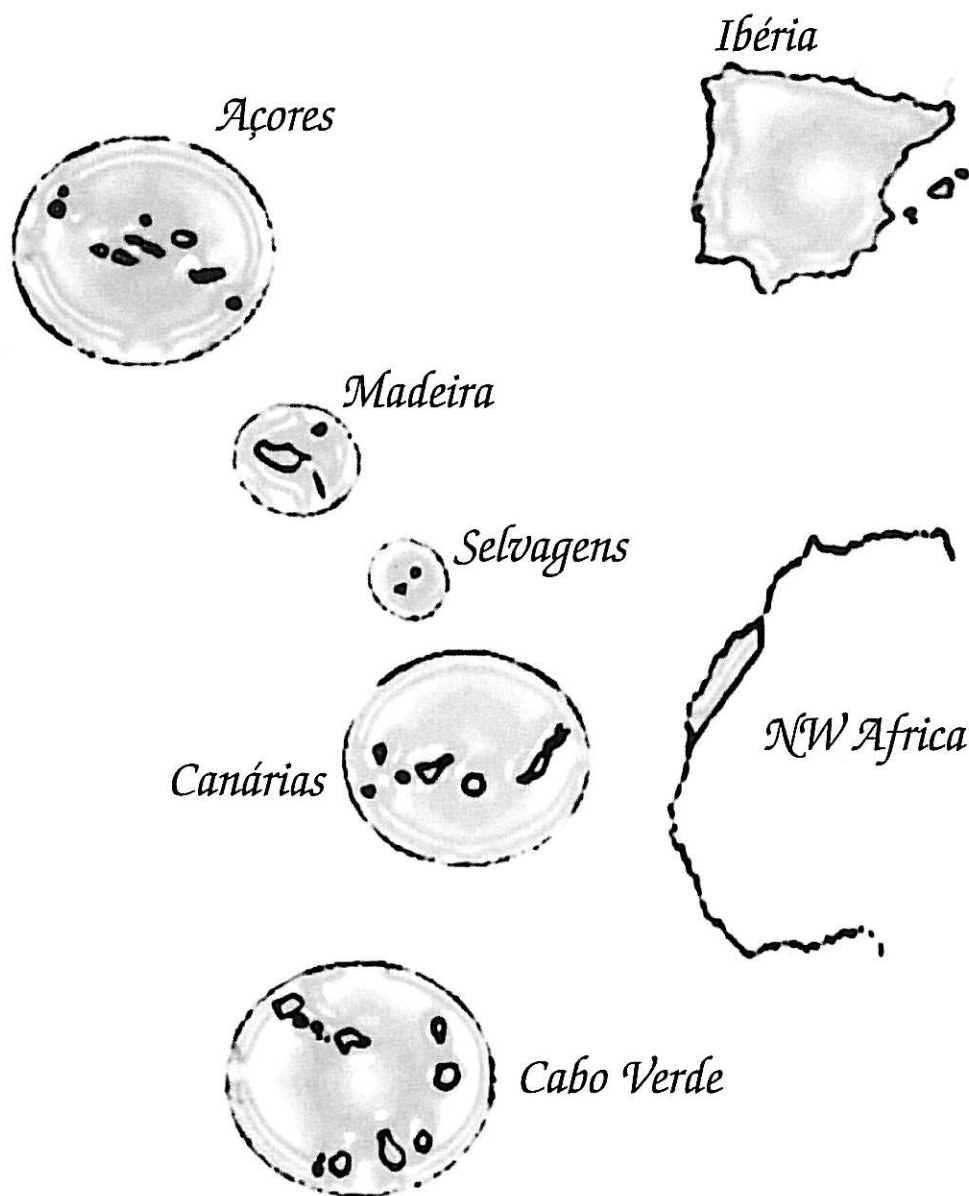


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## Relationship between local and regional species richness in azorean pasture arthropods.

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### RESUMO

Neste trabalho é investigada a relação entre a riqueza de espécies local e regional de insectos comedores de gramíneas e aranhas constructoras de teias em pastagens semeadas e semi-naturais de três ilhas dos Açores (Pico, Terceira e S. Maria). A comunidade de aranhas constructoras de teias mostra alguma evidência de saturação à escala local nos dois habitats estudados (o mesmo número de espécies nos campos experimentais das duas ilhas regionalmente mais ricas em espécies). A competição não parece ser o processo envolvido neste padrão, mas sim outros factores como os padrões de composição diferencial de famílias de aranhas, história das ilhas e perturbação pela herbivoria do gado. Pelo contrário, nos insectos comedores de gramíneas a riqueza local aumenta proporcionalmente com a riqueza regional. Por outro lado, os dados sazonais parecem ser tão informativos como os dados acumulados. Em conclusão, a riqueza de espécies local para os dois grupos de artrópodes estudados parece ser determinada principalmente por processos regionais. Para ilhas oceânicas, isto implica que a riqueza local de espécies é principalmente controlada por processos regionais como sejam a evolução (especiação) e os padrões de colonização e extinção.

### SUMMARY

The relationship between local and regional species richness was examined in respect of grass-feeding insect herbivores and web-building spider communities in sown and semi-natural pastures from three Azorean islands (Pico, Terceira and S. Maria). There is some indication that assemblages of web-building spiders are saturated with species at the local scale (same number of species in the field sites of the two regionally richest islands) in both habitats. Explanations for the "ceiling effect" obtained with this assemblage are discussed, but competition is probably not involved. A mixture of regional patterns in family composition and history of the islands, together with local processes like grazing disturbance and spatial heterogeneity, may be determining local richness in web-building spiders. The grass-feeding insect herbivores, in contrast, appear to be regionally enriched and show little evidence of saturation. Seasonal data seem to be as informative as pooled data in investigating local and regional species richness patterns. In conclusion, local richness seems to depend upon regional richness or at least is shaped by regional processes in sown and semi-natural pasture grass-feeding insects and web-building spiders. For oceanic islands, this implies that local species richness is controlled by regional processes, such as evolution (speciation) and colonization/extinction.

## INTRODUCTION

Since the influential work of Whittaker (1972), species richness in communities has been measured in several ways. Comprehensive revisions of the way later authors used such measures are available in Schluter & Ricklefs (1993a), Huston (1994) and Bisby *et al.* (1995). The simplest measure of species richness is its local component usually known as "alpha-diversity" and defined originally by Whittaker (1972) as the number of species found in a homogeneous sample representing a community. "Alpha-diversity" refers, therefore, to the number of species found within a homogeneous area of a given size (Huston, 1994), usually a field site. Another important measure of species richness is at a regional scale, a measure known as "gamma-diversity", and defined as the total number of species pooled from different communities found in a particular region (Whittaker, 1972).

An interesting issue, frequently addressed in the recent literature, concerns the way local and regional processes are structuring natural communities (see for instance Ricklefs & Schluter, 1993, a whole volume devoted to the subject). Two models were proposed to explain how local and regional species richness are related in natural communities (Cornell, 1985a and b; Ricklefs, 1987; Cornell & Lawton, 1992; Cornell, 1993; Cornell & Karlson 1997):

a) the proportional sampling model, in which local richness ("alpha-diversity") is independent of local processes and increases proportionately with regional richness (model I in Figure 1). In this model, regional processes such as historical and biogeographic constraints, as well as immigration and extinction events, can shape the species richness of local communities;

b) the local saturation model, local species richness reaches a ceiling in richer regions. In this model, local processes (e.g. biotic interactions between species, abiotic characteristics of the habitat, disturbance) limit the number of species that can coexist in a local community. Thus, local richness is largely independent of the pool of species occurring in the region (model II in Figure 1).

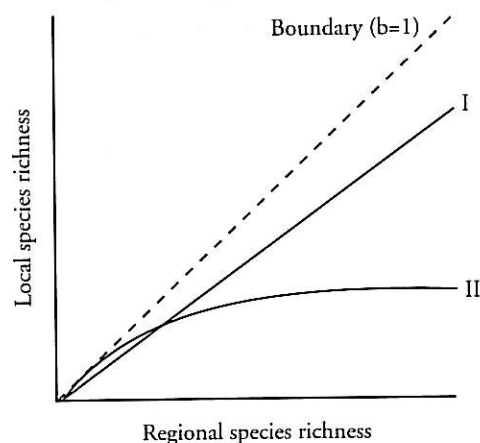


Figure 1 - Relationship between local species richness and regional species richness. Model I - "proportional sampling"; model II - "local saturation". The boundary line represents a situation in which local species richness equals regional species richness (slope = 1) (redrawn from Cornell & Lawton 1992; Cornell 1993).

Reviewing the available empirical tests of these two models, Cornell & Lawton (1992), Cornell (1993), Hawksworth *et al.* (1995) and Cornell & Karlson (1997) concluded that the "proportional sampling model" is an "assembly rule" in natural communities and, therefore, local assemblages are a proportional sample of the regional pool of species (Lawton 1996). In fact, most experimental work (e.g. Opler, 1974; Cornell, 1985a and b; Ricklefs, 1987; Compton *et al.*, 1989; Lawton, 1990; Hawkins & Compton, 1992; Cornell, 1993; Gaston & Gauld, 1993; Lawton *et al.*, 1993; Schluter & Ricklefs, 1993b; Dawah *et al.*, 1995; Hugueny & Paugy, 1995; Cornell & Karlson, 1996 and 1997; Griffiths, 1997 and others) supports the "proportional sampling model".

Local saturation was found to occur in helminth parasite richness in British freshwater fish (Kennedy & Guégan, 1994), while Aho & Bush (1993) found no consistent evidence supporting either regional or local processes in determining species richness, in spite of the fact that their results appeared more consistent with saturation. Earlier studies (e.g. Terborgh & Faarborgh, 1980; Tonn *et al.*, 1990) also suggested saturation in tropical bird and freshwater fish assemblages respectively, but the patterns were largely artefacts of the type of the analyses performed (Cornell, 1993). However, Griffiths (1997) disagrees and considers that the data of Terborgh & Faarborgh (1980) is consistent with saturation.

There are three aims in paper. First, to test the "proportional sampling model" as the null model (Cornell & Lawton, 1992; Cornell, 1993; Cornell & Karlson, 1997) in closely related groups of arthropods. As biotic interactions between species are more likely to occur in assemblages of species competing for a common resource, grass-feeding herbivores and web-building spiders were chosen as study groups. Grass-feeders share a common resource, the pasture grass species. Web-building spiders may compete for resources (Wise, 1995), but also for space where they can build the webs (Brown, 1991; Uetz, 1991). The absence of competing interactions between herbivorous arthropods is commonly reported (Strong *et al.*, 1984; but see Denno *et al.*, 1995 for some new insights about competitive processes on herbivore insects). I predict, therefore, that the "proportional sampling model" will explain the relationship between local and regional numbers in grass-feeding herbivorous insects. Because in predators competition is more likely to occur (Cornell & Karlson, 1997), I predict that web-building spiders are locally saturated. Second, I evaluate the importance of analyzing independently seasonal, between-year and pooled data in testing the above mentioned models. Third, the tested models can only be investigated within matched habitats (Cornell, 1993). As recent sown pastures and old semi-natural pastures were studied, and, young communities are less likely to be structured by competition than older ones (Arthur, 1987), I predict that evidences of saturation in local species richness will occur mainly in the semi-natural pastures.

## MATERIAL AND METHODS

### The data sets

Five data sets were built for herbivorous grass-feeders and web-building spiders. These data sets were the Spring,

Summer and Autumn 1994, Summer 1995 samples, and a pooled data set (see Appendix 1) comprising the data obtained in all the seasonal samples. Data were collected using pitfall traps, a suction machine (Vortis) and direct search, and for five seasonal samples in two years (see detailed experimental protocol in Borges, 1997 and 1999; Borges & Brown, 1999 and 2001).

The taxonomic composition of each of the studied assemblages comprised the following: grass-feeders - all the sucking and chewing herbivorous species sampled that were reported to feed on grasses; web-building spiders - Tetragnathidae, Araneidae, Linyphiidae, Theridiidae, Dictynidae, Oecobiidae, Mimetidae and Agelenidae. For the spiders, families were assigned to the web-building assemblage following Wise (1995) and Roberts (1995). The Mimetidae are not true web-builders. They are found in low vegetation as they search for webs of comparable size to invade (Roberts, 1995). They may, therefore, interact with other web spiders.

#### *Local and regional species richness estimates*

For the four seasonal data sets, local richness (= "alpha-diversity") was calculated as the number of species sampled at each field site in each season. As the pitfall traps sampled the arthropods over seven days in each season, and suction was performed in the best weather conditions, estimates of local richness are probably reliable, with few species being missed. For the pooled data set, local richness was calculated as the cumulative number of different species present in each field site pooled over all sampling occasions.

Regional richness (= "gamma-diversity") was calculated in the same way for the four seasonal samples and for the pooled data set. It is given as the number of different species pooled over all sites in a region. Each island is a region which subsumes four sites, two of sown pasture and two of semi-natural pasture. Therefore, this regional species richness estimate gives the pool of species that can potentially occur in pastureland (sown and semi-natural pastures) in each of the three studied regions (islands).

#### *Data analysis*

Species accumulation curves were built for each assemblage in each region (islands). Data from the five sampling periods were used for this purpose.

As the "proportional sampling" and "saturation" models predict that when the regional number of species is zero the local number of species should also be zero (Cornell & Lawton, 1992), the fitted lines were obtained following a conservative test of linearity forcing the regression line through the origin. The standard ordinary linear least-squares (OLS) regression was applied in both untransformed and double (log-log) transformed variables. As there are only three independent regions (islands), few degrees of freedom are available and no quadratic term can be added in order to test rigorously for curvilinearity. Therefore, the fitted lines should not be considered a rigorous statistical test. Additionally, the local estimates of species richness are not truly independent of the regional estimates of species richness, since regional richness was obtained from the local samples. However, it is still appropriate to plot local richness against regional richness and look for patterns of proportional increase or curvilinearity on the relationship

between local species richness and regional species richness. Obviously, with the small number of degrees of freedom available all the regressions performed must be interpreted with caution. If consistent patterns are found in all the seasonal and pooled samples, some inferences may be made about the mechanisms involved. All OLS regression statistics anchored through the origin were performed using Microsoft Excel 5.0 Macintosh statistical package. The graphs were created using a Macintosh package (Cricket Graph III).

## RESULTS

Species accumulation curves for the three islands (S. Maria, Terceira and Pico) are steep and only become asymptotic in the species poor island (Pico) and also in Terceira for the web-spinning spiders (Figures 2a and b). A different pattern was obtained for the richest island (S. Maria), where no plateau was reached for either of the assemblages. The latter also occurred with the herbivorous grass-feeders in Terceira (Figure 2a). This combined indicates that with more sampling further species are likely to be added to the regional pool of species in S. Maria and Terceira. However, as the last point is the only consistent complete sample in the second year, it represents an expected between year random variation with the inclusion of vagrant species. Moreover, after the third sampling event the slope of the curve becomes less steep, thereby suggesting that the censuses are almost complete.

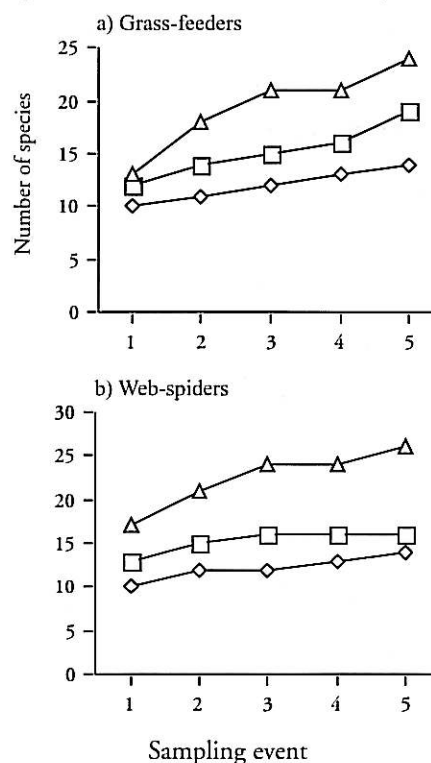


Figure 2 - Species accumulation curves for grass-feeding herbivores (a) and web-building spiders (b) in the three Azorean islands: S. Maria (triangles), Terceira (squares) and Pico (diamonds). The sampling events were as follow: 1 = Spring 1994; 2 = Summer 1994; 3 = Autumn 1994; 4 = Spring 1995; 5 = Summer 1995.



Only on two occasions (Autumn 1994 and pooled data) did the number of local species seem to be proportional to the number of regional species for the grass-feeding herbivores in sown pastures (see Table 1; Figure 3). On the other three sampling occasions, there is some tendency for local richness of sown-pasture grass-feeders to reach a ceiling (Figures 3a, b and d). For the grass-feeders in the semi-natural pastures, in all cases except Spring 1994 (Figure 4a; see also Table 1) there was a proportional increase of the local richness with regional richness. However, even in Spring 1994 there was no evidence of an asymptote in the curve.

For the web-building spiders similar OLS regressions of alpha on gamma diversities showed, with few exceptions, a non significance of the null model (Table 2; Figures 5 and 6). Only in the Spring and Autumn 1994, in the semi-natural pastures, was the null model supported (Figures 6a and c). However, as only four out of the twenty regressions were statistically significant (see Table 2), this result is expected to be obtained purely by chance. In all 1994 samples in the sown pastures, the low interval between the boundary curve and the data points for the web-building spiders occurring in the local sites from the poorest region (Pico) (Figure 5) is notorious. This suggests very low values of "beta-diversity", almost all of the species that occur regionally also occur locally. Therefore, the data suggest that local species richness of web-building spider predators does not increase linearly with regional species richness in the sown pastures trend also shown to some extent in the semi-natural pastures.

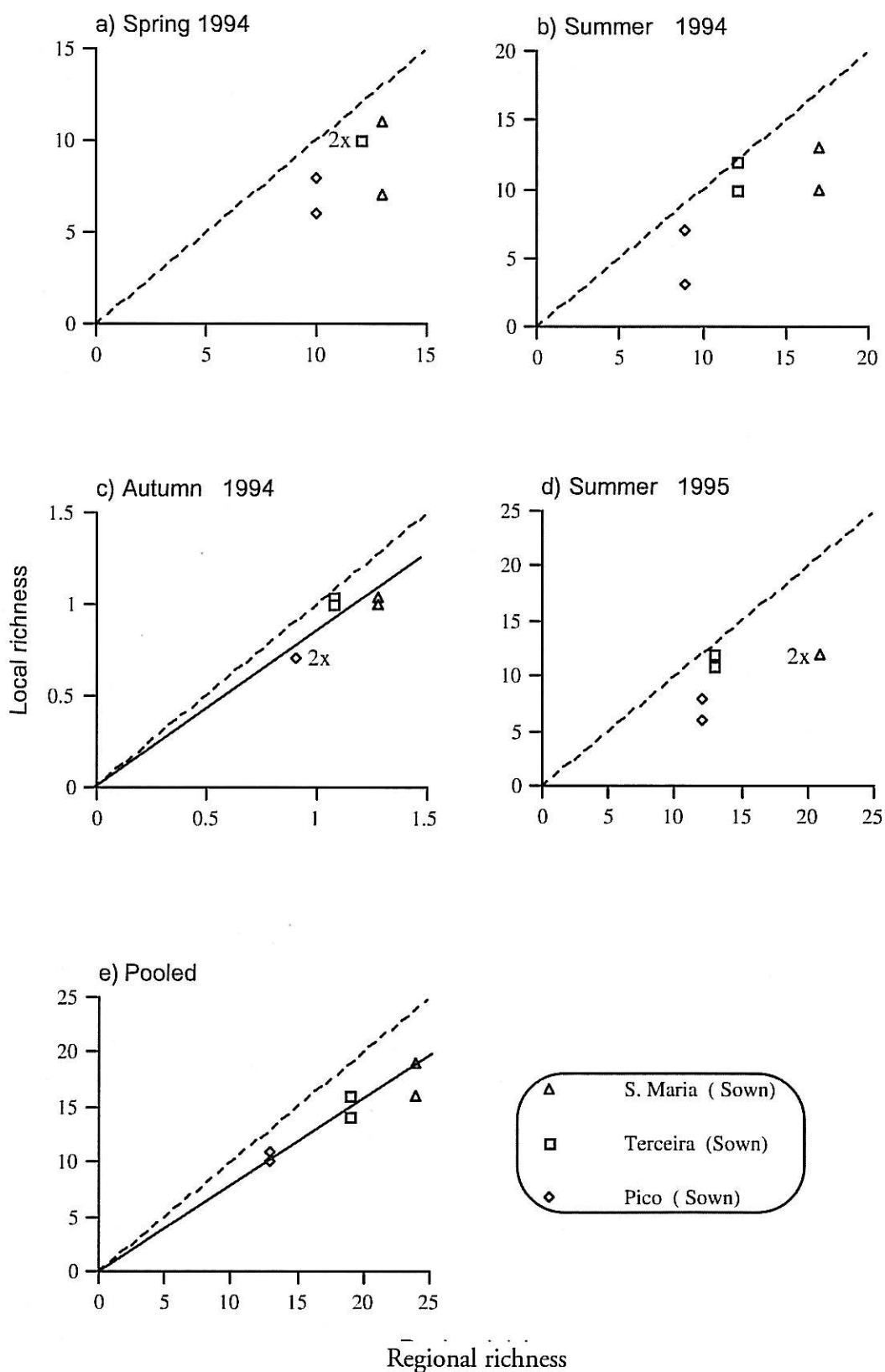
## DISCUSSION

This study was conducted over two years, using the same sampling protocol, thereby allowing a comparison between seasons and between years in the local-regional species richness relationship. The results show the importance of using seasonal data for a realistic interpretation of the relative importance of local and regional processes. The species accumulation curves showed that seasonal differences in species composition during the first year were more important, with a lesser contribution from the second year to the overall regional pool of species. It should also be emphasized that the "core" species, that is, those that persisted in the community in high abundance throughout all sampling occasions, have only slight effects on the curves. Therefore, the accumulation curves are due mainly to the addition of species with particular seasonal requirements, and also rare and vagrant species. It can be also argued that the inclusion of rare and vagrant species may overestimate the number of species in the species richer islands. However, such species are also likely to have a role in the communities (Gaston, 1994). The higher values of "beta-diversity" usually observed in the richer regional faunas may also account for the steeper curves in Terceira and S. Maria.

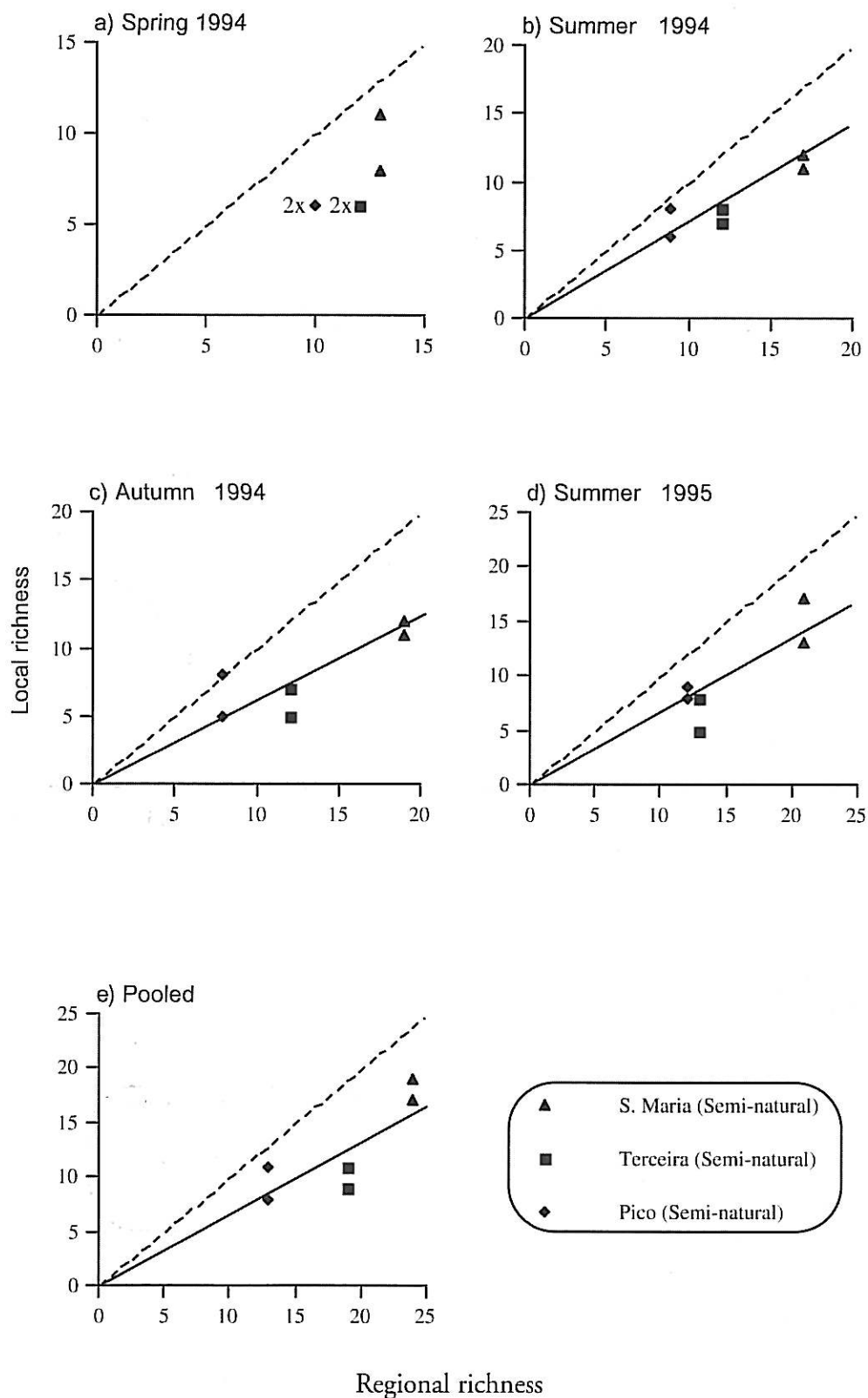
A major purpose of this work was to test the "proportional sampling hypothesis" as a null model explaining the relationship between local and regional species richness. I predicted that assemblages of herbivorous arthropods would not be structured by competition (see

Table 1 - Statistics for linear and log-log regressions of local against regional species richness for grass-feeding insects in sown (a) and semi-natural (b) pastures. See text for further details. n.s.= not significant; \*0.01 < p < 0.05; \*\*p < 0.01.

Regression type	Equation	r <sup>2</sup>	F	Regression type	Equation	r <sup>2</sup>	F
a) SOWN PASTURES				b) SEMI-NATURAL PASTURES			
Spring 1994				Spring 1994			
Linear model	y = 0.74x	0.29	n.s.	Linear model	y = 0.62x	0.38	n.s.
log-log model	log y = 0.87 log x	0.29	n.s.	log-log model	log y = 0.79 log x	0.37	n.s.
Summer 1994				Summer 1994			
Linear model	y = 0.72x	0.53	n.s.	Linear model	y = 0.68x	0.8	20.2*
log-log model	log y = 0.85 log x	0.45	n.s.	log-log model	log y = 0.85 log x	0.85	15.58*
Autumn 1994				Autumn 1994			
Linear model	y = 0.64x	0.46	n.s.	Linear model	y = 0.60x	0.64	9.03*
log-log model	log y = 0.84 log x	0.71	12.20*	log-log model	log y = 0.81 log x	0.52	n.s.
Summer 1995				Summer 1995			
Linear model	y = 0.64x	0.15	n.s.	Linear model	y = 0.67x	0.73	13.48*
log-log model	log y = 0.85 log x	0.37	n.s.	log-log model	log y = 0.83 log x	0.57	n.s.
Pooled				Pooled			
Linear model	y = 0.76x	0.83	25.2**	Linear model	y = 0.67x	0.68	10.55*
log-log model	log y = 0.91 log x	0.89	41.28**	log-log model	log y = 0.86 log x	0.6	7.54*



**Figure 3** - Relationship between local and regional species richness for grass-feeding herbivores of sown pastures (open symbols) in three Azorean islands: S. Maria (triangles), Terceira (squares) and Pico (diamonds). The dashed line represents the condition where every species occurs at every site. a), b) and c) give a seasonal perspective during 1994; b) and d) permit a between-year comparison; e) gives the pooled data. Data for Figure (c) is logarithmically transformed. A line is given only in the cases where a linear relationship between local and regional species richness was found at  $p = 0.05$ . See text for further details.



**Figure 4** - Relationship between local and regional species richness for grass-feeding herbivores of semi-natural pastures (filled symbols) in three Azorean islands: S. Maria (triangles), Terceira (squares) and Pico (diamonds). The dashed line represents the condition where every species occurs at every site. a), b) and c) give a seasonal perspective during 1994; b) and d) permit a between-year comparison; e) gives the pooled data. A line is given only in the cases where a linear relationship between local and regional species richness was found at  $p = 0.05$ . See text for further details.

Table 2 - Statistics for linear and log-log regressions of local against regional species richness for web-building spiders in sown (a) and semi-natural pastures (b). See text for further details. n.s.= not significant; \*0.01 &lt; p &lt; 0.05.

Regression type	Equation	r <sup>2</sup>	F	Regression type	Equation	r <sup>2</sup>	F
a) SOWN PASTURES				b) SEMI-NATURAL PASTURES			
Spring 1994				Spring 1994			
Linear model	y = 0.64x	-0.87	n.s.	Linear model	y = 0.62x	0.73	13.48*
log-log model	log y = 0.84 log x	-0.45	n.s.	log-log model	log y = 0.82 log x	0.81	21.13*
Summer 1994				Summer 1994			
Linear model	y = 0.72x	-0.02	n.s.	Linear model	y = 0.61x	0.35	n.s.
log-log model	log y = 0.87 log x	0.16	n.s.	log-log model	log y = 0.81 log x	0.46	n.s.
Autumn 1994				Autumn 1994			
Linear model	y = 0.69x	0.32	n.s.	Linear model	y = 0.69x	0.79	19.11*
log-log model	log y = 0.86 log x	0.42	n.s.	log-log model	log y = 0.85 log x	0.77	16.90*
Summer 1995				Summer 1995			
Linear model	y = 0.79x	-0.01	n.s.	Linear model	y = 0.64x	-0.55	n.s.
log-log model	log y = 0.90 log x	0.08	n.s.	log-log model	log y = 0.82 log x	-0.39	n.s.
Pooled				Pooled			
Linear model	y = 0.63x	-0.45	n.s.	Linear model	y = 0.59x	0	n.s.
log-log model	log y = 0.86 log x	-0.09	n.s.	log-log model	log y = 0.84 log x	0.41	n.s.

Strong *et al.*, 1984). Grass-feeding herbivores showed a consistent proportional increase in local species richness with increasing regional richness mainly in semi-natural pastures from three Azorean islands. Some evidence of curvilinearity in the relationship was found, but mainly in local sown pasture assemblages.

Competition may be more likely to occur between closely related taxa, because of similarity in feeding niche (Denno *et al.*, 1995). In this study, grass-feeders were selected regardless their taxonomic composition and are composed of very different taxonomic and ecological groups with different dynamics and particularly feeding behaviours (chewers and sap-feeders both above- and belowground). Grasses are not so varied in plant architecture and secondary compounds as forbs (Tschamtker & Greiler, 1995) and herbivores may compete more as a consequence of a limiting niche space. However, I suspect that the evidence of saturation is probably largely an artefact. It appears that the patterns are mainly a consequence of the variation in local species richness within the species richer island (S. Maria), surpassing in importance the differences in regional richness. In all 1994 samples in the sown pastures, the low interval between the boundary curve and the data points for the grass-feeders occurring in the local sites from Terceira (Figure 3) is remarkable. Therefore, almost all of the species that occur regionally also occur locally, which does not suggest competition. Moreover, considering that high levels

of disturbance may confuse the interpretation of empirical studies relating local and regional diversity (Caswell & Cohen, 1993; Cornell & Karlson, 1996), and that pastures can be considered a system under high disturbance regimes (grazing), it can be considered that the evidence of saturation obtained may be a consequence of the grazing management imposed to the experimental sites. Alternatively, both the occurrence of high proportions of "satellite" species coupled with high levels of species turnover throughout the seasons sampled in S. Maria, also support a ceiling generated by a stochastic equilibrium (see Cornell, 1993). Therefore, the number of species in each field site may not be limited by interspecific interactions, but by a balance between colonization and extinction processes.

Borges & Brown (2001) showed that grass species richness was a good predictor of grass-feeding insect species richness at local scale. Thus, the results obtained in the present analyses are not only a consequence of a regional effect. Instead, there are probably two processes operating: first, local grass-feeding insect assemblages are a collection of individuals representing those species that are available around (regional pool), i.e. this corresponds to the process of "proportional sampling" (Ricklefs, 1987; Cornell & Lawton, 1992; Cornell, 1993; Cornell & Karlson, 1997); second, local grass species composition may act as a selective force in determining the success of establishment of the colonizers. Moreover, the relative and absolute area of occupancy of the habitats in the three islands cannot be used to



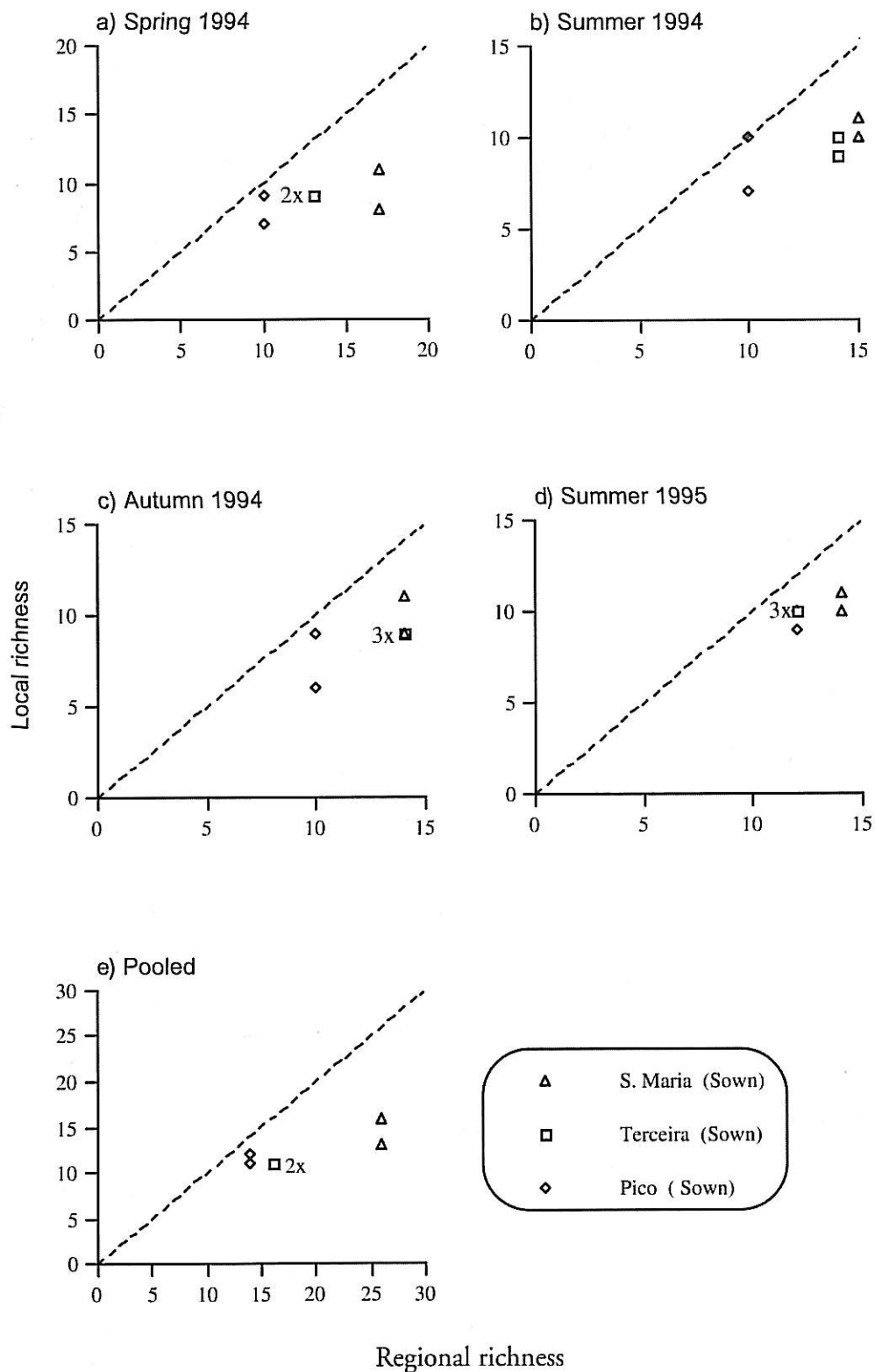
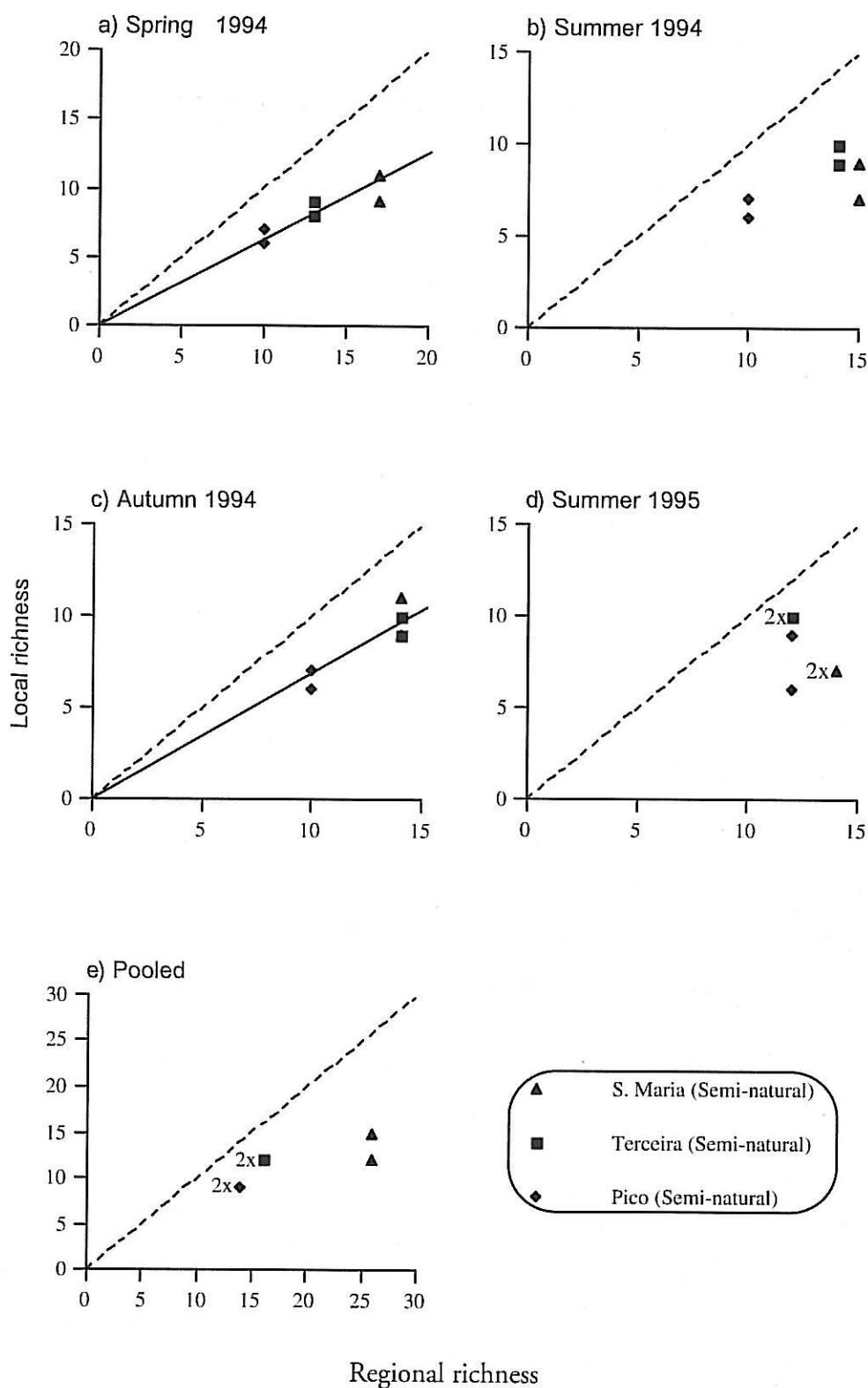


Figure 5 - Relationship between local and regional species richness for web-building spiders of sown pastures (open symbols) in three Azorean islands: S. Maria (triangles), Terceira (squares) and Pico (diamonds). The dashed line represents the condition where every species occurs at every site. a), b) and c) give a seasonal perspective during 1994; b) and d) permit a between-year comparison; e) gives the pooled data. See text for further details.



**Figure 6** - Relationship between local and regional species richness for web-building spiders of semi-natural pastures ((filled symbols) in three Azorean islands: S. Maria (triangles), Terceira (squares) and Pico (diamonds). The dashed line represents the condition where every species occurs at every site. a), b) and c) give a seasonal perspective during 1994; b) and d) permit a between-year comparison; e) gives the pooled data. A line is given only in the cases where a linear relationship between local and regional species richness was found at  $p = 0.05$ . See text for further details.

explain the local species richness of grass-feeders, since in all the three islands, pastureland is the most common habitat and the relationship between area of pastureland and local species richness of herbivorous arthropods is negative and not significant ( $\log \text{no. spp. herbivores} = 3.44 - 0.39 \log \text{area of pastureland}$ ;  $r^2 = 0.60$ ; n.s.).

Most of the experimental work already performed with herbivorous assemblages also supports the "proportional sampling hypothesis", that is, local richness is dependent upon the richness of the regional pool and independent of biotic interactions occurring at the local scale (Opler, 1974; Cornell, 1985a and b; Hawkins & Compton, 1992; Lawton *et al.*, 1993; Westoby, 1993). Therefore, I suggest that the mechanisms underlying the species richness patterns in local assemblages of sucking and chewing grass-feeding herbivores are mainly regional.

A typical "ceiling pattern" (sensu Cornell & Lawton, 1992; Cornell, 1993; Cornell & Karlson, 1997) was obtained for web-building spiders in both habitats, local species richness being independent of regional species richness. Natural experiments have shown clearer evidence of the impact of interspecific competition over short time scales in web-building spiders (Wise, 1995). Moreover, the spiders are considered a good taxonomic group for investigating the way in which species accumulate in differently aged and managed areas (Rushton *et al.*, 1989; Gibson *et al.*, 1992). Spiders might also be expected to have relatively predictable assemblages based on habitat structure (Brown, 1991; Uetz, 1991; Gibson *et al.*, 1992) (see also Borges & Brown, 2001). If competition is actually occurring in the web-building spiders, different features of the assemblages could be explained by the architecture of the vegetation of the habitats studied (Brown, 1991; Uetz, 1991). Borges & Brown (2001) showed that two measures of vegetation structure ("perennial grass cover abundance" and total vegetation "Williams's alpha diversity") were positively correlated with the abundance of web-building spiders. In sown pastures, the structure of the vegetation given by the "perennial grass cover abundance" was also less complex than in the semi-natural pastures (see also Borges & Brown, 2001). The analyses performed here suggested that sown-pastures are consistently more frequently saturated than semi-natural pastures (the "proportional sampling model" was rejected in all the seasons and in the pooled data in the sown pastures). However, the statistically significant correlations obtained in the semi-natural pastures (see Table 2) were expected to be obtained purely by chance, and should not be over-interpreted. These results did not confirm my initial predictions that competition would be more evident in the more mature habitat (see Arthur, 1987), no evidence have been found that this is so in the studied habitats.

Grazing management also affects the community structure of spider assemblages (Gibson *et al.*, 1992). Thus, the "ceiling effects" obtained in the spider assemblage may also be explained by disturbance effects of grazing. It could be hypothesized that, after a grazing event, higher extinction rates depressed the populations and that the time the vegetation had to recover before the sampling was performed was not enough to allow the populations recover through immigration from the surrounding landscape. However, this seems unlikely, since

most of the field sites were surrounded by a mosaic of pastures grazed in rotation. Plenty of source populations were, therefore, potentially available for recolonization ("mass effects" sensu Shmida & Wilson, 1985). Moreover, most of the web-building spiders are linyphiid spiders, engaged in aerial dispersal by "ballooning" (Wise, 1995). Because of their great dispersability, local extinctions are likely to be rare (Halley *et al.*, 1996).

Another possible explanation for the evidence of saturation found in the web-building spiders may be related to the family composition of the assemblage in the three islands: 79% of the web-building spiders found in Pico and 81% of the same group of species found in Terceira are linyphiids. In S. Maria, linyphiids represent only 31% of the web-building assemblage (41% in the Spring 1994; 53% in the Summer 1994; 50% in the Autumn 1994; 57% in the Summer 1995). The mechanisms producing these differential patterns in the pastureland of the three islands are most probably regional and related to long-distance dispersal, the age of the islands (see Borges & Brown, 1999), human interference (introductions) and speciating events (some of the non-linyphiid species found in S. Maria are endemic).

Having accounted for the above patterns in family composition of the web-building spiders, two possible explanations can be proposed to explain the observed ceiling effect:

i) first, as most of the non-linyphiids are less abundant and in some cases, very rare, the saturation evidence found for S. Maria could be an artefact; if this is true, the regional pool is overestimated by the inclusion of vagrant and rare non-linyphiid species, and together with great differences in species composition between sites (high "beta-diversity") in S. Maria, a saturation curve is artefactually generated;

ii) second, non-linyphiid species belong to several families, having probably different spatial and ecological requirements. However, if competitive interactions between species are actually occurring, they are likely to occur between the core species, mainly linyphiids. On the other hand, bodies of linyphiid specimens from S. Maria appeared to be larger (Borges pers. obs.) than those of specimens of the same species in the other two islands. This observation is contrary to the interactive model, since if competition is occurring in S. Maria I would not expect larger individuals there. However, the great proportion of core linyphiid species, together with low turnover in those species, may also indicate potential competitive interactions and true saturation.

Having in account the few degrees of freedom available in all the regression analyses performed all the above mentioned results should be interpreted very cautiously. Moreover, until further field experiments are carried out in order to test community-level effects of competition, the possible saturation pattern observed in the web-building spiders should not be taken as conclusive evidence that local competitive interactions are the main factor shaping the community structure of this assemblage in the Azorean pastures. What the results with this predatory assemblage suggest is that, even in cases where the local communities are saturated, history still exerts an influence (see Cornell, 1993). In this case, such influence is through differential family composition in the pool of web-building spider species in pastureland between the old island (S. Maria) and the recent islands (Terceira and Pico).

Regional processes are of overwhelming importance in shaping community processes (e.g. Ricklefs, 1987; Caswell & Cohen, 1993; Cornell, 1993; Lawton *et al.*, 1993; Ricklefs & Latham, 1993; Schluter & Ricklefs, 1993a and b; Westoby, 1993; Oberdorff *et al.*, 1995). For oceanic islands, the results imply that local species richness is controlled by regional processes like evolution (speciation) and colonization/extinction processes.

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**Appendix I.** List of 66 arthropod species (29 grass-feeding insects and 37 predatory web-building spiders) collected by means of direct search (#), suction (+) and pitfall traps (\*) in six sites of sown and six sites of semi-natural pasture in three Azorean islands (S. Maria, Terceira and Pico).

Species	S. MARIA				TERCEIRA			PICO			
	Sown		Semi-natural		Sown	Semi-natural		Sown	Semi-natural		
	1.1	1.2	2.1	2.2	3.1	4.1	4.2	5.1	5.2	6.1	6.2
<b>GRASS-FEEDERS</b>											
<b>ORTHOPTERA</b>											
Acrididae											
Gen. sp. a		#		#	#		#	#	#	#	#
Tettigoniidae											
Gen. sp. a	#	#	#	#							
Miridae											
<i>Pithanus maerkeli</i> (Herrich-Schaeffer)						+	*+	+	+	*+	+
<i>Trigonorylus caelestialium</i> (Kirkaldy)	+	*+	+		+						
<b>HOMOPTERA</b>											
Cicadellidae											
<i>Anoscopus albifrons</i> (Linnaeus)	*+	*+	*+	*+	*+	*+	*+	*+	*+	*+	*+
<i>Euscelidius variegatus</i> (Kirschbaum)	*+	*+	*+	*+	*+						
<i>Macrosteles sexnotatus</i> (Fallén)	*+		*+	+	*+	+	*+	+			
<i>Muellerianella</i> sp. a	*+	*+	*+	*+	*+	*+	*+	+	*+	+	+
Aphididae											
<i>Anoecia corni</i> (Fabricius)	*+		*+	*+	+		+	*+			+
<i>Rhopalosiphum insertum</i> (Walker)	*+	+	*+	+	+	*+	*+	*+	*+	*+	*+
<i>Rhopalosiphum padi</i> (Linnaeus)									+		
<i>Schizaphis graminum</i> (Rondani)	+										
<b>THYSANOPTERA</b>											
Phlaeothripidae											
<i>Haplothrips niger</i> (Osborn)	*+	*+	*+						*		
<i>Nesothrips propinquus</i> (Bagnall)	+	*+	+	*+							
Thripidae											
<i>Aptinothrips rufus</i> (Haliday)	*+	*+	*+	*+	*+	+	*+	*+	+		
<i>Plesiothrips perplexus</i> (Beach)			+	+							
<b>LEPIDOPTERA</b>											
Noctuidae											
<i>Agrotis ipsilon</i> (Hufnagel)	+		+								
<i>Agrotis segetum</i> (Denis & Schiffermüller)	*	*	*	*+	*						
<i>Mythimna unipuncta</i> (Haworth)	*+	*+	*+	*+	*+	*+	*+	*+	*+	*+	*+
<i>Noctua pronuba</i> (Linnaeus)	#			+				#	*	*	*
<i>Peridroma saucia</i> (Hübner)		*		+							
<i>Phlogophora meticulosa</i> (Linnaeus)	*	*	*+	*	*	*	*	*			
<i>Xestia c-nigrum</i> (Linnaeus)			*	#							
<b>COLEOPTERA</b>											
Scarabaeidae											
<i>Popillia japonica</i> Newman											
Rhynchophoridae											
<i>Sitophilus zeamais</i> Motschoulsky	*	*		*	*						
<i>Sphenophorus abbreviatus</i> (Fabricius)	*				*						
Curculionidae											
<i>Laparocerus azoricus</i> Drouet						*					
<i>Otiorhynchus sulcatus</i> (Fabricius)							+	*+	*		*+
<i>Otiorhynchus trophonius azoricus</i> Uyttenboog	*	*									
<b>WEB-BUILDING SPIDERS</b>											
<b>ARANEAE</b>											
Oecobiidae											
<i>Oecobius similis</i> Kulczynski		*									
Tetragnathidae											
<i>Leucognatha acorensis</i> Wunderlich			+								
<i>Meta merianae</i> (Scopoli)								*			
Araneidae											
Gen. sp. a					+						
<i>Gibbaranea occidentalis</i> Wunderlich			+								
<i>Mangora acalypha</i> (Walckenaer)	+		+	+							
<i>Neoscona crucifera</i> (Lucas)	+		+								

[illegible]