

## DEFORESTATION ALTERS PHYTOTELM HABITAT AVAILABILITY AND MOSQUITO PRODUCTION IN THE PERUVIAN AMAZON

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**Abstract.** We quantified the effects of deforestation, and subsequent cultivation and forest regeneration, on the abundance and composition of mosquito larval habitats, specifically phytotelmata (plant-held waters), in the western Amazon basin. Recently deforested sites were characterized by increased phytotelm density (1.6 phytotelmata/m<sup>2</sup>) and greater relative abundance of fallen-plant-part phytotelmata (76%) compared to intact forests (0.9 phytotelmata/m<sup>2</sup> and 25% fallen plant parts). As a result, the total volume of colonizable phytotelm water was significantly larger in new clearings. Subsequent cultivation of cleared land with mixed crops including pineapple and plantain had similar consequences: phytotelm density (2.2 units/m<sup>2</sup>) was significantly larger in plantations than in forests due to greater relative abundance of water-filled plant axils (71% vs. 39% in forest). Such axils are the preferred larval habitats for *Wyeomyia* spp. mosquitoes, which showed a similarly significant increase in production in plantations (0.25 larvae/m<sup>2</sup>) vs. forests (0.04 larvae/m<sup>2</sup>). Likewise, *Limatus* spp. mosquitoes were an order of magnitude more abundant in altered landscapes (especially in recently deforested and cultivated areas) than in mature forest, due to increased abundance of fallen-plant-part phytotelmata, in which they are typically the most common colonists. Because they are potential vectors of pathogens in a region of high endemic and emergent virus activity, increases in local abundance of *Limatus* spp. and *Wyeomyia* spp. due to large-scale deforestation and agriculture may influence rates of disease transmission.

**Key words:** Amazon; arthropods; deforestation; disease vector; diversity; larval mosquito habitat; *Limatus* spp.; mosquitoes; Peru; phytotelm; tropical forest; *Wyeomyia* spp.

### INTRODUCTION

Deforestation in the Amazon basin has wide-ranging social and environmental consequences, including the profound loss of biodiversity due to destruction of critical habitat (e.g., Dale et al. 1994, Fearnside 1999). Apart from the obvious and well-publicized effects of deforestation on intrinsic ecological processes, it also has important negative implications for human health. Specifically, deforestation may increase suitable habitat for vector species and thereby enhance the spread of arthropod-borne infectious diseases, including malaria (Walsh et al. 1993, Pope et al. 2005) and viral diseases such as encephalitis (Tesh 1994, Taylor 1997, Méndez et al. 2001, Alfonzo et al. 2005), which are diverse and common in the region (Turell et al. 2005). However, deforestation also may have the opposite effect (i.e., reduced vector densities) depending on the location, focal species, and timing of sampling (Suwonkerd et al. 2002, Overgaard et al. 2003). Tropical deforestation is

continuing at a phenomenal rate (Nepstad et al. 1999, Laurance et al. 2001a, 2004) while there is a growing threat of emergent diseases becoming pandemic, due to factors such as climate change and increased human mobility (e.g., Githeko et al. 2000). Thus, understanding the effects of land use and habitat conversion on distributions of pathogen vectors and their predators and competitors is increasingly important.

Despite changes in tropical deforestation practices over the past several decades (Perz 2002), much of the forest clearing in the western Amazon still stems from subsistence agriculture and is associated with construction of new roads (Fearnside 1987, Mäki et al. 2001). In this region, initial deforestation proceeds over several days to weeks, during which the forest understory is removed and most of the trees are felled. The largest trees are often left where they fall, either to partially dry before being cut into rough lumber, or to rot in place. Burning followed by 2–6 months of cultivation results in a plantation covering ~1 ha (locally and hereafter referred to as a “chacra”; Mäki et al. 2001). Chacras are typically planted with pineapple (*Ananas comosus* (L.) Merr., Bromeliaceae), plantain (*Musa* spp., Musaceae),

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sugar cane (*Saccharum officinarum* L., Poaceae), and manioc (*Manihot esculenta* Crantz, Euphorbiaceae) for several years until the soil is no longer fertile. The influx of pioneer species into abandoned chacras during the subsequent 5–10 years results in early-successional forest (locally and hereafter “purma”; Mäki et al. 2001), which differs dramatically from mature forest in terms of species composition (e.g., *Cecropia* spp. often dominate) and physical structure (<10 m canopy, dense understory; Peña-Claros 2003).

This deforestation–regeneration cycle results in a regional mosaic of successional habitat types. Their persistence times approximate a log distribution as follows: new clearings retain their general characteristics for up to 0.5 years, until the planted crops are tall enough to partially shade the soil; chacras persist for ~5 years, depending on edaphic factors and landowner investment; and purma begins to present the gross characteristics of mature forest in 30–50 years (Peña-Claros 2003). These transitional habitats typically have well-defined boundaries and commonly occur adjacent to mature forest, which may persist >500 years unless it is near human development.

Various types of phytotelmata (plant-held waters; Varga 1928, Maguire 1971) exist in all of the habitats just described. Phytotelmata are colonized by a broad range of invertebrate and vertebrate taxa, and are the principal larval microhabitats for many mosquito species (Fish 1983, Kitching 2000, Yanoviak 2001a). Frank and Curtis (1981) estimated that the aquatic stages of 22% of all Neotropical mosquito species occur in bromeliad axils. Many of the mosquitoes found in phytotelmata are important pathogen vectors. For example, tree-hole-inhabiting *Haemagogus* spp. remain the most important vectors of yellow fever virus in the Americas (e.g., Galindo et al. 1955), and *Anopheles* (*Kerteszia*) spp. are important malaria parasite vectors where epiphytic bromeliads are common. Finally, the Sabethini (e.g., *Limatus*, *Sabethes*, *Wyeomyia*) are often the most prominent mosquito inhabitants of phytotelmata, and are potential vectors of several encephalitis viruses (Jonkers et al. 1968, Theiler and Downs 1973, Turell et al. 2005).

Organisms living in phytotelmata show varying degrees of specialization for particular microhabitat classes (e.g., Bates 1949, Fish 1983). Within a given phytotelm unit, the species composition of the resident fauna depends on a variety of factors operating at different scales. These include the composition of the regional species pool and their vagilities, the distribution of predators (Yanoviak 2001b), the quantity and quality of nutrients (Yanoviak 1999a), and local abiotic conditions (Yanoviak 1999b, c, 2001c). Many of these factors are likely to differ among new clearings, chacra, purma, and mature forest habitats.

Here we investigate how typical deforestation practices in lowland forests of the western Amazon affect the abundance of small aquatic habitats, specifically phyto-

telmata, and their inquiline mosquitoes and other arthropods. Our primary goal was to quantify variation in phytotelm habitat availability and its consequences for the production of resident arthropods (particularly mosquitoes) in each of the four habitat types. We tested three hypotheses: (1) the density of phytotelmata and the total amount of phytotelm water available for colonization differ among the four habitats; (2) the relative abundance of different phytotelm types differs among habitats; and (3) variation in phytotelm characteristics among habitats alters the local species composition and production of mosquitoes.

We expected that mature forests would have a comparatively even distribution of phytotelm types, with tree holes being most abundant because they tend to occur at all levels (Yanoviak 1999c). We further predicted that fallen-plant-part phytotelmata would be most abundant in new clearings (e.g., leaves from numerous recently felled trees) and purma (associated with rapid vegetation turnover). Finally, we expected that habitats likely to have high densities of plant axil phytotelmata (e.g., chacras cultivated with pineapple) and fallen plant parts (e.g., new clearings) would produce significantly more mosquitoes, especially sabethines, per unit area than forest habitat.

#### METHODS

This project was conducted along the highway connecting the cities of Iquitos and Nauta in Loreto Province, northeastern Peru (3°45' S, 73°15' W). The region is dominated by lowland rain forest vegetation and receives ~3000 mm of precipitation per year. Rainfall in this part of Peru is minimally seasonal relative to other tropical forests (Whitmore 1998:12), receiving >100 mm per month, on average (Madigosky and Vatnick 2000). All data were collected in February–April 2003 and February–April 2004. There was a maximum of four consecutive rain-free days during these periods, and total monthly rainfall exceeded 125 mm (>200 most months; S. R. Madigosky and I. Vatnick, unpublished data). Mäki et al. (2001), Vásquez (1997), and Madigosky and Vatnick (2000) provide additional details about the region, the local climate, and the Iquitos–Nauta highway.

Three replicate study sites were located along the highway between 45 and 60 km south-southwest of Iquitos and within 3 km east or west of the road surface (between 4°09' S, 73°28' W and 4°17' S, 73°31' W). Large areas (2–3 ha patches) of three disturbed or regenerating habitat types (new clearing, chacra, purma), plus nearby continuous forest (i.e., located >100 m from the nearest large disturbance and connected to larger areas of forest) were selected for sampling at each site. The four habitat types within a replicate site were surveyed, and a square sampling area with dimensions 135 × 135 m was established in each. The area within the square was then divided into 81 15 × 15 m quadrats, and a random number table was used to select five quadrats for

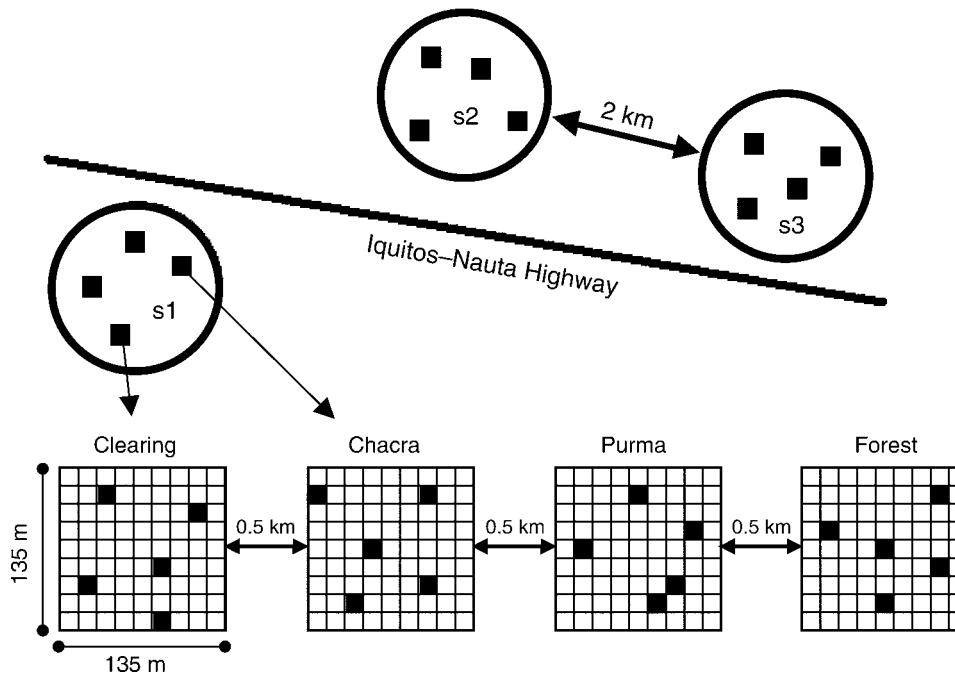


FIG. 1. Study design. Four habitat grids (clearing, chacra, purma, forest) were established in each of three replicate sites (s1–s3) along the highway (upper panel). Five  $15 \times 15$  m quadrats were randomly selected and sampled within each habitat grid (lower panel).

sampling within each grid (Fig. 1). Grids were  $\geq 0.5$  km apart within a site, and the replicate sites were separated by  $\sim 2$  km (Fig. 1). To avoid potentially confounding effects associated with the diversity of forest types present in the region, all forest grids used in this study were on upland (i.e., not seasonally inundated) clay soils.

Up to four people simultaneously and systematically searched each focal quadrat for any water-filled cavities within 2 m of ground level. We focused on phytotelmata (ignoring ground pools and stream or pond margins) and grouped them into four basic categories: tree holes (Kitching 1971), leaf axils (e.g., of tank bromeliads; Benzing 2000), *Heliconia* spp. flower bracts (Naem 1990), and fallen nonliving plant parts (water-filled leaves, fruit husks, palm fronds; e.g., Fish 1983, Caldwell 1993, Greeney 2001). The search time in a quadrat was  $\leq 90$  min, and all five focal quadrats of a given grid were generally sampled in a single day. Within each year of the study, sampling of individual habitat types and sites overlapped in time to distribute temporal variance as evenly as possible. The contents of each phytotelm unit were collected with a pipette and were transferred to a plastic bag for volume estimation and preliminary examination (Yanoviak and Fincke 2005). Any conspicuous predators found in the samples were placed in separate bags. Samples were transported to the lab in a cooler with several ice packs.

Fieldwork in 2003 focused only on chacra, purma, and forest understory up to 2 m. In 2004, we added the

vertical component of the forest habitat and three grids of recently cleared land associated with the three replicate sites. Deforestation is advancing rapidly in the region, and only one of the three forest grids sampled in 2003 remained sufficiently intact to be sampled in 2004. In that grid, we chose the largest tree within each of the same quadrats sampled in 2003 and climbed it using the single-rope technique (Perry 1978). When the largest tree within a quadrat was not suitable for climbing, we chose the nearest climbable tree. The two damaged forest grids were replaced with intact forest patches located  $< 5$  km from the original sites but  $> 2$  km apart. In each of these substitute forests, we climbed five trees spaced  $> 20$  m apart within a 1-ha square. During ascent and once in the crown of each tree, we scanned a  $15 \times 15$  m area of the surrounding forest and noted the presence of tree holes, bromeliads, and any other visible phytotelmata above 2 m. When possible, we collected the contents of the microhabitats, as in 2003. Canopy-level phytotelmata often were easily observed but not accessible within a reasonable amount of time. In such cases, we estimated their volumes by comparing their approximate size and number of axils (for bromeliads) with those of readily accessible phytotelmata, and we excluded them from analyses of the macroinvertebrate fauna. The resulting canopy phytotelm data were combined with the 2003 understory data for the analyses. Samples from individual phytotelmata having multiple water-filled subdivisions (e.g., the leaf axils of a single bromeliad, *Mauritia flexuosa* L.

palm, or plantain tree) were pooled in the field and were treated as a single unit for volume measurement and faunistic data. Collections from multiple bracts of a single *Heliconia* inflorescence were similarly combined. We pooled samples in this manner for convenience and to avoid pseudoreplication (Hurlbert 1984), but we recorded the number of individual subdivisions present in each phytotelm unit at the time of collection. We used this information to quantify the number of subunits present that were ignored by pooling samples in the field. For example, a 200-mL tree hole was treated as a single phytotelm unit with additional subdivisions = 0 and total volume = 200 mL, whereas a 200-mL bromeliad with five water-filled axils was treated as a single unit with additional subdivisions = 4 and total volume = 200 mL. This approach enabled us to quantitatively compare three basic physical characteristics among habitats types on a per quadrat basis: the number of independent phytotelmata (i.e., phytotelm density), the total phytotelm water volume available for colonization, and the degree of compartmentalization within structurally complex independent phytotelm units (e.g., bromeliads). The latter is ecologically relevant because the immature stages of many resident arthropods are unlikely to move voluntarily among the axils of a pineapple plant or the bracts of a *Heliconia* inflorescence.

Mosquito larvae were reared to adulthood and identified to species using the keys cited in Pecor et al. (2000) and Jones et al. (2004). Species within the genera *Limatus* and *Wyeomyia* sometimes co-occurred and could not be readily identified as larvae; thus we pooled them by genus for statistical analyses. Bunyaviruses have been isolated from both of the *Limatus* species that are common near Iquitos and from several Amazonian *Wyeomyia* species (Karabatsos 1985, Turell et al. 2005), so pooling in this manner did not affect the interpretation of results. Species identifications were confirmed by comparison with reference collections in Iquitos and at the Walter Reed Biosystematics Unit (WRBU), Suitland, Maryland, USA. Voucher specimens were deposited at WRBU and the Museo de Historia Natural Javier Prado, Lima, Peru. Non-mosquito taxa were identified to family or genus and were assigned to morphospecies when possible.

Statistical analyses focused on the effects of habitat types nested within the replicate sites, treating quadrats within habitats as the independent sampling units (i.e.,  $n = 5$  quadrats per habitat grid, 4 habitats per site, and 3 sites). This approach ignored variation among individual phytotelmata within a quadrat, but greatly improved normality in the data and provided spatially standardized results (revealing patterns at a scale of  $15 \times 15$  m). Phytotelm abundance, water volume, and number of subdivisions were compared among habitats (clearing, chacra, purma, forest) by using MANOVA (SAS Institute 2002). A separate MANOVA compared the relative abundance of the four phytotelm types (tree holes, plant axils, *Heliconia* bracts, and fallen plant

parts) among habitats nested within replicate sites. Both MANOVAs included contrasts of main effects with sequential Bonferroni adjustment (Rice 1989). Standardized canonical coefficients (SCCs) were used to determine the relative contribution of each variable to significant effects, as well as their relationship to each other (e.g., positive or negative; Scheiner 1993, SAS Institute 2002). Univariate normality was determined with Kolmogorov-Smirnov tests.

Mean macroinvertebrate density (number of individuals per unit phytotelm water per quadrat) and taxon density (number of taxa per unit phytotelm water per quadrat) were compared among replicate sites, habitats, and phytotelm types within habitats with nested ANOVAs. Raw abundance and volume data were pooled by phytotelm type within quadrats for these analyses. Production of *Wyeomyia* spp. and *Limatus* spp. mosquitoes (number of larvae per  $15 \times 15$  m quadrat) was compared among sites and habitats within sites with nested ANOVA. For all tests, non-normal count data were  $\log(x + 1)$ -transformed, and proportional data were arcsine square-root transformed before analysis (Sokal and Rohlf 1995).

## RESULTS

We collected the contents of 1142 phytotelmata; 31% occurred in new clearings, 44% in chacras, 7% in purmas, and 18% in forests. Individual samples ranged in volume from 1 mL to 6500 mL ( $59 \pm 289$  mL, mean  $\pm$  SD; median = 5 mL). Physical characteristics of phytotelmata differed among habitats (Fig. 2), with variation in the number of phytotelm subdivisions contributing the most to this result (Table 1). Phytotelmata in forests were characterized by high cumulative volume, moderate density, and a moderate amount of subdivision (Fig. 2). In contrast, chacra habitats contained many highly subdivided phytotelmata, clearings contained large numbers of minimally subdivided phytotelmata, and purma contained relatively few phytotelmata, with minimal subdivision and low cumulative volume (Fig. 2). No two habitats were similar in overall phytotelm structure (Table 1, Fig. 3).

With some minor exceptions, the distribution of phytotelm types among habitats supported our predictions (Fig. 3). The differences in phytotelm physical characteristics among habitats resulted from differences in the percentages of phytotelm types present (Table 2, Fig. 3). An abundance of plant axil phytotelmata (e.g., plantain trees and pineapple plants) in chacras led to a significantly larger number of subdivided phytotelmata in that habitat vs. intact forest (Figs. 2 and 3). Similarly, abundant fallen-plant-part phytotelmata in new clearings resulted in large cumulative water volume available for colonization, but significantly fewer subdivided phytotelmata than in forests. The few plant axils present in clearings were associated with bromeliads surviving in the crowns of felled trees. Likewise, fallen trees were an occasional source of tree holes in chacras (Fig. 3), with

some holes containing >5 L of water (e.g., those occurring in the cavities between buttresses and in deep trunk convolutions; Yanoviak and Fincke 2005). The low stature and small diameters of woody plants in purma habitat precluded the formation of tree holes in all but a few instances (Fig. 3). Plant axils were relatively more abundant than we expected in the forest habitats because there were large numbers of bromeliads in the canopy. Finally, physical characteristics and relative abundance of phytotelm types also differed marginally at the landscape scale (i.e., among the three replicate sites; Tables 1 and 2). However, univariate nested contrasts showed that differences in phytotelm characteristics between habitats (clearing, chacra, purma, and forest) were consistent across sites.

One-third (37%) of the phytotelm samples contained at least one macroinvertebrate. The frequency of positive samples differed among habitats (clearing, 26%; chacra, 45%; purma, 30%; forest, 48%;  $G_{adj} = 26.6$ ,  $df = 3$ ,  $P < 0.001$ ) and among phytotelm types (axil, 48%; *Heliconia*, 86%; fallen plant parts, 23%; tree holes, 51%;  $G_{adj} = 58.9$ ,  $df = 3$ ,  $P < 0.001$ ). Samples from fallen plant parts and axils that were low in total volume (less than the median volume for each phytotelm type) lacked macroinvertebrates more often than the expected frequencies ( $G_{adj} > 4.92$ ,  $df = 3$ ,  $P < 0.05$ ), whereas occupancy was not as closely associated with volume in tree holes or *Heliconia* bracts ( $G_{adj} < 1.79$ ,  $df = 3$ ,  $P > 0.10$ ).

Most (98%) of the 3020 collected macroinvertebrates were larvae of Diptera. Mosquitoes (Culicidae) represented 74% of the total collection and 75% of collected Diptera. In all, 35 different taxa or morphospecies were collected (Appendix). Given that our morphospecies designations for non-mosquito taxa were very broad, and that tropical tree holes alone may harbor diverse faunas (Yanoviak 2001a), the actual

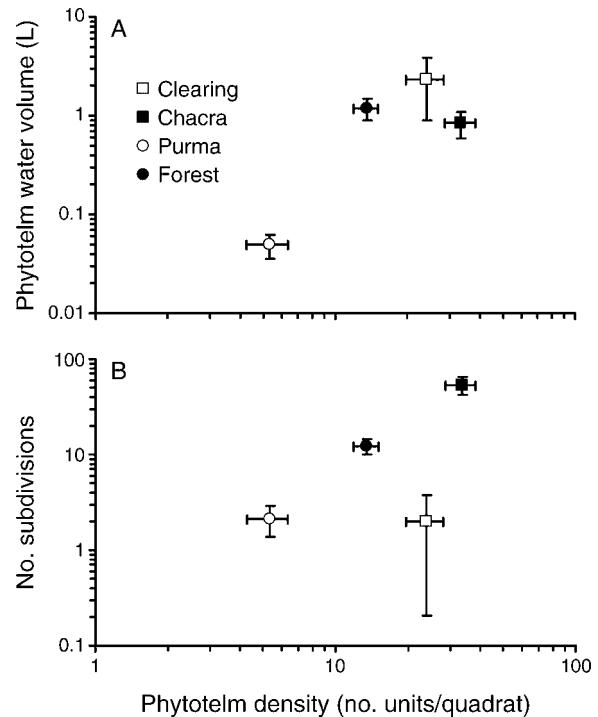


FIG. 2. Physical characteristics of phytotelmata in the four habitat types. (A) Total volume of phytotelm water collected per  $15 \times 15$  m quadrat and (B) the number of phytotelm units added by counting all axils and bracts independently (i.e., subdivisions) vs. phytotelm density (the number of independent units per quadrat). Values are means  $\pm$  SE for  $n = 15$  quadrats in each habitat. Note that the log scales and the y-axes span four orders of magnitude whereas the x-axis spans two.

number of species collected in this project is undoubtedly much higher.

Macroinvertebrate taxon density (number of species or morphospecies per unit volume of phytotelm water) and overall density (number of individual macroinverte-

TABLE 1. MANOVA output for variation in density, volume, and subdivision of phytotelmata among replicate sites and habitat types nested within sites.

Source	df	F	P	First SCCs		
				Density	Volume	Subdivision
Site	6, 94	2.62	0.022	1.96	-0.98	-0.50
Site 1 vs. 2	3, 46	2.97	0.041†	-1.99	1.02	0.72
Site 1 vs. 3	3, 46	5.58	0.002†	1.95	-0.96	-0.45
Site 2 vs. 3	3, 46	0.53	0.664†	1.63	-0.70	0.25
Habitat(Site)	27, 144	7.95	<0.001	-0.70	0.63	1.64
Forest vs. chacra	3, 46	11.98	<0.001‡	1.25	-1.56	0.93
Forest vs. clearing	3, 46	17.57	<0.001‡	-1.45	0.84	1.60
Forest vs. purma	3, 46	19.66	<0.001‡	-0.56	1.65	0.40
Chacra vs. clearing	3, 46	28.47	<0.001‡	-0.33	-0.35	1.86
Chacra vs. purma	3, 46	22.86	<0.001‡	0.39	0.40	1.05
Clearing vs. purma	3, 46	17.60	<0.001‡	0.87	0.91	-1.17

Notes: Standardized canonical coefficients (SCCs) show the relative contribution of each of the response variables to significant pairwise contrasts. F values are for Pillai's Trace.

† Bonferroni-adjusted  $\alpha = 0.017$ .

‡ Bonferroni-adjusted  $\alpha = 0.008$ .

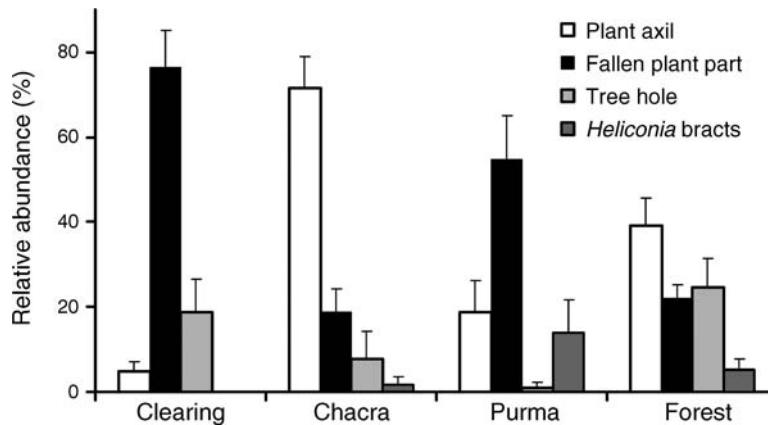


FIG. 3. Relative abundance (mean + SE) of different phytotelm types among the four focal habitats. Values are the percentages of each phytotelm type in  $n = 15$  quadrats within each habitat. MANOVA results are given in Table 2.

brates per unit volume) were correlated ( $r = 0.753$ ,  $P < 0.0001$ ). Both of these community parameters were significantly lower in new clearings than in forest habitat (Table 3, Fig. 4). Likewise, macroinvertebrate density and taxon density were generally highest in *Heliconia* bracts and lowest in tree holes and fallen plant parts, which did not differ (Table 3, Fig. 5).

The composition of resident faunas varied among the different types of phytotelmata, and *Limatus* spp. and *Wyeomyia* spp. mosquitoes accounted for more than half of the total collection (Table 4). Both showed strong associations with particular phytotelm types: *Wyeomyia* spp. comprised 92.5% of mosquitoes in plant axils and 98.8% of mosquitoes in *Heliconia* bracts; whereas *Limatus* spp. dominated the mosquito fauna of fallen plant parts (92.3%). Similar associations were found in other common taxa: *Culex urichii* was the most common mosquito in tree holes (58.2%), and most (82.6%) of the collected ceratopogonine midges were found specifically in pineapple axils. *Wyeomyia* spp. were very rare in

canopy phytotelmata; the most common mosquitoes encountered in canopy plant axils (bromeliads) were *Culex (Microculex)* spp., which have not yet been implicated in human disease transmission.

These mosquito–phytotelm microhabitat associations were reflected by differences in the production of certain taxa at larger spatial (i.e., habitat) scales. In particular, *Wyeomyia* spp. abundance was about one order of magnitude larger in chacras than in the other habitats (Table 5, Fig. 6). Likewise, *Limatus* spp. production generally followed the relative abundance of fallen-plant-part phytotelmata (Table 5, Fig. 6), except in chacras, where *L. flavisetosus* occasionally occupied axils and *Heliconia* bracts, as well as fallen plant parts (Figs. 3 and 6, Table 4).

Top predators (larvae of the damselfly *Microstigma rotundatum* [Odonata: Pseudostigmatidae], and the mosquitoes *Toxorhynchites haemorrhoidalis* and *T. nr. theobaldi*) were rare, in total representing only 0.5% of the macroinvertebrates collected. The odonates were

TABLE 2. MANOVA output comparing relative abundance of different types of phytotelmata (plant axil, fallen plant parts [FPP], tree hole, and *Heliconia* bracts) among replicate sites and habitat types (nested within sites).

Source	df	F	P	First SCCs			
				Axil	FPP	Tree hole	<i>Heliconia</i>
Site	8, 92	2.31	0.027	0.64	1.02	-0.33	-0.09
Site 1 vs. 2	4, 45	1.88	0.131†	-0.16	1.48	0.39	0.31
Site 1 vs. 3	4, 45	2.92	0.032†	0.60	1.09	-0.28	-0.07
Site 2 vs. 3	4, 45	2.07	0.101†	0.86	-0.12	-0.71	-0.38
Habitat(Site)	36, 192	2.77	< 0.001	0.70	-1.06	-0.63	0.01
Forest vs. chacra	4, 45	3.82	0.009‡	0.73	-0.61	-0.90	-0.30
Forest vs. clearing	4, 45	7.50	< 0.001‡	0.71	-1.03	-0.19	0.15
Forest vs. purma	4, 45	5.41	0.001‡	1.03	0.15	1.13	-0.03
Chacra vs. clearing	4, 45	17.39	< 0.001‡	0.81	-0.96	-0.55	0.04
Chacra vs. purma	4, 45	9.30	< 0.001‡	1.25	-0.28	0.28	-0.21
Clearing vs. purma	4, 45	6.32	< 0.001‡	0.18	1.26	1.25	-0.19

Notes: The  $F$  values are from Pillai's Trace. Standardized canonical coefficients (SCCs) show the relative contribution of each of the response variables to significant pairwise contrasts.

† Bonferroni-adjusted  $\alpha = 0.017$ .

‡ Bonferroni-adjusted  $\alpha = 0.008$ .

TABLE 3. Nested ANOVA output for macroinvertebrate density and macroinvertebrate taxon density among replicate sites, habitats within sites, and phytotelm types within habitats and sites.

Factor(s)	df	Type III ss	MS	F
Macroinvertebrate density				
Site	2	0.6152	0.3076	6.99*
Habitat(Site)	9	2.4153	0.2684	6.10***
Type(Habitat × Site)	25	2.9793	0.1192	2.71***
Error	71	3.1255	0.0440	
Macroinvertebrate taxon density				
Site	2	0.0570	0.0285	4.19*
Habitat(Site)	9	0.2844	0.0316	4.64***
Type(Habitat × Site)	25	0.3378	0.0135	1.98*
Error	71	0.4837	0.0068	

Notes: Macroinvertebrate density and macroinvertebrate taxon density are the number of individuals and number of taxa, respectively, per unit phytotelm water volume. Habitats include clearing, chacra, purma, and forest; phytotelm types include axil, fallen plant part, tree hole, and *Heliconia* bract.

\* $P < 0.05$ ; \*\*\* $P < 0.001$ .

found in forest tree holes only, whereas all of the *Toxorhynchites* larvae were found either in chacras or in new clearings (77% occurring in tree holes, 15% in axils, 8% in fallen plant parts).

#### DISCUSSION

Our results show that typical deforestation and subsequent land use for subsistence agriculture in the western Amazon increase the availability of microhabitats for colonization by mosquitoes and other arthropods that occupy plant-held waters. The process of clearing a patch of forest inevitably increases the local abundance of fallen plant parts, which are among the favored larval microhabitats of *Limatus* spp. mosquitoes. Larvae of *Limatus* spp. develop rapidly, and several generations may be produced in the time between clearing a patch of forest and burning the debris before

cultivation. Although the biology of disease transmission by sabethines remains largely unknown, Bunyamwera-group viruses and related pathogens have been isolated from *Limatus* spp. (Jonkers et al. 1968, Theiler and Downs 1973, Turell et al. 2005), and *Limatus* spp. in the Iquitos area frequently bite humans (Jones et al. 2004; S.Yanoviak, *personal observation*).

After the cleared land is planted (i.e., it becomes a chacra), the density of plant axil habitats may be two or more orders of magnitude greater than in the surrounding forest. The large numbers of water-filled axils in a new plantation cultivated with plantains and pineapples facilitate increased local production of *Wyeomyia* spp. mosquitoes and possibly ceratopogonid midges. Like *Limatus* spp., *Wyeomyia* spp. mosquitoes are potential vectors of Bunyamwera-group viruses (Theiler and Downs 1973, Turell et al. 2005). Also, preliminary identifications suggest that most of the collected ceratopogonids are in the genus *Culicoides*, which includes the principal vector of Oropouche virus (Watts et al. 1997a, b, Mercer and Castillo-Pizango 2005).

Although our results clearly demonstrate that deforestation enhances mosquito production on a local scale, several caveats must be considered. First, these effects may be less predictable on a larger spatial scale. As shown by differences among sites separated by as little as 2 km in this study, phytotelm densities and composition vary across the region. Tree holes and bromeliads are more common in some forests than in others (Kitching 2000), and fallen plant parts and *Heliconia* bracts may be locally very patchy in space and time. Moreover, land use practices are inconsistent; chacras are sometimes planted as monocultures of manioc or sugarcane, which generally provide no suitable phytotelmata for mosquito colonization. Second, this study focused on larval habitat availability as a mechanism for potential increases in vector abundance.

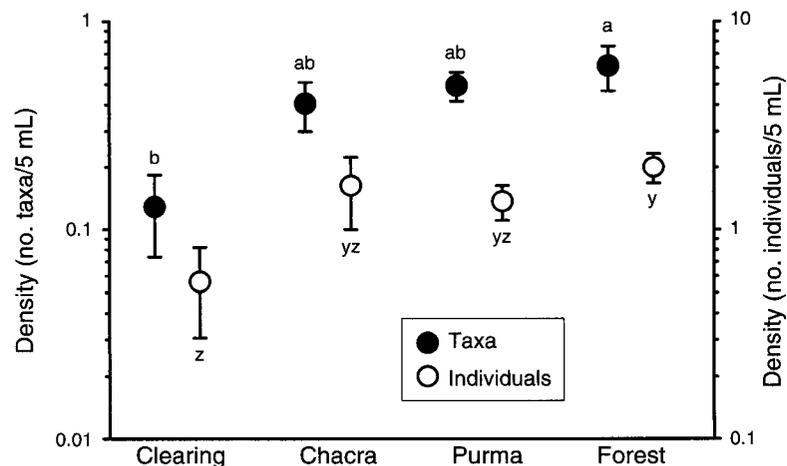


FIG. 4. Density (mean  $\pm$  SE) of macroinvertebrate taxa and of individuals in the different focal habitats. Densities per 5 mL are shown because this was the median sample volume for the entire collection ( $n = 15$  quadrats per mean). Identical letters indicate means that do not differ within density (y, z) or taxon density (a, b). Note the log scales for vertical axes.

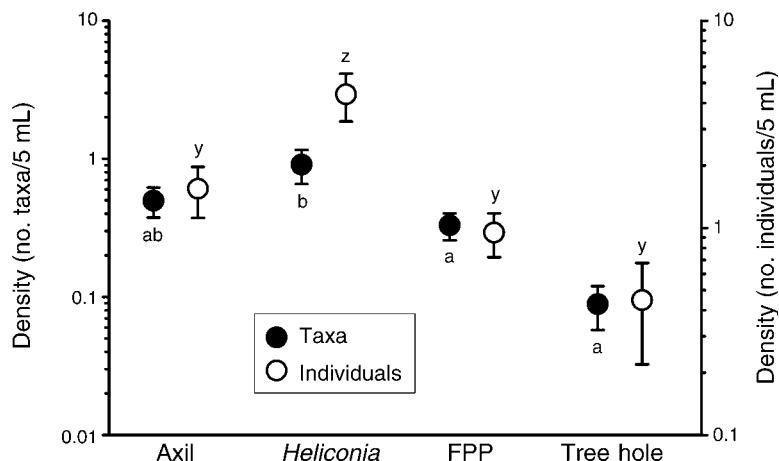


FIG. 5. Density (mean  $\pm$  SE) of macroinvertebrate taxa and of individuals (per 5 mL) among the different phytotelm types ( $n = 15$  quadrats per mean). FPP is fallen plant parts. Identical letters indicate means that do not differ, based on univariate tests within density (y, z) or taxon density (a, b). Note the log scales for vertical axis.

However, adults of many mosquito species are highly vagile, and larval distributions may not correlate with adult distributions or biting activity at the same site (e.g., Alfonzo et al. 2005). Results from a related study examining distributions of adult mosquitoes in the same chacra, purma, and forest sites showed that this is true for the Iquitos region; contrary to the larval results presented here, adult *Wyeomyia* and *Limatus* spp. were consistently more abundant in purma and forest than in chacras (S. Yanoviak, unpublished data). Finally, many factors influence the probability of disease transmission and the maintenance of sylvatic and peridomestic virus cycles, and local vector abundance (beyond a threshold)

TABLE 4. Distribution of selected taxa (those representing >1% of the total collection) among the four focal phytotelm types.

Taxon	Relative abundance				N	Portion of total (%)
	A	F	T	H		
<b>Diptera</b>						
Ceratopogonidae:	85	4	7	4	339	11
Ceratopogoninae						
Chironomidae	6	16	13	53	51	2
<b>Culicidae</b>						
<i>Culex conservator</i>	0	0	100	0	55	2
<i>Cx. urichii</i>	0	9	91	0	378	12
<i>Limatus</i> spp.†	5	79	16	<1	641	21
<i>Wyeomyia</i> spp.‡	79	<1	6	15	1084	36
Muscidae	81	19	0	<1	226	7
Psychodidae	68	0	9	23	104	3
Coleoptera: Scirtidae	29	0	71	0	35	1

Notes: Phytotelm abbreviations are: A, axil; F, fallen plant parts; T, tree hole; and H, *Heliconia* bract. Relative abundance is the percentage abundance among phytotelm types where present; rows sum to 100%. N is the number of individuals collected, and portion of total is the percentage abundance in the total collection.

† *L. durhamii* (90% found in fallen plant parts) and *L. flavisetosus* (71% in fallen plant parts).

‡ *W. aphobema*, *W. flui*, *W. melanocephala*, *W. pseudopecten*, and three morphospecies.

may not be critical among them. Additional research is needed to determine if abundance of *Limatus* and *Wyeomyia* limits potential outbreaks of pathogens such as Bunyamwera-group viruses. These and related viruses also have been isolated from aedine and culicine mosquitoes that do not breed in phytotelmata (Turell et al. 2005), and deforestation may or may not have similar effects on the production of species breeding in microhabitats such as stream margins or ground pools.

Distributions of the most common taxa among phytotelm types conformed to expectations based on other phytotelm studies (e.g., Fish 1983, Naeem 1990, Kitching 2000, Greeney 2001, Yanoviak 2001a) and our prior observations in the region. However, the overall low macroinvertebrate occupancy of phytotelmata (37%) was unexpected. We attribute this to the high relative abundance of fallen plant parts in highly exposed sites (clearings and chacras) and to the relatively small volume of water collected per sample from individual axil habitats, especially leaf axils of plantain trees. Likewise, differences in macroinvertebrate density and taxon density among phytotelm types can be explained, in part, by microhabitat volume and

TABLE 5. Nested ANOVA output for abundances of *Limatus* spp. and *Wyeomyia* spp. among replicate sites and habitats (clearing, chacra, purma, and forest) within sites.

Factor(s)	df	Type III ss	MS	F
<i>Limatus</i> spp.				
Site	2	2.6607	1.3304	0.79
Habitat(Site)	9	39.2385	4.3598	2.58*
Error	48	81.2480	1.627	
<i>Wyeomyia</i> spp.				
Site	2	3.8933	1.9466	1.16
Habitat(Site)	9	85.3389	9.4821	5.65***
Error	46	80.6057	1.6793	

\* $P < 0.05$ ; \*\*\* $P < 0.001$ .

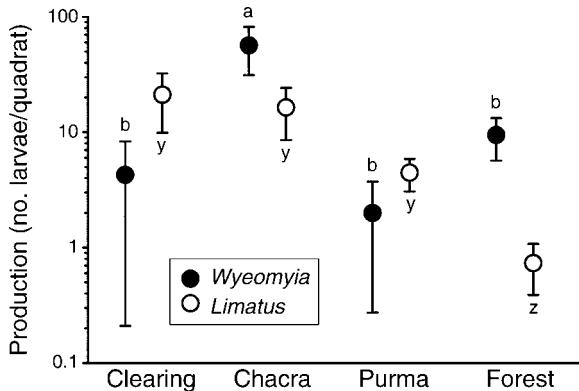


FIG. 6. Production (mean  $\pm$  SE) of larvae per  $15 \times 15$  quadrat by *Wyeomyia* spp. and *Limatus* spp. mosquitoes among the different habitats (all phytotelma types pooled within habitats;  $n = 15$  quadrats per mean). Identical letters indicate means that do not differ within *Wyeomyia* (a, b) or *Limatus* (y, z). Note the log scale for the vertical axis.

the resource base for the resident fauna. Tree holes and fallen plant parts tend to hold comparatively large volumes of water, and their faunas depend almost entirely on heterotrophic resources. In contrast, most plant axils and *Heliconia* bracts hold  $<100$  mL water, which is in contact with nonwoody (often photosynthetic) plant tissues, and may be augmented with secretions from the plant (Machado-Allison et al. 1983, Benzing 2000). The differences in mosquito production among habitats may be more extreme if *Limatus* and *Wyeomyia* have faster generation times in disturbed sites, where average temperatures are likely to be significantly higher, and where food webs and trophic characteristics in phytotelmata may differ greatly from those in shaded sites (Frank 1983).

There was no a priori reason to expect differences in macroinvertebrate density and taxon density among habitat types. However, as in similar studies of immature mosquito distributions (Alfonzo et al. 2005), we found more species in forested sites than cleared areas. The lower macroinvertebrate density and taxon density in new clearings is primarily attributed to the large relative abundance of fallen plant parts there. Such phytotelmata in clearings are often unprotected, potentially resulting in low colonization rates and high mortality due to extreme midday heat and washout during heavy rains.

Too few top predators were collected in this study to assess quantitatively the effects of deforestation on their distributions. However, data gathered here and in related projects (S. Yanoviak, unpublished data) strongly suggest that odonates are replaced by *Toxorhynchites* spp. in tree holes in deforested settings. Both taxa have strong effects on mosquito assemblages (Bradshaw and Holzapfel 1983, Lounibos et al. 1987, Fincke et al. 1997, Yanoviak 2001b). Determining how the effects of deforestation on top predator distributions may indi-

rectly influence mosquito productivity in tree holes would be an informative extension of this research.

In sum, much of the large-scale deforestation in the Amazon basin is associated with new road construction, which will continue for the next several decades (Laurance et al. 2001a, b, 2004, 2005, Fearnside et al. 2005). Roads promote immigration and development of sedentary populations with greater dependence on unsustainable, large-scale agriculture, in contrast to the traditional (and sustainable) shifting agriculture employed by Amazonian settlers (Whitmore 1998). Our results suggest that one potentially important consequence of this trend will be increased local production of *Limatus* and *Wyeomyia* mosquitoes, especially in new human settlements adjacent to intact forest. Unfortunately, relatively little is known of the biology of these taxa (but see, e.g., Frank 1983, 1986) and of the incidence of virus infections in humans caused by sabethines around Iquitos. We hope that this and related studies will stimulate further attention to these topics. Specifically, additional research is needed to assess the role of local *Limatus* and *Wyeomyia* abundance in limiting the transmission of pathogens, and to determine if effects of deforestation are applicable to groups of mosquitoes that occupy other habitats, such as ground pools, which are critical to the production of many other disease vectors (e.g., Alfonzo et al. 2005).

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#### LITERATURE CITED

- Alfonzo, D., M. A. Grillet, J. Liria, J.-C. Navarro, S. C. Weaver, and R. Barrera. 2005. Ecological characterization of the aquatic habitats of mosquitoes (Diptera: Culicidae) in enzootic foci of Venezuelan equine encephalitis virus in western Venezuela. *Journal of Medical Entomology* **42**:278–284.
- Bates, M. 1949. *The natural history of mosquitoes*. Macmillan, Gloucester, Massachusetts, USA.
- Benzing, D. H. 2000. *Bromeliaceae: profile of an adaptive radiation*. Cambridge University Press, Cambridge, UK.
- Bradshaw, W. E., and C. M. Holzapfel. 1983. Predator-mediated, non-equilibrium coexistence of tree-hole mosquitoes in southeastern North America. *Oecologia* **57**:239–256.
- Caldwell, J. P. 1993. Brazil nut fruit capsules as phytotelmata: interactions among anuran and insect larvae. *Canadian Journal of Zoology* **71**:1193–1201.

- Dale, V. H., S. M. Pearson, H. L. Offerman, and R. V. O'Neill. 1994. Relating patterns of land-use change to faunal biodiversity in the central Amazon. *Conservation Biology* **8**:1027–1036.
- Fearnside, P. M. 1987. Deforestation and international economic development projects in Brazilian Amazonia. *Conservation Biology* **1**:214–221.
- Fearnside, P. M. 1999. Biodiversity as an environmental service in Brazil's Amazonian forests: risks, value and conservation. *Environmental Conservation* **26**:305–321.
- Fearnside, P. M., W. F. Laurance, A. K. M. Albernaz, H. L. Vasconcelos, and L. V. Ferreira. 2005. Response [A delicate balance in Amazonia]. *Science* **307**:1045.
- Fincke, O. M., S. P. Yanoviak, and R. D. Hanschu. 1997. Predation by odonates depresses mosquito abundance in water-filled tree holes in Panama. *Oecologia* **112**:244–253.
- Fish, D. 1983. Phytotelmata: flora and fauna. Pages 1–27 in J. H. Frank and L. P. Lounibos, editors. *Phytotelmata: terrestrial plants as hosts for aquatic insect communities*. Plexus, Medford, New Jersey, USA.
- Frank, J. H. 1983. Bromeliad phytotelmata and their biota, especially mosquitoes. Pages 101–128 in J. H. Frank and L. P. Lounibos, editors. *Phytotelmata: terrestrial plants as hosts for aquatic insect communities*. Plexus, Medford, New Jersey, USA.
- Frank, J. H. 1986. Bromeliads as ovipositional sites for *Wyeomyia* mosquitoes: form and color influence behavior. *Florida Entomologist* **69**:728–742.
- Frank, J. H., and G. A. Curtis. 1981. On the bionomics of bromeliad-inhabiting mosquitoes. VI. A review of the bromeliad-inhabiting species. *Journal of the Florida Antimosquito Association* **52**:4–23.
- Galindo, P., S. J. Carpenter, and H. Trapido. 1955. A contribution to the ecology and biology of tree hole breeding mosquitoes of Panama. *Annals of the Entomological Society of America* **48**:158–164.
- Githeko, A. K., S. W. Lindsay, U. E. Confalonieri, and J. A. Patz. 2000. Climate change and vector-borne diseases: a regional analysis. *Bulletin of the World Health Organization* **78**:1136–1147.
- Greeney, H. F. 2001. The insects of plant-held waters: a review and bibliography. *Journal of Tropical Ecology* **17**:241–260.
- Hurlbert, S. H. 1984. Pseudoreplication and the design of ecological field experiments. *Ecological Monographs* **54**:187–211.
- Jones, J. W., M. J. Turell, M. R. Sardelis, D. M. Watts, R. E. Coleman, R. Fernandez, F. Carbajal, J. E. Pecor, C. Calampa, and T. A. Klein. 2004. Seasonal distribution, biology, and human attraction patterns of culicine mosquitoes (Diptera: Culicidae) in a forest near Puerto Almendras, Iquitos, Peru. *Journal of Medical Entomology* **41**:349–360.
- Jonkers, A. H., L. Spence, W. G. Downs, T. H. G. Aitken, and C. B. Worth. 1968. Arbovirus studies in Bush Bush Forest, Trinidad, W.I., September 1959–December 1964. *American Journal of Tropical Medicine and Hygiene* **17**:285–298.
- Karabatsos, N. 1985. International catalog of arboviruses including certain other viruses of vertebrates. Fourth edition. American Society of Tropical Medicine and Hygiene, San Antonio, Texas, USA.
- Kitching, R. L. 1971. An ecological study of water-filled tree-holes and their position in the woodland ecosystem. *Journal of Animal Ecology* **40**:281–302.
- Kitching, R. L. 2000. Food webs and container habitats: the natural history and ecology of phytotelmata. Cambridge University Press, Cambridge, UK.
- Laurance, W. F., A. K. M. Albernaz, and C. Da Costa. 2001a. Is deforestation accelerating in the Brazilian Amazon? *Environmental Conservation* **28**:305–311.
- Laurance, W. F., A. K. M. Albernaz, P. M. Fearnside, H. L. Vasconcelos, and L. V. Ferreira. 2004. Deforestation in Amazonia. *Science* **304**:1109–1111.
- Laurance, W. F., A. K. M. Albernaz, P. M. Fearnside, H. L. Vasconcelos, and L. V. Ferreira. 2005. Response [Underlying causes of deforestation]. *Science* **307**:1046–1047.
- Laurance, W. F., M. A. Cochrane, S. Bergen, P. M. Fearnside, P. Delamonica, C. Barber, S. D'Angelo, and T. Fernandes. 2001b. The future of the Brazilian Amazon. *Science* **291**:438–439.
- Lounibos, L. P., J. H. Frank, C. E. Machado-Allison, P. Ocanto, and J. C. Navarro. 1987. Survival, development and predatory effects of mosquito larvae in Venezuelan phytotelmata. *Journal of Tropical Ecology* **3**:221–242.
- Machado-Allison, C. E., D. J. Rodriguez, R. Barrera, and C. Gomez-Cova. 1983. The insect community associated with inflorescences of *Heliconia caribaea* Lamarck in Venezuela. Pages 247–270 in J. H. Frank and L. P. Lounibos, editors. *Phytotelmata: terrestrial plants as hosts for aquatic insect communities*. Plexus, Medford, New Jersey, USA.
- Madigosky, S. R., and I. Vatnick. 2000. Microclimatic characteristics of a primary tropical Amazonian rain forest, ACEER, Iquitos, Peru. *Selbyana* **21**:165–172.
- Maguire, B. 1971. Phytotelmata: biota and community structure determination in plant-held waters. *Annual Review of Ecology and Systematics* **2**:439–464.
- Mäki, S., R. Kalliola, and K. Vuorinen. 2001. Road construction in the Peruvian Amazon: causes and consequences. *Environmental Conservation* **28**:199–214.
- Méndez, W., J. Liria, J.-C. Navarro, C. Z. Garcia, J. E. Freier, R. Salas, S. C. Weaver, and R. Barrera. 2001. Spatial dispersion of adult mosquitoes (Diptera: Culicidae) in a sylvatic focus of Venezuelan equine encephalitis virus. *Journal of Medical Entomology* **38**:813–821.
- Mercer, D. R., and M. J. Castillo-Pizango. 2005. Changes in relative species compositions of biting midges (Diptera: Ceratopogonidae) and an outbreak of Oropouche virus in Iquitos, Peru. *Journal of Medical Entomology* **42**:554–558.
- Naeem, S. 1990. Resource heterogeneity and community structure: a case study in *Heliconia imbricata* phytotelmata. *Oecologia* **84**:29–38.
- Nepstad, D. C., A. Verssimo, A. Alencar, C. Nobre, E. Lima, P. Lefebvre, P. Schlesinger, C. Potter, P. Moutinho, E. Mendoza, M. Cochrane, and V. Brooks. 1999. Large-scale impoverishment of Amazonian forests by logging and fire. *Nature* **398**:505–508.
- Overgaard, H. J., B. Ekbom, W. Suwonkerd, and M. Takagi. 2003. Effect of landscape structure on anopheline mosquito density and diversity in northern Thailand: implications for malaria transmission and control. *Landscape Ecology* **18**:605–619.
- Pecor, J. E., J. Jones, M. Turell, R. Fernandez, F. Carbajal, M. O'Guinn, M. Sardelis, D. Watts, M. Zyzak, C. Calampa, and T. Klein. 2000. Annotated checklist of the mosquito species encountered during arboviral studies in Iquitos, Peru. *Journal of the American Mosquito Control Association* **16**:210–218.
- Peña-Claros, M. 2003. Changes in forest structure and species composition during secondary forest succession in the Bolivian Amazon. *Biotropica* **35**:450–461.
- Perry, D. R. 1978. A method of access into the crowns of emergent and canopy trees. *Biotropica* **10**:155–157.
- Perz, S. G. 2002. The changing social contexts of deforestation in the Brazilian Amazon. *Social Science Quarterly* **83**:35–52.
- Pope, K., P. Masuoka, E. Rejmankova, J. Grieco, S. Johnson, and D. Roberts. 2005. Mosquito habitats, land use, and malaria risk in Belize from satellite imagery. *Ecological Applications* **15**:1223–1232.
- Rice, W. R. 1989. Analyzing tables of statistical tests. *Evolution* **43**:223–225.
- SAS Institute. 2002. SAS/STAT user's guide. Version 9. SAS Institute, Cary, North Carolina, USA.
- Scheiner, S. M. 1993. Multiple response variables and multi-species interactions. Pages 94–112 in S. M. Scheiner and J.

- Gurevitch, editors. Design and analysis of ecological experiments. Chapman and Hall, New York, New York, USA.
- Sokal, R. R., and F. J. Rohlf. 1995. Biometry. Third edition. W. H. Freeman, New York, New York, USA.
- Suwonkerd, W., H. J. Overgaard, Y. Tsuda, S. Prajakwong, and M. Takagi. 2002. Malaria vector densities in transmission and non-transmission areas during 23 years and land use in Chiang Mai province, Northern Thailand. *Basic and Applied Ecology* **3**:197–207.
- Taylor, D. 1997. Seeing the forests for more than the trees. *Environmental Health Perspectives* **105**:1186–1191.
- Tesh, R. B. 1994. The emerging epidemiology of Venezuelan Fever and Oropouche Fever in tropical South America. Pages 129–137 in M. E. Wilson, R. Levins, and A. Spielman, editors. *Disease in evolution: global changes and emergence of infectious diseases*. Annals of the New York Academy of Science. Volume 740. New York Academy of Science, New York, New York, USA.
- Theiler, M., and W. G. Downs. 1973. The arthropod-borne viruses of vertebrates. Yale University Press, New Haven, Connecticut, USA.
- Turell, M. J., et al. 2005. Isolation of viruses from mosquitoes (Diptera: Culicidae) collected in the Amazon basin region of Peru. *Journal of Medical Entomology* **42**:891–898.
- Varga, L. 1928. Ein interessanter biotop der biocönose von wasserorganismen. *Biologisches Zentralblatt* **48**:143–162.
- Vásquez M., R. 1997. Flórula de las reservas biológicas de Iquitos, Perú. Monographs in systematic botany. Volume 63. Missouri Botanical Garden, St. Louis, Missouri, USA.
- Walsh, J. F., D. H. Molyneux, and M. H. Birley. 1993. Deforestation: effects on vector-borne disease. *Parasitology* **106**(Supplement):S55–S75.
- Watts, D. M., et al. 1997a. Venezuelan equine encephalitis and Oropouche virus infections among Peruvian army troops in the Amazon region of Peru. *American Journal of Tropical Medicine and Hygiene* **56**:661–667.
- Watts, D. M., I. Phillips, J. D. Callahan, W. Griebenow, K. C. Hyams, and C. G. Hayes. 1997b. Oropouche virus transmission in the Amazon River Basin of Peru. *American Journal of Tropical Medicine and Hygiene* **56**:148–152.
- Whitmore, T. C. 1998. An introduction to tropical rain forests. Second edition. Oxford University Press, Oxford, UK.
- Yanoviak, S. P. 1999a. Effects of leaf litter species on macroinvertebrate community properties and mosquito yield in Neotropical tree hole microcosms. *Oecologia* **120**:147–155.
- Yanoviak, S. P. 1999b. Distribution and abundance of *Microvelia cavicola* Polhemus (Heteroptera: Veliidae) on Barro Colorado Island, Panama. *Journal of the New York Entomological Society* **107**:38–45.
- Yanoviak, S. P. 1999c. Community structure in water-filled tree holes of Panama: effects of hole height and size. *Selbyana* **20**:106–115.
- Yanoviak, S. P. 2001a. The macrofauna of water-filled tree holes on Barro Colorado Island, Panama. *Biotropica* **33**:110–120.
- Yanoviak, S. P. 2001b. Predation, resource availability, and community structure in Neotropical water-filled tree holes. *Oecologia* **126**:125–133.
- Yanoviak, S. P. 2001c. Container color and location affect macroinvertebrate community structure in artificial treeholes in Panama. *Florida Entomologist* **84**:265–271.
- Yanoviak, S. P., and O. M. Fincke. 2005. Sampling methods for water-filled tree holes and their analogs. Pages 168–185 in S. Leather, editor. *Insect sampling in forest ecosystems*. Blackwell Science, London, UK.

#### APPENDIX

A list of macroinvertebrate taxa collected in the project (*Ecological Archives* A016-062-A1).