

Land Use Affects Macroinvertebrate Community Composition in Phytotelmata in the Peruvian Amazon

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ABSTRACT Patches of forest in the western Amazon often are converted to small-scale subsistence plantations (chacras), which become early successional forest (purma) when abandoned. Differences in abiotic conditions and phytotelm characteristics among chacras, purmas, and adjacent forest likely influence the distribution of phytotelm colonists. We sampled the contents of natural water-filled tree holes in the three habitat types and quantified differences in the abundance, species richness and composition of their macroinvertebrate communities. We additionally placed experimental tree-hole analogs (water-filled bamboo [*Guadua* sp.] internodes) in each of the habitat types and sampled their macroinvertebrate communities over 110 d. The species composition of macroinvertebrates in both tree holes and bamboo sections differed among habitats. Larvae of damselflies and crane flies, both important predators of mosquitoes, were replaced by larvae of the predatory mosquito *Toxorhynchites* spp. in chacras. Several mosquito species were relatively more abundant in chacra habitat. Macroinvertebrate abundance and species richness were correlated with water volume in tree holes and varied over time in bamboo sections. Species richness in bamboo did not differ among the three focal habitat types, but forest tree holes contained more species than tree holes in chacras. Differences in species composition between the two types of phytotelmata largely were attributed to the short duration of the bamboo experiment.

RESUMEN Los bosques primarios de la Amazonía peruana están siendo deforestados para la agricultura de pequeña escala (chacras). Las chacras forman bosques secundarios (purmas) después de ser abandonados. Las características del agua almacenada en plantas (fitotelmata) y las condiciones abióticas son diferentes entre chacras, purmas y bosques primarios. Se colocaron segmentos de bambú con agua en los tres hábitats y se cuantificaron la abundancia, riqueza y composición de especies de macroinvertebrados durante 110 días. La abundancia y riqueza de macroinvertebrados, y la conductividad y el pH del agua de los bambúes variaron durante el estudio, pero no hubo diferencias de estos factores entre hábitats. También, se estudiaron la fauna de huecos en árboles que contienen agua en los mismos hábitats. Encontraron correlaciones entre el volumen del hueco y la abundancia y riqueza de macroinvertebrados, pero no entre estas variables y las características del agua (pH y conductividad). La composición de especies en los bambúes y los huecos no fue igual entre hábitats. Las larvas de libélulas y moscas (Tipulidae), que son los depredadores principales de los mosquitos en este sistema, fueron reemplazados por otro depredador, el mosquito *Toxorhynchites* spp., en las chacras. Algunas especies de mosquitos fueron proporcionalmente más abundantes en las chacras. Ligeras diferencias en la composición de especies entre los dos tipos de fitotelmata pudieron resultar del poco tiempo que duró el experimento con el bambú.

KEY WORDS abundance, bamboo, deforestation, diversity, tree hole

Some of the most dramatic environmental consequences of deforestation in the Amazon include de-

struction of critical habitats and loss of biodiversity (Dale et al. 1994, Fearnside 1999). Effects of deforestation on human populations are often less immediately apparent and are more likely to be indirect (e.g., via climate change, Githeko et al. 2000). One such effect is increased availability of suitable habitat for arthropod vectors of human pathogens, such as mosquitoes, potentially enhancing the spread of infectious diseases (Alfonzo et al. 2005, Pope et al. 2005, Yanoviak et al. 2006; but see Overgaard et al. 2003). Deforestation in the Amazon is continuing at a phenomenal rate

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(Nepstad et al. 1999; Laurance et al. 2001, 2004); thus, understanding its effects on distributions of pathogen vectors and their predators and competitors is increasingly important.

Forest clearing in the western Amazon is generally associated with development along river margins and new roads (Fearnside 1987, Mäki et al. 2001). Both provide transportation and access to land for settlers, most of whom subsist via small-scale agriculture. In the western Amazon, typical subsistence farming involves deforesting, burning, and subsequently cultivating small patches of land (≈ 1 ha). The resulting plantation, or "chacra" (Mäki et al. 2001), is maintained in cultivation for several years until soil nutrients are depleted. The largest trees are sometimes cut for lumber or converted into charcoal a few months after deforestation, but many are left to rot where they fall. After a chacra is abandoned, colonizing pioneer plant species (e.g., *Cecropia* spp.) dominate the site, resulting in early successional forest locally called "purma" (Mäki et al. 2001). Purma habitat differs dramatically from both chacras and surrounding mature forests in terms of floristic composition and physical structure (Peña-Claros 2003).

Phytotelmata (plant-held waters; Varga 1928, Maguire 1971) exist in all of the habitats described above (Yanoviak et al. 2006). Water-filled tree holes (cavities in the woody portions of trees that collect rain water; Kitching 1971) are a specific type of phytotelmata that is common in many lowland tropical forests (Kitching 2000). Although one might expect tree holes to be rare in deforested areas such as chacras, the fallen trees left to rot in these habitats often collect rainwater in their trunks, thus producing many tree holes >5 liters in volume (Yanoviak et al. 2006). Neotropical tree holes harbor diverse macroinvertebrate faunas (Yanoviak 2001c). The properties of the communities that develop in a given tropical tree hole (abundance, species richness, and species composition) are influenced by factors such as the distribution of predators, the quantity and quality of nutrient inputs, and the local environmental conditions (Yanoviak 1999b,c 2001a,b). Many of these factors are likely to differ among chacra, purma, and mature forest habitats.

Understanding how macroinvertebrate communities in phytotelmata change along typical deforestation gradients in the western Amazon is important because tree holes and other phytotelmata are the principal larval microhabitats for many mosquito species (Fish 1983, Kitching 2000, Yanoviak 2001c), including several pathogen vectors. For example, tree hole-inhabiting *Haemagogus* are the most common enzootic vectors of yellow fever virus in the Americas (Galindo et al. 1955, Arnell 1973). Also, the Sabethini (e.g., *Limatus*, *Sabethes*, and *Wyeomyia*) are prominent mosquito inhabitants of phytotelmata and are potential vectors of encephalitis viruses (Jonkers et al. 1968, Theiler and Downs 1973, Karabatsos 1985, Turell et al. 2005). Although this study focused on tree holes, other phytotelmata (e.g., bromeliad axils and *Heliconia* spp. flower bracts) often are present in the three

habitats and contribute to the production of mosquitoes and other pathogen vectors (Yanoviak et al. 2006).

Tree holes are tractable systems for ecological studies in part because of their small size, and because they can be simulated with analogous containers, such as water-filled plastic cups and bamboo (*Guadua* sp.) internodes (Yanoviak and Fincke 2005). Such analogous habitats generally are colonized by the same fauna as natural tree holes (Kitching 2000; compare Louton et al. 1996 and Yanoviak 2001c). Based on our preliminary observations, this is true of the fauna in the common bamboo growing in the region included in this study. We took advantage of these similarities to investigate how typical deforestation practices in lowland forests of the western Amazon affect the structure of macroinvertebrate communities in experimental bamboo phytotelmata and their natural counterparts, water-filled tree holes.

The principal goal of this study was to determine whether macroinvertebrate communities developing in tree hole phytotelmata and water-filled bamboo internodes within chacra and purma habitats differ from those in intact forest. Based on previous observations in the region (Yanoviak et al. 2006) and similar studies (Alfonzo et al. 2005), we predicted that bamboo sections and natural tree holes located in chacra and purma habitats would contain fewer species than those in forest. We further expected that top predator distributions would differ among habitats, with *Toxorhynchites* spp. mosquitoes replacing damselflies (Odonata: Pseudostigmatidae) in chacra phytotelmata. Although *Toxorhynchites* spp. may preferentially oviposit in shaded forest habitats (Steffan and Evenhuis 1981), adult females frequently investigate shaded portions of fallen trees in deforested sites (S.P.Y., personal observation). In contrast, pseudostigmatids generally avoid large clearings (Fincke 2006).

Materials and Methods

Most of the fieldwork for this project was conducted along the Iquitos-Nauta highway in Loreto Province, northeastern Peru (3.75° S, 73.25° W). Additional field sites (Mishana and Explornapo; see below) are located within 100 km of Iquitos. Data were collected between January 2002 and May 2004. The region is classified as humid tropical lowland forest (Holdridge et al. 1974) and receives $\approx 3,000$ mm of moderately seasonal rainfall annually (Whitmore 1998, Madigosky and Vatnick 2000). Cumulative monthly rainfall exceeded 100 mm for all months of the study (S. Madigosky and I. Vatnick, unpublished data). Additional details about the region are provided by Vásquez Martínez (1997), Madigosky and Vatnick (2000), and Mäki et al. (2001).

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. Large patches (1–3 ha) of chacra and purma adjacent to mature forest were selected for sampling at each site. Each patch was surveyed and a sampling grid established for concurrent mammal and mosquito studies

(for details, see Yanoviak et al. 2006). All focal chacras had been cleared and cultivated at least a year before the start of the study, and all forest sites were on upland clay soils not subject to seasonal inundation.

Macroinvertebrates were sampled and abiotic characteristics were measured in water-filled tree holes and bamboo internodes at the study sites as described in more detail below. All collected mosquito larvae were reared to adulthood and identified to genus or species by using the keys cited in Pecor et al. (2000) and Jones et al. (2004). Identifications were confirmed by comparison with reference collections in Iquitos and at the Walter Reed Biosystematics Unit (WRBU, Suitland, MD). Nonmosquito taxa were identified to family or genus when possible and assigned to morphospecies. Voucher specimens were deposited at WRBU and the Museo de Historia Natural Javier Prado in Peru (Diptera), the University of Colorado Museum (Heteroptera), and the Illinois Natural History Survey (Annelida).

Overall similarity in macroinvertebrate taxonomic composition was compared between the bamboo internodes and tree holes with the classic incidence-based Sørensen index applied to the cumulative list of taxa, and within and between the two phytotelm types by using abundance-based Sørensen indices (Chao et al. 2005). The latter were calculated based on the total collection pooled by phytotelm type (tree hole or bamboo) within each habitat type (chacra, purma, or forest). Differences in mean abundance-based Sørensen similarity within and between the two phytotelm types were assessed with analysis of variance (ANOVA).

For all statistical tests, normality was determined with Kolmogorov–Smirnov tests and by examination of normal probability plots. Non-normal data were log transformed, and proportional data were arcsine square-root transformed before analysis (Sokal and Rohlf 1995). Bonferroni-adjusted α values were used for all multiple comparisons.

Bamboo Internodes. Several live stems of locally common bamboo (*Guadua* sp.) were harvested from a private residence in Iquitos and cut into sections just below each node to produce a series of open-top natural containers (Fig. 1). These containers were allowed to dry outdoors under cover for 2 mo before use. Drain holes were drilled ≈ 2 cm below the top margin to prevent overflow and washout, and the volume and inside diameter of each section was measured. Seven randomly selected bamboo sections were placed in each habitat at each replicate site during the first week of January 2003 ($n = 63$; three replicate sites by three habitats per site by seven bamboo sections per habitat). Each bamboo section was tied with polypropylene rope to a small tree 10–20 cm in diameter and 1.0–1.5 m above the ground (Fig. 1). Field observations during rain events showed that the rope facilitated conduction of stem flow to the bamboo interior (Yanoviak and Fincke 2005). Bamboo sections were numbered and located haphazardly within sites (partly depending on the distribution of small trees) at points separated by ≥ 15 m.



Fig. 1. Typical experimental bamboo section used in the project. The section shown is ≈ 30 cm in length and has an inside diameter of ≈ 6 cm.

One bamboo section from each site was selected using a random number table and destructively sampled 10 d after the experiment was established and every 14–20 d thereafter. Dissolved oxygen (DO) was measured in the field with a YSI meter (model 95, YSI Inc., Yellow Springs, OH) 4 cm below the water surface before disturbing the bamboo. The top half of the bamboo contents was subsequently decanted into a plastic bag, and the remaining contents were agitated and poured into a separate bag. The bamboo section was rinsed with water from the second bag at least twice and then placed into a larger plastic bag. All collected materials were then transported to the laboratory in an insulated box containing ice packs. Conductivity and pH were measured with a Hanna HI-991300 (Leighton Buzzard, United Kingdom) in the first sample bag in the laboratory, and the bamboo section was rinsed several times with tap water and inspected to ensure that no macroinvertebrates were missed.

Average bamboo size and relative abundances of common macroinvertebrate taxa were compared among sites and habitats within sites with nested ANOVAs (SAS Institute 2002). Relative abundances used in this analysis were calculated from data pooled across time. Macroinvertebrate community parameters (abundance and species richness) and water characteristics (DO, pH, and conductivity) in bamboo

Table 1. Mixed model repeated measures ANOVA output for effects of habitat (chacra, purma, and forest) and time on arthropod morphospecies richness and abundance, and on water characteristics in experimental bamboo sections

	Effect	df	F	P	Covariance parameters	
Abundance	Habitat	2, 40.8	1.76	0.186	Site	-0.0561
	Time	5, 21.9	3.28	0.023	Residual	1.0158
	Habitat × time	10, 35.6	0.79	0.639		
Richness	Habitat	2, 40.1	0.75	0.478	Site	0.0022
	Time	5, 19.9	4.25	0.009	Residual	0.1592
	Habitat × time	10, 35.4	0.37	0.954		
DO	Habitat	2, 28.1	0.21	0.812	Site	-0.0248
	Time	5, 19.2	1.18	0.354	Residual	0.2955
	Habitat × time	9, 25.1	1.15	0.366		
pH	Habitat	2, 34.6	1.74	0.190	Site	0.0389
	Time	5, 22.1	8.30	<0.001	Residual	0.1992
	Habitat × time	10, 31.6	1.19	0.331		
Conductivity	Habitat	2, 33.8	1.67	0.203	Site	-0.3199
	Time	5, 21.6	6.52	<0.001	Residual	0.8421
	Habitat × time	10, 28.2	0.64	0.764		

Decimal degrees of freedom (df) resulted from the Kenward–Roger method of df calculation.

sections were compared among habitat types over time with repeated measures ANOVAs by using mixed model procedures (Littell et al. 1996, Saavedra and Douglass 2002; SAS Institute 2002). Repeated measures analyses used autoregressive covariance structure with replicate sites as the error subject, and the Kenward–Roger method for estimation of degrees of freedom (SAS Institute 2002).

Natural Tree Holes. We surveyed natural water-filled tree holes in the chacra, purma, and mature forest at the three replicate sites described above. Holes in these sites were sampled several months to a year before establishment of the bamboo study. We additionally sampled tree holes at several other sites along the Iquitos-Nauta highway, near the town of Mishana on the Rio Nanay (3.88° S, 73.49° W), and near the Explornapo Camp on the Rio Sucusari (3.26° S, 73.92° W; Vásquez Martínez 1997).

The contents of each tree hole were removed with a large pipet (i.e., a turkey baster; Yanoviak and Fincke 2005) and transferred to a plastic pan or bag. The entire sample was transported to the laboratory for subsequent identification and rearing of the collected fauna. Characteristics of the water (DO, pH, and conductivity) and overall size (volume and approximate opening area) were measured for a subset of the tree holes.

Water-filled tree holes were not found in all habitat types at all replicate sites; thus, we pooled the data within habitats across sites for analysis to produce a more general comparison among chacra, purma, and forest. Macroinvertebrate species richness and abundance, and abiotic characteristics of tree holes were compared among the three habitats with one-way ANOVAs and post hoc Tukey tests. All of the holes were sampled only once, and sampling was distributed evenly among the three focal habitats over time.

Results

Volume was highly positively correlated with opening diameter in bamboo sections (Pearson $r = 0.91$,

$P < 0.0001$, $n = 63$) and with water surface area in natural tree holes ($r = 0.71$, $P < 0.0001$, $n = 48$), so subsequent analyses addressed phytotelm size in volume only.

Bamboo sections were reasonably good experimental analogs for tree holes; there was a moderate degree of taxonomic overlap between the two container types (incidence-based Sørensen index = 0.76). However, average (± 1 SD) abundance-based Sørensen values were significantly higher within tree holes (0.66 ± 0.095) and within bamboo (0.81 ± 0.061) than between the phytotelm types (0.42 ± 0.131 ; $F_{2,12} = 14.7$; $P < 0.001$). When compared on a per-habitat basis, the faunistic composition of bamboo more closely resembled that of tree holes in chacras (abundance-based Sørensen index = 0.59 ± 0.053) than tree holes in purma (0.29 ± 0.083) or forest (0.40 ± 0.078 ; $F_{2,6} = 13.4$; $P = 0.006$). Overall, the largest ecological differences between tree holes and bamboo pertained to the distributions of certain taxa as described below.

Bamboo Internodes. In total, 2,559 macroinvertebrates were collected from the bamboo sections. Macroinvertebrate abundance and species richness did not differ among chacra, purma, and forest, but varied significantly over time (Table 1; Fig. 2). Post hoc univariate tests showed a significant difference in abundance between chacra and forest on day 60, when one of the chacra bamboo sections contained only a single *Toxorhynchites haemorrhoidalis* (F.) mosquito larva.

The species composition of macroinvertebrates collected from bamboo sections differed among the three habitat types. Larvae of pseudostigmatid damselflies and crane flies (Diptera: Tipulidae) were not found in bamboo sections located in chacras, where they were replaced by the other important top predator in this system, larvae of *Toxorhynchites* spp. mosquitoes. *Toxorhynchites* spp. larvae were nearly absent in bamboo located in purma and forest, but they reached abundances as high as 23 individuals in a single bamboo in chacra habitat (Table 2). Bamboo sections differed from natural tree holes in having much larger

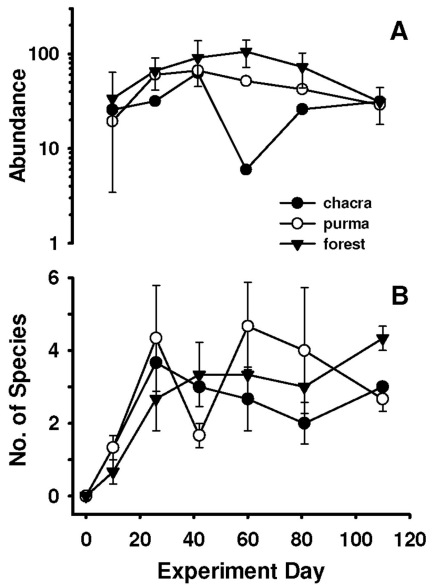


Fig. 2. Average \pm SE macroinvertebrate abundance (A) and species richness (B) in bamboo sections located in chakra, purma, and forest. $n = 3$ for each mean. Some error bars were omitted for clarity. The sharp decline in abundance in chakra on day 60 was caused by the predatory mosquito *T. haemorrhoidalis* (F.).

relative abundances of larvae of muscid flies and the mosquito *Trichoprosopon digitatum* (Rondani) (Table 2).

Despite being randomly assigned to the different habitats, bamboo sections located in chacras were significantly larger (498 ± 184.8 ml) than those in forest (364 ± 90.6 ml), whereas those in purma (400 ± 115.6 ml) did not differ from chakra or forest ($F_{2, 6} = 3.30$; $P = 0.008$). However, this minor size difference did not result in a detectable biological difference; there was no correlation between bamboo volume and macroinvertebrate abundance or species richness (Table 3). Other abiotic characteristics of the bamboo water did not differ among habitats (Table 1), and, except for a positive relationship between DO and macroinvertebrate species richness, abiotic and biotic factors were not correlated (Table 3). Conductivity and pH declined steadily over time in the bamboo sections (Fig. 3).

Natural Tree Holes. We sampled the contents of 131 natural tree holes, which contained a total of 3,708 macroinvertebrates. Most (72%) of the tree holes were found in chacras, 21% occurred in forests, and 6% in purmas. Macroinvertebrate abundance in tree holes was similar among habitats, but tree holes in mature forest contained more macroinvertebrate species than those in chacras (Table 4). There were no significant differences in abiotic characteristics of tree holes (vol-

Table 2. Abundance of selected macroinvertebrate taxa in bamboo and tree hole phytotelmata

Taxon	Bamboo		Tree hole	
	<i>n</i>	Abundance	<i>n</i>	Abundance
Annelida ^a	8	9.6 (5-78)	8	8.5 (1-200)
Odonata: Pseudostigmatidae				
<i>Microstigma rotundatum</i> Selys	2	0.1 (1-2)	15	0.8 (1-12)
Hemiptera: Veliidae	0	0 (0)	12	4.2 (1-65)
Coleoptera: Scirtidae	2	0.2 (1-5)	20	7.6 (1-41)
Diptera				
Ceratopogonidae				
Ceratopogoninae ^b	16	7.3 (1-27)	15	3.1 (1-20)
Forcipomyiinae	12	9.3 (1-50)	5	6.9 (5-218)
Culicidae				
<i>Culex conservator</i> Dyar & Knab	4	2.3 (1-47)	12	6.4 (1-78)
<i>Culex (Carrollia) spp.</i> ^c	20	15.2 (1-147)	31	19.7 (1-238)
<i>Haemagogus janthinomyia</i> Dyar	2	0.1 (1-2)	7	1.0 (2-10)
<i>Limatus spp.</i> ^d	0	0 (0)	10	4.1 (1-48)
<i>Orthopodomyia fascipes</i> (Coquillett)	10	11.4 (2-102)	4	7.3 (30-155)
<i>Sabethes spp.</i> ^e	5	0.7 (1-10)	4	0.2 (1-3)
<i>Toxorhynchites spp.</i> ^f	4	1.0 (1-23)	13	0.6 (1-4)
<i>Trichoprosopon digitatum</i> (Rondani)	13	15.6 (1-69)	2	0.8 (3-25)
<i>Wyeomyia spp.</i> ^g	2	0.7 (1-17)	11	3.5 (1-52)
Muscidae	22	21.6 (1-162)	1	<0.1 (1)
Psychodidae	13	3.6 (1-23)	16	3.0 (1-28)
Tipulidae: <i>Signatamera</i> spp.	5	0.2 (1-2)	6	0.6 (1-10)

Only taxa with occurrence frequency $\geq 0.5\%$ in the complete data set (bamboo and tree holes combined) are listed. *n*, number of bamboo sections (maximum of 63) or tree holes (maximum of 131) occupied by a taxon. Values are percent abundance within bamboo or tree hole phytotelmata. Values in parentheses indicate abundance ranges where a taxon was present.

^a *Dero* spp. plus one oligochaete morphospecies.

^b *Bezzia* spp. (80% overall) and *Culicoides* spp. (20% overall).

^c *Culex (Carrollia) bonnei* Dyar (0.6%), *Culex (Carrollia) infoliatum* Bonne-Wepster & Bonne (0.4%), and *Culex (Carrollia) urichii* (Coquillett) (99%).

^d *Limatus durhamii* Theobald (51%) and *Limatus flavisetosus* De Oliveira Castro (49%).

^e *Sabethes amazonicus* Gordon & Evans, *Sabethes cyaneus* (F.), *Sabethes melanocephala* Dyar & Knab, and one morphospecies.

^f *Toxorhynchites haemorrhoidalis* (F.) (90%) and *Toxorhynchites nr. theobaldi* (Dyar & Knab) (10%).

^g *Wyeomyia aphobema* Dyar (5%), *Wyeomyia flui* Bonne-Wepster & Bonne (91%), and three morphospecies (4%).

Table 3. Pearson correlations among biotic and abiotic characteristics in bamboo sections and natural tree holes

Bamboo	Abundance	Richness	Conductivity	DO	pH
Volume	-0.129 (63)	-0.070 (63)	0.111 (54)	-0.019 (46)	-0.035 (54)
pH	-0.042 (54)	-0.088 (54)	0.620** (54)	-0.226 (46)	
DO	0.195 (46)	0.439** (46)	-0.409** (46)		
Conductivity	-0.146 (54)	-0.201 (54)			
Richness	0.439** (63)				
Tree holes					
Volume	0.390** (129)	0.364** (129)	-0.037 (32)	-0.425 (20)	-0.265 (32)
pH	-0.181 (33)	-0.265 (33)	0.575** (33)	-0.179 (21)	
DO	-0.297 (21)	-0.436* (21)	-0.470* (21)		
Conductivity	0.119 (33)	0.099 (33)			
Richness	0.803** (131)				

Sample sizes are in parentheses. *, $P < 0.05$; **, $P < 0.005$.

ume, DO, pH, and conductivity) among the three habitat types (Table 4).

Relative abundances and distributions of top predator species in tree holes were similar to those in bamboo sections, especially in terms of their presence or absence in chacra habitat (Table 2; Fig. 4). Larvae of the mosquito *Haemagogus janthinomys* Dyar were collected from tree holes in all habitats and from bamboo in chacra habitat, but they were not found in bamboo in chacra habitat, but they were not found in bamboo in forest and purma (Fig. 4). Veliid hemipterans and *Limatus* spp. mosquitoes occurred in tree

holes, but they were absent from all bamboo collections (Table 2).

Macroinvertebrate abundance and species richness tended to increase with increasing volume of natural tree holes, and, as in the experimental bamboo sections, conductivity was significantly correlated with pH and DO in tree holes (Table 3). Species richness also was correlated with DO in tree holes, but the relationship was negative, unlike the positive correlation found in bamboo sections (Table 3).

Discussion

Historically, deforestation in the western Amazon took the form of a sustainable patchwork of small plantations separated in space and time (Whitmore 1998). More recently, road construction and increasing urbanization have facilitated and necessitated large-scale deforestation to support unsustainable semi-industrial agriculture (Whitmore 1998; Laurance et al. 2001, 2004). Our results suggest that the composition of macroinvertebrate communities in common natural container habitats is significantly altered by these landscape-level changes.

Although our prediction of reduced species richness in chacras relative to forests was not supported, our data suggest that overall biodiversity will be altered on a local scale as forest is converted to chacra. Specifically, at least two major tree hole-inhabiting taxa (pseudostigmatid damselflies and tipulid flies) will become rare. Both taxa include several species and are functionally important as significant predators of mosquitoes in phytotelmata (Lounibos et al. 1987, Fincke et al. 1997, Yanoviak 2001c). Apart from their ecological importance as predators in the larval stage, adult giant damselflies may be useful in local forest conservation efforts. They are attractive to collectors because they are elusive, visually appealing, and delicate, and the preserved specimens occasionally can be purchased in tourist markets (S.P.Y., personal observation).

Whereas pseudostigmatids and tipulids will likely become scarce in deforested areas, our results suggest that *Toxorhynchites* spp. mosquitoes will flourish in chacras. *Toxorhynchites* are voracious top predators (e.g., Lounibos 1979, Bradshaw and Holzapfel 1983),

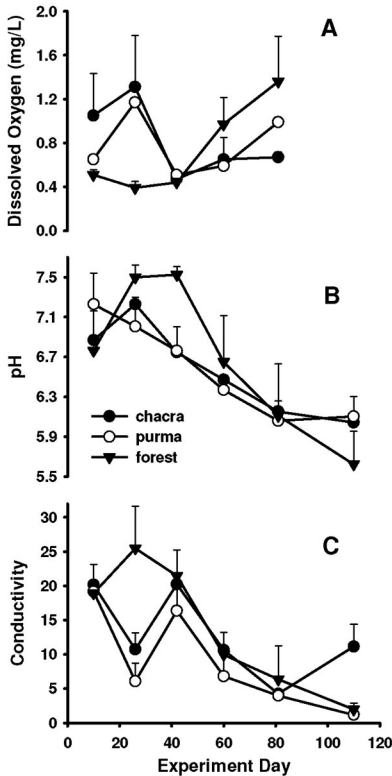


Fig. 3. Average \pm SE dissolved oxygen content (A), pH (B), and conductivity ($\mu\text{S} \times 100$) (C) of water in bamboo sections located in chacra, purma, and forest habitats. $n = 3$ for each mean. Some error bars were omitted for clarity.

Table 4. Means and ANOVA results for abiotic and biotic characteristics of natural tree holes in the three focal habitats

Characteristic	Chacra		Purma		Forest		df	SS III	F
	n	mean ± SE	n	mean ± SE	n	mean ± SE			
Vol (liters)	93	0.58 (0.149)a (0.002–10)	9	0.30 (0.065)a (0.020–0.600)	27	0.54 (0.300)a (0.005–8)	2, 126	5.989	0.76
pH	12	5.38 (0.277)a (3.86–6.85)	7	5.51 (0.526)a (3.73–7.32)	14	5.76 (0.278)a (3.85–7.37)	2, 30	0.997	0.42
DO (mg/liter)	8	1.61 (0.459)a (0.36–4.49)	5	0.60 (0.128)a (0.33–1.06)	8	1.99 (0.561)a (0.54–5.07)	2, 18	3.311	3.22
Conductivity (μ S)	12	328 (89.6)a (21–884)	7	398 (261.0)a (42–1955)	14	211 (51.8)a (29–640)	2, 30	0.264	0.20
Richness	95	1.5 (0.23)a (0–12)	9	3.3 (0.60)b (0–6)	27	2.7 (0.43)ab (0–10)	2, 128	24.963	5.01*
Abundance	95	30.8 (9.78)a (0–700)	9	34 (11.1)a (0–111)	27	17.6 (5.46)a (0–113)	2, 128	8.729	3.17

Ranges are in parentheses. SS III, type III sum of squares. Within rows, means followed by the same letter do not differ based on Tukey post hoc tests. *, P < 0.01.

and the magnitude of their local effects can be dramatic. For example, the significantly reduced macroinvertebrate abundance we observed in the chacra bamboo on day 60 was due to the presence of a single late instar *T. haemorrhoidalis*. Although *Toxorhynchites* prefer to oviposit in shaded forest microhabitats (Steffan and Evenhuis 1981), they are exposed to intraguild predation from odonates in forest tree holes (Fincke 1999); thus, colonization of phytotelmata in chacras and recently deforested sites may provide a refuge from interference competition. Community-level effects of shifting top predator identities are unknown, but other studies suggest that pseudostig-

matids are more selective than *Toxorhynchites* (S.P.Y., unpublished data).

The results of this and related studies (Yanoviak et al. 2006) indicate that conversion of forest to chacra increases the production of certain potential pathogen vectors. For some species, this may be a consequence of changed abiotic conditions. For example, repeated drying stimulates egg hatching in *H. janthinomys* (Galindo et al. 1955), a vector of yellow fever virus. In combination with the short duration of the experiment, this may explain the absence of *H. janthinomys* larvae in purma and forest bamboos, which were less exposed and experienced lower drying frequency and water fluctuations than bamboos in chacras (S.P.Y., personal observation). Similarly, our results suggest that some sabethine mosquitoes that are potential vectors of encephalitis and related viruses (e.g., *Limatus* spp. and *Wyeomyia* spp.; Jonkers et al. 1968, Theiler and Downs 1973, Turell et al. 2005) prefer to colonize container microhabitats in chacras.

We attribute differences in species composition between the phytotelm types (e.g., the absence of veliid hemipterans and *Limatus* spp. mosquitoes in bamboo) as well as differences in the relative abundances of muscoid flies, scirtid beetle larvae, and certain mosquitoes (e.g., *T. digitatum*) to differences in microhabitat preferences among species and to the younger age of the bamboo sections relative to natural tree holes. The moderate overlap in taxonomic composition between bamboo and tree holes observed in this study is similar to that found previously (Lounibos 1981) and indicates that bamboo internodes are good, but not perfect, analogs to tree holes.

Repeated observations of a subset of tree holes sampled in this study and that of Yanoviak (2001c) showed that they tend to attract a fairly consistent suite of colonists over periods of months and years. However, the maximum 110 d that the bamboo sections were available for colonization was just barely long enough for the development of consistent communities in terms of species composition and relative abundance. This is perhaps best demonstrated by the low frequency of pseudostigmatid damselflies and scirtid beetles in bamboo sections relative to tree

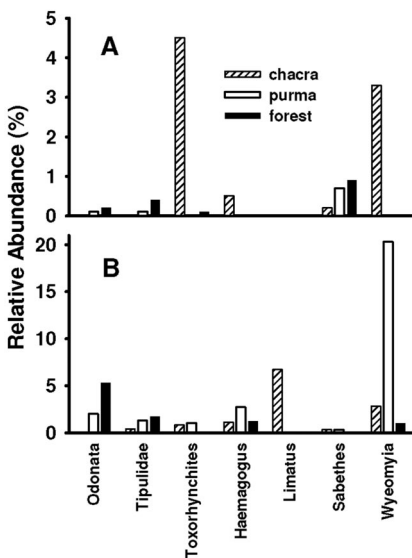


Fig. 4. Percent abundance of selected macroinvertebrate taxa (top predators and known pathogen vectors) where present in water-filled bamboo sections (A) and tree holes (B) located in chacra, purma, and forest habitats. Each bar in A represents pooled data from 18 bamboo sections in each habitat. Each bar in B represents data pooled from 95 tree holes in chacra, nine in purma, and 27 in forest. Percentages were calculated from total macroinvertebrate abundance in each phytotelm type within each habitat.

holes; these taxa often occur later in the early succession of tropical tree holes and their analogs (Yanoviak 2001c). The greater similarity between the fauna of chacra tree holes and the bamboo sections (in all habitats) suggests that the faunal assemblages in tree holes in highly exposed settings are maintained at a relatively early successional state due to frequent drying disturbance or extreme conditions that restrict colonization.

Larger tree holes sampled in this study tended to contain more macroinvertebrate species and individuals than smaller holes. This pattern also was observed in tree holes at other tropical sites (Yanoviak 1999a), but it may not be true for tree holes in all regions (Kitching 1971). The intentionally narrower range of volume variation and the relatively early successional status of the bamboo sections probably prevented a similar size–richness correlation. The lack of correlation between macroinvertebrate species richness and abundance with most other abiotic factors was consistent with the results of previous phytotelm studies (Yanoviak 1999a; but see Paradise and Dunson 1997a). The significant correlations between DO and macroinvertebrate species richness are probably spurious given their opposite slopes. Moreover, most container-inhabiting macroinvertebrates respire at the air/water interface, suggesting that DO content is not limiting their distributions. Finally, we attribute the changes in pH and conductivity in bamboo sections over time to leaching and conditioning of the bamboo material, although the resident fauna also may have influenced these parameters (Paradise and Dunson 1997b).

Artificial containers offer several advantages over natural tree holes for observational or manipulative experiments: they are portable, replicable, and have standardized ecological histories (Yanoviak and Fincke 2005). However, we found that one of the difficulties in using nonliving bamboo sections for long-term studies of phytotelm communities in the tropics is that they tend to degrade after 3–4 mo of exposure (especially those located in chacras). Bamboo sections not severely damaged by exposure were often destroyed by termites. Any bamboo modifications that avoid these problems without compromising their natural attractiveness to phytotelm colonists would greatly enhance the potential for long-term data collection in this system.

In sum, Neotropical deforestation is continuing at a rapid rate and at larger scales, which are unlikely to change in the near future (Nepstad et al. 1999; Laurance et al. 2001, 2004). Here, we show that the composition of macroinvertebrate communities in phytotelmata differs between forested and deforested habitats, with effects apparent among both potential disease vectors and the top predators that eat them. Additional studies are needed to determine how such shifts in the composition of the top predator guild directly and indirectly affect population-level characteristics of their prey. Given that container habitats are important breeding sites for pathogen vectors in the tropics, current trends in deforestation and land use may have broader implications for human health.

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