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ORIGINAL PAPER

An evaluation of the contribution of cultivated allspice (*Pimenta Dioca*) to vertebrate biodiversity conservation in Nicaragua

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Abstract Tropical deforestation has emerged as one of the most important conservation challenges of our time, both because of the high species diversity and rates of endemism of tropical forests, and because of the rapid rate at which this process is proceeding. Recent studies indicate that areas of low-intensity agroforestry have similar levels of vertebrate diversity as some primary habitats, leading some researchers and conservationists to conclude that this type of commodity production could contribute to the conservation of biodiversity. We compared the composition of bird, mammal and herpetofaunal communities in primary forest, secondary forest, and pasture—and within the allspice productive systems that have replaced pasture. We found that mammal species richness was higher in primary forest than all other habitats; however for resident and migrant birds, amphibians and reptiles, species richness was similar between primary forest and the other habitats. Despite similarities in overall numbers of species, there were numerous species that were encountered only in primary habitats. We conclude that the cultivation of allspice in a mixed productive system can offset some of the losses to biodiversity; however it should be complemented by the establishment and maintenance of protected areas to accommodate populations of primary forest specialists that are unable to persist in altered habitats.

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Introduction

Tropical deforestation has emerged as one of the most important conservation challenges of our time, both because of the high species diversity and rates of endemism of tropical forests, and because of the rapid rate at which this process is proceeding. Various initiatives have been forwarded to address this problem. Clearly, outright acquisition and strict protection is the most desirable approach from the perspective of biodiversity maintenance, although this solution is not feasible in many areas because it ignores political realities as well as the legitimate needs of the human population who are entitled to economic security and well-being (Kamaljit and Seidler 1998).

Some tropical habitats altered by low intensity cultivation of commercially valuable crops in combination with tree cover, or "agroforestry," support native tropical species. For example, numerous studies have reported that bird species richness in shade coffee is comparable to some natural habitats (Wunderle and Latta 1996; Greenberg et al. 1997a, b; Tejada-Cruz and Sutherland 2004). Similarly, cacao grown under diverse planted shade in Mexico appears to be good habitat for some migrant bird species (Greenberg et al. 2000; Reitsma et al. 2001). Hughes et al. (2002) found that "countryside habitats" were occupied by nearly 40% of native species detected in their sites in Costa Rica. These findings have led some to conclude that these habitats have an important role in augmenting habitat area, connectivity and range conditions represented by reserves (Daily et al. 2003).

Despite these findings, it is becoming clear that the propagation of these habitats cannot be a substitute for a program of rigorous habitat protection (Rappole et al. 2003a, b, Tejada-Cruz and Sutherland 2004). Although species diversity in some agroforestry systems is similar to primary forest, some forest residents are scarce or absent from cultivated habitats (Tejada-Cruz and Sutherland 2004), perhaps because of the absence of resources or substrates needed for Feeding and reproduction (Greenberg et al. 2000; Reitsma et al. 2001). The absence of these primary forest specialists from these managed forests point out the limitations of these systems, and thus the task has shifted to determining the role of altered forests in tropical biodiversity conservation.

For example, it is thought that the promotion of less intensive forms of cultivation might contribute to the conservation of some species, or might be useful as a buffer zone around existing preserves (Moguel and Toledo 1999; Tejada-Cruz and Sutherland 2004). Perhaps with knowledge of the relative value of various countryside habitats, biodiversity can be explicitly integrated into agricultural policy (Hughes et al. 2002; Daily et al. 2003).

In 1999, the Mesoamerican Development Institute (MDI) in cooperation with the Programa a Campesino a Campesino (PCAC), the Nicaraguan Government, and the World Bank/Global Environment Facility (GEF), initiated a program to develop and promote the cultivation of indigenous allspice (*Pimenta dioca*) on previously deforested parcels for the production of essential oils. Allspice, called locally "pimienta," is a native species in that region that occurs as a midstory tree, which is traditionally harvested by felling mature trees. Allspice is currently being cultivated by a cooperative of nearly 100 subsistence farmers (CoopeSiuna) in northern Nicaragua in the buffer zone of the largest remaining stand of tropical rain forest north of the Amazon basin—the BOSAWAS Biosphere Reserve (Smith, 2003). Within the buffer zone, which has been settled by ex-combatants from civil war, forest clearing for subsistence farming has increased along with extensive livestock operations, commercial logging, and mining. The estimated rate of deforestation in this region is 80,000 ha/year, or about 2.1% of remaining forest cover (Global Environment Facility (GEF) 1997). In an effort to develop an alternative to slash and burn agriculture and consequential advance of the agricultural frontier, which threatens the BOSAWAS, a program has been initiated through which indigenous allspice along with banana, cocoa, citrus, and other native shade trees have been introduced as a mixed-productive system on previously deforested parcels. These productive systems are to provide the raw products that will be processed to produce essential oils of allspice, lemongrass, vetiver, and ginger for a growing international market. Through this new agro-industrial activity, it is hoped that the cooperative members can break from the slash and burn cycle of subsistence farming and increase biodiversity within the buffer zone.

Allspice cultivated in mixed productive systems is characterized by a diverse, multistoried habitat similar to other types of crops known to support native biodiversity, such as coffee and cocoa. To determine the extent to which biodiversity conservation can be realized through the cultivation of allspice in a mixed productive system, we conducted an intensive, multi-taxon survey comparing species richness and composition of allspice plantations with that of primary forest, secondary forest and pasture.

Methods

Study area

The study took place in the region around Siuna, Nicaragua (13°40′ N, 85°50′ W) in areas consisting of tropical moist and wet forest between 170 and 600 m in elevation. The landscape in this area is a diverse mosaic of patches of remnant primary forest, degraded or regenerating secondary forest, ‘‘agroforestry systems’’ such as mixed plantings of coffee, cacao, citrus and native overstory trees, pasture and cereal crops. In recent years, allspice, which is native to the region and grows as a midstory tree in its natural state, has been cultivated as the principal plant in agroforestry systems for use in the production of essential oils. The earliest plantings took place in 1999, and new areas are currently being planted.

Vertebrate sampling

We sampled birds, mammals, amphibians and reptiles in several primary forest, secondary forest, allspice and pasture sites. Primary forest areas existed as large (>30 ha) patches of forest that had experienced no timber harvest, and were characterized by large, tall trees and open understory. Secondary forest had most of the original canopy removed, and had shorter, smaller trees and denser understory than primary forest. Allspice agroforestry systems consisted of allspice that had been planted in pasture with other commercially valuable species such as coffee, cacao, and citrus between 3 to 5 years before the commencement of the study. Allspice had shorter, smaller trees than secondary forest, but similar understory structure. Pasture consisted of grazed or recently grazed areas with grass or forb cover with scattered shrubs.

We sampled birds, mammals, reptiles and amphibians from July 2002 to April 2004. Mammals were sampled during the dry season (July–November) 2002 and 2003, and birds were sampled in the rainy season (January–April) 2003 and 2004. Sampling for birds was conducted at 23 sites, mammals at 27 sites, and herpetofauna at 19 sites. Although habitats were sampled in a random sequence within each season, it was not possible to randomize the selection of sites because of limited availability.

Bird species distribution and species composition were sampled using mist nets (Karr 1981). Ten 12 m × 3 m, 32 mm denier mist nets were deployed in each site 50 m apart in a grid pattern approximately 200 m × 250 m. Each site was sampled for 250 net hours. All birds captured were identified, and then marked to distinguish them from new captures subsequently by cutting the tip of a single rectrix (in the case of residents), or by banding with US Fish and Wildlife numbered bands (in the case of Neotropical migrants). Birds were then released near the point of capture. The identity of all species was established using field-guides, scientific keys and consultation with experts at the University of Nicaragua, Managua and elsewhere.

Mammals were sampled using a 40-m diameter circular trapping array with 15 sample points, 5 equally spaced on an inner 20-m diameter circle, and 10 on the outer 40 m diameter circle. Twenty Sherman folding traps (8 cm × 9 cm × 23 cm) were placed in pairs at each of the inner 5 points and at 5 alternate points of the outer circle, one on the ground and one approximately 1.5 m up in a tree or shrub. Small (15 cm × 15 cm × 48 cm) Tomahawk folding traps were placed at the remaining 5 outer sampling points. Care was used to minimize human scent, and all traps were placed as firmly as possible on the substrate and concealed with brush and leaves. Large (25 cm × 30 cm × 80 cm) Tomahawk folding traps were placed at the center of the 5 sections bounded by the inner and outer sampling rings. Finally, 5 1-m radius circular unbaited tracking stations were established per site by digging up and removing the ground litter and vegetation, and then smoothing the soil so that tracks could be observed and recorded.

Pitfall traps approximately 30 cm deep were placed between each of the inner sampling points. Each pitfall had 31-m long, 15 cm high vertical fences sunk into the ground radiating out from the pitfall traps at equal angles. Pitfall buckets were filled with water 5 cm deep and had 3-mm diameter holes drilled into the sides 5 cm from the bottom to keep them from overflowing in case of rain. In addition, searches for amphibians and reptiles were conducted during the 7 days of each trapping session.

Live traps were baited with bananas and peanut butter and checked every 24 h. Any animals captured were identified, marked by cutting a distinctive pattern in the pelage with scissors, and released, with the exception that voucher specimens were retained as needed in areas outside the biosphere reserve. Track stations were checked daily during the week-long trapping session and the presence and identity of tracks recorded. In cases where tracks could not be identified, sketches, notes and measurements were made at the site, and the soil smoothed out after each check. Pitfall traps were checked daily, and except for species which could be readily identified at the site, their contents was preserved in 10% alcohol and labeled for later identification.

On some of the sites, vegetation-sampling points were established on a random bearing 10 m from each of the 10 nets or the 10 outermost Sherman traps in a random direction. The number of times vegetation contacted a 3-m pole held vertically at this random point was recorded in 3 1-m height classes. In addition, the distance from that random point to the nearest tree that is part of the canopy was measured, as well as the species of tree.

Data analysis

Capture rates for each bird, mammal, amphibian, and reptile species were calculated by habitat as number of birds per 250 net hours, or captures per 7-day trapping period for mammals, amphibians, and reptiles.

Because species richness varies with sampling intensity, we analyzed species richness using rarefaction constructed from the means of 1,000 randomizations of sample order with the program ''EcoSim'' (Gotelli and Entsminger 2001). Expected values for richness and abundance for each level of sampling intensity were combined to produce a sample-based rarefaction curve in which the x axis was the number of individuals based on the number of samples chosen and the y axis was the corresponding number of species that were sampled. Rarefaction analyses were conducted separately for all bird species combined, and resident and Neotropical migrants separately. Species richness was compared among habitats by assessing the overlap of 95% confidence intervals at an intermediate level of sampling intensity (4 sites for bird data, 5 for mammals, 3 for reptiles and amphibians).

In addition rarefaction analyses we used Jaccard's coefficient to measure the similarity of habitat pairs. Where similarity = $2c/(a+b+c)$, and c is the number of species shared by two habitats, and a and b the total number of species in each habitat. Values of this index vary from 0 to 1; 0 indicates that assemblages differ totally, and 1 that they are identical. In addition to the calculation of similarity indices, we used multidimensional scaling (MDS) to calculate the similarity among samples based on their species composition and abundance. MDS is a procedure for fitting a set of points in a space such that the distance between points on the MDS plot corresponds to the dissimilarity among sampled sites. The fit of configuration distances to the original data was evaluated by calculating stress using Kruskall's stress formula, with values near 0 indicating a better fit. In addition, we examined Shepard diagrams (plots of the distance between points in the final plot with observed dissimilarities in the original data) to verify that they appeared as straight lines or smooth curves, also indicating good fit with the original data.

Vegetation variables were averaged for each plot, and compared among habitats using one-way ANOVA with Tukey's post hoc comparisons.

Results

Birds

We captured 1,433 individuals of 140 bird species during the 2 years of the study (Table 1). Of these, 89% were tropical resident species, and the remainder were

Table 1 Average capture rates (per 250 h) for birds in primary forest (n = 6), secondary forest (n = 5), allspice (n = 6) and pasture (n = 6) in north-central Nicaragua 2003–2004

Species	Status	Primary forest	Secondary forest	Allspice	Pasture	*n*
Variable Seedeater *Sporophila aurita*	r	1.333	2.600	6.833	8.167	111
White-collared Manakin *Manacus candei*	r	6.167	8.800	0.833	0.000	86
Scarlet-rumped Tanager *Ramphocelus passerinii*	r	1.000	2.800	4.000	6.833	85
Ochre-bellied Flycatcher *Mionectes oleagineus*	r	6.000	5.000	0.833	0.333	68
Long-tailed Hermit *Phaethornis superciliosus*	r	6.167	4.800	0.833	0.167	67
Blue-throated Goldentail *Hylocharis eliciae*	r	1.667	2.200	4.167	2.000	58
Blue-black Grassquit *Volatinia jacarina*	r	0.167	0.400	4.000	4.000	51
Buff-throated Saltator *Saltator maximus*	r	1.167	2.400	3.167	1.667	48
Yellow-faced Grassquit *Tiaris olivacea*	r	0.333	0.200	4.667	2.167	44
Blue-black Grosbeak *Cyanocompsa cyanoides*	r	2.333	3.400	0.333	0.000	33
Thick-billed Seed Finch *Oryzoborus funereus*	r	0.833	0.400	2.000	2.167	32
Red-headed Manakin *Pipra mentalis*	r	3.833	1.400	0.333	0.000	32
Little Hermit *Phaethornis longuemareus*	r	2.333	3.000	0.000	0.167	30
Orange-billed Sparrow *Arremon aurantiirostris*	r	1.500	3.000	0.000	0.000	24
Red-throated Ant-tanager *Habia fuscicauda*	r	2.000	1.600	0.333	0.000	22
Buff-throated Foliage-gleaner *Automolus ochrolaemus*	r	1.000	2.000	0.667	0.000	20
Wedge-billed Woodcreeper *Glyphorhynchus spirurus*	r	2.667	0.600	0.167	0.000	20
Band-tailed Barbthroat *Threnetes ruckeri*	r	0.667	2.400	0.500	0.000	19
Grey-headed Tanager *Eucometis penicillata*	r	0.667	1.400	1.167	0.000	18
House Wren *Troglodytes aedon*	r	0.000	0.000	2.167	0.833	18
Wood Thrush *Hylocichla mustelina*	m	1.000	1.600	0.500	0.000	17
Northern Bentbill *Oncostoma cinereigulare*	r	1.500	1.400	0.000	0.167	17
Stripe-headed Sparrow *Arremonops conirostris*	r	0.333	0.600	0.667	1.167	16
Groove-billed Ani *Crotophaga sulcirostris*	r	0.000	0.000	0.667	2.000	16
Indigo Bunting *Passerina cyanea*	m	0.167	0.200	0.833	1.333	15
White-ruffed Manakin *Corapipo leucorrhoa*	r	1.167	1.000	0.000	0.333	14
Yellow Bellied Elaenia *Elaenia flavogaster*	r	0.667	0.000	1.167	0.500	14
Ovenbird *Seiurus aurocapillus*	m	0.167	1.600	0.667	0.167	14
Clay-colored Robin *Turdus grayi*	r	0.667	0.800	1.000	0.000	14
Kentucky Warbler *Oporornis formosus*	m	0.333	1.400	0.667	0.000	13
Golden-crowned Spadebill *Platyrinchus coronatus*	r	2.000	0.200	0.000	0.000	13
Bronzy Hermit *Glaucis aenea*	r	0.500	0.400	1.000	0.000	11

Table 1 continued

Species	Status	Primary forest	Secondary forest	Allspice	Pasture	*n*
Stub-tailed Spadebill *Platyrinchus cancrominus*	r	1.000	1.000	0.000	0.000	11
Chestnut-sided Warbler *Dendroica pensylvanica*	m	0.333	0.200	0.833	0.333	10
Ruddy-tailed Flycatcher *Terenotriccus erythrurus*	r	1.333	0.400	0.000	0.000	10
Blue Ground-Dove *Claravis pretiosa*	r	0.000	0.000	0.833	0.667	9
Long-billed Gnatwren *Ramphocaenus melanurus*	r	0.333	1.00	0.167	0.167	9
Rufous-bellied Hummingbird *Amazilia tzacatl*	r	0.000	0.000	1.333	0.000	8
Dusky Antbird *Cercomacra tyrannina*	r	0.833	0.600	0.000	0.000	8
Spotted Antbird *Hylophylax naevioides*	r	1.000	0.400	0.000	0.000	8
Scaly-breasted Hummingbird *Phaeochroa cuvierii*	r	0.000	0.600	0.833	0.000	8
Wilson's Warbler *Wilsonia pusilla*	m	0.500	0.800	0.000	0.167	8
Tennessee Warbler *Vermivora peregrina*	m	0.000	0.000	1.00	0.333	8
Steely-vented Hummingbird *Amazilia saucerrottei*	r	0.000	0.000	1.167	0.000	7
Yellow Tyrannulet *Capsiempis flaveola*	r	0.000	0.000	1.000	0.167	7
Bicolored Antbird *Gymnopithys leucaspis*	r	0.500	0.800	0.000	0.000	7
Worm-eating Warbler *Helmitheros vermivorus*	m	0.500	0.800	0.000	0.000	7
White-breasted Woodwren *Henicorhina leucosticta*	r	0.833	0.400	0.000	0.000	7
Royal Flycatcher *Onychorhynchus coronatus*	r	0.333	0.800	0.167	0.000	7
Hooded Warbler *Wilsonia citrina*	m	0.667	0.600	0.000	0.000	7
Green Honeycreeper *Chlorophanes spiza*	r	0.000	0.000	1.000	0.000	6
White-necked Jacobin *Florisuga mellivora*	r	0.333	0.000	0.667	0.000	6
Blue Grosbeak *Guiraca caerulea*	m	0.000	0.200	0.000	0.833	6
Dotted-wing Antwren *Microrhopias quixensis*	r	0.833	0.200	0.000	0.000	6
Slaty Antwren *Myrmotherula schisticolor*	r	0.333	0.800	0.000	0.000	6
Rose-breasted Grosbeak *Pheucticus ludovicianus*	m	0.000	0.000	0.167	0.833	6
Barred Antshrike *Thamnophilus doliatus*	r	0.000	0.400	0.500	0.167	6
Black-faced Grosbeak *Caryothraustes poliogaster*	r	0.500	0.400	0.000	0.000	5
Plain-brested Ground Dove *Columbina minuta*	r	0.000	0.000	0.833	0.000	5
Barred Woodcreeper *Dendrocolaptes certhia*	r	0.833	0.000	0.000	0.000	5
Magnolia Warbler *Dendroica magnolia*	m	0.000	0.000	0.500	0.333	5
Mountain Elaenia *Elaenia frantzii*	r	0.000	0.600	0.000	0.333	5
Black-and-white Warbler *Mniotilta varia*	m	0.500	0.000	0.333	0.000	5
Great-crested Flycatcher *Myiarchus crinitus*	m	0.000	0.000	0.667	0.167	5

Table 1 continued

Species	Status	Primary forest	Secondary forest	Allspice	Pasture	*n*
Social Flycatcher *Myiozetetes similis*	r	0.000	0.000	0.500	0.333	5
Violet-crowned Woodnymph *Thalurania colombica*	r	0.667	0.200	0.000	0.000	5
Plain Xenops *Xenops minutus*	r	0.167	0.200	0.333	0.167	5
White-bellied Emerald *Amazilia candida*	r	0.333	0.200	0.167	0.000	4
Long-billed Starthroat *Heliomaster longirostris*	r	0.000	0.000	0.167	0.500	4
Sulphur-rumped Flycatcher *Myiobius sulphureipygius*	r	0.500	0.200	0.000	0.000	4
Ocellated Antbird *Phaenostictus mcleannani*	r	0.500	0.000	0.167	0.000	4
American Redstart *Setophaga ruticilla*	m	0.167	0.200	0.167	0.167	4
Blue-gray Tanager *Thraupis episcopus*	r	0.000	0.000	0.667	0.000	4
Mistletoe Tyrannulet *Zimmerius vilissimus*	r	0.000	0.000	0.667	0.000	4
Common Tody Flycatcher *Todirostrum cinereum*	r	0.000	0.000	0.667	0.000	4
Ruddy Foliage-gleaner *Automolus rubiginosus*	r	0.000	0.600	0.000	0.000	3
Common Ground Dove *Columbina passerina*	r	0.000	0.000	0.333	0.167	3
Shining Honeycreeper *Cyanerpes lucidus*	r	0.000	0.000	0.333	0.167	3
Blue-crowned Antbird *Gymnocichla nudiceps*	r	0.000	0.600	0.000	0.000	3
Spotted-crowned Woodcreeper *Lepidocolaptes affinis*	r	0.333	0.000	0.167	0.000	3
Buff-rumped Warbler *Phaeothlypis fulvicauda*	r	0.000	0.000	0.500	0.000	3
Eye-ringed Flatbill *Rhynchocyclus brevirostris*	r	0.500	0.000	0.000	0.000	3
Spotted-breasted Wren *Thryothorus maculipectus*	r	0.167	0.400	0.000	0.000	3
Violaceous Trogon *Trogon violaceus*	r	0.500	0.000	0.000	0.000	3
Golden-winged Warbler *Vermivora chrysoptera*	m	0.000	0.200	0.333	0.000	3
Blue-chested Hummingbird *Amazilia amabilis*	r	0.000	0.000	0.333	0.000	2
Yellow-billed Cacique *A mblycercus holosericeus*	r	0.000	0.400	0.000	0.000	2
Ruby-throated Hummingbird *Archilochus culibris*	m	0.333	0.000	0.000	0.000	2
Bright-romped Attila *Attila spadiceus*	r	0.333	0.000	0.000	0.000	2
Red-footed Plumeleteer *Chalybura urochrysia*	r	0.167	0.000	0.167	0.000	2
Short-billed Pigeon *Columba nigrirostris*	r	0.000	0.000	0.000	0.333	2
Tropical Pewee *Contopus cinereus*	r	0.000	0.000	0.333	0.000	2
Keel-billed Motmot *Electron carinatum*	r	0.333	0.000	0.000	0.000	2
Acadian Flycatcher *Empidonax virescens*	m	0.000	0.000	0.333	0.000	2
Gray-crowned Yellowthroat *Geothlypis poliocephala*	r	0.000	0.000	0.333	0.000	2
Lesser Greenlet *Hylophilus decurtatus*	r	0.000	0.000	0.333	0.000	2
White-whiskered Puffbird *Malacoptila panamensis*	r	0.333	0.000	0.000	0.000	2

Table 1 continued

Species	Status	Primary forest	Secondary forest	Allspice	Pasture	*n*
Checker-throated Antwren *Myrmotherula fulviventris*	r	0.333	0.000	0.000	0.000	2
Painting Bunting *Passerina ciris*	m	0.000	0.000	0.000	0.333	2
Crimson-collared Tanager *Phlogothraupis sanguinolenta*	r	0.000	0.000	0.000	0.333	2
White-throated Spadebill *Platyrinchus mystaceus*	r	0.000	0.400	0.000	0.000	2
Russet Antshrike *Thamnistes anabatinus*	r	0.333	0.000	0.000	0.000	2
Tropical Kingbird *Tyrannus melancholicus*	r	0.000	0.000	0.167	0.167	2
Green-breasted Mango *Anthracothorax prevostii*	r	0.000	0.000	0.167	0.000	1
Olive Sparrow *Arremonops rufivirgatus*	r	0.000	0.000	0.167	0.000	1
Rufous Motmot *Baryphthengus martii*	r	0.000	0.200	0.000	0.000	1
Northern Beardless-tyrannulet *Camptostoma imberbe*	r	0.000	0.000	0.000	0.167	1
Swainson's Thursh *Catharus ustulatus*	m	0.000	0.000	0.000	0.167	1
Ruddy Ground Dove *Columbina talpacoti*	r	0.000	0.000	0.000	0.167	1
Olive-sided Flycatcher *Contopus borealis*	m	0.167	0.000	0.000	0.000	1
Fasciated Antshrike *Cymbilaimus lineatus*	r	0.167	0.000	0.000	0.000	1
Blue Dacnis *Dacnis cayana*	r	0.000	0.000	0.167	0.000	1
Black-banded Woodcreeper *Dendrocolaptes picumnus*	r	0.000	0.000	0.167	0.000	1
Yellow Warbler *Dendroica petechia*	m	0.000	0.000	0.167	0.000	1
Yellow-bellied Flycatcher *Empidonax flaviventris*	m	0.000	0.200	0.000	0.000	1
Magnificient Hummingbird *Eugenes fulgens*	r	0.000	0.000	0.167	0.000	1
Gray-breasted Wood-wren *Henicorhina leucophrys*	r	0.000	0.200	0.000	0.000	1
Yellow-breasted Chat *Icteria virens*	m	0.000	0.200	0.000	0.000	1
Black-cowled *OrioleIcterus dominicensis*	r	0.000	0.000	0.167	0.000	1
Streaked-headed Woodcreeper *Lepidocolaptes souleyetti*	r	0.000	0.200	0.000	0.000	1
Gray-chested Dove *Leptotila cassinii*	r	0.167	0.000	0.000	0.000	1
Black-crested Coquette *Lophornis helenae*	r	0.000	0.000	0.167	0.000	1
White-fronted Nunbird *Monasa morphceus*	r	0.000	0.200	0.000	0.000	1
Dusky-capped flycatcher *Myiarchus tuberculifer*	r	0.000	0.000	0.167	0.000	1
Sulphur-bellied Flycatcher *Myiodynastes luteiventris*	r	0.000	0.000	0.000	0.167	1
Golden-olive Woodpecker *Piculus rubiginosus*	*r*	0.000	0.000	0.000	0.167	1
Hepatic Tanager *Piranga flava*	r	0.000	0.000	0.000	0.167	1
Summer Tanager *Piranga rubra*	m	0.000	0.200	0.000	0.000	1
Black-headed Saltator *Saltador atriceps*	r	0.167	0.000	0.000	0.000	1
Grayish Saltator *Saltator caerulescens*	r	0.000	0.200	0.000	0.000	1

Table 1 continued

Species	Status	Primary forest	Secondary forest	Allspice	Pasture	*n*
Thrushlike Manakin *Schiffornis turdinus*	r	0.000	0.200	0.000	0.000	1
Tawny-throated Leaftosser *Sclerurus mexicanus*	r	0.000	0.200	0.000	0.000	1
Lousiana Waterthrush *Seiurus motacilla*	m	0.000	0.200	0.000	0.000	1
Olivaceous Woodcreeper *Sittasomus griseicapillus*	r	0.167	0.000	0.000	0.000	1
Ruddy-breasted Seedeater *Sporophila minuta*	r	0.000	0.000	0.000	0.167	1
White-shouldered Tanager *Tachyphonus luctuosus*	r	0.000	0.200	0.000	0.000	1
Golden-hooded Tanager *Tangara larvata*	r	0.000	0.000	0.000	0.167	1
Great Antshrike *Taraba major*	r	0.000	0.200	0.000	0.000	1
Banded Wren *Thryothorus pleurostictus*	r	0.000	0.000	0.167	0.000	1
Black-throated Trogon *Trogon rufus*	r	0.000	0.200	0.000	0.000	1

Neotropical migrants. Overall bird species richness was highest in primary forest, secondary forest and allspice, and lowest in pasture (Fig. 1a), however, patterns of species richness differed between resident and migrant birds. Resident species exhibited similar richness in primary forest, secondary forest, and allspice, and significantly lower richness in pasture than all other habitats (Fig. 2a). In contrast, species richness of migrants was significantly lower in primary forest than secondary forest, and did not differ among primary, allspice and pasture, or among secondary forest allspice and pasture (Fig. 2b).

Bird species composition also differed among habitats. The similarity in both resident and migrant bird species composition between primary forest and secondary forest was greater than the similarity between allspice and either primary or secondary forest, and allspice and pasture were more or less equally similar to all other habitats (Fig. 3). This pattern was true for both resident and migrant birds, however the similarity values between allspice and primary forest were generally lower for residents than migrants Fig. 3). Similarly, the results of the multidimensional scaling showed considerable overlap of secondary forest, allspice and pasture, but less overlap between primary forest and allspice and pasture (Fig. 4). Finally, 18 bird species were captured only in primary forest, 23 only in secondary forest, 23 only in allspice, and 11 only in pasture (Table 1). There was no difference in the percentage of individual birds that were migrants among primary forest (5.2%), secondary forest (11.4%), allspice (9.7%) and pasture (11.1%; $F_{(3,22)} = 0.97$, $P = 0.43$).

Mammals

We captured 116 individuals of 28 mammal species during the 2 years of the study (Table 2). Overall mammal species richness was significantly higher in primary forest than all other habitats, did not differ between secondary forest and allspice, and was significantly lower in pasture than all other habitats (Fig. 5a). Mammal communities of primary forest had relatively low similarity to secondary forest (40%), allspice (44%) or pasture (20%) in contrast to the relatively high similarity between secondary forest and allspice (55%; Fig. 5b). Pasture had relatively low similarities to other habitats (≤25%). In contrast to the similarity analyses, the multidimensional scaling analyses indicated that there was substantial overlap in mammal species composition between primary and secondary forests and between pasture and allspice (Fig. 6). Nevertheless, the multidimensional scaling analyses indicated that there was less overlap between primary forest and allspice and pasture. Six mammal species were captured only in primary forest, 3 only in secondary forest, and 4 only in allspice (Table 2). No species were encountered only in pasture. Finally, we encountered two species of non-native rodent in allspice plantations (black rat, and house mouse), and one species in secondary forest (Norway rat).

Reptiles and amphibians

We encountered 128 individuals of 32 reptile and amphibian species during the 2 years of the study (Table 3). Rarefaction analysis indicated that species richness was highest in primary forest, secondary forest and allspice, and lower in pasture, however this difference was not significant (Fig. 7a). The similarity in species composition between primary forest and other habitats was low (≤17%), secondary

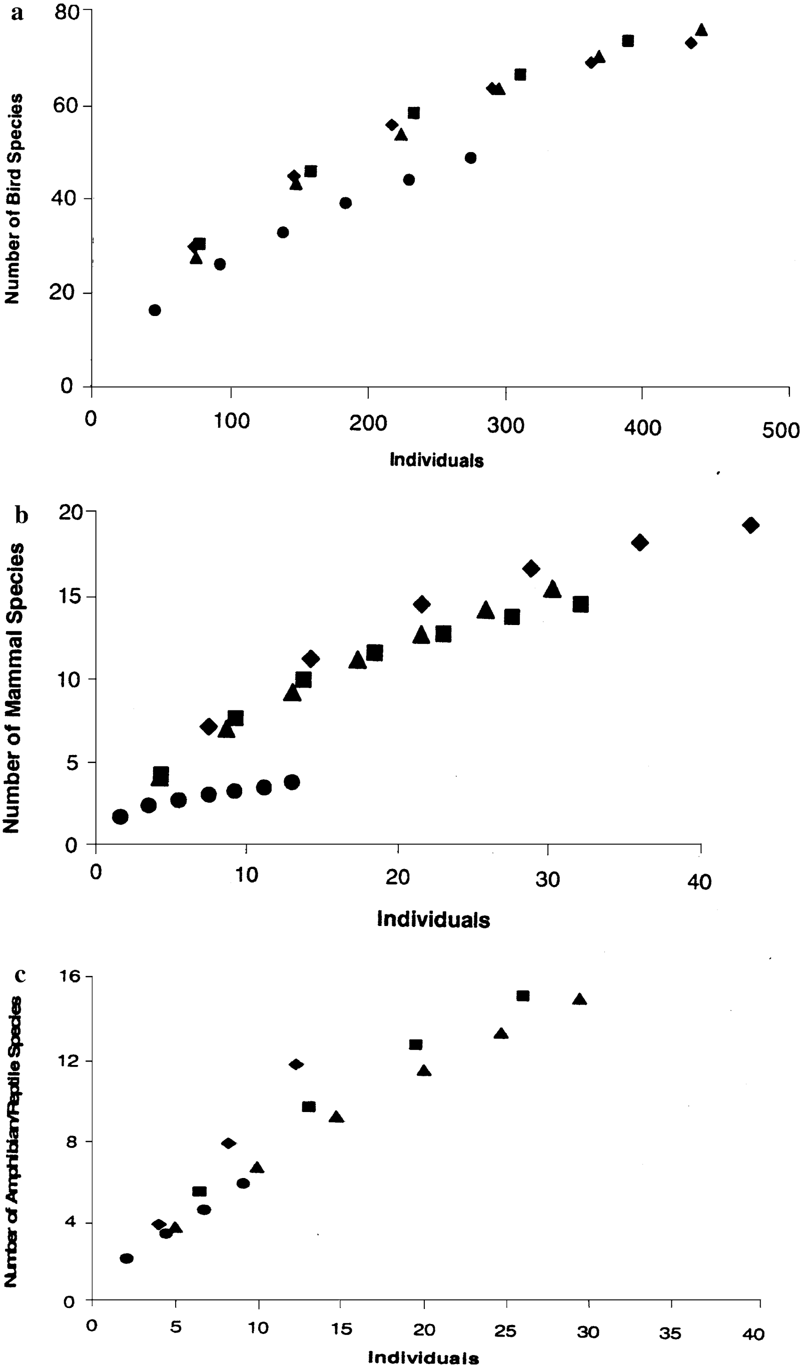

Fig. 1 Rarefaction curves for birds (**a**), mammals (**b**) and herpetofauna (**c**) in primary forest (◆), secondary forest (■), allspice (▲), and pasture (●)calculated from data collected in northcentral Nicaragua, 2002–2004. Primary forest, secondary forest and allspice generally have higher diversity of all taxa relative to pasture

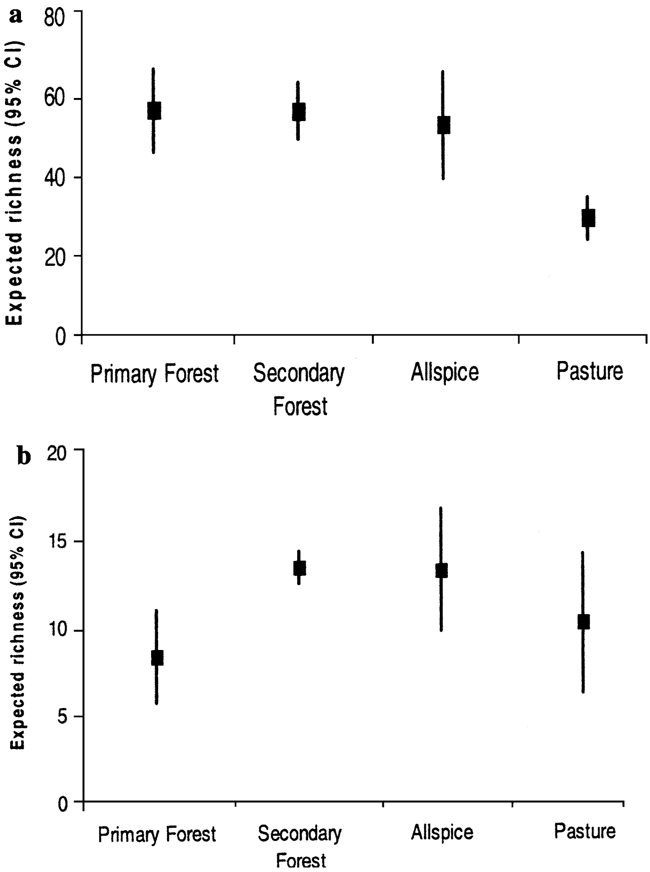

Fig. 2 Mean expected number of resident birds (**a**) and migrant birds (**b**) compared among habitats using rarefaction of data from 23 sites in north-central Nicaragua 2002–2004. Resident and migrant birds exhibit different patterns of species richness among habitats

forest and allspice were more similar (37%), and pasture was most similar to allspice (27%), less similar to secondary forest (20%), and least similar to primary forest (12%; Fig. 7b). Multidimensional scaling analyses indicated that there was substantial overlap between secondary forest, allspice and pasture, (Fig. 8) and less overlap between primary forest and pasture. Six species were captured only in primary forest, 4 only in secondary forest, 6 only in allspice, and 2 only in pasture (Table 3).

Habitat

Tree circumference and tree height were greater in primary forest than other habitats (Table 4). There were no significant differences among habitats in structure in any of the three strata, although structure tended to be higher between 0-1 m and lower 2-3 m above ground in pasture than other habitats. One-hundred-twenty-nine plant species were recorded in allspice plantations.

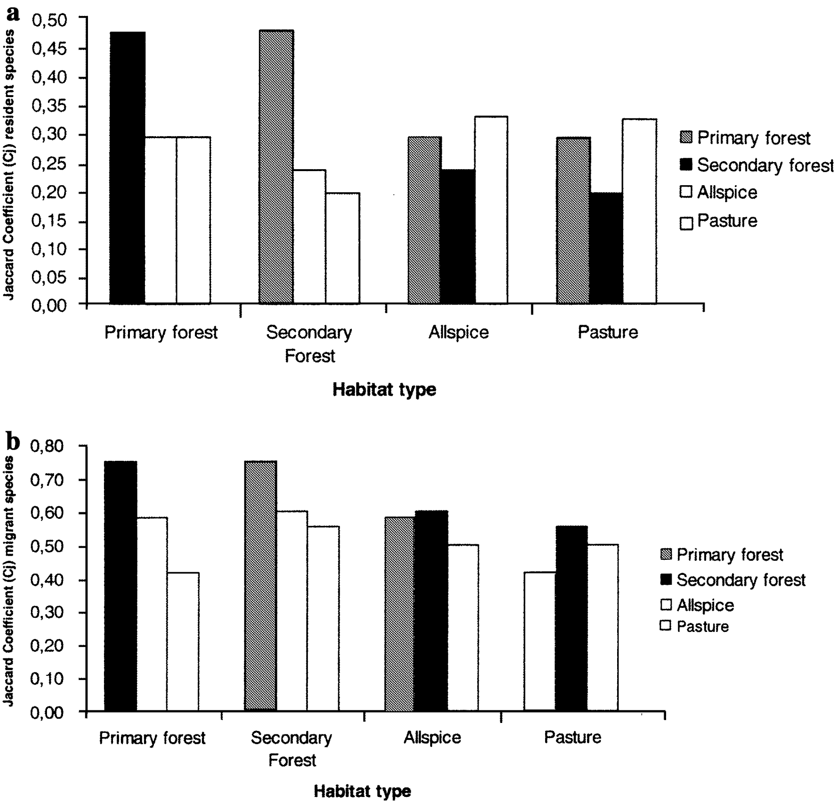

Fig. 3 Jaccard similarity coefficients of resident birds (**a**) and migrant birds (**b**) among habitats using data from 23 sites in north-central Nicaragua 2002–2004. For each habitat on the horizontal axis, the height of the three columns indicates the percentage of species shared with the other three habitats

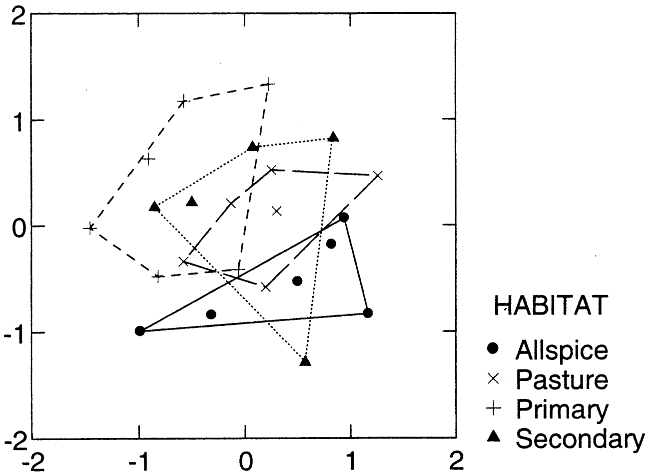

Fig. 4 Multi-dimensional scaling ordination of the abundances of bird species among habitats based on mist net captures of birds at 23 sites in north-central Nicaragua 2003–2004. Stress of final configuration was 0.01, proportion of variance (RSQ) was 0.69. The distance between points in this diagram illustrates the difference between sites in terms of their bird species composition

Table 2 Average capture rates (per 7 days) for mammals in primary forest (n = 7), secondary forest (n = 6), allspice (n = 7) and pasture (n = 7) in north-central Nicaragua 2002–2004

Species	Primary forest	Secondary forest	Allspice	Pasture	*n*
Common gray four-eyed opossum *Philander opossum*	0.5	0.57	0.57	0.86	17
Cotton rat *Sigmodon hispidus*	0.33	0.14	0.86	0.71	14
Common opossum *Didelphis marsupialis*	0.83	0.43	0.29	0	10
Big-eared climbing rat *Ototylomys phyllotis*	0.83	0.43	0.14	0	9
Dusky rice rat *Melanomys caliginosus*	0.5	0.14	0.43	0.14	8
Central American agouti *Dasyprocta punctata*	0.33	0.43	0.29	0	7
Virginia opossum *Didelphis virginiana*	0.33	0.43	0.29	0	7
Mexican mouse opossum *Marmosa mexicana*	0	0.57	0.29	0	6
Paca *Agouti paca*	0.5	0.14	0.14	0	5
Northern tamandua *Tamandua mexicana*	0.5	0.14	0	0	4
White-tailed deer *Odocoileus virginianus*	0.33	0.29	0	0	4
Striped hog-nosed skunk *Conepatus semiestratus*	0.33	0	0.14	0	3
Tayra *Eira barbara*	0.33	0	0.14	0	3
Brown four-eyed opossum *Metachirus nudicaudatus*	0.33	0	0	0	2
Northern raccoon *Procyon lotor*	0	0.29	0	0	2
White-nosed Coati *Nasua narica*	0	0.29	0	0	2
Central American Spiny Rat *Proechimys semispinosus*	0	0.14	0.14	0	2
Black rat *Rattus rattus*	0	0	0.14	0	1
Norway rat *Rattus norvegicus*	0	0.14	0	0	1
Mt. Pirri Isthmus Rat *Isthmomys pirrensis*	0.17	0	0	0	1
Big Pocket Gopher *Orthogeomys matagalpae*	0.17	0	0	0	1
Desmarest's spiny pocket mouse *Heteromys desmarestianus*	0.17	0	0	0	1
House mouse *Mus musculus*	0	0	0.14	0	1
White-throated rice rat *Oryzomys albigularis*	0.17	0	0	0	1
Nine-banded armadillo *Dasypus novemcinctus*	0	0	0.14	0	1
Two-toed sloth *Choloepus hoffmanni*	0	0	0.14	0	1
Jaguar Panthera onca	0.17	0	0	0	1
Unknown wild cat	0.17	0	0	0	1

Discussion

Differences in richness among habitats

We observed that species richness in allspice plantations was comparable to species richness in primary forest for some taxa. These results are similar to patterns reported in studies of vertebrates in other types of mixed agroforestry in the tropics. For example, coffee, cacao and other countryside habitats harbor a large number of native species (Wunderle and Latta 1996; Estrada et al. 1997; Greenberg et al. 1997a, b, 2000, Reitsma et al. 2001; Hughes et al. 2002; Daily et al. 2003; Perfecto et al. 2003; Tejada-Cruz and Sutherland 2004). These studies have been viewed in a positive light by many, and taken at face value, suggest that crops cultivated in a mixed productive system can ameliorate the effects of the destruction of primary forests on native forest biodiversity. The high species richness, as well as the high number of species reported only in allspice, is particularly striking considering that the oldest of these allspice plantations was only 5 years old. As time progresses, the structure of the habitat will become more similar to primary forest, and will likely support even more species.

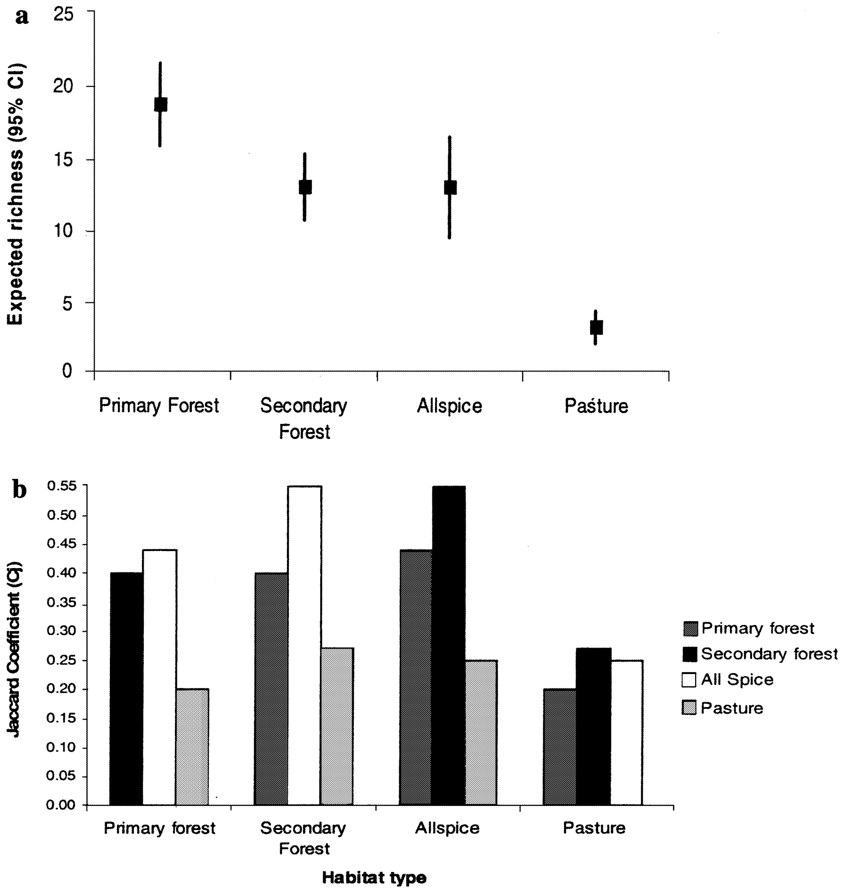

Fig. 5 Mean expected number of mammal species compared among habitats using rarefaction (**a**) and similarity in mammal species composition among habitats (**b**) using data from 27 sites in north-central Nicaragua 2002–2004

The abundance of Neotropical migrants in allspice is particularly notable given the numerous studies documenting declines in populations of these species (Rappole 1995), as well as the high species richness of these species in agroforestry systems. As in other studies, we observed that Neotropical migrant species richness was lowest in primary habitats and higher in habitats such as secondary forests, agroforestry systems (allspice) and pasture (Greenberg et al. 1997a, b, 2000, Reitsma et al. 2001; Hughes et al. 2002; Tejeda-Cruz and Sutherland 2004). Although their presence in human modified habitats may provide a first-order indication of their suitability for these species, survival rates of some migrants can be lower in human modified habitats due to predation (Rappole et al. 1989). Thus, the existence of these species in modified habitats might signify that preferred habitats are saturated, resulting in the exclusion of some individuals from preferred habitats (Winker et al. 1990; Marra et al. 1993). Furthermore, it is likely that we underestimated the differences between primary forest and other habitats for both migrants and residents because mist nets sample decreasing amounts of the avifauna [migrant as well as resident] with increasing canopy height (Rappole et al. 1998). More detailed studies of survival

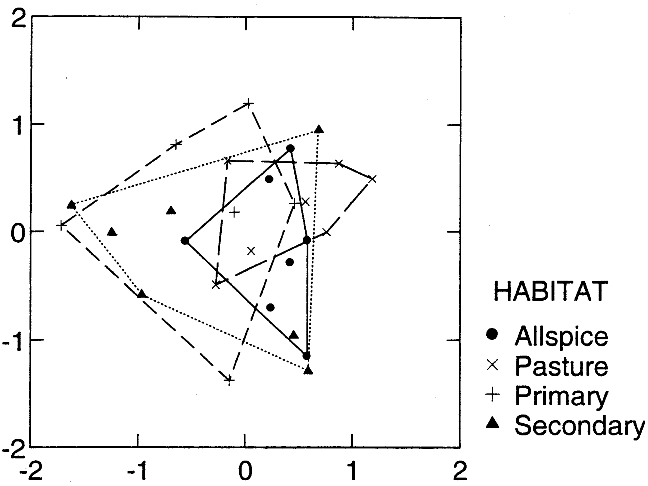

Fig. 6 Multi-dimensional scaling ordination of the abundances of mammal species among habitats based on trapping at 27 sites in north-central Nicaragua 2003–2004. Stress of final configuration was 0.02, proportion of variance (RSQ) was 0.80

rates of migrants in these different habitats are needed before we can conclude that allspice and other agroforestry systems are actually high quality habitat for the migrant species that use them (Greenberg et al. 2000; Reitsma et al. 2001; Tejada-Cruz and Sutherland 2004; Rappole et al. 2003a).

Allspice and vertebrate conservation

Despite the fact that species richness is comparable between allspice and primary forest for some taxa, there were substantial differences in species composition between primary forest and the other habitats. This is consistent with the findings of studies of other types of agroforestry systems (Heinen 1992; Greenberg et al. 2000; Reitsma et al. 2001; Tejada-Cruz and Sutherland 2004), and the limitations of these systems in conserving native biodiversity (Rappole et al. 2003; Naidoo 2004). Nevertheless, there are other ways in which allspice, as it is cultivated at our sites, can contribute to conservation of biodiversity beyond its direct habitat value. First, all of the sites used in this study were sites converted from intensive agriculture to allspice through plantings. Thus, at the most elementary level, the cultivation of allspice provides a more complex habitat that will support more native species than the pasture it is replacing, as well as potentially provide a buffer area for adjacent primary forest areas (Moguel and Toledo 1999; Tejada-Cruz and Sutherland 2004). Other types of agroforestry, such as coffee and cacao are also preferable to intensive agriculture because of relatively high species richness (Greenberg et al. 2000; Reitsma et al. 2001); however in many cases, these plantations have occurred at the expense of native forest (Rice and Greenberg 2000; Donald 2004). In contrast, the program encouraged by MDI involves the reclamation of formerly intensively cultivated agricultural land.

In addition to the value of allspice as habitat for tropical species, the cultivation of allspice will create economic incentives that will further contribute to the conservation of biodiversity. The cultivation of allspice will reduce the economic incentive

Table 3 Average encounter rates (per 7 days) for amphibians and reptiles in primary forest (n = 3), secondary forest (n = 5), allspice (n = 7) and pasture (n = 4) in north-central Nicaragua 2003–2004

Species	Primary forest	Secondary forest	Allspice	Pasture	n
Central American Whiptail *Ameiva festiva*	0.00	1.43	1.33	1.10	55
Speckled Racer *Drymobius margaritiferus*	0.00	0.50	0.29	0.25	7
Mexican Vine Snake *Oxybelis aeneus*	0.00	0.40	0.43	0.25	6
Red Eyed Tree Frog *Agalychnis callidryas*	0.33	0.40	0.29	0.00	5
Green Basilisk *Basiliscus plumifrons*	0.00	0.40	0.29	0.00	4
Smooth Skinned Toad *Bufo haematiticus*	0.33	0.40	0.00	0.00	4
Purple Caecilian *Gymnopis multiplicata*	0.33	0.20	0.14	0.25	4
Cukra Climbing Salamander *Bolitoglossa striatula*	0.33	0.20	0.14	0.00	3
Eyelasah viper *Brothiechis schlegelii*	0.00	0.40	0.00	0.00	3
Cane Toad *Bufo marinus*	0.00	0.00	0.43	0.00	3
Neotropical Green Anole *Norops biporcatus*	0.00	0.20	0.14	0.00	3
Rain Forest Frog *Rana vaillanti*	0.00	0.20	0.29	0.00	3
Tropical Rat Snake *Spilotespullatus*	0.00	0.60	0.00	0.00	3
Common Basilisk *Basiliscus basiliscus*	0.00	0.00	0.29	0.00	2
Helmeted Iguana *Corytophanes cristata*	0.00	0.20	0.14	0.00	2
Neotropical Racer *Drymobius chloroticus*	0.00	0.00	0.14	0.00	2
Tropical Water Snake *Hydromorphus concolor*	0.00	0.40	0.00	0.00	2
Bicolored Coral Snake *Micrurus multifasciatus*	0.33	0.00	0.14	0.00	2
Warschewitsch's Frog *Rana warszewitschii*	0.33	0.20	0.00	0.00	2
Misfit Leaf Frog *Agalychnis saltator*	0.00	0.00	0.14	0.00	1
Jumping Pit Viper *Atropoides nummifer*	0.33	0.00	0.00	0.00	1
Striped Basilisk *Basiliscus vittatus*	0.00	0.00	0.00	0.25	1
Fer de Lance *Bothrops asper*	0.33	0.00	0.00	0.00	1
Mussurana *Clelia clelia*	0.00	0.20	0.00	0.00	1
Mimicking Rain Frog *Eleutherodactylus mimus*	0.00	0.20	0.00	0.00	1
Purple Caecilian *Gymnopis multiplicata*	0.00	0.00	0.14	0.00	1
Common cat-eyed snake *Leptodeira annulata*	0.33	0.00	0.00	0.00	1
Central American Coral Snake *Micrurus nigrocinctus*	0.33	0.00	0.00	0.00	1
Red coffee snake *Ninia sebae*	0.00	0.00	0.14	0.00	1
Anolis sp. *Norops sp.*	0.00	0.00	0.00	0.25	1
Masked tree frog *Smilisca baudinii*	0.33	0.00	0.00	0.00	1
Turnip-tailed Gecko *Thecadactylus rapicauda*	0.33	0.00	0.00	0.00	1

for the felling of mature allspice trees in areas of virgin forest, as was the previous practice. Previously allspice was exported in its whole form, and thus, the fruits had little value added. With the introduction of the technology for the production of essential oils, wild allspice trees will increase in value, which will discourage Nicaraguans from harvesting allspice by cutting down fruiting trees. Furthermore, the semi-permanence of allspice plantations will yield repeated harvests from the same area, which will reduce the necessity of clearing additional virgin forest (Donald 2004), for which the protection of water supplies is an added incentive. Finally, the social and economic stability derived from the production of essential oils will result in the discouragement of indiscriminant deforestation by squatters, similar to that observed in cacao farming regions of eastern Brazil (Donald 2004).

The occurrence of non-native native species can be a problem in some kind of plantations through predation or competition with native species, or the transmission of disease (Daily and Erlich 1996; Laurance and Cochrane 2001). We encountered two species of non-native rodents in allspice plantations (black rat and house mouse). These species occurred in relatively low numbers, accounting for only 7% of

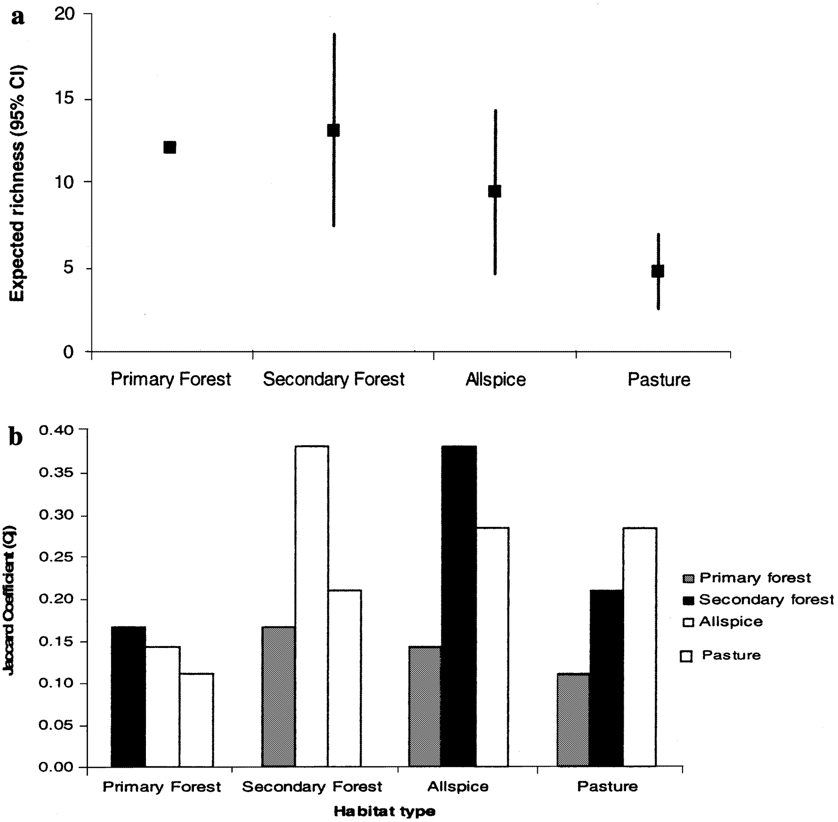

Fig. 7 Mean expected number of amphibian and reptiles compared among habitats using rarefaction (**a**) and similarity in herpetofaunal species composition among habitats (**b**) using data from north-central Nicaragua 2002–2004

species captured in allspice plantations. Thus, it appears unlikely that allspice plantations support numbers of non-native species sufficient to cause significant impacts on the native fauna, although this potential risk merits further investigation.

We conclude that the potential for allspice to contribute to biodiversity conservation by increasing the biodiversity of areas of former pasture and to reducing incentives for the clearing of additional primary forest is substantial. Care should be exercised, however, in indiscriminately promoting its cultivation on the basis of its biodiversity benefits. Shade coffee has been touted as a panacea for the conservation of tropical biodiversity, however it has become clear that, in the absence of rigorous certification programs based on scientifically established criteria combined with a detailed analysis of the effects of economic incentives associated with its promotion, it might in fact increase the loss biodiversity (Rappole et al. 2003a, b). As long as sufficient attention is given to the effect of the economic incentives on the agricultural practices in the region, allspice cultivation can improve the living standards of the human populace, and also improve the prospects for the native fauna of the region.

Although we found evidence of large mammals in the surrounding forest, such as droppings of tapirs (*Tapirus bairdii*), with the exception of white-tailed deer, larger

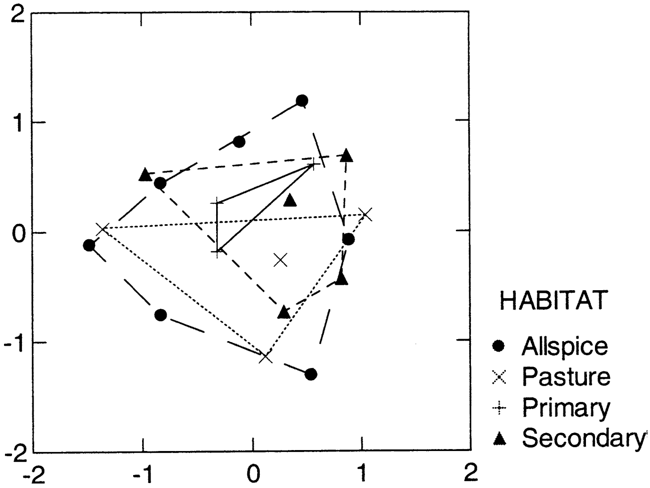

Fig. 8 Multi-dimensional scaling ordination of the abundances of reptile and amphibian species among habitats based on timed searches at 15 sites in north-central Nicaragua 2003–2004. Stress of final configuration was 0.005, proportion of variance (RSQ) was 0.84

Table 4 Average (standard error) habitat variables compared among primary forest, secondary forest, allspice and pasture at sampling sites in north-central Nicaragua 2003–2004

Habitat	Allspice	Pasture	Primary forest	Secondary forest	*P*-value
Circumference	41.8 (11.6)[b]	4.17 (1.23)[b]	141.1 (29.1) [a]	108.9 (20.0)[b]	*P*=0.005
Altura	7.06 (0.57)[b]	6.66 (2.53)[b]	23.7 (2.25) [a]	12.2 (0.70)[b]	*P*<0.002
Contacts 0–1	7.38 (1.70)	11.9 (0.48)	6.07 (1.63)	8.03 (1.56)	*P*=0.06
Contacts 1–2	5.53 (1.34)	4.88 (1.21)	4.10 (0.36)	5.33 (1.72)	*P*=0.88
Contacts 2–3	3.45 (1.31)	1.15 (0.79)	4.90 (0.90)	4.77 (0.68)	*P*=0.08

Common superscripts indicate means that did not differ significantly

[a]number of contacts of vegetation with a 3-m pole held vertically

mammals were notably absent from our study sites. This is probably due to the relative small scale of our sampling effort, which was constrained to relatively few, small trapping arrays. Wide ranging species dependent on forest should have high conservation priority (Daily et al. 2003), and might be particularly sensitive to habitat fragmentation, and we suggest that efforts to survey these species would be a valuable supplement to our investigation.

Conclusions and implications for conservation

Allspice cultivated in a mixed productive system provides habitat for a diverse community of resident and migrant birds, mammals, reptiles and amphibians. The habitat value of the multistoried, structurally complex habitats provided by allspice cultivation is only one way in which this form of agroforestry can contribute to the conservation of biodiversity. The cultivation of allspice will reduce the economic incentive for the felling of mature allspice trees in areas of virgin forest, as was the previous practice. In addition, the semi permanence of allspice plantations will yield repeated harvests from the same area, which will reduce the necessity of clearing additional virgin forest. Finally, it is expected that the social and economic stability derived from the production of essential oils will result in the discouragement of indiscriminant deforestation by squatters.

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