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Area-sensitivity of the sand lizard and spider wasps in sandy pine heath forests – umbrella species for early successional biodiversity conservation?

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Pine heath forests on sandy sediments occur as "biotope islands" all over Fennoscandia. An important component of the biodiversity within such pine heaths is early successional species restricted to open patches with sparsely vegetated sand. Surveys of the endangered sand lizard *Lacerta agilis* on a regional scale in south-central Sweden showed that populated pine heaths were significantly larger (median area 65 km^2) than those where the species was absent (median area 5 km^2). No effect of pine heath isolation was found. Moreover, on a landscape scale, occupied habitat patches within individual pine heaths were significantly larger than patches where the sand lizard had recently gone extinct. Patch isolation had no significant effect. Furthermore, an analysis of presence/absence of ground-nesting spider wasps (Hymenoptera: Pompilidae) on sandy pine heaths of different size showed that species composition was significantly nested. The highest diversity, of all species and red-listed ones, was found on the largest pine heaths, in sympatry with the sand lizard. It is argued that only the largest sandy pine heaths have provided historical continuity of suitable early successional habitat patches with exposed sand for the most dispersal-limited species. Because of forest fire suppression and afforestation since the beginning of the 20th century, many early successional species in sandy pine heath forests are now threatened due to loss of such patches. To provide habitat for these species, measures to re-create early successional patches must be taken. The sand lizard can be used as a cross-taxonomic umbrella species for red-listed spider wasps and other early successional species. However, to preserve the existing threatened biodiversity within a given pine heath (including the many pine heaths where the sand lizard is absent), a strategy of multiple umbrella species and demarcation of patches with key habitat components is needed.

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Patch dynamics in forest landscapes can be seen as a temporally dynamic process where habitat availability for a given species continuously changes with disturbances and forest regeneration (Pickett and Thompson 1978). Habitat fragmentation, however, may force populations to pass critical lower thresholds in the amount and distribution of preferred habitat required for long-term species survival in a given landscape (e.g. Andrén 1997, Angelstam 1997, Mönkkönen and Reunanen 1999, Fahrig 2001). For many threatened species, critical habitat threshold conditions are no longer met, and these species are expected to go extinct after some time delay in their response to environmental change. This so called extinction debt can be paid by either "allowing the species to go extinct or by improving the landscape structure sufficiently, before the species have gone extinct, such that the threshold conditions are met again" (Hanski and Ovaskainen 2002).

The conservation of biodiversity in boreal and hemiboreal forests has so far been focused on continuity of habitat for old-growth and/or wood-associated species (see Esseen et al. 1997, Niemelä 1999, Nilsson et al. 2001). Continuity of open habitat for early successional, ground-living species has received little attention. It is evident, however, that the latter group constitutes an important component of the biodiversity in pine forests on dry sites naturally regenerated by fire. In Scots pine *Pinus sylvestris* forests on sandy sediments in Fennoscandia, effective fire suppression and afforestation have caused an accelerating decline of open habitat patches since the beginning of the 20th century (e.g. Cederberg 1982, Väisänen et al. 1994, Berglind 1999). For two endangered species, the blue butterfly *Pseudophilotes baton* and the sand lizard *Lacerta agilis*, the resulting extinction debt has been paid by loss of local populations. However, recent active management measures have been undertaken locally such that habitat threshold conditions can be met again (Väisänen et al. 1994, Berglind 2000, 2004a).

Since dry pine heath forests on sandy sediments occur as islands in an archipelago all over Fennoscandia (Fig. 1), island biogeography theory may be relevant for conservation purposes. The degree of isolation from sources of colonisers would then determine the rate of immigration, while island area would determine the population size and thus the extinction rate. However, extinction is probably the dominant population process for low-vagility organisms in isolated transient landscapes, and the internal disturbance dynamics the critical key to long-term persistence (Pickett and Thompson 1978, Webb and Thomas 1994, Tiebout and Anderson 1997). If so, it is important to define the "minimum dynamic area" with a natural and anthropogenic disturbance regime which maintains internal re-colonisation sources and hence minimises local extinctions (Pickett and Thompson 1978). To identify this area, we would need to have knowledge of the size, frequency of inception and longevity of disturbance-generated patches, as well as of the mobilities of the most extinction-prone species (Angelstam et al. 2004).

Moreover, if the species composition on sandy pine heaths has long been shaped predominantly by local extinctions, a "nested subset" pattern may be expected among differently sized pine heaths, with impoverished species assemblages made up of non-random subsets of more species-rich ones (Patterson 1987, Cutler 1991). Analysis of nestedness may also reveal indicator species for high species richness (Fleishman et al. 2000). Furthermore, if the frequency of occurrence of an indicator is equal to that of sympatric species that share the same habitat or ecoregion and are threatened, it theoretically can confer protection to these and hence be used as an umbrella species (Andelman and Fagan 2000, Fleishman et al. 2001a, b, Roberge and Angelstam 2004).

In this study I compare on a regional and landscape scale (cf. Freemark et al. 2002) the occurrence of a threatened low-vagility vertebrate, the sand lizard, with the occurrence of spider wasps, which are associated with the same type of early successional habitat on sandy pine heaths in central Sweden. On a regional scale, I view sandy pine heaths as "landscapes" in a "matrix" dominated by spruce/mixed forests interspersed with agricultural land and lakes. On a landscape scale, individual pine heaths are composed of habitat patches, where the latter are basically reflections of soil texture, aspect and successional age.

Specifically, the aims are to 1) explore whether the presence of the sand lizard and rare spider wasps is determined by the size of individual pine heaths, 2) evaluate the importance of patch area and isolation within pine heaths for persistence of local sand lizard populations, and 3) identify potential indicator and umbrella species from red-listed taxa for biodiversity conservation on sandy pine heaths.

Methods

Study organisms

The sand lizard is considered primarily a "forest steppe" species and occurs in a variety of semi-open habitats from central Europe to central Asia (Bishoff 1984). It reaches the northern limit of its range in central Sweden with a few isolated populations confined to glaciofluvial sand deposits. These populations are considered to be relicts from the post-glacial warm period (ca 7000–500 B.C.), when the climate was warm enough for this egg-laying ectotherm to disperse northwards from central Europe throughout southern and central parts of Sweden. When the climate subsequently became cooler, the species retreated to southern Sweden but also survived on some sandy pine heaths in the central part of the country (Gislén and Kauri 1959, Andrén and Nilson 1979, Gullberg et al. 1998). It is red-listed as "Vulnerable" in Sweden and included in the EU Habitat Directive (Gärdenfors 2000). A number of early successional insect species are associated with similar habitats in Sweden, and their biogeographic histories may be analogous (Cederberg 1982, Berglind 2004b).

One insect family characteristic of open sandy patches are the spider wasps (Hymenoptera: Pompilidae). About 1/3 of the Swedish fauna of 61 species is red listed (Gärdenfors 2000), and the family is believed to include suitable indicators for threatened early successional habitats (Day 1991). The Fennoscandian species are 4–15 mm long, and all are predators of spiders (e.g. Oehlke and Wolf 1987, Schmid-Egger and Wolf 1992). Many are significant components of more or less open, sandy habitats, where they bury their paralysed prey in sand as food for their offspring. Most species have a long flight period, often 2–3 summer months with two generations per year (cf. Schmid-Egger and Wolf 1992), and they are highly attracted to yellow and white water traps. Thus, there is potentially a high probability of catching all or most species in one area during one summer season.

In addition to these focal study organisms, I present local occupancy of other red-listed and local species within the same habitats/patches, including 2 plants, 21 insects, and 3 birds, found on two of the largest and best studied of the sandy pine heaths investigated.

Sand lizard surveys

The sand lizard was surveyed in Värmland and Dalarna (ca 59–62°N), the two northernmost counties in Sweden where the species has been reported during recent decades. Värmland was surveyed mainly in 1984 and 1987 with complimentary surveys in later years/summers including 2002 (Berglind 2004b). The two largest sandy areas in Värmland (area 1 and 2, Brattforsheden and Sörmon, respectively; Fig. 1), have been monitored in most years between 1983 and 2003 (Berglind 2000, 2004b). Dalarna was surveyed mainly in 2001 (Wallgren and Berglind 2002).

Before the start of the surveys it was known that the sand lizard had been found on some of the largest sandy pine heaths with aeolian (wind blown) sand. Therefore all sand deposits > 4 km^2 and some smaller ones with aeolian sand, usually in the form of fossil sand dunes, were surveyed (n = 29). In addition, some other pine heaths > 1.0 km^2 with gravel-mixed sand, and close to dune areas, were surveyed (n = 11). Areas were localised and their size was measured from quaternary sediment maps, scale 1:200000 (G. Lundqvist 1948, J. Lundqvist 1958). Isolation was measured as the shortest distance across non-sandy soil from one sand deposit to the nearest other with

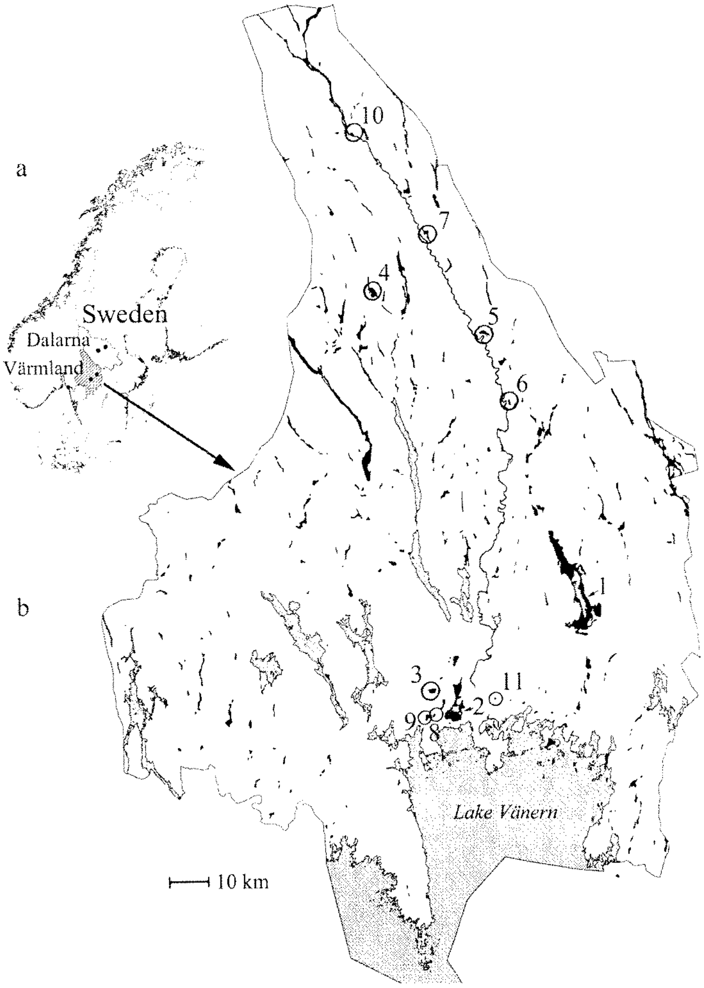

Fig. 1. a) The Värmland and Dalarna counties in central Sweden, which have been surveyed for the sand lizard *Lacerta agilis*. The dots show, from bottom to top, the four sandy areas with records of sand lizards: Sörmon, Brattforsheden, Mora-Bonäsfältet, and Orsa-Skattungbyfältet. b) Glaciofluvial sediments (sand and gravel) (black areas) in Värmland. Areas 1–11 refer to surveyed areas included in the nestedness analysis for spider wasps, and have been numbered in descending order according to their position in the nestedness matrix (see Table 1). Area 1 = Brattforsheden, 2 = Sörmon. Also indicated are larger waters (grey).

aeolian sand. Because the size of individual sand deposits is more or less the same as the size of the pine heath forests covering the same deposits, I use the terms "sand deposit" and "sandy pine heath" interchangeably in this article.

Localised sand deposits were subsequently studied on aerial photographs, and all open patches with or without exposed sand (except for mires) were noted on topographic maps. Thereafter the patches were visited in the field. When patches with suitable habitat, in the form of south-exposed sand patches in combination with a rich field layer of heather *Calluna vulgaris* or grasses/herbs (Berglind 1988, Wallgren and Berglind 2002), were found they were visually inspected for lizards, their egg burrows and/or foot prints in the sand for at least one hour during sunny weather. Patches without signs of sand lizards but with suitable habitat were surveyed on at least two separate days to minimise the risk of not detecting an occupied patch. Empty patches with older records of sand lizards between 1977 and 1992 (Berglind 2000, Wallgren and Berglind 2002) have been visited repeatedly (≥ 5 times) during several years by myself and/or other field workers. I consider the probability of not detecting an occupied sand lizard patch as very low, and on manyt of the empty patches the eurytopic close relative, the common lizard *Lacerta vivipara*, was found (for further details of field surveying techniques, see Taylor and Winder 1997, Moulton and Corbett 1999).

The size of habitat patches with extant or extinct sand lizard populations was estimated by visual inspection of those parts of the patches that contained acceptable habitat for foraging, shelter, dispersal, and/or egg-laying in 1998 (before some patches were subject to major habitat restoration during 1999–2002, which created 5–10 times larger habitat on each). Usually the habitat patches were delimited by closed pine stands and/or lakes. Isolation of habitat patches was measured as the shortest distance of unsuitable habitat (usually closed pine stands) between one patch to the nearest other inhabited patch in 1998.

Surveys of spider wasps and other taxa

In total, 11 sandy pine heaths were surveyed for spider wasps (Fig. 1 and Table 1). Their size was set equivalent to the size of the corresponding sand deposits, shown in Lundqvist (1958). Most of the pine heaths were chosen in connection with nature conservation work by the county administrative board of Värmland. The forest type is similar in all areas, with vegetation dominated by Scots pine forest with a ground and field layer dominated by reindeer lichens (*Cladonia* spp.), pleurocarpous mosses (mostly *Pleurozium schreberi* and *Dicranum* spp.), crow berry *Empetrum nigrum*, cow berry *Vaccinium vitis-idaea*, and sparse stands of *Calluna vulgaris*. Forest-fire suppression and conventional forestry keep most of the areas wooded with pine of various ages. On open, disturbed patches, the acrocarpous moss *Polytrichum piliferum* (< 3 cm high), occurs as a pioneer coloniser of dry, sun-exposed sand. Such patches often also have a mosaic field layer of *Calluna* and/or grasses and herbs. All surveyed pine heaths contain aeolian sand to some degree, except for area 10 and 11, which are dominated by gravel-mixed sand. The matrix in between the pine heaths is dominated by mixed spruce forest on moraine, or agricultural land on clay-dominated soils. Exceptions are the glaciofluvial sand deposits of area 5–7 and 10, which are situated along the eastern side of the Klarälven river valley and interconnected by a narrow strip of post-glacial sand deposits covered by mixed pine forest.

Within each pine heath the majority of existing open patches with a mosaic of south-exposed sand and a rich field layer were localised with the same technique as described for the sand lizard. The patches usually consisted of sand pits, sandy road verges (including S-oriented sand-cuts), power-line corridors, clear-cuts, or glades in younger post-fire pine stands. Water traps were placed on what were considered the most "optimal" patches for each pine heath. Most traps were placed on the ground at sharp interfaces between open sand and a dense field layer of *Calluna* or grasses/herbs, usually at south-oriented forest edges. Patches were considered separate if > 300 m of unsuitable habitat (usually closed pine stands) was situated in between. The majority of patches were separated by > 1 km.

On most surveyed patches one yellow and one white water trap were used, but the number per patch varied somewhat. Also the number of surveyed patches varied between the pine heaths, roughly in proportion to their size and occurrence of suitable patches (Table 1). For pine heaths that were investigated for more than one summer, only new patches were surveyed during the additional years. There was a significant positive correlation between the size of surveyed pine heath and both the number of traps used per pine heath (Spearman rank correlation $r_s = 0.68$, $p = 0.0223$) and number of surveyed patches per pine heath ($r_s = 0.69$, $p = 0.0198$). However, there was a significant negative correlation between the size of pine heath and the number of surveyed patches per km^2 ($r_s = -0.96$, $p < 0.001$). Thus, the absolute sampling effort was higher on larger pine heaths, but the relative sampling effort was higher on smaller ones.

The water traps consisted of plastic, round pans with a diameter of 23 cm and a height of 11 cm. They were 3/4 filled with water, some drops of detergent, and a bottom-layer of coarse salt (to slow down the decay of the caught insects). The traps were inspected and emptied at least once every second week from the end of May to late August. All spider wasps were preserved in 70% alcohol and later identified to species using Oehlke and Wolf (1987) and van der Smissen (1996). In total, ca 5000 specimens were examined. Other caught insect taxa were preserved and identified.

On area 1 (Brattforsheden), 6 surveyed patches were each occupied by a local sand lizard population, two of

Table 1. Presence-absence matrix and sampling effort for ground-nesting spider wasps (Hymenoptera: Pompilidae) on sandy pine heaths of different size (see Fig. 1). The matrix has been maximally packed according to the nestedness analysis (see Results). Also shown, within parenthesis, is presence-absence of the common lizard *Lacerta vivipara* and the sand lizard *Lacerta agilis* (these were not included in the nestedness analysis). Red-listed species are shown in bold. The name and main survey year (within parenthesis) of the areas are: 1 Brattforsheden (1988, 1990, 1997), 2 Sörmon (1989, 1990, 2001), 3 Mellbymon (2003), 4 Kristineforsheden (1990, 1991), 5 Halgådeltat (1989), 6 Säljeheden (1989), 7 Femtåheden (1990), 8 Törnmon (2002), 9 Algustadmon (2002), 10 Klarabro (1989), 11 Gräsås (1997).

	Area											
Species	1	2	3	4	5	6	7	8	9	10	11	No. of areas
Priocnemis perturbator	+	+	+	+	+	+	+	+	+	+	+	11
Priocnemis exaltata	+	+	+	+	+	+	+	+	+	+	+	11
Priocnemis schiödtei	+	+	+	+	+	+	+	+	+	+	+	11
Arachnospila anceps	+	+	+	+	+	+	+	+	+	+	+	11
Arachnospila spissa	+	+	+	+	+	+	+	+	+	+	+	11
Anoplius viaticus	+	+	+	+	+	+	+	+	+	+	+	11
(*Lacerta vivipara*	+	+	+	+	+	+	+	+	+		+	10)
Arachnospila trivialis	+	+	+	+	+	+	+	+	+			9
Evagetes crassicornis	+	+	+	+	+	+	+	+	+			9
Arachnospila fumipennis	+	+	+	+	+		+		+	+		8
Episyron albonotatum	+	+	+	+	+	+	+		+			8
Arachnospila hedickei	+	+	+	+	+	+		+	+			8
Evagetes sahlbergi	+	+	+	+	+	+	+	+				8
Arachnospila sogdiana	+	+		+		+	+	+				6
Pompilus cinereus	+	+	+	+				+				5
Ceropales maculata	+	+	+	+	+							5
Arachnospila wesmaeli	+	+	+					+	+			5
Arachnospila abnormis	+	+			+	+	+					5
Arachnospila opinata	+	+	+	+								4
Priocnemis parvula	+				+	+	+					4
Arachnospila westerlundi	+		+							+		3
Caliadurgus fasciatellus	+		+			+						3
Episyron rufipes	+	+	+									3
Evagetes alamannicus	+	+		+								3
Evagetes dubius	+	+										2
(***Lacerta agilis***	+	+										2)
Evagetes pectinipes		+										1
Priocnemis gracilis	+											1
No. of spider wasp species	25	22	19	17	15	15	14	13	12	8	6	
Size of area (km^2)	80	30	2.4	8	3.8	1.5	3.2	0.7	1.0	0.2	0.05	
No. of surveyed patches	25	10	2	4	2	1	2	3	1	1	2	
No. of surv. patches km^{-2}	0.3	0.3	3.3	0.5	0.5	0.7	0.7	4.3	3.0	5.0	20.0	
No. of traps	35	16	8	6	2	2	3	4	3	2	2	

which have recently gone extinct. In area 2 (Sörmon), 2 surveyed patches were each occupied by a local sand lizard population. Furthermore, insects have been surveyed on both areas by hand netting during several seasons between 1988 and 2003, and on area 1 also with both pitfall traps and UV-light traps in both 1988 and 1990. No additional spider wasp species have been found with these techniques. However, they have revealed many other insect species, making the species composition on these areas unusually well known with respect to sand-associated insects (see Berglind 2004b). Moreover, Brattforsheden has been surveyed with point counts for two pine heath birds, the nightjar *Caprimulgus europaeus* and wood lark *Lullula arborea*, in both 1986 and 1999 (Bengtsson unpubl.). These birds are listed on the EU Bird Directive (Gärdenfors 2000).

Data analyses

Determinants of local extinction

Potential environmental correlates of extinction for local sand lizard populations were analysed using stepwise logistic regression and the statistical software package BMDP

New System (Dixon 1992), ver. 2.0. Logistic regression quantifies how much independent (predictive or explanatory) variables can explain the variation in some dependent (outcome or response) variable. In this study the dependent variable was extinction or persistence of local sand lizard populations in patches known to have been occupied some time between 1977 and 1998, and the explanatory variables were patch area and isolation, as measured in 1998 (see further details under Sand lizard surveys). The effects of the two latter variables are considered as the first-order landscape effects on metapopulation persistence (Hanski 1999). The analysis was done as a forward stepwise logistic regression with 100 iterations, and with $p \leq 0.10$ for the explanatory variables to be entered into (or removed from) the model. A positive coefficient for a significant explanatory variable predicts increased extinction risk with lower values for that variable. I also used the BMDP New System software to conduct univariate non-parametric statistics on the sand lizard and spider wasp survey data.

Nestedness

A nested subset analysis for spider wasps was carried out based on a presence-absence matrix for those sandy pine heaths of different size that are presented in Fig. 1 and Table 1. Only ground-nesting species with known distributional limits in Fennoscandia covering the latitudes for the surveyed region were included. Furthermore, only those species restricted to more or less sandy habitats, and species with wide ecological affinities including sandy habitats, were included. Some species caught in low numbers prefer non-sandy and mesic/moist habitats and were excluded from the analysis (complete species lists for the two richest areas are given in Berglind 2004b).

I used Atmar and Patterson's (1993, 1995) Nestedness Temperature Calculator method and software to establish the extent at which my data were nested. Nestedness values can range from T = 0° for a perfectly ordered system (perfectly nested), to T = 100° for complete randomness. A presence-absence matrix that contains both a degree of nestedness and randomness will register an intermediate T-value between these two end-points (Atmar and Patterson 1995). The nestedness calculator by Atmar and Patterson runs a Monte Carlo simulation to estimate the distribution of nestedness scores expected in a randomly distributed data matrix of the same dimensions as the study data matrix. The actual nestedness score for the study data matrix is then compared against the distribution of randomly generated matrices to determine the probability of observing such a score by chance.

Umbrella index

To evaluate and rank potential umbrella species, the umbrella index developed by Fleishman et al. (2001a, b) was used. Originally, this index takes into account three components: mean co-occurrence of the species, its degree of ubiquity, and its sensitivity to human disturbance. For each species j, mean percentage of co-occurring species (PCS) is defined as

$$\sum_{i=1}^{I}\left[\left(S_i - 1\right) / \left(S_{max} - 1\right)\right] / N_j$$

where I is the number of locations (patches) in the data set, S_i is the number of species present at each location i, S_{max} is the total number of species present at all locations in the data set, and N_j is the number of locations at which species j occurs. PCS is quantified on a scale from 0 (tends to occur with few other species) to 1 (tends to occur with many other species).

The second component of the umbrella index is degree of ubiquity, or median rarity (R). Values for species with an intermediate degree of ubiquity approach 1, for rare or common species the values approach 0. For each species j, this parameter is calculated as

$$1 - 2 * \left|(N_j/I) - 0.5\right|$$

The third component of the umbrella index, sensitivity to human disturbance, was omitted in this study. Since life-history-related variables are poorly known for the majority of the analysed insect species, and the greatest threat can be assumed to be common to all species (shading of open habitat patches due to pine canopy formation) this omission was considered a reasonable approach. Thus, the umbrella index (UI) for each species was calculated by summing the scores for the first two components. Species with higher scores (maximum 2.0) are more likely to be effective umbrellas for their ecoregion and taxonomic group or guild.

$$UI = PSC + R$$

I calculated the umbrella index as a cross-taxonomic index for all red-listed and some other local species within the same guild found on the largest and most species-rich pine heath in this study, i.e. Brattforsheden (Fig. 1). This means that also clear differences in mobilities and area requirements between the taxa have to be considered in the evaluation of a species' suitability as an umbrella (see Discussion).

Results

Effects of area and isolation at a regional and landscape scale for occupancy of sand lizard populations

Sandy pine heaths occupied by the sand lizard in the counties of Värmland and Dalarna were significantly larger (range 30–90 km^2, median = 65.0; n = 4) than vacant pine

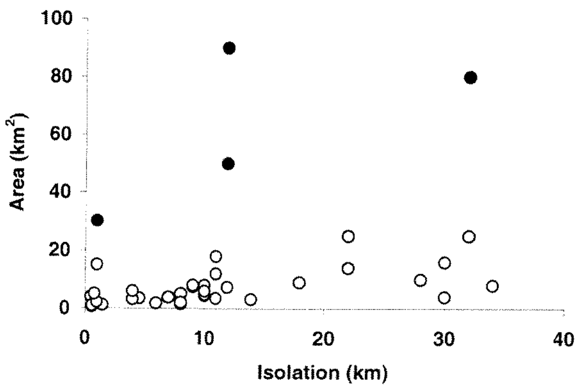

Fig. 2. Area and isolation of sandy pine heaths with (filled circles) and without (open circles) populations of the sand lizard *Lacerta agilis* in Värmland and Dalarna. Aeolian sand, usually with fossil sand dunes, were present at 29 (72%) of the 40 surveyed areas, including the four occupied areas. Isolation = shortest distance of non-sandy soil from one sand deposit to the nearest other with aeolian sand (see Methods for further details).

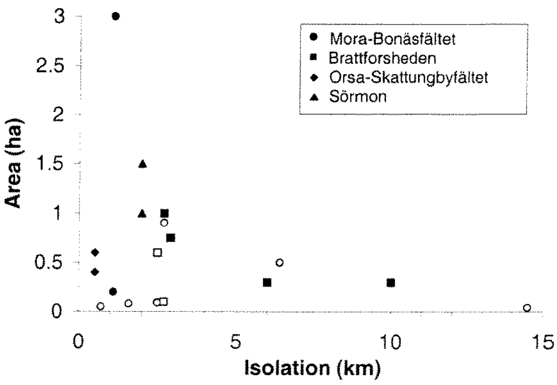

Fig. 3. Area and isolation of patches with extant (filled symbols) and extinct (open symbols) local sand lizard populations on the four occupied sandy pine heaths in Värmland and Dalarna in 1998 (see panel). Isolation = distance to the nearest other occupied sand lizard patch.

heaths (range 0.7–25 km^2, median = 5.0, n = 36) (Mann-Whitney U = 0.0, p = 0.0012) (Fig. 2). There was no significant difference in isolation for occupied pine heaths (range 1.0–32 km, median = 12.0, n = 4) vs vacant pine heaths (range 0.5–34 km, median = 9.0, n = 36) (Mann-Whitney U = 50.5, p = 0.332) (Fig. 2).

Within occupied pine heaths, the number of known local sand lizard populations between 1977 and 1998 was higher on the largest pine heaths. In total, 8 and 6 local populations, respectively, have been found on the two largest areas (Mora-Bonäsfältet and Brattforsheden, 90 and 80 km^2, respectively). Only 2 local populations have been found on each of the two smaller areas (Orsa-Skattungbyfältet and Sörmon, 50 and 30 km^2, respectively) (Fig. 3). In spite of the small sample size, there was an almost significant positive correlation between the number of local sand lizard populations and the size of occupied pine heaths (Spearman rank correlation r_s = 0.949, p = 0.051, n = 4).

Within occupied pine heaths, suitable habitat patches with extant sand lizard populations were significantly larger in 1998 (range 0.2–3.0 ha, median = 0.75, n = 10) than those where the sand lizard had gone extinct (range 0.05–0.75 ha, median = 0.095, n = 8) (Mann-Whitney U = 66.5, p = 0.0183) (Fig. 3). No significant difference in isolation was found between patches with extant populations (range 0.5–10.0 km, median = 2.0, n = 10) vs patches with extinct populations (range 0.7–14.5 km, median = 2.6, n = 8) (Mann-Whitney U = 28.0, p = 0.2843) (Fig. 3). Moreover, a logistic regression model examining extinction or not of local populations supported the notion that extinction risk increased significantly with decreasing patch area, whereas patch isolation had no significant additional effect (Table 2).

Table 2. Effects of area and isolation on extinction probabilities of local sand lizard populations according to a stepwise logistic regression model. Number of patches with extinct populations = 8, number of patches with extant populations = 10. The tabulated χ^2 is the improvement-χ^2 of the variable in the final model, and p the corresponding p-value (at 1 DF). The goodness of fit of the final model (deviance statistic) was χ^2 = 18.46, DF = 16, p = 0.298.

Variable	Coefficient ± SE	χ^2	DF	p
Significant (step 2)				
Area	3.41 ± 1.85	6.27	1	0.012
Constant	–1.42 ± 0.94	2.72	1	0.099
Non-significant (step 1)				
Isolation		1.35	1	0.246

Nestedness and species-area relationship of spider wasps

The spider wasp communities on the surveyed pine heaths were clearly nested (Fig. 4a and Table 1). The matrix nestedness temperature $T = 7.19°$ was highly significantly lower than the mean score for the randomised matrix ($T \pm SD = 54.1° \pm 6.37°$; $p = 9.73 \times 10^{-14}$; Monte Carlo runs total = 500). This means that the faunas of low-diversity pine heaths tended to be predictable subsets of the faunas with higher diversity. However, there were eight species and four pine heaths for which the nestedness temperatures were higher than for the matrix as a whole (Fig. 4b–c). This suggests different biogeographic histories for these species and pine heaths compared with those that governed the formation of nestedness in the overall matrix.

Moreover, there was a strong positive correlation between the number of spider wasp species and the size of pine heaths (Spearman rank correlation $r_s = 0.91$, $p = 0.0001$, $n = 11$) (Fig. 5), where the two most species-rich pine heaths were occupied also by the sand lizard (area 1 and 2; Table 1). The number of spider wasp species found per pine heath was also significantly correlated with the number of traps used per pine heath ($r_s = 0.77$, $p = 0.0059$, $n = 11$) and number of surveyed patches per pine heath ($r_s = 0.66$, $p = 0.0266$, $n = 11$). Pine heath size, number of traps and number of surveyed patches per pine heath were also significantly correlated, as mentioned in the methods section.

For the two largest pine heaths (area 1–2; Table 1), significantly more spider wasp species per patch were found on the most species-rich patches that also contained sand lizards (range = 17–22 species, median = 18.5, n = 6) than on the most species-rich patches on the four richest of the smaller pine heaths without sand lizards (area 3–6) (range = 14–17 species, median = 15.0, n = 7) (Mann-Whitney U = 1.00, p = 0.0038). Since there was no significant difference in the number of traps used per patch on the richest patches on the largest pine heaths (range = 2–4 traps, median = 2, n = 6) vs the richest patches on the smaller pine heaths (range = 1–4 traps, median = 2, n = 7) (Mann-Whitney U = 15.00, p = 0.3614), the difference in species number per patch seems not to be an effect of unequal sampling effort.

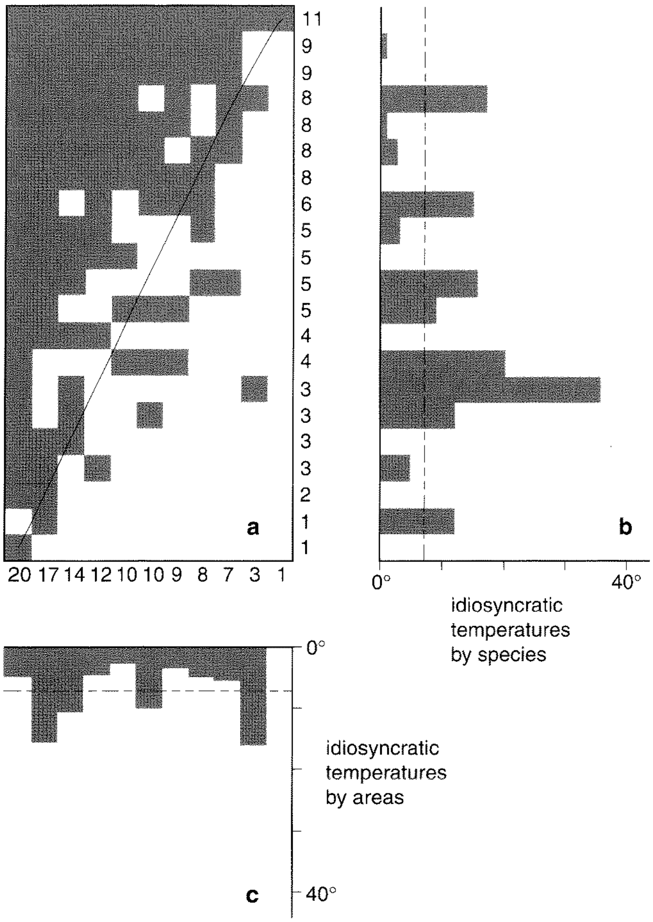

Fig. 4. a) Nestedness matrix of spider wasp faunas on 11 sandy pine heaths in Värmland. Species are listed from top to bottom, and pine heaths from left to right in order of decreasing species richness. The matrix is packed so as to minimize the distance of unexpected presences and absences from the calculated extinction threshold line (diagonal). Note: 5 duplicate "all grey" rows were removed from the top of the matrix; thus all column totals displayed are 5 less than the original data matrix (Table 1). b) Idiosyncratic temperatures by species. c) Idiosyncratic temperatures by pine heaths. Species and pine heaths that generate specifically higher temperatures than the matrix as a whole are above the dashed line.

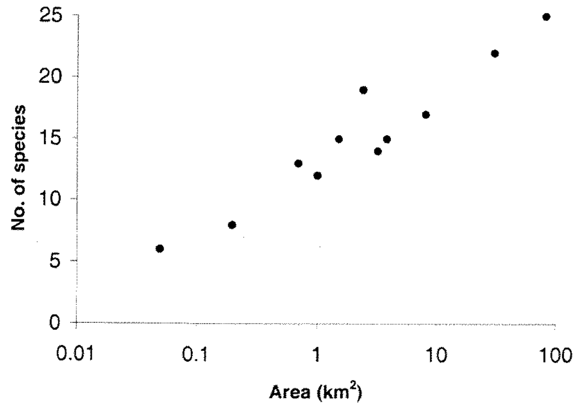

Fig. 5. Correlation between the number of spider wasp species and the size of pine heaths. The investigated pine heaths are presented in Fig. 1 and Table 1. The regression line: number of species = 13.08 + 5.88 × log Area, Pearson's r = 0.96, $p = 3.96 \times 10^{-6}$, n = 11.

Potential indicator- and umbrella species

Within pine heaths occupied by the sand lizard in areas 1 and 2, i.e. the most species-rich areas with respect to spider wasp diversity (Table 1), significantly more red-listed spider wasp species were found within sand lizard patches (range = 3–5 species, median = 3.5, n = 8) than on patches without the sand lizard (range = 0–5, median = 1.0, n = 27) (Mann-Whitney U = 28.5, p = 0.00137). Furthermore, of a total of 28 red-listed species from all taxa found on areas 1 and 2 (Table 3), significantly more species were found within sand lizard patches (range 5–12 species, median = 11.0, n = 8) than on patches without sand lizards (range = 0–13 species, median = 2.0, n = 27) (Mann-Whitney U = 24.5, p = 0.00094). Thus, pine heaths and patches with sand lizards indicate presence of a disproportionately large number of other red-listed species on, respectively, a regional and landscape scale.

Nevertheless, the sand lizard was also absent from several pine heaths and patches that harboured red-listed spider wasps and other red-listed taxa (Tables 1, 3 and Fig. 6), suggesting that additional indicators would be useful to identify. Although there is a significant correlation between the number of spider wasp species and size of pine heath (see above) as well as between the number of red-listed spider wasp species and size of pine heath (Spearman rank correlation $r_s = 0.72$, p = 0.01, n = 11), the nestedness analysis suggests that few red-listed species are reliable indicators for high regional species richness (Table 1). The most suitable species seem to be *Priocnemis gracilis* and *Evagetes dubius* since they were found exclusively on the two most species-rich pine heaths and lack unexpected absences or "holes" in the nestedness matrix. However, when looking at the local distribution on area 1, these two species failed to indicate the presence of respectively two or three other red-listed spider wasps (*Arachnospila opinata, A. wesmaeli* and *A. westerlundi*), and *E. dubius* co-occurred with the sand lizard on only one patch (Fig. 6).

The cross-taxonomic umbrella index calculated for 25 red-listed and five other local species occurring on area 1 (Brattforsheden) gives further guidance to species that may be useful indicators and umbrellas for biodiversity conservation on a landscape scale (Table 3). The tiger beetle *Cicindela sylvatica* has the highest rank, i.e. it co-occurred with many red-listed species and it had an intermediate degree of ubiquity. Furthermore, the spider wasps *Priocnemis gracilis* and *Episyron albonotatum* and the digger wasp *Ammophila campestris* scored almost as high. The three vertebrates, the wood lark *Lullula arborea*, the nightjar *Caprimulgus europaeus*, and the sand lizard, scored lower but still had among the highest ranks (Table 3).

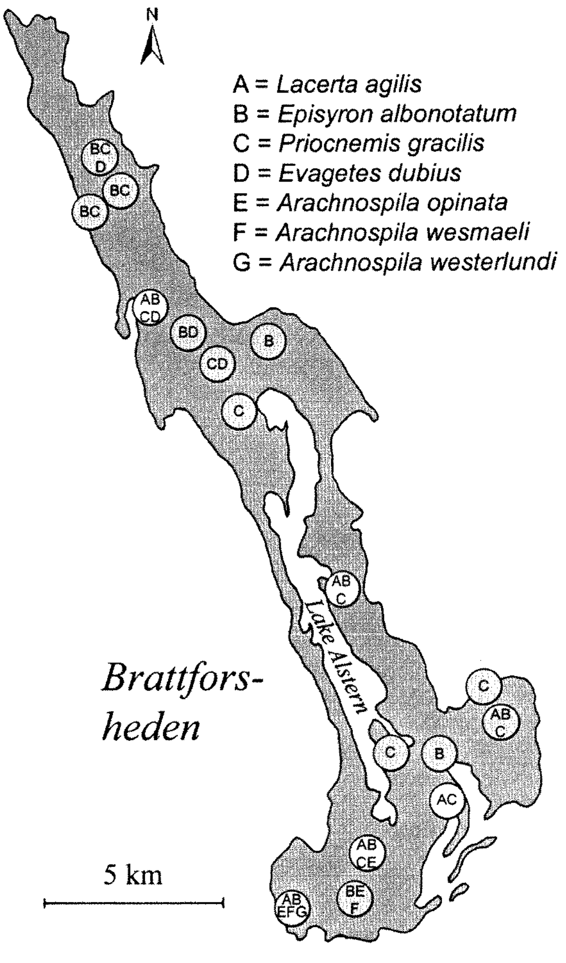

Fig. 6. Patches with known local populations of the sand lizard and red-listed spider wasps on Brattforsheden between 1988 and 2001 (16 out of 25 surveyed patches). In all cases, > 0.5 km of unsuitable habitat (predomintaly closed pine stands) was situated in between the patches. Note the clustering of occurrences of the rarest spider wasps (species D–G). White circles = patches with extant sand lizard populations.

Table 3. Red-listed and some other local species recorded in dry, sandy habitats on the two largest sandy pine heaths in Värmland county: Sörmon (30 km^2) and Brattforsheden (80 km^2). Red-list categories according to Gärdenfors (2000): VU = Vulnerable, NT = Near Threatened, – = not red-listed. The number of patches refers to only those where insects were sampled with water traps. These patches include all red-listed early successional species found on the areas, but some of the species where also found on additional patches, for example *A. vernalis* (3 additional patches on Brattforsheden in 2003), *L. c. chamaecyparissus* (6 additional patches on Sörmon in 2003), and *C. europaeus* (2 additional patches on Sörmon in 2002 and 8 on Brattforsheden in 1999). Numbers within parenthesis refer to the number of patches with co-occurrence of the sand lizard *Lacerta agilis* (2 patches on Sörmon and 6 patches on Brattforsheden). The cross-taxonomic umbrella index is based on those 25 patches on Brattforsheden where insects were sampled with water traps. Note that Diptera and Coleoptera species, except for *C. sylvatica*, have been surveyed less intensively than the other taxa. Umbrella index in bold = the 10 species with the highest rank (for definitions, see Methods).

		Number of patches		Umbrella index (UI) (Brattforsheden)			
Species	Red list category	Sörmon (n=10)	Brattfors-heden (n=25)	PCS	R	UI	Rank
Plants							
Anemone vernalis	VU	Extinct?	1 (1)	0.30	0.24	0.54	14
Lycopodium complanatum ssp. *chamaecyparissus*	VU	1 (1)	0				
Insects							
Hymenoptera							
Pompilidae, spider wasps							
Priocnemis gracilis	VU	0	12 (5)	0.20	0.96	**1.16**	**3**
Arachnospila opinata	NT	1 (1)	3 (2)	0.37	0.24	0.61	12
A. westerlundi	NT	0	1 (1)	0.31	0.08	0.39	20a
A. wesmaeli	NT	4 (2)	2 (1)	0.36	0.16	0.52	15
Evagetes dubius	–	4 (2)	4 (1)	0.26	0.32	0.58	13
Episyron albonotatum	NT	5 (2)	12 (5)	0.22	0.96	**1.18**	**2**
Formicidae, ants							
Formica cinerea	–	0	2 (1)	0.32	0.16	0.48	17
Eumenidae, solitary wasps							
Stenodynerus dentisquama	NT	0	2 (1)	0.26	0.16	0.42	19
Sphecidae, digger wasps							
Ammophila campestris	NT	2 (1)	10 (6)	0.23	0.88	**1.11**	**4**
Lestica subterranea	NT	0	1	0.41	0.08	0.49	16a
Belomicrus borealis	NT	0	1	0.10	0.08	0.18	22a
Crossocerus heydeni	NT	0	1	0.41	0.08	0.49	16b
Andrenidae, sand bees							
Andrena argentata	VU	0	6 (3)	0.26	0.48	**0.74**	**8**
Panurgus banksianus	VU	2 (1)	1	0.41	0.08	0.49	16c
Lepidoptera							
Hesperidae, skippers							
Hesperia comma	NT	0	1	0.41	0.08	0.49	16d
Lycaenidae, blues							
Glaucopsyche alexis	NT	1	1	0.10	0.08	0.18	22b
Noctuidae, noctuid moths							
Spaelotis suecica	NT	1	1	0.41	0.08	0.49	16e
Zygaenidae, burnets							
Adscita statices	NT	0	1	0.41	0.08	0.49	16f
Diptera							
Asilidae, robber flies							
Cyrtopogon luteicornis	NT	2 (1)	4 (2)	0.33	0.32	**0.65**	**9**
Therevidae, stiletto flies							
Psilocephala imberbis	NT	0	2	0.19	0.16	0.35	21
Coleoptera							
Carabidae, ground beetles							
Cicindela sylvatica	–	6 (2)	12 (6)	0.24	0.96	**1.20**	**1**
Bembidion nigricorne	NT	0	5 (2)	0.30	0.32	0.62	11
Amara infima	NT	1 (1)	4 (2)	0.39	0.24	**0.63**	**10**
Cymindis macularis	NT	0	1 (1)	0.38	0.08	0.46	18a

Table 3. Continued.

Species	Red list category	Number of patches Sörmon (n=10)	Brattfors-heden (n=25)	Umbrella index (UI) (Brattforsheden) PCS	R	UI	Rank
Buprestidae							
Buprestis octoguttata	NT	1 (1)	1 (1)	0.38	0.08	0.46	18b
Curculionidae							
Strophosoma fulvicorne	NT	2 (1)	0				
Neuroptera							
Myrmeleontidae, ant lions							
Myrmeleon bore	VU	5 (2)	0				
Reptiles							
Lacerta agilis	VU	2	6	0.30	0.48	**0.78**	7
Birds							
Caprimulgus europaeus	VU	6 (2)	17 (5)	0.19	0.64	**0.83**	**6**
Lullula arborea	–	6 (2)	9 (5)	0.25	0.72	**0.97**	**5**
Riparia riparia	–	0	1 (1)	0.31	0.08	0.39	20b

Discussion

Area sensitivity for focal species at regional and landscape scales

This study has shown that sand lizard populations on the northern periphery of the species' range occurred on only a few, unusually large sandy pine heaths. The occupied areas are four of the largest glaciofluvial sand deposits in the southern half of Sweden, and they also contain four of the largest fields of fossil inland dunes (see Bergqvist 1981). Isolation of pine heaths had no effect on sand lizard occupancy. Generally, if isolation predicts "island" occupancy, a focal species may be present on small islands if they are close enough to a source population for immigration rates to compensate for high extinction rates (Lomolino 1999). In spite of the fact that the distance between several of the surveyed pine heaths were within the dispersal capacity of the sand lizard (≤ 2 km, see Berglind 2000), and the intervening habitat no more inhospitable than closed pine stands, only size of pine heath seemed to influence occupancy. The explanation for this pronounced area effect on a regional scale is probably that sand lizard occupancy has been shaped by selective extinctions since the end of the postglacial warm period (ca 500 B.C. when these sand areas were part of a larger habitat continuum, until climate changed), and that only the largest sand areas have provided continuity of suitable habitat patches for population survival. This hypothesis is also supported by the fact that the two smaller occupied pine heaths in this study contained fewer local populations. Also in other studies of reptiles on islands including habitat fragments, island area was of critical importance for long-term persistence (Foufopoulos and Ives 1999, Diaz et al. 2000).

The same pattern of occupancy was also reflected on a landscape scale, where occupied patches within individual pine heaths were significantly larger than patches where the sand lizard had recently gone extinct. Patch isolation had no significant effect. Thus, there is no support for a classical metapopulation structure, with a balance between distance-dependent re-colonisation and spatially independent extinctions (see Harrison and Taylor 1997). Instead, local extinctions of the sand lizard on these pine heaths seems to occur in accordance with a non-equilibrium, habitat-tracking metapopulation model, i.e. extinction occurs mainly when disturbance or succession cause the loss of suitable habitat. The species' abundance and distribution will remain roughly constant only if the rates of habitat loss and renewal happen to be roughly equal (Thomas 1994) (see also under Disturbance dynamics and population survival). The overall number of potential habitat patches for the sand lizard within occupied sandy pine heaths are very small today, as shown by the number of patches on Brattforsheden that contained a combination of critical habitat components (Fig. 7). Stochastic extinctions do, however, also occur before complete loss of habitat, as indicated in Fig. 3 (see also Berglind 2000).

The strong positive correlation between number of spider wasp species and size of pine heath, in combination with the significantly nested subset pattern, supports the notion that rare species on large sandy pine heaths are less prone to extinction than rare species on smaller ones. Several of the more area-sensitive spider wasp species in this study, seem to have a disjunct or fragmented distribution pattern in NW Europe and are known from few localities in central Sweden (Schmid-Egger and Wolf 1992, van der Smissen 1996). *Priocnemis gracilis* has its main known occurrence in Fennoscandia on Brattforsheden, where it in-

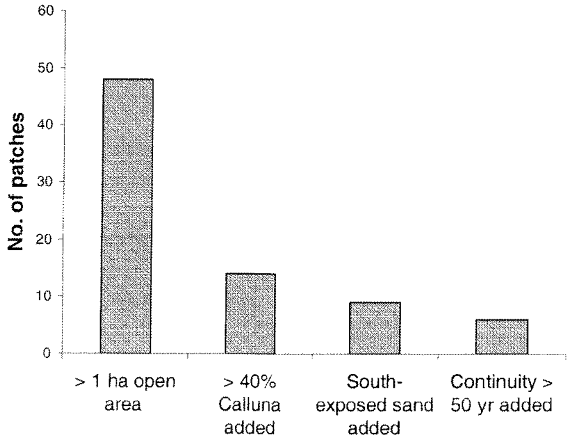

Fig. 7. Schematic illustration of number of patches with four key habitat components for occurrence of the sand lizard in the sandy pine heath forest of Brattforsheden in 1988 (before habitat restorations started). The components have been added from left to next bar to the right. There were 48 open patches > 1 ha (including clear-cuts and some suitable sand road sections; left bar), but only six patches with a combination of all four components (right bar). Only the latter patches were occupied by the sand lizard in 1988. Open area = area with < 20% tree coverage, Calluna = coverage of *Calluna vulgaris* field layer.

habits open sites with a mosaic of exposed sand, heather, grasses, reindeer lichens, and scattered bushes. *Evagetes dubius* is found only on three of the four sandy pine heaths where the sand lizard occurs, but not always on the same patches (Fig. 6). In south Sweden the area of occupancy for both *E. dubius* and the sand lizard is larger and their habitat niches broader (see Berglind 2004b). This type of north-south gradient in ecological range is not unusual in thermophilous ectotherms in NW Europe (Thomas et al. 1999). A third example of a species with a fragmented occurrence is *Arachnospila wesmaeli*, which, however, also occurred on some small pine heaths in this study. This species is more or less strictly confined to coastal and inland dune areas with large patches of open, aeolian sand. On a landscape scale for Brattforsheden, it seems that the two latter species, among others, have a metapopulation structure restricted to two smaller parts of this pine heath, whereas *P. gracilis* is locally distributed over most of the area (Fig. 6).

Disturbance dynamics and population survival

In order for the sand lizard and other early-successional, low-vagility species to survive on the central Swedish sandy pine heaths after the end of the postglacial warm period, there must have been disturbance regimes that continuously created open sand patches. In the past, dry Scots pine forests were probably made up of multi-layered stands strongly shaped by forest fires (Angelstam 1997, 1998, Esseen et al. 1997, Angelstam and Kuuluvainen 2004). Most likely, fire was the dominant disturbance factor until at least the 17th century, after which the influence of human activities in the forests became more prominent (see Angelstam 1997, Niklasson and Drakenberg 2001). There is much evidence that fire recurrently created open patches with exposed sand in boreal and hemiboreal pine heath forests with fossil sand dunes until as late as the beginning of the 20th century (Bergqvist and Lindström 1971, Lindroos 1972, Bergqvist 1981). Since aeolian sand is one of the most well-sorted materials in nature, and lacks finer particles that retain moisture, it has extremely low water-holding capacity (Bergqvist 1981). Thus, burns that consume most of the humus layer on aeolian sand, especially on south-facing slopes, produce vegetation-free patches that remain exposed for a long time (cf. Oksanen 1983, and Fig. 2 in Berglind 2000).

Extensive human activities like forest grazing by cattle, charcoal production, and tree harvesting, also contributed to keeping the central Swedish forests, including the forested inland dune areas, relatively open between at least ca 400–100 yr ago (Cederberg 1982, Angelstam 1997). During recent decades, open patches with exposed sand have been created only at a small, local scale, mainly at sand roads and sand pits. Clear-cuts do not offer open sand habitats, since the humus-layer is left intact after tree harvesting.

The structural components crucial for the sand lizard in sandy pine heath forests include a mosaic of open sand patches for egg-laying, and a rich field-layer of *Calluna vulgaris* and/or grasses for shelter and foraging (Berglind 1999). During recent decades the sand lizard on the central Swedish sandy pine heaths has been found within ca 0.1–3 ha patches of suitable habitat (Fig. 3), including: sand road verges (Fig. 8), sand pits, power-line corridors, old fire fields, and lake shores. Since all these populations have declined and some gone extinct (Berglind 2000, Wallgren and Berglind 2002), such small patches do not seem large enough for long-term persistence. This notion is supported by an age-structured, stochastic population viability analysis for the sand lizard on Brattforsheden. This analysis indicated a quasi-extinction risk (threshold ≤ 10 females, including hatchlings) of ca 60% for 1 ha habitat patches over a 50-yr horizon. In contrast, 5 and 10 ha patches have quasi-extinction risks of only 6 and 1%, respectively, which can be considered acceptably low risks over a 50-yr horizon (Berglind 2004a).

Under a natural fire regime and past human activities, sand lizard colonisations and extinctions probably occurred in a shifting spatiotemporal mosaic, with lizards tracking early successional habitats within their dispersal distance (cf. Thomas 1996, Tiebout and Anderson 1997). It is likely that there was spatiotemporal variation in growth rates within such sand lizard metapopulation networks, due to differences in successional stage, patch size, local topography (affecting microclimate and egg hatching success), catastrophic short-term effects of forest fires etc.

Fig. 8. Example of "key habitat" for biodiversity conservation in sandy pine heath forests. South-oriented sand-cut in a fossil sand dune at a small sand road. The latter was probably created some 300–400 yr ago. The sand-cut has contributed to continuity in open habitat for egg-laying by the sand lizard and several red-listed insect species. Brattforsheden, Djäknetjärn in 1990. Photo: S.-Å. Berglind.

Causes of nestedness

The investigated spider wasp communities were highly significantly nested, with the faunas of low-diversity pine heaths being predictable subsets of the faunas of high-diversity ones. If species richness decreases with declining habitat area, a nested subset structure might allow one to predict future faunal composition in a habitat subjected to reduction or fragmentation (Worthen 1996). Nestedness is frequent in insular habitats and it can principally be explained by: selective extinctions, selective colonisations, habitat nestedness, and passive sampling (e.g. Wright et al. 1998). Future work on nestedness among spider wasp communities should try to tease apart the relative importance of these processes, which are briefly discussed below.

Selective extinction refers to systems where species disappear from habitat patches or islands in a predictable sequence according to their lower threshold area requirements, without replacement by nearby colonists "relaxation" (Wright et al. 1998). In accordance with the suggested extinction dynamics for the sand lizard, selective extinctions may have caused spider wasp species that were formerly widely distributed to survive only on the larger sandy pine heaths. *Evagetes dubius* supports this hypothesis in that it is only found on the same areas as the sand lizard (Table 1).

Selective colonisations may have contributed to the observed nestedness pattern if there are pronounced differences in dispersal abilities among spider wasp species. Then poorer dispersers would tend to be present only on the largest or richest pine heaths, where extinction rates are lower, whereas better dispersers would tend to be present on most pine heaths because local extinctions would be quickly reversed (Cook and Quinn 1995). Haeseler (1988) showed that common species of spider wasps had colonised young dune islands up to 7 km off the North Sea coast. Two of the species encountered, *Episyron rufipes* and *Evagetes pectinipes*, prefer coastal sand habitats. This may explain why they occurred mainly on pine heaths close to the "inland sea" lake Vänern in my study (Fig. 1 and Table 1), where they also inhabit small sandy shores.

A nested distribution of habitats among islands may also result in nestedness of species assemblages (Calmé and Desrochers 1999). Although not obvious to the human eye, it is possible that large sandy pine heaths offer sandy microhabitats (including microclimates and/or species interactions) rarely found on smaller ones, and that this is reflected in the occurrences of rare species. High richness of sandy microhabitats may explain the surprisingly high species richness of area 3 (Table 1), considering its small size. A large proportion of this area (almost 40%) contained open sand in the form of sand pits (in different successional stages), as opposed to the other areas, where the relative amount of exposed sand was much smaller. The high species richness of this area may also relate to the previous hypothesis, and the one below.

Passive sampling may also cause nestedness, whereby abundant species have a higher probability of being sampled than rare ones (Andrén 1994, Wright et al. 1998). Moreover, the species-area relationship may arise because large areas sample more individuals from a species pool than small areas and therefore have more species (Connor and McCoy 1979). Although the nestedness calculator programme used in this study tends to overestimate the degree of nestedness and its statistical significance (Fischer and Lindenmayer 2002), the low nestedness temperature in my dataset is likely to reflect a genuine signal, rather than being an artefact of passive sampling. This is supported by the fact that the number of spider wasp species per patch was significantly higher on the largest areas than on smaller ones. Furthermore, the potential to find the majority of species in a spider wasp community on individual pine heaths seems to be high. Although the largest studied area, area 1 (Brattforsheden), has been surveyed with varying intensity and local focus for several seasons on a total of 25 patches between 1988 and 2003, it is noteworthy that 23 species out of 25 (92%) of the sand-associated spider wasp fauna known today were caught in water traps from only 7 patches in the first survey season. Two additional species were caught in the second season, on patches not investigated before. However, two species (*Arachnospila wesmaeli* and *A. westerlundi*) have been found with only 3 and 1 specimens, respectively, indicating that the rarest species might be overlooked by chance.

Potential indicator and umbrella species

Pine heaths and patches with the sand lizard had a disproportionately large number of red-listed spider wasps and other early successional species on a regional and landscape scale. Because of the sand lizards' restricted dispersal capacity and association with structurally complex sand habitats (see above), this species indicates historical continuity of such habitats. Since the sand lizard is also conspicuous and rather easy to survey, it can be considered a suitable indicator species for patches of high early successional biodiversity value. Furthermore, potential habitat patches for the sand lizard are fairly easy to identify (Fig. 7), which make surveys for "hot spot" patches straightforward.

In addition, since the sand lizard requires relatively large patches on at least a 50-yr horizon (> 5–10 ha; see above), it makes it a suitable umbrella species for early successional biodiversity conservation on large sandy pine heaths. This was also supported by the relatively high score of the umbrella index calculated for red-listed species on Brattforsheden (Table 3). However, two drawbacks with the sand lizard as an umbrella species for biodiversity conservation in pine heath forests are its restriction to the largest sandy areas, and its rarity within these at present. An ideal umbrella species should be neither too ubiquitous nor too rare but instead strike a balance between these two extremes (Fleishman et al. 2001b). Sites that are identified with an umbrella species should also encompass viable populations of both the umbrella and its beneficiary species (Caro 2003, Roberge and Angelstam 2004). Importantly, this could be achieved after habitat restoration and subsequent population growth.

Although they are less species-rich overall, smaller sandy pine heaths can also be inhabited by red-listed early successional species (Table 1). On such smaller areas, spider wasp species such as *Episyron albonotatum* and *Arachnospila wesmaeli* and the digger wasp *Ammophila campestris*, can be useful umbrellas and/or indicators (Table 3). Moreover, the number of red-listed spider wasp species per patch is significantly positively correlated with the number of other red-listed aculeate Hymenoptera per patch (mostly digger wasps and solitary bees) (data from the areas in Table 3; unpubl.).

Among other insects, the umbrella index suggests that the diurnal, easily observed and identified tiger beetle *Cicindela sylvatica* (for presentation, see Lindroth 1985) is an especially suitable candidate as an umbrella species, since it indicated high red-listed species richness and had an intermediate degree of ubiquity (Table 3). Pearson and Cassola (1992) argued that tiger beetles in general make good indicator taxa for biodiversity conservation because of their conspicuous appearance and often strict association to early successional and threatened habitats.

Among vertebrates, the wood lark and the nightjar scored higher as potential umbrella species than the sand lizard on Brattforsheden; the nightjar mainly because it occurred on relatively many patches, whereas the wood lark better indicated species-rich patches with respect to red-listed early successional taxa (Table 3). However, one disadvantage with these high-vagility species is that they are not dependent on continuity of open habitats, which make them less sensitive than the sand lizard as indicators and umbrellas for threatened, low-vagility species.

Obviously, no one species studied here can be used as an umbrella for all other threatened species on sandy pine heaths, so a strategy of multiple umbrella species (Lambeck 1997), and demarcation of patches with key habitat components (cf. Fig. 7), would be a suitable approach for early successional biodiversity conservation.

Implications for conservation action

I concur with Linder et al. (1997) and Sutherland (1998) that active management of threatened early successional habitats and species must play a larger role in conservation, as opposed to the passive form of management usually applied in forest reserves. The efficiency of afforestation and fire suppression accelerated during the 20th century, and the Swedish boreal forest is now generally much denser than before (Linder and Östlund 1998). The conservation of the sand lizard and other thermophilous, ground-dwelling, early successional species in sandy pine heath forests requires action to reduce closed canopy formation and subsequent shading, and to re-establish new open habitat patches at suitable locations. On Brattforsheden, ca 20 new 5–15 ha sand lizard habitat patches divided into at least six networks are planned to be restored over the coming years, with the management measures described in Figs 9–10. Since natural colonisation of sand lizards to restored, distant, empty patch networks, is unlikely within the foreseeable future, reintroduction of juveniles is planned to take place (Berglind 2004a).

Several sound, general suggestions for biodiversity restoration in dry pine forests, including use of prescribed burnings, are given by Fries et al. (1997) and Angelstam (1998). It is, however, as Granström (2001) points out, vital to designate selected stands and landscapes with long-term plans for the use of fire. Prescribed burnings may be a suitable long-term way to recreate suitable mosaics of open sand patches and a dense field layer of *Calluna vulgaris* at some distance from sand lizard patches (fire within habitat patches can cause major mortality among sand lizards; e.g. Moulton and Corbett 1999). This more "natural" method of restoration has the advantage of also attracting pyrophilous and thermophilous wood-associated insects (Wikars 1992, Ehnström 1999).

Besides restoration of early successional patches, we must also start focusing on existing habitat patches of conservation importance in sandy pine heath forests. The sand lizard and many other red-listed species often occur in or

Fig. 9. Part of sand lizard habitat patch ten years after habitat restoration (cutting of a 40 yr old pine stand, patch-soil scarification, and excavation of bare sand patches). Note the high coverage of *Calluna vulgaris*, regrown from the existing seed bank, and the excavated sand patches in the fore- and background (on top of fossil sand dunes). Before restoration, the ground was shaded by closed pine canopy, and almost completely covered by a ground layer of reindeer lichens, with only a minute field layer of *Vaccinium vitis-idaea* and *Calluna vulgaris*. The patch is today also habitat for the wood lark, nightjar, and the rare spider wasp *Priocnemis gracilis*. To keep restored patches in such an early successional stage, recurrent management is planned to take place ca every 20th yr, by felling of pine shrubs, mechanical sand disturbance, and/or small-scale burning on a rotational basis. Brattforsheden, site SB (northern part of the southern patch in Fig. 10, view towards NW) in August 2002. Photo: S.-Å. Berglind.

Fig. 10. Aerial photograph of two newly restored habitat patches connected by a dispersal corridor for the sand lizard on Brattforsheden, site SB in 2000. The non-restored area between the patches was less suitable to restore since it has a northerly aspect. Within the patches, pine trees have been cut down, except for groups of ca 5–10 trees. The patches have been subject to patch-soil scarification to allow regrowth of *Calluna vulgaris* from the seed bank, and thus provide shelter and foraging opportunities for the sand lizard. The sand patches have been created on fossil sand dunes with a southerly aspect by an excavator for egg-laying by sand lizards. The unusually broad, open verges (10 m on each side) of the sand road have been created to reduce the amount of shade per day from surrounding tree canopy so as to allow inter-patch dispersal by the lizards. The 12-yr old restoration patches from 1988 were the main ones inhabited by lizards when the photograph was taken in 2000. Photo: Lantmäteriet.

close to sand/gravel pits (Berglind 2004b). These are very important habitats for early successional biodiversity conservation and should in many cases be classified as "key habitats", and kept permanently open, perhaps through subsidies to land-owners. Furthermore, sandy road verges with a southerly aspect often represent high quality habitats for reproduction and dispersal for both the sand lizard (Dent and Spellerberg 1988) and invertebrates (Vermeulen 1993, Eversham and Telfer 1994) (Fig. 8). By clearence of trees at least 5–10 m on each side of the verges along suitable road sections (cf. Fig. 10), the amount of shade per day can be reduced and habitat offered for many more years than is normally the case (due to tree canopy formation and shading).

Is biodiversity conservation in sandy pine heath forests important?

One might argue that the peripheral populations of red-listed species that occur in the Fennoscandian sandy pine heath forests are on the brink of extinction anyway, the positive effects of increased global warming not withstanding, and that conservation resources should be directed towards, for example, threatened boreal species occurring closer to their centres of range. However, recently Channel and Lomolino (2000) showed that peripheral populations are no more "doomed to extinction" than populations in the centre of a species' range, and in fact often less so. Furthermore, peripheral populations often exhibit unique genetic characteristics that make them especially valuable for biodiversity conservation (Lesica and Allendorf 1995), which has in fact been demonstrated for the central Swedish sand lizard populations (Gullberg et al. 1998). Large sandy pine heath forests may also be viewed as "archives" with regard to early successional species connected to historical ecological processes, including forest fires and associated open sand habitats, which have only relatively recently been suppressed by human activities. Thus, there are strong reasons to direct conservation management priorities towards these heath forests without further delay.

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