Evaluating Effects of Habitat Loss and Land-Use Continuity on Ant Species Richness in Seminatural Grassland Remnants

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Abstract: *Seminatural grasslands in Europe are susceptible to habitat destruction and fragmentation that result in negative effects on biodiversity because of increased isolation and area effects on extinction rate. However, even small habitat patches of seminatural grasslands might be of value for conservation and restoration of species richness in a landscape with a long history of management, which has been argued to lead to high species richness. We tested whether ant communities have been negatively affected by habitat loss and increased isolation of seminatural grasslands during the twentieth century. We examined species richness and community composition in seminatural grasslands of different size in a mosaic landscape in Central Sweden. Grasslands managed continuously over centuries harbored species-rich and ecologically diverse ant communities. Grassland remnant size had no effect on ant species richness. Small grassland remnants did not harbor a nested subset of the ant species of larger habitats. Community composition of ants was mainly affected by habitat conditions. Our results suggest that the abandonment of traditional land use and the encroachment of trees, rather than the effects of fragmentation, are important for species composition in seminatural grasslands. Our results highlight the importance of considering land-use continuity and dispersal ability of the focal organisms when examining the effects of habitat loss and fragmentation on biodiversity. Landscape history should be considered in conservation programs focusing on effects of land-use change.*

Key Words: Formicidae, grassland restoration, habitat fragmentation, management continuity, species-area relationship, traditional farming systems

Evaluación de los Efectos de la Pérdida de Hábitat y de Continuidad en el Uso de Suelo sobre la Riqueza de Especies de Hormigas en Remanentes de Pastizales Seminaturales

Resumen: *Los pastizales seminaturales de Europa son susceptibles a la destrucción y fragmentación del hábitat que tienen efectos negativos sobre la biodiversidad debido al incremento del aislamiento y de los efectos de área sobre la tasa de extinción. Sin embargo, hasta los pequeños parches de pastizales seminaturales pueden ser de valor para la conservación y restauración de la riqueza de especies en un paisaje con una larga historia de gestión, que ha sido relacionada con el incremento en la riqueza de especies. Probamos si las comunidades de aves han sido afectadas negativamente por la pérdida de hábitat y el incremento del aislamiento en pastizales seminaturales durante el siglo veinte. Examinamos la riqueza de especies y la composición de la comunidad en pastizales seminaturales de diferente extensión en un paisaje heterogéneo en Suecia central. Los pastizales bajo gestión continua por siglos albergaron comunidades de hormigas ricas en especies y ecológicamente diversas. El tamaño del remanente de pastizal no tuvo efecto sobre la riqueza de especies de hormigas. Los remanentes pequeños no albergaron un subconjunto anidado de especies de*

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hormigas de hábitats más extensos. La composición de la comunidad de hormigas fue afectada principalmente por las condiciones del hábitat. Nuestros resultados sugieren que el abandono del uso tradicional de suelos y la invasión de árboles, no los efectos de la fragmentación, son importantes para la composición de especies en pastizales seminaturales. Nuestros resultados resaltan la importancia de considerar a la continuidad en el uso del suelo y de la habilidad dispersora de los organismos focales cuando se examinan los efectos de la pérdida de hábitat y de la fragmentación sobre la biodiversidad. La historia del paisaje debería ser considerada en los programas de conservación que enfocan los efectos del cambio en el uso del suelo.

Palabras Clave: continuidad de gestión, fragmentación de hábitat, Formicidae, relación especies-área, restauración de pastizales, sistemas de cultivo tradicionales

Introduction

Habitat destruction and fragmentation are the most likely causes of the recent loss of biodiversity (Groombridge 1992; Harrison & Bruna 1999; Henle et al. 2004). Seminatural farmland habitats of Northern Europe are susceptible to habitat destruction and fragmentation due to intensification of agriculture and the abandonment of traditional management practices (Hallanaro & Pylvänäinen 2001). For example, in Sweden seminatural grasslands used for grazing have been reduced by almost 90% over the past 80 years (Bernes 1994). Such habitat loss should have consistently negative effects on biodiversity due to increased habitat isolation and area effects on extinction rate (Debinski & Holt 2000; Fahrig 2003). This might not hold if there are long time lags before the extinction of many of the species (Eriksson 1996) or if there are species living in small fragments with high dispersal rates counteracting extinctions of small populations. For example, results of studies on the richness and distribution of plant species in seminatural grasslands show a slow response to abandonment and habitat loss (Cousins & Eriksson 2002; Eriksson et al. 2002).

Long continuity of grazing and mowing is thought to be one of the main factors causing high plant species richness in seminatural grasslands (Zobel 1992; Austrheim et al. 1999; Pärtel & Zobel 1999). This also holds for small habitat patches (Cousins & Eriksson 2001). Consequently, even small remnants of seminatural grasslands might be of value for conservation strategies aimed at maintaining and restoring the species richness of a landscape. Most of these propositions have been derived from studies of vascular plants (e.g., Cousins & Eriksson 2002; Eriksson et al. 2002), and only a few studies addressing this topic have concerned fauna (e.g., Söderström et al. 2001; Tscharntke et al. 2002).

Ants are sensitive to fragmentation (Golden & Crist 2000; Braschler & Baur 2003), and species composition of ant communities in fragmented forests is affected by remnant size (Sobrinho et al. 2003; Schoereder et al. 2004). Hence, we hypothesized that ant communities have been negatively affected by the habitat loss and increased isolation of seminatural grasslands during the 1900s. Ants are of interest because they are an important part of biodiversity, influencing other organisms and soil processes (e.g., Dauber & Wolters 2000; Lenoir et al. 2001). They can alter the composition and diversity of plant species (King 1977; Dean et al. 1997) and affect each other and other arthropod predators by interference or intraguild predation (e.g., Laakso & Setälä 2000; Hawes et al. 2002). This means ants can affect the overall biodiversity of a particular site or habitat.

We investigated species richness and community composition of ants in seminatural grasslands of different size in a mosaic landscape in Sweden. Up to the beginning of the 1900s these grasslands have had a long history of continuous grazing (Dahlström 2001). Since then they have undergone considerable habitat loss because of abandonment and afforestation. Taking into account historical landscape pattern is important for assessing effects of land-use change on organisms (e.g., Swetnam et al. 1999; Kiss et al. 2004; Schrott et al. 2005).

We asked the following questions. Do smaller patches generally contain fewer ant species than larger patches, and is the set of species on smaller patches a predictable subset of the species on larger patches (Debinski & Holt 2000; Ganzhorn & Eisenbeiß 2001)? Alternatively, do ants respond to a long history of management in the same way as plants, so that small patches have equal or even higher species richness than large patches (Cousins & Eriksson 2002)?

Are wood ants an important structuring force in grassland ant communities, as they are in forest fragments (Puntilla et al. 1994)? Small forest fragments are inhabited mainly by monogynous (one queen per colony) and monodomous (one colony inhabiting one nest) ants, whereas large fragments tend to be monopolized by polydomous (one colony inhabiting several nests) colonies (Vepsälainen & Wuorenrinne 1978; Puntilla 1996). We also investigated whether monodomous and polydomous wood ants affect the composition of the other ant species.

Does the higher edge-to-interior relationship in small remnants allow for an invasion of generalist species (i.e., species that tend to prosper in the "matrix" surrounding the habitat remnants, as reported by Kiviniemi and Eriksson [2002] for plant communities and Schoereder et al. [2004] for ant communities in forest fragments)? Diversity patterns of ants can differ significantly between edges and centers of agricultural habitats (Peck et al. 1998; Dauber & Wolters 2004).

Study Area and Methods

History of Swedish Seminatural Grasslands

During the late Iron Age an increased need for winter fodder for livestock led to the creation of a system of infields (arable fields and meadows) close to the villages and outlands farther away, used as pasture and for collecting fodder and fuel (Eriksson et al. 2002). Many centuries of regular mowing or grazing resulted in sparsely wooded, fairly open landscapes, often forming a transitional zone between more open fields and true forest (Hallanaro & Pylvänäinen 2001). Additionally, small nonarable areas of moraine or rocks formed midfield islets in the infields. These were grazed in the past and have remained unfertilized (Dahlström 2001).

The infield and outfield system existed until the beginning of the twentieth century. The intensification of agriculture in Northern Europe has resulted in the abandonment of traditional land-use practices. Many grasslands have become overgrown, and the remaining farmland has deteriorated for many organisms due to the use of fertilizers and pesticides. Nowadays, many midfield islets have been removed and none of the remaining ones are grazed.

Study Region

We carried out our study on Selaön, the biggest island in Lake Mälaren, Central Sweden (59°23'N, 17°08'E). The island has 10,210 ha of agricultural fields, forests, and seminatural grasslands. Mean annual precipitation is 600–700 mm, mean annual temperature is 7° C, elevation ranges between 2 and 25 m asl. The bedrock is dominated by sedimentary gneiss. The soil and subsoil, distributed in a fine-grained mosaic, varies from podzol in the coniferous forests to brown and organic soils in the agricultural areas.

According to a historical survey, land use on Selaön did not change much in the centuries preceding the twentieth century (Dahlström 2001). The historical mosaic pattern of infields and outland is still visible, but the infields are nowadays more intensively managed, with wheat, rape, and ley the dominant crops. Land use of the outland has changed as well, and only a little grassland is still grazed. The grassland cover of the outland patches associated with bare bedrock has been fairly stable but a lot has been converted to forest. The smallest patches we studied were midfield islets. A recent investigation of the vegetation in large parts of Selaön Island (S. A. O. Cousins, unpublished data) characterized about 30 sites as remnants of seminatural grasslands. Most grasslands undergo succession and show a large variation in the cover of trees and shrubs. However, in some remnants, trees have been cut and parts of the grasslands have been restored for grazing.

Sampling Design

As study sites, we selected four large (mean size 8.96 ha), five medium (2.90 ha), and 13 small grasslands (midfield islets, 0.18 ha; Fig. 1). We excluded all remnants that were completely reforested. On the large sites, we selected six

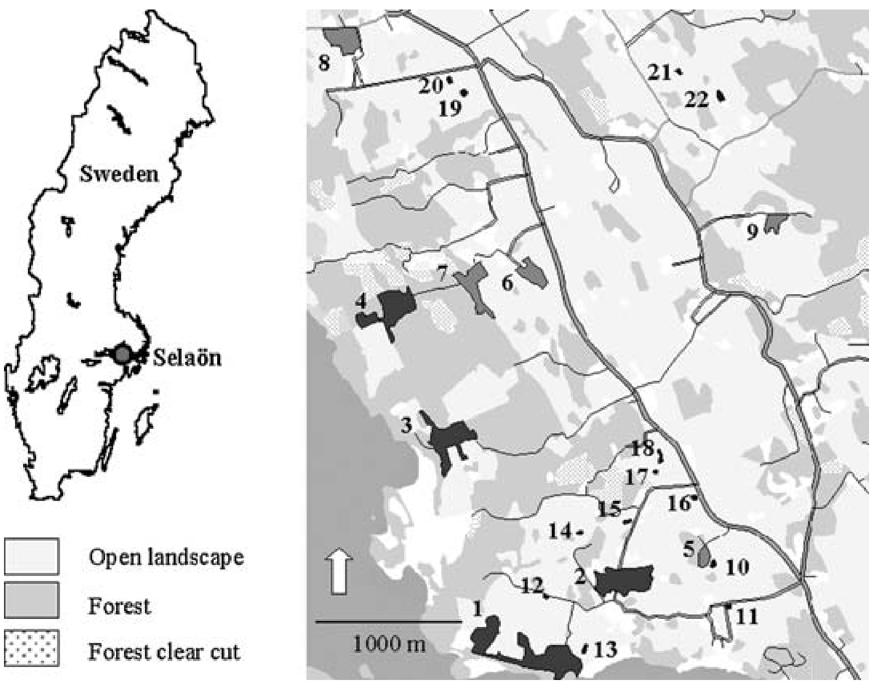

Figure 1. Map of the study region showing the position of the 22 study sites (darkest shading) on Selaön, an island in Lake Mälaren, Södermanland, Sweden. The study sites are divided into three size classes: 1–4, large sites; 5–9, medium sites; and 10–22, small sites.

sample plots: two at the edges to the infields and four at the center of each site. On the medium sites, we selected four sample plots: two plots at the edge and two plots at the center. The small sites contained only one sampling plot, resembling an edge plot. In each sampling plot, we installed seven pitfall traps: 30-mL plastic cups 3 cm in diameter buried level to the ground surface. The traps were filled with 15 mL of a 50% solution of propylene glycol. The minimum distance between the traps was 5 m, and the maximum distance was 10 m. In the edge plots, the traps were positioned along a transect of increasing distance to the infields. The minimum distance of a trap to the infield edge was 1 m, and the maximum distance was 25 m. In the center plots, traps were randomly distributed. The pitfall traps were exposed for 4 days between August 22 and August 25, 2003. We sorted all ants from the traps and identified them to species level based on Seifert (1996) and Seifert (2000). We counted only worker ants.

Environmental Data

We differentiated between plots that were grazed by cattle and plots that were not grazed. Furthermore, based on the recent history of the plots, we identified plots that were restored for grazing by clearcutting of trees. We estimated the percentage of tree cover as percent area of the plot under the canopy and the total percent vegetation cover of herbs, grasses, and mosses. Size of the study sites was obtained from digital land-cover maps with ArcView 3.2 geographic information system software (ESRI, Redlands, California).

Data Analyses

We calculated species frequency as the percentage of traps within a plot in which a particular species was caught. Due to the chosen distance between traps, frequency provides a good estimation of the colony density of small species with limited movement ranges (e.g., *Myrmica* spp., *Lasius* spp., *Leptothorax* spp.) and of the activity density of bigger species with wider movement ranges (e.g., *Formica* spp.). Species richness of ants was the total number of species found on the sites. To correct the counts for the different numbers of traps exposed on the different-sized sites, we used the first-order jackknife richness estimator in EstimateS 5.0.1 (Colwell 1997).

To assess the effect of habitat area of each site on species richness, we calculated a linear regression with the ln-transformed power function $\ln S = \ln c + z \ln A$, where S is number of species, A is area, and c and z are constants fitted to data. To estimate the importance of small habitat remnants for species richness, we used cumulative species-area curves (Quinn & Harrison 1988). Cumulative species richness was plotted against cumulative site area. The shape of the resulting curve depended on the sequence of the addition of habitat area: sites were ranked by their area in ascending (i.e., starting with the smallest areas) or in descending order (i.e., starting with the largest areas). If the ascending curve lies above the descending curve, sets of small sites contain more species than sets of large sites of the same total area (Peintinger et al. 2003).

We compared species composition of plots in different size classes and in different locations (edge vs. center) with the Jaccard similarity index (Southwood & Henderson 2000). We used principal component analysis (PCA) on species frequency data to outline the general structure of the ant species composition on the plots. Only species occurring on more than five plots were included in the analysis. We chose PCA because the gradient length for the ordination axes was close to 3.0, indicating appropriateness of a linear-response model (Leps & Smilauer 2003). We pooled and summed the frequencies of the species of the *Leptothorax s. str.* group, namely *Leptothorax acervorum*, *L. muscorum*, and *L. gredleri*. Environmental parameters were added to the analysis as supplementary variables to facilitate the interpretation of the PCA but did not influence the ordination. We added the categorical variables management, size class, and location as dummy variables (Leps & Smilauer 2003).

We tested patterns in the occurrence of the two most common generalist species (i.e., *Lasius niger* and *Myrmica rubra*) in edge plots along a transect of traps of increasing distance to the edge with logistic regression analyses. Correlations between the distance of a trap to the infields in edge plots and species richness were calculated with Spearman correlation. We tested differences in the mean species richness of ants in edge and center plots of medium and large sites and differences in the frequencies of the habitat generalists by one-way analysis of variance (ANOVA). The appropriateness of statistical models was checked by plotting residuals against fitted values and by normal probability plots. Homogeneity of variances was tested with Levene's test.

We examined whether the wood ant species of the subgenus *Formica s. str.* (i.e., *Formica rufa*, *F. polyctena*, and *F. pratensis*) were negatively distributed in relation to each other by examining whether the observed number of sites with two and three co-occurring species differed from that expected by chance. We conducted a randomization test on an MS Excel spreadsheet in which the expected probabilities of occurrence were determined by their respective distributions. We analyzed whether the presence of wood ants (any of the three species above) was related to the distribution of other ant species with pair-wise G tests (Sokal & Rohlf 1995).

Linear regression, logistic regressions, Spearman correlation, ANOVA, and PCA were performed using the STATISTICA for Windows Package (version 6, StatSoft, Tulsa, Oklahoma).

Table 1. Ant species occurrence (%) on seminatural grasslands on Selaön, Sweden.*

	Plot size		
Species	*large (24 plots)*	*medium (20 plots)*	*small (13 plots)*
Camponotus ligniperda (Latr. 1802)	0	5	15
Formica exsecta Nyl. 1846	4	20	0
Formica fusca L. 1758	83	45	100
Formica polyctena Först. 1850	29	35	31
Formica pratensis Retz. 1783	17	10	0
Formica pressilabris Nyl. 1846	4	0	0
Formica rufa L. 1761	13	40	31
Formica rufibarbis Fabr. 1793	25	25	15
Formica sanguinea Latr. 1798	4	20	0
Formicoxenus nitidulus (Nyl. 1846)	0	0	8
Lasius flavus (Fabr. 1781)	25	40	38
Lasius fuliginosus (Latr. 1798)	0	0	8
Lasius niger (L. 1758)	50	35	15
Lasius platythorax Seifert 1991	21	25	23
Leptothorax acervorum (Fabr. 1793)	17	5	38
Leptothorax gredleri Mayr 1855	4	0	15
Leptothorax muscorum (Nyl. 1846)	0	5	8
Myrmica lobicornis Nyl. 1846	67	75	85
Myrmica lonae Finzi 1926	4	10	8
Myrmica rubra L. 1758	4	10	15
Myrmica ruginodis Nyl. 1846	63	70	85
Myrmica scabrinodis Nyl. 1846	88	75	85
Myrmica schencki Viereck 1903	58	70	38

**The percent occurrence of the species in plots of large, medium, and small size is shown.*

Results

Remnant Size Effects on Species Richness

We found 23 ant species on the grasslands (Table 1). The assemblage of species was characterized by a wide spectrum of habitat and niche preferences, ranging from typical wood-living ants (e.g., *Formica rufa*, *Lasius platythorax*) to species typical for open grasslands (e.g., *Formica rufibarbis*) and from species preferring cool and wet habitats (e.g., *Myrmica ruginodis*) to species preferring warm and dry environments (e.g., *Myrmica schencki*). Total species richness was 19 on large and medium sites combined, and 18 on small sites. The curves of species richness obtained through the jackknife estimation showed that the estimated numbers of species resembled the numbers of species caught (Fig. 2). The curve for

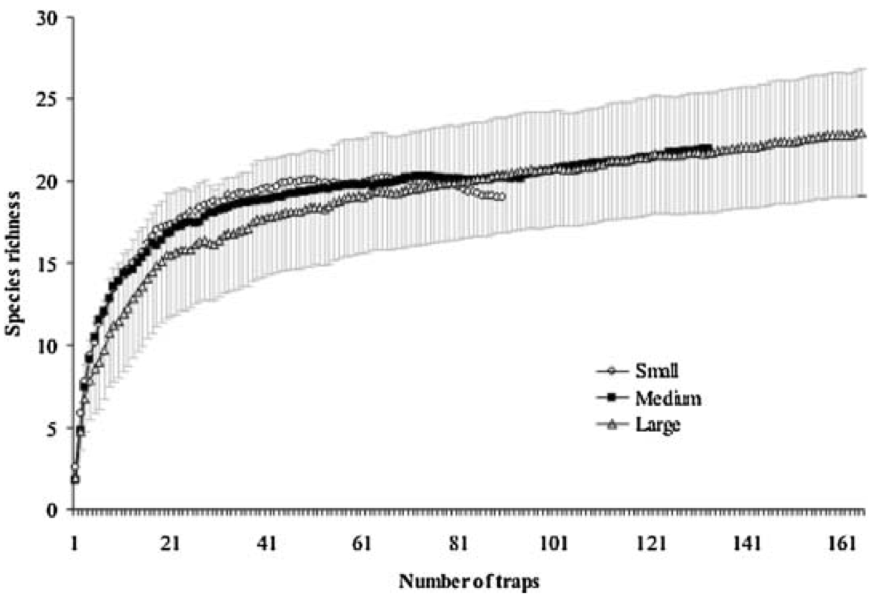

Figure 2. First-order jackknife estimation of ant species richness of the three different size classes of grasslands used to correct for variation in sampling size (number of runs = 100). Whiskers show the 95% confidence interval of the curve calculated for the large sites.

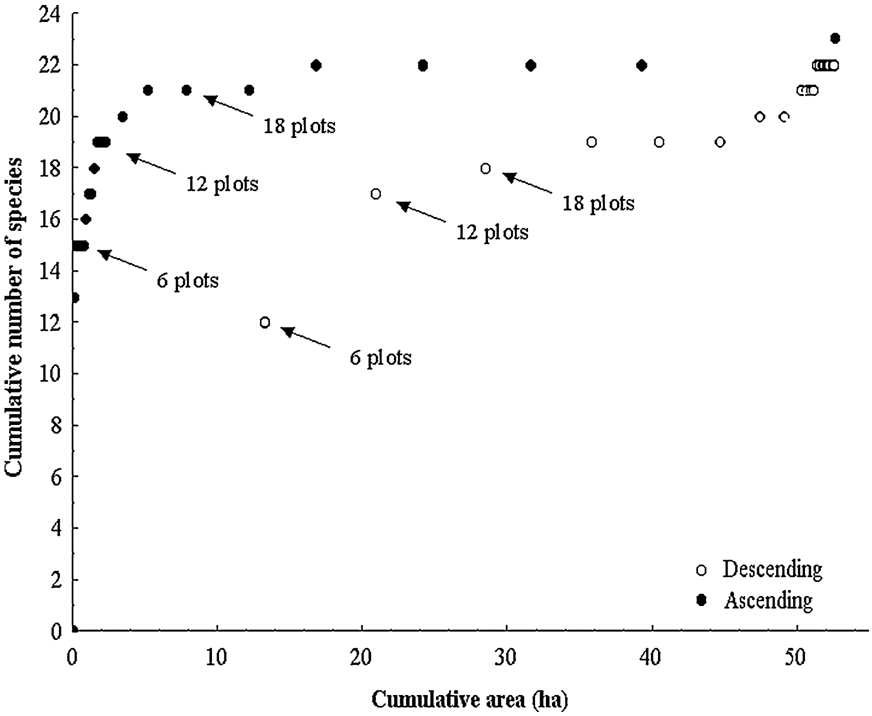

Figure 3. Cumulative species-area relationships for ants in seminatural grasslands in Selaön, Sweden, plotted against cumulative area. Study sites are ranked along the x-axis in the order of ascending (i.e., starting with the smallest areas; filled symbols) or descending area (i.e., starting with the largest areas; open symbols). The shape of the curves can be biased by the nonproportional sampling effort on the remnants of different size. Therefore, arrows indicate points on the curves with similar sampling effort (i.e., same number of sample plots).

the small sites reached saturation at around 19 species, whereas the medium and large sites had slightly higher saturation points (23 species for large sites). The confidence interval for the species richness of the large sites included both other curves, indicating that the species richness of the habitat remnants was independent of the size classes.

There was no significant relationship between species richness and habitat area (i.e., size of the single study sites in hectares) (ln$c$ = 1.78 ± 0.06 SD; $z = -0.04 \pm 0.03$ SD; $F = 1.6$; $p = 0.21$; $R^2 = 0.03$). The slope of the power function did not differ from zero. The ascending cumulative species-area curve was above the descending curve (Fig. 3). The shape of the curves (Fig. 3) may have been biased by the nonproportional sampling effort on the remnants of different size. Therefore, we also marked points on both of the curves that represent an equal sampling effort. A comparison of these points showed the same trend: a certain number of plots sampled on many small sites yielded more species than the same number of plots sampled on a few large sites (Fig. 3).

Remnant Size Effects on Species Composition

Species composition showed no obvious differentiation among the different-sized sites (Table 1). About half the species occurred regularly on all size classes, and only species with a more incidental occurrence were missing in one or two of the size classes. A comparison of the species compositions of sites of different size classes showed similarities ranging from 30 to 40% both within and between size classes (Table 2). This indicates that species composition on sites of the same size class showed the same amount of variation as species composition on sites of different size classes. Most of the single sites contained only a small subset of the total species pool of grasslands, but they were complementary so that

Table 2. Similarity (mean Jaccard indices ±SD) of ant community composition among plots in different size and location categories.

Size	*Location*	*Large all*	*Medium all*	*Small edge*	*Medium edge*	*Medium center*	*Large edge*	*Large center*
Large	all	0.38 ± 0.16						
Medium	all	0.33 ± 0.10	0.33 ± 0.11					
Small	edge	0.38 ± 0.12	0.34 ± 0.11	0.41 ± 0.09	0.40 ± 0.11	0.31 ± 0.09	0.41 ± 0.11	0.37 ± 0.14
Medium	edge				0.35 ± 0.06	0.33 ± 0.08	0.41 ± 0.09	0.34 ± 0.06
Medium	center					0.30 ± 0.05	0.29 ± 0.04	0.32 ± 0.10
Large	edge						0.49 ± 0.07	0.37 ± 0.11
Large	center							0.36 ± 0.10

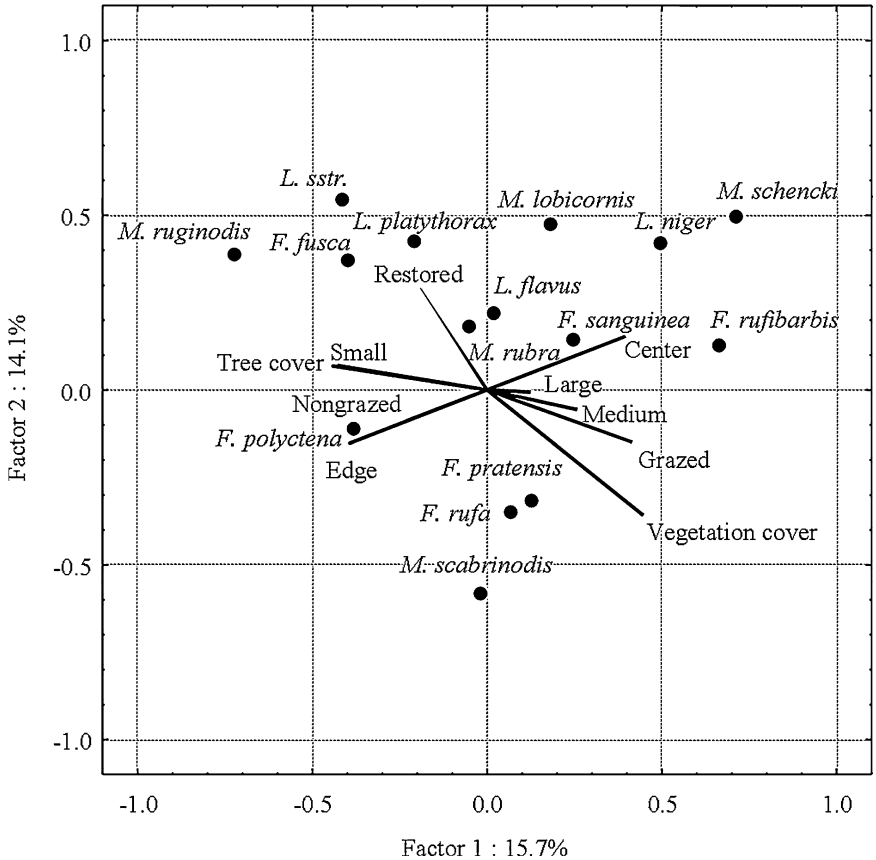

*Figure 4. Ordination diagram showing species scores from the principal component analysis (PCA) of ant species composition at the 22 study sites (*L. sstr. = Leptothorax s. str. *group). Environmental variables are represented by arrows indicating the direction of increasing values of the respective variable. The environmental parameters were added to the analysis as supplementary variables to facilitate the interpretation of the PCA results but did not influence the ordination. The first axis differentiates between forest and open landscape species. The second axis is related to vegetation cover in open grasslands. Only species occurring on more than five plots were included in the analysis.*

the size classes showed similar total species assemblages (Table 1).

In the PCA (Fig. 4), the first axis accounted for 15.7% (eigenvalue: 2.36) of the variance in ant species composition, and the second axis accounted for 14.1% (eigenvalue 2.11). Along the first axis there was a clear differentiation between thermophilous, open-landscape species (i.e., *F. rufibarbis*, *M. schencki*) and forest species (i.e., *M. ruginodis*, *Formica fusca, Leptothorax s. str.*). The ordination of species along the second axis was less pronounced. Here *Myrmica scabrinodis*, an open-landscape species that can cope with denser vegetation in grasslands, was differentiated from both open-landscape and forest species. The correlations of the environmental variables with the PC axis are given as vectors in the biplot (Fig. 4). The first axis was correlated to the tree cover, grazing, size classes, and the location of the study plots. The differentiation between the forest and the open-landscape species along this axis indicated that tree cover and grazing were the most important factors structuring the ant communities. Furthermore, the forest species showed high frequencies on restored grasslands, still reflecting the past habitat conditions.

Wood ants were a typical component of the ant communities of seminatural grasslands. Sixty-two percent of the study plots were colonized by wood ants of the subgenus *Formica s. str.* or other polydomous *Formica* species, such as *Formica sanguinea* or *F. exsecta* and *F. pressilabris*. Both wood ant species—the mainly monogynous and monodomous *F. rufa*, and the mainly polygynous and polydomous *F. polyctena*—inhabited study sites of all size classes (Table 2). In contrast, *F. pratensis* and the other polydomous *Formica* species could not be found on the small sites (Table 2).

Effects of Wood Ants on Occurrence of other Ant Species

In most cases, only one wood ant species was found in a plot. Two or three wood ant species were found together on 5 of the 57 plots. In 27 of 100 simulations, the number of plots with two or three species was 5 or less, indicating that the observed number of co-occurrences did not differ from that expected by chance (and the probability 27% showed that more simulations were not needed). Hence, in general, the occurrence of one wood ant species did not exclude the occurrence of another wood ant species. Logistic regression analyses could not reveal any significant effects of the size of the individual sites on the occurrence of wood ants of the subgenus *Formica s. str*.

The occurrence of wood ants (one or more species of the subgenus *Formica s. str.*) did not affect the occurrence of any other ant species significantly (G tests, $p > 0.05$ in the 10 cases with sufficient n values). Furthermore, species richness was unaffected by the presence or absence of wood ants (ANOVA: df = 1, $F = 2.16$, $p = 0.14$).

Edge Effects

Edge effects were tested for two different spatial scales: First, we tested—in edge plots only—whether species richness and the occurrence of two generalist species (*L. niger* and *M. rubra*) within the single traps ($n = 212$) were affected by distance to the edge. There was no significant correlation between species richness and distance of the traps to the edge (Spearman: $R = 0.06$, $p = 0.4$). *L. niger* did not occur significantly more often closer to the edge (logistic regression: $\chi^2 = 11.685$, $p = 0.0006$, $-1.343 + [-0.37549]^{*}x$). Distance to the edge did not significantly affect the occurrence of *M. rubra* (logistic regression: $\chi^2 = 2.887$, $p = 0.089$, $-2.8378 + [-0.36715]^{*}x$). *M. rubra* was missing on the edge plots of the large and medium sites. However, logistic regression restricted to the small sites showed that the occurrence of *M. rubra* closer to the edge was not significant.

Second, we investigated whether ant species richness, community composition, or the frequencies of *L. niger* and *M. rubra* were different between the edge plots (n = 18) and the interior plots (n = 26) of the large and medium sites. Species richness was not significantly different between the edge plots and the interior plots (edge: 5.7 ± 2.0 SD, interior: 6.2 ± 2.0 SD; ANOVA: df = 1, $F = 0.49$, $p = 0.49$). Neither the frequency of *L. niger* (edge: 8.2 ± 11.8 SD, interior: 8.0 ± 11.0 SD; ANOVA: df = 1, $F = 0.03$, $p = 0.9$) nor of *M. rubra* (edge: 0, interior: 3.5 ± 10.7 SD; ANOVA: df = 1, $F = 1.9$, $p = 0.17$) differed significantly between the edge plots and interior plots. The comparison of the species composition of edge plots and interior plots among and between different size classes did not show considerable differences. The similarities ranged between 29 and 49% (Table 2).

Discussion

Size and Management Effects

Our results showed that seminatural grasslands with a long history of continuous management located in a heterogeneous landscape can harbor species-rich and ecologically diverse ant communities. The species we found represented about 30% of the known ant species of Sweden (Douwes 1995). Size of the grassland remnants had little effect on ant species richness. Small midfield islets contained as many and sometimes even more species than large grassland patches. This result is in accordance with the finding of Cousins and Eriksson (2002) that small patches with a long management continuity may have equal or higher plant species richness than large patches of the same management continuity. Punttila et al. (1994) found that the number of wood ant species in larger forest fragments tends to be lower than in smaller fragments. However, our finding that patch size had no effect on species richness is in contrast to the inferences of most habitat fragmentation experiments in general (Debinski & Holt 2000) and for ants in particular (Golden & Crist 2000; Braschler & Baur 2003). This discrepancy might primarily be due to the fact that in these studies habitat patches were created that were much smaller than in our study sites.

If higher extinction rates on small remnants were important, this would cause changes in the similarity of species composition between small sites and larger sites. Both random extinction and random recolonization from the matrix with first colonizers dominating the community (Elmes et al. 1998) should lead to reduced similarity between individual small sites and between small and larger sites. In contrast to this expectation, our results showed that species richness and composition were comparable between small and large remnants, and similarities among small sites were as high as among larger sites. Therefore, continuity and predictability of a habitat might be seen as a driver of local species richness that counteracts the drivers of the species-area relationship (i.e., increased extinction risk on small islands and increased isolation). Vulnerable species of land snails can be supported on small forest islands of areas from 0.5 to 5 ha if the islands have a long continuity as forest habitats (Bengtsson et al. 1995).

Cousins et al. (2003) suggest that high plant species richness on small patches like midfield islets could be explained by grassland plant species persisting on these patches because the isolation of midfield islets within arable fields inhibits secondary-successional species from colonizing. This explanation does not hold for the species-rich assemblages of ants on small midfield islets observed in our study because the secondary-successional ant species would be forest species, and they were equally present on small and larger sites. The composition of the subset of species on a site was not defined by the vulnerability of certain species to habitat fragmentation (i.e., fragment size) as proposed by the concept of nested species assemblages (Ganzhorn & Eisenbeiß 2001), but by the habitat and niche preferences of the species.

The small midfield islets in our study were inhabited by subsets of the total species pool that were comparable to the subsets found on the larger sites. This indicates that dispersal between sites is not a big problem in our landscape. An alternative explanation might be that as a consequence of long-term fragmentation species sensitive to fragmentation have already been lost from even the large remnants. We cannot fully discount this alternative because data from large and contiguous grasslands are missing and sensitivity of ant species to fragmentation is not well studied. Plant species richness of seminatural grasslands in Sweden is not related to present-day landscape configuration but is a legacy of habitat connectivity occurring 50–100 years ago (Lindborg & Eriksson 2004). We expect that ants as long-lived "organisms" also show a time lag between the onset of landscape change and response to fragmentation. Many ant species respond slowly when habitats are abandoned and undergo succession (Steiner & Schlick-Steiner 2002). However, we recorded most of the known Swedish ant species with preferences for mesic grasslands and semiopen habitats in the remnants. The majority of the remaining 70% of species prefer very different types of habitats, are very rare, or simply do not occur in the study region (Douwes 1995; Seifert 1996).

The PCA showed that the species composition on the different plots was best explained by the environmental differences between the study plots. Also, the cumulative-species-area curve (Fig. 3) indicated that several small sites had more species at an intermediate total area than a few large remnants of the same total cumulative area. Different organisms have different requirements (e.g., food resources); thus, habitat heterogeneity is likely to be associated with higher biodiversity in the agricultural landscape (Benton et al. 2003). In our study, past and present land use and tree and vegetation cover were important factors explaining variation in ant species composition. This corroborates the results of Morrison (1998), who compared insular ant populations on small Bahamian cays and found plant species richness and not island area was the best single predictor of ant species richness.

Wood Ants as a Structuring Force of Ant Communities

We found no effects of wood ants on the frequency or abundance of other ant species or on community composition. This is not in agreement with other studies. Punttila (1996) showed that young forests with an open canopy are colonized by territorial ant species such as *F. sanguinea* and *F. exsecta*. Territorial ant species, and encounterers such as *Camponotus* spp. and *L. niger*, are aggressive and are expected to exclude each other (Savolainen et al. 1989). However, submissive species, such as *F. fusca*, *L. acervorum,* and *Myrmica* species, may co-occur with stronger species, but their activity density may be depressed (Vepsäläinen & Savolainen 1990; Punttila et al. 1996). Most studies on competition, interference, and coexistence among different ant species have been carried out in taiga forest habitats. The larger number of coexisting ant species in our study site might indicate that the vegetation structure on Selaön is more heterogeneous than, for example, in the taiga biome and thus can harbor a larger array of ant species.

Edge Effects

In a landscape context, the species-area relationship can be clouded by "spillover" into habitat patches from the surrounding matrix (Cook et al. 2002). Small habitat islands might be equally or more species rich because matrix species invade the habitat and keep species richness high (Ås 1999; Gibb & Hochuli 2002). We found no significant differences between edge plots and center plots in either ant species richness or in the frequency of individual ant species. Only the generalist *L. niger* showed higher occurrence in edge-plot traps positioned closer to the infields. Similarity of species composition did not differ between or among edge and center plots. Therefore, we found no influence of the surrounding landscape matrix on the grasslands studied, which is, for example, in contrast to ant communities in forest fragments in Brazil (Schoereder et al. 2004).

One important reason for the lack of a spillover effect from the matrix is that the infields are situated in a matrix of species-poor habitats subject to agricultural practices, such as tilling, in most years. Species composition of the matrix is only slightly overlapping with that of the grassland remnants. In wheat, rape, and ley fields on Selaön only five ant species (*Lasius niger*, *L. flavus*, *Myrmica scabrinodis*, *Formica polyctena*, and *F. pratensis*) were found (L. L., unpublished data). From these, only the *Lasius*-species and *M. scabrinodis* were able to establish nests in arable land. The *Formica* species only entered the fields for foraging. Wood ants can be found in arable fields at 100 m from their nests, but the number of ants declines dramatically with distance to the nest (K. J. Pålsson, unpublished data). Four ant species (i.e., *M. rubra*, *M. ruginodis*, *L. niger*, and *L. flavus*) were recorded in wheat fields, and four additional species (i.e., *M. schencki*, *M. scabrinodis*, *M. sabuleti*, and *Formica cunicularia*) were recorded in intensively managed grasslands in Lower Saxony, Germany (J.D., unpublished data).

Implications for Conservation

Intensification and abandonment of agricultural practices have drastically altered farmland landscapes in Europe, and many noncrop habitats have become increasingly fragmented. Habitat loss is a serious threat to many of the rare or declining animal and plant species in Europe (Fuller 1987; Pain & Pienkowski 1997). Therefore, all over northern Europe today there is considerable interest in the conservation of various types of traditional farmland habitats and their characteristic flora and fauna.

One of the major goals is to ensure the survival and restoration of the remaining areas of traditional farmland and seminatural grasslands because these grasslands harbor a diverse flora and fauna as a result of mowing and grazing over a long period (Hallanaro & Pylvänäinen 2001). One important question when considering conservation or restoration of these grasslands concerns the ecological role of small remnants as a refuge for species dependent on these habitats and as a source population for grasslands under restoration.

Our results showed that the small grassland remnants were species rich and did not harbor a nested subset of the ant species of larger habitats. This might be due to the dispersal capabilities of the ants being sufficient enough so that the habitat fragments in the study landscape were not isolated from each other (Duelli et al. 1989; Mabelis 1994). When comparing the same total area, many small patches together showed higher species richness than a few large patches, due to the higher heterogeneity of environmental conditions. An important driver of habitat degradation of seminatural grasslands is the abandonment of traditional land use and the encroachment of trees. A few trees on the grasslands maintain their ecotone characteristics and thereby high species richness, but too many trees lead to a shift toward species-poor woodland ant communities.

Our results highlight the importance of considering land-use continuity and dispersal ability of the focal organisms when examining the effects of habitat loss and fragmentation on biodiversity. A general implication for conservation is that current spatial patterns of biodiversity are often a legacy of historical landscape patterns, and our results suggest that conservation programs focusing on land-use change should consider the history of a landscape.

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