



Distribution of ground-dwelling arthropods in tropical countryside habitats

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Abstract

The future of biodiversity depends to a great extent on the conservation value of human-dominated and semi-natural habitats. In a mixed agricultural landscape in southern Costa Rica, we compared the richness and composition of terrestrial arthropod communities occurring in three habitat types along a gradient of increasing disturbance: in a large (227 ha) forest fragment, small (3.8–5.3 ha) forest fragments, and sun coffee (1–3 ha) plantations. Pitfall trap sampling revealed decreasing morphospecies richness with increasing disturbance. Moreover, the number of species unique to a habitat type was lower in the smaller forest fragments and the coffee sites. We found significant changes in community composition associated with habitat at the levels of order (all arthropods), family (beetles), and morphospecies (carabids, scarabs, and ants). We identified no significant correlation of richness among the taxonomic orders, meaning these taxa are unable to serve as biodiversity indicators (for each other or for all arthropods) in the study region. Arthropod diversity presently found in countryside habitats is certainly lower, and perhaps less sustainable, than that of the extensive forested habitats fragmented > 40 years ago. It nonetheless remains substantial, suggesting a conservation opportunity in human-dominated landscapes of the tropics.

Introduction

In landscapes worldwide, ongoing fragmentation and clearance of native habitat is spawning complex mosaics of natural, semi-natural, and human-dominated habitats. As the extent of relatively natural habitat shrinks, the future of biodiversity depends increasingly on the conservation potential of rural “countryside” – agricultural plots, managed forest, gardens, and remnants of native habitat embedded in landscapes devoted primarily to human activities (Daily (1999, 2001); Rosenzweig 1999). A major challenge for conservation biologists is to understand the capacity of countryside habitats to support biodiversity and, conversely, the capacity of different taxa to exploit such habitats.

Ideally, one would like to know the composition and abundance of species likely to be sustained under alternative patterns of land cover. To forecast changes in biodiversity, recent approaches combine species’ habitat affiliations with alternative scenarios of change in land cover (e.g., Hughes et al. (2002)). Some projections incorporate other information, such as species’ area requirements and gap-crossing abilities (Dale et al. 1994; White et al. 1997; Pärt and Söderström 1999; Pearson et al. 1999). Because such information is so limited, however, the studies undertaken so far typically base their analysis on a small number of vertebrate and plant species (usually \leq 10, up to \sim 30); an exception is Dale et al. (1994), which incorporates general information on scarab beetles and euglossine bees.

Improving forecasts of changes in biodiversity, and relating these to ecosystem function and services (Didham et al. 1996; Chapin et al. 2000; Sala et al. 2000), will require much greater understanding of the impacts of habitat alteration on arthropods (Wilson 1987; McKinney 1999). Although limited in extent, work to date reveals several pertinent insights and priorities for further investigation. First, tropical countryside habitats can retain remarkably diverse arthropod assemblages decades after large-scale destruction of native habitat (Perfecto et al. 1996; Kitching et al. 2000; Ricketts et al. 2001, Devine et al. in press). There is, however, strong reason to expect a decline in diversity even with no further change in land cover, resulting from the slow but entrained reduction in plant diversity as particular species (e.g., long-lived forest trees) fail to recruit sufficiently (Benitez-Malvido 1998; Bruna 1999). In addition, microclimatic changes and other consequences of fragmentation can impact dynamics of invertebrate communities of remnant forest fragments (Didham et al. 1996; Laurance and Bierregaard 1997).

Second, some arthropod taxa show species-area effects in native habitats (Daily and Ehrlich 1995; Richardson et al. 1999) while others appear not to (at the scale of landscapes) (Daily and Ehrlich (1995, 1996); Ozanne et al. 2000). The capacity of scattered small (10^{-1} to 10^2 ha) fragments of native habitat to conserve diversity remains unknown for most arthropod taxa. Third, even closely related arthropod taxa, such as butterflies and moths, may not serve well as indicators of one another (Daily and Ehrlich 1996; Ricketts et al. 2002). It is clear that multi-taxon assemblages will be required for indicators (of either biodiversity or environmental quality; Kremen (1994) and Oliver and Beattie (1996), Kotze and Samways (1999), Kitching et al. (2000)), and that more extensive information on most taxa and their interspecies relationships will be required to plan and ensure their conservation.

Deeper understanding of these observations is crucial to predicting the long-term future of biodiversity and to generating the information and tools to manage it. The particular aims of this study were to: (i) compare the richness and composition of the ground-dwelling arthropod fauna occurring in forested habitats (large and small) and agricultural habitats of a tropical countryside; (ii) assess the utility of Carabidae, Scarabaeidae, and Formicidae as biodiversity indicators of all arthropods; (iii) gain insight to the faunal change likely to occur with continued forest

clearance and fragmentation; and (iv) provide a baseline for future comparisons.

Materials and methods

Study area

We conducted the study in Coto Brus, southern Costa Rica, where extensive forest clearance occurred approximately 40 years ago, primarily for small-scale coffee and cattle production. We worked at the Las Cruces Biological Field Station of the Organization of Tropical Studies during the wet season in June and August of 1999. The station is contiguous with the largest (227-ha) mid-elevation (~ 1100 m) forest fragment in the 15 km-radius study area. This forest and various smaller fragments (mostly < 5 ha) are embedded in a mosaic of pastures (typically 5 – 50 ha), coffee (typically < 2 ha), other agricultural plots (typically < 0.5 ha), and towns.

We sampled three habitat types: the large Las Cruces forest (“LC Forest”), three sites spaced as far apart as possible (pairwise distances of 300 m, 900 m, and 1200 m), to minimize effects of pseudoreplication; “Fragment,” three nearby smaller forest fragments, ranging from 3.8–5.3 ha, one site each (400, 500, and 2300 m from Las Cruces forest); and “Coffee,” three moderately sized sun coffee plantations, 1–3 ha with 2–3 m high shrubs, and similar in age, one site each (spaced ≥ 1 km apart). In fragment and coffee sites, traps were situated ≥ 10 m and < 20 m from the fragment / coffee plot edge. Steep topography constrained trap locations in the LC Forest habitat type; all were situated ≥ 10 m and < 200 m from the forest edge. The elevation of all sites was ca. 1100 m.

Sampling design and protocol

In each site we placed four pitfall traps (BioQuip Product #2838, with a ca. 10 cm diameter opening) randomizing the location of each trap while ensuring that the traps were separated by ≥ 25 m, for a total of 36 traps. In placing them, we took pains to minimize disturbance of soil and detritus. To prevent flooding and overflow from rain, we covered each trap with a white plastic plate, mounted above the trap to leave a ca. 3 cm-high entrance on all sides. We used a solution of 50% ethylene glycol and 50% water in the trap.

We obtained twelve 24-hour pitfall trap samples from each plot (4 traps \times 3 samples). We waited one week between sampling periods at a site and rotated among sites at random to minimize phenological and weather effects.

We identified all specimens to order using Borror and White (1970) and Borror et al. (1989) and measured their length. We identified beetles to family using White (1998). Finally, DMG identified carabids (Carabidae), scarabs (Scarabaeidae), and ants (Formicidae) to morphospecies, in accordance with the guidelines of Oliver and Beattie (1996).

Statistical analyses

To examine the effect of habitat type on arthropod richness, abundance, and length, we conducted one-way analyses of variance. For these analyses, we pooled the data from the 4 traps within each site. To compare the relative evenness of abundance of taxa across habitat types, we used J' , calculated as $-\sum p_i \ln p_i / \ln S$ where p_i is the proportion of a sample made up of the i th species and S is the total number of species in the sample (Pielou 1966). We also calculated the number of "unique" taxa for each habitat type, defined as those taxa represented by at least two specimens in a single habitat type and no specimens in the other two habitat types.

We used the Bray-Curtis similarity coefficient (Bray and Curtis 1957) to quantify and compare the similarity of community composition among habitats. This index is calculated as $S_{jk} = 100 \{1 - \sum_{i=1, p} |y_{ij} - y_{ik}| / \sum_{i=1, p} (y_{ij} + y_{ik})\}$, where p represents the total number of species to be compared across sites j and k and y_i is the sampled abundance of species i . The index thus varies between 0 and 100, with 100 indicating identical community composition. We then used a multidimensional scaling (MDS) algorithm (SYSTAT 7.0 1997) to test for clustering of sites by community composition. This procedure yields two-dimensional plots in which the proximity of sites is proportional to their degree of similarity. Finally, to calculate the probability of acquiring a given level of clustering by chance, we used a randomization program (Anosim; Carr (1997)).

Results

Effects of habitat type

In 9 weeks of sampling, we collected 5976 arthropods representing 20 orders. The three habitat types were comparably rich at the order level: we found 14 orders represented in LC Forest sites, 17 in Fragment sites, and 15 in Coffee sites. Among ants and scarabs, the LC Forest sites yielded the greatest number of morphospecies, followed by Fragment sites; these differences were not statistically significant, however. Among the carabid morphospecies, Coffee sites contained none, and Fragment sites had more than the LC Forest sites.

Community composition differed strikingly across habitat types as visualized in similarity plots based on Bray-Curtis coefficients (Figure 1). Relative evenness in species diversity was substantially higher in LC Forest and Fragment than in Coffee sites. These results are summarized in Table 1. We found significant differences across habitat type in the number of individuals for Coleoptera ($F = 6.75$, $p < 0.05$), Diptera ($F = 12.22$, $p < 0.01$), Orthoptera ($F = 7.09$, $p < 0.05$), and Blattaria ($F = 15.30$, $p < 0.01$); in each case, the LC Forest and Fragment sites had greater abundance than the Coffee sites.

To identify more precisely the compositional change associated with a change in habitat, we looked at the taxa unique to each habitat type in our sample for each taxonomic level in our study. The number of unique arthropod orders did not differ significantly across habitat types. Nonetheless, some trends appear evident. The LC Forest sites generated the largest number of unique groups among the coleopteran families (8) and the pooled morphospecies data (24; for Formicidae, Carabidae, and Scarabaeidae). The Coffee sites had the next highest level of uniqueness in these groups.

The 545 Coleoptera specimens comprised 25 families. Evenness on the family level was comparable across habitat types, but the LC Forest site was richer than the others (Table 2). We found differences in number of individuals trapped across habitat types for Leptodiridae ($F = 11.18$, $p < 0.01$), Staphylinidae ($F = 13.46$, $p < 0.01$), and Carabidae ($F = 4.98$, $p = 0.053$). Coffee, in all these cases, had significantly lower abundances than the other habitat types. For Staphylinidae and Leptodiridae a greater abundance was observed in the Fragment sites and for Carabidae more individuals were present in LC Forest samples.

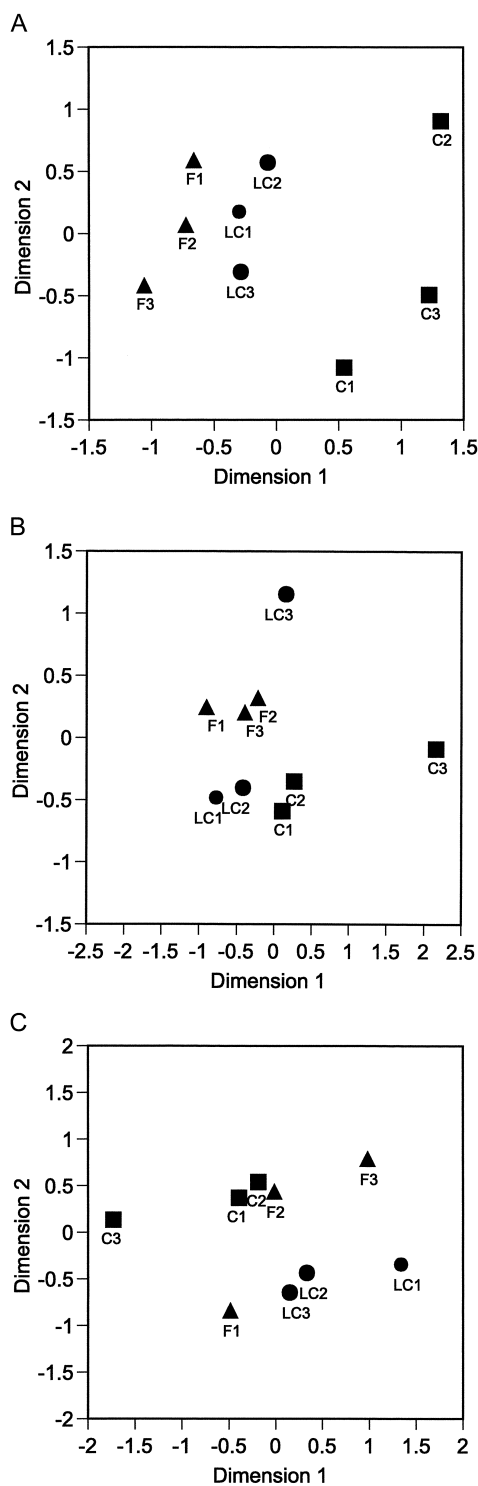


Figure 1. Similarity plots of Bray-Curtis coefficients among the 9 sampling sites. (a) Order-level analysis, pooling all arthropod orders plus ants; stress = 0.03, $p = 0.007$, $R = 0.531$. (b) Family-level analysis, pooling all coleopteran families; stress = 0.06, $p = 0.014$, $R = 0.342$. (c) Morphospecies-level analysis, pooling data on ants, carabids, and scarabs; stress = 0.11, $p = 0.039$, $R = 0.300$. Circles represent sites from the Las Cruces forest, triangles the Fragment sites, and squares the Coffee sites. Plots a and b were generated from 4th-root-transformed data; plot c is based on presence/absence data (because ant abundance was not well censused in our design). Stress represents the accuracy of the Euclidean distances in the figure in representing the similarity coefficients; R is a measure of the sum of the variance within habitat groups.

We found little evidence for a general relationship between body size (as approximated by length) and habitat type. Collembola were smaller in Coffee sites than in LC Forest and Fragment sites ($F = 185.53$, $p < .001$). Other length differences within order, family, and morphospecies across habitat types were not significant.

Evidence for indicator taxa

To test for the ability for the sampled taxa to serve as biodiversity indicators on the scale of this study, we calculated the correlation (as Pearson's correlation coefficient) in richness between taxa across the nine sites (Table 4). All correlations were positive but none was significant, including those incorporating the pooled morphospecies richness advocated by Oliver and Beattie (1996).

Discussion

Effects of habitat type

Forest fragmentation and replacement of forest vegetation with sun coffee plantations in the Las Cruces region are associated with substantial changes in the arthropod community sampled by pitfall traps. These changes were significant on all taxonomic levels studied, involving alteration in the numbers of individuals, morphospecies, and families of major taxa.

There was no clear trend in community composition across the habitats studied, with the exception of significantly higher abundance of some of the more diverse arthropod groups (Coleoptera, Diptera) in the forested sites. Although the richness of orders was comparable across habitat types, evenness of abundance declined with increasing anthropogenic disturbance. We observed a decrease in the richness of coleopteran families with increasing disturbance. There was also a sharp decrease in coleopteran abundance in the coffee plantations sampled in our study.

Ecosystem processes and services

One of the consequences of changes in insect communities as a result of forest fragmentation and clearance is the disappearance of "beneficial" insects and the "ecosystem services" they provide. Declines in key insect-driven ecosystem functions such as pollination, predation, parasitism and decomposition have

Table 1. Summary of arthropod individuals captured in pitfall traps, by order and habitat type.

	LCForest		Fragment		Coffee		ANOVA
	Total	Variance	Total	Variance	Total	Variance	
Collembola	464	3796.3	332	1025.3	1735	158152.3	ns
Diptera	407	3070.3	742	5058.3	111	28.0	0.008
Hymenoptera	166	236.3	167	70.3	299	2232.3	ns
Coleoptera	238	961.3	234	93.0	73	258.3	0.029
Orthoptera	145	460.3	264	1372.0	31	82.3	0.026
Acarina	59	24.3	92	466.3	42	28.0	ns
Araneae	25	24.3	28	37.3	75	217.0	ns
Hemiptera	33	147.0	14	10.3	50	366.3	ns
Homoptera	16	16.3	7	0.5	38	132.3	ns
Blattaria	8	0.3	21	3.0	6	1.0	0.004
Isopoda	7	2.3	13	24.3	0	–	ns
Opiliones	4	2.0	9	0.5	2	–	ns
Dermoptera	4	2.0	3	0.5	1	–	ns
Chelonethida	0	–	4	0.3	1	–	ns
Mallophaga	0	–	0	–	1	–	ns
Scorpionida	0	–	1	–	0	–	ns
Siphonaptera	0	–	0	–	1	–	ns
Strepsiptera	0	–	1	–	0	–	ns
Thysanoptera	0	–	1	–	0	–	ns
Thysanura	1	–	0	–	0	–	ns
Total Orders	14	–	17	–	15	–	–
Unique Orders	0	–	0	–	0	–	–
Total Individuals	1577	–	1933	–	2466	–	–
Shannon (H')	1.85	–	1.81	–	1.15	–	–
Evenness (J')	0.70	–	0.64	–	0.43	–	–

been noted in various studies (Didham et al. 1996; Klein 1989; Souza and Brown 1994), and in this study, we also observed declines in some important groups such as scarab and carabid beetles. All the scarabs caught in pitfall traps were dung beetles and their abundance in fragments and coffee plantations declined by 67% and 30% respectively when compared to the forest plots, although the differences were not significant. A large decline in dung beetle abundance may cause pronounced reductions in decomposition rates (Klein 1989), slowing the recycling of nutrients into the soil. This may result in more nutrient-poor soils, in changes in forest fragment plant communities, and possibly in elevated transmission rates of some diseases (because various disease-causing pathogens that live in excrement are killed by dung beetles; Klein (1989)).

There was also a significant decline in carabid abundance in forest fragments and coffee plantations.

In fact, we captured no carabids in coffee plantation pitfall traps, which is disconcerting considering the abundance of carabid beetles in all kinds of ground habitats (Borror and White 1970). Carabid beetles are important predators of many invertebrates, including agricultural pests like snails (Borror and White 1970)

Indicator taxa

Although our sampling regime was not designed to identify biodiversity indicators along a disturbance gradient, our results speak to the capacity of the taxa selected to serve as indicators of arthropod diversity. Carabid and scarab beetles, along with ants were selected for morphospecies analysis in this study based on the 1996 paper by Oliver and Beattie suggesting that richnesses of these three taxonomic groups are inversely correlated and that the combined richness may correlate with measures of local diversity. (We

Table 2. Summary of coleopteran individuals captured in pitfall traps, by family and habitat type.

	LCForest		Fragment		Coffee		ANOVA
	Total	Variance	Total	Variance	Total	Variance	
Staphylinidae	84	129.0	127	60.3	19	0.5	0.006
Scarabaeidae	63	372.0	22	16.3	34	74.3	ns
Erotylidae	22	14.3	22	26.3	6	1.0	ns
Carabidae	17	8.3	7	4.5	0	–	0.053
Scolytidae	9	4.0	10	4.3	4	0.0	ns
Leptodiridae	3	0.5	19	8.3	0	–	0.009
Ptilidae	6	2.0	10	4.3	4	0.3	ns
Nitidulidae	9	0.5	3	–	0	–	ns
Chrysomelidae	3	0.5	1	–	2	–	ns
Curculionidae	4	–	1	–	1	–	ns
Scydmaenidae	3	0.5	0	–	1	–	ns
Byrrhidae	0	–	4	2.0	0	–	ns
Leiodidae	1	–	3	0.0	0	–	ns
Bruchidae	0	–	4	–	0	–	ns
Mycetophagidae	3	–	0	–	0	–	ns
Tenebrionidae	2	–	0	–	0	–	ns
Anthicidae	1	–	0	–	1	–	ns
Cryptophagidae	1	–	0	–	1	–	ns
Bostrichidae	2	0.0	0	–	0	–	ns
Monommidae	1	–	0	–	0	–	ns
Pselaphidae	1	–	0	–	0	–	ns
Anthribidae	0	–	1	–	0	–	ns
Melandryidae	1	–	0	–	0	–	ns
Hydrophilidae	1	–	0	–	0	–	ns
Nosodendridae	1	–	0	–	0	–	ns
Total Families	22	–	14	–	10	–	–
Unique Families	3	–	2	–	0	–	–
Total Individuals	238	–	234	–	73	–	–
Shannon (H')	2.02	–	1.68	–	1.56	–	–
Evenness (J')	0.65	–	0.64	–	0.68	–	–

excluded pselaphid beetles, advocated in the same paper, from our analysis because of insufficient abundance in our samples.) The positive correlations of richness derived among all taxa investigated in our study, combined with the contrasting results of the work of Oliver and Beattie performed in the Australian tropics, supports the hypothesis that relationships among taxa will vary with location (May 1992). We found no significant correlation between any of our richness values at any level of taxonomic organization across the nine sites in this study. This further diminishes support for the search to identify invertebrate indicators for biodiversity in land use planning on the scale of this study (Daily and Ehrlich 1996; Prendergast 1997; Flather et al. 1997). The progress

in the search for biodiversity indicators at larger spatial scales (such as among biomes) suggests that investigation may still be warranted (Weaver 1995; Wilcox et al. 1986).

Faunal change

Our study demonstrated not only changes in community composition with increasing human activity, but also a differential morphospecies turnover among the habitat types investigated. This sort of information may serve as a basis for projecting the effects of future changes in land use on local biodiversity. For instance, we found a trend of declining unique ant morphospecies richness with increasing disturbance

Table 3. Summary of individuals captured in pitfall traps, by morphospecies and habitat type. Data on abundance of Formicidae are excluded because of the lack of independent capture in the sampling regime.

	LCForest	Fragment	Coffee	Total
Formicidae				
Morphospecies	37	32	27	61
Unique Morphospecies	9	2	7	–
Scarabaeidae				
Individuals	62	22	34	118
Morphospecies	12	9	6	20
Unique Morphospecies	6	2	1	–
Carabidae				
Individuals	17	7	0	24
Morphospecies	2	4	0	5
Unique Morphospecies	1	0	0	–
Total Morphospecies	51	45	33	86
Total Unique	16	4	8	–

(Table 3). Furthermore, we found that 19 species unique to the union of the LC Forest and Fragment sites would likely be lost if both site types were converted to agriculture. This number is considerably greater than the number of species that occur in each of these habitat types and the Coffee sites independently. There were many ant morphospecies found in the Fragment sites that were not found in the Coffee, suggesting that smaller fragments may contribute substantially to regional ant richness. A hypothetical situation representing extreme clearance of forest habitats, in which all specimens from the LC Forest and Fragment habitat types are eliminated from our analysis, would result in 27 morphospecies in the sample, as compared to the 46 ant species that would remain in a hypothetical region maintaining a patchy distribution of small forest fragments. It is important to emphasize that fragment populations in this study are not geographically isolated and may be supported

Table 4. Correlation matrix (reporting Pearson's r) of the richness of different taxa across the 9 sites. "All MS" represents comparisons performed on the pooled morphospecies data. Few carabid morphospecies were sampled, making the robustness of values for carabids low.

	Formicidae	Scarabidae	Carabidae	Coleoptera	All Orders	All MS
Formicidae	1.00	0.28	0.31	0.34	0.03	–
Scarabidae		1.00	0.46	0.26	0.46	–
Carabidae			1.00	0.74	0.54	–
Coleoptera				1.00	0.31	0.50
All Orders					1.00	0.39
All MS						1.00

by populations in the larger forest fragments of the region. If such reinforcement of populations is occurring we would expect our estimate of morphospecies loss with complete removal of the LC Forest to be falsely optimistic.

A recent study of arthropods in this fragmented landscape has demonstrated a halo of elevated moth diversity surrounding the LC Forest (Ricketts et al. 2001). If such a halo exists for the taxa studied here, then projections based on our findings will be overly optimistic. In conservation planning for arthropods, it will be important to understand the dependence of species occurring in agricultural habitats on resources from forest remnants, in order to assess more accurately the effects of additional deforestation on regional biodiversity (Estrada et al. 1998; Golden and Crist 2000; Didham et al. 1998; Gibbs and Stanton 2001).

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