiocolea* and Jamesonielloideae, usually treated as parts of Lophoziaceae, do not belong there. But even after excluding these elements, the group is almost certainly paraphyletic as, e.g. Cephaloziaceae and Cephaloziellaceae and some other minor elements are nested within and/or at least sister to the rest. We have not included the last two families so the investigated group is not monophyletic although all investigated species are related.

As many species are very badly known, both taxonomically (the “Linnean shortfall” of Brown and Lomolino, 1998) and distribution (the “Wallacean shortfall” of Lomolino, 2004), it is difficult to find information on them (especially tropical and antipodal species) we have restricted this work to species occurring north of the Tropic of Cancer. However, we have investigated those species worldwide. We thus ended up with 174 species in this analysis.

### 2.2. Distribution ranges

Distribution data has been collected from hundreds of published sources over the last 20 years (sources not given here). The classification of distribution ranges follows Brummit (2001). Distribution ranges are scored on three levels. Level 1 is basically the continents and has nine units. Level 2 is regions within continents and has 51 units. Level 3 are basically countries except that large countries (e.g. Russia and Canada) are separated in smaller units and that very small countries are included in a neighbour (e.g. Andorra in Spain and Luxembourg in Belgium). We also recognize the following countries at level 3 although not recognized in Brummit (2001): Estonia, Latvia, Lithuania, Czech Republic, Slovak Republic, Slovenia, Croatia, Serbia-Monte Negro and FYR Macedonia). This gives a total of 379 units worldwide (183 north of Tropic of Cancer).

We have scored the number of units at each level a species occur in, mainly by scanning the literature, using floras and reports from a large number of scientific journals.

We calculated a rarity index using the same formula as the Shannon–Wiener diversity index (Zar, 1984) as

$$H' = -\sum p_i \ln p_i$$

where $p$ is the proportion of level 3 areas occupied in each level 2 area. We also calculated the index with proportion of level 3 areas in each level 1 area, and proportion of level 2 areas in each level 1 area. The three measures were highly correlated. The level 3 in level 2 showed most resolution and is thus used here. With this definition, the $H'$ value is an index on how large the chance is to find the same species in the next level 2 area visited.

We defined range restricted species as the c. 25% with lowest $H'$ using the nearest natural cut off limit (see Section 3).

The proportion of range restricted species was calculated for each level 3 area. In order to downgrade the effects of a restricted species in areas with very few species we calculated a rarity index as

$$\mathrm{RI_D} = p_r^* n_r$$

where $p_r$ is the proportion of the species occurring in the area that are range restricted and $n_r$ is the number of range restricted species in that area.

### 2.3. Habitat use

Also habitats were scored at three levels, macro-, meso- and microhabitats. Macrohabitats are sometimes called biomes and we registered them using 10 units, although we registered occurrences in only seven of them. Mesohabitats are often termed habitats in the literature. Our species are registered from 30 mesohabitats. Microhabitats are what we usually call substrates. We split these microhabitats further into moisture classes (dry, moist, wet), acidity classes (acid, neutral, basic), decay stages (early, middle, late) and bark quality (smooth, rough) where appropriate. We have thus registered the species from 138 different microhabitats.

We first scored the number of macro-, meso- and microhabitats each species occurred in. In addition, we combined the levels and scored how many combinations they occurred in (Microhabitats in a Mesohabitat in a Macrohabitat; MaMeMi). Note that the geographical regions are strictly nested within each other which the habitats are not.

We defined habitat specialists as the c. 25% of the investigated species occurring on fewest habitats using the nearest natural cut off limit (see Section 3).

Also here we calculated the proportion of habitat specialists in each area and downgraded the effects of a specialist in an area with few species by calculating a rarity index as

$$RI_H = p_r^* n_r$$

where $p_r$ is the proportion of the species occurring in the area that are habitat specialists and $n_r$ is the number of habitat specialists in that area.

### 2.4. Data analysis

Statistical analysis was performed in SPSS version 14.0. The variables were not normal distributed and all correlations were for this reason performed with Spearman correlation coefficient. Linear regression was used to identify outliers (species, regions or habitats) both at distribution ranges and habitat specificity. For this analysis MaMeMi was log transformed. A 99% confidence interval for individual points was used in every regression in order to identify species, habitats or regions deviating significantly from the regression line.

## 3. Results

### 3.1. Distribution ranges

The correlation between distribution at the three levels are all strongly positively correlated (0.817–0.978; $p < 0.001$; $n = 174$).

We are for this work defining range restricted species (the c. 25% most restricted) as $H' < 1$ (47 sp, 27%; Table 1). The c. 25% most range restricted species based on number of occurrences in level 3 units ($\leqslant 4$) do not differ much from those defined by the $H'$ value. Only two species, *Scapania sphaerifera* and *Scapania hians* deviate. *S. sphaerifera* occurs in many (six) areas in one region (Siberia), but only in one area outside that. Therefore, the $H'$ will be lower as the evenness component (cf. Zar, 1984) will be very low. *S. hians* occurs in just three areas in two regions giving it a relatively high evenness component. It is thus among the rarest c. 25% in number of level 3 areas, but not in the rarity index. However, the rarity index falls just above the cut off for us to consider it rare even at this level.

Alaska has the highest number of species (90) followed by Norway (89), Northern European Russia (83), Sweden, (82) and West Siberia (81; Fig. 1).

The arctic and the boreal regions have very few range restricted species ($H' < 1$). Nepal has most restricted species (19) followed by South-central China (17), East Himalaya (14) Japan (10) and Tibet (5).

Himalaya and surrounding areas have a large proportion of range restricted species. Only Nepal, South-central China, East Himalaya and West Himalaya have an $RI_D$ over 400 (Fig. 2).

Number of range restricted species in level 3 areas north of the Tropics of Cancer is positively correlated with number of species (correlation coefficient 0.437, $p < 0.001$, $n = 183$). Only four areas, Nepal, south-central China, East Himalaya and Japan, fall outside the 99% confidence interval for individual areas in the linear regression (Fig. 3).

### 3.2. Habitat specificity

Habitat specificity at different levels is strongly correlated. Correlation coefficients (including combined number of habitats, MaMeMi) varies between 0.692 and 0.799 ($p < 0.001$ for all combinations).

The vast majority of the species use a very limited number of habitats at all levels. There are 68 species confined to one macrohabitat, 42 species to one mesohabitat and 38 species to one microhabitat. Using the combination of all habitats (MaMeMi), 29 species are still registered for only one habitat type and another 11 species for two habitat types. However, some species use a large number of habitats, with nine species using over 100 habitats (max. 209 for *Scapania irrigua*; Fig. 4).

For this paper we define habitat specialist species (the c. 25% using fewest habitats) as those with log MaMeMi <1 (i.e. using one or two habitats). This gives 40 species (23%; Table 1).

The investigated group is most species rich in alpine macrohabitats, but also boreal, arctic and temperate macrohabitats host a lot of species. Fewer species occur in Mediterranean, Tropical deciduous forest and Tropical evergreen forest macrohabitats. However, the last two macrohabitats are almost lacking north of the Tropic of Cancer. Number, and also proportion, of habitat specialists are highest in alpine environments (21% and 16%, respectively).

The species are registered from 30 mesohabitats. Cliffs and rocks have most species (91), followed by mesic subalpine forests (69), streams (61) and tundra heathlands (61). Most habitat specialists are found in mesic subalpine forests (11) and on cliffs and rocks (10). Those habitats also have the highest proportion of habitat specialists (16% and 11%, respectively) if only habitats with more than 10 species are considered. The mesohabitats can be combined into 13 habitat groups. Of these, bedrock habitats are the most species rich (112 species), subalpine forests and bedrock habitats have most habitat specialists (11 and 13, respectively) and the last two habitat groups also have the largest proportion of specialists (15% and 12%, respectively) when only groups with more than 10 species are considered.

The investigated group of species is registered from 103 microhabitats. The microhabitats where most species can be found are moist decaying logs in intermediate decay stage (50 species), moist acid soil (46) and moist neutral soil (38). Most habitat specialists can be found on moist neutral soil (6), moist neutral rocks (5), moist basic soil (4) and moist decaying logs in intermediate stages (4). Considering only microhabitats with over 10 species, the highest proportion of habitat specialists are found on moist basic soil (18%), wet decaying logs at intermediate stages (17%), moist neutral rocks (16%), moist neutral soil (16%) and moist neutral sand (15%).

The microhabitats can be grouped into 19 microhabitat groups. Of these groups, soil is the most species rich (105 species) followed by epilithic (75) and decaying logs (61). These microhabitat groups also have the largest number of habitat specialists (12, 12 and 6, respectively) and proportion of spe-

**Table 1 – Species classified into four groups of rarity using habitat restriction and distribution ranges**

| | Restricted species ($H' < 1$) | Widespread species ($H' \geqslant 1$) |
|---|---|---|
| Habitat generalists (logMaMeMi ⩾ 1) | *Anastrophyllum lignicola*<br>*Diplophyllum serrulatum*<br>*Diplophyllum trollii*<br>*Gottschelia patoniae*<br>*Hattoria yakushimensis*<br>*Lophozia setosa*<br>*Scapania ampliata*<br>*Scapania davidii*<br>*Scapania griffithii*<br>*Scapania hirosakiensis*<br>*Scapania karl-muelleri*<br>*Scapania koponenii*<br>*Scapania pseudocontorta*<br>*Scapania serrulata*<br>*Scapania sphaerifera*<br>*Scapania subnimbosa* | The other 118 species |
| Habitat specialists (logMaMeMi < 1) | *Anastrophyllum tenue*<br>*Gerhildiella rossneriana*<br>*Gymnocolea borealis*<br>*Gymnocolea fascinifera*<br>*Lophozia austri-sibirica*<br>*Lophozia herzogiana*<br>*Lophozia lantratroviae*<br>*Lophozia nakanishii*<br>*Lophozia nepalensis*<br>*Lophozia pallida*<br>*Lophozia subapiculata*<br>*Scapania bhutanensis*<br>*Scapania contorta*<br>*Scapania diplophylloides*<br>*Scapania fulfordiae*<br>*Scapania gigantea*<br>*Scapania harae*<br>*Scapania himalayica*<br>*Scapania hollandiae*<br>*Scapania integerrima*<br>*Scapania komagadakensis*<br>*Scapania matveyevae*<br>*Scapania nipponica*<br>*Scapania orientalis*<br>*Scapania pseudocalcicola*<br>*Scapania rotundifolia*<br>*Scapania schljakovii*<br>*Scapania secunda*<br>*Scapania sinikkae*<br>*Scapania spiniloba*<br>*Scapania zhukovae* | *Barbilophozia hyperborea*<br>*Diplophyllum nanum*<br>*Diplophyllum obtusatum*<br>*Lophozia alboviridis*<br>*Lophozia hyperarctica*<br>*Scapania ciliatospinosa*<br>*Scapania imbricata*<br>*Scapania maxima*<br>*Scapania microdonta* |

cialists (11%, 16% and 10%, respectively). Two other habitat groups also had large proportion of habitat specialists, hollows (18%, 11 species) and litter (17%, 6 species).

Number of habitat specialists in macrohabitats, mesohabitats and microhabitats is positively correlated with number of species. Additionally, no macrohabitat, mesohabitat group or microhabitat group differ significantly from the linear regression.

Himalaya and the surrounding areas have most habitat specialists. Only Nepal, East Himalaya and South-central China have $RI_H$ over 200 (Fig. 5). In fact these are only ones with $RI_H$ over 100.

### 3.3. *Relation between habitat specificity and distribution ranges*

Number of range restricted species in macrohabitats, mesohabitats and microhabitats is positively correlated with number of species. Again, no macrohabitat, mesohabitat group or microhabitat group differ significantly from the linear regression.

Number of habitat specialists in level 1 areas is positively correlated with number of species for all levels. No area differs significantly from the linear regression at level 1.

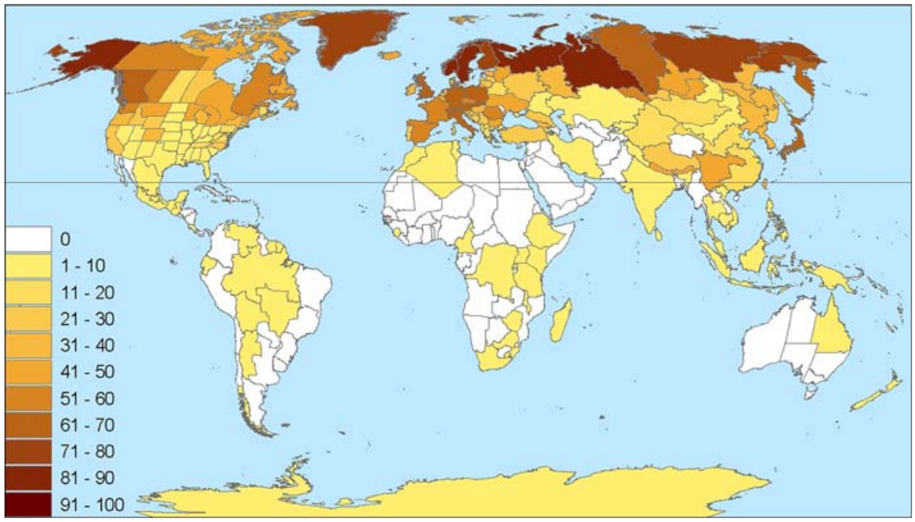


**Fig. 1 – Number of investigated species in each level 3 area. The line is the Tropic of Cancer and only species occurring north of this line is scored. The area south of this line is shown only for the completeness of the distributions.**


**Fig. 2 – Importance for range restricted species ($RI_D$) of each level 3 area.**

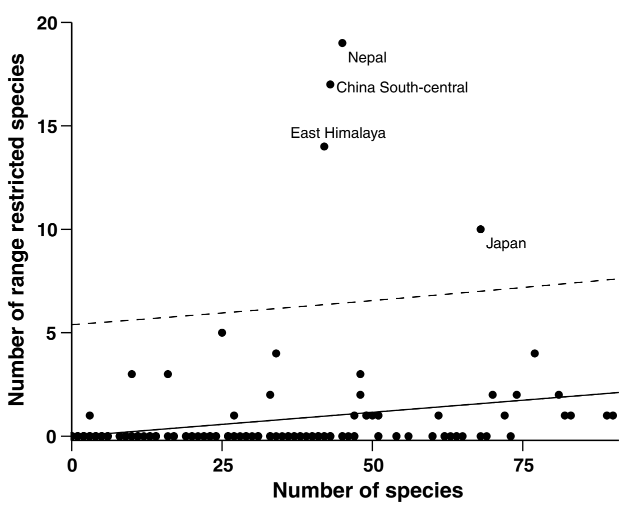


**Fig. 3 – The relation between number of species and number of range restricted species in each level 3 area, the linear regression line ($y = -0.012 + 0.023x$; $p < 0.001$; $n = 183$; $R^2 = 0.055$) and the 99% confidence interval for individual areas (broken line). Only areas outside the confidence interval are labelled.**

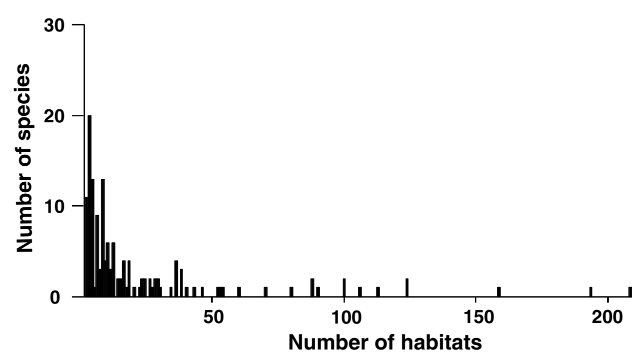


**Fig. 4 – Number of habitats used by investigated species.**

Only Indian subcontinent (incl. Himalaya) has significantly more habitat specialist species than expected from the linear regression (Fig. 6).

Number of habitat specialists in level 3 areas is also positively correlated with number of species. Four areas, East Himalaya, south-central China, Nepal and Japan have significantly more rare species than expected from the linear regression (Fig. 8).

There is a strong positive correlation between species distribution and habitat use (correlation coefficient 0.835, $p < 0.001$; $n = 174$) and all but seven species falls within the 99% confidence interval of the linear regression (Fig. 8). The seven deviating are all more habitat generalists than expected from their distribution and the species fall into three clusters. *Scapania koponenii* and *Gottschelia patoniae* are restricted but use many habitats, *Scapania gracilis*, *Scapania compacta* and


**Fig. 5 – Importance for habitat specialist species ($RI_H$) of each level 3 area.**

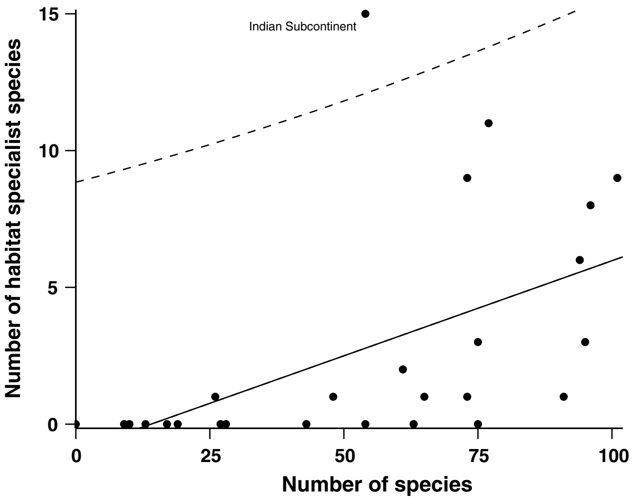


**Fig. 6 – Number of species and habitat specialists in each level 2 areas north of the Tropic of Cancer, the linear regression line ($y = -0.98 + 0.70x$; $p = 0.007$; $n = 26$; $R^2 = 0.268$) and the 99% confidence interval for individual areas (broken line). Only areas outside the confidence interval are labelled.**

*Douinia ovata* are fairly common species and *Scapania nemorea* and *S. irrigua* are the two species registered from most habitats and among the most widespread of all species.

Using the rarity limits defined in this study 31 species are rare on both parameters, 9 species habitat specialists but not range restricted, 16 species range restricted but not habitat specialists, and the remaining 118 species are not rare on any of the investigated parameters (Table 1).

## 4. Discussion

### 4.1. *Conservation priorities*

As a rare species is more vulnerable for changes in the environment they are also more vulnerable for extinction. It is thus important to be able to identify the rare species, and the type of rarity they show, in order to prioritize the conservation efforts. Analysis of rarity along more than one parameter have been done for some animals, e.g. population size and resource use in frugivorous birds (Walker, 2006) and distribution ranges and niche width in Amphiopoda (Gaston and Spicer, 2001), and for plants (e.g. population sizes, distribution ranges and niche width in forest plants; Kolb et al., 2006). However, most interest has been on distribution ranges and local population sizes (e.g. Symonds and Johnson, 2006) and conservation aspects have not been evaluated.

This study shows that rarity along two important parameters, distribution ranges and habitat specificity is not independent. A habitat specialist is thus most often also range restricted and vice versa. We identify 56 species as rare for one or both of the criteria using our limits for rarity (Table 1). The species that are rare both on distribution ranges and habitat specialisation should be the first ones evaluated for conservation need. If there is a threat to their habitats, the effect on the populations is faster than for more widespread species. We have managed to identify 31 species (18% of the total number of species evaluated) to give highest priority. Other habitat specialist species should also be evaluated for threats to their habitats, but as they occur over a larger area, their risk to go extinct within a short time-period is lower. For range restricted species that are habitat generalists, the population dynamic is more important to study and include in threat analysis.

It is notable that the genus *Scapania* is so well represented among the rare species (62% while only 42% in the whole dataset). This is a monophyletic group (cf. e.g. Schill et al., 2004; Davis, 2004; Yatsentyuk et al., 2004) while the other species are phylogenetically much more diverse. It is thus tempting to conclude that rarity does have a phylogenetic component that we know very little about at this stage.

### 4.2. *Species richness and occurrence of rare species*

Conservation biogeography is a relatively recent subfield of conservation biology (Whittaker et al., 2005) where biogeographical principles and methods are applied on conservation issues, e.g. in identifying "hot spots" for conservation. The results of such analysis are highly dependent on the spatial and temporal scales applied and on the parameters used (cf. Whittaker et al., 2005). We have here used a coarse-grained system to analyse the distribution range and range restrictions. A more fine-grained system may have given different results but the lack of detailed distribution data ("the Wallacean shortfall") presently prevents us from doing this with any credibility.

The northern species of the Lophoziaceae/Scapaniaceae complex are markedly arctic and boreal in its distribution, but also to some degree oceanic and alpine/montane. Range restricted species are concentrated to Himalaya and surrounding areas of China, and to Japan. If areas with very few species recorded (mainly under-explored areas) are excluded, these areas also show the highest proportion of their species to be range restricted. In fact, Nepal, East Himalaya, South-central China (including Yunnan and Sichuan) and Japan show significantly more range restricted species than expected from the number of species occurring there. Those areas are known for high endemism also in other organism

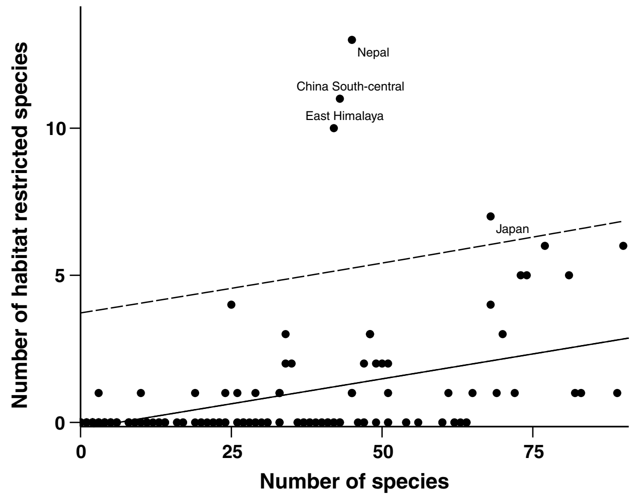


**Fig. 7 – Number of species and habitat specialists in each level 3 area, the linear regression line ($y = -0.124 + 0.034x$; $p < 0.001$; $n = 183$; $R^2 = 0.189$) and the 99% confidence interval for individual areas (broken line). Only areas outside the confidence interval are labelled.**

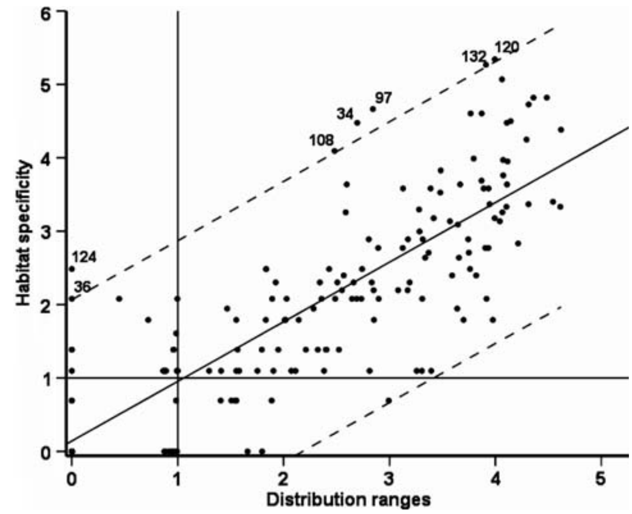


**Fig. 8 – Relation between distribution range ($H'$) and habitat specificity (log MaMeMi), the linear regression line ($y = 0.812 + 0.142x$; $p < 174$; $n < 0.001$; $R^2 = 0.666$; black solid line) and the 99% confidence interval for individual areas (black broken line). The solid lines delimit the rarity level for distribution range ($H' < 1$) and habitat specificity (log MaMeMi < 1). Only species outside the confidence interval are labelled (36 = *G. patoniae*, 124 = *S. koponenii*, 34 = *D. ovata*, 97 = *S. compacta*, 108 = *S. gracilis*, 120 = *S. irrigua*, 132 = *S. nemorea*).**

groups (Groombridge and Jenkins, 2002). They are also rather isolated areas (mountain ranges and islands) which may restrict the possibilities to disperse, at least for sexually non-reproducing species without suitable diaspores (cf. Söderström and Herben, 1997). However, the linear regression only explains 5.5 percent of the variation so it is clear that other factors than number of species is important.

Several regions do have more habitat specialists than expected from the number of species. Nepal deviates most with 13 habitat specialists instead of 5 or less expected from the linear regression for an area with that number of species. Also South-central China (11 instead of ⩽5), East Himalaya (10 instead of ⩽5 and Japan (7 instead of ⩽6) are areas with a high number of habitat specialists (Fig. 7). It must, however, be stressed that the number of species does not explain more than 20% of the number of habitat specialist species occurring there. This also means that no habitat specialist species is necessary for areas under at least 100 species and areas with only 1 species may also have a habitat specialist.

### 4.3. *Range sizes and habitat specialisation*

Number of habitat specialists in any of the habitats is strongly correlated with the number of species occurring there. This means that the most species rich habitat at any level also holds the highest number of habitat specialists, and no microhabitat group seems to be so special that species occurring there can not occur on other microhabitats.

No habitat at any level has more range restricted species than expected from the number of species in that habitat. The reason for this pattern is probably the strong correlation between habitat specificity and distribution range. Thus, at this point it is difficult to separate between them and say which factor is most important.

However, there are seven species that are less habitat specialists than expected from their distribution range (Fig. 8). Of these, two (*S. koponenii* and *G. patoniae*) were recently described and at the same time recorded from relatively many substrates. It may be expected that they will be found also in other areas and thus may not be so distribution limited. The next group includes three species (*S. gracilis*, *S. compacta* and *D. ovata*) with a marked oceanic occurrence. Our habitat recording does not recognize oceanity very well and the species are probably limited by macroclimate more than anything else. Therefore, they tend to occur on many habitats where they occur at all. Two of the most widespread species (*S. irrigua* and *S. nemorea*) are also occurring on a very wide range of habitats.

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## Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.biocon.2006.10.012.

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