

The value of primary, secondary, and plantation forests for Neotropical epigeic arachnids

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Abstract. Plantations and secondary forests are becoming dominant components of many tropical forest landscapes. Yet we have an insufficient understanding of the value of these habitats for biodiversity conservation, and almost none for most arthropods in species-rich tropical forests. We sampled epigeic arachnids (Amblypygi, Araneae, Opiliones, Scorpiones, and Uropygi) in primary, secondary (14–19 years), and *Eucalyptus* plantation (4–5 years) forests in the Jari region of northeastern Brazilian Amazonia. We sampled five independent sites in each forest type between January and June 2005, collecting a total of 4824 individuals (3177 adults, 112 species), including 1864 adults (75 species) in *Eucalyptus*, 776 (60) in secondary forest, and 536 (72) in primary forest. We compared species richness, species-abundance distributions, and community structure, between the three forest types and identified the species that were characteristic of each forest type. Rarefaction analyses showed that undisturbed primary forest harbored significantly more species and a similar overall abundance as second-growth forest; while levels of species richness were similar between secondary forest and *Eucalyptus*. The species composition and abundance structure of arachnid assemblages was distinct in all three forest types. Considering all species sampled, 19% were only sampled in primary forest, 4% in secondary forest, and 19% in *Eucalyptus*. Most species sampled in plantation forests are known to be wide-ranging habitat generalists. Our data indicate that regenerating forests are not biological deserts (57% and 56% of species sampled in primary forest were also captured in secondary and plantation forests respectively) and can, therefore, help mitigate some of the negative effects of deforestation for epigeic arachnids. However, these replacement habitats do not provide a substitute for primary forest and may fail to conserve many of those species most at risk from extinction.

Keywords: Araneae, Opiliones, Scorpiones, tropical forests, biodiversity, deforestation

The rapid rate of forest conversion in the tropics (FAO 2006) is expected to lead to a massive extinction of tropical forest species (Pimm & Askins 1995; Pimm & Raven 2000). However, the loss of intact forest is being partially offset by the growth of regenerating and planted forests, which are becoming increasingly common across the tropical forest biome (Wright 2005; Grainger 2008), leading to suggestions that the predicted loss of species might be premature (Wright & Muller-Landau 2006). However, these claims are controversial and have been hotly contested due to the lack of empirical evidence that demonstrates the ability of these replacement forests to support native forest species (Gardner et al. 2007a; Laurance 2007), thereby highlighting the importance of research to determine the potential contribution of tropical secondary and planted forests for biodiversity conservation.

At present the conservation value of secondary forests and different plantation forests, from exotic monocultures to mixed-native species stands, remains poorly understood (Freitas et al. 2002; Reid & Huq 2005; Gardner et al. 2007a). Existing studies are few, and often present contradictory conclusions regarding patterns of conservation value depending on the particular taxon sampled and research methods used (Barlow et al. 2007a, 2007c, 2007d; Gardner et al. 2007a, 2007b). Part of the explanation behind the lack of consensus in these studies is the ubiquity of various methodological shortcomings and differences in analytical approach (Gardner et al. 2007a). Typical limitations of studies concerned with the effect of habitat change on tropical forest species include the lack of an undisturbed baseline, non-

independence among samples due to limitations in the spatial extent of the study, poor sample representation through low capture or trapping success, and inappropriate analyses (Gardner et al. 2007a). Furthermore, studies of habitat change and tropical forest biodiversity have largely been biased towards birds and terrestrial vertebrates and our understanding of cross-taxon variability in response patterns is embryonic (Barlow et al. 2007a).

We attempted to address the problems outlined above by making a comprehensive and robust evaluation of the value of primary, secondary, and plantation forests for a Neotropical epigeic arachnid fauna (encompassing the orders Amblypygi, Araneae, Opiliones, Scorpiones, and Uropygi). The Brazilian Amazon is a priority area for research on the effects of land-use change on arachnids because the absolute rate of deforestation is among the highest recorded anywhere in the world (Fearnside 2005). Our understanding of the diverse Amazonian arachnid fauna is largely restricted to a small number of well-studied areas of relatively pristine habitat (Heyer et al. 1999), and knowledge of many groups is limited to higher taxa (Adis 2002). Secondary forests are an increasingly dominant feature of the Amazon, following the rapid abandonment of large areas of land in the wake of deforestation (Houghton et al. 2000). In addition a large expansion in the plantation-forest estate is predicted during the coming decades in response to the burgeoning global demand for timber (FAO 2006), with much of the increase expected to occur in Brazilian Amazonia (Fearnside 1998).

By sampling a landscape created by a large-scale forestry project, we minimized the confounding influence of edge

effects and habitat fragmentation and maximized the spatial independence among sites of each forest type. To evaluate the biodiversity consequences of clearing areas of native forest for tree plantations and the potential for faunal recovery through natural regeneration, we examined patterns of alpha and beta diversity for leaf-litter arachnids among the three forest types and compared species-abundance distributions and patterns of assemblage structure and characteristic species in each forest. To our knowledge this is the first ecological study of the value of planted and regenerating forests for arachnids in the neotropics.

METHODS

Study area and site selection.—Sampling was conducted within the Jari Celulose/Grupo Orsa, a 1.7 Mha landholding on the Jari River between the states of Pará and Amapá in north-eastern Brazilian Amazonia (00°27'00"–01°30'00"S, 51°40'00"–53°20'00"W). Sampling was conducted only in the state of Pará. At the time of sampling the landholding was characterized by 53,000 ha of *Eucalyptus* plantations and 50,000 ha of regenerating native vegetation. Fifteen transects were established, with five replicate sites in each of primary, secondary and plantation forests (see either Barlow et al. 2007c or Gardner et al. 2007b for a map). The scale of the landscape enabled us to select study sites that minimized edge effects (the average size of *Eucalyptus* and secondary forest blocks are 17 km² and 27 km², respectively) and that were spatially independent (average distances between replicate sites within primary, secondary and *Eucalyptus* were 30 km, 9 km, and 11 km respectively). *Eucalyptus* and secondary forest sites were located at similar distances from the nearest areas of continuous primary forest (average distances were 1.1 km and 1.3 km, respectively). The areas of plantation and fallow land we studied were embedded in a large and virtually undisturbed primary forest matrix (> 5000 km²).

Primary forest sites are dominated by Burseraceae, Sapotaceae, Lecythidaceae, Mimosaceae, and Lauraceae, and are characterized by low levels of anthropogenic influence. The areas of secondary and plantation forest were first cleared (through cutting and burning) between 1970 and 1980. The secondary forest sites are all between 14–19 years of age and are characterized by an abundance of palms, *Inga* spp. and other pioneers. The *Eucalyptus* plantations were sampled between ages 4–5, and are characterized by an understory of annual plants (including many Asteraceae, Rubiaceae, Piperaceae, Poaceae, and Cyperaceae), lianas (e.g., *Davilla* spp., Dilleniaceae) and small trees such as *Vismia* spp. (Clusiaceae), *Mabea taquari*, and *Aparisthium cordatum* (Euphorbiaceae). Each of the three habitats are distinct with respect to the structure of the canopy, understory and leaf-litter vegetation layers (see Barlow et al. 2007b).

Arachnida sampling.—The arachnids were sampled between January and June 2005 using large dry pitfall traps (35 L buckets, 450 mm deep, with mouth diameter of 350 mm) suitable for sampling a wide range of epigeic organisms including small vertebrates. The buckets were arranged in four-trap arrays, with a 6 m long by 50 cm high plastic drift fence connecting them in a Y-shaped design - composed of one central bucket and one bucket at the end of each arm. Ten consecutive arrays were arranged 100 m apart along each

transect. Each sample comprises all arachnids collected over 7 consecutive days in one pitfall array. To minimize loss of specimens to predation and degradation inside the buckets, each array was inspected daily, and all arachnids removed. A total of 50 arrays were sampled over a 14 day period (2 × 7 day samples) in each forest type, producing a total of 100 samples per forest type, and 300 samples in total. Sampling was always conducted across three sites simultaneously, and in nearly every case we sampled sites from different forest types in each sampling session. Consequently the sampling in any given forest type (pooling across all sites) encompassed a wide range of environmental conditions.

All the analyses are based only on adult arachnids. Voucher specimens are stored in the collection of Museu Paraense Emílio Goeldi (MPEG) in Belém, Pará, Brazil. Identification was made using the MPEG reference collection and identification keys (see Adis 2002). Furthermore, some arachnids were identified by specialists at Universidade de São Paulo (Opiliones) and Instituto Butantan (some true spider families and Scorpiones) both in São Paulo, Brazil. A morphospecies number was used when the specific names were unknown (75% of the total number of species, with 56% being identified to the genus level).

Data analysis.—Patterns of species richness between forest types were analyzed by visual inspection of the 95% confidence intervals of individual-based rarefaction curves (EstimateS v.7.5, Colwell 2005). Standardized species-abundance “Whittaker” plots were used to compare species-abundance patterns between different forest types and species assemblages. Non-metric multidimensional scaling (NMDS) was used to define the overall differences in assemblage structure and composition within and among forest types. Ordinations were undertaken for both quantitative (abundance based using square-root transformed site-standardized data and the Bray-Curtis index) and qualitative (presence absence based, Sørensen index) data. We used the similarity percentage (SIMPER) analysis of Clarke & Warwick (2001) to determine the contribution that individual species made toward distinguishing differences in quantitative assemblage structure among forest types. Multivariate analyses were implemented in Primer v.5.

RESULTS

A total of 4824 individuals (3177 adults, 112 species including morphospecies) were collected, including 536 adults (72 species) in primary forest, 777 (60) in secondary forest, and 1864 (75) in *Eucalyptus* plantations. True spiders (Araneae) comprised the majority of the total arachnid fauna constituting 1939 adults (84 species). We sampled more than 71% of the expected number of species in each of the three forest types (Table 1), suggesting that our comparisons of species richness among the three forest types are valid. Sixty-four per cent of all species were recorded in primary forest, and 19% of all species were unique to this habitat (Fig. 1). The same proportion (19%) of the total number of species was also unique to *Eucalyptus* plantations (Fig. 1). By contrast few species (4%) were only found in secondary forest samples. Among the species collected in primary forest, 25% were rare (singletons and doubletons), while in secondary forest and plantations 5% and 20% respectively were rare by this classification.

Table 1.—Species richness, and sample completeness for arachnids sampled in primary, secondary and plantation forests in Jari region, Brazil. ^aNumber of individuals captured; ^bNumber of species observed; ^cNumber of species observed as a percentage of the estimated total richness (averaged from 3 estimators, Chao 1, Jack 1 and ACE, Colwell 2005); ^dPercentage of exclusive species sampled (i.e., not sampled elsewhere); ^eNumber of species observed as a percentage of the landscape total (all forest types) per site and per forest type.

Forest type	Site	N ^a	Sobs ^b	Coverage ^c	% Exclusive species ^d	Completeness ^e
Primary	Bituba	113	32	77.0	1.8	28.6
	Castanhal	100	28	71.6	1.8	25.0
	Estacao	70	26	60.9	5.4	23.2
	Pacanari	123	33	61.7	1.8	29.5
	Quaruba	130	34	72.2	3.6	30.4
	All	536	72	71.2	18.8	64.3
Secondary	Area 55	78	20	62.8	0.9	17.9
	Area 56	160	30	69.0	0.0	26.8
	Area 75	362	37	75.9	0.9	33.0
	Area 86	43	21	75.2	0.9	18.8
	Area 91	134	17	60.3	0.0	15.2
	All	777	60	81.1	4.4	53.6
<i>Eucalyptus</i>	Area 10	372	32	57.9	3.6	28.6
	Area 127	229	35	47.0	4.5	31.3
	Area 14	766	36	62.5	0.9	32.1
	Area 52	292	21	77.8	0.9	18.8
	Area 95	205	35	57.2	2.7	31.3
	All	1864	75	71.6	18.8	67.0
All Data		3177	112			

Undisturbed primary forest harbored significantly more species of Arachnida than either secondary forest or *Eucalyptus* plantations, although none of the accumulation curves are close to being saturated (Fig. 2). Following the rank abundance analyses, the species-abundance distributions are similar in each forest type (Fig. 3A). Furthermore, the rank-order of species abundances in primary and secondary forest is similar, whereas the species that are superabundant in *Eucalyptus* plantations are either very rare, or not found, in either primary or secondary forests (Fig. 3B). Differences in

assemblage structure among habitats were significant for all species assemblages whether they were based on quantitative (ANOSIM, $R = 0.59$, $P < 0.001$, Fig. 4) or qualitative data (ANOSIM, $R = 0.46$, $P < 0.001$). Furthermore, pairwise comparisons revealed that each of the forest types hosted a distinct arachnid assemblage (Fig. 4, quantitative data – $R > 0.36$, $P < 0.02$). The SIMPER analysis illustrated that most of the observed differences in assemblage structure among forest types cannot be attributed to a small number of species (Table 2). However, many of the same species were revealed as being important in distinguishing the arachnid assemblages that were sampled in individual forest types (e.g., *Ancylometes rufus* and *Ananteris pydanieli*, Table 2).

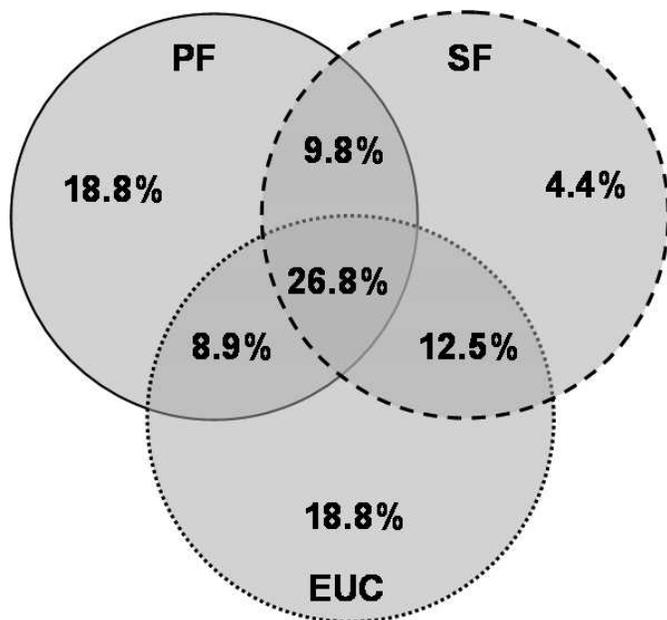


Figure 1.—Venn diagram of all species of arachnid sampled between primary (PF), secondary (SF), and *Eucalyptus* forests (EUC) in our study region.

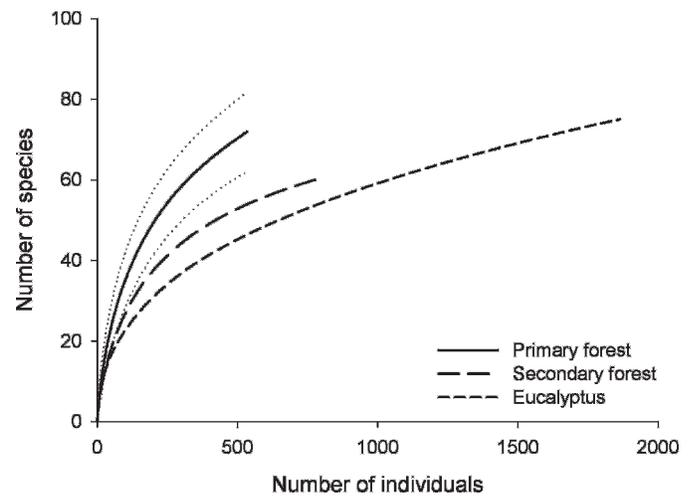


Figure 2.—Individual based rarefaction curves for arachnids in primary, secondary and *Eucalyptus* plantation forests. Fitted dotted lines indicate 95% confidence intervals (shown only for primary forest).

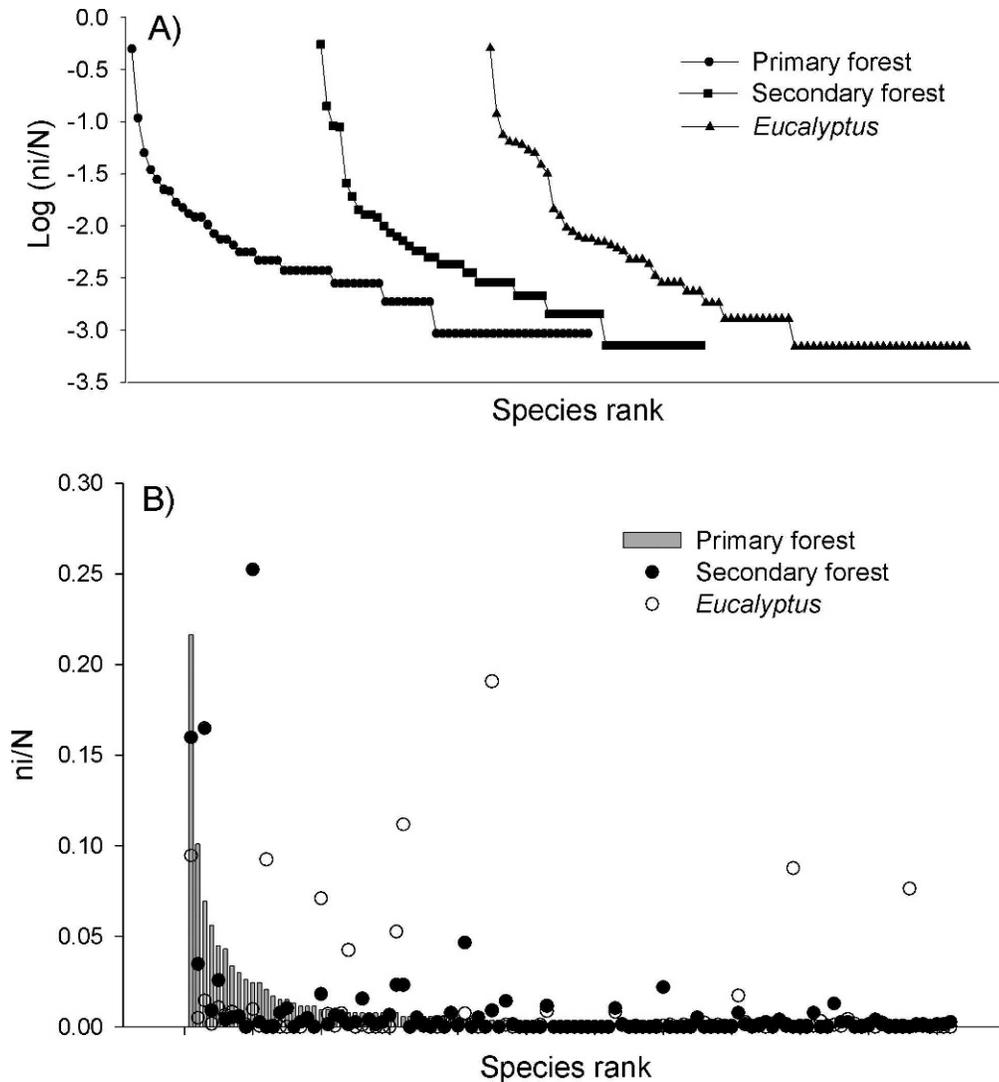


Figure 3.—(A) Dominance diversity (Whittaker) plots for arachnids in primary, secondary and plantation forests of northeastern Brazilian Amazon. Species are ranked according to the number of individuals of each species (n_i) and the total of individuals of all species (N) for each forest type. (B) Relative abundance (n_i/N) of all species in primary forest. Superimposed are the relative abundances of the same species sampled in secondary forest (filled circles) and *Eucalyptus* plantations (open circles).

DISCUSSION

This study presents the first data comparing patterns of arachnid diversity between primary, secondary, and *Eucalyptus* plantations in the Amazon region. We examine our results with respect to difficulties in the design of biodiversity field studies, patterns of species richness and species composition, and the importance of known environmental associations in explaining species-specific responses to landscape change.

Sampling issues in biodiversity studies.—Understanding the conservation value of human-dominated forest landscapes presents a significant challenge, particularly because of the high cost of biodiversity research (Gardner et al. 2008a) and the lack of investment in taxonomic research (Sheil 2001). This is particularly problematic for arachnids, as the majority of the tropical species are unknown (Redak 2000; Harvey 2002). However the results of many existing biodiversity studies are also confounded because they have been conducted over a

small spatial and temporal scale, are vulnerable to edge effects, and often lack independent replication (Gardner et al. 2007a).

We were able to overcome many of the potential methodological problems involved in understanding the conservation value of human-dominated forest landscapes by using a replicated experimental design in large study blocks that minimized edge effects. Even so, our study is not without its own set of problems; 84% of our sample could only be identified to morpho-species (without full Latin binomials), rarefaction curves suggest that our survey was far from complete in any of the habitats and many components of total epigeic arachnid assemblage, especially the small specimens, were not captured by our sampling method (e.g., Oonopidae, Schizomida). There may also be a seasonal bias due to our samples being taken mostly in the wet season, although Adis et al. (1987) did not observe any significant differences in the number of arachnid species captured between the dry and wet seasons in a neotropical secondary forest site.

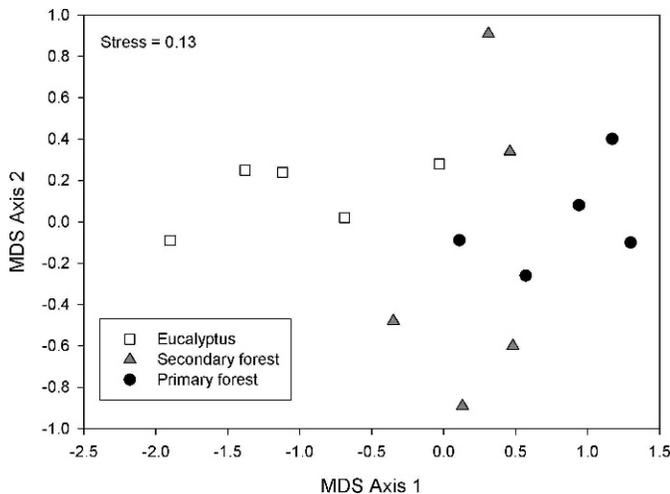


Figure 4.—Multi-Dimensional Scaling (MDS) ordination of arachnid community structure across primary, secondary and *Eucalyptus* forests. Ordination analyses are based on quantitative dissimilarity matrices.

Patterns of species richness.—We found significantly more species of epigeic arachnids in primary forest when compared to secondary forest and *Eucalyptus* plantation, while secondary forest and *Eucalyptus* had similar numbers of species. Barlow et al. (2007a) compared patterns of species richness between epigeic arachnids and 14 other taxa (including other invertebrates, vertebrates and trees) sampled at the same set of study sites and during the same time period. This broad analysis revealed a high level of inter-taxon variability in response patterns to the same gradient of landscape change with individual taxa falling into five major response groups (Barlow et al. 2007a). Epigeic arachnids with significantly more species in primary forest, and no observable difference in species richness between secondary and plantation forests, exhibited the same response pattern as dung beetles (Coleoptera: Scarabaeinae), lizards, and bats (see Gardner et al. 2007b, 2008b).

Patterns of species composition and species turnover.—Despite the fact that each forest type exhibited similar species-abundance distributions, patterns of species composition and community structure were distinct in all three forest types (Fig. 1), matching most other invertebrate and vertebrate taxa sampled at the same sites (Barlow et al. 2007a). Furthermore, these patterns were relatively insensitive to differences in the type of data used (incidence or abundance).

Perhaps surprisingly the same numbers of species were unique to *Eucalyptus* and primary forest sites in our samples (19% of the landscape total in each case), while only five species (4% of total) were caught only in secondary forest. Many of the dominant identified species found in plantation sites can be characterized as wide ranging habitat generalists (e.g., wolf spiders) and are common in open areas (Jocqué & Alderweireldt 2005). The three forest types harbored 30 species that occur in common (27% of total), while 10% and 9% of species were found only in primary and secondary and primary and plantation sites respectively (Fig. 1). These findings were supported by Ferreira & Marques (1998) in the Brazilian Atlantic forest, who show that leaf-litter

arthropods sampled in secondary forest more closely reflected primary forest communities than those found in *Eucalyptus* tree monocultures.

The observed dissimilarity in assemblage structure between forest types was only partly driven by differences in abundance of common species (versus differences in species composition) and as such there are few focal species that serve to effectively characterize the different forests in our samples.

Nevertheless, there are some examples where particular forest types are characterized by groups of species, as in the case of the wolf spiders (Lycosidae). It is well known that representatives of Lycosidae are favored by simplified habitats such as grasslands (Jocqué & Alderweireldt 2005) as well as forest areas with shallow leaf litter cover (Uetz 1979). Vegetation structure can have a marked influence on the distribution of arachnid fauna through the provision of suitable microhabitats, including the availability of suitable refuges and appropriate substrata for web attachment (Wise 1993; Indicatti et al. 2005). The fact that representatives of the Lycosidae were absent from both primary and secondary forest samples may indicate that *Eucalyptus* plantations present an appropriately simplified habitat for these species, while it is inaccessible to other species groups.

One particular species that was found only in *Eucalyptus* plantations was the miturgid *Teminius insularis* (Lucas 1857) a widespread species that occurs from Northern Argentina to Florida (Platnick & Ramírez 1991). Although to our knowledge nothing has yet been published on the ecology of this common species, its occurrence in our plantation sites, as well as other anthropogenic environments in Brazilian Amazonia suggests that it represents a true habitat generalist. In contrast, several species which were found to be very common in *Eucalyptus* plantations in this study were previously known from very few specimens elsewhere in Amazonia, and may even represent undescribed species (e.g., *Nops* spp., *Actinopus* spp.). It is possible that these species are opportunists which occupy a niche space (e.g., particular microhabitat) that is rare in primary forest but common in open, disturbed habitat. Marked increases in the abundance of species that are rarely found in native habitat (closed canopy forest) in plantation and secondary forest samples has been observed for many other taxonomic groups (e.g., heliothermic lizards, Gardner et al. 2007b).

A number of recent empirical studies have suggested that secondary forest regeneration can restore conditions suitable for supporting a significant number of primary forest species within decadal time scales (e.g., Dunn 2004; Quintero & Roslin 2005). These positive, yet preliminary results have supported optimistic claims as to the value of secondary forests for the conservation of tropical forest species (Wright & Muller-Landau 2006). Our results partly support this claim in that investment in the conservation of secondary forest may represent an investment in conserving part of the tropical forest biota for our study region (57% and 56% of species sampled in primary forest were also captured in secondary and plantation forests respectively). However, while regenerating forests can mitigate some of the negative effects of deforestation for epigeic arachnids, primary forest represents a seemingly irreplaceable habitat for many species (19% of landscape total in our samples of arachnids) as well as

Table 2.—Pairwise dissimilarities between the different forest types as defined by arachnid assemblages. For each pair of forest types, the top 10 ranked species that contribute to between forest type differences in assemblage structure are listed together with the average abundance in each of the two habitats, the ratio of the average dissimilarity between the two habitats to its standard deviation, and the contribution of that species to the overall observed dissimilarity between the two habitats. Primary (PF); Secondary (SF) and *Eucalyptus* forests (EUC).

PF-SF	Total dissimilarities 60.9%			
	SF	PF	Diss/SD	Contrib%
<i>Ancylometes rufus</i> (Walckenaer 1837)	25.6	7.4	1.11	4.12
Cosmetidae sp. 1	39.2	2.6	1.03	3.91
Ctenidae sp. n. 3	5.4	10.8	1.9	2.97
Ctenidae sp. n. 2	0.6	4.6	1.26	2.77
<i>Broteochactas mapuera</i> Lourenço 1988	1.4	6	1.66	2.74
<i>Fufius</i> sp. 1	7.2	0.4	1.12	2.67
<i>Paratropis</i> sp. 1	0	2.8	1.05	2.43
<i>Hapalopus</i> sp. 1	0.4	2.6	1.49	2.34
<i>Acanthoscurria</i> sp. 2	0.8	3.6	1.26	2.32
<i>Stygnus</i> sp. 1	3.6	0.8	1.08	2.17
<i>Actinopus</i> sp. 1				

PF-EUC	Total dissimilarities 73.9 %			
	EUC	PF	Diss/SD	Contrib%
<i>Nops</i> sp.1	71	0.4	1.96	4.78
Lycosidae sp. 1	32.6	0	1.37	4.35
Ctenidae sp.n. 3	1.8	10.8	2.73	3.64
<i>Teminius insularis</i> (Lucas 1857)	28.4	0	1.02	3.25
<i>Broteochactas mapuera</i> Lourenço 1988	0.6	6	2.45	3.19
<i>Acanthoscurria</i> sp.1	34.4	2.2	1.47	3.11
<i>Ananteris pydanieli</i> Lourenço 1982	26.4	1	1.85	3.08
<i>Ancylometes rufus</i> (Walckenaer 1837)	5.4	7.4	1.35	3.04
<i>Brotheas amazonicus</i> Lourenço 1988	35.2	23.2	1.08	3.03
<i>Stygnus</i> sp. 1	19.6	0.8	1.58	2.6

SF-EUC	Total dissimilarities 67.9 %			
	EUC	SF	Diss/SD	Contrib%
<i>Ancylometes rufus</i> (Walckenaer 1837)	5.4	25.6	1.34	5.96
Lycosidae sp. 1	32.6	0	1.35	5.25
<i>Nops</i> sp.1	71	1.4	1.55	4.59
<i>Acanthoscurria</i> sp. 1	34.4	0	1.68	4.54
<i>Teminius insularis</i> (Lucas 1857)	28.4	0	1.01	3.93
Cosmetidae sp. 1	3.6	39.2	1.02	3.9
<i>Brotheas amazonicus</i> Lourenço 1988	35.2	24.8	1.13	3.76
<i>Abapeba</i> sp. 1	15.8	0.2	2.63	3.22
<i>Actinopus</i> sp. 1	41.6	3.6	0.86	3.02
<i>Ananteris pydanieli</i> Lourenço 1982	26.4	2.8	2	2.94

representing a unique source of colonization for species able to move into degraded habitats (see also Floren & Deeleman-Reinhold 2005).

The results from our study are likely to represent a conservative estimate of the number of species found exclusively in primary forest (both due to taxonomic restrictions and sampling limitations – e.g., we didn't sample in the canopy). Nevertheless, the results presented here, and for other taxa sampled at the same study sites (e.g., dung beetles, Gardner et al. 2008b) suggest a more pessimistic picture of the value of regenerating forest land for native forest species than has been suggested elsewhere (Wright & Muller-Landau 2006). The discrepancy between the results from the Jari landscape and those of studies elsewhere in the tropics is likely to be partly explained by important differences

in biogeographical and landscape context, together with the influence of systematic sampling biases. These factors confound our ability to draw general patterns and indicate the danger of understating the tropical forest biodiversity crisis (Laurance 2007). To be effective, management strategies for production landscapes need to emphasize the importance of protecting remaining areas of primary forest. In areas where this is not possible, it is vital that the key methodological and ecological considerations highlighted in our study are given priority when assessing the conservation value of human-dominated forest lands.

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