ORIGINAL ARTICLE

Landscape heterogeneity at multiple spatial scales enhances spider species richness in an agricultural landscape

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Abstract Landscape supplementation, which enhances densities of organisms by combination of different landscape elements, is likely common in heterogeneous landscapes, but its prevalence and effects on species richness have been little explored. Using grassland-dwelling spiders in an agricultural landscape, we postulated that richness and abundances of major constituent species are both highest in intermediate mixtures of forests and paddy fields, and that this effect derives from multi-scale landscape heterogeneity. We collected spiders in 35 grasslands in an agricultural landscape in Japan and determined how species richness and abundances of major species related to local and landscape factors across different spatial scales. We used a generalized linear model to fit data, created all possible combinations of variables at 15 spatial scales, and then explored the best models using Akaike's information criterion. Species richness showed a hump-shaped pattern in relation to surrounding forest cover, and the spatial scale determining this relationship was a 300–500-m radius around the study sites. Local variables were of minor importance for species richness. Abundances of major species also exhibited a hump-shaped pattern when plotted against forest cover. Thus, a combination of paddy fields and forests is important for enhancement of grassland spider species richness and abundance, suggesting habitat supplementation. The effective spatial scales determining abundances varied, ranging from 200 to >1000 m, probably representing different dispersal abilities. Landscape compositional heterogeneity at multiple spatial scales may be thus crucial for the maintenance of species diversity.

Keywords Fractal-like landscape · Grassland · Landscape complementation · Landscape supplementation · Mosaic structure · Satoyama

Introduction

Spatial heterogeneity influences biodiversity in terrestrial ecosystems (e.g., Fahrig 2003). Over spatial scales, species richness of local communities is often determined by both landscape- and site-level factors (e.g., Holland et al. 2004; Bennett et al. 2006). There are two mechanisms whereby local species richness at the landscape scale may be enhanced, namely, by spill-over or mass effects from different habitats (e.g., Kunin 1998; Tscharntke et al. 2005) or by the addition of new species to the focal habitat through landscape complementation or supplementation (e.g., Dunning et al. 1992; Kato et al. 2010). Processes of landscape complementation and supplementation occur when organisms require different habitats for the provision of non-substitutable and substitutable resources, respectively. These are regarded as processes that emerge only when two landscape elements combine (Bennett et al. 2006; Fahrig et al. 2011). Although a combination of different habitats is not essential for landscape supplementation, the probability of organisms occurring at a local site should increase as a result of elevated population densities so that landscape supplementation will contribute to enhanced species richness.

Although landscape complementation or supplementation is thought to be common, most of the earlier studies

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did not explicitly demonstrate that this effect enhances species richness, because high species richness at local sites surrounded by a mixture of different landscape elements may result from an assemblage of species that prefer either of the two habitat types (Fig. 1a). One way of exploring the importance of habitat complementation/supplementation is to determine whether each species responds to the gradient of landscape mixtures surrounding a given habitat. If species richness peaks in a landscape with an intermediate mixture of different landscape elements, and most species have corresponding abundance patterns, it is likely that heterogeneity per se increases species richness through landscape complementation or supplementation (Fig. 1b).

Spiders in agricultural landscapes are ideal model organisms for testing this concept because they are known to respond to spatial heterogeneity in landscapes that include crop fields, fallow lands, and woodlots (Schmidt et al. 2005; Schmidt and Tscharntke 2005; Öberg et al. 2007; Batáry et al. 2008; Drapela et al. 2008; Pluess et al. 2010). This spider assemblage includes species that differ in responses to landscape compositions (Schmidt et al. 2008). Almost all studies have demonstrated that spiders respond to non-crop habitats positively and have concluded that habitat heterogeneity is important. However, a monotonic positive response does not necessarily imply that habitat heterogeneity has a role, but may indicate simply that non-crop habitats enhance species richness.

Here, we focus on spider communities inhabiting grasslands distributed sparsely across a traditional "satoyama" agricultural landscape in Japan. The satoyama landscape is composed of habitat mosaics, including paddy fields, grasslands, secondary forests, and farm ponds that are rich in biodiversity (Washitani 2001; Kobori and Primack 2003). For centuries, grasslands were maintained by burning or mowing (Washitani 2001), but abandonment of this form of management over the past century has

decreased the grassland area in Japan by 90 % (Ministry of Agriculture, Forestry and Fisheries 2005). Concomitant with this decrease, many species of plants and butterflies that were once widespread have become endangered (Takahashi 2002). As most of these grasslands are located near paddy fields and these two habitats are structurally similar, grasslands are thought to function as refuges or source habitats for predators of rice plant pests (Murata 1999). Therefore, exploring factors that determine spider species richness and abundance in this habitat will likely contribute to the conservation of ecosystem services in satoyama landscapes.

Our study area was located in a typical satoyama landscape in Japan composed mostly of paddy fields and forests. Paddy fields appear to be sink habitats for most grassland spider species because rice plants are present only from May to September and the fields are almost bare in other seasons. However, during the growing season, paddy fields may function as substitutable habitats for grassland spiders (Murata 1999). Likewise, the forest margin is expected to provide complemental habitats for grassland spiders by providing refuges or by supplementation of prey insects. Accordingly, we postulated that richness and abundances of major constituent species are both highest in intermediate mixtures of forests and paddy fields. Furthermore, because different species likely have different dispersal abilities, we postulated that spider species respond to landscape heterogeneity at different spatial scales.

Methods

Study area

Field surveys were conducted on Sado Island (38°N, 132°E; altitude 50–300 m) in central Japan. The survey

Fig. 1 Two cases where local species richness exhibits a hump-shaped pattern along the gradient of mixture of two landscape elements. *Solid* and *broken lines* indicate species richness and abundance of spiders, respectively. **a** Assemblage of species preferring either of the two habitat types. **b** Assemblage of species preferring heterogeneous landscape per se
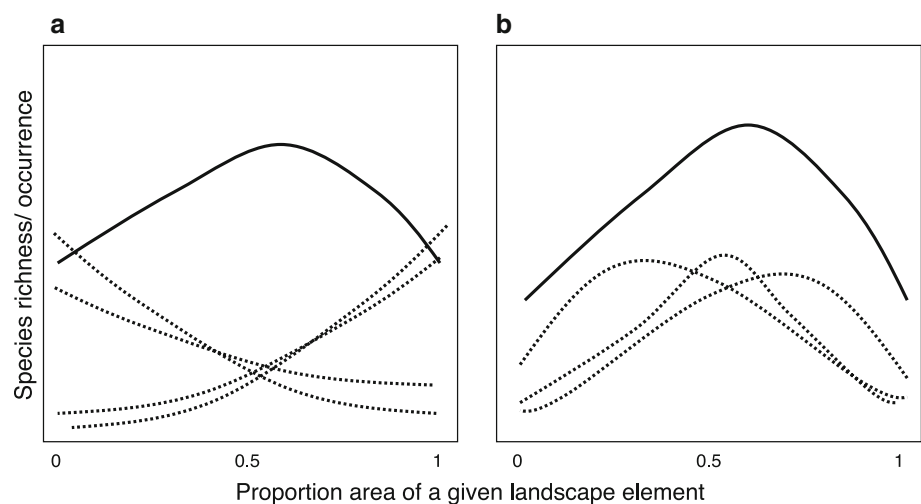
covered approximately 200 km^2, and the landscape elements were mostly paddy fields (40 %) and forests (50 %), ranging from forest-dominated hills to rice-dominated plains along an east to west axis (see Kato et al. 2010 for the landscape). The forest tree species included native deciduous hardwoods (such as *Quercus serrata* Murray, *Carpinus tschonoskii* Maxim., *Acer* spp.) mixed with patchy plantations of Japanese cedar (*Cryptomeria japonica* D. Don). We selected 35 grasslands located near rice fields and with varying degrees of surrounding forest cover (0–98 % within a 500-m radius). The distance between grassland sites ranged between 0.7 and 21.8 km (mean 8.0 km, SD 3.8 km). These grasslands were scattered in the landscape and largely maintained by mowing once or twice a year. Most of the grasslands were long (>20 m), narrow (2–3 m) strips whose patch boundaries were difficult to discern. No herbicides and insecticides were applied to these tracts of land. Species compositions of grasslands were variable, with mixed herbs (*Artemisia indica* H.Hara, *Vicia sativa* Ehrh., *Erigeron philadelphicus* Pers.), grasses (*Miscanthus sinensis* Andersson, *Imperata cylindrica* P.Beauv.), and ferns (*Equisetum arvense* L.).

Sampling

We collected spiders at each site in mid-May 2009 using insect sweep nets (40 cm in diameter). The middle of May is a good time of year in central Japan for examining spider species composition (Miyashita and Takada 2007). We made 50 sweeps at each site, and spiders collected were immediately preserved in bottles with 70 % ethanol. We recorded the coverages of dicotyledons, graminoids, and ferns, and vegetation heights at 10 points at each site; these data were used as local environmental variables. Because samplings were conducted before first mowing, there was likely little anthropogenic disturbance of spider communities immediately prior to collection.

GIS analysis

Landscape variables were explored using a geographic information system (GIS; ArcGIS9.3 ESRI) and a digital vegetation map downloaded from the Japan Integrated Biodiversity Information System (J-IBIS; http://www.biodic.go.jp/J-IBIS.html; Ministry of the Environment, Japan). As nearly 90 % of the landscape in this region consists of forest and paddy fields, we used percent forest cover and percent of grassland cover as landscape variables to avoid multicollinearity. We also calculated forest edge length as a measure of landscape configuration as complexity of boundaries may affect habitat suitability of spiders. To discern appropriate spatial scales of landscape factors affecting the richness or abundance of target species, we generated differently sized circular buffers around each site, ranging from 50 and 100 m to 1500 m at 100-m intervals, and extracted landscape variables for 16 spatial scales. We set 1500 m as the maximum spatial scale to minimize overlaps of buffer circles between sites. More than 90 % (32 out of 35 sites) of buffers with a 1500-m radius were non-overlapping.

Statistical analysis

We examined factors affecting species richness and abundance of spiders using a generalized linear model with either a Poisson error distribution or a negative binomial error distribution, depending on the degree of overdispersion of dependent variables. The independent variables (Table 1) were classified into local and landscape categories depending on differences in spatial scales. Four variables were used to represent the local level: altitude, mean vegetation height, and the first and second principle components (PC) of plant functional compositions calculated from the coverage of grasses, herbs, and ferns. The component loadings of PC1 for grasses, herbs, and ferns were 0.903, −0.996, and 0.317, respectively, and those of PC2 were 0.429, 0.09, and −0.948, respectively. Patch sizes of the grasslands were not used, as it was impossible to discern patch boundaries due to the extremely long strip-shape of this element of terrain.

We used four landscape variables for the analyses: percent forest cover (forest cover)^2 percent of grassland cover, and the residual of forest edge length. The residual of forest edge length was calculated by regressing forest edge length against forest cover with a second-order polynomial equation, as forest area and its perimeter is interrelated in a convex manner. Both forest cover and forest edge length were centered on mean values for computational convenience.

An information theoretic approach based on Akaike's information criterion (AIC; Burnham and Anderson 2002) was used to select the generalized linear model that best explained species richness and abundances of spiders. This approach is superior to traditional stepwise procedures because it accounts for uncertainties concerning model structure and parameter estimation when there are several competing models with respect to their performance on the observed dataset (Whittingham et al. 2006). To identify environmental factors and spatial scales affecting species richness and abundances, we calculated ΔAIC (ΔAIC = AIC − AIC$_{lowest}$) for all possible models at all spatial scales (64 combinations of independent variables × 16 spatial scales). According to Burnham and Anderson (2002), we employed the following criteria for determining the performance of a particular model relative to the best model, i.e., ΔAIC <2: substantial support, AIC <7:

Table 1 Independent variables used in generalized linear models to explain species richness and abundance of spiders in grasslands

Variable name	Description	Mean	Max	Min	SE (n = 35)
Local-level					
Altitude	In meter	139.8	500.6	4.9	21.4
Vegetation height	In centimeter	47.5	66.0	23.0	1.5
Vegetation PC1	Coverages of grasses, herbs and ferns	5.10	16.20	−3.26	0.93
Vegetation PC2	Coverages of grasses, herbs and ferns	−1.01	2.06	−7.24	0.35
Landscape level					
Grassland cover	In proportion within a buffer circle (50–1500 m), only values at 500 m-radius shown	0.11	0.22	0.00	0.01
Forest cover	In proportion within a buffer circle (50–1500 m), only values at 500 m-radius shown	0.49	1.00	0.00	0.06
(Forest cover)^2	In proportion within a buffer circle (50–1500 m), only values at 500 m-radius shown	0.35	1.00	0.00	0.06
Residual of forest edge	In meters, residuals from the regression of forest edge against forest cover	0	1941	−2895	144

considerably less support, ΔAIC >10: essentially none. Because models with ΔAIC <2 are considered to be competitors with similar performance, no single best model may be chosen in such circumstances. We therefore calculated Akaike weights (w_i), which represent the probability that model i is the best model in the set of models considered (Burnham and Anderson 2002). To determine which variable was more important, we computed the weighted average of z values (Z_i) for each variable i using Akaike weights,

$$Z_i = \Sigma w_{ij} Z_{ij},$$

where w_{ij} is the Akaike weight of variable i in model j, and Z_{ij} is the corresponding z value (estimate/SE). When variable i was not included in model j, the estimate (regression coefficient) was set to zero. Variables with z values >2 were considered to be influential in the model (Burnham and Anderson 2002).

To examine the influence of spatial autocorrelation on species richness and abundances of spiders, we calculated Moran's I using residuals of each dependent variable from the best model having the lowest AIC. Moran's I was calculated for 15 distance classes (1000-m interval, up to 15000 m). Statistical significance was tested after Holm's sequential Bonferroni adjustment, with 15 comparisons.

All statistical procedures were performed with the R-2.6.2 statistical software package (R Development Core Team 2005).

Results

We collected 800 individuals of spiders by sweeping and identified 530 to the species level [Table S1 in Electronic

Supplementary Material (ESM)]. Using Chikuni's (1989) description of main habitat types for each spider species, we categorized 42 species as grassland or open habitat dwellers, and 17 species as forest margin or shrub dwellers.

Analysis of species richness demonstrated that ΔAIC value of the null model was 9.67, indicating little support for the null model relative to the best model. All the competing models included forest cover and its squared term (Table S2 in ESM), and z values of these were both >2 (Fig. 2), implying that they were influential in determining species richness of spiders. Furthermore, the coefficient of the squared term was negative, indicating a hump-shaped fit to forest cover (Fig. 3a). Because forest cover was centered at the mean value, models with negative coefficients of linear and squared terms imply a hump-shaped pattern with a center at <50 % forest cover, while those with positive coefficients of the linear term and negative coefficients of the squared term imply a hump-shaped pattern with a center at >50 % forest cover. Local variables had much smaller z values and were of minor importance (Fig. 2). The spatial scale that influenced species richness was 300–600 m, as indicated by the ΔAIC values of competing models (Fig. 4a).

We analyzed abundance patterns of eight species with >20 individuals captured across all study sites. For all species other than *Tetragnatha squamata* Karsch, the best model showed a considerably higher performance than the null model, as ΔAIC values were clearly larger than 4 (Table S2 in ESM). Landscape variables were generally more important than local variables for the abundance of each species (Fig. 2). Concerning the forest cover, six species had average z values larger than or close to 2 in forest cover and its squared term (Fig. 2); this produced a hump-shaped pattern when abundance was plotted against
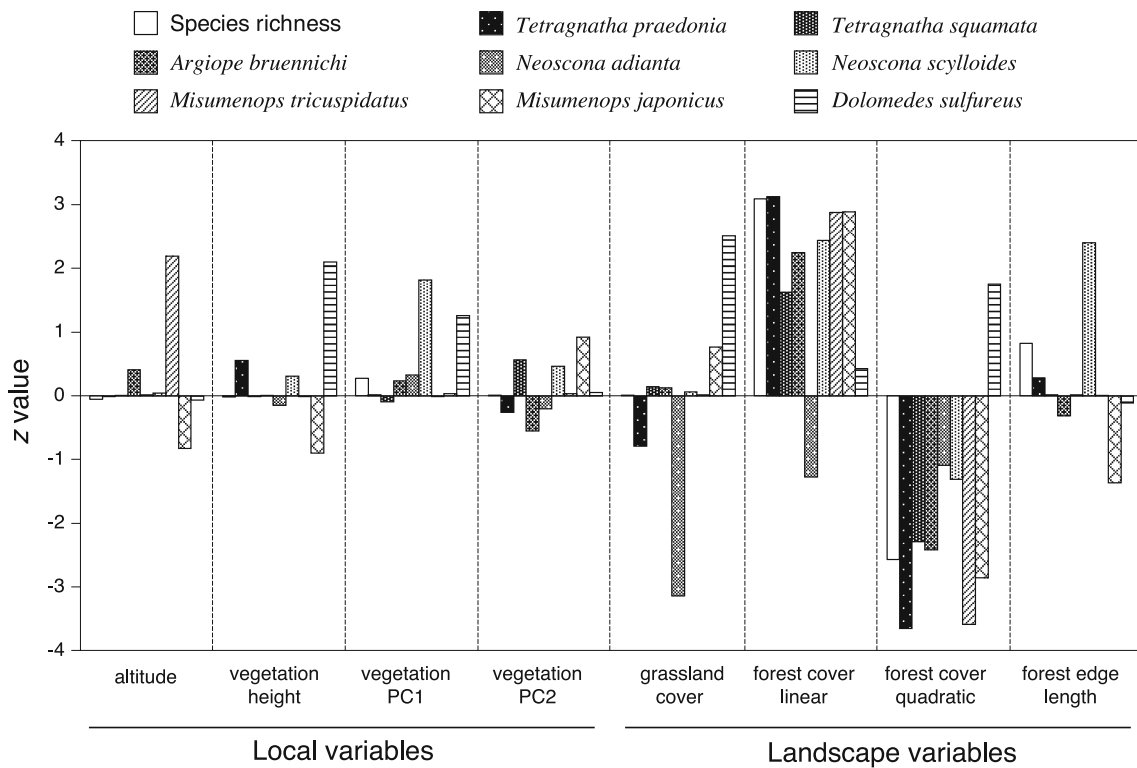
Fig. 2 The z value weighted by Akaike weight for each variable used for analysis. Absolute values >2 indicate strong effects of those variables
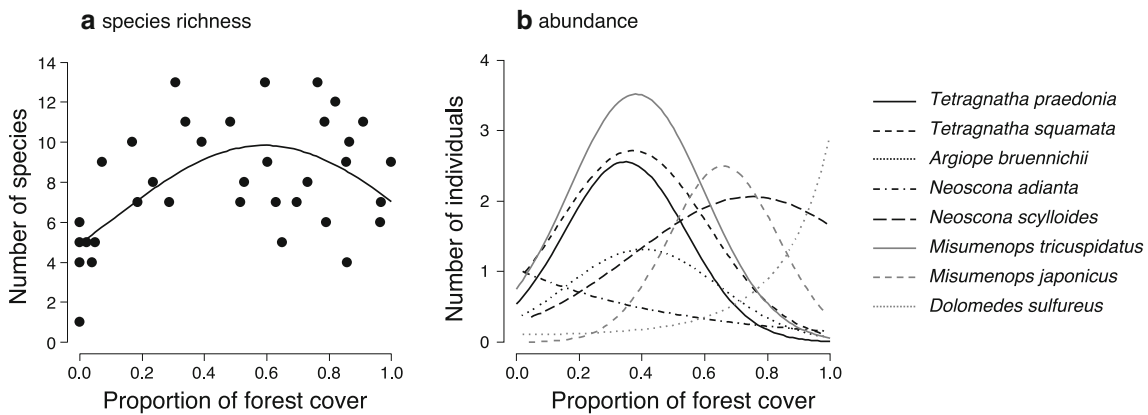
Fig. 3 Species richness of spiders (**a**) and abundance of each spider species (**b**) in grasslands along the gradient of forest cover. *Dots* in **a** represent study sites, and *lines* in **a** and **b** represent regression curves

forest cover (Fig. 3b). For the remaining two species, *Neoscona adianta* Walckenaer showed a week negative response to forest cover, while *Dolomedes sulfureus* L.Koch showed an acceleratingly increasing response to forest cover (Fig. 3b). Grassland area in surrounding landscapes was important for only two species, with *N. adianta* being less abundant and *D. sulfureus* more abundant in sites with high grassland cover. Some local variables were important for these species, as indicated by the positive z values in altitude for *Misumenops tricuspidatus* Fabricius and in grass height for *D. sulfureus*.

The spatial scales that influenced the abundances of spiders differed among species. *Argiope bruennichi* Scopoli, *Neoscona adianta, N. scylloides* Bos. et Str. and *Misumenops japonicus* Bos. et Str. had smallest ΔAIC values at around 500 m or less buffer radius (Fig. 4d–f, h). *Misumenops tricuspidatus* had the smallest ΔAIC values larger than the above species, at the range of 600–1000 m (Fig. 4g). Finally, two *Tetragnatha* species and *Dolomedes sulfureus* had the smallest ΔAIC values at more than 600 m but did not exhibit clear spatial scales (Fig. 4b, c). These results suggest that the effective spatial scales determining
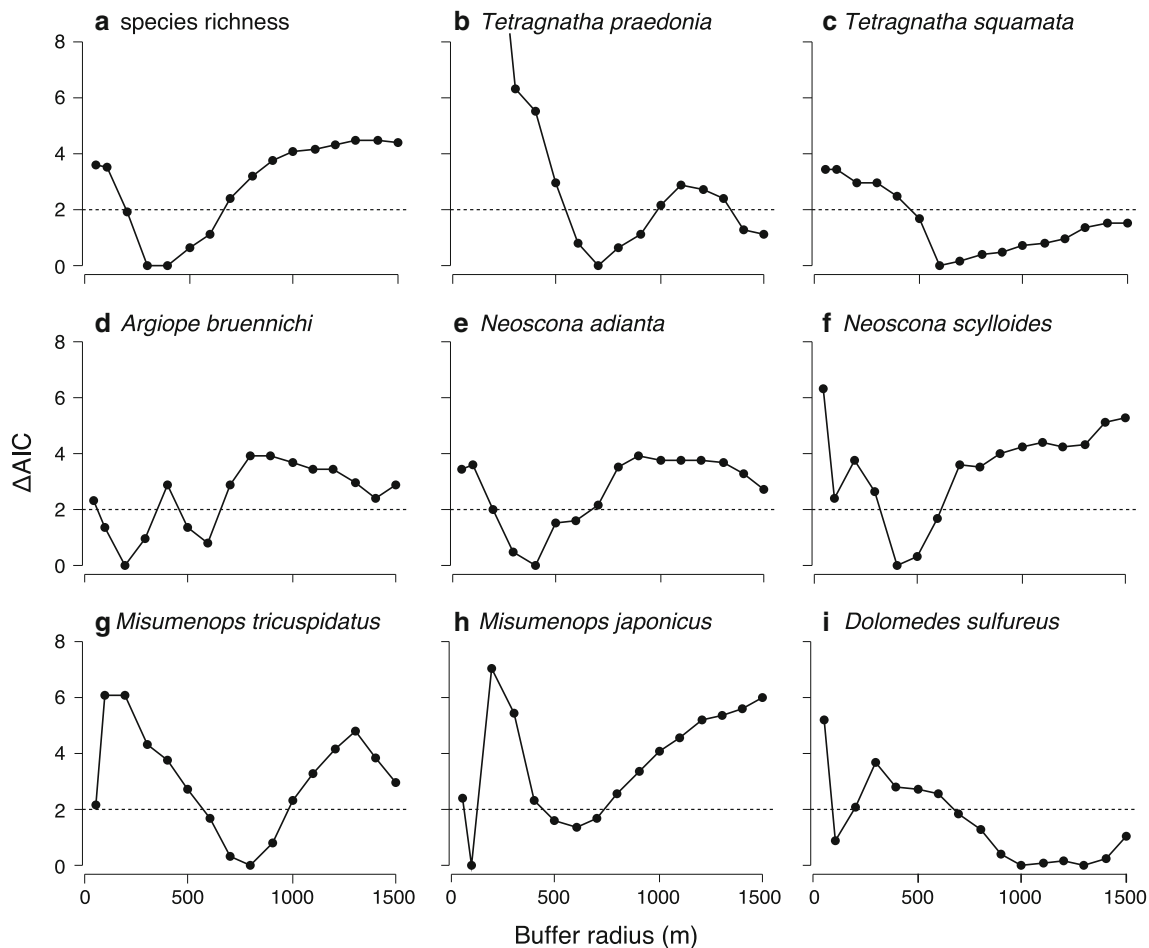
Fig. 4 The ΔAIC value of the best model in response to the change in buffer radius (spatial scale). *Broken lines* indicate ΔAIC = 2. Models with ΔAIC <2 indicate competing models

the abundances of spiders differ among species in both magnitude and sensitivity.

None of the spatial autocorrelations estimated by Moran's I was significant for either species richness or abundance [except for a distance class of 600–700 m in *Neoscona scylloides* (adjusted $P = 0.045$) and that of 12000–13000 m in *Misumenops japonicas* (adjusted $P = 0.015$)]. Thus, spatial autocorrelation had little effect on the patterns described.

Discussion

Species richness of spiders in grasslands exhibited a hump-shaped pattern with respect to percent forest cover in surrounding landscapes. This finding was statistically robust because (1) all competing models included both forest cover and (forest cover)^2, and the coefficients of the squared terms were negative, and (2) model-averaged z values of the both terms were >2. Moreover, local factors

were not important in explaining species richness. Thus, spider species richness in grasslands was mostly determined by landscape factors, and landscapes with intermediate mixtures of forest and paddy fields were most species rich. Earlier works demonstrated that the extent of non-crop habitats, such as fallow fields and woodlots, was an important predictor of spider species richness in arable landscapes (Schmidt et al. 2005, 2008; Öberg et al. 2007; Drapela et al. 2008; Pluess et al. 2010). Although these previous studies did not statistically test non-linear responses to the availability of non-crop habitats, inspection of their graphs leads us to conclude that the patterns were indeed monotonic rather than convex. We examined grassland spider assemblages while previous works studied spiders in heavily managed arable fields. This difference may explain the disparities in the responses to non-crop habitats. Although the grasslands in our study system were periodically mown, they were present year-round and relatively stable in comparison to arable fields. Hence, the arable fields examined in earlier studies provided sink or

ephemeral habitats for most spiders, and spillover effects from surrounding habitats may have been dominant influences. The grasslands we studied were probably not merely sink habitats for most spider species, as demonstrated by the fact that more than 70 % of species sampled were grassland-dwellers.

When looking at the abundance response of each species, 6 of 8 species analyzed had highest abundances in landscapes with intermediate levels of forest cover in surrounding landscapes. As with species richness, this finding is statistically robust because (1) almost all competing models included both forest cover and (forest cover)^2, (2) model-averaged z values were >2 or $\sim$2, and (3) local factors were rarely included in competing models. Thus, a combination of paddy fields and forests is important for these species, strongly suggesting an effect of habitat supplementation. Although we were able to analyze abundance distributions for only a small fraction of species, habitat supplementation contributed, at least in part, to high species richness in landscapes with intermediate levels of forest cover. Importantly, a large proportion of the spiders collected were grassland-inhabiting species, which suggests at least two mechanisms underlying habitat supplementation. First, the forest margins may serve as refuges when the grasslands are disturbed by periodic mowing. This mechanism was suggested for arable-land spiders in Europe (Schmidt and Tscharntke 2005; Drapela et al. 2008; Pluess et al. 2010). However, this postulate does not explain why spiders were less abundant in landscapes with high levels of forest cover in the surroundings we examined. Second, prey subsidies from adjacent forests and paddy fields might increase or stabilize food supplies for grassland spiders, thereby enhancing their population densities (Bianchi et al. 2006). Indeed, some insect taxa, such as chironomids and leafhoppers are temporarily very abundant in paddy fields (Kajimura et al. 1995; Settle et al. 1996), while insects from forest edges or brush are more diverse in taxa and phenology (Shimazaki and Miyashita 2005) and their populations are relatively stable over time. Furthermore, prey insects themselves may have increased in abundance through resource subsidization or provision of alternative food. Food web analysis including spiders and their prey insects across grasslands, forests, and paddy fields will determine whether this is a plausible set of explanations.

In addition to forest cover, forest edge length was an important landscape variable determining the abundance of *Neoscona scylloides*. Importantly, this was the only species (among the eight we analyzed) for which the forest margin is the major habitat (Chikuni 1989); this spider is the only one that makes webs between tree branches. Spill-over from such forest margin habitats may have enhanced the abundance of this species in adjacent grasslands.

We also found that spatial scales matter for determining species richness and abundance for most spider species. For species richness, a radius of 300–600 m was most effective, while very small (<100 m) and large (>1000 m) scales had little effect. The effective scale size we identified was largely consistent with those reported in some previous studies (Drapela et al. 2008; Pluess et al. 2010), but smaller than that reported by Schmidt et al. (2008). Concordance among studies is intriguing because, despite large differences among geographic regions (Europe, Israel, and Japan) and taxonomic identities, the spiders responded similarly to spatial scales in agricultural landscapes. Spider abundance responses fell into three groups differentiated by spatial scale. The first group responded to a small spatial scale of <600 m (*Argiope bruennichi, Neoscona adianta, N. scylloides* and *Misumenops japonicus*), the second group responded to an intermediate spatial scale of around 600–1000 m (*Misumenops tricuspidatus*), and the third group responded to radii of more than 600 m (two *Tetragnatha* species and *Dolomedes sulfureus*). As speculated in earlier studies, these differences may reflect differences in dispersal ability among spider species; the first group has relatively low dispersal ability while the third group could probably disperse beyond 1500 m. However, it is important to note that the spatial scale does not simply reflect dispersal ability, as grasslands are not sink habitats for grassland spiders, and their populations are likely to persist without spill-over effect from surrounding habitats. Thus suitable spatial scales may imply the area necessary to sustain high density of each species. This is equivalent to the concept of niche space in spatial contexts proposed by Holt (2009).

Differences in spatial scales among species that appeared to require habitat supplementation indicates that compositional heterogeneities at multiple spatial scales may be crucial for maintaining species diversity in a given assemblage. Although such a perspective has been conceptually proposed for species richness in agricultural landscapes (Benton et al. 2003), to our knowledge, our study is the first to empirically demonstrate such a possibility. Because habitat supplementation is an emergent property derived from heterogeneous environments (Bennett et al. 2006), landscape supplementations at multiple spatial scales may be viewed as a multiple emergent-properties.

We consider two different cases in which multi-scale habitat supplementation is operational. In the first, combinations of landscape elements contributing compositional heterogeneity differ at different spatial scales. This case is readily exemplified in agricultural landscapes, e.g., forest–cropland combinations at large scales, while crop species or crop-hedge combinations at smaller scales (Benton et al. 2003; Werling and Gratton 2010). In the second case, even

Fig. 5 Comparison of suitable habitats for two types of species differing in their effective spatial scales (300 vs. 600 m buffer radius) in our study landscape. *Grey area* represents suitable habitat and *black* and *white areas* are forest and paddy fields, respectively. The suitable habitats are the grasslands having 40–60 % forest cover in a given buffer radius

300 m-radius   600 m-radius

■ Forest   □ Paddy fields   ▨ Suitable habitat
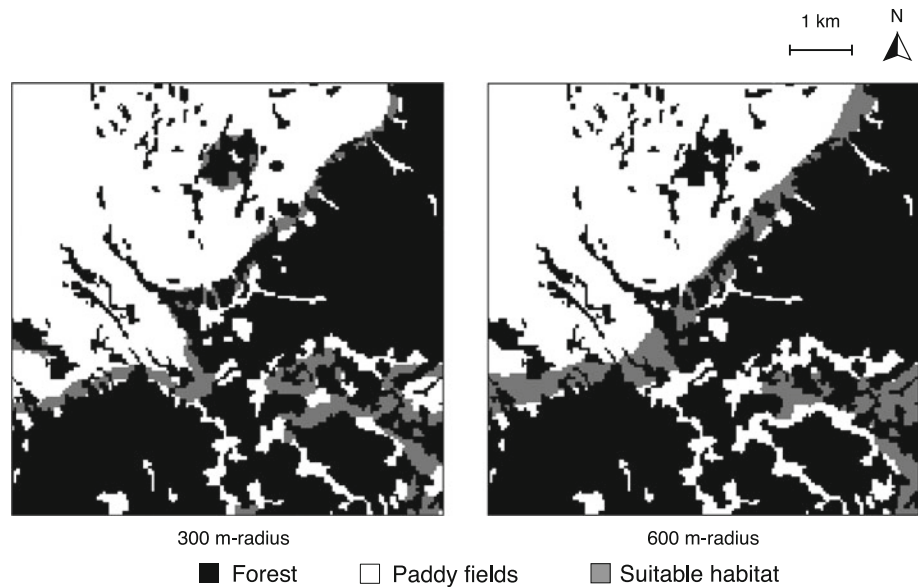
if the combinations of landscape elements do not change with scales, multi-scale habitat supplementation is important in fractal-like landscapes because it leads to segregated local distributions of species with different spatial niche scales, which could minimize competition and hence allow coexistence (Holling 1992; Peterson et al. 1998; Szabo and Meszena 2006). This is visualized by an actual complex landscape in our study area (Fig. 5). Consider two species of animals which require both rice paddies and forests to complete their life cycles. The landscape compositions suitable for the two species are the same for both species (40–60 % forest cover surrounding a focal rice paddy), but the effective spatial scales for the landscape differ between the species (A: 300 m radius from a paddy, B: 600 m radius from a paddy). The estimated distributions for the two species mapped in the landscape are somewhat segregated (Fig. 5); species A appears to occupy fine-scale mosaic structures to a greater degree than does species B, as a result of the smaller spatial scale necessary for species A. Accordingly, the fractal like landscape may promote a high beta-diversity of grassland spiders through multi-scale habitat supplementation. This postulate should be tested for future studies.

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