

Methods for conservation outside of formal reserve systems: The case of ants in the seasonally dry tropics of Veracruz, Mexico

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Abstract

Like most ecosystems of the world, tropical dry forests of the central coast of the Gulf of Mexico are inadequately preserved. Given that reserve expansion is unlikely, it is imperative that the conservation capacity of the matrix surrounding reserves is enhanced. Here, we examine the habitat value of isolated pasture trees and patches of secondary regrowth in terms of their terrestrial and arboreal ant assemblages in both a wet and dry season. These simplified wooded systems increase species densities within the agricultural matrix and provide habitat for some forest ant species. Estimated species richness of arboreal ants was particularly low on isolated trees, highlighting an important limitation. This was not the case for terrestrial ants, which were particularly species rich under isolated trees. We also found that the inter-site variations in species densities and similarity to the forest ant assemblage for terrestrial and arboreal strata were not correlated, suggesting that responses to restoration may not be as uniform as often thought. This has important implications for the use of indicator taxa in suggesting the response of other taxa. In terms of species composition, neither secondary regrowth nor isolated trees were appropriate replacements for forest fragments, even though the studied forest fragments were small (13–32 ha). The ant assemblages did not exhibit a seasonal change in composition. However, season influenced the contrast between habitats, with isolated trees being more distinct from pasture, and regrowth more closely resembling forests, during the wet season. Microclimatic variables indicate that the forests were least affected by the tropical dry season, and this may contribute to their characteristic fauna. We conclude that even small forest patches make a unique contribution to landscape conservation and that, where reserves are limited, conscientious management of the landscape matrix may provide some species with sufficient new habitat to survive outside of reserve systems. These conclusions are influenced by both season and strata studied.

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1. Introduction

Janzen (1988) declares tropical dry forests to be the world's "most endangered major tropical ecosystem". Wilson (1992, p. 377) was prompted to say, "Among the concerns of ecologists, tropical deciduous forests have stood in the shadow of the rain forests, but they are in even greater peril...they are among the most heavily

exploited of the world's land environments". The disproportionate endangerment of dry forests is mainly a consequence of the extended dry season, which allows the forest to be cleared using fire and for regrowth to be readily controlled. The climate is considered to be particularly suitable for livestock and agriculture, and human population densities are also higher in dry forest regions than in any of the world's other major tropical ecosystems (Murphy and Lugo, 1986). The central region of Veracruz, Mexico once supported an area of approximately 800,000 ha of tropical dry forest (Rzedowski, 1978), but most of this has been cleared and only 46 ha

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of forest are protected. Given small range sizes and high turnover rates of tropical insect assemblages, many species will not be preserved in such systems, and will be dependent upon the surrounding matrix habitats for their survival.

Although conservation of tropical dry forest has reached a stage where restoration has overtaken the task of protection (Janzen, 1988), complete restoration is often not possible, particularly in areas of continued agricultural use. For example, proposed reserve extensions in Mexico do not include central Veracruz, and do not adequately protect lowland areas, due mainly to high population densities in those areas (Cantú et al., 2004). For such areas, it is crucial to develop methods for conservation that are compatible with these high population densities and to emphasize the potential conservation value of this human-dominated matrix.

Several studies have demonstrated the value of tropical agricultural landscapes as habitat for invertebrates (e.g., Perfecto et al., 1997; Ricketts et al., 2001; Goehring et al., 2002; Perfecto and Vandermeer, 2002; Horner-Devine et al., 2003; Perfecto et al., 2003). However, these studies focus on coffee plantations at mid altitudes, while human population pressures are at their highest in lower tropical zones where agricultural practices and their effects may differ. Lowland dry forest areas require particular attention, possibly with their own unique approach to conservation in the matrix, such as the integration of remnant vegetation with grazing. Where isolated trees have been studied in the context of lowland pastures and agriculture, they have been found to support insect faunas which complement those of the surrounding agricultural matrix, leading to recommendations for their retention for conservation purposes (Majer and Delabie, 1999; Dunn, 2000). However, this method of enhancing diversity has never been studied year round, and never in a tropical dry forest region. In lowland dry forests, secondary regrowth has also been found to have significant plant conservation value (Gordon et al., 2004). Therefore, in addition to examining the value of isolated trees, we also test the conservation value of secondary growth in the region. Few studies have concurrently focused on the response of both the terrestrial and arboreal ant assemblages (but see Majer and Delabie, 1999), probably because they are generally considered to be correlated (Lawton et al., 1998). Here, we compare the responses of both the arboreal and terrestrial strata to habitat retention.

Seasonality interacts with habitat fragmentation in both tropical (Laurance and Williamson, 2001) and temperate environments (Barbosa and Marquet, 2002). In view of the fact that tropical dry forests are characterized by a distinct dry season which lasts several months, seasonality may affect the relative contribution of different landscape elements to conservation of local biota. To understand how ant species composition and diversity

might be conserved in the extensively degraded dry forest landscapes of Mexico and beyond, and to most thoroughly understand the value of these off-reserve habitats, we sample across strata and across seasons. Specifically, we aim to compare the conservation value of isolated pasture trees and secondary regrowth with that of small forest fragments and, at the other end of the spectrum, open pasture.

2. Methods

2.1. Study area and design

The study was undertaken in the central coastal plain of Veracruz, Mexico. The landscape is a mosaic of pastures, agriculture, human habitations and secondary regrowth in various stages of succession. The climate is warm sub-humid, with a rainy season occurring from June to September. Average annual precipitation is approximately 1200 mm and mean monthly temperature ranges from 20.3 to 26.7 °C, with the cooler months occurring from November to March (K. Mehltreter, unpublished data).

We sampled three different habitat types: forest, secondary regrowth and pastures. Pastures included samples in both the open pasture and isolated remnant trees. We sampled three sites within each habitat, and within each of these sites we sampled four trees (see Appendix 1 for detailed site descriptions). Sampled trees were at least 10 m apart but, wherever possible, distances were generally, far greater (mean distance to nearest neighbouring tree = 164 m). The forest fragments ranged in size from 13 to 32 ha and the areas of regrowth ranged from 50 to 98 ha.

Most sampling was associated with *Diphysa robinoides* (Leguminosae), a small tree common in the region. *D. robinoides* is deciduous at the study site and has a variety of uses, including firewood, building materials and 'live fences' (Niembro Rocas, 1986). We chose this species due to its local abundance and frequent occurrence as an isolated tree. We occasionally substituted additional species for *D. robinoides* when it was not accessible (see Appendix 1 for details of substitutions). No tree species had specific ant-plant relationships (Díaz-Castelazo et al., 2004; A. Gove, personal observation), and the effect of plant species on ant fauna was considered minimal.

2.2. Ant sampling

We sampled the terrestrial ant assemblage using pit-fall traps which consisted of disposable plastic drinking cups (70 mm diameter), half-filled with ethylene glycol, and set flush with the ground surface. We placed traps 1 m to the north and south of each tree trunk. We sampled

the open pasture with a similar configuration, with the pair of traps placed 5 m to the north of the drip line of the nearest sampled tree. We left pitfall traps open for 96 hours.

We sampled the arboreal ant assemblage by beating each tree with a 2.5 m bamboo pole, and collecting ants as they fell on to ten 1 × 1 m cloth trays suspended beneath each tree. We chose this method because its relatively low impact allows repeated sampling and it was least problematic to land managers. In a comparison of methods, [Basset et al. \(1997\)](#) found beating to be particularly effective. We beat each portion of the tree overhanging a collecting sheet until no further ants were collected. Where large nests were located throughout the tree (e.g., *Azteca* species, *Crematogaster torosa* or *Myrmelachista* sp.1), ants almost continually fell from the tree. In these cases, we counted a maximum of 200 individuals of these species.

We sampled at the end of the wet-season (November 2001) and in the mid-late dry season (March 2002).

2.3. Microclimate

We recorded ground surface temperature and relative humidity, and soil temperature (10 cm depth) at all sites. We placed a data logger (Onset Hobo H8 Pro logger for surface temperature and humidity; Onset Optic Stow-Away Temp logger for soil temperature) at a central location, and all records were related back to this logger. We then expressed each measure as a deviation from the benchmark's record at precisely the same time as the individual field recordings. Readings were taken between 10:00 and 16:00 h. In each season, we took the readings twice, with the ordering of sites varying between the two sessions within a season. The mean value of these two readings was then used for analysis. At the benchmark site, we logged surface temperature and relative humidity and soil temperature at a depth of 10 cm.

We took each measure 1.25 m to the north of the tree trunk, or equivalent position in the pasture. We measured temperature and humidity with a digital thermo hygrometer (Forestry Supplies #76255), and measured soil temperature with a digital thermometer with probe (Forestry Supplies #89102).

2.4. Analysis

We used repeated-measures ANOVA to test the effect of month and habitat type on species density and ant abundance. Month and habitat type were both considered fixed factors. As three different sites were considered within each habitat treatment, we employed a nested ANOVA design. Multiple comparisons between the three habitat types were performed using Ryan's test, based on the *F*-ratio ([Day and Quinn, 1989](#)). We screened all data to ensure error structures were nor-

mally distributed and that variances were homogeneous. In the case of terrestrial abundance, values were log₁₀-transformed before analysis. As arboreal ant activity was only considered as 'high' when sampling reached 200 individuals, activity level was treated as a discrete variable, with which we performed the Wilcoxon signed rank test to test the effect of month, and the Kruskal–Wallis test for the effect of habitat type. We analyzed microclimate variables using MANOVA. All conventional analyses were performed using SPSS 10.00.

We estimated the total species richness for each habitat with species accumulation curves created using EstimateS ([Colwell, 2000](#)). We estimated species richness with the Incidence-based coverage estimator (ICE), which utilizes presence–absence data.

We used linear regression to test whether the species density and assemblage similarity to forest of both the terrestrial and arboreal ant assemblages were correlated. This was aimed at testing whether management of either stratum would automatically implicate the other.

Given the configuration of this study – widely dispersed sites, each with a cluster of sampled trees – we controlled for the effect of geographic configuration, by using partial Mantel tests, to test the hypothesis that there are distinct ant assemblages associated with each habitat type. We employed the program ZT ([Bonnet and Van de Peer, 2002](#)), and performed a separate test for each season. As there are no formal post hoc tests, we carried out a series of pair-wise Mantel tests to illustrate level of discrimination between habitat types. In each test, 9999 permutations were used, and the assemblage matrix was based on Sørensen's coefficient of dissimilarity.

3. Results

3.1. Overview

During the study, we sampled 92 species or morpho-species of ants in 35 genera (summarized in [Appendix 2](#)). Seventy nine species occurred in pitfall traps and 62 were sampled through tree-beating; 49 species occurred in both strata. In pitfall traps, 35 species occurred in pasture (21 genera), 53 species (26 genera) at the base of isolated trees, 47 species (27 genera) in regrowth and 38 species (19 genera) in forest. In tree-beating samples, 33 species (18 genera) occurred in isolated trees, 51 species (22 genera) in regrowth and 40 species (13 genera) in forest.

3.2. Species density

Habitat types did not differ in terms of arboreal ant species density ($F_{2,27} = 2.66$, $p = 0.088$), although it tended to decrease from isolated trees to forest ([Fig. 1\(a\)](#)). Significant variation in arboreal species density was explained by the variation among sites within a

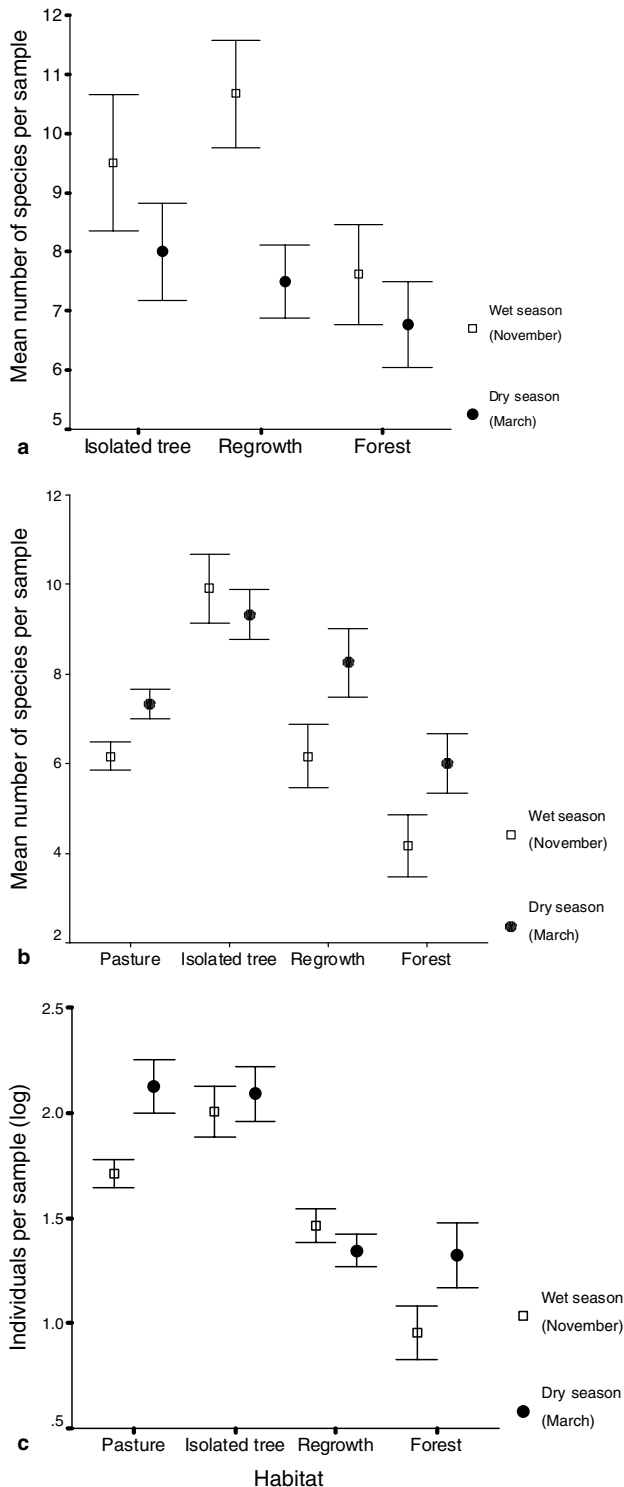


Fig. 1. (a) Mean species densities of arboreal species, (b) mean species density of terrestrial species and (c) mean abundance of ants in the wet and dry season. Error bars represent one standard error.

habitat type ($F_{26,27}=4.16$, $p=0.004$). Species density in the canopy was higher during the wet season than during the dry season ($F_{1,27}=15.29$, $p=0.001$; Fig. 1(a)). Arboreal ant activity, as measured by relative numbers of ants

collected from beating trays, was consistent across habitats (November, Kruskal–Wallis $\chi^2=2.87$, d.f. = 2, $p=0.238$; March, Kruskal–Wallis $\chi^2=0.4$, d.f. = 2, $p=0.819$) and season (Wilcoxon signed rank $Z=-0.95$, $p=0.342$).

In the case of both terrestrial species density and mean abundance, a season–habitat interaction occurred (species density, $F_{3,36}=4.00$, $p=0.013$; abundance, $F_{3,36}=4.13$, $p=0.013$). Species density increased in pasture, regrowth and forest during the dry season, while remaining constant under isolated trees (Fig. 1(b)). Isolated trees supported the highest average species density (9.63 species), and had, on average, 2.8 species more than open pastures. Forests possessed the lowest mean species density (5.08 species). Activity levels tended to fall into two groups: high activity in open sites (pasture and isolated trees) and low activity in wooded sites (Fig. 1(c)). Activity increased in the dry season in all habitats except regrowth.

3.3. Estimates of total species richness

Estimated richness for the arboreal ant assemblage was lowest in isolated trees and highest in secondary regrowth and forest (Table 1). Patterns in the total species richness of the terrestrial assemblage were more complex: terrestrial species richness was similarly low in the forest and grassland, and highest in isolated trees. When both strata were combined, isolated trees and wooded habitats (forest and regrowth) were equally species rich, but comparison of the two strata demonstrates that this richness was distributed quite differently in different habitats.

3.4. Correlation of strata

The terrestrial and arboreal assemblages were not correlated in terms of either species density ($r^2=0.124$, $p=0.261$) or similarity to forest ($r^2=0.046$, $p=0.506$). This suggests that the two assemblages are influenced by different factors, and should be considered as separate subsets of the fauna.

3.5. Multivariate analysis of the ant assemblage

Ant species composition in both the terrestrial and arboreal ant assemblages differed between habitat types (Table 2). Assemblage composition of each habitat did not differ among seasons (diagonal in Table 3).

Table 1

Estimated species richness within each habitat type, based on the ICE estimator

Habitat	Arboreal	Pitfall traps	All strata
Pasture	–	46.64 (35)	46.64 (35)
Isolated tree	35.71 (33)	68.38 (53)	75.68 (65)
Regrowth	62.64 (51)	58.47 (47)	76.68 (70)
Forest	63.21 (40)	45.05 (38)	78.20 (60)

Numbers in brackets are the observed species richness.

Table 2
Results of simple and partial Mantel tests of matrix correlations

	November 2001 (wet season)		March 2002 (dry season)	
	<i>r</i>	<i>p</i>	<i>r</i>	<i>p</i>
<i>(A) Pitfall traps</i>				
Habitat type	0.282	<0.001	0.236	<0.001
Geography	0.593	<0.001	0.558	<0.001
Habitat geography*	0.193	<0.001	0.140	<0.001
<i>(B) Tree beating</i>				
Habitat type	0.307	<0.001	0.328	<0.001
Geography	0.373	<0.001	0.324	<0.001
Habitat geography*	0.220	<0.001	0.256	<0.001

p is derived from number of occurrences of observed *r* value in a randomized data set (9999 permutations).

* |geography indicates a partial correlation controlling for effect of geographic configuration.

Generally, each habitat assemblage was distinct, but with several important exceptions. In both the terrestrial and canopy samples, the regrowth assemblage was more similar to the forest assemblage during the wet season than in the dry season. In the terrestrial assemblage, there was a significant difference between the forest and terrestrial assemblage during the dry season ($p=0.014$), but not during the wet season ($p=0.054$). A similar pattern occurred in the arboreal assemblage, with the difference between regrowth and forestry assemblages being stronger in the dry season ($p=0.015$) than in the wet season ($p=0.219$). Conversely, the ant assemblage below isolated trees was more distinct from the pasture assemblage during the wet season ($p=0.014$) than in the dry season ($p=0.251$).

3.6. Species responses of note

The habitat value of isolated trees and secondary growth was most readily highlighted by occurrence of

arboreal genera. Species of the arboreal genera *Cephalotes* and *Pseudomyrmex* both survived in isolated trees and regrowth. Although several arboreal species had a preference for wooded habitats, they were also found in isolated trees (e.g., *Azteca* sp. 3, *Dolichoderus lutosus*, *Camponotus linnaei*, *C. novagranadensis* and *Pseudomyrmex gracilis*), while several other arboreal species responded favourably to tree isolation (e.g., *Camponotus zoc*, *Cephalotes scutulatus*, *Pseudomyrmex caeciliae* and *Pseudomyrmex bruneus*). The two litter-dwelling specialist fungivores, *Mycocephurus smithii* and *Cyphomyrmex costatus*, were only ever sampled from the forest fragments. Opportunistic ant species, *Dorymyrmex* sp. 1 and *Ectatomma tuberculatum*, and the hot-climate specialist, *Forelius pruinosus* (Bestelmeyer, 2000), were present in all habitats except forest fragments.

3.7. Microclimate

A habitat \times season interaction was revealed by the MANOVA of microclimate variables ($F_{9,108}=5.34$, $p<0.001$). Contrasts between habitat types were stronger in the dry season than in the wet season, and most of this contrast was due to the effect of the forest possessing lower temperatures and maintaining higher humidity. In the dry season, the forest was more than 6 °C cooler and more than 10% more humid than all other habitats. Regrowth was more similar to the other secondary habitats than forest.

4. Discussion

Isolated pasture trees and patches of secondary regrowth both provide conservation value to degraded landscapes in which there is a limited network of conservation reserves. Regrowth most closely resembles

Table 3
P values based on pair-wise Mantel tests comparing species composition between habitat type and season

	Pasture	Isolated	Regrowth	Forest	
<i>(A) Pitfall traps</i>					
Pasture	0.590	0.251	0.001	<0.001	
Isolated	0.014	0.147	0.018	<0.001	Dry season
Regrowth	<0.001	<0.001	0.136	0.014	
Forest	<0.001	<0.001	0.054	0.132	
	Wet season				Season
<i>(B) Tree beating</i>					
		Isolated	Regrowth	Forest	
Isolated		0.331	0.003	<0.001	
Regrowth		<0.001	0.571	0.015	Dry season
Forest		<0.001	0.219	0.418	
		Wet season			Season

The diagonal (gray) is the comparison between the two seasons, within the same habitat type. The upper right corner is the comparison in dry season (March), and the lower left corner is the comparisons in the wet season (November). *P* values are included for comparison only and have therefore not been adjusted for multiple comparisons.

small forest fragments and provides habitat for certain species that are not likely to survive in more open habitats. In addition to conserving high species densities, single isolated trees provide habitat for some elements of the woodland ant assemblage in what are otherwise simplified systems (see also Majer and Delabie, 1999; Dunn, 2000). Importantly, isolated trees conserve a number of arboreal species, such as *Cephalotes* and *Pseudomyrmex* species, which would not otherwise occur in pastures. The demonstrated habitat value of these secondary habitats supports the suggestion that agricultural landscape can be managed to maximize arthropod conservation (Roth et al., 1994; Perfecto et al., 1997; Perfecto and Vandermeer, 2002; Benton et al., 2003; Horner-Devine et al., 2003). This potential may also encompass birds (Hughes et al., 2002) and mammals (Daily et al., 2003). Janzen (1988) suggests that reducing tropical dry forest to “fencerows, ditch-sides, unkempt pastures, and woodlots” would reduce species diversity by 90–95%. Our findings suggest that with conservation of these features, species loss could be far less. Although not tested here, small forest fragments such as those we studied may still act as essential sources of immigrants for colonisation of secondary habitats, such as isolated trees (see also Horner-Devine et al., 2003).

We believe that consideration of both species density and species richness is important in identifying the habitat value of these features. For example, when one considers the total species richness of arboreal ants in isolated trees relative to that in forest fragments and other habitats, the isolated trees actually conserve fewer species. Estimated total arboreal species richness was lowest in isolated trees, as the same subset of species is repeatedly conserved in a number of trees. Sampling more trees in forests continued to yield more arboreal ant species, whereas sampling more isolated trees did not. Even though a single isolated tree may conserve many species (e.g., Majer and Delabie, 1999), a series of isolated trees does not conserve a great deal more species. Since most authors that have considered isolated trees have looked at species density rather than species richness, this result has been missed. This is not the case for the terrestrial ant assemblage, as estimated species richness was particularly high below isolated trees when compared to other habitats. This may be explained by a higher diversity of habitats occurring beneath trees than in the canopy.

Arboreal ant samples, at this scale, indicate that the conservation of larger remnants will preserve more species than the conservation of many smaller habitats such as isolated trees (SLOSS debate; Wilson and Willis, 1975; Soulé and Simberloff, 1986). We do not suggest that isolated tree faunas are a mere subset of forest fragment faunas (Patterson and Atmar, 1986), as isolated trees provide unique habitat for some arboreal species such as *Cephal-*

otes species. We recommend that the preservation of a range of fragment sizes, including isolated trees is the most effective approach to landscape management.

Low arboreal species richness in isolated trees demonstrates that they are a useful conservation tool, but one with obvious limitations. Also in their favour, is the fact that if all isolated trees were cleared from the region's pastures, we would probably lose more than 45% of ant species from those habitats and most of the ecological interactions in which they play a role.

The lack of a correlation between the terrestrial and arboreal ant assemblage, in terms of similarity to the forest assemblage and species density, highlights the fact that arboreal and terrestrial ants may respond differently to habitat alteration. At larger scales, species richness of canopy and terrestrial ant assemblages are correlated in at least some regions (Lawton et al., 1998) and, although we may not expect a close relationship between unrelated organisms (Goldstein, 1997; Kerr, 1997), we may expect one between the ant assemblages of two strata. That even canopy ants are poorly correlated with ground-dwelling ants, suggests that forest organisms may respond to disturbance in a more complex manner than is often thought. These findings have important implications for the use of single species assemblages to predict the response of other assemblages, and suggest that groups within the same taxa may not be relied upon to indicate the response of others.

At the ground level particularly, both the species density and estimated species richness of ants in the forest is impoverished compared to other habitat types. This is most likely due to decreased activity levels associated with lower levels of insolation (e.g., Kotze and Samways, 2001) and with lower levels of species turnover associated with lower habitat homogeneity. These forests also have particularly low densities of specialized litter ant species. The relatively high density of ant species in isolated trees is partially attributable to the overlap of two distinct ant faunas, that of pastures and that of forests, in and near isolated trees. Consequently, the highest density of species in pitfall traps was found under isolated trees. Other studies have produced similar results with other types of habitat transitions (e.g., Lovejoy et al., 1986; Bedford and Usher, 1994). Lovejoy et al. (1986), found that butterfly species density was highest in forest fragments due to the influx of sun-loving species associated with the increase in light levels.

In terms of species composition, the recognized conservation value of isolated trees and regrowth differed depending upon the season in which they were sampled. Microclimate data demonstrated that forests were less susceptible to seasonal climatic oscillation than were the other habitat types, being more than 5 °C cooler and 10% more humid than the other habitat types during the

dry season. The increased sensitivity of secondary habitats to seasonality also manifests itself in changes in the species composition of ants. The resemblance of the regrowth ant assemblage to that in the forest declines with the dry season, while the assemblage of ants beneath isolated trees more closely resembles that of the surrounding pasture. In the dry season, in these habitats, there is more activity from opportunistic and thermophilic ants, such as *Dorymyrmex* and *Forelius pruinosus*, while specialized species become less active. For example, at the base of isolated trees, dry season activity of *Pseudomyrmex* spp., *Solenopsis* spp., *Strumigenys* sp. 1, several *Pheidole* species and *Dolichoderus lutosus* is reduced.

Several rare species occur only in forest fragments (e.g., *Camponotus sericeiventris*, *Cephalotes minutus*, *Cephalotes umbraculatus*, *Cyphomyrmex costatus* and *Pseudomyrmex spiculus*). Given this rarity, it is not possible to completely separate their occurrences from random sampling. However, a deeper understanding of these rare species, and their habitat requirements, is particularly required. It is of great concern to think that if these species are lost from the forest fragments, their presence in the entire landscape will be doubtful.

Despite their small size (13–32 ha), the tropical dry forest fragments in this study possess significant conservation value when compared to other elements of the landscape, including secondary regrowth, which covered greater areas (50–98 ha). Evolved tolerance of dry forest species to the harsh climatic conditions of the seasonally dry tropics may increase the habitat value of the region's small forest fragments. This value may be more so than in the humid tropics, where detrimental edge effects (e.g., Kapos, 1989; Camargo and Kapos, 1995; Williams-Linera et al., 1997) do not have such a strong seasonal analogue to which species have evolved.

As there are still many species that have not been noted in association with isolated trees or secondary regrowth (e.g., *Mycocepurus smithii*, and rare species listed above), core reserves such as the current La Mancha ecological reserve are required. However, given small species range sizes such a reserve is almost certainly not enough to service the entire central coast of Veracruz. Many species must survive in the surrounding landscape. For example, several species not necessarily associated with disturbed habitats, such as *Cephalotes pallens* and *Mycetosoritis* sp. 1, have only been recorded outside the reserve and, although common, *Pogonomyrmex barbatus* has not been recorded within the reserve. Although the agricultural landscapes studied here generally offer some levels of habitat protection, a more comprehensive reserve system is required for a forest region that formally occupied approximately 800,000 hectares.

The situation may be more complex than simply retaining isolated trees in farmland areas. The ANOVAs

indicate a significant level of variation in species density being explained by the site itself. This suggests that more should be done to examine effects on species composition at the farm level; for example, the density of isolated trees, and nature of surrounding vegetation. Weibull et al. (2003) identify farm scale management to be the most important scale for managing diversity of invertebrates. However, Dunn (2000) was unable to identify an effect of isolated tree density or border condition on species richness of ants or beetles at this scale. Nonetheless, more work is required to identify why one farmland property may conserve more species than another.

Areas such as the lowland tropical areas of Mexico have highly valued ecosystems, combined with particularly dense human populations. Reserve systems are inadequate but are also unlikely to be enlarged. Therefore, conservation strategies will require integration of conservation and production landscapes. We suggest that isolated trees and secondary regrowth are no substitute for even small forest fragments, but do provide further conservation value to agricultural landscapes. Assessment of the conservation value of these features depends upon both the sampled strata and the season in which they are sampled.

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Appendix 1. Site descriptions

Dry forest

The trees sampled in dry forests were apportioned between three sites, two of which were located within the La Mancha ecological reserve (Centro de Investigaciones Costeras La Mancha, 19°35'N, 96°23'W), and the third on private land, approximately 33 km to the south of La Mancha near La Antigua (19°20'N, 96°19'W).

The two different forests were sampled in the La Mancha ecological reserve, managed by the Mexican Instituto de Ecología. They occupy two separate valleys, separated by a grass-covered ridge.

The La Mancha forests were 32 hectares of medium semi-deciduous forest (*selva mediana subcaducifolia*), and 13 hectares of low deciduous forest (*selva baja caducifolia*). (See Castillo-Campos and Medina-Abreo, 2004). The third forest fragment was the Chalchihuecan forest ejido (19°20'N, 96°18'W) - This is a mature but slightly disturbed medium semi-deciduous forest (*selva mediana subcaducifolia*) in which there has been no recent history of clearing. The fragment is approximately 15 hectares surrounded by recent clearing, small farms, and coastal dunes. In the first forest fragment, sampled trees were *Diphysa robinoides*, *Brosimum alicastrum*, *Gymnanthes lucida* and *Hyperbaena jalcomulcensis*, while in the second fragment *Coccoloba barbadensis*, *Eleodendron trichotomum* and two *Gymnanthes lucida* were sampled. Sampling in the privately owned forest focussed on four *Diphysa robinoides* individuals.

Pasture and isolated trees

The pasture and isolated tree sites were, in effect, the same areas and were distributed between three sites, one near the township of La Antigua (19°20'N, 96°19'W) and the other two, approximately two km to the south (19°18'N, 96°19'W). These pasture sites were all cleared at least 20 years ago, and had scattered remnant trees.

Secondary regrowth

The secondary woodland sites (*acahual*) were distributed between three areas, Rancho Riaño (75 hectares, 19°21'N, 96°19'W), La Antigua (98 hectares, 19°20'N, 96°19'W) and at a site approximately three km south of La Antigua (50 hectares, 19°18'N, 96°19'W). These sites were cleared for agriculture or grazing and were abandoned in the last 10–20 years. They possess scattered forest trees (*Ficus* spp. *Enterolobium cyclocarpum*, *Cedrela odorata*, *Acacia pennatula* and *Diphysa robinoides*), with a denser covering of opportunistic small tree species (*Glyricidia sepium*, *Guazuma ulmifolia* and *Acacia cornigera*).

Appendix 2

Summary of ant species or morphospecies sampled during the study

Subfamily Species	Sampling method and habitat type						
	Pitfall traps				Arboreal		
	Pasture	Isolated tree	Regrowth	Forest	Isolated tree	Regrowth	Forest
Myrmicinae							
<i>Atta cephalotes</i> (Linnaeus)	0	1	2	0	0	0	0
<i>Cardiocondyla venustula</i> Wheeler	0	2	0	0	3	1	0
<i>Cephalotes minutus</i> (Fabricius)	0	0	0	0	0	0	1
<i>C. pallens</i> (Klug)	0	0	1	0	0	2	0
<i>C. scutulatus</i> (Smith)	0	3	1	1	11	5	2
<i>C. umbraculatus</i> (Fabricius)	0	0	0	0	0	0	1
<i>Crematogaster torosa</i> Mayr	1	7	6	2	10	8	3
<i>C. sp. 2</i>	0	0	1	1	0	0	0
<i>C. sp. 3</i>	1	0	6	4	0	5	3
<i>Cyphomyrmex costatus</i> Mann	0	0	0	2	0	0	0
<i>C. minutus</i> (Fabricius)	2	7	3	3	0	2	1
<i>Leptothorax subditivus</i> (Wheeler, W.M.)	1	4	3	0	0	0	0
<i>L. echinatinodis</i> Forel	0	0	0	2	6	3	3
<i>L. wilda</i> M.R. Smith	0	4	2	0	6	5	0
<i>Monomorium cyaneum</i> Wheeler, W.M.	11	10	8	1	5	3	1
<i>M. gp. minimum</i>	0	0	0	0	0	1	3
<i>Mycocepurus smithii</i> Forel	0	0	0	6	0	0	0
<i>Mycetosoritis</i> sp. 1	1	0	0	0	0	0	0
<i>Pheidole</i> sp. 1	0	0	2	4	0	1	1
<i>P. sp. 2</i>	0	1	0	0	0	0	1
<i>P. sp. 3</i>	1	0	1	0	0	0	0

(continued on next page)

Appendix 2 (continued)

Subfamily Species	Sampling method and habitat type						
	Pitfall traps				Arboreal		
	Pasture	Isolated tree	Regrowth	Forest	Isolated tree	Regrowth	Forest
<i>P.</i> sp. 7	0	0	1	6	0	1	3
<i>P.</i> sp. 8	2	1	0	0	0	0	0
<i>P.</i> sp. 9	9	11	4	2	0	0	1
<i>P.</i> sp. 10	3	0	0	1	0	0	0
<i>P.</i> sp. 11	2	0	3	1	0	0	0
<i>P.</i> sp. 12	2	2	0	2	0	0	0
<i>P.</i> sp. 13	0	1	0	0	0	0	0
<i>P.</i> sp. 14	0	1	0	0	0	0	0
<i>P.</i> sp. 16	0	0	0	2	0	0	0
<i>Pogonomyrmex barbatus</i> (Smith, F.)	2	0	0	0	0	0	0
<i>Pyramica</i> sp. 1	0	0	0	0	1	0	0
<i>Solenopsis geminata</i> Forel	5	6	0	5	0	5	3
<i>S. tenuis</i> Mayr	0	1	0	0	0	2	0
<i>S.</i> sp. 4	0	2	1	0	2	1	1
<i>S.</i> sp. 5	0	0	0	3	0	0	0
<i>S. (Diplorhoptrum)</i> sp. 1	7	4	4	2	0	2	1
<i>S. (Diplorhoptrum)</i> sp. 2	4	6	6	4	0	0	0
<i>Strumigenys</i> sp. 1	0	1	1	0	0	0	0
<i>Tetramorium spinosum</i> (Pergande)	4	4	2	1	1	0	0
<i>Trachymyrmex saussurei</i> (Forel)	5	10	12	7	0	0	0
<i>Wasmannia auropunctata</i> (Roger)	0	0	3	3	1	1	0
<i>Xenomyrmex</i> sp. 1	0	0	0	0	0	1	0
Dolichoderinae							
<i>Azteca</i> sp 1	1	1	0	0	2	0	3
<i>Azteca</i> sp. 2	0	0	2	0	0	2	1
<i>Azteca</i> sp. 3	0	0	2	4	2	3	6
<i>Dolichoderus diversus</i> Emery	0	2	0	0	0	1	3
<i>D. lutosus</i> (Smith)	0	1	2	4	4	8	10
<i>Dorymyrmex</i> sp. 1	11	11	5	0	9	2	0
<i>Forelius pruinosus</i> (Roger)	5	4	2	0	4	1	0
<i>F.</i> sp. 2	3	1	0	0	0	0	0
<i>Tapinoma</i> sp. 1	0	2	0	0	0	1	1
<i>Tapinoma</i> sp. 2	0	0	1	0	0	1	0
Ecitoninae							
<i>Eciton burchelli</i> (Westwood)	0	0	1	0	0	0	0
<i>Neivamyrmex adnepos</i> (Wheeler, W.M.)	1	1	0	0	0	0	0
<i>N. opacithorax</i> (Emery)	1	2	0	0	0	0	0
<i>N. pilosus</i> (Smith)	0	2	0	0	0	0	0
<i>Nomamyrmex</i> sp. 1	0	2	2	0	0	0	0
Formicinae							
<i>Brachymyrmex</i> sp. 1	5	6	6	0	0	1	0
<i>Brachymyrmex</i> sp. 3	4	5	1	0	4	4	0
<i>Camponotus atriceps</i> (Smith, F.)	2	5	3	1	6	1	1
<i>C. coloratus</i> Forel	0	3	1	0	5	5	4
<i>C. hirsutinasus</i> Wheeler	0	2	1	1	6	4	5
<i>C. linnaei</i> Forel	0	0	0	0	2	3	10
<i>C. longinoi</i> Mackay	0	0	0	0	0	1	0
<i>C. novagranadensis</i> Mayr	0	0	0	2	1	2	7

Appendix 2 (continued)

Subfamily Species	Sampling method and habitat type						
	Pitfall traps				Arboreal		
	Pasture	Isolated tree	Regrowth	Forest	Isolated tree	Regrowth	Forest
<i>C. planatus</i> Roger	1	1	1	7	5	10	10
<i>C. pullatus</i> Mayr	1	1	1	0	0	0	1
<i>C. sericeiventris</i> (Guerin)	0	0	0	2	0	0	3
<i>C. sharpi</i> Forel	0	0	2	3	0	0	0
<i>C. striatus</i> (Smith, F.)	0	0	1	0	0	2	0
<i>C. zoc</i> Forel	0	3	0	2	6	2	1
<i>C. sp. 10</i>	0	0	0	0	0	3	0
<i>C. sp. 12</i>	0	0	0	0	0	0	1
<i>Myrmelachista</i> sp. 1	0	0	5	0	5	6	0
<i>Paratrechina guatamalensis</i> (Forel)	3	2	3	1	0	1	0
Ponerinae							
<i>Ectatomma tuberculatum</i> (Olivier)	7	7	8	0	0	4	0
<i>Leptogenys</i> sp. 2	0	0	0	1	0	0	0
<i>Odontomachus</i> sp. 1	2	2	4	1	0	0	0
<i>Pachycondyla villosa</i>	0	1	0	0	2	1	4
<i>P. sp 1</i>	1	1	3	3	0	0	0
Pseudomyrmicinae							
<i>Pseudomyrmex bruneus</i> (Smith)	0	2	2	0	6	3	0
<i>P. caeciliae</i> (Forel)	1	2	0	0	9	4	0
<i>P. cubaensis</i> (Forel)	0	0	0	0	7	4	1
<i>P. ejectus</i> (Smith, F.)	0	2	0	0	0	1	0
<i>P. elongatulus</i> (Dalla Torre)	0	1	0	0	2	5	1
<i>P. ferrugineus</i> (Smith, F.)	0	1	3	1	0	0	0
<i>P. filiformis</i> (Fabricius)	0	0	0	0	0	0	1
<i>P. gracilis</i> (Fabricius)	1	1	0	0	1	8	8
<i>P. ita</i> (Forel)	0	0	0	0	1	2	4
<i>P. simplex</i> (Smith, F.)	0	2	0	0	10	9	5
<i>P. spiculus</i> Ward	0	0	0	0	0	0	1
<i>P. tenuisimus</i> (Emery)	0	0	0	0	3	4	4

Wet and dry season samples are combined. Numbers are number of sample-points at which the species occurred (maximum 12).

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