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Reports

Competitive exclusion within the predator community influences the distribution of a threatened prey species

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Abstract. While much effort has been made to quantify how landscape composition influences the distribution of species, the possibility that geographical differences in species interactions might affect species distributions has received less attention. Investigating a predator–prey setting in a boreal forest ecosystem, we empirically show that large-scale differences in the predator community structure and small-scale competitive exclusion among predators affect the local distribution of a threatened forest specialist more than does landscape composition. Consequently, even though the landscape parameters affecting Siberian flying squirrel (*Pteromys volans*) distribution (prey) did not differ between nest sites of the predators Northern Goshawks (*Accipiter gentilis*) and Ural Owls (*Strix uralensis*), flying squirrels were heterospecifically attracted by goshawks in a region where both predator species were present. No such effect was found in another region where Ural Owls were absent. These results provide evidence that differences in species interactions over large spatial scales may be a major force influencing the distribution and abundance patterns of species. On the basis of these findings, we suspect that subtle species interactions might be a central reason why landscape models constructed to predict species distributions often fail when applied to wider geographical scales.

Key words: Accipiter gentilis; *competitive exclusion; Siberian flying squirrel; habitat selection; landscape composition; Northern Goshawk; predator community;* Pteromys volans; *spatial distribution; species interactions;* Strix uralensis; *Ural Owl.*

Introduction

The theory of habitat selection (Fretwell and Lucas 1970, Rosenzweig 1981, Morris 2003) assumes that species select the best habitat patch available in the landscape, e.g., regarding where to forage and to reproduce. While time constraints and imperfect information on patch quality may render optimal decisions impossible in reality (e.g., Sutherland 1996), it is clear that habitat choice constitutes one of the most fundamental processes in ecology dictating species' spatial distribution (Fretwell and Lucas 1970, Morris 2003, Ydenberg et al. 2004). In spite of this consensus and the fact that various environmental characteristics such as availability of food, predation pressure, and the presence of con- or heterospecifics (Brown 1988, Lima and Dill 1990, Quinn and Kokorev 2002, Sergio et al. 2004, Forsman et al. 2009) are known to affect the distribution and population densities of species, the relative importance of the cues individuals use when performing habitat choice are seldom explored (Brown 1988, Goodale et al. 2010).

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If one disregards obvious biogeographical reasons, such as distribution barriers and historical origins of species, little is known about which way differences in local environmental characteristics, e.g., predation risk, explain differences in species abundance patterns as observed over large spatial scales (but see Martin 1995, McKinnon et al. 2010). Furthermore, there exist, to our knowledge, no studies investigating whether competitive exclusion (i.e., the situation where a dominant species, by its presence, spatially excludes a subordinate one) among members of a predator community have repercussions for spatial distribution of prey species. A better understanding of such interactions would not only be of pure scientific interest, but could also be of importance for various ecological applications. For example, if landscape structure alone is used as a rationale for designing reserve networks (e.g., Hartig and Drechsler 2009), integrating species interactions into the area selection algorithm is needed if geographical differences in predator community structure influence the distribution of the species in target of conservation.

By investigating a predator–prey setting in the Finnish boreal forest where the dominant Northern Goshawk *Accipiter gentilis* L. (hereafter goshawk) and the subordinate Ural Owl *Strix uralensis* Pall. act as predators, we tested to what degree (1) large-scale

differences in species composition of local predator assemblages and (2) competitive exclusion among the predators locally have repercussions for the distribution of their shared prey (Hanski et al. 2000, Selonen et al. 2010), the nationally threatened Siberian flying squirrel *Pteromys volans* L. (Rassi et al. 2010; hereafter, flying squirrel). Because landscape composition in addition to other factors usually limit species distributions (Brown 1988, Andrén 1994, Watling et al. 2011), we further investigated (3) to what extent landscape composition explains prey distribution while simultaneously accounting for potentially confounding effects (vegetation zone shift, small-scale spatial correlations). If landscape composition is the major determinant of flying squirrel distribution locally and because the Ural Owl and the flying squirrel both are nocturnal, whereas the goshawk is diurnal, we predicted (1) that flying squirrels should be relatively less frequent at Ural Owl nest sites (high predation risk) than at goshawks nest sites (moderate predation risk) in regions where both raptor species occur. However, sites without predators (low predation risk) should always be favored, provided that the proportion of landscape components of importance for flying squirrels at predator-free sites does not differ from that of predator sites. Alternatively, if predation risk overrides the importance of landscape composition, and because the goshawk competitively excludes, and occasionally even kills the Ural Owl (Mikkola 1983), we predicted (2) that goshawks and flying squirrels should aggregate heterospecifically (Forsman et al. 2009) in regions where Ural Owls and goshawks co-occur. This is because goshawk sites then will constitute enemy-free refuge against the Ural Owl, which poses a bigger predation threat to flying squirrels than the goshawk (Hanski et al. 2000). Under the same scenario in regions where Ural Owls are not a part of the local predator community, we predicted no or only limited spatial association between goshawks and flying squirrels.

Methods

Study species, study sites, and study design

Goshawks and Ural Owls are among the most common forest birds of prey in southern Finland and typically occur with 2–4 breeding pairs/100 km^2 (Väisänen et al. 1998). Even though it is known that the hunting ranges of neighbor pairs may overlap to some extent, both within and among species (P. Byholm, *personal observations*; P. Saurola, *personal communication*; see also Tornberg et al. 2006), breeding goshawks and Ural Owls spend most of their time close to the active nest from late March (Ural Owls) or early April (goshawks) until the young reach independence in July–August, after which the young disperse (Mikkola 1983, Tornberg et al. 2006). The flying squirrel uses multiple nests during the whole year (both for breeding and daytime resting) spaced randomly within the home range (Hanski et al. 2000), which varies in size between 1 ha and 90 ha (100% minimum convex polygon [MCP]) depending on sex and sexual state (Hanski 1998, Reunanen et al. 2002*a*). Although the Ural Owl and the flying squirrel are nocturnal and the goshawk is diurnal, all three species show the same general preference for mature mixed-spruce forest stands (Mikkola 1983, Hanski 1998, Tornberg et al. 2006). Both predators occasionally prey on flying squirrels (Selonen et al. 2010), but the Ural Owl is clearly more specialized on small mammals (Korpimäki and Sulkava 1987), including the flying squirrel (Hanski et al. 2000), than the goshawk, whose diet is dominated by avian prey (Tornberg et al. 2006). Although Ural Owls may breed in old goshawk nests (Mikkola 1983), they normally avoid breeding closer than one kilometer from nests that are occupied by goshawks (Solonen 1993). In this way, they may not only avoid direct predation impact by the goshawks (Mikkola 1983), but also reduce energetic and physiological negative effects that likely arise from (repeated) encounters with dominant predators (Creel and Christianson 2008).

To investigate the hypothesized effect of predator presence/absence on the local distribution of prey, we conducted a field study in the cross section of the southern and middle boreal vegetation zones (Ahti et al. 1968) in Suupohja (SP), western Finland (62°50′ N, 22°00′ E; Fig. 1). A second study area was established in Varsinais-Suomi (VS), situated within the southern boreal vegetation zone north of the town of Salo (60°30′ N, 22°60′ E; Fig. 1). These two study areas are situated ca. 250 km apart, and while flying squirrels are about equally common in both areas (Hanski 2008), both Ural Owls and goshawks are central members of the raptor community in SP, but Ural Owls are lacking from VS (Valkama et al. 2011).

Forming an expansion of a long-term study on forest raptors (e.g., Byholm and Nikula 2007, Byholm and Kekkonen 2008, Byholm et al. 2011), local flying squirrel occurrence was mapped within 150 m from 30 occupied goshawk nests and 35 Ural Owl nests in SP, and 30 goshawk nests in VS in early–mid May during 2006–2010. This scale was chosen as a rationale based on previous knowledge of landscape composition preference by flying squirrels at the patch scale (e.g., Mönkkönen et al. 1997, Hanski 1998). Every nest (N) was assigned with two distinct reference plots: genuine references (G) and random references (R). Both types of reference plots were always located on mineral soil characterized by forest vegetation, but, while the random references were scattered in any kind of forest habitat of any age and type, including clearcuts and plantations, the genuine references were subjectively localized to forest stands of the same size and with the same stand structure (tree age, tree species composition, percent canopy cover, and so on) as the nest sites. Because the flying squirrel is arboreal as well as nocturnal, it is extremely difficult to observe directly. Therefore, following the procedure used by established mammalogists, flying squirrel presence was inferred from systematically scanning

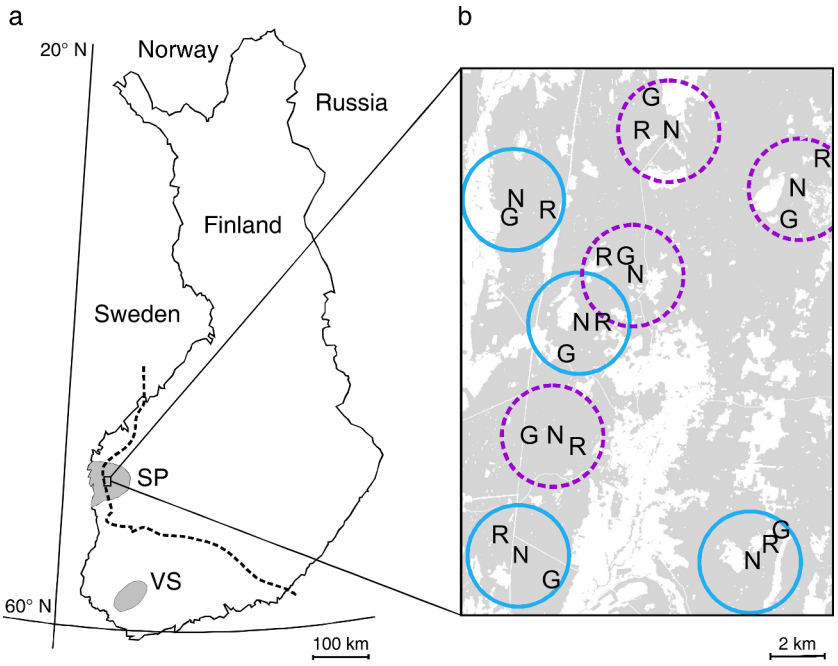


FIG. 1. (a) Map of Finland with the study areas Suupohja (SP) and Varsinais-Suomi (VS) in gray and the border between the southern and midboreal vegetation zones (dashed line) indicated. (b) Detailed view of part of the SP study area showing Northern Goshawk *Accipiter gentilis* L. (solid blue circles) and Ural Owl *Strix uralensis* (dashed purple circles) territory clusters (radius = 2 km) containing the three different types of sampling plots: nest site (N), genuine reference (G; forest stand of the same size with the same stand structure as the nest site), and random reference (R; any kind of forest habitat of any age and type). Gray represents forest habitats, and white shows open habitats (see *Methods* for further details).

for droppings commonly found at the base of trees in stands where flying squirrels are present (Reunanen et al. 2002*a*). This is by far the most accurate mapping method available (Reunanen et al. 2002*b*). To account for potential spatial small-scale correlation in the distribution of flying squirrels, the reference sites were clustered within 1063 ± 419 m (mean ± SD) from the actual nest sites. Since the average minimum nearest neighbor distance was 5678 ± 4917 m between owl nests and 4551 ± 2409 m between hawk nests, this study design resulted in the three sampling plots belonging to the same cluster being far more aggregated spatially than the territory clusters themselves (Fig. 1). Whereas the distance from nests to reference plots did not differ between treatments, either in SP (generalized linear model [GLM], raptor identity × sampling plot, $F_{1,\ 128} = 1.96$, $P = 0.16$) or VS (sampling plot, $F_{1,59} = 2.77$, $P = 0.10$), there was more variation in landscape composition among the random reference plots (because they are scattered randomly in the landscape) than among the genuine reference plots (Appendix A). Thus, this study design allowed controlling for the effects of habitat (random references) and predator absence/presence (genuine references) independently.

Landscape measurements

Land cover classification based on a Landsat TM 5 satellite image (path 192, row 16, date 12 July 2005) in pixel size 25 × 25 m (Muukkonen et al. 2012) was used to infer land use and forest composition in SP. To double-check the accuracy in the classifications as well as to extrapolate additional land cover classes, we merged and compared this classification with the Corine Land Cover 2000 data with the same pixel resolution (CLC2000-Finland 2005). Altogether, nine landscape components were distinguished: (1) mature coniferous forest (MCF; covering 9% of the SP study area), (2) mature mixed forest (MMF; 3%), (3) young coniferous forest (YCF; 20%), (4) young mixed forest (YMF; 12%), (5) clearcuts and plantations (CCP; 16%), (6) peat land with no or sparse tree vegetation (PL; 9%), (7) fields (FI; 15%), (8) built-up areas (BUP; 4%), and (9) water bodies and wetlands (WA; 12%). Among the forest variables (landscape classes 1–5, 60% of area) areas logged less than ~10 years ago were assigned to the class CCP, whereas the mature forest classes (MCF and MMF) were areas in which the forest structure was characterized by later successional forest, including trees typically older than 80 years. The age of trees in both the forest categories YCF and YMF were of intermediate age. Using this material, the proportion of landscape components was calculated at three different distances (50 m, 150 m, 500 m) from a total of 186 flying squirrel sampling plots (nine sampling plots were located outside the image border) to get a general impression of the landscape composition at mapped sites in the SP area (see Appendix A) using the package Patch Analyst (grid)

3.0 within ArcView based on a Fragstats algorithm (McGarigal and Marks 1995).

Statistical analyses

The distribution of flying squirrels in relation to landscape composition was modeled as a binomial response (presence = 1, absence = 0) using generalized linear mixed modeling (GLMM) where the proportions of landscape components within 150 m from the three types of sampling plots (N, G, R) were set as fixed effects. Since only one of the total of 35 pairwise correlations between landscape variables was marginally greater than ±0.5 (OCF vs. YMF, −0.59), evidence for high collinearity between variables was limited in our data set. With that, there was no need to re-classify the variables (cf. Rhodes et al. 2009) using linear combinations or biased estimation procedures, a conclusion that was also supported from inspections of variance inflation factors (VIF($\acute{\alpha}$i) $\leq$ 3.1 in all model combinations). To keep the models biologically relevant (Mönkkönen et al. 1997, Hanski et al. 2000, Reunanen et al. 2002*a*), as well as to limit the amount of alternative models, only models with different combinations of forest variables (landscape components 1–5) were analyzed. Akaike information criterion (AIC; Burnham and Anderson 2002) was then used as a guide to rank the alternative landscape models.

In the model used to investigate if competitive exclusion of predators would explain the local distribution of flying squirrels within SP (only there both raptors are present), flying squirrel occurrence was modeled as a function of the variables raptor identity (goshawk, Ural owl) and sampling plot (N, G, R). Acknowledging that the border of the southern and middle boreal vegetation zone is crossed when moving from west to east within SP (Fig. 1), the normalized (zero mean and unit variance) east coordinate (longitude) was included as explanatory variable in all of the models to account for potential large-scale differences in flying squirrel occurrence due to spatial variation in vegetation complexity. At this stage, if differences in flying squirrel distribution were detected, potential differences in the proportions of landscape components of importance for predicting flying squirrel occurrence between treatments was inferred. Patch occupancy patterns of flying squirrels in relation to large-scale differences in raptor assemblage species composition was modeled as a function of the variables area (SP, both raptors present; VS, only goshawk present) and sampling plot. In addition to the main effects, the first-order interactions of the fixed effects were included in both models.

Because of the spatially structured study design (Fig. 1) and to account for possible small-scale spatial correlation in flying squirrel distribution, the variable cluster (see Fig. 1) was set as a random effect in all models. When performing model averaging, maximum likelihood (ML) estimation was used since models had different fixed-effects structures (Crawley 2002). All modeling was done in R 2.10.1, using the glmm ML library specifically for mixed models (R Development Core Team 2011).

Results

When analyzing the impact of forest structure at the 150-m scale for flying squirrel presence/absence in SP, three alternative forest models were constructed and compared with the null model (Appendix B: Table B1). As judging from AIC comparisons, the model containing the landscape components YCF, YMF, CCP, and longitude ranked best. Even though all three landscape components showed negative parameter estimates, only clearcuts and plantations (CCP), in addition to longitude, significantly correlated negatively with flying squirrel occurrence probability (Appendix B: Table B2).

In the model addressing whether competitive exclusion affects flying squirrel distribution, the interaction between sampling plot and raptor identity was highly significant (GLMM, $z > 2.9$, $P < 0.004$; Appendix C: Table C1). This was due to the finding that flying squirrels were practically absent at Ural Owl's nest sites, while the probability of flying squirrels to occur at goshawk sites was ~67% (Fig. 2a), even though the proportion of clearcuts and plantations (the only landscape component affecting local flying squirrel distribution negatively; Appendix B: Table B2) did not differ as compared between the nest sites of the two species (Mann-Whitney U test, $Z = -1.58$, $P = 0.11$; Appendix A: Table A1). In addition to this, and in congruence with the result from the landscape composition model, there was evidence that flying squirrels decreased with increasing longitude within SP.

Where Ural Owls were not a part of the raptor community, this positive association between goshawks and flying squirrels disappeared. Consequently, while in SP goshawk nest sites more often host flying squirrels than any other type of sampling plot, in VS flying squirrels are about equally frequent at nest sites and genuine reference sites, albeit overall flying squirrel density did not differ regionally (GLMM, $z > 1.9$, $P < 0.056$; Fig. 2b; Appendix C: Table C2). Moreover, flying squirrel occurrence probability also differed between territory clusters as such as inferred from the random-effect estimates in both models (1.01 ± 0.51 and 0.82 ± 0.43 [mean ± SE], respectively).

Discussion

In line with earlier findings (Hanski 1998, Reunanen et al. 2002*a*) and following our landscape-effect prediction, marks of flying squirrels were observed more often at genuine reference sites (high forest quality) than at random reference sites (low forest quality). This observation is well in line with general theoretical predictions (Tilman and Kareiva 1997) and with previous abundant empirical evidence (e.g., Andrén 1994, Fahrig 2003) that landscape composition is of importance for species' occurrence and distribution patterns in fragmented landscapes. However, although

the number of clearcuts and plantations less than 10 years old (the only landscape parameter adding significantly to flying squirrel presence/absence) did not differ between raptor nest sites, flying squirrels were close to eight times more frequent at goshawk nest sites than at Ural Owl sites, which were avoided. This finding provides strong evidence that not only may predator presence affect the spatial distribution of species (Forsman et al. 2001, Ydenberg et al. 2004, Ripple and Beschta 2006), but also that competitive exclusion among species within the predator community may override landscape composition for explaining the local distribution of threatened forest specialist (prey) species. We suspect that this might be the case in many other situations as well, in particular, as animals commonly appear to assess predation risk effects when deciding where to settle (Creel and Christianson 2008). However, while tremendous effort has been devoted to explaining habitat preference and spatial distribution of species in relation to landscape structure and composition (e.g., Fahrig 2003, Turner 2005), there have been far fewer investigations assessing the importance of nonlethal species interactions (but see Caro 2005, Thomas et al. 2009).

Since goshawks and Ural Owls both prey on flying squirrels (Selonen et al. 2010), a question that inevitably arises here is why do flying squirrels in the Suupohja study area aggregate spatially with one of their natural enemies? Although it was not possible to directly observe, we see no other reasonable explanation than that this pattern must be the result of active movements, i.e., that flying squirrels are heterospecifically attracted by goshawks (Goodale et al. 2010). Interestingly, when Ural Owls were not a part of the predator community, the spatial aggregation between the two breaks down (Fig. 2b). Jointly, these findings suggest that, when evaluating local habitat quality, species (here the flying squirrel), not only assess the predation risk as posed by a single predator (here the goshawk), but that they also may balance the predation danger of one predator against that of other predators (here the Ural Owl). Consequently, prey may rank habitat patches occupied by one of their natural predator as being of better quality than corresponding predator-free reference sites if the predator spatially displaces species imposing higher predation danger. In this respect, the goshawk, in fact, provides habitat facilitation (Bertness and Callaway 1994) to its threatened prey, the flying squirrel. Although it was not possible to tell whether predation, predator avoidance, or both were the reason(s) why flying squirrels were lacking at Ural Owl nest sites, our findings demonstrate that the way species are distributed in space depends on the complexity of species interactions and that habitat selection is a highly dynamic process that involves decisions at the individual level (Nathan et al. 2008).

Aside from species interactions and landscape composition, we also found evidence that the local distribution of flying squirrels is dictated by a set of additional factors acting at multiple spatial scales. Apparently, due to general shifts in vegetation complexity as a consequence of that the border between the southern and middle boreal zones was crossed when moving from west to east within Suupohja, flying squirrels were more abundant closer to the coast than inland. Similarly, as inferred from the random-effect estimates, the probability of flying squirrel occurrence differed between different nest clusters. In combination with the fact that flying squirrels distribute themselves differentially in relation to predator presence/absence when compared between two study areas situated 250 km apart, these findings are likely to greatly undermine the effectiveness of tools addressing which landscape components add to the spatial distribution of species in fragmented landscapes. Thus, our study provides a concrete explanation for why landscape models often do not perform particularly well in predicting species occurrence and abundance in relation to landscape

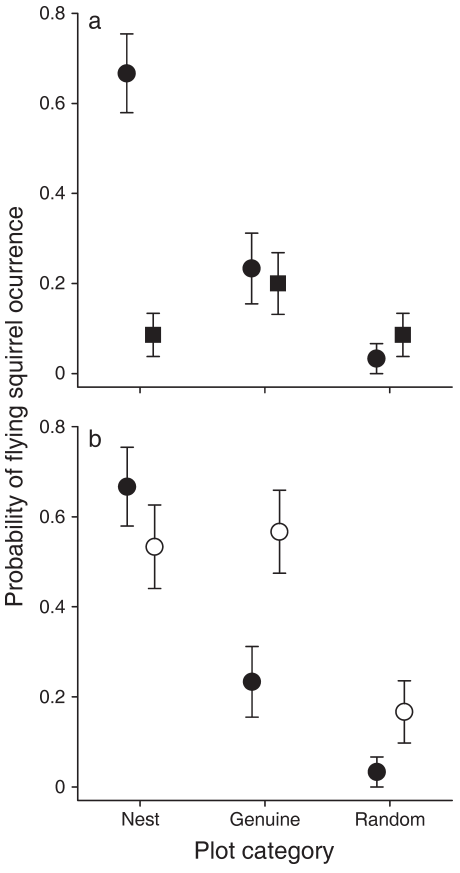


FIG. 2. Probability of occurrence (mean ± SE) for flying squirrels (*Pteromys volans* L.) in the three types of sampling plots (see Fig. 1 for descriptions) in (a) relation to predator identity (Northern Goshawk, circles; Ural Owl, squares), and (b) as compared between regions with different predator community structures (the presence of both goshawks and Ural Owls is indicated with solid circles; goshawk presence only is shown with open circles).

composition over large scales (e.g., Heikkinen et al. 2006), including Finnish flying squirrels (Reunanen et al. 2002*b*).

On the basis of our results we suspect that differences in competitive exclusion and other subtle nonlethal species interactions at regional to national levels may have more profound ramifications for the distribution and abundance of species than considered heretofore. We therefore encourage participants involved in the development of strategies for the management threatened species in fragmented landscapes to pay more attention to species interactions than heretofore. Although we acknowledge that the relative roles of disturbances and species interactions will probably vary depending on landscape context, our results clearly show that there is a risk that the area selection may turn out to be nonoptimal if concentrating solely on landscape composition and structure when deciding which areas to protect. Since species distributions are ultimately the result of decisions made by individuals, more attention should be paid to better understand the exact clues individuals use when selecting where to settle (Nathan et al. 2008, Morales et al. 2010).

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Supplemental Material

Appendix A

A table with the percentages of landscape components where both raptor species coexist (*Ecological Archives* E093-159-A1).

Appendix B

Model selection addressing occurrence of flying squirrel as function of landscape composition (*Ecological Archives* E093-159-A2).

Appendix C

Two tables with the outputs from modeling flying squirrel presence as function of competitive exclusion between raptors and as function of differences in predator community structure (*Ecological Archives* E093-159-A3).