LOSSES OF RARE FOREST INVERTEBRATES AND DIVERGENT RATES OF LITTER DECOMPOSITION UNDER DIFFERENT LAND USES

by

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Habitat destruction and fragmentation are dominant disturbances in tropical landscapes, but consequences of these changes for invertebrates and ecosystem functioning are poorly described and explained. In northwestern Costa Rica I used pitfall sampling and litter bag experiments to investigate consequences of two land-use changes (forest conversion to orange groves and forest fragmentation) for litter invertebrates and decomposition. I infer effects of forest conversion and fragmentation based on comparisons of intact forest with orange groves and forest fragments, respectively.

Invertebrate diversity differed among habitat types. Invertebrate family richness and evenness in orange groves were 24% and 56% lower, respectively, relative to intact forest. Beta diversity (dissimilarity in invertebrate composition) among orange groves was high, likely due to variation in microclimate with grove age and/or management regime. Forest patch diversity was similar to that of intact forest, and composition was marginally more dissimilar between forest patches than between intact forest sites. Consistency in local richness between intact and fragmented forest was largely attributed to a suite of disturbance-adapted taxa detected exclusively in forest patches. Approximately 11% of the families that were naturally common in intact forest were rare or range-limited in forest fragments. These results emphasize the need for large forest reserves to prevent considerable losses of intact forest fauna. Losses of intact forest invertebrates in both orange groves and forest patches were explained by habitat modification (increases in litter temperature) and were more likely for families that are naturally rarer.

Forest conversion and fragmentation had divergent effects on litter decomposition. During the wet season, decomposition was 9% faster in orange groves relative to forest. This pattern was explained by higher temperatures and lower litter cover in orange groves; I discuss both indirect and direct microenvironment mechanisms. In contrast, dry season decomposition rates were 7% slower in forest fragments than those in intact forest. Fragmentation effects on decomposition were explained by the action of shredder and/or saprophagous macroinvertebrates, which enhanced decomposition rates in intact forest but not in forest patches. The seasonal aspect of these results emphasizes the importance of accounting for intra-annual variation when assessing disturbance effects in natural systems.
PREFACE

M.C. was the principal author of this research and completed all fieldwork, data analyses and thesis preparation. However, Chapters 2 and 3 are written in first-person plural as they have been prepared to submit for publication. Diane Srivastava was M.C.’s supervisor throughout all stages of this research and provided guidance on study design, methodology and thesis preparation. Both research chapters will be submitted for publication under the co-authorship of M.C. and D.S.
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1 INTRODUCTION

Anthropogenic disturbances have transformed landscapes in most ecosystems and regions of the world. Scientists have issued warnings for several decades of high biodiversity losses resulting from extensive human impact on natural systems (e.g. Myers 1988, Western 1992, Pimm et al. 2000, Ehrlich and Pringle 2008, Bradshaw et al. 2009). Global biodiversity is currently threatened with extinction rates comparable in magnitude only to handful of cataclysmic mass extinctions in the Earth's geological history (May et al. 1995, Pimm et al. 1995). This biodiversity crisis is the result of the separate and synergistic effects (Brook et al. 2008) of disturbances such as land-use change, climate change, pollution, introduced species, and exploitation (Sala et al. 2000, Novacek and Cleland 2001).

While disturbance may reduce landscape- and regional-level biodiversity, species richness may increase locally due to responses of disturbance-adapted taxa (Tocher et al. 1997, Lewis 2009). Individual species may have positive, negative or negligible responses to disturbance and local communities will reflect these varied responses (e.g. Robinson et al. 1992, Margules et al. 1994, Ingham and Samways 1996, Didham et al. 1998a, Davies et al. 2000, Debinski and Holt 2000, Daily et al. 2003). It is desirable to document these changes from both an academic and a conservationist's point of view. Understanding biodiversity changes under different disturbance scenarios can yield insight into community interactions and assembly processes. It is also important for efforts to mitigate human impacts in natural systems. We need to be able to predict extinction probabilities to understand and manage biodiversity changes under shifting patterns of land cover. However, information gaps hinder our ability to predict and stem biodiversity losses for many taxonomic groups, ecosystems, and disturbance scenarios. This gap is particularly noticeable in the tropics and for highly diverse, poorly described components of biodiversity such as invertebrates (McKinney 1999, Dunn 2005, Collen et al. 2008).

Concerns in the scientific and conservation communities regarding biodiversity losses have naturally led to questions regarding the consequences of these losses for ecosystem functioning (Chapin et al. 2000). During the last two decades a body of research has grown to test the biodiversity ecosystem function (BDEF) hypothesis of enhanced ecosystem functioning
with increases in biodiversity (Hooper et al. 2005, Srivastava and Vellend 2005, Cardinale et al. 2006). Several (nonexclusive) mechanisms can explain positive BDEF relationships. First, ecosystem functions may be enhanced with greater biodiversity because a greater number of species is more likely to include species with greater contributions to ecosystem functions (sampling mechanism: Huston 1997, Tilman et al. 1997, Ives et al. 2005). Second, more complex competitive interactions in biologically rich systems can yield a more efficient use of resources and therefore elevated ecosystem function rates (complementarity mechanism: Tilman et al. 1997, Loreau 2000). Third, BDEF relationships may be explained by facultative interactions, which are more prevalent in more diverse communities (facilitation mechanism: Heard 1994, Cardinale et al. 2002). In general, evidence supports the BDEF hypothesis (Balvanera et al. 2006, Cardinale et al. 2006). However, research indicates that relationships between biodiversity and ecosystem functioning can be both positive and negative (Ives et al. 2004, Srivastava et al. 2009) and when observed, BDEF relationships vary in magnitude (Balvanera et al. 2006, Cardinale et al. 2006).

The majority of BDEF research has been carried out under controlled conditions and/or in simple systems with few, clearly defined trophic levels. While these design characteristics have been helpful, and often necessary, in determining the presence and causes of BDEF relationships, they can be problematic when making generalizations that apply to real world situations (Srivastava and Vellend 2005, Duffy et al. 2009). We now recognize that BDEF relationships differ among extinction scenarios; stronger BDEF relationships are often evident under realistic patterns of species extinctions than under the random extinction scenarios commonly used in experimental BDEF studies (Srivastava and Vellend 2005, Duffy et al. 2009). BDEF research in multi-trophic systems subject to realistic extinction patterns is needed to understand the nature and generality of BDEF relationships in nature and strengthen conservation arguments based upon the BDEF hypothesis (Srivastava and Vellend 2005, Duffy et al. 2007, Duffy et al. 2009).

Here I present a study of land-use effects on invertebrate communities and litter decomposition functions in a fragmented landscape in northwestern Costa Rica. Two disturbance processes have transformed my study landscape: conversion of native tropical moist forest for agriculture (principally orange groves), and fragmentation of forest into smaller patches. I make
inferences regarding the effects of these two processes based on comparisons among four habitats; intact forest, large and small forest patches, and orange groves. First I report results of an observational study of land-use effects on meso- and macroinvertebrates in ground litter communities (Chapter 2). I sampled invertebrates using pitfall traps in the four habitats to assess the effects of forest conversion (intact forest vs. orange groves) and fragmentation (intact vs. fragmented forest) on community characteristics. I investigate relationships between changes in the litter microenvironment and in invertebrate communities. I also test whether two traits, abundance and spatial variability in abundance, predict the responses of intact forest fauna to the disturbances of forest fragmentation and conversion. This study contributes to our understanding of in situ responses to landscape alteration within a diverse but poorly described taxonomic group, and the use of two easily measured traits in predicting those responses. The results also provide insight regarding the conservation value of small forest fragments for invertebrate fauna typical of tropical moist forest, and complement the relatively greater amount of data available from biodiversity studies in human-dominated landscapes in temperate regions.

Second, I present the results of an in situ experimental study of land-use effects on leaf litter decomposition (Chapter 3). Results are based on litter bag decomposition measurements in the four habitats, in both dry and wet seasons. I investigate contributions of both habitat (microenvironment) modification and macroinvertebrates to forest conversion and fragmentation effects on decomposition. I assessed the role of macroinvertebrates in mediating litter bag loss by comparing decomposition rates in the two litter bag treatments: one mesh size allowed entry of macroinvertebrates, and the second restricted their entry. The combined results from Chapters 2 and 3 allow me to infer BDEF relationships for a component of complex, multi-trophic communities following different land uses in the tropics.
2 LAND-USE EFFECTS ON LITTER INVERTEBRATE COMMUNITIES AND
LOSSES OF RARE FOREST INVERTEBRATES IN A TROPICAL FRAGMENTED
LANDSCAPE

2.1 Summary

I investigated land-use effects on litter invertebrates with an observational study (pitfall sampling) in the four main habitats (intact forest, large and small forest patches, orange groves) in my study landscape. The two disturbances of forest fragmentation and conversion to orange groves differed in their effects on invertebrate communities. Forest conversion reduced local invertebrate diversity: average family richness and evenness were 24% and 56% lower, respectively, in orange groves relative to intact forest. Community composition differed between intact forest and orange groves, and was related to lower litter biomass in orange groves. In orange groves on average, I failed to detect 27% of invertebrate families typical of intact forest. Average similarity in invertebrate composition between orange groves was 25% lower than between forested sites. In contrast, forest fragmentation did not affect aggregate measurements of invertebrate diversity. However, community measurements masked losses of approximately 11% of intact forest taxa in forest patches. Richness in patches was sustained by a large suite of families detected exclusively in fragmented forest. Local extirpations of intact forest fauna in both forest patches and orange groves were explained by higher temperatures in these habitats, and were more likely for taxa that were naturally rarer. Results emphasize the value of small forest fragments in maintaining local richness of invertebrate families but suggest large forest reserves are necessary to maintain intact forest invertebrates in disturbed landscapes.

2.2 Introduction

Habitat destruction and fragmentation are dominant threats to animal communities worldwide (Sala et al. 2000, Fahrig 2001) and the effects of these disturbances have been investigated for many taxa (Fahrig 2003). Biodiversity is generally negatively affected by habitat fragmentation (Turner 1996), but empirical studies indicate varying species-specific responses (Robinson et al. 1992, Margules et al. 1994, Ingham and Samways 1996, Debinski and Holt 2000, Daily et al. 2003) in remnant habitat patches. At the within-patch scale, species are
affected by concurrent changes in habitat area and quality. First, island biogeography theory (MacArthur and Wilson 1967) predicts fewer species in smaller areas of forest due to reduced habitat heterogeneity and because reduced resource availability in smaller patches can support smaller populations that are in turn more vulnerable to extinction. Stochastic models of population extinction predict greater extinction risk in smaller populations because of density dependence in the proximate causes of extinction such as environmental and demographic stochasticity (Lawton 1994). In general, species with low abundance (Caughley 1994, Andrén 1996, Foufopoulos and Ives 1999) and high population variability (Didham et al. 1998a, Heino et al. 1997, Fagan and Holmes 2006) are more vulnerable to chance losses of individuals and are predisposed to local extinction following habitat reduction.

Second, populations can be affected by deterministic changes in habitat quality associated with patch size (Bierregaard et al. 1992, Laurance 1997, Laurance et al. 1997). Changes in vegetation structure and microenvironment at the edges of remnant forest patches (Didham and Lawton 1999) can affect animal populations directly (if conditions pose a desiccation risk or otherwise exceed physiological tolerances), or indirectly, via changes in resource availability or species interactions (Kareiva 1987, Kruess and Tscharntke 1994, Laurance et al. 2002). These edge effects have been shown to affect individual species either positively (Fowler et al. 1993, Brown and Hutchings 1997, Didham et al. 1998b, Davies et al. 2001) or negatively (Brown and Hutchings 1997, Spector and Ayzama 2003), and differ with regional context (Harper et al. 2005). In communities affected by edge effects on forest quality, richness may either increase or decrease with changes in patch size (Ries and Sisk 2008).

Populations in remnant forest patches can also be affected by between-patch processes that mediate the importance of changes in habitat area and quality at the within-patch scale. Terrestrial fragmented landscapes are the result of two concurrent but distinct processes of land-use change: fragmentation of native vegetation into patches and its clearance for conversion to other (matrix) habitat. When the matrix is inhospitable to forest fauna, island biogeography (MacArthur and Wilson 1967) and metacommunity theory (Leibold et al. 2004) predict decreased richness in forest fragments due to increased isolation and decreased immigration rates. However, matrix habitats vary in their permeability to forest animals’ movements (Ricketts 2001) and disparate matrices support different portions of forest biodiversity (e.g. Daily et al.
2001, Daily et al. 2003, Summerville and Crist 2004). Patch-centric studies fail to acknowledge variability in matrix habitat quality and linkages between forest and non-forest habitat (Koelle and Vandermeer 2005). Forest species' responses to the within-patch effects of habitat reduction and modification may differ depending on whether the matrix serves as a barrier, conduit for dispersal among forest remnants, or suitable habitat (Warburton 1997, Gascon et al. 1999, Daily et al. 2001).

Matrix habitat can further affect communities in remnant forest by providing a source of new species. In matrix habitat, altered habitat structure and associated changes in microclimate and resource availability often result in losses of forest specialists and replacement with a smaller number of generalist, disturbance-adapted taxa (Ricketts et al. 2001, Daily et al. 2003, Lövei et al. 2006). Immigration of new taxa (Laurance 1991, Laurance and Bierregaard 1996, Tocher et al. 1997, Ricketts et al. 2001) can affect forest richness either positively or negatively, depending on the relative numbers of new taxa that add to the forest species pool and taxa that replace previous residents. Colonizations of matrix taxa in forest edges may lead to local increases in forest patch richness, but this is not necessarily reflected at the landscape scale because disturbance-adapted taxa tend to be widespread species (Ingham and Samways 1996, McKinney and Lockwood 1999). Landscape diversity reflects the complementary among sites within a landscape with respect to habitat type and the species complement of each habitat (Chan and Daily 2008). Landscape diversity is thus influenced by species richness within patches and within the matrix, as well as differences in community composition (beta diversity) between habitats.

Invertebrates represent a large portion of tropical biodiversity, but effects of different land uses on this group are both poorly described and often complex in pattern (Davies et al. 2001, Laurance et al. 2002). In this study, we investigate the effects of tropical forest fragmentation and conversion to orange groves on leaf litter invertebrates. We first contrast the effects of forest fragmentation with those of forest conversion on invertebrate community diversity and composition, as well as on a subset of invertebrates typical of intact forest. After testing for patterns, we then test for mechanisms. We investigate relationships between land-use effects on the litter microenvironment and on invertebrate community structure and ask if microenvironment changes explain land-use effects on intact forest invertebrates. We also test if
the demographic traits of low abundance and high spatial variability in abundance predispose forest invertebrates to extinction.

We predicted lower invertebrate richness in orange groves relative to forest for two reasons. First, lower litter cover in the orange groves provides fewer resources for litter invertebrates. Second, higher temperatures and lower litter moisture may impose desiccation stress on litter fauna and reduce invertebrate populations in orange groves. Implicit in these predictions are changes in community composition between habitats. We expect lower richness in orange groves to reflect losses of invertebrate families typical of intact forest, particularly families that are naturally rarer and/or that have more variable abundances among intact forest sites. We also predicted greater similarity in composition both within and between different orange groves, relative to forest, because habitat is homogenized following forest conversion.

If habitat modification within fragmented forest is important, lower invertebrate richness might be predicted in smaller forest patches relative to larger patches and/or intact forest because edge effects that create unfavourable microclimate conditions (higher temperature, lower litter moisture via increased exposure: Frith and Frith 1990, Cadenasso et al. 1997, Didham and Lawton 1999) are more prevalent in smaller patches. On the other hand, higher wind disturbance and treefall in small patches can create more ground litter (Laurance et al. 2000, Harper et al. 2005) and would be expected to have a positive effect on invertebrate richness. If stochastic extinctions within patches are important, losses in fragmented forest should be higher among forest taxa with lower abundances that are more spatially variable. We expected species composition in forest patches to be less heterogeneous than in intact forest, because of decreased microhabitat variability and/or replacement of forest diversity with fewer widespread immigrant taxa from matrix habitat. If movements between fragmented forest and orange groves are important and orange groves serve as sources of individuals or invading species to fragments, community richness and composition should be more similar between orange groves and forest patches than between orange groves and continuous forest.
2.3 Methods

**Site description**

We sampled litter invertebrate communities in a 10 x 10 km landscape adjacent to the Área de Conservación Guanacaste (ACG), northwestern Costa Rica. This area has a distinct dry season from January through May (115.9 ± 50.0 mm average monthly rainfall) and receives 325.6 ± 44.1 mm/month during the remainder of the year (April 2006 - March 2007, M. M. Chavarria, pers. comm.). The landscape covers an elevation range of 1035 - 1645 m. Much of the native tropical moist forest has been fragmented by land-use changes into remnant patches (0.4 - 36.7 ha, > 20 years since fragmentation). Forest clearance has been motivated by human settlement, cattle ranching and increasingly by agriculture. Principal land-use categories in this region are now, from most to least common, orange groves, secondary forest, pasture and pineapple plantations. Habitats surrounding forest patches are predominantly orange groves, with some pasture land. Orange agriculture near the ACG is dominated by Del Oro, S.A.

**Sampling**

Sampling was based on a contrast of four habitats common within the study landscape: intact forest, large (6.1 - 21.4 ha) and small (0.6 - 4.0 ha) forest patches, and orange groves. We selected five sites within each of the four habitat categories, along the landscape’s elevation range (Figure 2.1). Intact forest sites were chosen to represent the different structures of intact forest throughout the study landscape, and encompass a range of succession stages. We considered different forest patches to be separate sites and excluded patches with swamp sections from site selection. Sites were spaced by a minimum of 100 m and sites within each habitat category were spaced by a minimum of 390 m. Forest patches were all bordered by orange groves, with the exceptions of one small (S5) and one large (L3) patch (Figure 2.1), which were located in young teak (*Tectona grandis*) plantation and regenerating pasture, respectively. Two patches (L3 and S4) were moderately affected by human disturbance. Three orange grove sites (O1, O2 and O3) were managed by Del Oro, S.A. The other two orange groves (O4 and O5) were managed by small private farms. O5 was no longer harvested at the time of this study, and was covered in several years’ overgrowth. Agrochemicals were not applied to orange groves with the exception of O4, to which fertilizer was sprayed twice yearly.
Invertebrate samples and microenvironmental measurements were taken from plots located along transects within each site. We used this sampling design to ensure data represented a broad area of central habitat in each site. Transects began 250 m from forest edge in intact forest and 15 m from edges in orange groves. The forest patch transects were positioned about the geometric center of each patch; plots in small and large forest patches were located 26 - 100 m and 50 - 212 m from patch edge, respectively. We sampled five 8 x 8 m plots spaced every 20 m along transects in each site. Plots were located 5 m perpendicular to walked transects to minimize disturbance by observers. All plots were located ≥ 10 m from streams.

**Invertebrate samples**

We sampled litter invertebrates from 19 May – 11 June during the 2007 dry season. Given our objective of comparing communities among different habitats, we selected pitfall sampling as the most reliable trapping method for this study. Pitfall sampling may be biased against taxa and/or trophic groups in upper sections of the litter layer (Prasifka et al. 2007). However, these biases are assumed consistent among samples, and pitfall samples are assumed to reflect trends characteristic of litter invertebrate communities across sites. Pitfall sampling allows for greater sampling effort than invertebrate extraction from mesh litter bags. Different sampling methods based on Winkler extraction of invertebrates from litter scoop samples or mesh bags also fail to sample all taxa with equal efficiency (Prasifka et al. 2007). Furthermore, the sensitivity of Winkler extraction to climate (Didham et al. 1998b) and difficulties in standardizing litter scoops across disparate ground vegetation in forest sites and orange groves (M. C., pers. obs.) made these methods less reliable than pitfall sampling for comparative purposes.

We prepared pitfall traps using plastic cups of 9 cm internal diameter and 10.8 cm depth. One cup was placed in the center of each plot with its upper rim flush with the solid soil surface. A plastic rain cover (26 cm diameter) was suspended at a height of 30 cm over each pitfall trap using wooden stakes. One third of each pitfall trap (~190 mL) was filled with a solution of scentless detergent and salt to reduce surface tension and slow the sample’s degradation. Each trap was retrieved after 6 d (total sampling effort 600 trap days). Trapped invertebrates were preserved in 70% ethanol following trap retrieval. Invertebrates were enumerated and sorted to family. In the few cases (7 of 16 orders) where identification to family was not possible,
individuals were sorted to order. Richness counts therefore represent conservative estimates of richness at the family level, but will be referred to hereafter as family richness. Pitfall data were pooled by site for all data analyses.

**Microenvironment measurements**

We used litter depth, standing litter biomass, and litter moisture content, slope, elevation, location coordinates, and temperature to characterize the leaf litter microenvironment. Litter measurements were taken from 5 May - 4 July 2007 during the late dry season. We measured litter depth at the beginning of the field season in five undisturbed locations in each plot. A 20 x 20 cm leaf litter sample was scraped from the solid soil surface in an undisturbed location in each plot. The wet biomass of each litter sample was recorded before drying, within 12 h of collection. Each sample was then dried to constant mass (standing litter biomass, ± 0.001 g). We estimated the litter moisture content of each litter sample as 100% x (wet mass-dry mass)/dry mass. Litter depth, standing litter biomass, and litter moisture were each averaged by site. Topographic slopes were measured with a clinometer (+ 0.5°) in the center of each plot and averaged by site. Elevation and location along the north-south axis of the study landscape were recorded for each site using a handheld GPS unit (GARMIN Geko 201, ± 9.5 m) to account for spatial correlation between sites. We recorded elevation and location in the center of each forest patch and at 350 and 20 m from edges in intact forest and orange grove sites, respectively.

Temperature measurements were taken during the 2007 wet season (26 October – 18 December) using an electronic temperature probe (Hanna Instruments HI 9024, ± 0.4° C). We recorded air (1.5 m above ground) and leaf litter (half-litter depth) temperatures at five-minute intervals for one hour, while moving among four randomly selected locations in a 12 x 12 m plot centered at the positions of GPS measurements. Temperature measurements were taken in all weather conditions, for logistical purposes. In an attempt to account for diurnal weather variation, all temperature records were taken within one hour of local solar noon, during which time incoming solar radiation is fairly consistent. We repeated measurements at each site on two different days to account for daily weather differences. We calculated the average air and leaf litter temperatures for each site.
Data analyses

Univariate invertebrate community measurements

We used analyses of variance (ANOVAs) to compare the three univariate community measurements of total abundance, rarefied richness and evenness among habitats (intact forest, large and small forest patches, orange groves). Each measure was calculated at the site level. Richness and evenness represent separate components of invertebrate family diversity. Family richness was rarefied (to n = 338) to make comparisons among sites with disparate abundances. Family evenness was calculated as \( E_{1/D} \) (based on a common form of Simpson’s dominance index of diversity: Smith and Wilson 1996), which deemphasizes families more susceptible to sample size effects. We ran separate one-way ANOVAs for each of the three response variables of abundance, rarefied family richness and family evenness. Post-hoc pairwise comparisons between habitats were made using Tukey-Kramer HSD tests. Sequential Bonferroni corrections (Peres-Neto 1999) were applied to account for our use of multiple response variables for ANOVAs, but did not affect conclusions.

Habitat effects on invertebrate community composition

Patterns in community composition among sites were first graphically examined using non-metric multidimensional scaling (NMDS: Clarke 1993). NMDS ordination was based on Bray-Curtis similarity measures derived from invertebrate abundance data. Bray-Curtis similarity measures most strongly emphasize changes in relative abundances. Relative abundances were \((\log_{10} + 1)\)-transformed to downweight the influence of numerically dominant taxa and smooth variation due to habitat heterogeneity. We then assessed differences in community structure among the four habitats using an analysis of similarity (Clarke 1993). This analysis was carried out using the ANOSIM procedure in the program PRIMER (Clark and Gorly 2001) and was also based on the Bray-Curtis similarity measurements. ANOSIM uses a resampling algorithm to test for significant differences in community composition between treatments, based on the scaled difference between average similarity between habitats and average similarity within habitats (\( R \), ranges from 0 to 1). Finally, we investigated habitat effects on dissimilarity in family composition among sampling locations (a form of beta diversity). We assessed beta diversity at two scales: between sites, and between plots within a site. Beta diversity between sites was measured using similarity measures among replicate sites within
We tested habitat effects on beta diversity among sites using a Monte Carlo randomization test (PopTools in Excel, version 3.0.6: http://www.cse.csiro.au/poptools/) to account for non-independence between similarity measures. Beta diversity between plots was measured for each site as the average Bray-Curtis similarity between plots. Between-plot similarities were calculated from $(\log_{10} + 1)$-transformed relative abundance data. We tested habitat effects on beta diversity within sites using a one-way ANOVA. The ANOSIM, Monte Carlo test and ANOVA were followed by post-hoc pairwise comparisons between habitats, with sequential Bonferroni corrections for multiple tests.

We next examined the responses of intact forest invertebrates to different land-uses. In the absence of a list of invertebrate families that typify intact forest fauna in the region, we refer to the set of families we collected in intact forest as intact forest fauna. The fraction by which this list was reduced was calculated for each forest patch and orange grove. These fractions will be referred to as each site’s “forest family extirpations”. The effect of type of disturbance (forest fragmentation vs. forest conversion) on forest family extirpations was analyzed using a generalized linear model (GLM) with quasibinomial errors. Recorded “extirpations” from the intact forest pool of families include true family losses as well as sampling error (undetected families). Since the probability of sampling errors increases with family rarity, we restricted these analyses to invertebrate taxa that were common in intact forest. We excluded families that were spatially rare (in < 40% of intact forest sites) and/or numerically rare (< 50 individuals detected in total across intact forest traps) from calculations of forest family extirpations.

**Invertebrate-environment relationships**

We predicted that habitat effects on invertebrate community structure and forest family extirpations would be related to differences in microenvironment among habitats. One-way ANOVAs were used to test for differences in microenvironmental measurements among habitats. Significant ANOVAs were followed with pairwise comparisons between habitats. Sequential Bonferroni corrections were applied to account for our use of multiple response variables for ANOVAs, but did not affect conclusions.

We investigated relationships between biotic patterns and measured environmental variation using RELATE and BIOENV procedures (Clarke and Ainsworth 1993) in PRIMER.
RELATE was used to test the relationship between invertebrate community structure (the Bray-Curtis similarity matrix underlying the NMDS ordination) and the matrix of normalized Euclidean similarity measurements derived from sites’ microenvironmental measurements, using Spearman’s rank order correlations. BIOENV identified microenvironment variable(s) with the highest rank correlation with invertebrate community structure.

Finally, we examined whether land-use disturbances on forest family extirpations could be explained by measured environmental differences among habitats. We included our microenvironmental measurements as predictors in the earlier GLMs with quasibinomial errors. Specifically, we tested if disturbance (either forest fragmentation or conversion) was still a significant predictor of forest family extirpations after including microenvironment variables in the model. If environmental differences among habitats explain disturbance effects on forest family extirpations, then disturbance should no longer be significant after accounting for these differences.

**Responses of invertebrate families to disturbances**

We next investigated the responses of individual invertebrate families to land-use differences. We used similarity percentages (SIMPER) procedures in PRIMER to calculate invertebrate families’ contributions to dissimilarities between forested and non-forested habitats (forest conversion effects) and between intact forest and forest fragments (forest fragmentation effects). The abundances of the top six discriminating taxa identified by SIMPER routines were tested for responses to each of forest fragmentation and forest conversion using Wilcoxon (Kruskal-Wallis) tests with significance levels adjusted for multiple tests.

An invertebrate family's susceptibility to disturbance may be affected by its abundance or population variability. We used GLMs with quasibinomial errors to assess the effects of these attributes on extirpation probabilities of intact forest families first in forest fragments, and second in orange groves. Family abundances were calculated as averages in intact forest sites and were (log\(_{10}\) + 1)-transformed to meet model assumptions. Population variability was calculated for each family as the coefficient of variation in abundance among the five intact forest sites. We calculated extirpation probabilities for each family (or order, when identification to family level was not possible) separately for forest patches and for orange groves, as the
fraction of disturbed sites in which that family was not trapped. Spatially and numerically rare taxa, as previously defined, were excluded from these analyses.

All ANOVAs and GLMs were performed in R (version 2.7.2: R Development Core Team 2008).

2.4 Results

Univariate invertebrate community measurements

We collected a total of 13805 individuals in pitfall traps representing 16 orders (123 taxa total, of which 116 were identified to family and 7 identified to order). Total invertebrate abundance was similar among sites ($F_{3,16} = 1.78, p = 0.19$; Figure 2.2). Raw richness did not differ among habitats ($F_{3,16} = 1.41, p = 0.28$). However, rarefied richness differed marginally among habitats ($F_{3,16} = 3.18, p = 0.05$; Figure 2.2). This difference was largely driven by lower richness in orange groves (on average 24% and 19% lower than average richness in intact forest and forest patches, respectively: Figure 2.2), although post-hoc pairwise comparisons were not significant. Family evenness was low in all sites; in each site, more than 46% of all individuals were accounted for by the site’s four most abundant taxa. Evenness differed among habitats ($F_{3,16} = 4.82, p = 0.01$; Figure 2.2). Family evenness in orange groves was approximately half of that in forested sites (Tukey-Kramer HSD; Figure 2.2).

Habitat effects on invertebrate community composition

Invertebrate community structure differed among habitats (ANOSIM: $R = 0.26, p < 0.01$). Forest communities were clearly separated from orange grove communities (Figure 2.3). The abandoned orange grove (O5) was an exception to this pattern, and was more closely clustered with forest sites than with other orange groves. Invertebrate composition differed between orange groves and each of large (ANOSIM: $R = 0.52, p < 0.01$) and small (ANOSIM: $R = 0.48, p < 0.01$) forest patches, as well as between intact forest and orange groves (ANOSIM: $R = 0.52, p < 0.01$). Large and small forest patches were only weakly differentiated in NMDS space, and tended to cluster with intact forest sites (ANOSIM: all pairwise comparisons among forested sites, $p > 0.05$; Figure 2.3).
Beta diversity between sites differed among habitats (Monte Carlo ANOVA: $F_{3,36} = 34.52, p < 0.01$; Figure 2.3). On average, community composition was 25% more variable among orange groves than among replicate forest sites ($p < 0.01$ for each comparison of orange groves with a forested habitat). Beta diversity between sites increased marginally with reduction in forest area; mean similarity was 3% lower among large patches than among intact forest (intact vs. large: $p = 0.08$) and 3% lower among small patches than among large patches (large vs. small: $p = 0.07$). Community composition was 6% more variable, on average, among small forest patches than among intact forest (small vs. intact: $p < 0.01$). As expected, beta diversity was always greater between sites than between plots for each habitat. Within a site, beta diversity between plots did not differ among habitats (ANOVA: $F_{3,16} = 2.37, p = 0.11$).

Of the 79 taxa present in intact forest sites, 22 were numerically and spatially common (>50 individuals trapped in ≥40% of intact forest sites, see Appendix). This set of 22 taxa was used in analyses of disturbance effects on forest family extirpations and were also common throughout the landscape: each was detected in at least 40% of disturbed sites. Losses of intact forest families were significant in both forest patches and orange groves (both $p < 0.03$) but differed between the two disturbances of forest fragmentation and conversion ($F_{13,14} = 4.53, p = 0.05$). On average, more than twice as many intact forest taxa (21-35%) were locally extirpated from orange groves ($t = -2.74, p = 0.02$) than were extirpated in forest patches (11-15%, $t = -5.78, p < 0.01$).

**Invertebrate-environment relationships**

Microenvironment measures were related to patterns in invertebrate community structure (RELATE: $\rho = 0.41, p = 0.01$). The best correlation between environment and community composition was given by a combination of litter biomass and litter depth (BIOENV: $\rho = 0.68$). Location and climate measures were poorly associated with invertebrate community structure (Table 2.1).

Most microenvironment measures were similar among habitats (Table 2.1). However, both litter biomass and litter temperature differed among habitats (Table 2.1); orange groves had lower litter biomass and higher litter temperature than forested habitats (Tukey-Kramer HSD;
Figure 2.4). Litter temperature was moderately correlated with changes in litter biomass \((r = -0.54, p = 0.01)\).

Of the two microenvironmental measures that differed among habitats, only litter temperature affected forest family extirpations (litter temperature: \(p = 0.04\), litter biomass: \(p = 0.30\)). For every \(1^\circ\) C increase in litter temperature, forest family extirpations in disturbed habitats increased by 53 - 60%. We assessed whether litter temperature could explain disturbance effects on forest family extirpations. Neither forest conversion nor fragmentation affected forest family extirpations after accounting for changes in litter temperature \((p = 0.51)\).

**Invertebrate families’ responses to disturbances**

A broad range of taxa contributed to differences in invertebrate communities among habitats. 13 families were only found in orange groves. Of the 37 taxa that were only trapped in forested (intact or fragmented) sites, three families were only detected in intact forest and 18 families, 1 order were detected solely in forest patches (Appendix). 54 taxa were detected in all of orange groves, intact and fragmented forest.

We examined in detail the six taxa most responsible for each of forest conversion and fragmentation effects on community composition. Together the top six discriminating taxa for each land-use effect accounted for 33% of the cumulative dissimilarity between orange groves and forests and 22% of the cumulative dissimilarity between intact forest and forest patches (Table 2.2). Three beetle families and the order Colembolla each contributed more than 5% to dissimilarities in community composition between disturbed habitat and intact forest (Table 2.2). Abundances of Colembolla, Phoridae, Opiliones and four beetle families (Bostrichidae, Pselaphidae, Scarabaeidae, Staphylinidae) were greater in forests than in orange groves whereas one taxon, Formicidae, reached highest abundances in orange groves (Table 2.2; Figure 2.5). However, none of the top discriminating taxa differed in abundance between intact forest and forest patches (Table 2.2).

Forest taxa with higher abundances in intact forest had lower extirpation probabilities in both orange groves \((F_{1,20} = 17.01, p < 0.01)\) and forest fragments \((F_{1,20} = 10.51, p < 0.01; \text{Figure 2.6a})\). Taxa with more variable abundances among intact forest sites also had higher extirpation probabilities in both types of disturbed habitat (orange groves: \(F_{1,20} = 9.50, p < 0.01\), forest...
fragments: $F_{1,20} = 7.64, p < 0.01$; Figure 2.6b). Both attributes explained more of the changes in forest family extirpations in orange groves than in forest patches (Figure 2.6). Population variability was inversely proportional to abundance in intact forest ($r = -0.63, p < 0.01$). After statistically accounting for taxon abundance, population variability no longer explained extirpation probabilities in either forest fragments ($F_{1,20} = 0.90, p = 0.34$) or orange groves ($F_{1,20} = 0.40, p = 0.53$).

### 2.5 Discussion

Invertebrate communities differed in composition between forests and orange groves and beta diversity was greater between disturbed sites than among intact forest sites. These land-use effects, in addition to extirpations of intact forest taxa in disturbed habitats, were explained by habitat modification as well as attributes of the invertebrate families themselves.

The litter microenvironment explained land-use effects on invertebrates. In our landscape changes in community composition were correlated with leaf litter amount, which was lower in orange groves than in forest. Microclimate change explained forest family extirpations in both forest patches and orange groves; increases of 1°C litter temperature predicted losses of 48% intact forest taxa. Litter quantity and temperature have also been shown to mediate forest fragmentation effects in other landscapes (Didham et al. 1998a, Ferguson 2004). Environmental effects on invertebrates may be direct, such as increased desiccation risk in hotter temperatures, or indirect, via influences on species interactions and/or influxes of disturbance adapted taxa. We cannot distinguish between direct and indirect microenvironment effects in this study without greater resolution of the food web. Litter temperature was more severely affected by forest conversion than fragmentation because canopy shading is lower in orange groves than in forest. On average, more than twice as many intact forest taxa were locally extirpated from orange groves than from forest fragments. The high effect size for temperature is of concern given trends of climate change in the tropics (Thompson et al. 2006).

We expected population variability to confer higher extirpation risk to forest invertebrates in disturbed habitats because more variable populations are also more vulnerable to stochastic extinctions (Gaston 1994, Heino et al. 1997). Population variability was negatively correlated with abundance in our landscape, as in other tropical invertebrate communities.
(Didham et al. 1998a), and did not explain further variation in forest family extirpations after we statistically accounted for the dependence of population variability on abundance. Population fluctuations may lead to extirpation only below small, population-specific abundances (Brook et al. 2006, Traill et al. 2007).

As predicted, abundance was useful in predicting forest family extirpations; rarer intact forest taxa were less likely to be detected in both forest fragments and orange groves. Other studies of fragmentation effects on invertebrates either contradict (Didham et al. 1998a) or corroborate (Schoener 1992, Warburton 1997, Davies et al. 2000, Korkeamaki and Suhonen 2002) this pattern. There are reasons to predict either lower or higher extinction risk in patches for less abundant taxa. Pre-adaptions may confer better dispersal abilities to species that occur naturally at low abundances (Tilman et al. 1994). These species may be buffered against local extinction following fragmentation if movement between patches is important for species' persistence (Didham et al. 1998a). On the other hand, abundances of already rare taxa should be more likely to fall below minimum viable population sizes after forest loss, and subsequently lead to local extinction. Our data support the latter prediction, which is based on the importance of within-habitat reductions of populations rather than between-patch processes. It is possible that other traits that co-vary with abundance contribute to the effect of rarity on invertebrate extirpations in disturbed habitats. Ecological specialization is often associated with both rarity (Lawton 1994) and higher extinction rates (Foufopoulos and Ives 1999, Owens and Bennet 2000, Harcourt et al. 2002, Korkeamaki and Suhonen 2002, Krauss et al. 2003). In our landscape, habitat modification explained forest family extirpations in both fragmented forest and orange groves. Rare forest families may be more sensitive to differences in microenvironment because they are less capable of adapting to environmental change by diet or range shifts. Species traits of abundance and specialization can act synergistically to increase species' sensitivities to habitat fragmentation (Davies et al. 2004). Analyses at a lower level of organization may reveal different patterns in invertebrate responses to land-use differences (Ingham and Samways 1996, Davies et al. 2000). The generality of our conclusions regarding trait predictors of sensitivity to differences in land use depends on the extent to which traits are shared by related taxa within families.
**Forest conversion effects**

Our data reveal large losses in invertebrate biodiversity in cleared habitat. On average, rarefied family richness and evenness were 24% and 56% lower, respectively, in orange groves relative to intact forest. These differences reflect local extirpations of some invertebrate orders in addition to losses at the family level. Abundances were also lower in orange groves than in forests for most of the common taxa for which we tested habitat effects on abundance. Because declines in abundance can be a precursor of local extinction (Gaston 1994), our estimates of forest conversion effects on family richness may be conservative. The negative effect of forest conversion on family richness in our landscape is consistent with previous reports of reduced invertebrate richness in cleared habitats (clear-cut forest: Klein 1989, coffee plantations: Goehring *et al.* 2002) but contrasts with other studies that have reported similar invertebrate richness between agricultural plantations and reference intact forest (Davies *et al.* 2001, Ricketts *et al.* 2001, Estrada and Coates-Estrada 2002). These inconsistencies may be explained by variation in matrix habitats' shade and ground cover. In our study, effects of forest conversion on community composition, as well as forest family extirpations in particular, were related to changes in the litter microenvironment. Persistence of forest invertebrates likely differs among matrix habitats with disparate ground litter, as do persistence of other animal groups among matrices with different habitat structure (Daily *et al.* 2003, Kupfer *et al.* 2006).

Although invertebrate richness was lowest in orange groves, beta diversity (dissimilarity in community composition) was greater among orange groves than among forested sites. Differences in community structure between orange groves were comparable in magnitude to differences between orange groves and forested sites. This result opposes our predictions and was somewhat unexpected given the environmental homogenization in orange groves, relative to forest. Grove age and management regimes (e.g. frequency of clearing ground vegetation) varied among groves. Disparities in orange tree age and litter layer structure among orange groves in this landscape may enhance beta diversity across orange groves. For example, invertebrate community structure, litter amount and temperature in the abandoned orange grove (O5) are more similar to that of forests than to other orange groves. Landscape-level losses of invertebrate diversity in orange groves may be higher when grove age, structure and management are more consistent across the landscape.
We expected homogenization of litter structure to decrease beta diversity within orange groves, but beta diversity between plots did not differ between orange groves and forests. This result may be explained by marked differences in exposure between plot locations under and between trees in most orange grove sites (data not shown). Strong influences of temperature on litter invertebrates in orange groves are evidenced by increases in forest family extirpations with temperature. Shade has been shown to mitigate forest conversion effects on ground-foraging ants (Perfecto and Vandermeer 2002). Shade under orange trees may provide some refuge for litter invertebrates from the physiological challenges of high temperatures and low litter cover in orange groves. These refuges may partially offset invertebrate losses in plots under, but not between, orange trees, and thus bolster beta diversity between plots despite reductions in environmental variation within orange groves. Local invertebrate diversity may not be similarly buffered in other types of agricultural habitat with lower shade and more homogeneous environments (e.g. pineapple plantations).

**Forest fragmentation effects**

In contrast to our predictions and previous reports of decreased invertebrate abundance (Klein 1989, Estrada and Coates-Estrada 2002) and richness (Klein 1989, de Souza and Brown 1994) in fragmented forest, neither invertebrate community abundance nor diversity differed between intact and fragmented forest in our landscape. This result would be expected if invertebrate immigration rates from orange groves are high. However, community composition in orange groves was not more similar to that in fragmented than to continuous forest, as would be expected if influxes of individuals and new invertebrate taxa from orange groves were important in bolstering community richness in forest fragments. Instead, consistency in local richness levels between intact and fragmented forest was largely attributed to a suite of invertebrate families that were detected exclusively in forest patches. These families could be specialists of disturbed forest. Alternatively, they could be emigrants from matrix habitat other than orange groves; parts of three of our study fragments were adjacent to regenerating pasture, and one fragment (S5) was embedded in teak plantation. Species richness in forest fragments can differ within a landscape depending on the type of matrix habitat adjacent to the fragments (Daily et al. 2003). In our study landscape, proportional changes in intact forest- and
disturbance-adapted invertebrates may vary among forest patches embedded in different landscape contexts (orange groves, pasture, teak plantations, pineapple plantations).

Community-level variables do not always capture differences among community members’ responses to habitat fragmentation (Robinson et al. 1992). In this study, aggregate community measures (richness, abundance, evenness, similarity) masked fragmentation effects on taxa typical of intact forest. We failed to detect, on average, 11% of common intact forest families in forest fragments. Higher litter temperatures in fragments explained these extirpations, although wet season temperature differences between intact and fragmented forests were not significant. We suspect that temperature differences between intact forest and forest fragments are stronger in the dry season, when we sampled invertebrates.

Aggregate community measures were similar between large and small patches. Our results agree with some previous research that report negligible changes in invertebrate richness with habitat area (Robinson et al. 1992, Davies and Margules 1998, Davies et al. 2001, Estrada and Coates-Estrada 2002) and indicate low influences of changes in patch area over the range of patch sizes in our study landscape. Other research report conflicting responses of invertebrate communities to reduced habitat size (e.g. Collinge and Forman 1998, Summerville and Crist 2004). In our study, irregular patch shapes may have allowed edge effects to extend even to the center of large patches (Laurance 1997), reducing the effect of patch size per se.

Contrary to predictions, beta diversity between forest patches was marginally higher than that between intact forest sites. This result may reflect differences in the extent of edge effects among fragment centers. Invertebrate community composition was strongly correlated with litter cover, which was highest near the edges of our study fragments (see Chapter 3). Invertebrate taxa associated with intact forest also responded to changes in temperature, which is often higher closer to forest edges. Edge effects on tropical ground invertebrates have been shown to penetrate forests to distances up to 200 m (Laurance et al. 2002). Our sampling in patch centers took place between 26-212 m from patch edge. Differences in edge effects among our plots in forest fragments could have positively influenced beta diversity between fragments. Beta diversity may be lower among the centers of larger fragments that are less influenced by edge effects. Without invertebrate samples from plots in both intact forest and fragments at equivalent
distances to forest edge, we are unable to separate the contributions of edge effects from those of patch isolation.

**Implications**

Invertebrates are diverse, abundant, and have important functional roles in decomposition and as herbivores, predators and prey in both forest and agroecosystems (Seastedt 1984, Janzen 1987, Estrada and Coates-Estrada 1991, Didham *et al.* 1996, Huhta 2007), yet invertebrate communities' responses to disturbance are poorly described and explained. This information deficiency is particularly noticeable for tropical regions, where invertebrates are most diverse (Hawkins 2001) and where forest destruction and fragmentation are leading drivers of contemporary extinctions (Groombridge 1992, Purvis *et al.* 2000). Our results suggest that changes in within-habitat quality (microenvironment) mediate effects of both forest fragmentation and conversion on litter invertebrates. Local abundance is an easily assessed trait for tropical invertebrates and was useful at the family level for predicting land-use effects on forest invertebrates: extinction risk decreased with abundance in both forest fragments and orange groves in our study landscape. Species with low abundances often occupy higher trophic positions, thus, land-use differences may also affect the trophic structure of litter invertebrate communities. To investigate this, we would require invertebrate identifications at a finer resolution.

Our analyses of land-use effects on extirpations of intact forest invertebrates are conservative for three reasons. First, our reference data are derived from intact forest are representative of the different succession stages typical of intact forest in our landscape. We do not know the degree to which communities in our intact forest sites differ from those in completely undisturbed forest. Second, we examined invertebrates only in fragment centers, where any edge effects of exposure and influences of adjacent matrix habitat are minimized. Third, our estimations of extirpation probabilities exclude numerically and spatially rare taxa, that is, the very taxa that are more likely to be locally extirpated from disturbed sites. Despite the conservative nature of our extirpation estimations, we failed to detect 11% and 27% of intact forest taxa in forest patches and orange groves, respectively. These findings corroborate myriad other studies calling for large forest reserves as a requirement in maintaining tropical forest biodiversity.
While there is no substitute for large undisturbed tracts of tropical forest, trends of increasing forest conversion for agriculture imply agroecosystems will play an important role in determining the degree of biodiversity preserved in tropical landscapes (FAO 2000, Tilman et al. 2001). Agricultural matrix habitats can support some existing populations and can also contribute new species to landscapes (Gascon et al. 1999, Daily et al. 2001, Ricketts et al. 2001, Estrada and Coates-Estrada 2002, Daily et al. 2003, Mayfield and Daily 2004). Despite the large number of forest invertebrate families that declined or were absent in orange groves, nearly two thirds of the total invertebrate taxa we trapped were detected in orange groves, and 11% were detected exclusively in orange groves. Orange grove biodiversity also appeared to be somewhat buffered at the landscape scale by differences in grove age and/or management among orange groves. A mosaic of matrix habitats with different litter environments may support more diverse litter fauna than a landscape with fewer matrix types (Estrada and Coates-Estrada 2002, Krauss et al. 2003, Steffan-Dewenter 2003).

Forest fragments in our study landscape harbored a considerable portion of the invertebrate biodiversity in our study landscape, despite their small size. Forest patches of the sizes we sampled in this study (< 36 ha) are increasingly typical of tropical countryside as continuing fragmentation reduces the size of forest remnants in Costa Rica and elsewhere in the tropics (Sánchez-Azofeifa et al. 2001, Terborgh and Feeley 2008). On average, we detected 89% of the total invertebrate families trapped in intact forest in forest patches (compared with 73% in orange groves). Forest fragments also supported a large portion of invertebrate biodiversity (17 families and one order of 123 total taxa trapped) not detected in either intact forest or orange groves. These data emphasize the importance of small forest remnants for maintaining biodiversity in agricultural landscapes (Turner and Corlett 1996, Chan and Daily 2008).
Table 2.1 Spearman rank correlations between individual microenvironment measures and invertebrate community structure (matrix of Bray-Curtis similarity measures based on sites' relative abundances of invertebrate taxa). F ratios are derived from one-way ANOVAs testing for differences in each measure among habitats. Asterisks indicate significant differences in habitat microenvironment, following sequential Bonferroni corrections for multiple tests.

<table>
<thead>
<tr>
<th>Microenvironment measure</th>
<th>Spearman rank correlation</th>
<th>$F_{3,16}$ (p-value)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Litter biomass</td>
<td>0.56</td>
<td>10.41 (&lt; 0.01)*</td>
</tr>
<tr>
<td>Litter depth</td>
<td>0.48</td>
<td>0.91 (0.46)</td>
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<tr>
<td>Litter temperature</td>
<td>0.29</td>
<td>4.08 (0.03)*</td>
</tr>
<tr>
<td>Air temperature</td>
<td>0.18</td>
<td>2.26 (0.12)</td>
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<tr>
<td>Litter moisture</td>
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</tr>
<tr>
<td>Slope</td>
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<td>1.09 (0.38)</td>
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<tr>
<td>Elevation</td>
<td>0.18</td>
<td>0.71 (0.56)</td>
</tr>
<tr>
<td>Location</td>
<td>0.06</td>
<td>0.93 (0.45)</td>
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</tbody>
</table>
Table 2.2. Ecological attributes and responses to different land uses for the top six discriminating taxa between forests and orange groves (forest conversion effects) and between intact and fragmented forest (forest fragmentation effects). The percentage contributions of each taxon to forest conversion and fragmentation effects on community composition were calculated using SIMPER procedures. Taxa are arranged in the table in order of decreasing percent contribution to composition differences between intact forest and orange groves. Chi-square test statistics and associated p-values are reported for Wilcoxon (Kruskall-Wallis) tests of disturbance (forest conversion and fragmentation) effects on the abundances of each taxon. Asterisks indicate significant effects after sequential Bonferroni corrections for multiple tests. The abundance and coefficient of spatial variation (CV) for each taxon are averaged over intact forest sites. Extirpation probabilities represent the fractions of disturbed sites (orange groves, forest patches) in which we failed to detect each taxon.

<table>
<thead>
<tr>
<th>Order</th>
<th>Family</th>
<th>Type of land-use change</th>
<th>Percent contribution to difference between habitats</th>
<th>Disturbance effects on abundance $\chi^2 (1)$ (p-value)</th>
<th>Mean abundance in intact forest sites (SE)</th>
<th>CV in intact forest sites</th>
<th>Extirpation probability (SE)</th>
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</thead>
<tbody>
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<td>Coleoptera</td>
<td>Pselaphidae</td>
<td>Forest conversion</td>
<td>6.86</td>
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<td>Staphylinidae</td>
<td>Forest conversion</td>
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<td>9.08 (&lt; 0.01) *</td>
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<td>Phoridae</td>
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<td>4.96</td>
<td>8.56 (&lt; 0.01) *</td>
<td>51.80 (11.15)</td>
<td>0.48</td>
<td>0.00 (0.00)</td>
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<td>Type of land-use change</td>
<td>Percent contribution to difference between habitats</td>
<td>Disturbance effects on abundance $\chi^2$ (p-value)</td>
<td>Family attributes</td>
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<td></td>
<td></td>
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<td>Mean abundance in intact forest sites (SE)</td>
<td>CV in intact forest sites</td>
<td>Extirpation probability (SE)</td>
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<td>105.00 (31.68)</td>
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</tbody>
</table>
2.7 Figures

Figure 2.1 Sampling sites north of the Estación Biológica Pitilla, ACG, and south of the community of Santa Cecilia, north-western Costa Rica. Dashed lines indicate dirt roads and solid lines are paved. One intact forest site (I2) is located within the ACG. Shaded areas indicate forest habitat. Intact forest sites: I1, I2, I3, I4, I5. Large forest patches: L1, L2, L3, L4, L5. Small forest patches: S1, S2, S3, S4, S5. Orange groves (stippled area): O1, O2, OP3, O4, O5.
Figure 2.2 Average (+ 1 SE) invertebrate diversity components for each habitat. Evenness values (E₁/D, Smith and Wilson 1996) have been multiplied by 100. Averaged total invertebrate abundances (SE) are 588.6 (44.5) in intact forest, 727.4 (50.4) and 570.6 (70.9) in large and small patches, respectively, and 709.4 (94.9) in orange groves.
Figure 2.3. NMDS ordination of relative invertebrate community composition. Stress value = 0.07. Circles represent forested sites (black: intact forest sites, grey: large forest patches, white: small forest patches) and triangles represent orange groves. Sites are labeled as in Figure 2.1.
Figure 2.4 Litter temperature and litter biomass differ among habitats. Circles represent forested sites (black: intact forest sites, grey: large forest patches, white: small forest patches) and triangles represent orange groves. Sites are labeled as in Figure 2.1.
Figure 2.5 NMDS ordinations of relative community composition. Stress value = 0.07. Circles are scaled to relative mean abundances of A) Pselaphidae; B) Staphylinidae; C) Colembolla; D) Bostrichidae; E) Phoridae; F) Formicidae. Selected families were identified by SIMPER as the top discriminating families between forests and orange groves (forest conversion effects). Sites are labeled as in Figure 2.1.
Figure 2.6 Changes in extirpation probabilities in forest patches (open circles) and orange groves (filled circles) with invertebrate family a) abundance and b) spatial variability in abundances in intact forest. Abundance and population variability (coefficient of spatial variation) for each taxon were averaged over intact forest sites. Abundances are (log_{10}+1)-transformed. Lines were fitted with separate GLMs for forest patches (dotted lines) and orange groves (solid lines), with quasibinomial errors. Taxa trapped ≤ 50 times total in < 40% intact forest sites were excluded from regressions.
3 DIVERGENT EFFECTS OF DIFFERENT LAND USES ON RATES OF TROPICAL LITTER DECOMPOSITION

3.1 Summary

In Chapter 2 I described effects of forest conversion on invertebrate community diversity and differences between the litter environments of orange groves and intact forest. I also reported differences in invertebrate community composition attributable to both forest conversion and fragmentation. Here I examine the consequences of these differences for decomposition. Forest fragmentation and forest conversion had divergent effects on decomposition rates. Decomposition rates were 7% slower in forest patches during the dry season than in intact forest, and this result was mediated by forest fragmentation effects on shredder and/or saprophagous macroinvertebrates. Decomposition rates were 9% higher in orange groves during the wet season, relative to intact forest. This result was explained by higher litter temperatures and lower litter cover in orange groves.

3.2 Introduction

Anthropogenic habitat fragmentation and habitat conversion are dominant disturbances in natural landscapes (Groombridge 1992, Purvis et al. 2000, Fahrig 2001). In tropical forests, such disturbances are most rapidly occurring for agricultural purposes (World Resources Institute 1994, FAO 2000). Given the prevalence of these processes, we understand their influences on ecosystem functioning. Decomposition is an important control of nutrient release (Swift et al. 1979, Aerts and De Caluwe 1997) and is particularly important in tropical ecosystems, many of which have naturally low nutrient availability (Jordan 1982). The conversion of organic carbon to carbon dioxide, a key part of the global carbon cycle and consequently global climate change models, is also largely regulated by decomposition (Raich and Schlesinger 1992, herbivory has a minor role: Cebrian and Duarte 1995, Cebrian and Lartigue 2004). Decomposition is important from a utilitarian perspective in agroecosystems, because of its influence on plant productivity.

Detrital breakdown is mediated by microbes and invertebrate fauna as well as passive leaching. Decomposition rates are reflective of three main groups of driving factors: the
chemical composition of the decomposing matter itself (Swift et al. 1979, Seastedt 1984, Beare et al. 1992, Lavelle et al. 1993), characteristics of the abiotic environment and communities of invertebrates and microbes. In this study we examined differences in the litter microclimate and invertebrates under different land uses and the consequences of these differences for decomposition. Disturbances associated with forest fragmentation and converting forest to agroecosystems have been shown to affect both the abiotic microenvironment and invertebrate communities in ground litter systems (Klein 1989, Didham and Lawton 1999, Bierregaard et al. 1992, Davies et al. 2001, Ricketts et al. 2001, Estrada and Coates-Estrada 2002, Perfecto and Vandermeer 2002).

In Guanacaste province, Costa Rica, conversion and fragmentation of tropical rain forest has been largely driven by agriculture, particularly orange groves. We measured rates of leaf litter loss for a common brown litter source in intact forest, the centers of forest patches, and orange groves to facilitate assessment of forest fragmentation (intact vs. fragmented forest) and forest conversion (intact forest vs. orange groves) effects on decomposition. We used different litter bag mesh sizes to separate influences of macroinvertebrates from effects of the abiotic environment and microbiota on decomposition in each habitat. We also investigated effects of patch area and distance to edge on decomposition rates in forest fragments.

In forest patches, previous studies report increased ground litterfall (Laurance et al. 2000, Harper et al. 2005) as well as hotter, drier conditions, relative to continuous forest. These fragmentation effects have opposing implications for decomposition rates. Increased litterfall improves conditions for litter invertebrates and microbes (e.g. Duncan 1969, Frith and Frith 1990), so was expected to increase decomposition rates in forest patches relative to intact forest. In contrast, we expected increases in temperature (and lower moisture) to decrease decomposition rates in forest fragments due to adverse effects of high temperature extremes on litter invertebrates in tropical climates (e.g. Janzen 1973, Levings and Windsor 1984). Fragmentation effects on decomposition should therefore depend on relative changes in litter cover and temperature. Finally, we expected fragmentation effects on the litter microenvironment to be stronger closer to patch edges (Kapos et al. 1997, Didham and Lawton 1999). As the centers of most small patches are closer to their edges than the centers of large
patches, we also predicted fragmentation effects on decomposition to be greatest for the smallest patches.

Our predictions regarding decomposition in orange groves depend on the relative influences of leaching and macroinvertebrates on aboveground litter decomposition rates. We predicted low litter cover and shading in orange groves would negatively affect abundances and richness of litter macroinvertebrates and therefore reduce rates of litter decomposition, relative to intact forest. In contrast, if passive leaching dominates control of decomposition rates, we expected increased exposure in orange groves to increase decomposition rates, especially in the wet season when rain storms are more common.

3.3 Methods

Site description

We measured decomposition rates in a 10 x 10 km landscape adjacent to the Área de Conservación Guanacaste (ACG), northwestern Costa Rica. This area has a distinct dry season from January through May (115.9 ± 50.0 mm average monthly rainfall) and receives 325.6 ± 44.1 mm/month during the remainder of the year (April 2006 - March 2007, M. M. Chavarria, pers. comm.). The landscape covers an elevation range of 1035 - 1645 m. Much of the native tropical moist forest has been fragmented by land-use changes into remnant patches (0.4 - 36.7 ha, > 20 years since fragmentation). Forest clearance has been motivated by human settlement, cattle ranching and increasingly by agriculture. Principal land-use categories in this region are now, from most to least common, orange groves, secondary forest, pasture and pineapple plantations. Habitats surrounding forest patches are predominantly orange groves, with some pasture land. Orange agriculture near the ACG is dominated by Del Oro, S.A.

Site selection was based on a contrast of four habitats common within the study landscape: intact forest, large (6.1 - 21.4 ha) and small (0.6 - 4.0 ha) forest patches, and orange groves. We selected five sites within each of the four habitat categories, along the landscape’s elevation range (Figure 2.1). Intact forest sites were chosen to represent the different structures of intact forest throughout the study landscape, and encompass a range of succession stages. We considered different forest patches to be separate sites and excluded patches with swamp
sections from site selection. Sites were spaced by a minimum of 100 m and sites within each habitat category were spaced by a minimum of 390 m. Forest patches were all bordered by orange groves, with the exceptions of one small (S5) and one large (L3) patch (Figure 2.1), which were located in young teak (*Tectona grandis*) plantation and regenerating pasture, respectively. Two patches (L3 and S4) were moderately affected by human disturbance. Three orange grove sites (O1, O2 and O3) were managed by Del Oro, S.A. The other two orange groves (O4 and O5) were managed by small private farms. O5 was no longer harvested at the time of this study, and was covered in several years’ overgrowth. Agrochemicals were not applied to orange groves with the exception of O4, to which fertilizer was sprayed twice yearly.

Decomposition and microenvironment measures were taken during the late dry season (5 May - 4 July 2007) and the wet season (26 October - 18 December 2007). Dry season records were taken from five 8 x 8 m plots located along transects in each site. These plots were spaced by 20 m and located 5 m perpendicular to walked transects to minimize disturbance by observers. Dry season transects began 250 m from forest edge in intact forest and 15 m from edges in orange groves. We positioned the forest patch transects about the geometric center of each patch; dry season plots in small and large forest patches were thus located 26 - 100 m and 50 - 212 m, respectively, from patch edge.

Wet season records were taken from a single 12 x 12 m center plot in each site. These plots were located 350 m from intact forest edges and 20 m from orange grove edges. In forest patches, we established wet season plots at the maximum distance from the edge, 26 -121 m in small patches and 50 - 217 m in large patches. We established additional plots during the wet season to distinguish effects of area and edge in forest patches. 8 x 8 m plots were established along transects at 0, 10 and 20 m from edges in the four smallest forest fragments (S1, S2, S3 and S4) and at 0, 10, 20, 50 and 100 m from edges in the four largest fragments (L1, L3, L4 and L5). As in the dry season, we spaced all wet season plots 5 m away from walked transects to minimize disturbance. Edge transects were all oriented perpendicular from south-west facing edges and adjacent to orange groves, with the exceptions of those in L3 and L5, which were adjacent to regenerating pasture. All dry and wet season plots were located ≥ 10 m from streams.
Decomposition measures

Decomposition rates were measured as changes in leaf litter mass over time using mesh litter bags. We measured decomposition in two litter bag treatments: 9-mm mesh bags to allow macroinvertebrate entry (+MI treatment) and 1-mm mesh control bags to restrict macroinvertebrates’ entry (-MI treatment). Litter bag estimates show good agreement with predictions of litter loss based on respirometric measurements (Swift et al. 1979) and are the most common method for measuring terrestrial litter decomposition. Although the litter bag method may underestimate true decomposition rates due to pre-drying leaf contents (Taylor 1998) or otherwise bias decomposition rate estimates due to microclimate alterations (Heal et al. 1997), we assume that biases due to changes in leaf chemistry are consistent among bags and thus allow comparisons of decomposition rates between MI treatments and among sites.

In the dry season, we placed six litter bags (three +MI bags and three -MI bags) in each plot (total 600 bags). All litter bags were filled with naturally abscised leaves hand-collected from Conostegia xalapensis pasture trees. We selected this filling instead of a natural leaf mixture from each site (Vasconcelos and Laurance 2005) because it allowed us to separate changes in decomposition due to differences in microclimate, fauna or microflora from changes due to the chemical composition of sites’ litter resources (Jonsson and Malmqvist 2000; Bradford et al. 2002). Conostegia xalapensis was common throughout the landscape and recorded in at least 16 of our 20 sites. Each litter bag was 20 x 20 cm and filled with approximately 4 g whole leaves for consistent leaf mass and compression among litter bags. We recorded the initial dry mass (± 0.001 g, following oven drying at 60° C) of each litter bag prior to field placement. Litter bags were placed on the solid soil surface and were left in plots for ≥ 2 weeks to allow time for invertebrate colonization. One randomly selected litter bag of each MI treatment was retrieved after each of 2, 3 and 6 weeks from each plot. Within 12 hours of bag retrieval, we dried each bag’s contents to constant mass and recorded its final dry mass.

Decomposition measurements were repeated in the wet season plots. We placed eighteen litter bags (9/MI treatment) in each center plot and eight litter bags (4/MI treatment) in each edge transect plot (total 616 bags). After 17 and 40 days, two litter bags/MI treatment from each edge plot and four bags/MI treatment from each center plot were randomly selected and their litter contents were dried to constant mass.
**Microenvironment measurements**

We characterized the leaf litter microenvironment with litter depth, standing litter biomass, litter moisture content, temperature, slope, elevation and location coordinates. Litter depths were measured at the beginning of each field season in undisturbed locations from five locations in each dry season plot, and at 20 and nine locations in each of the center and edge wet season plots, respectively.

20 x 20 cm leaf litter samples were scraped from the solid soil surface in undisturbed locations in each grove season. One litter sample was taken from each dry season plot and wet season edge plot. We took four litter samples from each wet season center plot. Each litter sample was dried to constant mass (standing litter biomass, ± 0.001 g). In addition, we recorded the wet biomass of each dry season litter sample before drying, within 12 h of collection. We estimated the litter moisture content of each dry season litter sample as:

\[ 100\% \times \frac{\text{wet mass} - \text{dry mass}}{\text{dry mass}} \]

Relative differences between sites’ dry season litter moisture content were assumed to be representative of litter moisture content differences among sites in the wet season. In the dry season we averaged litter depth, biomass and moisture content by site, and we averaged litter depth and biomass by plot in the wet season.

Air and leaf litter temperatures were measured at 1.5 m above ground and at half-litter depth, respectively. All temperature measurements were taken during the wet season using an electronic temperature probe (Hanna Instruments HI 9024, ± 0.4° C). We recorded both air and leaf litter temperatures at 5-minute intervals for one hour, while moving among four randomly selected locations in each wet season center plot. We also recorded temperature in the centers of edge transect plots while walking back and forth along each transect for one hour.

We measured temperatures in all weather conditions and in coordination with litter bag retrieval. To account for diurnal weather variation, all temperature records were taken within one hour of local solar noon, during which time incoming solar radiation is fairly consistent. We repeated measurements in each center plot and transect for two different days, in an attempt to account for daily weather differences, and averaged air and leaf litter temperatures for each plot.
Relative differences between sites’ wet season temperature records are assumed representative of relative temperature differences among sites in the dry season.

Using a clinometer (± 0.5°), we measured slopes in the center of each dry season plot and wet season edge plot. We recorded the slope for each wet season center plot as the average of measurements in 4 random locations. The elevation and location along the north-south axis of the study landscape were recorded in the center of each site using a handheld GPS unit (GARMIN Geko 201, ± 9.5 m) to account for spatial correlation between sites.

Earthworms can influence aboveground litter decomposition by transporting litter belowground (Brown 1995). We removed one 250 cm$^3$ soil sample from each dry season and wet season edge plot, and four soil samples from each wet season center plot. All earthworms (Oligochaeta excluding Enchytraeidae) in each sample were counted and their lengths measured. Earthworm biomass was recorded for each sample, and the four samples from each wet season center plot were averaged.

Data analyses

We assessed landscape effects on decomposition rates using two sets of linear mixed models. The first set of models was used to examine the effect of habitat (intact forest, large and small forest patches, orange groves) and the second set was used to examine the fragmentation effects of area and distance to edge, only in forest patches. Before running these regression models, we first calculated decomposition rate constants (response variables) and summarized a set of microenvironment predictor variables using factor analyses.

Calculation of decomposition rates

Exponential decay models best describe the litter decomposition process (Jenny et al. 1949, Wieder and Lang 1982). A single exponential model of the form

$$X = Ce^{-k_{exp}t}$$

where $X =$ percent remaining leaf mass at time $t$, $k_{exp} =$ exponential decomposition rate, and $C = X$ at $t = 0$ is commonly used to describe litter bag mass loss over time (e.g. Olson 1963; Rubinstein and Vasconcelos 2005). However, other decay functions with poorer biological
realism often produce better statistical fits when modelling litter breakdown over time (Wieder and Lang 1982). The linear decomposition model of the form
\[ X = C - k_{\text{lin}}t \]
where \( k_{\text{lin}} \) = linear decomposition rate, is often suitable for describing decomposition over shorter periods of time (Taylor 1998).

We investigated the fit of both single exponential and linear models for our data. We first calculated decomposition rates for each site by MI treatment combination using litter bag data from the dry season, using both single exponential and linear decomposition models. Plot data were pooled for each site. Because the objective of fitting decomposition models was to obtain decomposition rates that were comparable among sites, we fit both types of model with the restriction that \( X = 100 \) at \( t = 0 \) (Wieder and Lang 1982). Both models fit the data equally well (paired sample t-test, \( t_{39} = 0.49, p = 0.62, n = 40 \); average \( R^2 \) = 0.80 and 0.82 for linear and single exponential models, respectively). Both linear (one sample t-test, \( t_{39} = -1.70, p = 0.10, n = 40 \)) and single exponential (one sample t-test, \( t_{39} = 0.18, p = 0.86, n = 40 \)) models with unfixed intercepts reliably predicted an intercept of \( X = 100 \) at \( t = 0 \). We used linear decomposition rates with fixed intercepts as response variables in the habitat and fragmentation regression models.

Linear decomposition models with fixed intercepts were used to calculate decomposition rates for sites’ wet season center and edge transect plots. Wet season linear decomposition models with unfixed intercepts also reliably predicted intercepts of \( X = 100 \) at \( t = 0 \) (one sample t-test, \( t_{39} = -1.34, p = 0.19, n = 40 \)).

**Microenvironment factor analyses**

Factor analyses were used to summarize the variation among microenvironmental variables in a reduced set of orthogonal factors for use in subsequent regression models (Tabachnik and Fidell 2001). We began each factor analysis with a principal components analysis on the correlation matrix to remove differences in measurement scales among variables. Two separate analyses were completed; one for the regression models to explain habitat effects and one for the regression models to explore fragmentation effects in patches. The first factor analysis (for the habitat regression models) involved all microenvironmental measures and all sites’ data from both seasons with the exceptions of forest patch edge transect data. Litter biomass was \( \log_{10} \)-transformed before inclusion in this factor analysis. Dry season litter moisture
values were used for the wet season and wet season temperatures were used for the dry season. The substitution of these variables did not affect the factor separations of other variables. Five principal components were retained for factor analysis, and together represented 96.2% of the total sample variance from the original variables. We created factors using a varimax orthogonal rotation. Factor 1 was positively related to location and air temperature, and negatively related to elevation; this factor will hereafter be referred to as the “elevation factor”. Factor 2 loaded strongly on both litter depth and litter biomass (“litter amount factor”). Factor 3 was related to leaf litter temperature and moderately so to air temperature; this factor will be referred to as “temperature factor”. We labeled the remaining two factors as the “litter moisture” and “slope” factors after the variables they represented.

We performed the second factor analysis (for the fragmentation regression models) using wet season forest patch data, including those from edge transects. Litter depth and litter biomass were both log\(_{10}\)-transformed. Three principal components were retained for factor analysis, and together represented 89.7% of the total sample variance from the original variables. We created edge factors using a varimax orthogonal rotation. The first edge factor (“temperature edge factor”) was positively related to air and leaf litter temperatures. Edge factor 2 (“litter edge factor”) was positively related to both litter depth and litter biomass. The third factor was labeled “slope edge factor” because of strong loading on this variable. All factor analyses were performed in SAS (version 9.1.3, SAS Institute Inc. 2005).

**Habitat regression models**

We analyzed habitat effects on decomposition rates using three separate mixed regression models and all center plot data. MI treatment and season were included in these models as fixed effects, as were all two and three-way interactions.

First, we assessed habitat effects by including habitat as a predictor after accounting for variance explained by MI treatment and season. Second, we examined whether these habitat effects could be explained by differences in measured environmental predictors (earthworm biomass, microenvironment factors) among habitats. If environmental differences among habitats explain habitat effects on decomposition, then the habitat predictor should no longer be significant after accounting for these differences. Third, environmental predictors may explain residual variance in decomposition rates not explained by the habitat categories we selected. The
effects of earthworm biomass and the five microenvironment factors were each assessed after accounting for differences in decomposition rates among habitats.

We did an additional analysis to investigate influences of field workers on decomposition in orange groves. We re-calculated orange grove decomposition constants after excluding data from litter bags in locations most likely to be trampled by workers and then repeated habitat regression models using these new constants with significance levels adjusted for multiple tests.

**Fragmentation regression models**

Fragmentation effects (forest patch area and distance to edge) on decomposition rate were assessed using only wet season data from forest patches (both center and edge plots). We examined separately the effects of patch area and distance to edge in models after accounting for MI treatment as a fixed effect. We also examined changes in the litter microenvironment (earthworm biomass, edge microenvironment factors) along edge transects.

**Regression model construction**

All habitat and fragmentation regression models included random effects associated with site. Within-group errors were greater for the +MI treatment than for the –MI litter bags, and greater for the wet season than for the dry season. These heteroscedasticities were modeled with different within-group variances (Pinheiro and Bates 2004). Decomposition rates, earthworm biomass, patch area and distance to edge were log$_{10}$-transformed to meet assumptions of normality. Earthworm biomass was tested as a predictor only for the +MI litter bags, as mesh size excluded earthworms from the -MI litter bags.

Fixed effects were tested using conditional F-tests (Pinheiro and Bates 2004). Likelihood ratio tests were used to evaluate random effects, and to compare within-group variances and nested models (Pinheiro and Bates 2004). Significance levels in multiple tests of habitat effects on different environmental predictors and multiple regression models testing the environmental predictors' effects on decomposition were adjusted using sequential Bonferroni corrections (Peres-Neto 1999). All regression analyses were performed in R (version 2.7.2, R Development Core Team 2008).
3.4 Results

Habitat effects on decomposition

Decomposition rates were 11 - 16% higher in litter bags with macrofauna (F_{1,56} = 28.93, p < 0.01). However, macrofauna effects differed among habitats (F_{2,56} = 6.88, p < 0.01); decomposition rates differed between MI treatments in intact forest and orange groves, but not in forest patches (Figure 3.1a). Decomposition was marginally slower in forest patches relative to intact forest in +MI bags (t_{17} = -2.01, p = 0.06) but not in -MI litter bags (t_{17} = 0.95, p = 0.36). Decomposition rates were not significantly different between large and small forest patches (L. Ratio = 0.27, p = 0.87, Figure 3.1a), and we lumped the two patch size categories for model simplification. Decomposition was faster in orange groves relative to forested habitats (t_{17} = 2.28, p = 0.04). This habitat effect was largely driven by a 10% reduction in decomposition in forest patches relative to orange groves in +MI bags (Figure 3.1a). Decomposition rates did not differ between orange groves and intact forest in either +MI (t_{17} = 1.05, p = 0.31) or -MI (t_{17} = 1.86, p = 0.08) bags.

Decomposition rates were 7 - 10% higher in the dry season than in the wet season F_{1,56} = 41.69, p < 0.01). There was a marginally significant interaction between season and habitat effects on decomposition (L. Ratio = 5.74, p = 0.06, Figure 3.1b,c). Decomposition in +MI bags was marginally lower in forest patches than in intact forest in the dry, but not wet, season (dry season: t_{17} = -1.95, p = 0.07, wet season: t_{17} = 0.00, p = 0.89). Decomposition in -MI bags did not differ between forest patches and intact forest in either season (both seasons p > 0.10). Decomposition was 5 - 13% faster in orange groves than in intact forest in the wet (F_{2,56} = 6.88, p < 0.01) but not dry season (p > 0.10). This conclusion did not change when we excluded litter bags most susceptible to orange grove workers’ disturbances.

Each environmental predictor was tested for differences between habitats. Of the five microenvironmental factors, only litter amount and temperature varied among habitats (Table 3.1). Orange groves had lower amounts of litter (t_{16} = -2.51, p = 0.02) and higher temperatures (t_{16} = 1.89, p < 0.01) than intact forest (Figure 3.2). Earthworm biomass did not differ among habitats (Table 3.1).
We assessed whether those environmental predictors that differed among habitats could explain effects of habitat on decomposition. Once we accounted for differences in either litter amount or temperature, the difference in decomposition between orange groves and forests was no longer significant (p > 0.05 after each factor). However, neither of these microenvironment factors explained differences in macrofaunal effects among habitats (MI treatment x habitat interaction still p < 0.05 after accounting for either factor).

Finally, we examined whether environmental predictors that did not necessarily differ amongst habitats might explain some of the residual variance in decomposition in this landscape. Both temperature (L. ratio = 12.99, p < 0.01) and litter moisture (L. ratio = 5.14, p = 0.02) explained residual variance not captured by MI treatment, season and habitat. Decomposition rates increased by 4% and 5% with increases of 1° C temperature and 10% litter moisture, respectively. No other microenvironmental factor explained residual variance (all p > 0.05).

**Fragmentation effects on decomposition**

Decomposition rates were 4 - 9% slower in –MI bags relative to +MI bags in forest patch edge transects (F1,71 = 7.65, p < 0.01), but there were no interactive effects of MI treatment and either area or edge on decomposition rates. Decomposition rates were not predicted by forest patch area (F1,8 = 0.57, p = 0.47; Figure 3.3a). Changes in decomposition rates were highly variable within edge transects but did not change monotonically with distance to edge (F1,70 = 2.95, p = 0.09; Figure 3.3b). Of the three edge microenvironmental factors, only litter amount predicted that decomposition rates (Table 3.1) increased with amount of standing litter. Distance to edge was negatively but weakly correlated with litter amount (Spearman’s rho = -0.29, n = 41, p = 0.06).

**3.5 Discussion**

The two land-use effects of forest conversion and forest fragmentation had divergent effects on litter decomposition. Decomposition rates were reduced in forest fragments and this effect was mediated by macroinvertebrates. Conversely, decomposition was faster in orange groves relative to forested sites because of differences between the abiotic environments of these habitats and possibly the action of microbiota. We examine each of these patterns in detail.
Forest fragmentation effects

Decomposition rates were lower in forest fragments than those in either intact forest or orange groves. This effect of forest fragmentation is attributed to the action of macroinvertebrates, as only the +MI bags demonstrate a difference in decomposition between intact and fragmented forest. Macroinvertebrates may affect decomposition in three ways. Feeding by predatory macroinvertebrates can reduce mesoinvertebrates' predation pressure on microorganisms, with consequent positive effects on decomposition rates (indirect-indirect macrofauna effects, Bradford et al. 2002). Other macrofauna that break litter into smaller fragments can indirectly increase decomposition rates by facilitating decomposer microorganisms' activities (direct-indirect macrofauna effects e.g. shredders, earthworms). Finally, saprophagous macroinvertebrates can directly increase measured rates of litter loss (direct-direct macrofauna effects). Our litter bag treatment isolates the combined direct-direct and direct-indirect macrofauna controls on decomposition; indirect-indirect effects of macroinvertebrates can have top-down control on invertebrate communities in both -MI and +MI bags. Earthworms can be important regulators of mass loss rates via direct-indirect effects and also speed litter loss from +MI litter bags by transporting litter bag contents belowground (Brown 1995). Our earthworm measurements did not differ between intact and fragmented forest (see Chapter 2) and did not explain forest fragmentation effects on decomposition in this study. Our data thus suggest that losses of shredder and/or saprophagous macroinvertebrates 1-9 mm in size explain observed forest fragmentation effects.

Given the high trophic diversity within tropical invertebrate families (Giller 1996) we require species-level data to identify specific saprophagous and/or shredder taxa responsible for our observed fragmentation effects on decomposition. Invertebrate pitfall samples from our study sites during the 2007 dry season indicate negligible effects of forest fragmentation on either total abundance or diversity at the community level (see Chapter 2). However, in forest patches we recorded average losses of 11% invertebrate families sampled in intact forest (Chapter 2). If these taxa were involved in facultative interactions (Cardinale et al. 2002) their losses may explain reduced decomposition rates in patches. Invertebrate taxa that were extirpated from patches may have included keystone taxa that are important for decomposition.
Forest fragmentation can modify habitat microenvironment (Kapos et al. 1997, Didham and Lawton 1999) and invertebrate communities (Didham et al. 1998a). Changes in abiotic or biotic factors with distance to edge can affect rates of litter loss in forest fragments (Didham 1998). Smaller patches often have higher temperatures and lower litter moisture due to exposure effects on their edges (Cadenasso et al. 1997, Kapos et al. 1997). We therefore expected fragmentation to negatively affect litter invertebrates and reduce decomposition rates if macroinvertebrates are important in regulating decomposition. Wet season decomposition rates were not affected by either fragment area or distance to patch edge in our landscape. In the wet season, we did not detect trends in microenvironment or decomposition with patch size or distance to edge. However, we expect temperature differences between intact and fragmented forest to be more severe in the dry season, when MI fragmentation effects were evident. Any effect of fragmentation on litter temperature has substantial consequences for litter invertebrates; forest family extirpations increased by 50% with every 1°C increase in litter temperature in our landscape (see Chapter 2).

There are at least two additional explanations for the lack of area or edge effects on decomposition in this study. First, forest patches in our landscape might have been buffered against edge microclimate effects as their edges were mostly sealed by dense growth of climbers and were maintained by orange grove workers. Both of these edge features help to reduce the magnitude and penetration distance of edge effects (Didham and Lawton 1999, Laurance et al. 2002, Harper et al. 2005). Second, although macroinvertebrates mediated forest fragmentation effects on decomposition, MI effects did not change with distance to patch edge or patch size. Edge effects can affect litter invertebrates at more than 200 m from edge (Ewers and Didham 2008). Because our forest fragments were very small (our plots at patch centres were located between 26 m – 217 m from edge), litter communities and their functions may not vary with distance to edge or among the different patch sizes in this landscape. The role of edge exposure in affecting decomposition in these forest fragments would be clarified by sampling litter invertebrates and measuring decomposition along edge transects in the dry season, when fragmentation effects on decomposition were observed.
Forest conversion effects

Decomposition rates were unaffected by forest conversion during the dry season but 9% faster in orange groves than those in intact forest during the wet season. Trampling disturbances by orange grove workers could have artificially increased mass loss measurements in orange groves. We distributed litter bags in orange groves evenly among three different types of locations: under trees, between trees, and between tree rows. Most of the orange grove workers’ movements occurred between orange tree rows. However, trampling by orange grove workers did not appear to affect our results: wet season decomposition rates were also faster in orange groves than in intact forest when we excluded data from bags likely to be trampled. Forest conversion effects were explained by changes in the litter microenvironment; higher temperatures and lower litter amount in orange groves each explained increases in decomposition rates.

The microenvironment in orange groves may have enhanced decomposition rates directly and/or indirectly. Our results agree with our predictions based on forest conversion affecting decomposition primarily via microenvironment effects on leaching rates. Wetting/drying cycles may have been more dynamic in orange groves and directly increased mass loss rates by enhancing comminution (physical breakage of leaf cell walls). Although our instantaneous litter moisture measurements did not differ between orange groves and forest, we did not measure variability in litter moisture over time. Reduced canopy cover and litter amounts left the soil surface more exposed in orange groves and subject to greater variability in temperatures and moisture levels (M. Cuke, pers. obs.). Rains are more frequent during the wet season and would be expected to enhance this mechanism. The occurrence of forest conversion effects during the wet, but not the dry, season corroborates the conclusion that leaching (direct microenvironment effects) explains differences in decomposition between orange groves and intact forest.

Alternatively, microclimate may have affected decomposition rates in orange groves indirectly via effects on litter fauna. In our study landscape, invertebrate community composition was altered by forest conversion and diversity was reduced in orange groves (Chapter 2). MI treatment effects did not differ between forests and orange groves and so do not explain forest conversion effects on decomposition. However, indirect-indirect macroinvertebrate effects may increase decomposition rates (Bradford et al. 2002), and these effects were not separated by the
MI treatments. Effects of forest conversion on meso- and microinvertebrates may also have played a role in affecting decomposition. For example, Collembola were almost completely excluded from orange grove invertebrate samples (Chapter 2, Figure 2.5) and have been shown to affect fungal species’ growth rates with knock-on effects on decomposition rates (Newell 1984). Direct enumeration of fauna in bags would also allow us to investigate the relative roles of direct and indirect (via microbiota or macroinvertebrate predators) effects of microclimate change in orange groves.

**Methodological issues**

Conclusions regarding macroinvertebrates’ effects on decomposition rates can be limited in three ways when based on a mesh size treatment that excludes a component of the ground litter community: a) different mesh sizes are unable to discriminate indirect-indirect effects of fauna surrounding litter bags from invertebrate effects directly mediated on litter inside the litter bags; b) measured litter loss may be artificially increased in litter bags with greater mesh sizes when transporting litter bags to and from the field; and c) invertebrate or microbial activity inside litter bags may be altered via mesh size effects on microclimate within bags.

First, because indirect-indirect effects of macroinvertebrates can have top-down control on communities in both +MI and -MI bags, the influences of these effects relative to direct-indirect or indirect-indirect effects are unknown. Data with higher taxonomic resolution would allow us to examine land-use effects on the trophic structure of litter communities in closer detail and assess indirect-indirect macroinvertebrate effects on decomposition in disturbed habitats. Indirect-indirect effects of macroinvertebrate will increase decomposition rates (Bradford et al. 2002). The MI treatment effects measured in this study should thus be interpreted as a minimum of net potential macroinvertebrate effects *in situ*.

The second two issues are possible artefacts of mesh size. We placed an extra set of litter bags of both MI treatments in the field and immediately retrieved them. We dried those bags’ litter contents in order to quantify mass losses due to litter bag transportation, field placement and retrieval, following Harmon *et al.* (1999). Transportation losses were confirmed as negligible relative to differences in litter loss among bags after 2 weeks *in situ* (data not shown). Finally, depending on litter moisture status, decomposition in litter bags with finer mesh size can
be affected (positively or negatively) by altered microclimate effects on microorganisms or decreased because of reduced rates of litter colonization by microbes and microfauna (Wise and Schaefer 1994). Bradford et al. (2002) detected significant effects imposed by 100 µm mesh relative to mesh sizes of 2 mm and 4.7 mm but not between the two latter mesh sizes. As the smallest mesh size we used was 1 mm, we do not expect mesh size effects to be relevant in our study.

**Implications**

The two dominant processes of land-use change in our landscape differed in the timing and nature of their effects on decomposition. Relative to intact forest, decomposition rates were 7% lower in forest fragments during the dry season, but 9% higher in orange groves during the wet season. The seasonal aspect of our results suggests that the functional consequences of different land uses can only be understood with studies that account for intra-annual variation. In our study region, there has been a recent increase in settlement and agricultural development, threatening the remaining forest fragments. Because different land uses affected decomposition in opposite directions, consequences of land-use change at the landscape scale will depend on the relative increases of fragmented forest versus orange groves over time. Any effect of land-use change on nutrient turnover has implications for forest and agricultural productivity, as well as longer term patterns of soil carbon stores and fluxes. The degree to which the land-use effects on decomposition we observed in this study translate into changes in nutrient cycling within ecosystems will depend on whether land-use effects on belowground decomposition mirror those aboveground.
3.6 Tables

Table 3.1 Conditional F tests for (A) differences in microenvironment factors and earthworm biomass among habitats after accounting for season and (B) microenvironment and earthworm effects on decomposition rates along edge transects in forest patches. F tests condition on estimated random effect parameters (sites). Asterisks indicate significance after sequential Bonferroni corrections for sets of six (habitat regression models) and four (fragmentation regression models) multiple tests. Earthworm effects were only examined in +MI litter bags.

(A) Habitat regression models

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(B) Fragmentation regression models

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3.7 Figures

![Graph a](image1)

- **Graph a**: Comparison of decomposition rate across different habitats with and without MI (Multiple Interventions). The x-axis represents different habitats (Intact forest, Large patches, Small patches, Orange fields), and the y-axis shows the decomposition rate. The graph indicates a higher decomposition rate under +MI conditions compared to -MI conditions.

![Graph b](image2)

- **Graph b**: Comparison of dry season decomposition rate across different habitats with and without MI. Similar to Graph a, the x-axis represents the same habitats, and the y-axis shows the dry season decomposition rate. The graph shows a similar trend with a higher decomposition rate under +MI conditions.
Figure 3.1 MI treatment effects on differences in mean decomposition rates (d$^{-1}$, ± 1 SE) among habitats in a) the pooled seasons’ data and separately for each of the b) dry and c) wet seasons. Decomposition rates were fitted with linear mixed models, and are log$_{10}$-transformed. Large and small forest patches are shown separately, but were lumped for analyses.
Figure 3.2 Differences in mean (+ 1 SE) litter amount and temperature factor scores among habitats, after accounting for season. Asterisks indicate different habitat categories at significance levels adjusted with sequential Bonferroni corrections. Mean factor scores were fitted with linear mixed models. Litter amount and temperature increase with corresponding factor scores.
Figure 3.3 Changes in log$_{10}$-transformed decomposition rates ($d^{-1}$) with (a) forest patch area (−MI: open circles, +MI: filled circles) and (b) distance to patch edge (−MI litter bags only). Lines in (b) are locally weighted separately for each forest patch. Patch area and distance to edge are both plotted on log scales. All data are from forest patches in wet season.
4 CONCLUSIONS

In north-western Costa Rica tropical forest is increasingly cleared for agricultural use, resulting in landscapes of forest fragments that are often embedded in plantations of orange trees. These different land uses affected both litter invertebrate communities and ecosystem functioning, but effects differ between processes of forest fragmentation and conversion. Invertebrate diversity was similar between intact and fragmented forest but diversity was lower in orange groves relative to intact forest (24% and 56% lower richness and evenness, respectively). Both types of disturbance resulted in losses of rare forest specialists. On average, I detected 11% fewer invertebrate families typical of intact forest within forest patches, and an average of 27% fewer intact forest taxa in orange groves. The disturbances of forest fragmentation and conversion had divergent effects on litter decomposition rates: decomposition was 7% slower in forest patches and 9% faster in orange groves than in intact forest. Disturbance effects on decomposition were also mediated by different pathways. Forest conversion only affected decomposition in the wet season, and these effects were explained by abiotic effects. Forest fragmentation only affected decomposition in the dry season, and these effects were mediated by the action of macroinvertebrates. My results are strengthened by good replication and repeated decomposition measurements in both the dry and wet seasons. Many in situ studies of forest fragmentation suffer from inadequate and/or pseudoreplication (Murcia 1995). High variability in litter communities and decomposition rates both within and among forest patches and orange groves in my landscape demonstrates the need for proper replication. The seasonal aspect of my decomposition results highlights the importance of studies that account for intra-annual variation.

4.1 Landscape Invertebrate Diversity

Diversity in landscapes is determined by diversity within sites (alpha diversity) as well as differences in composition among sites (beta diversity). Alpha diversity was lower in orange groves than in forested habitat. Beta diversity was high among orange groves in my study landscape and was related to differences in the groves’ litter environment. High beta diversity among groves was likely explained by differences in their management regimes: frequency of grass cutting and orange harvests (one site was no longer harvested) varied among orange groves.
as did their litter layers. Future studies of the relationship between invertebrate diversity and grove management would confirm this. I predict higher beta diversity in landscapes with a greater variety of agricultural management regimes. There has been much habitat conversion in my study landscape to pineapple plantations. I predict lower alpha and beta diversity in pineapple plantations than in orange groves because of higher temperatures and lower, more homogeneous litter cover in pineapple plots. Future projections of invertebrate diversity in this landscape will depend on the relative proportions of different agricultural crops and the invertebrate diversity maintained therein.

The remnant forest fragments in my study landscape are very small (< 36 ha) and are typical in size of patches that make up a large proportion of existing tropical forest (Terborgh and Feeley 2008). Despite my patches’ small sizes, they have considerable conservation value in sustaining alpha diversity. Invertebrate richness in patches was greater than that in orange groves and similar to richness levels in intact forest because of a large suite of families that we detected exclusively in forest fragments. Beta diversity among patches was also similar to beta diversity among plots in intact forest. However, I predict future disturbances will further deplete invertebrate diversity in this landscape. As in other areas of the tropics (Terborgh and Feeley 2008), forest clearance and conversion are progressing at an exponential rate in this landscape (M. C., pers. obs.). M. C. also observed additional disturbances (hunting, selective timber harvest for local use, water pipes and trails) which can be synergistic with fragmentation effects in patches (Gascon et al. 2000). In addition, family richness in forest patches was elevated due to a large number of disturbance-adapted taxa. Longer term invertebrate richness may be lower depending on the relative numbers of transient and established species. Finally, despite high beta diversity among disturbed sights and alpha diversity within forest patches, local extirpations of intact invertebrate families were also high in both orange groves and forest fragments. My estimates of local extirpations were conservative (Chapter 2) and are only indicative of forest fragmentation effects on the ground-dwelling proportion of litter invertebrates. Losses of forest invertebrates increased with litter temperatures and were non-random depending on natural abundances in intact forest. Given projected changes in temperature due to global climate change (Cox et al. 2000) and the high prevalence of rare species in tropical invertebrate communities there may be further depletion of invertebrate diversity beyond that observed in my study. My
results suggest large forest reserves will be required to maintain rare forest invertebrates in tropical countryside.

4.2 Diversity-Function Relationships

Concern regarding high biodiversity losses in natural systems, particularly in the tropics, has given rise to a large body of research investigating the relationship between biodiversity and ecosystem functioning (BDEp). Most tests of this relationship reveal positive effects of diversity on ecosystem function, including those examining detritivore effects on decomposition rates (Cardinale et al. 2006, Srivastava et al. 2009). However, neither forest conversion nor forest fragmentation effects on decomposition in my study could be explained by a positive relationship between invertebrate family richness and ecosystem function. In terms of forest conversion, invertebrate family richness was reduced in orange groves but decomposition rates were faster relative to intact forest. In terms of forest fragmentation, invertebrate community diversity did not differ between fragments and intact forest, but decomposition was slower in patches.

These results do not necessarily contradict the consensus on BDEp relationships. Although most studies report a positive BDEp relationship, many show the opposite pattern (Balvanera et al. 2006, Cardinale et al. 2006). This may be particularly true for in situ communities that have lost species due to disturbance (Ives and Cardinale 2004), as species’ extinctions are non-random with respect to their functional traits (Rafaelli 2004, Larsen et al. 2005). In such natural systems, BDEp relationships are more variable than in communities with random species losses, as they depend on the functional importance of taxa most affected by disturbance (Ives et al. 2004, Gross and Cardinale 2005). My research adds to the relatively few studies examining the functional consequences of diversity losses in communities with multiple trophic levels and realistic extinction scenarios following disturbance (Rafaelli 2004).

Numerous studies have shown that species composition effects on function are at least as strong as those of diversity (Hooper et al. 2005). Although invertebrate family richness was similar between intact and fragmented forest in my landscape, our data reveal losses of forest specialists in forest patches and differences in macroinvertebrates’ activity between intact and fragmented forest. These biotic changes explained slower decomposition rates in patches. This
result suggests there are particular macroinvertebrates (such as shredders and/or saprophytes) that have a disproportionate influence on decomposition regulation.

Land-use effects on BDEF relationships would be clarified with further sampling in communities of litter invertebrates and other detritivores. I chose pitfall methods to sample invertebrates in the interest of obtaining comparative samples among disparate habitats for a large component of in situ litter communities (Chapter 2). These samples may only partially reflect the communities acting on litter within litter bags, as pitfall samples are biased against invertebrates that are more active in the upper parts of the litter layer. I am thus only able to draw indirect inferences regarding influences of macroinvertebrate diversity on decomposition. Direct invertebrate samples in bags of each mesh size would be useful for identifying particular macroinvertebrates responsible for fragmentation effects on decomposition and confirming linkages between diversity, composition of faunal assemblages, and decomposition rates in disturbed habitats. Finally, future studies investigating the effects of forest conversion on microinvertebrates, protozoa, fungal and microbial communities would clarify diversity-decomposition relationships in orange groves.

Consumer-resource dynamics can be affected by changes in either consumer or resource diversity. In this study I investigated top-down control of decomposition rates. Meta-analysis of studies investigating decomposition responses to changes in consumer and resource diversity in detritus-consumer food webs indicates top-down control of BDEF relationships is more important than bottom-up (detrital diversity) effects on the breakdown of brown litter (Srivastava et al. 2009). Top-down BDEF regulation was important in forest patches: rates of decomposition were slower in patches due to fragmentation effects on macroinvertebrate communities and their action on decomposing litter. I am uncertain whether forest conversion affected decomposition via top-down BDEF control: decomposition in orange groves was faster due to either changes in consumer diversity (microfauna) or direct microclimate effects.

Bottom-up (resource) diversity effects may also influence decomposition in disturbed sites. Decomposition is slower in lower quality litter (Vasconcelos and Laurance 2005) and litter quality is likely affected by the disturbances of forest fragmentation and conversion. For example, Laurance et al. (1998) documented greater proportions of successful plant species in forest fragments due to edge exposure effects on patch microclimate. Nutrient quality of
successional plant litter is poor for detritivores and may thus be expected to reduce decomposition rates in forest patches (Taylor et al. 1989, Mesquita et al. 1998). Further study of the nature and magnitude of bottom-up (detrital) diversity effects on decomposition rates in disturbed sites is the next step in providing a comprehensive description of forest fragmentation and conversion effects on BDEF relationships. Feedback patterns of soil nutrient mineralization will depend on the independent and interactive effects of top-down and bottom-up influences on BDEF relationships in disturbed sites, as will consequences for seedling dominance, productivity in fragmented forest and agroecosystems, and longer term effects on soil carbon stores and fluxes.
REFERENCES


Duffy, E., Srivastava, D. S., McLaren, J., Sankaran, M., Solan, M., Griffin, J., Emmerson, M. and K. E. Jones. 2009. Forecasting decline in ecosystem services under realistic scenarios of


APPENDIX

Cumulative list of invertebrate taxa sampled in pitfall traps. Forest obligates are taxa not detected in orange groves. A taxon is considered to be part of the intact forest fauna if it was detected in intact forest sites. Bold taxa were trapped in forest patches but were not found in intact forest. For taxa present in orange groves, asterisks indicate taxa that are not found in any forested sites. Forest obligates with asterisks are only present in intact forest. (c) indicates a taxon for which > 50 individuals were trapped across ≥ 2 intact forest sites.

<table>
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<th>Taxa present in orange groves</th>
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<th>Forest obligates</th>
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Taxa present in orange groves, intact and fragmented forest

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73
Taxa present in orange groves, intact and fragmented forest

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