

## Assessment of the probability of colonization of local spider communities in an experimental landscape

Ronei Baldissera<sup>1</sup>, Everton N. L. Rodrigues<sup>2</sup> and Sandra M. Hartz<sup>1</sup>: <sup>1</sup>Programa de Pós-Graduação em Ecologia, Departamento de Ecologia, Instituto de Biociências, Universidade Federal do Rio Grande do Sul – UFRGS, Av. Bento Gonçalves, 9500, setor 4, prédio 43422, sala 102. Caixa postal 15007, CEP 91501-970, Porto Alegre, RS, Brazil. E-mail: roneibaldissera@yahoo.com.br; <sup>2</sup>Programa de Pós-Graduação em Biologia, Universidade do Vale do Rio dos Sinos – UNISINOS. Avenida Unisinos 950. Caixa postal 275, CEP 93022-000, São Leopoldo, RS, Brazil

**Abstract.** Establishment of communities is a dynamic process initiated by immigration. Therefore, movements of individuals within a metacommunity are important for maintaining and increasing species distribution. We present results of a small landscape-level experiment that manipulated habitat size and diversity. We examined the rates of colonization of spider species, and the richness, abundance and composition of foliage-dwelling spiders. Estimation of colonization rates was based on maximum likelihood. The experimental landscape was composed of five blocks with four patches (two large, 1 m<sup>2</sup>; two small, 0.25 m<sup>2</sup>). Less diverse patches had seedlings of one plant species, whereas more diverse patches had four species with diverse structures. Eight periodic censuses of spiders arriving in the patches were performed (average interval between censuses, 28 days). The initial composition of colonizers was significantly different from the final composition, but rates of colonization did not differ between sizes and diversities, or their interaction. Abundances of spiders were positively influenced by patch size. Compositions in each temporal sample were determined by differences in the species pool migrating and arriving at an experimental landscape irrespective of habitat size or diversity. Larger patches were more likely to receive more colonists representing a wider array of species than small patches. The probability of colonization was independent of patch size and diversity, which contradicts theoretical predictions. The results highlight the high colonization capacity of spiders on spatial and temporal scales.

**Keywords:** Community composition, immigration, passive sampling, temporal variation

The process of colonization includes survival and establishment, as well as immigration (Lomolino 1990). Immigration is the movement of organisms from the regional pool of species to a target habitat. It follows the phenological development of organisms in that habitat, which enhances the probability of reproduction that would establish a population of a species. Then the population growth in the local community is determined by the set of available resources and the interactions with other species. There is a limit to population growth, and individuals exceeding the limit must either die or disperse to other habitats, restarting the colonization process. Colonization is a key process in the Theory of Island Biogeography (TIB) (MacArthur & Wilson 1967), which proposes that the number of species arriving on a given island should depend on the size of the island in question, as well as on its distance from a mainland that serves as a species pool (Clark & Rosenzweig 1994). Larger islands receive more immigrants and, therefore, should show higher species richness. This is the definition of the area per se hypothesis for explaining the species-area relationship (Connor & McCoy 2001). Alternatively, the habitat diversity hypothesis postulates that larger areas may have more kinds of habitats, and hence more species, than small areas (Williams 1964; Nilsson et al. 1988). The TIB was appropriated in early years of fragmentation research to fit the patterns of richness observed in habitat islands, but ecological processes in remnants are in various ways critically influenced by direct interactions with surroundings, whereas such interactions are negligible on oceanic islands (Haila 2002). Ultimately, the matrix structure sets the pool of species that is able to act as immigrants.

In this paper, we present a small-scale landscape experiment that manipulated habitat size and diversity in a randomized

block design. Our main goal was to examine whether rates of colonization of spider species are influenced by the size and diversity of vegetation patches. To achieve this we employed a method based on maximum likelihood estimation to assess colonization rates from periodic surveys (Clark & Rosenzweig 1994). We assumed the presence of adult spiders in the patches as the final stage of a colonization event. Additionally, we assessed the patterns of abundance, richness, and composition of foliage-dwelling spider species in the vegetation patches. The experimental landscape was manipulated in such a manner that confounding variables supposed to influence the spider responses were controlled (Ewers & Didham 2006). Therefore, shape of patches, distance among patches and matrix surroundings were all held constant during the study period.

The experimental landscape was composed of five blocks with two levels of patch area: large and small; and two levels of patch diversity, more and less diverse. The comparison among these different patch treatments provides insight into the relative importance of size and diversity for spider colonization. When patch size is important independent of patch diversity, we may infer that the area per se hypothesis (Connor & McCoy 2001) is the main mechanism shaping the colonization; although the richness and abundance response to the size effect may reflect sampling artifacts like passive sampling of the regional pool of species (Schoereder et al. 2004). If patch diversity is important, independently of size, the probable important mechanism influencing colonization is habitat heterogeneity (Cramer & Willig 2005). If size and diversity both influence the colonization rates in the same direction, the increase in patch diversity is linked to increasing

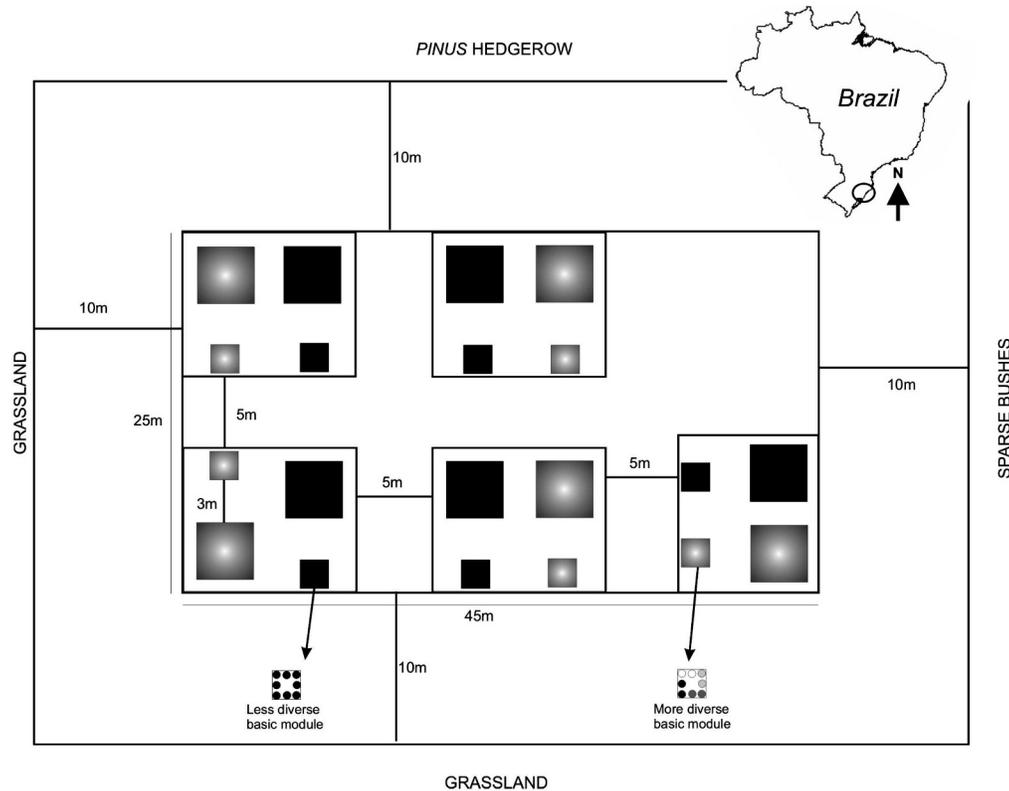


Figure 1.—Experimental landscape showing arrangements of the five blocks with the two levels of factors. Black squares = less diverse patches, shaded squares = more diverse patches. The matrix was set in a managed grassland. Factor levels were assigned randomly to each patch within a block. The less and more diverse basic modules were composed of the eight seedlings shown.

patch size. We expected an increase in colonization rates of spider species in larger and more diverse patches, based on the predictions of island biogeography theory and on the assumption that spider distribution and occurrence are strongly influenced by diversity in habitat structure (Uetz 1991; Wise 1993).

## METHODS

**Experimental design.**—We conducted the study in an area of grassland on the coastal plain of southern Brazil (29°20'06" S, 49°43'37" W) (Fig. 1). The experimental landscape consisted of ca. 1125 m<sup>2</sup> of grassland surrounded by early successional vegetation (mainly sparse bushes) and a *Pinus* hedgerow (Fig. 1). In order to minimize the effect of the surroundings (nuisance factor) in the analyses, we utilized a randomized block design. The experiment was composed of two treatments (factors), area and diversity, randomly assigned to four experimental units in each one of five blocks. In ANOVA, inclusion of the block factor tends to improve power if the blocks are markedly more homogeneous than the whole area (Seltman 2012). In our case, the “whole” was the surroundings with different vegetation, which could influence the pool of species immigrating to the experimental units. Therefore, we had two treatments, area and diversity. Area had two levels: large or small, and diversity also had two levels: more or less diverse. The experimental unit was a plant patch that contained four size × diversity treatment combinations in each block. Therefore, we had 20 experimental units in the whole five-block experimental design. A two-factor fixed

effects model was used to address 1) area main effects, 2) diversity main effects and 3) interaction between area and diversity. All factorial ANOVAs performed during the analyses used blocks of experimental units as the blocking factor.

**Experimental units.**—The experimental units were formed on a basic module of vegetation composed of eight seedlings. We used three native plant species [*Citharexylum montevidense* (Spreng.) Moldenke (Verbenaceae), *Eugenia uniflora* L. (Myrtaceae) and *Tabebuia chrysotricha* (Mart. ex A.DC.) Mattos (Bignoniaceae)] and one artificial seedling (Table 1). Each native seedling was rooted in a 2-l plastic pot. The artificial seedling was composed of three 20-cm-long wooden rods mimicking vegetation twigs, with five artificial leaves made of nonwoven tissue in each rod. The rods were partly buried in sand within the 2-l plastic pots. The basic module was thus composed of eight pots, with the seedlings situated in a 0.25 m<sup>2</sup> square (Fig. 1). The top of each seedling (leaf to leaf) was ca. 10 cm distant from the others. The basic module of the more diverse patches was composed of two pots of each natural seedling (six pots) and two pots of the artificial seedling, while the basic module of the less diverse patches was composed with only one previously randomly selected seedling (*E. uniflora*).

For the area treatment, the small patch level was simply the basic module patch (0.25 m<sup>2</sup>), with either the more or the less diverse basic module, while the large patch level was composed of four basic modules distributed in a large square patch (1 m<sup>2</sup>) (Fig. 1). We randomly assigned the position of each seedling

Table 1.—Mean  $\pm$  standard deviation of the morphological structures from 10 randomly selected individuals of three plant species and one artificial seedling used in the vegetation patches. Artificial seedlings did not have branches, leaves were directly inserted in the artificial shoot.

	Shoot height	Internodes length (cm)	Number of branches	Branch length (cm)	Leaf length (cm)
<i>Citharexylum montevidense</i>	77.3 $\pm$ 5.4	11.2 $\pm$ 1.1	6.6 $\pm$ 0.7	5.4 $\pm$ 0.5	7.7 $\pm$ 0.3
<i>Eugenia uniflora</i>	43.4 $\pm$ 3.1	16.6 $\pm$ 1.9	9.3 $\pm$ 1	3.2 $\pm$ 0.3	3.9 $\pm$ 0.3
<i>Tabebuia chrysotricha</i>	80.7 $\pm$ 4.1	8.4 $\pm$ 0.4	7.8 $\pm$ 0.7	8.5 $\pm$ 1	7.9 $\pm$ 0.3
Artificial	30 $\pm$ 0	3.7 $\pm$ 0.1	0	0	4.4 $\pm$ 0.1

group in each experimental unit, as well as the position of each experimental unit within each block.

**Sampling procedure.**—We removed the insects and spiders (defaunation) from seedlings prior to first spider collection by manual collecting and by shaking the branches taking care to not defoliate the seedlings. After the defaunation, we did eight periodic censuses during which we manually collected all spiders occurring in the experimental units. We spent one day sampling each block (four experimental units) so the whole census lasted five days in each period. The first sample was carried out in December 2010, thirty days after the defaunation. The mean days between two consecutive samples varied from 27.3 to 30.4 depending on the block. The spiders were collected in dry days, and the variation in the intervals of days between samples reflect rainy days that postponed the sample in that particular period. The month-long interval between censuses enabled us to analyze the first stage of community assembly: immigration and early establishment of adult spiders in the experimental units. All collected spiders were put in vials with alcohol, and the adult individuals were identified at species level whenever possible. Any adult male or female found in an experimental unit was considered a potential breeding individual. We utilized only adult spiders for the calculation of colonization rates and discarded the juveniles for two basic reasons. First, juvenile spiders are not suitable for identification at species level so they cannot be used to measure the colonization rate of species. Second, we found recently hatched spiderlings in various patches during the samplings, which could introduce bias in the analysis of abundance patterns. Voucher species are deposited in the spider collection of Museu de Ciências Naturais de Fundação Zoobotânica do Rio Grande do Sul, in Porto Alegre, Brazil.

**Colonization rate measurement and analyses.**—We utilized the method for estimating colonization rates from census data developed by Clark & Rosenzweig (1994). The method estimates the colonization rate for one species by first calculating parameter  $k$ , which equals the number of transitions from absence to presence of individuals in a patch during transitions of time, and parameter  $l$ , which equals the number of transitions from absences to absences. The first period ( $T_0$ ) considered for the colonization rate calculation was the defaunation day. Therefore, there were eight time transitions from  $T_0$  to  $T_8$ . For each experimental unit (vegetation patch) we computed  $k$  and  $l$  parameters for each species, based on the eight transitions. The colonization rate  $\lambda$ , where  $\lambda = k / (k + l)$ , is the probability that a species not present in the community will enter it in the time interval of approximately 28 days. In order to calculate the colonization rate of the entire community, we summed the  $k$  and  $l$  data for all species (Clark & Rosenzweig 1994) occurring in each experimental unit during the time periods and recalculated the

colonization rate  $\lambda$ . Clearly, the  $k$  and  $l$  parameters are influenced by the frequency of occurrence of each species and, consequently, by the abundances because more abundant species are likely to be more frequently found than rare ones. Nevertheless,  $k$  is positively related to the abundances, whereas  $l$  is negatively related to the abundances. In that sense, the denominator of the formula sets the weight of  $k$  and  $l$  to the measurement of colonization rate. If there are more transitions from absence to absence, the  $l$  parameter contributes more to the weight, while if there are more transitions from absence to presence, it is the  $k$  parameter that contributes more. Therefore, rare species (less frequent) contribute more with the  $l$  parameter, while dominant species (more frequent) contribute more with the  $k$  parameter. This characteristic prevents the bias that dominant/rare species may exert on the colonization rate estimate. This characteristic is apparent from the lack of influence of the adult spider abundances on the calculated colonization rates ( $R^2 = 0.021$ ;  $P = 0.55$ ). The influence of area, diversity and the interaction term on colonization rates was analyzed with a factorial ANOVA in the software Systat v. 11.00.01.

**Composition analyses.**—The variation in the composition of spider species over time was analyzed with a repeated measures two-factor permutational MANOVA, based on a chord distance dissimilarity matrix between experimental units. In that sense, we were able to assess possible interactions between the effects of time and space on community composition. The abundance matrix was subjected to a  $\log(x + 1)$  transformation in order to dampen the effects of dominant species. The repeated measures analyses were performed by restricting random allocations within the time periods. This approach allowed us to evaluate the variation in spider composition between the time periods, between the two factors, and the interaction terms (1000 permutations). We used the software Multiv v.2.63b to perform the analysis. It uses randomization tests based on resemblance measures between experimental units. The results are interpreted similarly to the ones in an analysis of variance table. The method uses as the test criterion a sum of squares between groups of experimental units, as described by Pillar & Orlóci (1996).

**Diversity analyses.**—We tested the influence of size and diversity on adult spider abundance; i.e., the spiders that were identified at species level. In that sense, we considered adult abundance as a measure of successful colonization; i.e., potential breeding individuals that either mature or disperse as adults to the experimental units. Richness took into account the number of species found in each experimental unit. We utilized the adult abundances as a covariate in the species richness analysis in order to account for a sampling effect (passive sampling hypothesis). We pooled the periodic

measurements of adult abundances and richness in order to perform two-factor ANOVAS. Analyses were performed in Systat 11.00.01.

## RESULTS

We collected 2183 spiders belonging to 19 families. Fifty spider species were identified from 575 adults (Table 2). Web spiders were the most speciose and abundant spider group, with 33 species (66% of total richness) and 394 individuals (69% of total abundance). Among web spiders, the most speciose and abundant family was Theridiidae with 22 species and 345 individuals. The cursorial family, Salticidae, was the second most speciose family with seven species. The three most abundant web spider species were theridiids: *Cryptachaea hirta* (Taczanowski 1873) ( $n = 129$ ), *Theridula gonygaster* (Simon 1873) ( $n = 109$ ), and *Anelosimus ethicus* (Keyserling 1884) ( $n = 25$ ). *Cheiracanthium inclusum* (Hentz 1847), the only Miturgidae (cursorial) species was also abundant with 102 individuals.

We did not find significant effects of the interaction between area and diversity on spider community colonization rates (ANOVA,  $F_{1,16} = 0.04$ ,  $P = 0.83$ ) and the main effects of patch size (ANOVA,  $F_{1,16} = 0.8$ ,  $P = 0.38$ ) and diversity (ANOVA,  $F_{1,16} = 1.8$ ,  $P = 0.2$ ) were also non-significant. Most of species (86%) showed less than 50% colonization probability during the experiment. As expected, the four most abundant species showed 100% of establishment probability. However, *Eustala saga* (Keyserling 1893) ( $n = 9$ ) also showed high colonization potential.

We did not find significant effects of the interaction between time and patch size (PERMANOVA,  $SS = 5.0$ ,  $P = 0.22$ ) or patch diversity (PERMANOVA,  $SS = 4.7$ ,  $P = 0.37$ ) on spider composition, but the interaction was significantly different among time periods (PERMANOVA,  $SS = 9.2$ ,  $P = 0.001$ ). Therefore, the composition responded only to the temporal effect. The PCoA ordination (Fig. 2) shows the species with the highest correlation coefficients with axes 1 and 2 based on chord distance dissimilarity between time periods. There are clearly three distinct spider compositions corresponding to initial, intermediate and final sampling periods.

We did not find significant effects of the interaction between area and diversity on spider community abundances (ANOVA,  $F_{1,16} = 0.4$ ,  $P = 0.55$ ). However, we found a significant effect of patch size on abundance (ANOVA,  $F_{1,16} = 71.7$ ,  $P < 0.001$ ) (Fig. 3). Patch diversity did not affect spider abundances (ANOVA,  $F_{1,16} = 0.9$ ,  $P = 0.34$ ). Regarding spider richness, we found no interaction between patch size and diversity (ANOVA,  $F_{1,15} = 1.4$ ,  $P = 0.26$ ). The resulting model of spider richness responses showed a significant effect of the adult abundances (ANOVA,  $F_{1,15} = 7.4$ ,  $P = 0.016$ ) (Fig. 4), but patch size (ANOVA,  $F_{1,15} = 0.2$ ,  $P = 0.64$ ) and patch diversity (ANOVA,  $F_{1,15} = 4.0$ ,  $P = 0.06$ ) did not influence mean richness.

## DISCUSSION

We found that the rates of colonization of spider species in the experimental landscape were not affected by size or diversity of habitat patches, in spite of temporal changes in the composition of colonizers. We sampled the community at very short periods, which emphasized the capacity of spider community to initiate rapid succession after disturbances

(Stefano et al. 2007; Fattorini & Borges 2011). The local community structure underwent continuous adjustment under the regime of continuous change in its composition (Loreau et al. 2001). However, the alterations in the regional community structure did not translate into changes in the likelihood of colonization.

Our experiment showed a continuous flux of immigrants on the landscape that was able to arrive at the vegetation patches, a pattern also found for a spider community in a Brazilian cerrado experiment, where spiders were the only taxon that continuously colonized litter plots (Vasconcelos et al. 2009). Initial spider community composition was largely determined by temporal differences in the pool of species that arrived and established at the experimental landscape, irrespective of habitat size or diversity. These changes in the regional pool of species composition did not affect the likelihood of local colonization over time; i.e., the process of local habitat colonization did not respond to changes in the structure of regional community. If the system was subjected to unpredictable spatial disturbances, temporal variation might constitute a major source of spatial patchiness, and species would differ in their responsiveness to temporal environmental variation (Wiens 1976). In the present experiment, we continuously disturbed the spider community structure, which placed it in the first stage of succession, with steady vegetation patch condition over time. In that sense, we reproduced the non-equilibrium approach to community structure, which states that community structure is primarily determined in a non-equilibrium fashion by the interactions of the heterogeneity of the physical environment (size and diversity factors), disturbance (spider census) and recruitment (colonization) (Reice 1994).

We found that adult abundance was the only community characteristic responsive to the imposed factors; it was higher in the larger patches. The result indicates that a positive relationship may be established between abundance and area during the early colonization of patches, matching the passive sampling hypothesis (Connor & McCoy 2001). The short time frame between consecutive samples in the experiment allowed us to discard strong interspecific interaction effects in structuring the initial spider community. Hypotheses linked to equilibrium theory, like resource concentration (Root 1973), may be disregarded as an explanation for the pattern. Therefore, mechanisms linked to populations' changes in abundance must be considered to explain area effects. Ham-bäck and Göran (2005) emphasized the importance of the search mode of animals in the observed relationships between insect density and patch size. In that sense, spider behavior may be equivalent to some contact searchers (Bukovinszky et al. 2005), which are essentially unable to identify suitable habitat before alighting on the substrate. Consequently, dispersers have little control over their ultimate destination, and the decision to stay or leave a substrate is based on tactile clues after landing. Therefore, larger patches may passively receive more immigrants. Additionally, abundance explained richness. In that sense, higher richness in larger patches was an artifact of sampling, which implies that the actual species richness is unaffected by size (Schoereder et al. 2004).

Other studies have also failed to find a significant relationship between plant diversity and arthropod abun-

Table 2.—List of spider species collected during the eight time periods (T1 to T8) of the experiment. *n* = abundance.

Species	T1	T2	T3	T4	T5	T6	T7	T8	<i>n</i>
Anyphaenidae									
<i>Tasata</i> sp.	1	0	0	0	0	0	1	0	2
<i>Teudis</i> sp.	3	9	0	0	0	0	0	0	12
Araneidae									
<i>Araneus unanimus</i> (Keyserling 1879)	1	0	0	0	0	0	0	0	1
<i>Argiope argentata</i> Tanikawa & Ono 1993	0	0	0	0	1	0	0	0	1
<i>Bertrana rufostriata</i> Simon 1893	0	0	0	2	1	1	0	0	4
<i>Eustala saga</i> (Keyserling 1893)	3	2	1	1	0	1	0	1	9
<i>Eustala albiventer</i> (Keyserling 1884)	0	0	0	0	0	0	0	1	1
Corinnidae									
<i>Meriola cetiformis</i> (Strand 1908)	0	0	1	0	0	0	0	0	1
Deinopidae									
<i>Deinopis amica</i> Schiapelli & Gerschman 1957	0	0	0	0	0	0	1	0	1
Linyphiidae									
<i>Anodoration claviferum</i> Millidge 1991	0	2	1	0	0	0	0	0	3
<i>Lygarina silvicola</i> Millidge 1991	0	0	0	2	1	0	3	9	15
<i>Lygarina</i> sp.	1	4	0	0	0	0	0	0	5
<i>Sphecozone rubescens</i> O. P.-Cambridge 1870	0	5	2	0	0	0	1	0	8
<i>Triplogyna ignitula</i> (Keyserling 1886)	0	0	0	0	0	0	0	1	1
Miturgidae									
<i>Cheiracanthium inclusum</i> (Hentz 1847)	18	10	9	8	32	12	3	10	102
Oxyopidae									
<i>Oxyopes salticus</i> Hentz 1845	0	1	4	5	6	3	1	0	20
Philodromidae									
<i>Berlandiella magma</i> Mello-Leitão 1929	4	1	0	0	0	0	0	0	5
Salticidae									
<i>Aphirape uncifera</i> (Tullgren 1905)	0	2	0	0	0	2	2	0	6
<i>Mopiopia labyrinthea</i> (Mello-Leitão 1947)	0	0	1	4	4	1	0	0	10
<i>Salticidae</i> sp.1	0	0	2	2	1	1	0	0	6
<i>Salticidae</i> sp.2	0	0	1	1	1	0	0	0	3
<i>Salticidae</i> sp.3	0	1	1	1	1	0	0	0	4
<i>Salticidae</i> sp.4	0	0	0	0	2	0	0	0	2
<i>Tariona</i> sp.	0	1	0	0	0	0	0	0	1
Scytodiidae									
<i>Scytodes imbituba</i> Rheims & Brescovit 2009	0	1	1	1	1	0	0	0	4
Theridiidae									
<i>Anelosimus ethicus</i> (Keyserling 1884)	8	8	1	1	2	3	0	2	25
<i>Chryso pulcherrima</i> (Mello-Leitão 1917)	0	0	0	2	1	1	1	0	5
<i>Cryptachaea hirta</i> (Taczanowski 1873)	18	21	19	21	21	15	5	9	129
<i>Cryptachaea passiva</i> (Keyserling 1891)	0	0	0	1	1	0	0	0	2
<i>Cryptachaea pinguis</i> (Keyserling 1886)	3	1	2	0	3	1	0	0	10
<i>Cryptachaea rioensis</i> (Levi 1963)	3	4	0	0	1	0	0	0	8
<i>Cryptachaea sicki</i> (Levi 1963)	2	0	1	0	0	0	0	0	3
<i>Dipoena</i> sp.	1	0	1	0	0	0	0	0	2
<i>Exalbidion</i> sp.	0	0	0	1	0	0	0	0	1
<i>Neospintharus rioensis</i> (Exline & Levi 1962)	0	0	1	0	2	0	0	0	3
<i>Parasteatoda tessellata</i> (Keyserling 1884)	0	1	0	0	0	0	0	0	1
<i>Phycosoma altum</i> (Keyserling 1886)	0	0	0	1	2	0	4	6	13
<i>Steatoda iheringi</i> (Keyserling 1886)	0	2	0	0	0	0	0	0	2
<i>Theridion bisignatum</i> (Mello-Leitão 1945)	3	6	3	0	2	1	0	0	15
<i>Theridion pernambucum</i> Levi 1963	1	0	0	0	0	0	0	0	1
<i>Theridion plaumanni</i> Levi 1963	2	1	0	0	0	1	1	4	9
<i>Theridion</i> sp.	0	0	0	0	0	1	0	1	2
<i>Theridula gonygaster</i> (Simon 1873)	4	8	10	16	26	34	10	1	109
<i>Thwaitesia affinis</i> O. P.-Cambridge 1882	1	0	1	0	0	0	0	0	2
<i>Thymoites</i> sp.1	0	0	0	0	0	1	0	0	1
<i>Thymoites</i> sp.2	0	0	0	0	0	0	0	1	1
<i>Tidarren haemorrhoidale</i> (Bertkau 1880)	0	1	0	0	0	0	0	0	1
Thomisidae									
<i>Misumenops maculissparsus</i> (Keyserling 1891)	0	0	0	1	0	0	0	0	1
<i>Misumenops</i> sp.	0	0	0	1	0	0	0	0	1
<i>Thomisidae</i> sp.1	1	0	0	0	0	0	0	0	1
TOTAL	78	92	63	72	112	79	33	46	575

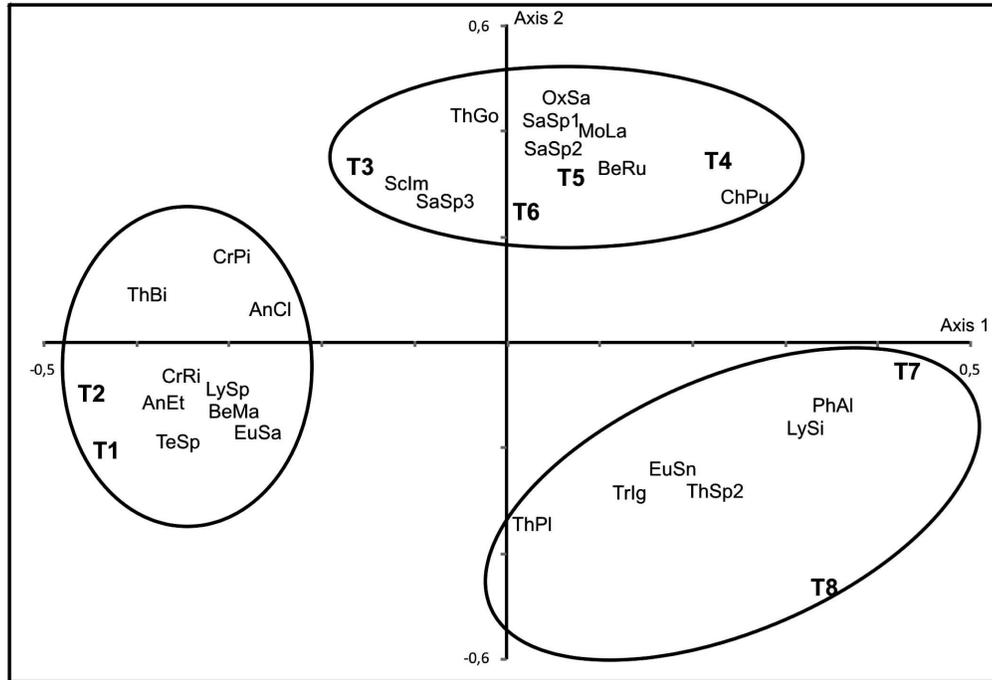


Figure 2.—PCoA ordination based on chord distance dissimilarity between the eight time periods. T1... T8 = time periods. Variation explained: axis 1 = 34.7%, axis 2 = 29.1%. Species showing the highest correlation coefficients with the axes: AnCl: *Anodoration claviferum*, AnEt: *Anelosimus ethicus*, BeMa: *Berlandiella magna*, BeRu: *Bertrana rufostriata*, ChPu: *Chryso pulcherrima*, CrPi: *Cryptachaea pinguis*, CrRi: *Cryptachaea rioensis*, EuSa: *Eustala saga*, EuSn: *Eustala albiventer*, LySi: *Lygarina silvicola*, LySp: *Lygarina* sp., MoLa: *Mopiopia labyrinthea*, OxSa: *Oxyopes salticus*, PhAl: *Phycosoma alta*, SaSp1: *Salticidae* sp.1, SaSp2: *Salticidae* sp.2, SaSp3: *Salticidae* sp.3, ScLm: *Scytodes imbituba*, TeSp: *Teudis* sp., ThBi: *Theridion bisignatus*, ThGo: *Theridula gonygaster*, ThPl: *Theridion plaumanni*, ThSp2: *Thymoites* sp.2, Trlg: *Triplogyna ignitula*.

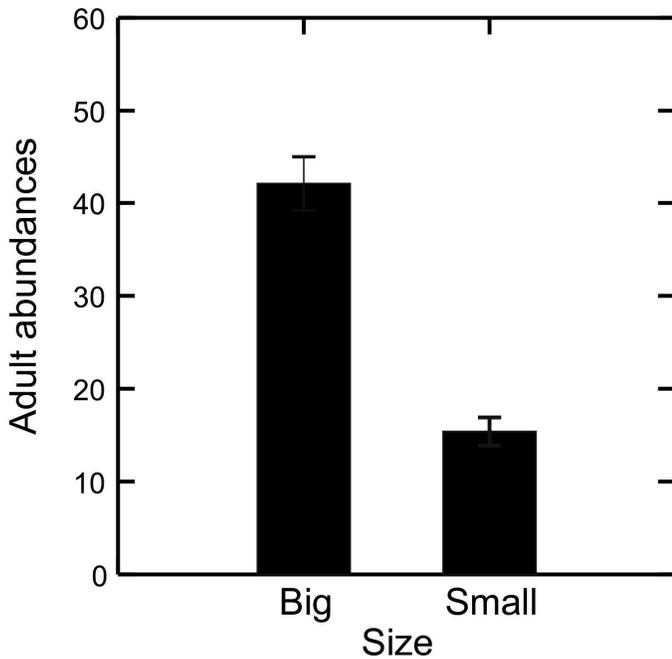


Figure 3.—Comparison of the means ( $\pm$  standard error) of adult abundance of spiders collected in large and small experimental patches of vegetation. Large patches = 1 m<sup>2</sup> (n = 10); small patches = 0.25 m<sup>2</sup> (n = 10).

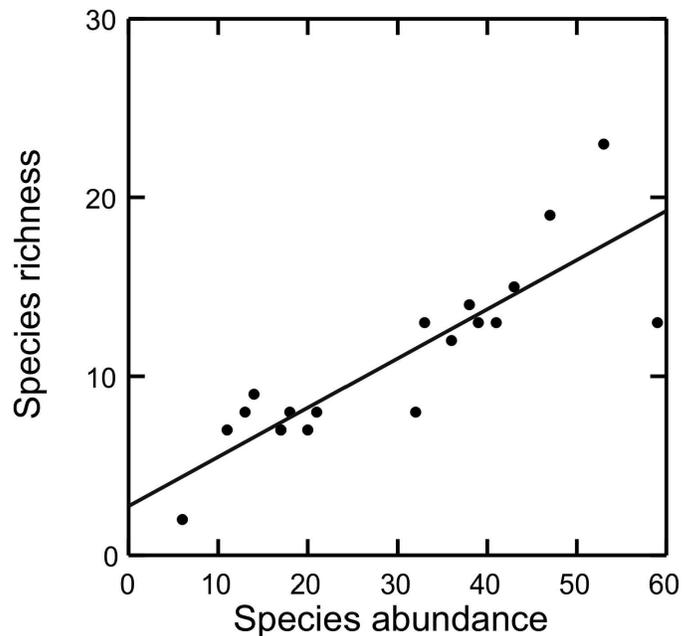


Figure 4.—Relationship between adult spider richness and abundance in 20 experimental vegetation patches ( $R^2 = 0.75$ ,  $P < 0.001$ ).

dance, but there was evidence of increased predator abundance in areas of high plant productivity and low diversity (Siemann 1998; Koricheva et al. 2000; Perner et al. 2005). Possible effects linked to prey abundance seem to be unimportant in shaping spider abundance in the experiment because there was not enough time between consecutive samples to allow important interactions between the spider community and other arthropods. Therefore, the equal abundance and richness of adult spiders in more and less diverse patches can be a response of the spider community to other aspects of habitat structure. Because web spiders comprised 70% of immigrants, it may be that the plant habitat in less diverse patches provides particular structures to support web construction. However, because the experimental design did not randomize the less diverse patches among the four seedlings, the diversity effect may be confounded by the presence of a plant identification effect that had a disproportional beneficial impact on the presence of web building spiders.

In the manipulative experiment employed in this study, we were able to physically manipulate attributes of the landscape in a controlled manner, while varying only patch size and diversity. Therefore, possible confounding factors like patch isolation, shape, and matrix were controlled. Additionally, the short interval between two consecutive samples maintained the spider communities at initial succession stage. In the experimental fragmented landscape, the responses of the spider community contradicted theoretical predictions about the influence of size and diversity on colonization rates. The community structure of spiders in this particular fragmented landscape is determined mainly by the continuous colonization process of the regional pool of species that settles the initial stage of community succession after disturbances. However, we must stress that spiders have a high dispersal ability and even at large landscapes spider metacommunities may be not limited by dispersal (Baldissera et al. 2012). The small spatial and temporal scales used in this study restrict generalizations about the influence of area and diversity on a spider community. Therefore, we suggest the use of the present experimental design for future studies focusing on longer colonization periods and larger-scale plots in order to better understand the responses of spider communities in fragmented landscapes.

#### ACKNOWLEDGMENTS

We thank Carla Rosana Cramer for fieldwork assistance. RB and SMH received CNPq doctoral and researcher scholarships (# 140220/2008-9 and # 306816/2010-5 respectively). Spider collection was permitted by license number 15260-1 (IBAMA – Brazilian Environmental Institute). We thank two anonymous reviewers, who made valuable comments on the original version of the manuscript.

#### LITERATURE CITED

Baldissera, R., E.N.L. Rodrigues & S.M. Hartz. 2012. Metacommunity composition of web-spiders in a fragmented neotropical forest: relative importance of environmental and spatial effects. *PLoS ONE* 7(10):e48099.

Bukovinszky, T., R.P.J. Potting, Y. Clough, J.C. van Lenteren & L.E.M. Vet. 2005. The role of pre- and post-alighting detection

mechanisms in the responses to patch size by specialist herbivores. *Oikos* 109:435–446.

Clark, C.W. & M.L. Rosenzweig. 1994. Extinction and colonization processes: parameter estimates from sporadic surveys. *American Naturalist* 143:583–596.

Connor, E.F. & D.D. McCoy. 2001. Species-area relationships. *Encyclopedia of Biodiversity* 5:397–411.

Cramer, M.J. & M.R. Willig. 2005. Habitat heterogeneity, species diversity and null models. *Oikos* 108:209–218.

Ewers, R.M. & R.K. Didham. 2006. Confounding factors in the detection of species responses to habitat fragmentation. *Biological Reviews* 81:117–142.

Fattorini, S. & P.A. Borges. 2011. Biogeographical kinetics on an island volcano (Capelinhos, Azores): fast colonization rates and dominance of arthropod exotic species. *Insect Conservation and Diversity* 5:358–366.

Haila, Y. 2002. A conceptual genealogy of fragmentation research: from island biogeography to landscape ecology. *Ecological Applications* 12:321–334.

Hambäck, P.A. & E. Göran. 2005. Patch area, population density and the scaling of migration rates: the resource concentration hypothesis revisited. *Ecology Letters* 8:1057–1065.

Koricheva, J., C.P.H. Mulder, B. Schmid, J. Joshi & K. Huss-Danell. 2000. Numerical responses of different trophic groups of invertebrates to manipulations of plant diversity in grasslands. *Oecologia* 125:271–282.

Lomolino, M.V. 1990. The target area hypothesis: the influence of island area on immigration rates of non-volant mammals. *Oikos* 57:297–300.

Loreau, M., S. Naeem, P. Inchausti, J. Bengtsson, J.P. Grime, A. Hector, D.U. Hooper, M.A. Huston, D. Raffaelli, B. Schmid, D. Tilman & D.A. Wardle. 2001. Biodiversity and ecosystem functioning: current knowledge and future challenges. *Science* 294:804–808.

MacArthur, R.H. & E.O. Wilson. 1967. *The Theory of Island Biogeography*. Princeton University Press, Princeton, New Jersey.

Nilsson, S.G., J. Bengtsson & S. Ås. 1988. Habitat diversity or area per se? Species richness of woody plants, carabid beetles and land snails on islands. *Journal of Animal Ecology* 57:685–704.

Perner, J., C. Wytrykush, A. Kahmen, N. Buchmann, I. Egerer, S. Creutzburg, N. Odat, V. Audorff & W. Weisser. 2005. Effects of plant diversity, plant productivity and habitat parameters on arthropod abundance in montane European grasslands. *Ecography* 28:429–442.

Pillar, V.D. & L. Orlóci. 1996. On randomization testing in vegetation science: multifactor comparisons of relevé groups. *Journal of Vegetation Science* 7:585–592.

Reice, S.R. 1994. Nonequilibrium determinants of biological community structure. *American Scientist* 82:424–435.

Root, R.B. 1973. Organization of a plant-arthropod association in simple and diverse habitats: the fauna of collards (*Brassica oleracea*). *Ecological Monographs* 43:95–124.

Schoereder, J.H., C. Galbiati, C.R. Ribas, T.G. Sobrinho, C.F. Sperber, O. DeSouza & C. Lopes-Andrade. 2004. Should we use proportional sampling for species-area studies? *Journal of Biogeography* 31:1219–1226.

Seltman, H.J. 2012. *Experimental design and analysis*. Online at: <http://www.stat.cmu.edu/~hseltman/309/Book/Book.pdf>

Siemann, E. 1998. Experimental tests of effects of plant productivity and diversity on grassland arthropod diversity. *Ecology* 79:2057–2070.

Stefano, F., C. Marco, B. Tiziano, G. Paolo & M. Giorgio. 2007. Colonisation by ground and edaphic invertebrates of soil patches with different pollution levels. *Periodicum Biologorum* 109:37–45.

Uetz, G.W. 1991. Habitat structure and spider foraging. Pp. 325–348. *In* *Habitat Structure: The Physical Arrangement of Objects in Space*. (S.S. Bell, E.D. McCoy & H.R. Mushinsky, eds.). Chapman and Hall, London.

- Vasconcelos, H.L., R. Pacheco, R.C. Silva, P.B. Vasconcelos, C.T. Lopes, A.N. Costa & E.M. Bruna. 2009. Dynamics of the leaf-litter arthropod fauna following fire in a Neotropical woodland savanna. *PLoS ONE* 4(11):e7762.
- Wiens, J.A. 1976. Population responses to patchy environments. *Annual Review of Ecology and Systematics* 7:81–120.
- Williams, C.B. 1964. Patterns in the balance of nature and related problems in quantitative ecology. Academic Press, London.
- Wise, D.H. 1993. Spiders in ecological webs. Cambridge University Press, Cambridge.

*Manuscript received 10 July 2012, revised 30 April 2013.*