

# Effects of aerial dispersal, habitat specialisation, and landscape structure on spider distribution across fragmented grey dunes

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Species distribution patterns have been explained by Hutchinson's niche theory, metapopulation theory and source-sink theory. Empirical verification of this framework, however, remains surprisingly scant. In this paper, we test the hypothesis that landscape characteristics (patch size and connectivity), aerial dispersal ability and niche breadth interact in explaining distribution patterns of 29 spider species inhabiting fragmented grey dunes. Distribution patterns only depended on aerial dispersal potential, and the interaction between patch connectivity and area. Niche breadth, measured as the degree of habitat specialisation in the total coastal dune system, did not contribute to the observed distribution patterns. Additional variation in patch occupancy frequency was strongly species-dependent and was determined by different responses to the degree of patch connectivity for ballooning dispersal. Results from this study suggest that dispersal ability largely affects our perception of a species "fundamental niche", and that source-sink and metapopulation dynamics may have a major impact on the distribution of species. From a conservation point of view, specialised (and hence intrinsically rare) species can be predicted to become rarer if fragmentation increases and connectivity decreases. This study is, to our knowledge, one of the few linking species distribution (and not patch occupancy, species diversity or richness) to landscape ecological (patch connectivity and area) and auto-ecological (niche breadth, dispersal potential) features.

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Hutchinson's niche theory, metapopulation theory and source-sink theory combined, provide a solid conceptual framework for the study of species distribution patterns (Pulliam 1988, Hanski 1998, 1999a, 1999b, Pulliam 2000). Empirical verification of this framework, however, remains surprisingly scant (Pulliam 2000). Besides, case studies examining the effects of organism-based parameters and landscape structure on distribution patterns often yield inconsistent results. For instance, species regularly prove absent from 'suitable habitat' (as predicted by the modified Hutchinson's n-dimensional niche concept; Hutchinson 1957) and present in 'less suitable' one (Pulliam 2000).

Patterns of distributions in heterogeneous landscapes thus reflect complex biotic interactions, such as between species competition, dispersal, niche breadth and the distribution of environmental parameters in space and time (e.g. Pulliam and Danielson 1991, Moilanen and Hanski 1998, Pulliam 2000).

Metapopulation theory states that local population extinctions are not as uncommon as previously thought (Brooker and Brooker 2002, Smith and Hellmann 2002) and may result from stochastic changes in habitat quality and demography combined with poor ability of dispersal (Hanski 1998). The latter has been widely identified as a key process in both population regulation

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and spatial distribution in plants and invertebrates (e.g. Malmqvist 2000, Thomas 2000, Johnson et al. 2001, Verheyen and Heryn 2001, Hedenäs et al. 2003). Yet, other studies have failed to demonstrate clear-cut relationships between dispersal and distribution (e.g. Andersson et al. 2000, Malmqvist 2000, Clarke et al. 2001, Rundle et al. 2002) or have revealed counter-intuitive patterns (e.g. Guitierrez and Menéndez 1997). Habitat fragmentation may both promote and reduce mobility, depending on the degree of resource or habitat specialisation (Wiens 2001). Thus, ecologically related species occupying the same environment may differ markedly in their responses to landscape change and fragmentation, depending on how dispersal and niche breadth are expressed in their respective populations, possibly as a result of local adaptation. Moreover, levels of habitat specialisation and of dispersal ability have been previously shown to be interrelated in spiders from fragmented grey dune habitats (Bonte et al. 2003d).

Despite the above, few studies have attempted to integrate species-level and landscape-level variables to explain patterns of species distribution (Thompson et al. 1999) or patch occupancy (Lens et al. 2002). We apply such approach to study the distribution of spider (Araneae) species across a network of grey dune patches along the Belgian coast. Due to increased urbanisation for tourist facilities, the total area of dune habitat in Belgium has decreased from 6000 ha to 3800 ha since the beginning of the 20th century, and became increasingly fragmented (Vermeersch 1986). In addition, local farmers started to abandon their agropastoral activities after the Second World War, resulting in a steady increase of sea buckthorn-shrubs *Hippophae rhamnoides*. This, in combination with a crash of the rabbit population *Oryctolagus cuniculus* due to viral diseases myxomatosis and VHS, lead to a further reduction and fragmentation of grey dune vegetation (Provoost et al. 2002). An earlier survey of spider species in remaining grey dune fragments revealed a positive relationship between presence of typical grey dune species and patch size (Bonte et al. 2002). Such a relationship may both reflect poor colonization ability, high sensitivity to environmental stress, or interactive effects between these (and other) variables. In this paper we test the hypothesis that characteristics at landscape level (patch size and isolation) and population level (dispersal ability and niche breadth) interact when affecting distribution patterns of spiders in a heterogeneous and severely fragmented coastal dune landscape.

## Material and methods

### Study area and species

Fieldwork was conducted in the Flemish coastal dunes, located between the cities of Nieuwpoort-Lombardsijde

and De Panne (Belgium, 51°08'N-51°05'N, 2°45'-2°32'E) and consisting of 149 discrete grey dune patches. Mean patch size is 1.41 ha and ranges from 0.07-22.54 ha. Patch size and patch connectivity, as calculated for ballooning dispersal (see further), are significantly related (Bonte et al. 2003c), indicating that smaller patches are generally more strongly isolated.

All studied species (Table 1) are common in the Flemish coastal dunes, but specialised species may be rare at regional (Maelfait et al. 1998) or global level (Hänggi et al. 1995). They represent >85% of the total number of individuals caught with pitfall traps (Table 1) and were the only collected in sufficiently numbers to perform tests on their aerial dispersal propensity (see below). Spiders from grey dunes are generally small-sized and most active during autumn and spring (Bonte and Mertens 2003). Stenotopic microsheit webspiders (Linyphiidae) are characterised by one generation in one year and have semi-sessile life habits, while larger species of crabspiders (Thomisidae) and wolfspiders (Lycosidae) have one generation yearly or bi-yearly (Bonte and Maelfait 1998, Bonte and Maelfait unpubl.). Most species live on the surface, or have a burying life style (*Arctosa* and *Alopecosa* species). Voucher specimens are deposited at the Royal Belgian Institute of Natural Sciences in Brussels; nomenclature follows Platnick (2002).

### Patch occupation and landscape characteristics

Presence-absence data of 29 spider species were derived from pitfall records in 19 grey dune patches. Each fragment was sampled during one year between 1995 and 2002 with five pitfall traps (the traps consist of uncovered glass jam jars with a diameter of 9.5 cm, filled with a 10% formaline soap-solution). The traps were emptied fortnightly. All species included in the analysis are easily captured with pitfall traps because of their high degree of mobility and the short vegetation structure (Bonte et al. 2003a). Pitfall data therefore reliably reflect species occurrence.

Patches were digitised from aerial orthophotographs with a Geographic Information System (Arcview 3.1) and discrimination of vegetation types was based on vegetation-specific red (RED) and near-infrared (NIR) reflectance values (Provoost et al. 2002). Patch connectivity ( $S_i$ ) was estimated as  $S_i = a_j^{-d_{ij}} N_j$  (Hanski 1999a) with  $a$ =constant describing the strength of the inverse relationship between numbers of migrants from patch  $j$  and distance between patches,  $d$ =the geographic distance between patch  $i$  and  $j$ , and  $N$ =population size at patch  $j$ .  $N$  was set as one for all patches, so  $S_i$  reflects the optimal patch connectivity, irrespectively of the patch occupancy status. Based on literature data (Thomas 1996) we assigned  $a=4$  for

Table 1. Degree of habitat specialisation (data from Bonte et al. 2002), frequency of tiptoe behaviour (data from Bonte et al. 2003d), the number of tested individuals n (with notes on the number of mothers in case of laboratory rearing), relative abundance within pitfall traps (total abundance=8887 individuals) and percentage patches occupied by 29 Araneae species from coastal grey dunes (on 19 grey dune patches).

Species and family	Habitat specialisation	Tiptoe freq. (%)	n	Relative abundance (%)	Patch occupation (%)
<i>Alopecosa barbipes</i> (Sundevall, 1833) (Lycosidae)	3	8.95	67 (6)	1.66	84.10
<i>Alopecosa fabrilis</i> (Clerck, 1757) (Lycosidae)	6	0.00	21	0.34	31.57
<i>Alopecosa pulverulenta</i> (Clerck, 1757) (Lycosidae)	2	16.36	55 (4)	1.67	100.00
<i>Arctosa perita</i> (Latreille, 1799) (Lycosidae)	2	20.90	110 (7)	0.72	78.94
<i>Argenna subnigra</i> (O.P.-Cambridge, 1861) (Dictynidae)	1	40.00	35	1.41	78.94
<i>Centromerita concinna</i> (Thorell, 1875) (Linyphiidae)	2	56.36	55	8.19	94.73
<i>Erigone atra</i> Blackwall, 1833 (Linyphiidae)	1	96.00	300	13.42	100.00
<i>Erigone dentipalps</i> (Wider, 1834) (Linyphiidae)	2	73.21	56	4.96	100.00
<i>Hypsosinga albovittata</i> (Westring, 1851) (Araneidae)	3	33.33	15	0.45	47.36
<i>Meioneta rurestris</i> (C.L. Koch, 1836) (Linyphiidae)	2	77.50	40	0.88	100.00
<i>Ozyptila simplex</i> (O.P.-Cambridge, 1862) (Thomisidae)	2	32.35	34	0.49	78.94
<i>Pachygnatha degeeri</i> Sundevall, 1830 (Tetragnathidae)	2	35.59	59	2.89	89.47
<i>Parapelecopsis nemoralis</i> (O.P.-Cambridge, 1884) (Linyphiidae)	2	10.56	123	0.92	68.42
<i>Pardosa monticola</i> (Clerck, 1757) (Lycosidae)	4	8.08	569 (22)	18.59	68.42
<i>Pardosa nigriceps</i> (Thorell, 1856) (Lycosidae)	1	42.26	97 (6)	1.97	100.00
<i>Pardosa pullata</i> (Clerck, 1757) (Lycosidae)	2	15.73	89 (7)	0.34	68.42
<i>Pelecopsis parallela</i> (Wider, 1834) (Linyphiidae)	5	20.58	34	4.01	63.15
<i>Styloctetor romanus</i> (O.P.-Cambridge, 1872) (Linyphiidae)	6	12.68	134	0.38	78.94
<i>Tenuiphantes tenuis</i> (Blackwall, 1852) (Linyphiidae)	1	85.29	34	1.40	100.00
<i>Thyphochrestus digitatus</i> (O.P.-Cambridge, 1872) (Linyphiidae)	5	10.95	210	6.43	73.68
<i>Tiso vagans</i> (Blackwall, 1834) (Linyphiidae)	3	46.87	32	0.60	78.94
<i>Trichopterna cito</i> (O.P.-Cambridge, 1872) (Linyphiidae)	3	22.98	87	3.42	73.68
<i>Walckenaeria monoceros</i> (Wider, 1834) (Linyphiidae)	2	45.83	48	0.60	73.68
<i>Walckenaeria stylifrons</i> (O.P.-Cambridge, 1875) (Linyphiidae)	6	4.34	23	0.51	57.89
<i>Walckenaeria antica</i> (Wider, 1834) (Linyphiidae)	1	88.23	34	0.19	94.73
<i>Xysticus kochi</i> Thorell 1872 (Thomisidae)	3	32.30	65 (3)	4.31	94.73
<i>Xysticus ninnii</i> (Thorell, 1872) (Thomisidae)	5	0.00	21 (1)	0.19	15.78
<i>Xysticus sabulosus</i> (Hahn, 1832) (Thomisidae)	4	13.63	110 (6)	0.97	57.89
<i>Zelotes electus</i> (C.L. Koch, 1839) (Gnaphosidae)	2	36.00	25	3.52	100.00

dispersal by ballooning (see below) independently of the surrounding matrix type. Values of patch size and patch connectivity were ln-transformed to approach normality. For this study, we selected grey dune patches in which patch size and connectivity were not significantly ( $r_{18}=0.289$ ; NS) related.

### Habitat specialisation

Species-specific levels of habitat specialisation were estimated from the level of maximal indicator value (IndVal) in a dichotomous and hierarchical clustering of pitfall data from different coastal dune habitats (details in Bonte et al. 2002, Bonte et al. 2003d) as an approach of eurytopicity (Dufrêne and Legendre 1997). This approach determines indicator species at different hierarchical or non-hierarchical levels of clustering by combining relative species abundance with its relative frequency of occurrence in the various groups of site within each level of clustering. Species with maximal IndVal at the last level (level 6) occur only in very specific habitats (grey dune), while those with a maximal IndVal at intermediate division levels are bound to more than one type of typical coastal dune habitat. Dispersing individuals accidentally trapped in a particular habitat

only marginally influence the IndVal calculation due to the specific algorithm used (Dufrêne and Legendre 1997). Additionally, because only data from three patches, included in this study, were used for this IndVal calculation, circular argumentation was avoided.

### Aerial dispersal

Potential long-distance dispersal in Araneae species mainly occurs via passive transport in air currents, so-called ballooning dispersal (Weyman 1993), while short-distance dispersal is also possible by cursorial dispersal, especially in wolf spiders Lycosidae (Samu et al. 2003). Ballooning dispersal is initiated by tiptoe behaviour, i.e. stretching of the legs and raising of the abdomen prior to silk thread production from the spinnerets (Duffey 1998). Earlier studies confirmed that the frequency of tiptoe behaviour under laboratory conditions could be used as a reliable estimator of ballooning propensity in the field (Richter 1970, Weyman 1993, Bonte et al. 2003c, d). To study tiptoe behaviour, spiders were either collected in the field (families Araneidae, Dictynidae, Linyphiidae, Gnaphosidae and Tetragnathidae) or reared from cocoons collected in the field (families Lycosidae and Thomisidae; protocol as described in Bonte et al.

2003d). Only adult Linyphiidae and small juvenile spiders from the other genera were used for the experiment, since these have ideal masses for aerial dispersal (B1 mg; Greenstone 1990). Tiptoe behaviour was studied following Legel and Van Wingerden (1980) and Bonte et al. (2003d). Spiders were placed on a plastic frame, individually or in groups of two to five individuals (in case of *Pardosa* juveniles reared in the lab) as to reduce the level of intraspecific interaction. The frame was placed in a windtunnel with an upward current of 1-1.2 ms<sup>-1</sup> at a temperature of 30±2°C and an aerial humidity of 40-50%. To prevent spiders from escaping by walking, the frame was placed in water. Observations were conducted during 20 min. Observations of tiptoe behaviour of three seconds or more were considered valid (Bonte et al. 2003b). Since nutritional conditions influence ballooning (Bonte et al. 2003b), spiders were fed with *Isotoma viridis* (Collembola) ad libitum before starving them for one week prior to the experiment.

### Statistical analysis

Data on the occupancy of each species within each patch (binomial response; 0 or 1) were analysed with a mixed logistic regression model with logit link (glimmix procedure in SAS 8.1). Variables ‘tiptoe frequency’, ‘habitat specialisation’, ‘patch area’, ‘patch connectivity’ and all relevant two-way interactions were modelled as continuous factors, with the degrees of freedom being approximated using Satterthwaite’s procedure. Variable ‘species’ and the two-way interactions with variables ‘patch area’ and ‘patch connectivity’ were included as random factors and tested against the  $\chi^2$  distribution (DF=1) of the Log-Likelihood-difference between the models with and without variable of interest. Non-significant variables were eliminated by a backward-stepwise procedure.

### Results

Data on patch occupancy, tiptoe frequency and degree of habitat specialisation are summarized in Table 1.

The probability of patch occupancy was positively related to the frequency of tiptoe behaviour. The regression slope was estimated to 2.8689±2.598, back-transformed equalling 0.935 (range 0.515-0.995) (Table 2, Fig. 1). The effect of patch connectivity depended on patch area, as shown by a significant areaxconnectivity interaction (Table 2). When both area and connectivity increased, fragments were more likely to be occupied. However, connectivity did not affect patch occupancy when patches were small (Fig. 2). Patch occupancy varied significantly between species ( $s^2=0.408$ ), with the effect of species depending on the degree of

Table 2. Logistic regression model analysing the effects of tiptoe frequency (TTfreq), degree of habitat specialisation (IndVal), patch area (Area) and patch connectivity (S) on patch occupancy by 29 Araneae species from coastal grey dunes.

Variable	Num. DF	Den. DF	F	p
TTfreq	1	40.9	24.56	B0.001
IndVal	1	302	0.30	0.584
Area	1	519	1.31	0.254
S	1	517	8.56	0.004
TTfreqxIndVal	1	20.1	0.06	0.815
AreaxS	1	519	6.20	0.013
AreaxTTfreq	1	50	1.18	0.282
AreaxIndVal	1	43	0.25	0.624
SxIndVal	1	241	0.62	0.432
SxTTfreq	1	410	0.73	0.392
Variable		$s^2$	$\chi^2$	p
Species		0.408	98.2	B0.0001
SpeciesxS		0.013	10.7	0.0005
SpeciesxArea		B0.001	0.114	0.735
SpeciesxAreaxS		B0.001	0.008	0.928

connectivity (speciesxconnectivity:  $s^2=0.013$ ) (Table 2). The residual variance equalled 0.764. The goodness-of-fit of the models was significant ( $\chi^2_{327}=359.11$ , pB0.0001).

### Discussion

The distribution of spider species depended on their aerial dispersal potential, and the interaction between patch connectivity and area. Niche breadth, measured as the degree of habitat did not directly contribute to the observed distribution patterns, but may shape distribution through its relation with the measures of ballooning propensity. Residual variation was explained by species-specific responses to the degree of patch connectivity for ballooning dispersal.

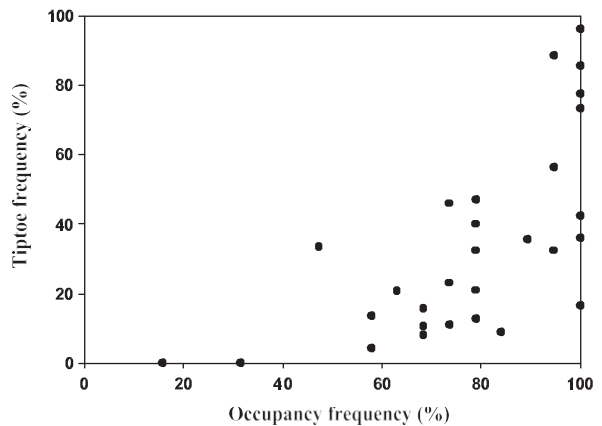


Fig. 1. Relationship between frequency of tiptoe behaviour and the number of occupied patches by 29 spider species of fragmented grey dunes.

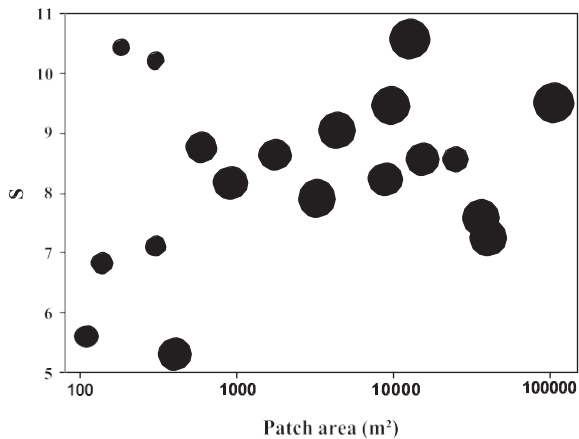


Fig. 2. Number of species per patch for 29 spider species in relation to landscape levels of patch connectivity and patch size. Sizes of the dots reflect the proportion of present species on the total number of studied species.

Ballooning is presumed to be an efficient mechanism for distant dispersal and hence for colonisation of suitable but unoccupied habitats (Toft 1995, Duffey 1998). In this study, we estimated ballooning propensity and hence dispersal potential by measuring the frequency of tiptoe behaviour. This estimate, of course, should not a priori be related to effective dispersal events since proximal factors may both influence dispersal initiation (local food deprivation, crowding) and colonisation success (suitability of the habitat, presence and density of con- and heterospecifics) (Weyman 1993). As shown by Samu et al. (2003), short-distance dispersal may be more effective by terrestrial dispersal in lycosid spiders, certainly if suitable habitat is available within the proximity of the core habitat. Therefore, we believe that this measure is only an estimate of the long-distance dispersal potential beyond the species home range, and a good approximation for dispersal efficiency at longer time scales.

In severely fragmented landscapes, suitable habitats are patchily distributed within an unsuitable matrix. Especially for species with strict and specialised habitat requirements, aerial dispersal may involve a high risk in reaching potential suitable habitats. This was confirmed in an earlier study on dispersal by spiders in grey dunes where selection against ballooning dispersal in specialist species was believed to result from local adaptation (Bonte et al. 2003d). Effective wind dispersal has been strongly linked to colonisation ability in a number of plant species (e.g. Dwzonko and Loster 1992, Nakashizuka et al. 1993, Stöcklin and Bäumler 1996), while ballooning in spiders has also been shown to be effective in the colonisation of recently cleared land (Meijer 1977, Weyman and Jepson 1994). As mentioned before, long-distance dispersal by ballooning is supposed to be the major relevant dispersal mode for (distant) patch colonisation. A recent study of a

spatially-structured population of wolf spiders (Bonte et al. 2003c), however, failed to confirm the importance of ballooning in short-term colonisation, although it was the best predictor for patterns of patch occupancy resulting from long-term colonisation and extinction dynamics. Results from this study generalise this conclusion that long-term patch occupancy patterns are related to ballooning dispersal for the entire spider assemblages of grey dunes.

This study, however, does not show a relationship between level of habitat specialisation and species distribution, which would be expected if specialist spiders were more sensitive to changes in habitat quality. It does neither explain patterns in species distribution in interaction with connectivity, which would indicate different sensitivities to patch isolation for specialist and generalist species. Such a relationship would be expected if generalist species survived better in other habitat types in the shrub matrix and were able to disperse in a more cursorial way through this matrix. When a different, completely independent, index of niche breadth was used (negative logarithm of the number of suitable habitats of the species in central Europe; details in Bonte et al. 2003d), comparable results were obtained (data not shown), confirming the validity of our conclusions. Because niche breadth and ballooning propensity are positively related (Bonte et al. 2003d), low occurrence of specialised species in small and isolated grey dune fragments (Bonte et al. 2002) seems largely due to their low potential ballooning ability. As a result, specialised (hence intrinsically rare) species can be predicted to become rarer if fragmentation increases and connectivity decreases.

Since we used the degree of habitat specialisation in coastal dunes as a measure of niche breadth, effects of realised niches rather than of Hutchinson's fundamental niches were analysed. As pointed out by Pulliam (2000), species can survive outside their fundamental niche, although local mortality may exceed recruitment in case of a source-sink population structure. We recorded the presence of species for which the presumed optimal habitat is productive (often arable) grasslands (*Erigone atra*, *E. dentipalpis*, *Meioneta rurestris*, *Tenuiphantes tenuis*; Hänggi et al. 1995). Because prey abundance tends to decrease during summer (Bonte and Mertens 2003), summer mortality can be expected to be very high for these grassland species. Their presence in grey dunes was therefore probably mediated through continuous aerial colonisation from neighbouring source habitat (i.e. dune slacks, wet meadows). In contrast, specialist species for which the fundamental niche consists of grey dunes (*Alopecosa fabrilis*, *Styloctetor romanus*, *Walckenaeria stylifrons*) can be expected to be absent due to limited dispersal ability. Results from our study therefore suggest that dispersal ability largely affects our perception of a species "fundamental niche" (Pulliam 2000),

and that source-sink and metapopulation dynamics may have a major impact on the distribution of species. If effects of fundamental niche breadth (e.g. through study of desiccation resistance and/or temperature optima; Almquist 1970, Almquist 1971) rather than realised niche breadth could be analysed, model outcomes might differ in the direction expected. Yet, in a study on regional and national distribution patterns of herb species (Thompson et al. 1999) the degree of habitat specialisation (realised niche) rather than germination temperature (fundamental niche) explained the largest variation species range.

Apart from species-specific traits, landscape characteristics significantly explained variation in patch occupancy. Regression coefficients describing the relationship between patch occupancy and patch connectivity, varied between -2.12 and 2.13 (29 species tested; after Bonferroni correction none of the regressions were significant). Such variation was likely due to the presence of other dispersal modes, i.e. cursorial dispersal, which may be more efficient in larger lycosid species as demonstrated by Bonte et al. (2003c) for the wolfspider *Pardosa monticola* (Clerck 1757). Besides, individual- and population-level factors such as longevity, population size, population density, and sensitivity to low densities (Allee effect; Stephens and Sutherland 1999) may affect extinction probability and hence distribution patterns.

In conclusion, we have provided substantial correlative evidence that aerial, passive dispersal shapes species distribution. The inclusion of data on niche breadth, although here not contributing to the overall model, may elucidate species distributions, apparently not influenced by dispersal characteristics (Andersson et al. 2000, Malmqvist 2000, Clarke et al. 2001). From a conservationist point-of-view, our results show that fragmentation will accelerate the extinction of specialised species if fragmentation rates of their habitat keep on increasing.

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