DIVERSITY, RESOURCE PARTITIONING, AND SPECIES TURNOVER IN NEOTROPICAL SAPROXYLIC BEETLES (COLEOPTERA: CERAMBYCIDAE, CURCULIONIDAE) ASSOCIATED WITH TREES IN THE BRAZIL NUT FAMILY (LECYTHIDACEAE)

by

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Abstract

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by

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Deforestation and global changes in temperature and moisture associated with rising levels of greenhouse gases are expected to have strong, direct effects on abundance of wood-boring beetles through loss of larval feeding substrates, and indirect effects through climate and microclimate change. This dissertation examines Neotropical saproxylic beetle (Coleoptera: Curculionidae) diversity, niche breadth, and resource partitioning, and predicts possible impacts of climate change. Data from beetle rearing experiments conducted in French Guiana and Peru were analyzed to assess species richness, abundance, host specificity, seasonality and stratification of wood-boring beetles associated with the Brazil nut family (Lecythidaceae). Niche stability was assessed over time (French Guiana 1995-96, 2007-08) and space (Peru 2003-05). In French Guiana, resource partitioning was analyzed among the most abundant subfamilies of Curculionidae (Conoderinae, Scolytinae, Platypodinae) and Cerambycidae (Cerambycinae, Lamiinae). Species richness was higher in Peru than French Guiana, with high beta-diversity between sites; largely due to the prevalence of rare species in Peru. In both localities, most

beetle species were disproportionately associated with the host *Eschweilera coriacea* (DC) S.A. Mori. In French Guiana, comparatively large cerambycids were more abundant during the dry season and seemed relatively drought tolerant. Small-bodied curculionids were most abundant during the rainy season, with weevils and platypodines best represented at ground stratum. In Peru, weevils were more abundant during the dry season. Cerambycinae, which are preferentially associated with the dry season canopy stratum, are expected to thrive should regional climates become warmer and drier. Lamiinae may respond by seasonally alternating stratum. Many Neotropical weevils and bark/ambrosia beetles seem strongly moisture-dependent, and populations are expected to be negatively impacted by increased drought. The Brazil nut family is threatened by both habitat fragmentation and climate change. The favored host species, *E. coriacea*, has a wide geographic distribution that extends into western Amazonia, which is not expected to experience severe precipitation changes, and could provide refuge for saproxylic beetles currently associated with Lecythidaceae. Saproxylic beetles, especially curculionids, may be less impacted by direct effects of host loss than indirect effects of climate change, especially northeast Amazonia which is expected to experience declining precipitation and longer dry seasons.

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CHAPTER 1

Introduction

To date, 1.7 million species of flora and fauna have been described worldwide. Global diversity estimates range from 5million to over 30 million species (Erwin, 1982; Novotny *et al*., 2002). Tropical rainforests contain the majority of global species diversity, yet they are poorly sampled – particularly for invertebrates (Hartshon, 2000). It is estimated that only about 20% of tropical insects having been described (Godfray, 1999). Unfortunately, estimating global species diversity is notoriously difficult. Erwin (1982) proposed that global species richness might be 30 million, using estimates of host specificity and stratification of beetles collected from the canopy of a single tropical tree species, *Luehea seemannii*. Later studies suggest that he overestimated not only the percent host specificity of beetles (at 20%), but also general tropical beetle diversity (at 40% of all species) and the proportion of beetles found in the canopy (Basset *et al.*,1996; Ødegaard *et al*., 2000; Novotny *et al.*, 2002). In a study of phytophagous beetles in Panama, Ødegaard *et al*. (2000) determined that the percent of species restricted to a single host species was only 6-12%, much lower than Erwin's estimate. Additionally, they estimated that beetles constituted only about 20% of tropical insect species, and calculated global species richness at 5-15 million species. Weiblen *et al.* (2006) examined the distribution of insect herbivores (caterpillars, beetles, and grasshoppers) on woody plants in a New Guinea rainforest, and found that community similarity was highest among congeneric plant hosts (50%) with familial overlap of 20-30%, showing that insects are often clade specialists. Novotny *et al*.'s (2002) study of herbivorous insects in New Guinea found that only about 33% of the insect species were shared between phylogenetically different hosts, but monophagy was rare because tropical genera are so species rich. Due to lower anticipated host specificity, they decreased estimated global species richness to 4-6 million species.

The global extinction rate for plant and animal species is currently estimated at 1% per century, which is 10,000 times higher than the normal rate seen in the fossil record. The global extinction rate is calculated using the current rate of habitat loss and estimated global species richness (Levinton, 2000). Habitat loss through deforestation is around 13 million hectares per year. While some deforestation has natural causes, such as fire and drought, most loss is from conversion of tropical forests into agricultural lands (Nepstad *et al*., 2008; FAO, 2010). Logging to clear agricultural land reduces large tracts of forest to small randomly arranged fragments. These fragments are often 50 ha or less in size, and interspersed among monocultures of sugar cane, coffee, etc. Fragments tend to be drier and receive more sunlight than the interior of larger forests, which may lead to reduced functional plant diversity and only a fraction of the species richness (Girão *et al.*, 2007). Fragmentation increases biotic homogenization by increasing the abundance of short-lived deciduous or semi-deciduous pioneer tree species (Lobo *et al*., 2011; Tabarelli *et al*., 2010). Fragmentation also affects insect diversity. In Malaysia, ant species richness and nest density were significantly higher in continuous forests than in fragments (Brühl *et al*., 2003). Grimbacher *et al*. (2006) found that drier habitat associated beetle species in Northeast Queensland, Australia, were more abundant in forest fragments whereas wetter habitat associated species were more abundant in forest interiors.

The global climate is expected to change considerably in patterns of moisture levels and drought over the next century (Stork, 2010). Global circulation models predict a decline in average rainfall of >20% in the Neotropics by the end of the century (Nepstad *et al*., 2008). Neotropical rainforests will be dramatically affected by increased dry season duration and decreased rainy season moisture (Miles *et al*., 2004). Increases in sea surface temperatures associated with increases in atmospheric greenhouse gases have already caused increases in drought occurrence and severity in the Amazon. Increased incidences of drought, in combination, with logging are expected to lead to the loss of 55% of Amazonian closed-canopy forest by 2030 (Nepstad *et al*., 2008) and, as a consequence, the loss of biodiversity inhabiting Neotropical rainforests.

Changes in rainfall and temperature are not expected to be evenly spatially distributed across the Neotropics. With just a 1% compounded annual increase in atmospheric CO_2, South American weather patterns are forecasted to shift toward longer duration of the dry season duration and less moisture in the rainy season. However, these changes will not be evenly distributed across the continent. While NE Amazonia is expected to experience a significant moisture deficit, with a forecasted decrease of 1200-1750 mm in precipitation per year, SW Amazonia is expected to experience only a mild to moderate decrease in yearly precipitation of 150-450 mm per year (Miles *et al*., 2004). The effects of decreased moisture availability may be mitigated in part by large tracts of forest, because larger tracts are better able to recycle moisture through evapotranspiration and precipitation than smaller tracts (Borchert, 1998).

Host specific insect species will probably be adversely affected by alteration of global climate because changes in moisture availability may result in changes in host distribution or size and structure of host assemblages (Lewinshon *et al*., 2005). Insect herbivores must be able to track host plants across distances and then disperse to their hosts. Plants with limited geographical distributions are not likely to support many specialized insect herbivores, whereas plants with larger distributions may support more specialized insect species (Novotny *et al*., 2007). Similarity in the compositions of tropical tree and insect communities declines with distance due to limited geographical distributions (Condit *et al*., 2002; Novotny *et al*., 2007).

The number of species present, their ranges, and ecology are used to estimate rates of species extinction and decline as well as to determine conservation priorities. Additionally, insect species richness is used to assess the diversity in a single location (α-diversity) or between multiple locations (β-diversity), and host and habitat specificity are considered fundamental factors determining variation in diversity, whether due to abiotic or biotic factors (Ødegaard, 2006).

Insect diversity is influenced by both biotic factors (resource availability, interactions with other organisms) and abiotic factors (light, temperature, moisture, barriers to dispersal). These factors all contribute to habitat specificity, insect seasonality and vertical stratification. For instance, ant species in Panama are more abundant and active during the rainy season, when there is less risk of desiccation (Kaspari & Weiser, 2000). In a study focusing on seasonal changes in beetle species composition in Uganda, Wagner (2003) found that overall abundance was lower in the dry season. Although Curculionidae (weevils, the focus of these studies) were more abundant during the dry season, most species were small and aggregated in relatively humid sites in the canopy. Charles and Basset (2005) found a greater abundance of leaf-feeding chrysomelid beetles in the canopy than the understory, with stratification much more pronounced in wet than dry forest. In Panama, saproxylic, moribund wood associated, beetles showed only low levels of similarity between the canopy and understory strata (Ødegaard, 2004). However, Stork and Grimbacher (2006) found 72% shared beetle species richness between strata in North Queensland, Australia, with cerambycids, curculionids, and platypodines more abundant in the canopy and scolytines more abundant on the ground. In French Guiana, cerambycid beetles that appeared to be stratum generalists were actually shifting from ground stratum during the dry season to canopy stratum during the rainy season (Lee, 2010).

Forest moisture regime also influences insect diversity in tropical forests. Charles and

Basset (2005) found that chrysomelid beetle diversity was higher in a dry forest habitat than in a wet forest. However, Ødegaard (2006) found that Panamanian wet forest was 37% more species rich than dry forest, primarily due to the increased presence of saproxylic and flower visiting beetle species. Additionally, saproxylic beetle species were more species rich and host specific in wet forest.

Saproxylic beetles (Curculionidae and Cerambycidae, but in particular curculionids) are the focus of these studies. Most major insect orders include saproxylic species. They include the insects that feed on dead wood or the fungi associated with it, as well as their parasites, parasitoids, and predators (Grove, 2002; Ødegaard, 2006). Saproxylic beetles are an especially important part of forest ecosystems because their larvae develop within or under the bark of moribund or dead wood, forming galleries and tunnels. They facilitate wood decomposition by initiation of wood fragmentation and deposition of microbe containing frass (Schowalter *et al*., 1992; Calderon & Berkov, 2012). Cerambycids, weevils, and bark and ambrosia beetles are the generally the first beetles to colonize dead or dying wood (Madoffe & Bakke, 1995; Jacobs *et al*., 2007). In Panama, Ødegaard (2006) found that saproxylic beetle species tended to be more host specific than leaf chewers. This is not surprising since many saproxylic beetles are more intimately associated with their hosts and the early colonists, in particular, may need resistance to any residual chemical defenses remaining in moribund or dead wood (Novotny and Basset, 2005; Mattson *et al.*, 1988).

Weevils (superfamily Curculionoidea) consist of 62,000 described species in over 5600 genera. Based on the high proportions of undescribed species that have been collected in large ecological surveys, the estimate for overall global diversity is 220,000. The largest family of the Curculionoidea is the Curculionidae, with 51,000 described species in 4,600 genera (Oberprieler *et al*., 2007). In spite, or perhaps because, of this diversity, the phylogeny of weevils is unsettled and contested. While Curculionidae is monophyletic (Marvaldi *et al*, 2002; McKenna *et al*., 2009), the relationships between subfamilies within the curculionids is as yet undetermined. Curculionids are grouped by two major morphological characteristics. They have geniculate (elbowed) antennae and an elongated snout, or rostrum, a character that has been lost in some species (Anderson, 1995; Oberprieler *et al*., 2007). The evolution of the rostrum was a key factor in the diversification of weevils. The mouthparts are located at the end of the rostrum, and its primary function is for feeding. However, the rostrum has a secondary function; female weevils use it to prepare oviposition pits. By laying their eggs inside the pit they larvae are protected against parasites, predators and adverse weather conditions (Anderson, 1995). The larvae are mostly endophytic and found in plants and seeds with some ectophytic on the roots or leaves of the plant (Anderson, 1995; Oberprieler *et al*., 2007). The incredible diversity of Curculionoidea can also be attributed, in part, to their wide array of feeding habits. Various species feed on nearly every part of angiosperm and gymnosperm plants, as well as the fungi and other insects that inhabit those plants. They occur worldwide in a wide variety of habitats from the arctic and subarctic to deserts and rainforest (Oberprieler *et al*., 2007).

Many curculionid subfamilies include saproxylic species that are associated with moribund wood; their larvae develop endophytically. These subfamilies include, but are not limited to, Conoderinae, Cossoninae, Cryptorhynchinae, Molytinae, Platypodinae, and Scolytinae; little is known about the host preferences of most species. Conoderinae weevils consist of 200 genera with 1500 species and are very abundant in the tropics. Their larvae develop in dead or fallen wood, leaf petioles, and seeds (Lyal, 1986; Kojima and Lyal, 2002). Conoderinae is often grouped with Baridinae (Oberprieler *et al*., 2007), but support for the relationship is not strong (Marvaldi *et al*., 2002). Not much is known about the feeding habits of conoderines, although some have been found to be cleptoparasitic, feeding on the ambrosia fungi in platypodine larval galleries (May, 1997; Jordal *et al*., 2011).

Cossoninae consists of 1700 species whose larvae develop in dead or dying wood. The adult females lay their eggs into the stems and trunks of trees that are in an advanced stage of decay (Oberprieler *et al*., 2007). Cryptorhynchinae have a worldwide distribution and consist of 6000 species in 500 genera. These weevils are small, inconspicuously colored and their larvae develop in stressed, dying roots and branches of plants (Astrin and Stubin, 2008). Molytinae is a polyphyletic subfamily into which the majority of wood-boring taxa have been placed; however not all species within the Molytinae are wood-borers. Cryptorhynchinae has been placed within this subfamily in the past (Oberprieler *et al*., 2007); however the relationship between these subfamilies remains unclear (McKenna *et al*., 2009). Molytinae (including Cryptorhynchinae) includes 10,000 species and the larvae of wood-associated species develop in dead or dying wood, as well as the stems, trunks, and roots of living plants (Oberprieler *et al*., 2007).

Platypodinae and Scolytinae contain weevil species that no longer have a rostrum. The loss of the rostrum is a derived characteristic shared by these two subfamilies (Jordal *et al*., 2011); however their phylogenic relationship remains unclear (Marvaldi, *et al*., 2002; McKenna *et al*., 2009). Platypodinae consists of 1500 species worldwide (Oberprieler *et al*., 2007). They are specialized wood borers called ambrosia beetles; their larvae develop on ambrosia fungi that they inoculate into the wood, rather than through ingestion of the wood itself (Hulcr, *et al*., 2007; Oberprieler *et al*., 2007). Scolytinae is made up of around 6000 species (Oberprieler *et al*., 2007). The subfamily includes both ambrosia beetles, which feed on ambrosia fungi, and bark beetles, which feed directly on the host plant tissue (Hulcr, *et al*., 2007). In a study of ambrosia and bark beetles in Papua New Guinea, Hulcr *et al*. (2007) found that 95% of ambrosia beetles sampled were generalists that fed readily on congeneric or heterogeneric host species. The diet of bark beetles, however, was restricted to species in a single genus or family.

Cerambycids constitute approximately 35,000 described species, with over 1400 species known from French Guiana (Berkov & Tavakilian, 1999; Tavakilian *et al*., 1997). Adults deposit eggs into naturally occurring crevasses or grooves cut into tree bark. Upon hatching, larvae bore into wood and roots, where they tunnel and form galleries as they feed directly on host tissue (Turnbow & Thomas, 2002). In French Guiana, Tavakilian *et al*. (1997) found that host specialists outnumbered generalists three to one; however, specialists were defined as feeding primarily on species in a single family or genus. Few were monophagous on a single host species.

Host specificity can be difficult to determine with some methods of specimen collection. Many collection methods, *e.g.*, fogging, flight intercept traps, etc., may result in the collection of tourist species or specimens that yield no host data (Basset, 1999; Godfray, 1999). This issue can be addressed by implementing experiments that include feeding observations with herbivores or, for saproxylic groups, rearing data (Berkov & Tavakilian, 1999; Tavakilian *et al*., 1997).

The studies performed for this thesis concentrated on beetles associated with tree species from the Brazil nut family (Lecythidaceae) (Table 1; Figures 1.1 - 1.3), which is one of the most abundant Neotropical plant families. Lecythidaceae is a pantropical plant family with species in Madagascar, Africa, Asia, Australia, and South America. In the Neotropics, species

Table 1.1: Species of Brazil nut tree (Lecythidaceae) sampled in two studies in French Guiana (1995, 2007) and one study in Peru (2003)

Species	Code[1]	*N*	Functional Group	Forest type	Phylogeny	Location
Allantoma decandra (Ducke) S.A.Mori, Y.-Y. Huang & Prance	AD	4[2]	Canopy	Non-flooded	Polytomy	FG 95, Peru 03
Bertholletia excelsa Bonpl.	BE	4[2]	Emergent	Non-flooded	*Bertholletia* clade	Peru 03
Corythophora amapaensis Pires ex S.A. Mori & Prance	CA	4 - 5[1]	Canopy	Non-flooded	*Bertholletia* clade	FG 95
Couratari macrosperma A.C. Sm.	CM	1[2]	Emergent	Non-flooded	Polytomy	Peru 03
C. stellata A.C. Sm.	CS	4 - 5[1]	Emergent	Non-flooded	Polytomy	FG 95
Eschweilera coriacea (DC) S.A. Mori	EC	4[3] - 5[1]	Canopy	Non-flooded	*Bertholletia* clade	FG 05, 07; Peru 03
E. tessmannii R. Knuth	ET	4[2]	High Canopy	Mostly non-flooded	*Bertholletia* clade	Peru 03
Gustavia augusta L.	GA	4[2]	Understory	Riverine to non-flooded	Basal	Peru 03
G. hexapetala (Aubl.) Sm.	GH	1[3], 4 - 5[1]	Understory	Non-flooded to periodically flooded	Basal	FG 95. 07
Lecythis poiteaui Berg	LP	4[3] - 5[1]	High Canopy	Non-flooded	*Bertholletia* clade	FG 95, 07

[1] Five individuals were sampled 15 - 24 September 1995 and four were sampled 4 - 10 January 1996; [2]individuals were sampled16 - 19 August 2003 and 10 - 24 January 2004 (in some cases different individuals were sampled); [3]individuals sampled in 1995 were resampled 26 - 28 August 2007 and 17 - 20 January 2008; [4]NA = no data available; [5]FG = French Guiana; Data from Mori *et al*., 2010 onward or Berkov, pers. comm.

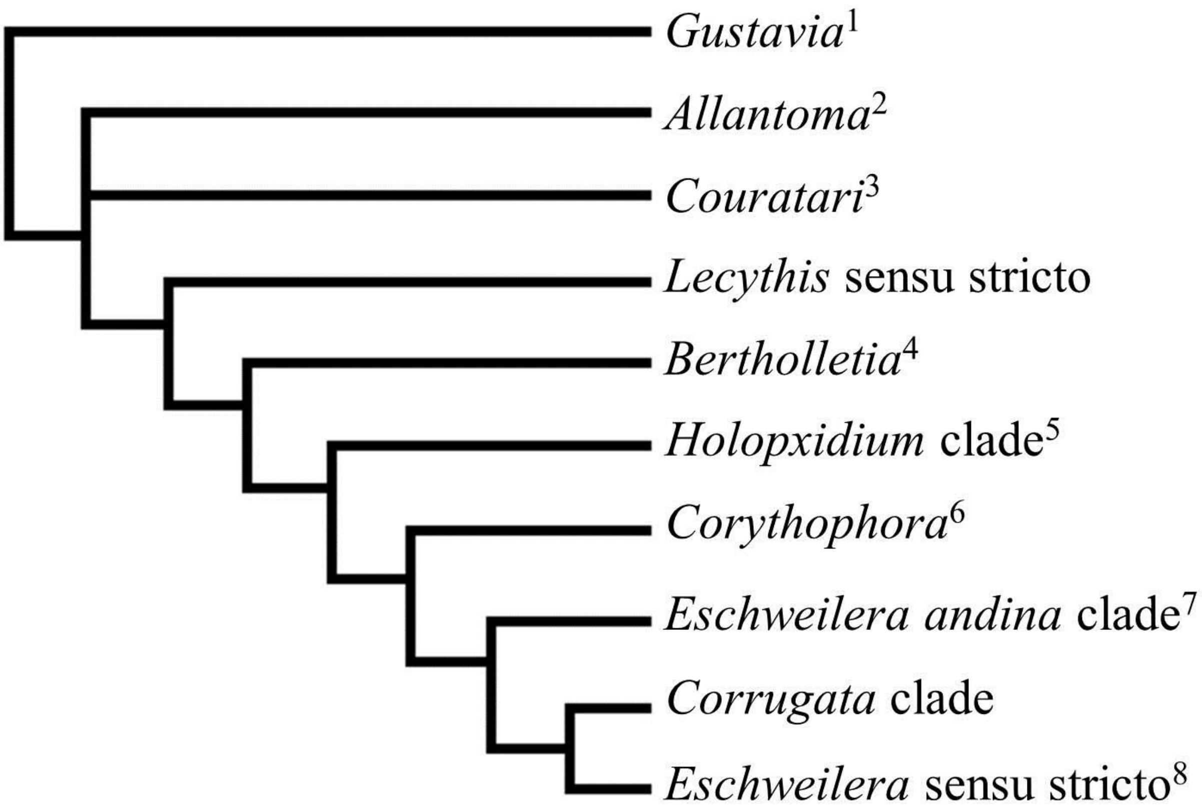

Figure 1.1: Phylogenetic tree of Lecythidaceae. Numbers indicate clades including sampled host tree species: 1 = basal species *Gustavia augusta* and *G. hexapetala*; 2 = *Allantoma decandra* and 3 = *Couratari macrosperma* and *C. stellata* form a polytomy with the *Bertholletia* clade; and 4 = *Bertholletia excelsa*, 5 = *Lecythis poiteaui*, 6 = *Corythophora amapaensis*, 7 = *Eschweilera tessmannii*, and 8 = *E. coriacea* are members of the large *Bertholletia* clade. Adapted from Huang, 2010.

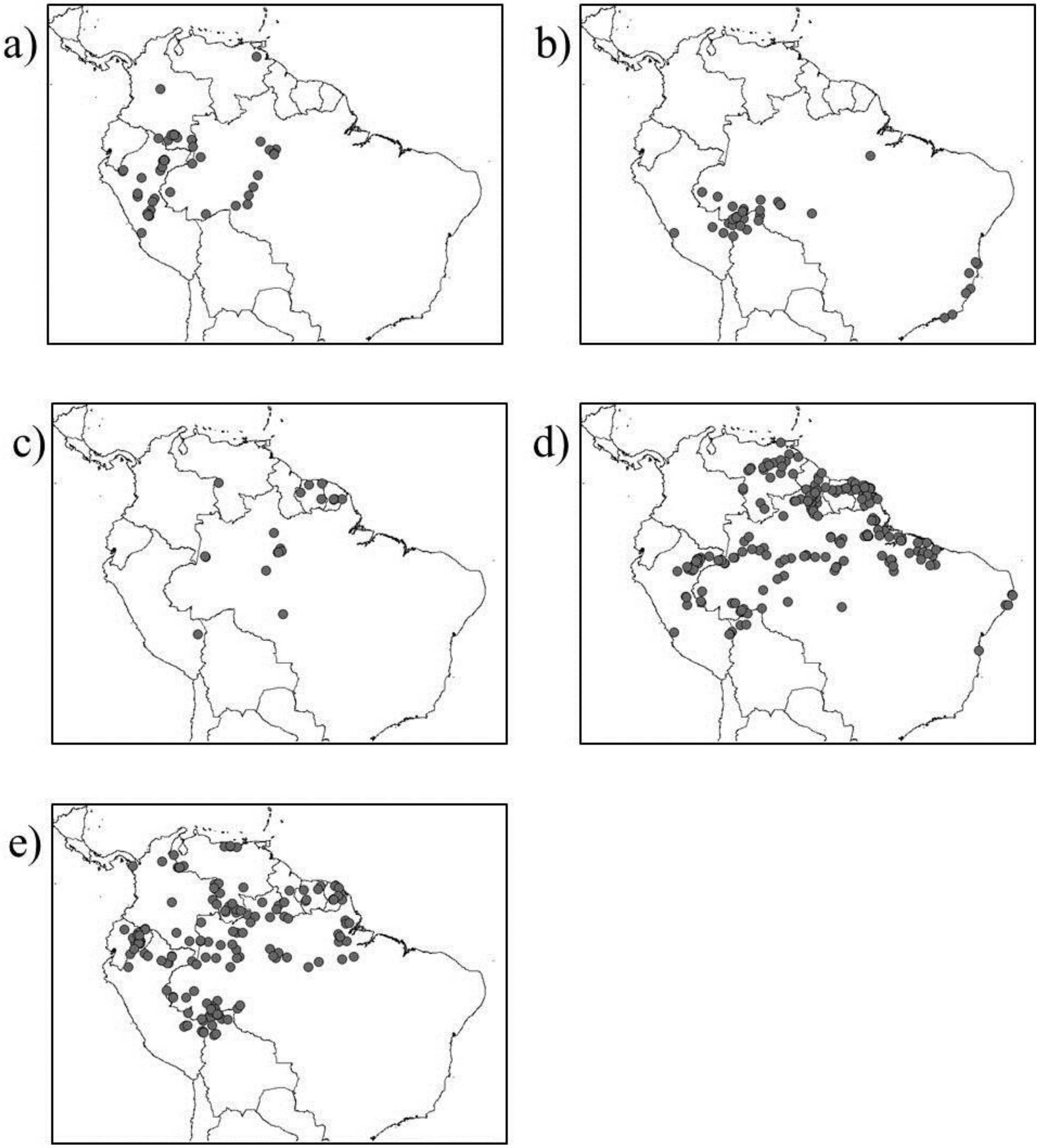

Figure 1.2: South American distributions of Lecythidaceae sampled during rearing studies. a) *Allantoma decandra* (AD), b) *Couratari macrosperma* (CM), and c) *Couratari stellata* (CS) form polytomies with the *Bertholletia* clade; d) *Gustavia augusta* (GA) and e) *Gustavia hexapetala* (GH) are basal species; Data from Mori *et al.*, 2010 onward.

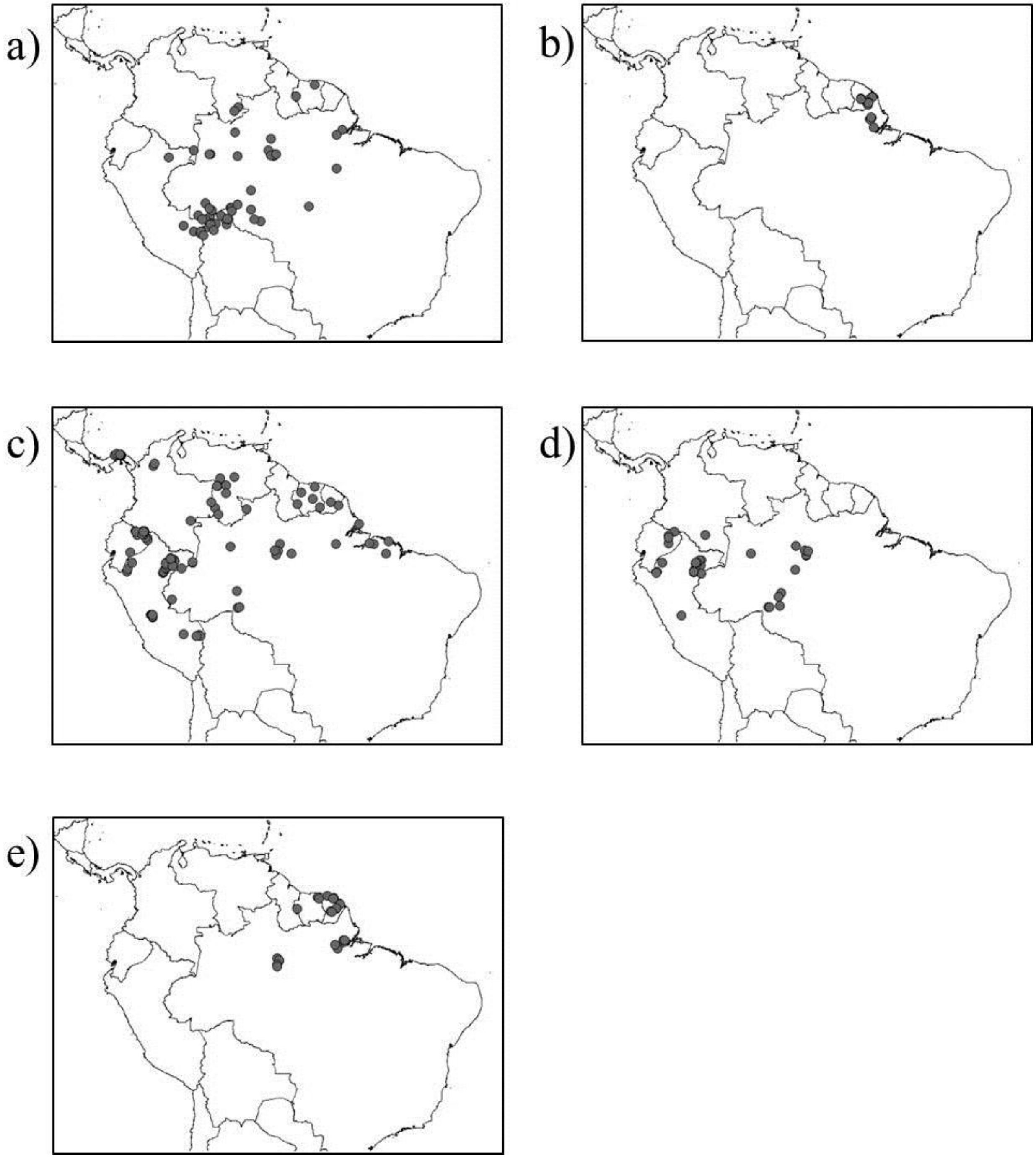

Figure 1.3: South American distributions of Lecythidaceae from the *Bertholletia* clade sampled during the rearing studies. a) *Bertholletia excelsa* (BE); b) *Corythophora amapaensis* (CA); c) *Eschweilera coriacea* (EC); d) *Eschweilera tessmannii* (ET); e) *Lecythis poiteaui* (LP). b) Data from Mori *et al.*, 2010 onward.

distributions range from Vera Cruz, Mexico to Paraguay, with some species in the Caribbean and Trinidad and Tobago (Mori, 2007). Neotropical Lecythidaceae consist of about 200 species and all but one genus, *Asteranthos*, are members of the monophyletic subfamily Lecythidoideae (Mori, 1992; Mori, 2007). Brazil nuts are harvested from a species of Lecythidaceae, *Bertholletia excelsa*, making the Brazil nut one of the most economically important plant families in Amazonia (Mori, 1992).

The purpose of this dissertation was to assess niche associations, resource partitioning, and species richness and abundance in Neotropical saproxylic wood-boring beetles reared from host species in the Brazil nut family (Lecythidaceae). Data were collected from two studies performed in French Guiana (1995, 2007) and a study performed in Peru (2003) (Figure 1.4). The analyses included herein are:

1) The first study evaluated resource partitioning and niche breadth of wood-boring weevils (Conoderinae, Cryptorhynchine, and Molytinae) collected in two studies in French Guiana (1995, 2007). I expected weevil species to show consistent association with host species between the two years. I also expected weevil species to be more abundant during the rainy season and at the ground stratum due to moisture abundance at that time and decreased risk of desiccation.
2) The second study evaluated abundance, species richness, beta-diversity, and niche breadth of wood-boring weevils (Conoderinae, Cryptorhynchine, and Molytinae) collected in French Guiana (1995, 2007) and Peru (2003). I expected weevil species in Peru to show preference for hosts in the *Bertholletia* clade, particularly *Eschweilera* species, and to emerge in greater

abundance from branches in the rainy season. I expected species turnover to be high due to the distance between the two sites and Peru to have greater species richness due to higher plant productivity.

3) The third study evaluated resource partitioning and niche breadth of wood-boring beetles (Cerambycidae: Cerambycinae and Lamiinae; Curculionidae: Conoderinae, Platypodinae, and Scolytinae). I expected the small-bodied weevils, bark beetles, and ambrosia beetles to be more diverse at the moist ground stratum and in the rainy season due to decreased risk of desiccation in that microclimate. I expected larger-bodied cerambycids, which are likely more desiccation resistant, to be more abundant than curculionids during the dry season.

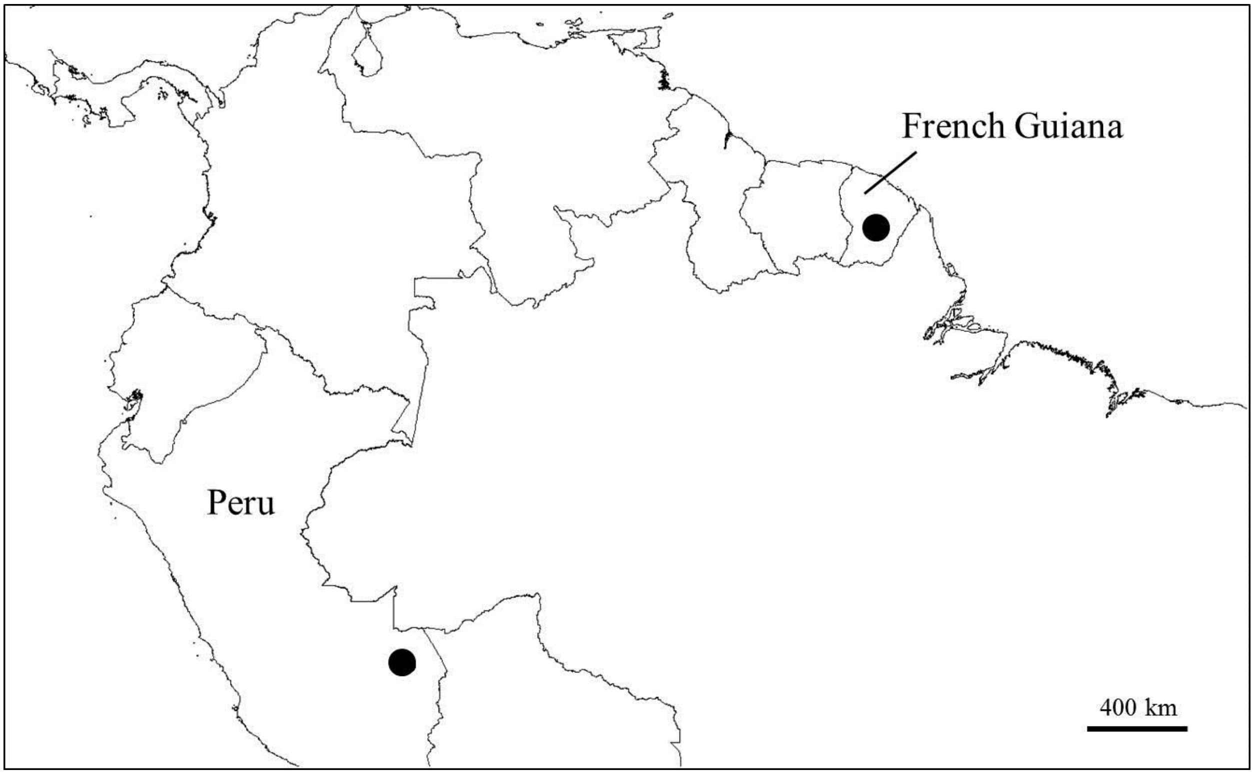

Figure 1.4: Study sites in French Guiana (1995, 2007) and Peru (2003).

CHAPTER 2

Niche associations of wood-boring weevils (Coleoptera: Curculionidae) in French Guiana

Abstract

The loss of tropical forests has a strong direct effect on the abundance of wood-boring beetles through the loss of larval feeding substrates and indirect effects through climate and microclimate changes in forest fragments. In this study, baseline data on niche associations of wood-boring weevils were collected in the minimally disturbed moist forest of French Guiana. Two rearing experiments (1995, 2007) were conducted to assess host specificity, seasonality, and stratification of wood-boring weevils associated with dead wood from tree species in the Brazil nut family (Lecythidaceae). We hypothesized that weevil species would be host specialists and more abundant in moist microhabitats. G-tests for goodness of fit were conducted on the 2007 data to determine whether weevil abundance was proportional to resource availability. Multivariate analyses (two-way cluster, canonical correspondence, and indicator species) were conducted to explore community structure. The studies yielded 2,247 weevils of 38 species; ten species in the subfamily Conoderinae accounted for 83% of the specimens. Weevils were disproportionately associated with the tree species *Eschweilera coriacea.* Bait branches in the warmest, driest microhabitat were rarely used as hosts, while the branches with the most beetles emerged from bait branches in the coolest, moistest microhabitat. The Brazil nut family is most abundant and diverse in old-growth forests, and is expected to suffer under biotic homogenization, but the favored host species is widely distributed. Weevils may be more impacted by indirect effects of forest fragmentation than by direct effects of habitat loss.

Introduction

Worldwide habitat loss through deforestation is estimated to be 13 million hectares per year. While some deforestation results from natural causes such as fire, most loss is from conversion of tropical forests into agricultural lands (FAO, 2010). Conversion of Amazonian rainforests has resulted in a plethora of forest fragments (often no larger than 50 hectares) interspersed among sugar cane or other agricultural fields. Fragments, over time, begin to exhibit reduced functional diversity and retain only a fraction of the species richness of the interior of large forest tracts (Girão *et al.*, 2007). Forest edges and fragments also show a marked increase in biotic homogenization when compared to the forest interior. Flora in fragments consists predominantly of short-lived, small-seeded pioneer semi-deciduous or deciduous tree species (Lobo *et al.*, 2011; Tabarelli, *et al.*, 2010).

Increased deciduousness of Neotropical rainforests is thought to be driven by global climate change. Decrease in annual rainfall leads to a longer dry season and an increase in drought-tolerant, deciduous trees. In times of water stress, such trees are more likely to wilt or lose their leaves to minimize water loss, causing a reduction in canopy cover, leading to a decrease in evapotranspiration and precipitation (Borchert, 1998) as well as an increase in the number of forest fires. Forest fires, drought, and logging convert a forest ecosystem into a brush or grassy habitat, thereby increasing a forest's future risk of burning by increasing the amount of material that is available as fuel for fire. An estimated 55% of Amazonian forest will be cleared, logged, or damaged by drought or burning by the year 2030 (Nepstad *et al.*, 2008).

Habitat loss has a strong direct effect on the diversity of forest-associated insects by reducing species richness and abundance—especially of saproxylic species that are dependent upon dead wood (Grove, 2002). The saproxylic guild includes representatives from all major insect orders that feed on dead wood or dead wood-associated fungi, plus their parasites, parasitoids, and predators (Grove, 2002; Ødegaard, 2006). Saproxylic species are often concealed feeders that have physically intimate associations with the host, and would tend to be more specialized than external feeders (Mattson *et al.*, 1988; Novotny & Basset, 2005). In French Guiana, host specific wood-boring cerambycids outnumber generalists three to one, but specialists are usually associated with a particular plant genus or family (Tavakilian *et al*., 1997). In New Guinea, ambrosia beetles (Platypodinae, Scolytinae) that feed on dead wood-associated fungi are host generalists, while bark beetles (Scolytinae), which feed directly on host tissues, show strict congeneric/ confamilial specificity (Hulcr *et al*., 2007). Other curculionid subfamilies, including Cossoninae, Conoderinae, some Cryptorhynchinae, and some Molytinae, include species associated with dead wood (Oberprieler, 2007), but almost nothing is known about their host preferences.

Global climate change is expected to have a strong indirect effect on saproxylic species, especially in moisture-dependent tropical forests. In Panama, a wet tropical forest harbored nearly twice as many species as a dry forest, primarily due to an increased abundance of saproxylic beetles including Curculionidae (Conoderinae, Cryptorhynchinae, and Molytinae) (Ødegaard, 2006). Neotropical weevils are also seasonal, with sharp increases in abundance at the beginning of the rainy season (Wolda *et al.*, 1998). Given their apparent preference for moister habitats, it may become increasingly difficult for some saproxylic weevils to locate suitable oviposition substrates—as precipitation decreases and the length of the dry season increases in areas of the tropics over the coming decades (Miles *et al*., 2004).

Wood-boring weevils, the focus of this study, are one of the first groups of saproxylic beetles to colonize moribund wood (Madoff & Bakke, 1995). Females form oviposition pits using their elongated rostrum, allowing them to place their eggs into the bark of the tree. The larvae develop endophytically, where they are protected from the weather and predators (Lyal, 1986; Anderson, 1995). They create feeding galleries through which other organisms of decay (fungi, bacteria, etc.) can enter the tree to further decompose the dead wood, returning its nutrients to the soil (Maser & Trappe, 1984).

This study evaluates niche associations of wood boring weevil larvae that feed on trees in the Brazil nut family, an iconic family of Neotropical moist forests. Data collected from two year-long rearing experiments, performed at the same site in French Guiana, twelve years apart (1995-96 and 2007-08), are compared. Weevil species reared from the same host tree species in both experiments are expected to exhibit consistent associations with those species. Weevil species should be more abundant during the rainy season, and at the ground level, because abundant moisture (Lee, 2010) decreases the risk of desiccation for both larvae and adults (Addo-Bediako *et al.*, 2001). Baseline data collected in this relatively undisturbed forest is used to assess species richness, host specificity, and seasonality; these will make it possible to detect changes as forests become fragmented, and to make predictions about weevil responses to climate change.

Materials and Methods

Study Site

Both studies took place in a lowland moist forest near Les Eaux Claires (3^o37-39’N, 53^o12-13’W); a homestead located approximately seven kilometers north of Saul, French Guiana. The terrain is hilly with altitudes ranging from 200-400 m above sea level, and soils are well-drained. Cumulative rainfall measured from 26 August 2007 to 31 July 2008 was 2894.7 ml (Lee, 2010). The rainy season in 2007 began in November and lasted through July. The main dry season was between August and November with a short, mild dry season in April. Mean daily temperatures during the dry season ranged from approximately 24-25° C (ground and canopy) and during the rainy season from approximately 22-23º C (ground and canopy) (Lee, 2010). See Berkov and Tavakilian (1999) for full details on the 1995 study.

Tree selection

The Brazil nut family (Lecythidaceae) has a Pantropical distribution; it is particularly abundant and species-rich throughout the new world tropics (Mori et al., 2007). Host tree species were selected because of their relative abundance at the study site. They include both early and later diverging members of the Neotropical subfamily Lecythidoideae (Huang, 2010): Gustavia hexapetala (Aubl.) Sm. (an early-diverging species); Corythophora amapaensis Pires ex S.A. Mori & Prance, Eschweilera coriacea (DC.) S.A. Mori, and Lecythis poiteaui Berg, (members of the derived Bertholletia clade); and Couratari stellata A.C. Sm. (a member of a polytomy that includes the Bertholletia clade).

In 1995, five tree species were sampled and vouchered: Couratari stellata (CS), Corythophora amapaensis (CA), Eschweilera coriacea (EC), Gustavia hexapetala (GH), and Lecythis poiteaui (LP). Five individuals of each species were sampled in the dry season cut, and four individuals in the rainy season. All trees were located within one km of the homestead (see Supp. 1 for voucher numbers and tree details).

In 2007, nine individual trees belonging to three species of Lecythidaceae were resampled (Supp. 1), focusing on the two most productive species: EC (N = 4) and LP (N = 4). A single individual of GH was sampled because in 1995 it was sparsely colonized by weevils.

Branch Sampling (2007)

Branches were cut from the sample trees during both dry and rainy seasons, and placed in the canopy and on the ground as bait to attract wood-boring beetles. The dry season branches were cut on 26-28 August 2007. The rainy season branches were cut on 17-20 January 2008. The same procedure was followed in both seasons. One branch was cut from each tree. A section (~8 cm diameter by 65 cm length) was severed and suspended as bait in the canopy in the tree from which it was cut. The rest of the branch was placed on the forest floor as a ground bait. Bait branches were collected after approximately three months. Ground baits were cut into three thick (~8 cm x 65 cm) and six thin (~2 cm x 65 cm) sections. Three rearing cages were generated per tree: one containing the canopy bait, one with three thick ground baits, and one with six thin ground baits. In 1995, cages were constructed from plastic screen, mosquito netting, and no-seeum insect netting. In 2007, all cages were constructed from no-seeum insect netting.

All cages were checked manually at least once per day for recently emerged adult beetles, which were given a preliminary identification and preserved in 70 % (1995) or 100 % (2007) ethanol. Specimens were transported to City College of New York (CCNY). Weevil species were identified by Dr. Charles O’Brien, or by comparing specimens to his previously identified reference collection. Specimens are available at the American Museum of Natural History (1995), and CCNY (2007).

Data analysis

These analyses focus on Curculionidae excluding the subfamilies Scolytinae and Platypodinae, which are discussed elsewhere. Species were classified as specialists if 90 % of the specimens were associated with a single host, season, stratum, or branch diameter (a simple quantification that has been used for both host and habitat specificity; Novotny & Basset, 2005; Wardhaugh et al., 2012). Species with fewer than 10 individuals were excluded from specialist classifications due to insufficient data; classifications are considered tentative when sample sizes are small. Species richness data were compared between year, season, and host.

A goodness of fit test (G-test) was performed on the 2007 data to determine whether weevil abundance was proportional to the number of branch sections available at each stratum per season (dry canopy, dry ground, rainy canopy, rainy ground) (Sokal & Rohlf, 1995; McDonald, 2009). Only data from thick canopy and thick ground branches were included in G-test analyses (data from the sparsely colonized thin branches were excluded because it was not clear whether resource availability would be better described by branch circumference or biomass). Abundance by season was calculated for the weevil genera belonging to three common subfamilies. Indicator species analysis, which combines frequency and abundance data, was performed on the combined 1995/2007 dataset to determine if any weevil species were predictively associated with season. Indicator values were calculated with the Dufrêne and Legendre method on a presence / absence dataset (recommended when comparing results from separate studies) using PC-ORD (McCune &Mefford, 2011). A Monte Carlo test of the significance of observed maximum indicator values was performed where p = (1 + number of runs $\geq$ observed) / (1 + number of randomized runs).

A second G-test was performed on the 2007 data to determine whether weevil abundance was proportional to the number of branch sections available from each host tree species. Abundance by host was calculated for the weevil genera belonging to three common subfamilies. Indicator species analysis was performed on the combined 1995/2007 dataset, as previously described, to determine if any weevil species were predictively associated with a particular tree species. A two-way cluster analysis was performed with PC-ORD on the 1995/2007 data to analyze weevil community structure with a dataset including the following categorical factors: host species (CA, CS, EC, GH, or LP), year (1995 or 2007), and season (rainy or dry). Group average linkage method and Sorensen (Bray-Curtis) distance measure were used for analysis. For all PC-ORD analyses, weevil species were included if they were represented in more than one sample.

Patterns of weevil community structure were further explored between years using canonical correspondence analysis (CCA) within PC-ORD (ter Braak, 1986). Abundance data were log (x+1) transformed before analysis. The dataset included the following factors: host species (EC, GH, or LP), season (rainy or dry), and year (1995 or 2007). CA and CS were excluded from the combined 1995/2007 analysis because they were not sampled in 2007. Axis scores were standardized by Hill’s (1979) method and scaled to optimize representation of explanatory variables. The statistical significance of the correlation between species and environment was evaluated using a Monte Carlo permutation test (998 permutations) where $p = (1 + \text{no. permutations} \geq \text{observed}) / (1 + \text{no. permutations})$.

Results

Collections yielded six subfamilies of Curculionidae sensu stricto: Conoderinae, Cryptorhynchinae, Dryopthorinae, Molytinae, Scolytinae and Platypodinae. Scolytinae and Platypodinae were treated in a later study. No Cossoninae specimens were collected in either year.

Species richness

The two studies yielded 2248 weevils in 38 species, belonging to four subfamilies of Curculionidae: Conoderinae (*N* = 1834), Cryptorhynchinae (*N* = 343), Dryopthorinae (*N* = 3), and Molytinae (N = 66) (Appendix 1). In 1995, 986 individuals in 27 species were reared, and in 2007, 1262 individuals in 24 species were reared. Fourteen species were collected only in 1995, eleven were collected only in 2007, and thirteen were collected in both years. Ten of the species that were reared in both 1995 and 2007 belong to the subfamily Conoderinae; these accounted for 83 % of the specimens. In 2007, four conoderine species were represented by > 100 individuals and made up > 79 % of the total abundance: *Copturomorpha* sp.1 (*N* = 175), *Piazurus incommodus* (*N* = 289), *P. pseudoalternans* (*N* = 404), and *Piazurus* sp. 3 (*N* = 132). In 1995 only one of these four species, *P. incommodus*, was represented by > 100 individuals, along with the cryptorhynchine *Pisaeus* sp. 1.

Seasonality

In 1995, weevil abundance was similar from dry and rainy season branches (dry season *N* = 516, rainy season *N* = 470) (Appendix 1). In 2007, the rainy season branches produced both the highest weevil species richness (dry season *N* = 11, rainy season *N* = 19) and abundance (dry season *N* = 89, rainy season *N* = 1173) (Fig. 2.1). In 2007, seasonality was not an artifact of resource availability (Table 2.2). Bait branches cut during the dry season were sparsely colonized at both canopy and ground stratum, but 90 % of the adults were from ground branches. Bait branches cut during the rainy season were well colonized, with 84 % of the adults from ground branches (G = 907.2275, df = 3, p < 0.00001).

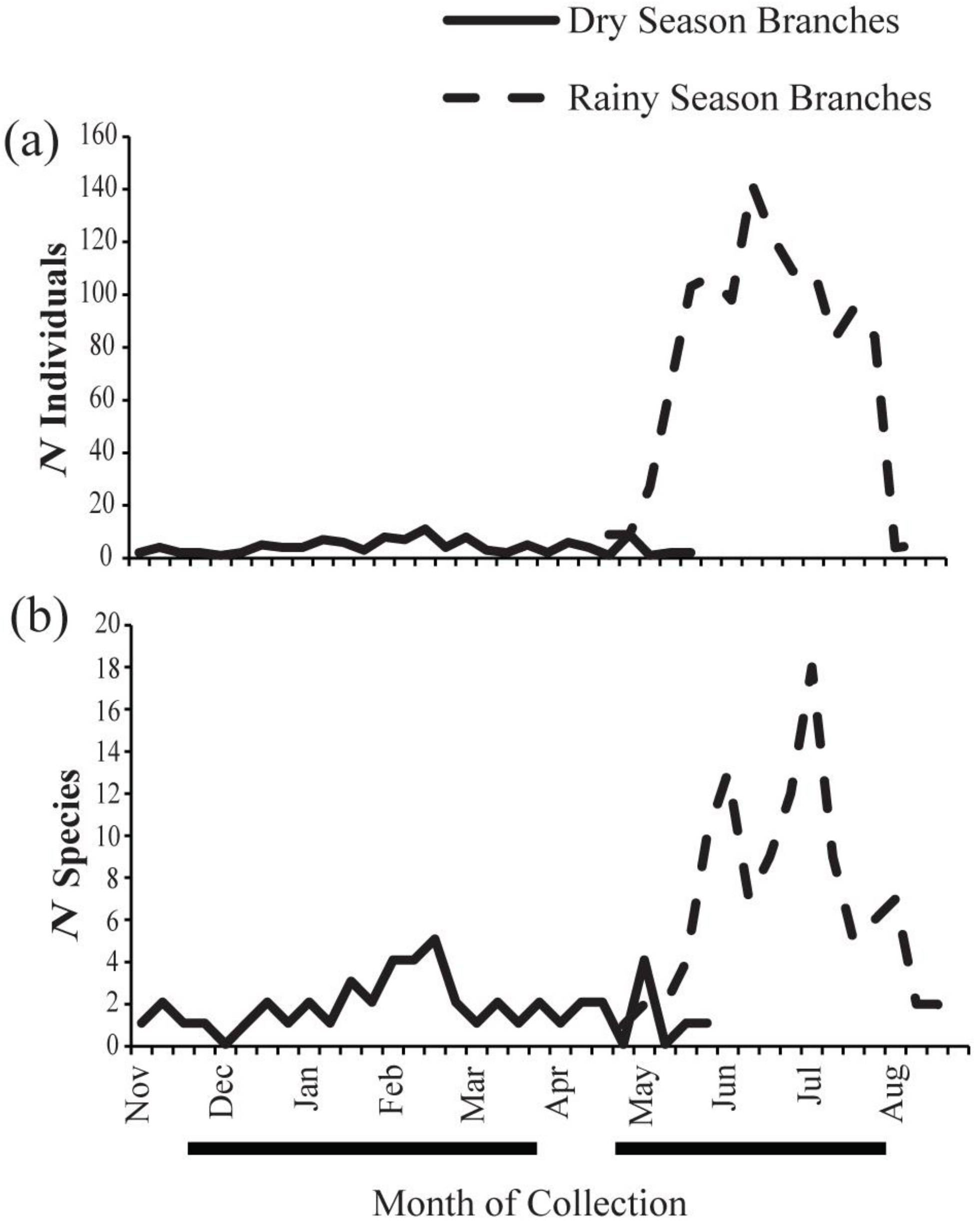

Figure 2.1: Weevils collected per week in 2007-2008 emerged in (a) greater abundance and (b) higher species richness from rainy season branches. Black bars indicate rainy season.

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Table 2.1: A G-test of weevils collected from canopy and ground strata during the dry and rainy seasons indicates that weevils were preferentially represented during the rainy season.

Season	**Stratum**	**Branch[1] *N***	**Ind. Obs.[2]**	**Ind. Exp.[3]**	**Ratio obs./exp.[4]**	**df**	***G***	**p**
Dry	Canopy	9	9	131.5	0.068	3	907.2275	<0.00001
	Ground	27	74	394.5	0.188			
Rainy	Canopy	9	185	131.5	1.407			
	Ground	27	784	394.5	1.987			

[1]Number of bait branch sections from each stratum, excluding thin branches from ground, [2]Observed number of individuals reared from branches, [3]Number of individuals expected to be reared from branches, [4]Ratio of observed individuals to expected individuals.

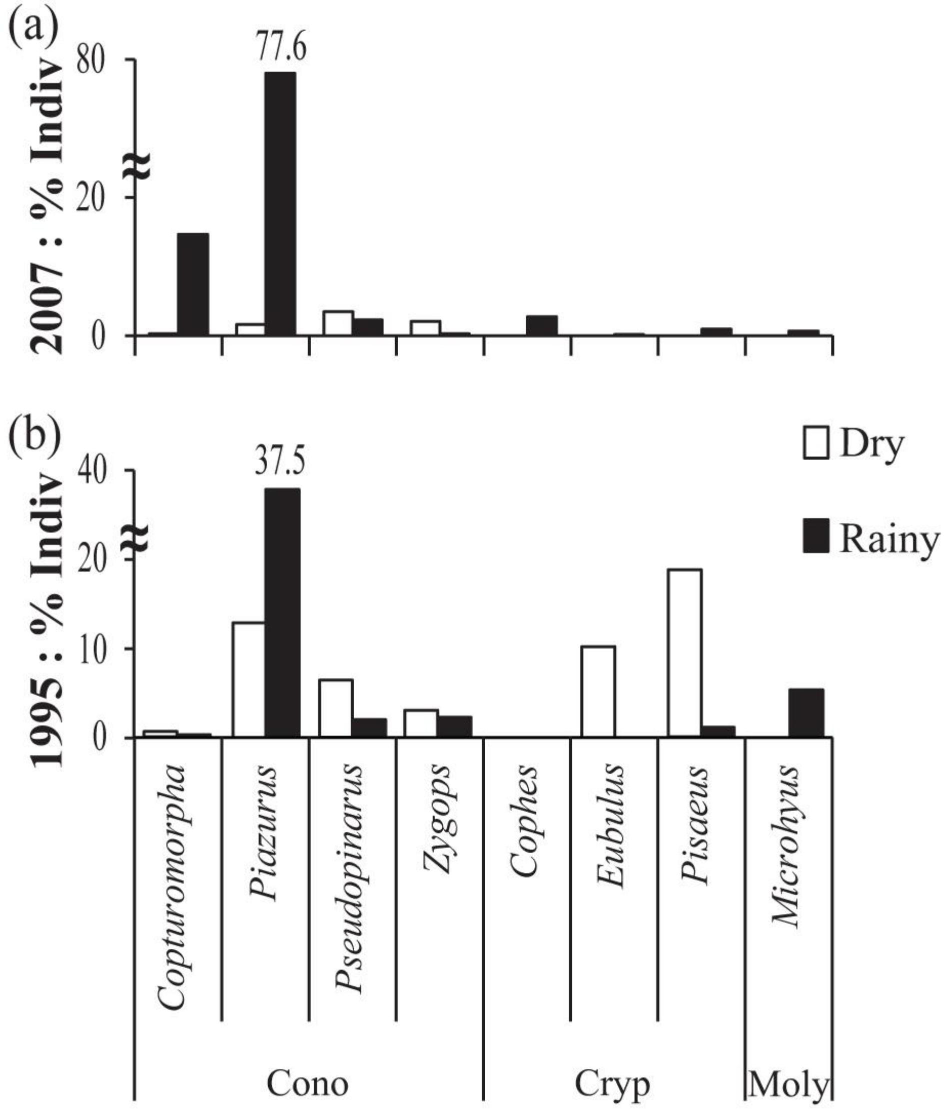


Figure 2.2: Seasonality of weevil genera in (a) 2007 and (b) 1995 indicates that *Piazurus* is dominant during the rainy season. Subfamilies are abbreviated: Cono = Conoderinae, Cryp = Cryptorhynchinae, Moly = Molytinae.

In both 1995 and 2007, weevils in the conoderine genus *Piazurus* emerged in higher numbers from the rainy season branches, while weevils in the conoderine genera *Pseudopinarus* and *Zygops* emerged in higher numbers from dry season branches (Fig. 2.2). In 1995, the cryptorhynchine genera *Eubulus* and *Pisaeus* were also more abundant in dry season branches, while the molytine genus *Microhyus* emerged in higher numbers from rainy season branches. Among weevil species represented by at least ten individuals, the ratio of dry season specialists: season generalists : rainy season specialists was 4:5:4 in 1995, and 1:1:8 in 2007 (Appendix 1). None of the 2007 species exhibited statistically significant indicator values for season. However, of twelve weevil species reared in both 1995 and 2007 and represented by at least ten individuals, four species (33 %) retained the same seasonal classification (Appendix 1). *Piazurus alternans*, *Piazurus* sp. 3, and *Microhyus* sp. 1 emerged consistently during from rainy season branches, while *Zygops histrio* emerged consistently from both dry and rainy season branches. One of these, *Piazurus* sp. 3, was the sole canopy specialist.

Host association

In both 1995 and 2007, *Eschweilera coriacea* was the most productive host species (1995: *Corythophora amapaensis* (CA) = 8, *Couratari stellata* (CS) = 10, *Eschweilera coriacea* (EC) = 817, *Gustavia hexapetala* (GH) = 56, *Lecythis poiteaui* (LP) = 95, and 2007: EC = 934, GH = 57, LP = 271; Appendix 1). In 2007, the difference between expected and observed numbers of weevils collected from each host species was significantly greater than could be explained by variation in branch number ($G = 455.7$, $df = 2$, $p < 0.00001$; Table 2.3).

In both 1995 and 2007, weevils in the dominant conoderine genus, *Piazurus*, emerged in higher numbers from EC, with LP yielding the second highest abundance (Fig. 2.3). *Pseudopinarus*, while reared from a variety of hosts, was most abundant from GH. In 2007, *Cophes* and *Zygops* were more abundant from LP branches, but in 1995 no *Cophes* were collected, and *Zygops* was more plentiful in EC than LP. The remaining genera were collected in higher numbers from EC (Fig. 2.3). Two weevil species exhibited statistically significant indicator values for EC (*Copturomorpha* sp.1, p = 0.001 and *Piazurus* sp. 3, p = 0.0012), and one species had a statistically significant indicator value for GH (*Pseudopinarus cerastes*, p = 0.0112). Host associations were consistent for ten of the twelve species (83 %) reared during both 1995 and 2007 (Appendix 1). Six species were reared almost exclusively from EC (*Copturomorpha* sp. 1, *P. alternans*, *Piazurus* sp. 3, *Pseudopinarus* sp. 2, *Pisaeus* sp. 1, and *Microhyus* sp. 1, one species was reared exclusively from LP (*Pseudopinarus* sp. 1), and three were reared consistently from both EC and LP (*Piazurus incommodus*, *P. pseudoalternans*, and *Zygops histrio*). In addition, *Pseudopinarus cerastes* was reared in greatest abundance from GH in 1995 and exclusively from GH in 2007.

In the two-way cluster analysis (Fig. 2.4), CS and one sample of CA (from 1995) clustered with the basal species GH because they produced occasional specimens of *P. cerastes*, The other sample of CA clustered with LP and EC, each of which forms an individual cluster. While EC yielded six weevil species that were never reared from an alternate host, most of the species reared from LP were also reared from EC.

Table 2.2: A G-test of weevils collected from three host tree species in 2007 indicates that *Eschweilera coriacea* is the favored host.

Year	**Host**	**Branch[1] *N***	**Ind. Obs.[2]**	**Ind. Exp.[3]**	**Ratio obs./exp.[4]**	**df**	***G***	**p**
FG07	GA	1	57	140.22	0.41	2	455.7	<0.00001
	LP	4	271	560.89	0.48			
	EC	4	934	560.89	1.67			

[1] Number of bait branch sections from each host, excluding thin branches from ground, [2] Observed number of individuals reared from branches, [3] Number of individuals expected to be reared from branches, [4] Ratio of observed individuals to expected individuals.

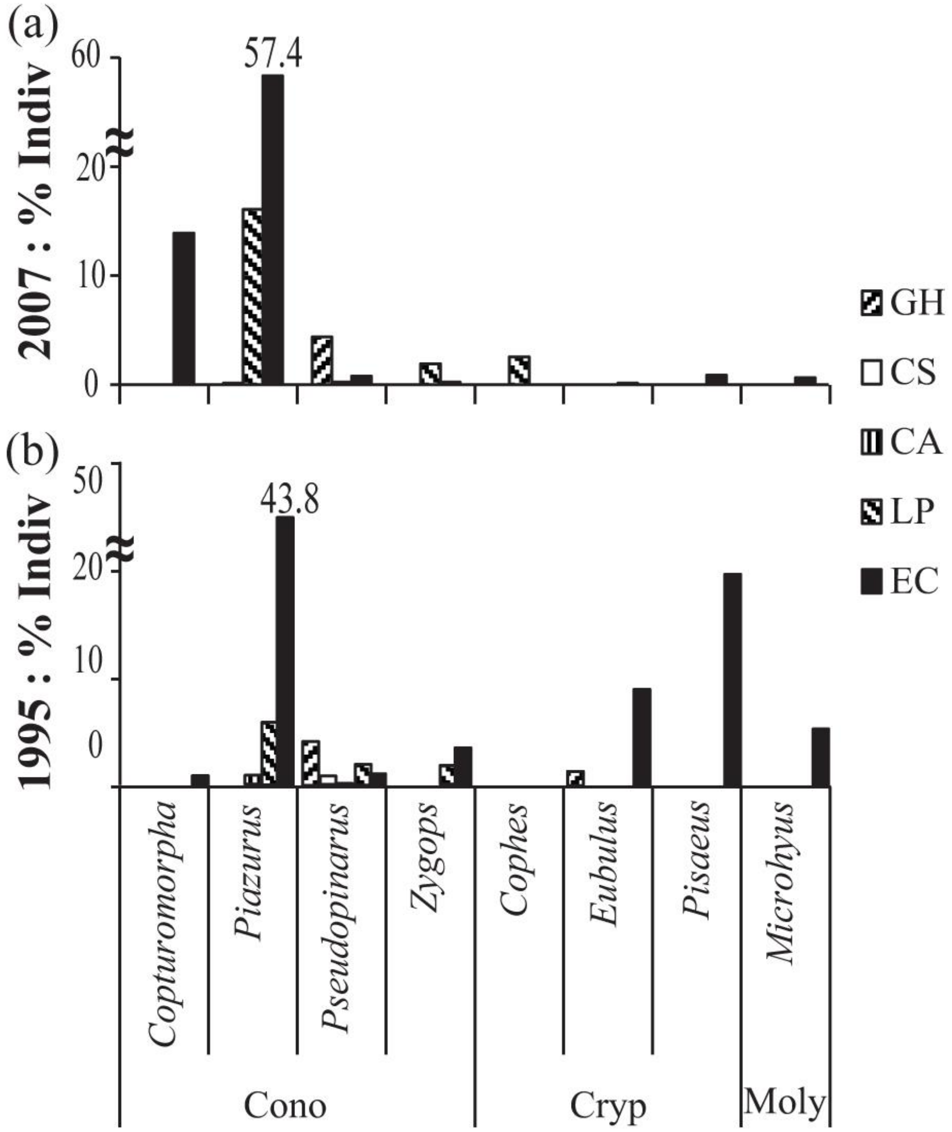
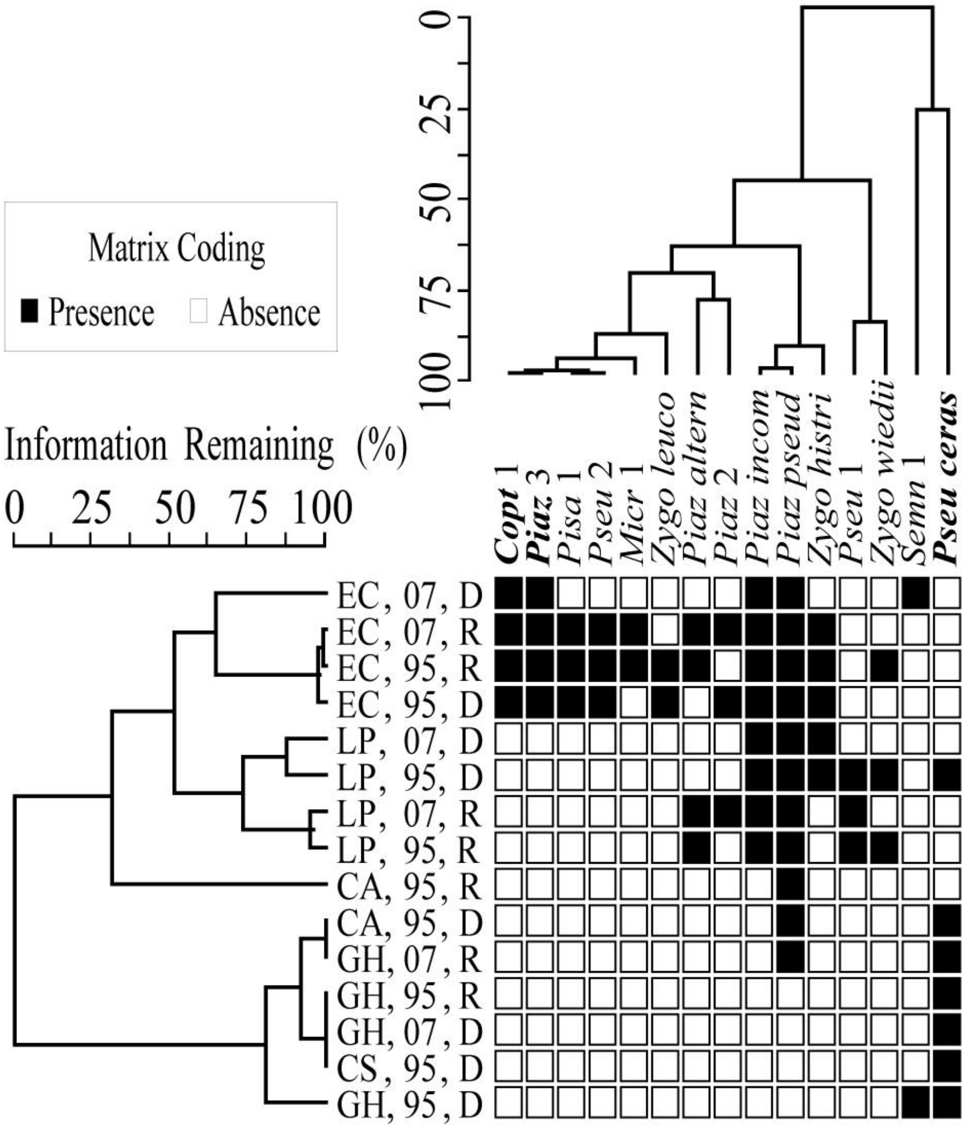


Figure 2.3: Host associations of weevil genera in (a) 2007 and (b) 1995 indicate that *Eschweilera coriacea* is the most densely colonized host. Subfamilies are abbreviated: Cono = Conoderinae, Cryp = Cryptorhynchinae, Moly = Molytinae. Tree species are abbreviated: CA = *Corythophora amapaensis*, CS = *Couratari stellata*, EC = *Eschweilera coriacea*, LP = *Lecythis poiteaui*, GH= *Gustavia hexapetala*.



	Copt 1	***Piaz*** 3	*Pisa* 1	*Pseu* 2	*Micr* 1	*Zygo leuco*	*Piaz altern*	*Piaz* 2	*Piaz incom*	*Piaz pseud*	*Zygo histri*	*Pseu* 1	*Zygo wiedii*	*Semn* 1	***Pseu ceras***
EC, 07, D	■	■	□	□	□	□	□	□	■	■	□	□	□	■	□
EC, 07, R	■	■	■	■	■	□	■	■	■	■	■	□	□	□	□
EC, 95, R	■	■	■	■	■	■	■	□	■	■	■	□	■	□	□
EC, 95, D	■	■	■	■	□	■	□	■	■	■	■	□	□	□	□
LP, 07, D	□	□	□	□	□	□	□	□	■	■	■	□	□	□	□
LP, 95, D	□	□	□	□	□	□	□	□	■	■	■	■	■	□	■
LP, 07, R	□	□	□	□	□	□	■	■	■	■	□	■	□	□	□
LP, 95, R	□	□	□	□	□	□	■	□	■	■	□	■	■	□	□
CA, 95, R	□	□	□	□	□	□	□	□	□	■	□	□	□	□	□
CA, 95, D	□	□	□	□	□	□	□	□	□	■	□	□	□	□	■
GH, 07, R	□	□	□	□	□	□	□	□	□	■	□	□	□	□	■
GH, 95, R	□	□	□	□	□	□	□	□	□	□	□	□	□	□	■
GH, 07, D	□	□	□	□	□	□	□	□	□	□	□	□	□	□	■
CS, 95, D	□	□	□	□	□	□	□	□	□	□	□	□	□	□	■
GH, 95, D	□	□	□	□	□	□	□	□	□	□	□	□	□	■	■

Figure 2.4: Two-way cluster analysis of weevil community structure shows that *Gustavia* and *Couratari* are separated from most members of the *Bertholletia* clade. Samples are labeled as follows: host species: CA = *Corythophora amapaensis*, CS = *Couratari stellata*, EC = *Eschweilera coriacea*, LP = *Lecythis poiteaui and* GH = *Gustavia hexapetala;* year: 95 or 07; and season: D = dry, R = rainy.

Effect of host tree and season on weevil community composition

When data from 1995 and 2007 were combined, the cumulative variance explained by the three CCA axes was 35.4 %, again suggesting correlations between environmental factors and weevil abundance (total inertia = 1.673; cumulative explained inertia = 0.593; Fig. 2.5). The remaining variance was unexplained (64.6 %). The correlation between species and environment was statistically significant (p = 0.013). In spite of the substantial inter-annual variation discussed above, the samples separated by both host and season; in EC and GH, most of the inter-annual variation was along the season axis.

Discussion

Of the 38 weevil species reared from Lecythidaceae in French Guiana, only 33 % were reared in both 1995 and 2007, but these species accounted for much of the abundance. Although it was not reflected in the indicator species analysis, probably due to patchy distribution, most were consistent in their host associations over time. Comparative data from unrelated host plants, akin to Tavakilian *et al.*'s (1997) compilation for Neotropical cerambycids, are not available for most wood-boring weevils. Nevertheless, weevil species would not be expected to emerge consistently from particular tree species by chance alone, and the common conoderines are probably Lecythidaceae specialists. Weevils, like cerambycids, roughly tracked plant phylogeny (Fig. 2.4; Huang, 2010). In both families, beetles associated with the fetid species *Gustavia hexapetala* seldom emerge from tree species in the *Bertholletia* clade , and beetles associated with trees in the *Bertholletia* clade seldom emerge from *Gustavia* (Berkov *et al.*, 2000; Fassbender and Berkov, unpubl. data). The widespread, mid-canopy tree species

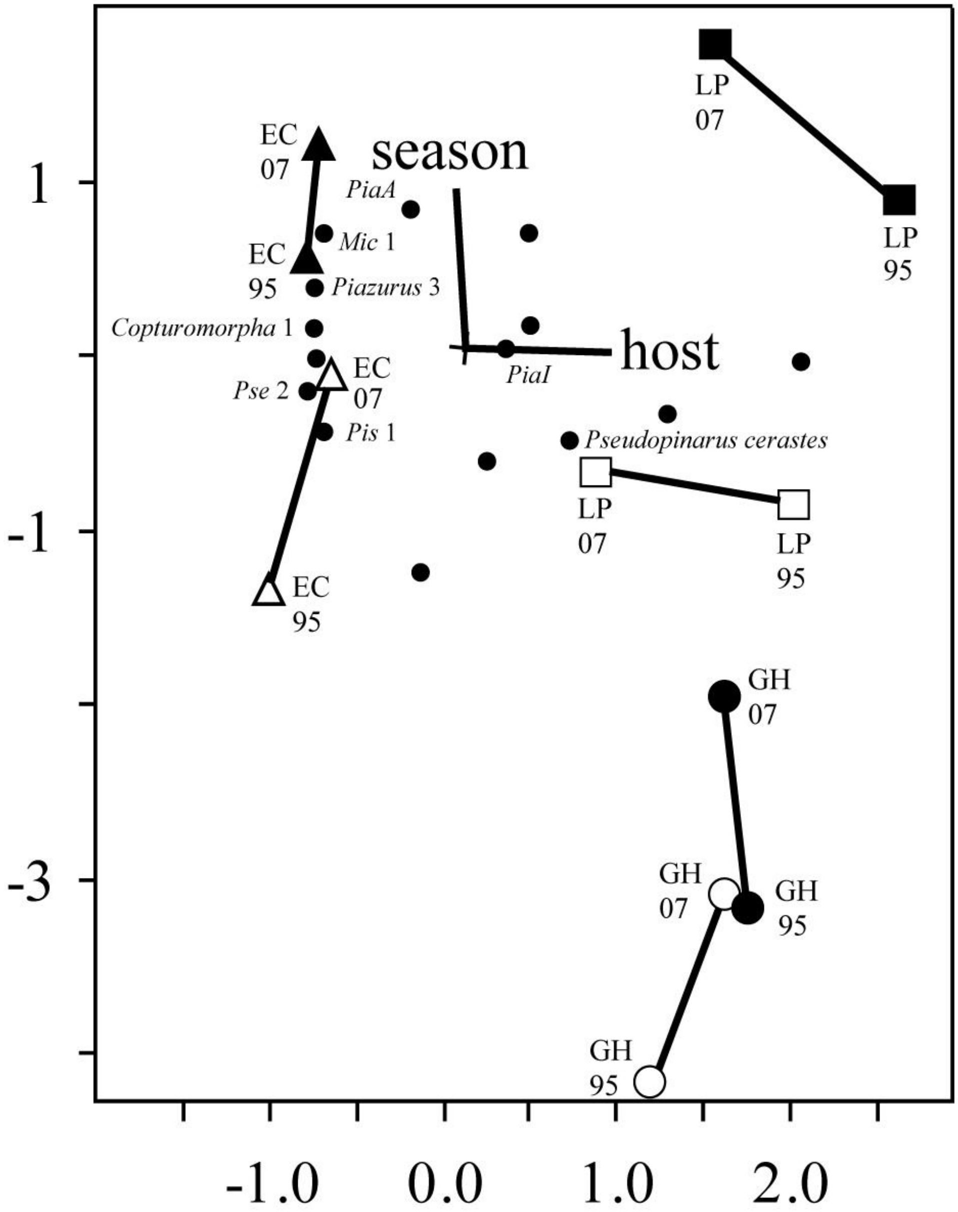


Figure 2.5: Canonical correspondence analysis (CCA) of the distribution of weevil species by host species and season for 1995 and 2007**.** Triangle = *Eschweilera coriacea* (EC), circle = *Gustavia hexapetala* (GH), square = *Lecythis poiteaui* (LP); empty symbols = dry season, filled symbols = rainy season; vectors link equivalent samples from 1995 and 2007. Small dots represent individual weevil species; those indicated by name had significant indicator values for host; those indicated by codes are also considered specialists.

Eschweilera coriacea (Mori & Prance, 2010 onwards) is a preferred host; the geographically restricted, emergent tree species *Lecythis poiteaui* is, for some species, an important secondary host.

Unlike host associations, seasonality varied dramatically between the two studies. In 1995 the dry season baits yielded 52 % of the weevils, while in 2007 they yielded only 7 %, and only 33 % of the seasonal classifications were consistent over time. This variation was probably influenced by both modification in the rearing protocol, and inter-annual differences in precipitation. In 1995, the dry season bait branches were exposed to beetles until late December (Berkov and Tavakilian, 1999), while in 2007 they were collected and caged in November near the beginning of the rainy season. Therefore, the 1995 dry season branches were available to weevils at onset of the rains, which, at least in Panama, is the period of peak adult abundance (Wolda *et al.*, 1998). This probably led to colonization of dry season branches by weevils that prefer a moist substrate (such as *Piazurus*). In addition, 2007 received approximately 25 % more rain than 1995 (Berkov, unpubl. data); this may have inhibited colonization by cryptorhynchines that were abundant in 1995. Overall, conoderines in the genus *Piazurus* appear to be strongly moisture dependent, while those in the genus *Zygops* and weevils in the subfamily Cryptorhynchinae appear to be more drought-tolerant; it would be informative to compare these data with results from long-term monitoring studies that more precisely correlate local precipitation and periods of adult activity.

Canopy baits, which are typically well-colonized by cerambycids (Lee, 2010), were sparsely colonized by weevils. Weevils preferentially colonized rainy season ground stratum branches, which were almost devoid of cerambycids. During the dry season, canopy temperatures can exceed 34° C and relative humidity drops below 50 % (Lee, 2010); this would increase the probability of desiccation and potentially result in decreased survival of small larvae (Addo-Bediako *et al*., 2001). Temperatures at ground stratum during the rainy season seldom exceed 26° C and relative humidity seldom drops below 90 %; this would present little risk of desiccation and probably explains why weevils were preferentially reared from bait branches in this microhabitat. It is not clear why cerambycids are uncommon in rainy ground branches (Berkov and Tavakilian, 1999; Lee, 2010), but high bark moisture content prevents some early instar cerambycid larvae from reaching their optimal feeding zone near the cambium, and they fail to pupate (Hanks *et al*., 1999). Weevils appear to overcome this barrier by using their elongate rostrum to penetrate the bark when forming oviposition sites. This secondary use of the rostrum, in addition to its primary purpose of feeding, is considered a "key innovation" that has promoted extreme species diversity in weevils (Anderson, 1995). Eggs are placed within the bark and the larvae are closer to the most nutritious host tissues. The ability to colonize wet branches may reduce intraguild competition with, or possible predation by, cerambycids (Dodds *et al*., 2001).

The Brazil nut family is restricted to moist tropical habitats (Mori & Prance, 2010 onwards); it is not surprising that its most common wood-boring weevil associates appear to be moderately to strongly moisture-dependent. Of the 85 species of Neotropical Lecythidaceae currently included on the IUCN Red List, 23 are endangered or critically endangered, and 45 are considered vulnerable (IUCN, 2012). Decreased abundance of host species will adversely affect wood-boring weevil species that specialize on Lecythidaceae through the loss of larval rearing substrate. *Eschweilera coriacea*, the favored host species in this study, has a widespread geographic distribution and tends to be locally abundant (Mori & Prance, 2010 onwards); climate permitting, it could provide a refuge for many saproxylic weevils associated with the Brazil nut family. South American rainforests are, however, projected to experience increased moisture deficits and decreased evapotranspiration over the next 50 to 75 years (Miles *et al*., 2004). Increased severity and duration of drought periods would be expected to have a negative fitness impact on moisture dependent saproxylic insects, particularly weevils in the genus *Piazurus*.

CHAPTER 3

Species richness, abundance, and diversity of saproxylic weevils (Curculionidae) in disjunct Neotropical forests

Abstract

Plant and animal diversity form gradients across Amazonia from east to west, with western Amazonia having the greatest overall species diversity. For this study, data on wood-boring weevils were collected to assess diversity, niche breadth, and resource partitioning in disjunct moist Neotropical forests in French Guiana and Peru. Rearing experiments (French Guiana: 1995, 2007; Peru: 2003) were conducted to assess species richness, abundance, beta-diversity, host specificity, and seasonality of wood-boring weevils associated with the Brazil nut family (Lecythidaceae). I hypothesized that weevil species would be preferentially associated with trees in the *Bertholletia* clade, and, due to their relatively small body size, be most abundant in moist microhabitats. I also hypothesized that Peru would have higher weevil abundance and species richness, and that species turnover between sites would be high due to the distance between them (>3300km). G-tests for goodness of fit were conducted (Peru) to determine whether weevil abundance was proportional among 1) host species and between 2) seasons. Multivariate analyses (two-way cluster, canonical correspondence, and indicator species) were conducted to explore community structure. The studies yielded 5177 specimens in 93 beetle species; thirteen species in the subfamily Conoderinae accounted for 78% of the specimens. Weevils were disproportionately associated with the tree species *Eschweilera coriacea*, but only one species was considered an indicator species for the tree. Bait branches in the dry microhabitat were poorly colonized in French Guiana (2007), but densely colonized in Peru. Abundance and species richness were higher in Peru than in French Guiana and species turnover between the sites was high. Lecythidaceae abundance may decline in response to global climate change, but the favored host species is widely distributed and apparently tolerates some

environmental heterogeneity, therefore it may provide a refuge for many of the saproxylic species associated with the Brazil nut family.

Introduction

Neotropical rainforests vary in both soil fertility and seasonality, with corresponding differences in plant productivity, and in plant and animal diversity. Soil fertility increases in a westerly direction across Amazonia with the peak close to the Andes (Hoorn *et al*., 2010). The soils in western Amazonia have been laid down relatively recently by erosion of the Andes (< 1.8 million years ago) and exhibit only slight to moderate weathering and thus are relatively high in nutrients (Quesada, *et al*., 2011). North of the Amazon, on the Guiana Shield, soil fertility is fairly low (Lescure and Boulet, 1985; ter Steege *et al*., 2006). The soils were first laid down approximately 1700 million years ago and show strong weathering and extremely advanced development, indicating that they release only a minute amount of nutrients (Quesada, *et al*., 2011). Contrary to the soil fertility gradient, seasonality decreases in severity in a westerly direction across Amazonia. The dry season is longer (ter Steege *et al*., 2006) and mean annual air temperature higher (Legates and Willmott, 1990) in eastern Amazonia than in western Amazonia (ter Steege *et al*., 2006)

The composition of Neotropical plant communities is highly influenced by the soil fertility gradient. The more fertile soils of western Amazonia yield higher plant productivity and increased plant diversity (Hoorn *et al*., 2010; ter Steege *et al*., 2006). Highly productive areas of western Amazonia have a larger percentage of smaller seeded species with less wood mass (ter Steege *et al*., 2006) than in the forests of northeast Amazonia which contain a greater diversity of slow growing, large seeded species that thrive in older, well established forests (ter Steege *et al*., 2009). Differences in tree species composition can have a strong influence on insect diversity even across relatively short distances. Tropical tree communities typically decline in species composition similarity with geographic distance (Condit *et al*., 2002). In Papua New Guinea, caterpillar communities feeding on multiple hosts shared over 50% species richness at sites 500 km apart; however, no monophagous species, which fed on only one host plant species, were shared between these sites (Novotny *et al*., 2007). High species turnover across even short distances indicates that species' abilities to track plant resources and disperse across distances may play a role in maintaining insect diversity.

In moist tropical rainforests, insect species richness and abundance are also strongly affected by moisture availability and season length, because these factors play a large role in insect survival due to their influence on water loss (Addo-Bediako *et al*., 2001). In Panama, Ødegaard *et al*. (2006) found that a wet tropical forest had nearly twice the insect species richness of a dry tropical forest, primarily due to a higher proportion of saproxylic (dead wood associated) weevils. Distinct seasonal preferences have also been shown in Neotropical weevils. In French Guiana in 2007, wood-boring weevil species richness was nearly 50% greater in the rainy season than the dry season (Fassbender, Chapter 2). Increases in dry season length or severity may cause a decline in moisture dependent insect species.

Shifts in the geographic distributions of host plants, as well as changes in size and structure of local or regional host assemblages (Lewinsohn *et al*., 2005), would have major effects on organisms with narrow niches—such as insect larvae that develop endophytically. Concealed feeders, including endophytic weevil larvae, are more intimately associated with the host, potentially leading to greater specialization (Novotny & Basset, 2005; Mattson *et al*., 1998). Predictions about the host specificity of saproxylic curculionids seem to depend largely on feeding strategy; whether they feed on fungi associated with dead wood, rather than directly on wood or bark. In New Guinea, bark beetles (Scolytinae) feed directly on host tissues and show strict congeneric / conspecific host specificity, whereas ambrosia beetles (Platypodinae and some Scolytinae), which feed on fungi they inoculate into dead or dying wood, show no such host specificity (Hulcr *et al*., 2007). Little is known about the feeding habits of other saproxylic weevils. In French Guiana, weevils associated with the Brazil nut family showed a preference for hosts within the *Bertholletia* clade, with 53% of the weevil species showing a selective preference for *Eschweilera coriacea,* a widely distributed host species within that clade (Fassbender, Chapter 2). If host specificity is a common phenomenon, loss of host species would result in a decrease in weevil species diversity due to the loss of the larval habitat.

The purpose of this study was to assess abundance, species richness, niche breadth, and beta-diversity, and of communities of saproxylic weevils associated with tress in the Brazil nut family in disjunct Amazonian forests (French Guiana and Peru). I expected Peru to yield greater weevil species richness and abundance due to the influences of higher plant productivity. Due to the 3300 km distance between the two study sites (Fig. 3.1), I also expected to find high species turnover. I expected weevils from both locations to prefer host species within the more derived *Bertholletia* clade of the Lecythidaceae (Fig. 3.2), particularly for *Eschweilera*, as shown in French Guiana (Fassbender, Chapter 2). I hypothesized that weevils would emerge in greater abundance in the rainy season because increased moisture during the rainy season decreases the chances of desiccation in adults.

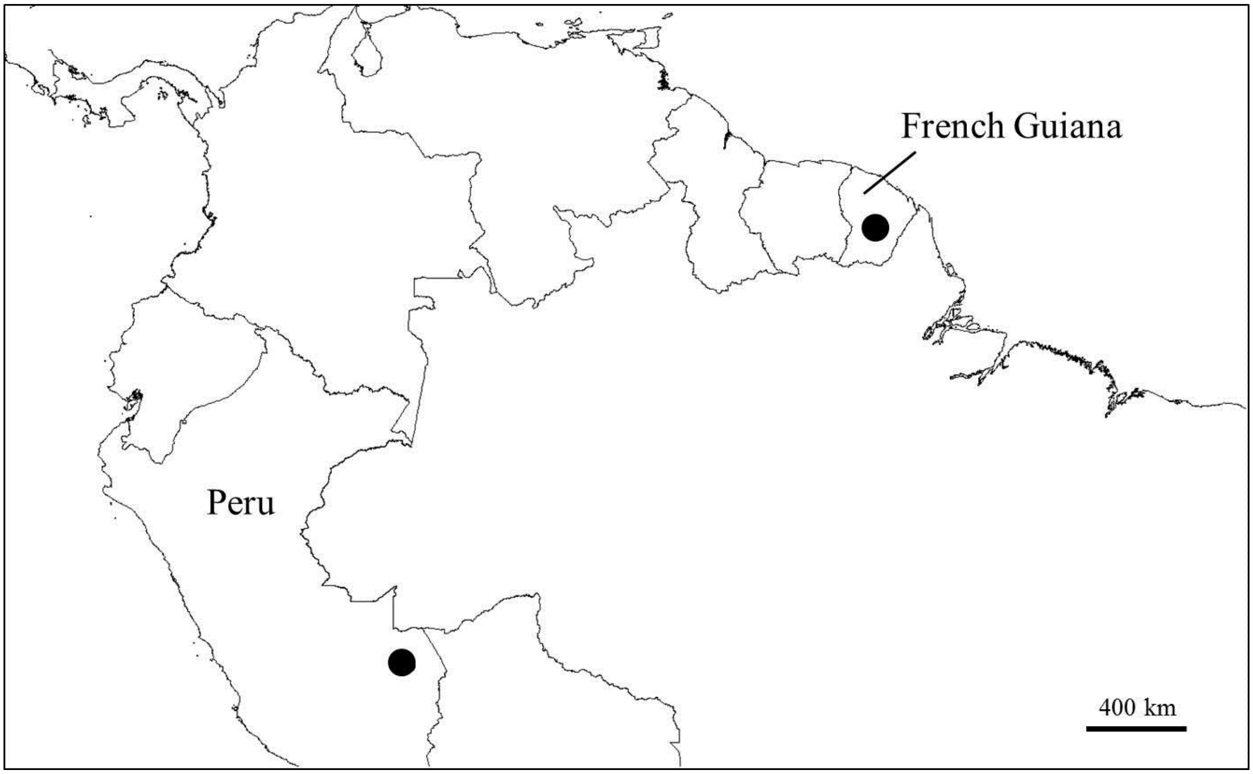


Figure 3.1: Study sites in French Guiana (1995 and 2007) and Peru (2003).

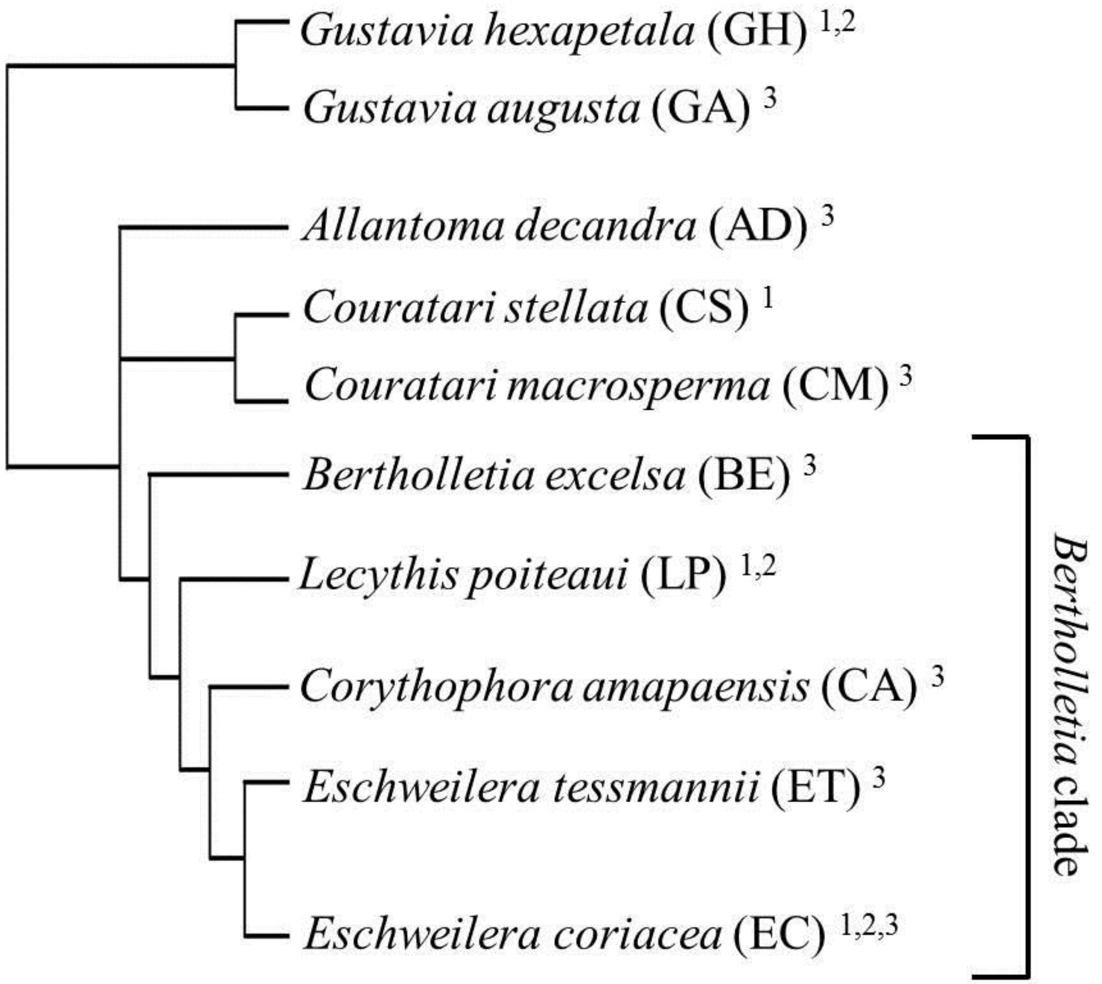


Figure 3.2: Phylogeny of Lecythidaceae host species sampled for saproxylic beetles (adapted from Huang, 2010); [1] French Guiana 1995; [2] French Guiana 2007; [3] Peru 2003.

Materials and Methods

The two study sites in this study were located in southeast Peru, and central French Guiana (Fig. 3.1), and the trees sampled belong to the Brazil nut family (Lecythidaceae, Fig. 3.2). Trees in this family were fairly abundant at both study sites. Because the Brazil nut is largely restricted to lowland moist tropical forest, and is not typically well-represented in secondary forest (Cornejo et al., 2008 onward) this suggests that even though the two sites were separated by vast distances and the Amazon River, similar forest types were sampled.

Forty seven percent of Peru's total land area is covered by primary forest (60,200 ha; 27% protected). French Guiana, while much smaller in size, has 94% of its land area covered with primary forests (7,700 ha; 30% protected) (FAO, 2010). Southeast Peru is located at the junction of two extremely productive ecoregions: the pantanal wet forest and Andean yungas. French Guiana is in the humid Guyana ecoregion (Morrone, 2006). This area of Peru has high levels of species richness for many organisms including birds, mammals, and plants, while French Guiana has relatively moderate levels of species richness (Bass, *et al*., 2012). Peru's soils are composed primarily of relatively young, fertile cambisols whereas French Guiana's soils are composed predominantly of much older and less fertile ferralsols. Tree productivity and species richness are higher in southeast Peru than in French Guiana; however, Lecythidaceae diversity is higher in French Guiana (ter Steege *et al*., 2006). This may be due to the presence of extensive primary forests in French Guiana (FAO, 2010), because Lecythidaceae are most grow best in old growth primary forests (Mori *et al.*, 2010 and onward).

Study Site

The French Guiana studies (1995 and 2007) took place in a lowland moist forest at near Les Eaux Claires (3°37-39’N, 53°12-13’W), located approximately seven kilometers north of Saul, French Guiana. The site was approximately 200 - 400 m above sea level. The terrain was hilly with well-drained soils. Forests were primary growth forests with little human disturbance (Berkov, pers. comm.). Cumulative rainfall for the 2007 study (recorded August 2007 through July 2008) was 2894.7 mm (Lee, 2010). The rainy season was from November to June with mean daily temperatures ranging from 22 - 23°C. The dry season was from July to October with mean daily temperatures ranging from 24 - 25°C (Lee, 2010).

The Peru study took place in a lowland moist forest at Los Amigos Research Center (Centro de Investigacion y Capacitation Rio Los Amigos, (CICRA) (12°32-34’S, 70° 05-06’ W), located approximately three kilometers north of Boca Amigos in the department of Madre de Dios, Peru). The site was approximately 268 m above sea level, and included terraced upland forest 41m above the Madre de Dios River. The forest was a mosaic of primary and secondary growth, and had been selectively logged for commercially valuable species (Pitman, 2008; Berkov, pers. comm.). Upland soils were typically sandy, acidic, and nutrient-poor relative to floodplain soils. Mean annual rainfall is close to 3000 mm per year, with 80% falling during the rainy season (October – May). Monthly mean temperatures range from 21 – 26° C; however, temperature extremes have been recorded of 39° C in summer and 8° C in winter (Pitman, 2008).

Tree selection

Lecythidaceae (the Brazil nut family) has a pantropical distribution and is particularly abundant and species-rich throughout the Neotropics (Mori *et al*., 1997). Trees sampled in the study represent major clades of Lecythidaceae (Huang, 2010) (Fig. 3.2): *Gustavia augusta* L., *Gustavia hexapetala* (Aubl.) Sm. (basal species); *Bertholletia excelsa* Bonpl., *Corythophora amapaensis* Pires ex S.A. Mori & Prance, *Eschweilera coriacea* (DC) S.A. Mori, *Eschweilera tessmannii* R. Knuth, and *Lecythis poiteaui* Berg, (members of the derived *Bertholletia* clade); and *Allantoma decandra*(Ducke) S.A.Mori, Y.-Y. Huang & Prance, *Couratari macrosperma* A.C. Sm., *Couratari stellata* A.C. Sm.. (members of a polytomy that includes the *Bertholletia* clade).

In French Guiana (FG) in 1995, five tree species were sampled and vouchered: CS, CA, EC, GH, and LP (Figures 3.3). Five individuals of each species were sampled in the dry season cut, and four individuals in the rainy season cut. Plant vouchers were deposited at the Herbier de Guyane (CAY), Cayenne, French Guiana and the New York Botanical Garden; see Berkov and Tavakilian (1999) for full details.

In Peru in 2003, six tree species were sampled and vouchered: AD, BE, CM, EC, ET, and GA (Figures 3.4). Four individuals of each species, except CM (*N* = 1), were sampled for both the dry and season cuts. Individuals of CM used for sampling differed between seasons. Replicates of CM were not included because nearby specimens were part of an unrelated long-term study. Tree species were identified by P. Centeno and A. Berkov using a key to local species prepared by S. A. Mori, and plant vouchers were collected for the local CICRA herbarium, Peru.

In French Guiana in 2007, nine individual trees belonging to three species of Lecythidaceae were resampled, focusing on the two most productive species: EC (*N* = 4) and LP (*N* = 4). A single individual of GH was sampled because the previous specimens in 1995 were sparsely colonized by weevils; see Fassbender, Chapter 2 for full details.

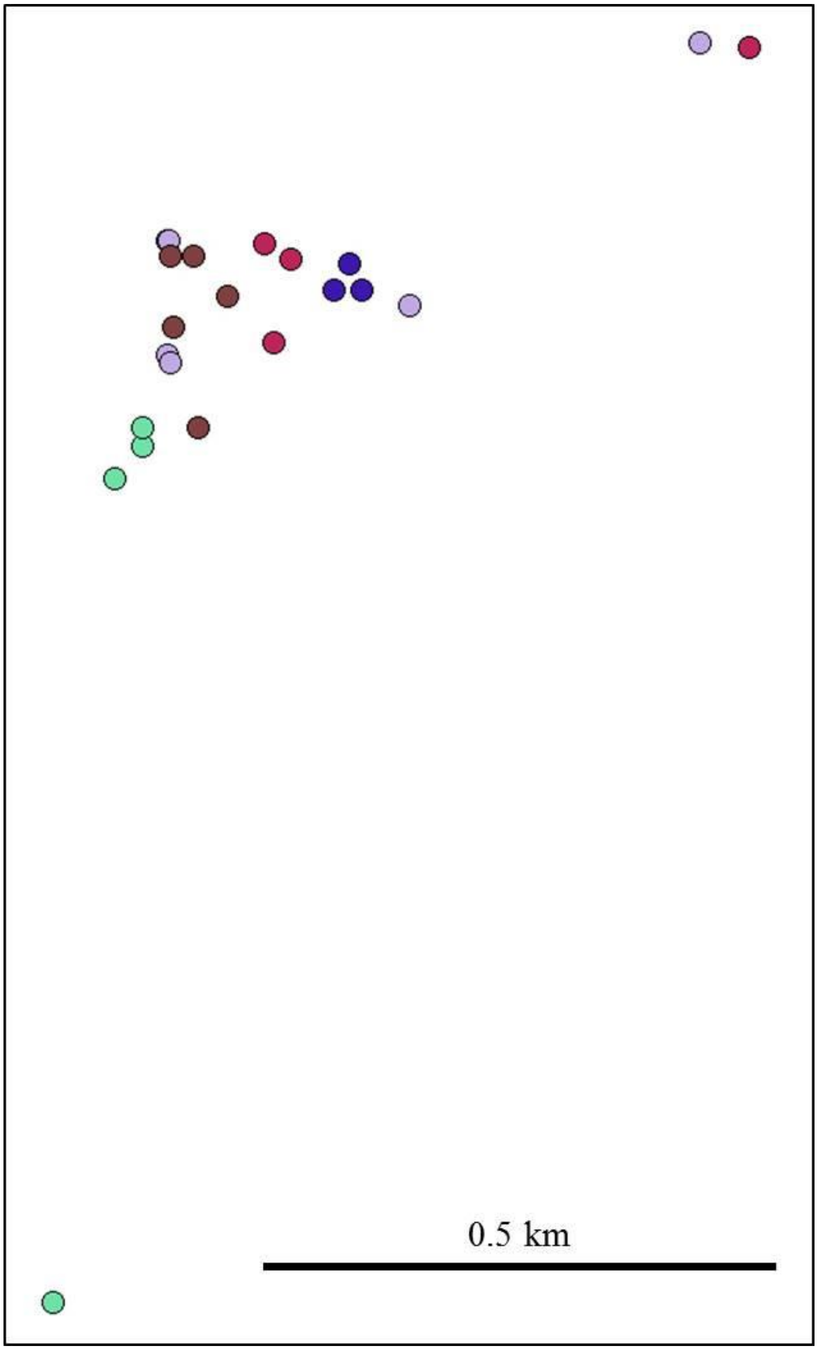


Figure 3.3: Location of trees in French Guiana: most were located along a one km section of the Sentier Botanique (1995 and 2007). Circles: Red = CA; Brown = CS; Green = EC; Blue = GH; Lavender = LP.

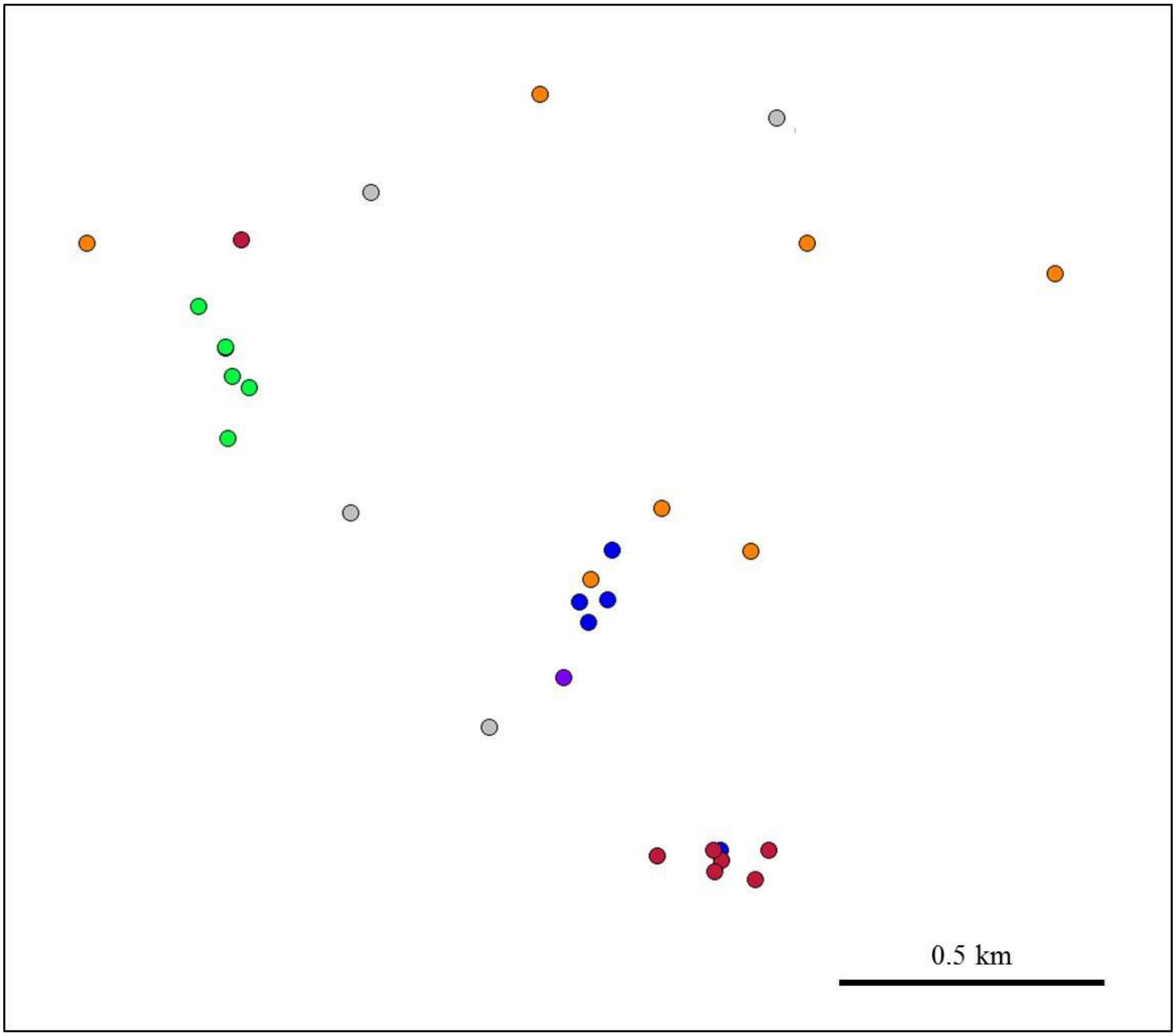


Figure 3.4: Location of trees in Peru; they were scattered along trails on both the upland plateau and in the low forest (2003). Circles: Orange = AD; Grey = BE; Purple = CM; Green = EC; Blue = ET; Red = GA.

Branch Sampling

Branches were cut from the sample trees during both dry and rainy seasons as bait to attract wood-boring beetles. The same procedure was followed in both seasons (see Berkov & Tavakilian (1999) for modifications during the original study). One branch was cut from each tree. A section (approximately 70 cm length) was severed and suspended as canopy bait in the tree from which it was cut. The rest of the branch was placed on the forest floor as ground bait. Bait branches were collected after approximately three months. Ground branches were cut into three thick (approximately 8 cm) and six thin (approximately 2 cm) sections. Three rearing cages were generated per tree: one containing the canopy sample, one with three thick ground samples, and one with six thin ground samples (Fig. 3.5).

All cages were monitored daily for emergence of adult beetles. Most branches stopped yielding specimens by January 2005. Each beetle was given a preliminary identification to species and preserved in 100% ethanol. Specimens were transported to the City College of New York (CCNY), New York, NY, USA, and identified by Charles O'Brien (Green Valley, AZ), or by comparing specimens to a reference collection of specimens previously identified by him. Beetle specimens from Peru were deposited in the Museo Nacional de San Marcos, Lima, Peru and are available at the American Museum of Natural History, New York, NY, USA.

Data analysis

Species richness data were compared by year, season, and host. Chao 1 species richness estimates and reciprocal Simpson's index (1/D) were calculated for both Peru (03) and French Guiana (07) with EstimateS 8.2 (Colwell, 2005). Chao 1 uses abundance data to calculate an estimate of minimum species richness. The measure is based on the rare species in a sample.

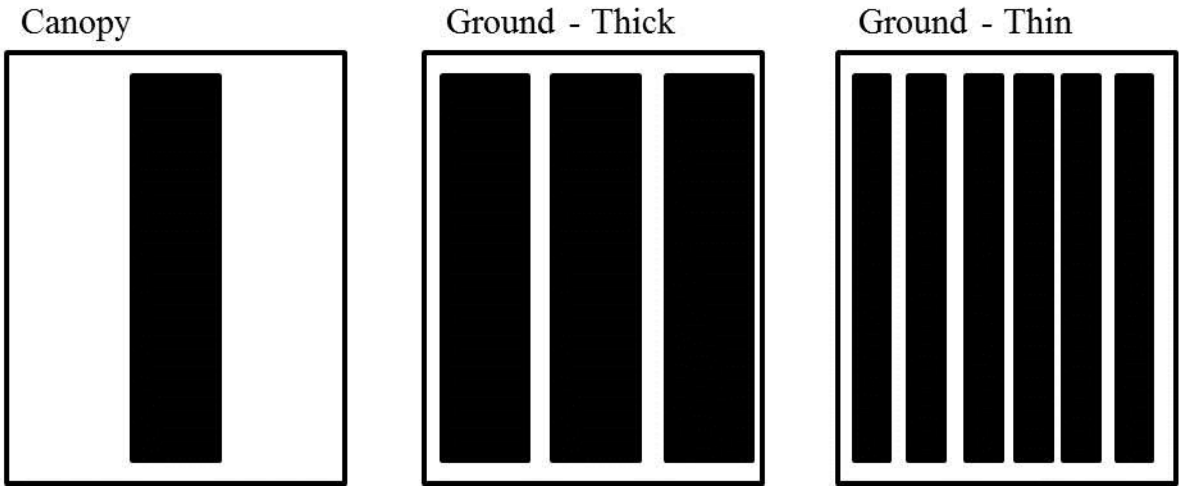


Figure 3.5: Branch number and quantity per rearing cage: branch length: ~ 70 cm, branch width: thick ~ 8 cm, thin ~ 2 cm.

Reciprocal Simpson's index is robust to rare species (Magurran, 2004). The Peru 03 dataset of weevil species samples were sorted by: host species (AD, BE, EC, ET, and GA), season (rainy or dry), and stratum (ground or canopy). Specimens lacking stratum data were excluded from the analysis. In the French Guiana 2007 weevil dataset, samples were also sorted by: host species (EC, GH, or LP), season (rainy or dry) and stratum (ground or canopy). Reciprocal Simpson's index was then used to calculate evenness ($E_{1/D}$):

$$\frac{1/D}{S}$$

where 1/D = reciprocal Simpson's and S = total species richness (Magurran, 2004). The Morisita-Horn index (C_{MH}) was calculated with EstimateS to assess species turnover between French Guiana (1995 and 2007 combined) and Peru 03 using a dataset including the following factors: Location (Peru or FG), Host (AD, BE, CM, EC, ET, GA, GH, or LP), and season.

Indicator species analysis was performed on the FG 07 / Peru 03 dataset to determine if any weevil species were predictively associated with location. Data were first transformed by general relativization to minimize the influence of extremes in absolute abundance. Then indicator values were calculated with the Dufrêne and Legendre (1997) method using PC-ORD 6.0 (McCune & Mefford, 2011). A Monte Carlo test of the significance of observed maximum indicator values was performed where p = (1 + number of runs $\geq$ observed) / (1 + number of randomized runs). For all PC-ORD analyses, weevil species not represented in two or more samples were excluded from analyses. Patterns of weevil abundance per location were explored using canonical correspondence analysis (CCA) (ter Braak, 1986) within PC-ORD 6.0. Weevil abundance data were log (x+1) transformed before analysis. The dataset included the following categorical factors: location (FG 95, FG 07, and Peru 03) and season (rainy or dry). Axis scores were standardized by Hill's (1979) method and scaled to optimize representation of explanatory variables. The statistical significance of the correlation between species and environment was evaluated using a Monte Carlo permutation test (998 permutations) where p = (1 + no. permutations ≥ observed) / (1 + no. permutations).

A goodness of fit test (G-test) was performed on the Peru 03 data to determine whether weevil abundance was proportional among seasons (Sokal & Rohlf, 1995; McDonald, 2009). Weevil abundance per season was calculated for the weevils belonging to the three most abundant subfamilies in all three experiments (FG 95, FG 07, and Peru 03), and also for the weevil genera belonging to the most abundant subfamily. Indicator species analysis was performed on the FG 07 / Peru 03 dataset to determine if any weevil species were predictively associated with season. Data were first transformed by general relativization to minimize the influence of extremes in absolute abundance. Then indicator values were calculated with the Dufrêne and Legendre (1997) method using PC-ORD 6.0 (McCune & Mefford, 2011). A Monte Carlo test of the significance of observed maximum indicator values was performed where p = (1 + number of runs ≥ observed) / (1 + number of randomized runs). A second G-test was performed on the Peru 03 data to determine if weevil abundance was proportional between host tree species. Abundance by host was calculated for the two locations and for each year sampled (FG 95, FG 07, and Peru 03). Indicator species analysis was performed as previously described on the FG 07 / Peru 03 dataset to determine if any weevil species were predictively associated with a particular tree species. A two-way cluster analysis was performed with PC-ORD 6.0 on the Peru 03 data to assess consistency of weevil host and season association across all host trees. The analysis was performed on a weevil dataset including the following categorical factors: host species (AD, BE, CM, EC, ET, or GA) and season (rainy or dry). Group average linkage method and Sorensen (Bray-Curtis) distance measure were used for analysis.

For the Peru 03 data, species were classified as specialists if 90% of the specimens were associated with a single host, season, or stratum. Species with fewer than 10 individuals were excluded from specialist classifications due to insufficient data; classifications are considered tentative when sample sizes are small. Patterns of weevil habitat use were further explored for Peru 03 using canonical correspondence analysis (CCA) within PC-ORD 6.0. Abundance data were log (x+1) transformed before analysis. The dataset included the following categorical factors: host tree species (AD, BE, GA, EC, or ET), and season (rainy or dry). CM was excluded due to unequal sampling. Axis scores were standardized by Hill's (1979) method and scaled to optimize representation of explanatory variables. The statistical significance of the correlation between species and environment was evaluated using a Monte Carlo permutation test (998 permutations) where p = (1 + no. permutations $\geq$ observed) / (1 + no. permutations).

Results

Species Richness and Diversity

The three rearing studies (French Guiana (1995, 2007) and Peru (2003) yielded 5177 weevil specimens in 93 species (Appendix 2; excluding Scolytinae and Platypodinae). Peru 03 had greater species richness than French Guiana (Fig. 3.6). From similar wood volumes, French Guiana (1995) yielded 986 individuals in 27 weevil species and Peru (2003) yielded 2929 individuals in 72 species (Table 3.1). French Guiana (2007), which included fewer samples but focused on the most productive host species, yielded 1262 individuals in 24 species. Twenty-one weevil species were collected only in FG (1995 and 2007), while 54 species were collected only in Peru, and eighteen species were shared between the two locations. Thirteen of the species reared in both locations belong to the subfamily Conoderinae; these accounted for 78% of total specimens. In Peru (2003), seven conoderine species were represented by >100 individuals and made up 95% of abundance: *Piazurus alternans* (*N* = 138), *P. incommodus* (*N* = 124), *P. pseudoalternans* (*N* = 186), *Pseudopinarus cerastes* (*N* = 136), *Zygops histrio* (*N* = 296), *Z. leucogaster* (*N* = 1331), and *Zygops* sp. 4 (*N* = 420). In French Guiana (1995, 2007), only four of these seven species were represented by >100 individuals as well as two additional species: a conoderine, *Piazurus* sp. 3, and the cryptorhynchine *Pisaeus* sp. 1 (Appendix 3).

In Peru, the species richness of saproxylic weevils associated with the Brazil nut family was estimated to be more than twice as high as in French Guiana (Peru 03: *N* = 56, Chao 1 = 104; FG 07 *N* = 24, Chao 1 = 48) (Table 3.1). Due to the relatively high species richness, but low evenness in Peru, Simpson's reciprocal diversity index indicated that species diversity was equal between locations (Peru 03 = 5.19; FG 07 = 5.19). Species turnover was high between sites (Morisita-Horn index =0.177); however, the shared species accounted for much of the weevil abundance (Table 3.1). Two species had statistically significant indicator values for Peru 03 (*Zygops leucogaster*, *p* = 0.026; *Zygops* sp. 4, *p* = 0.004), while one species exhibited a statistically significant indicator value for French Guiana (*Piazurus pseudoalternans*, *p* = 0.018). Two of these species were, however, reared at both sites. The number of species reared was less than the lower confidence interval of the Chao 1 estimate for both locations. The canonical correspondence analysis shows clear separation of weevil communities by location. The cumulative variance explained by the three CCA axes was 73.8% (axis 1: 38.2 %, axis 2: 14 %, axis: 21.6 %), suggesting a moderate correlation between host and season and weevil abundance (total inertia = 0.6699; cumulative explained inertia = 0.4944; Fig. 3.7). The remaining variance was unexplained (26.2%). The correlation between species and environment was not statistically significant (*p* = 0.4645).

Table 3.1: Species richness and diversity by subfamily shows that Peru 03 had the greatest overall species richness and abundance.

	***N* species**	***N* Individuals**
FG 95	27	986
FG 07	24	1262
Peru 03	72	2929
	***N* Shared Species**	**% Ind in Shared Species**
FG 95 and 07	13	90
FG 95 and Peru 03	14	90
FG 07 and Peru 03	15	58
All FG and Peru	18	91
Species Richness	**Peru 03**	**FG 07**
N species	56*	24
Chao 1[1]	104	48
Chao 1 CI[2]	73-191	27-191
1 / D[3]	5.19	5.19
Evenness	0.09	0.22

[1] Chao 1 = Chao 1 richness estimator; [2] Chao 1 CI = Chao 1 95% Confidence interval; [3] 1 / D = reciprocal Simpson's index. *Species lacking stratum data were excluded from analysis.

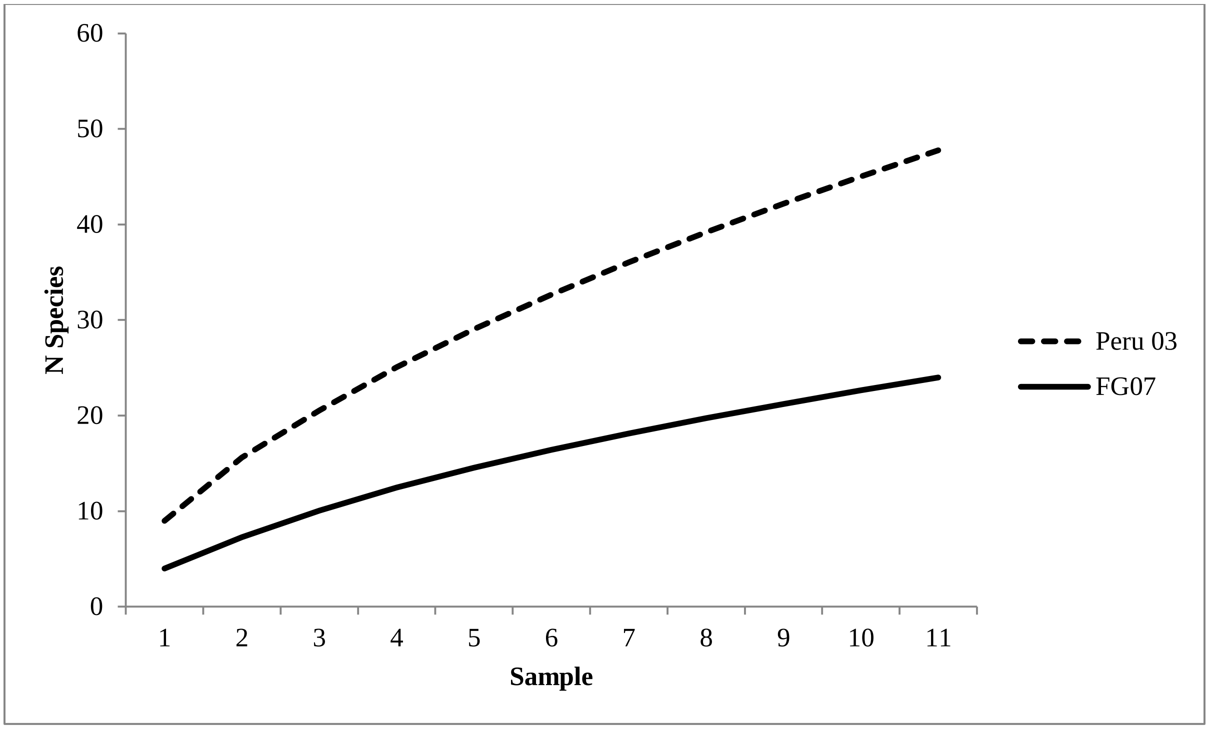


Figure 3.6: Species accumulation by locality shows that Peru 03 had higher species richness than French Guiana.

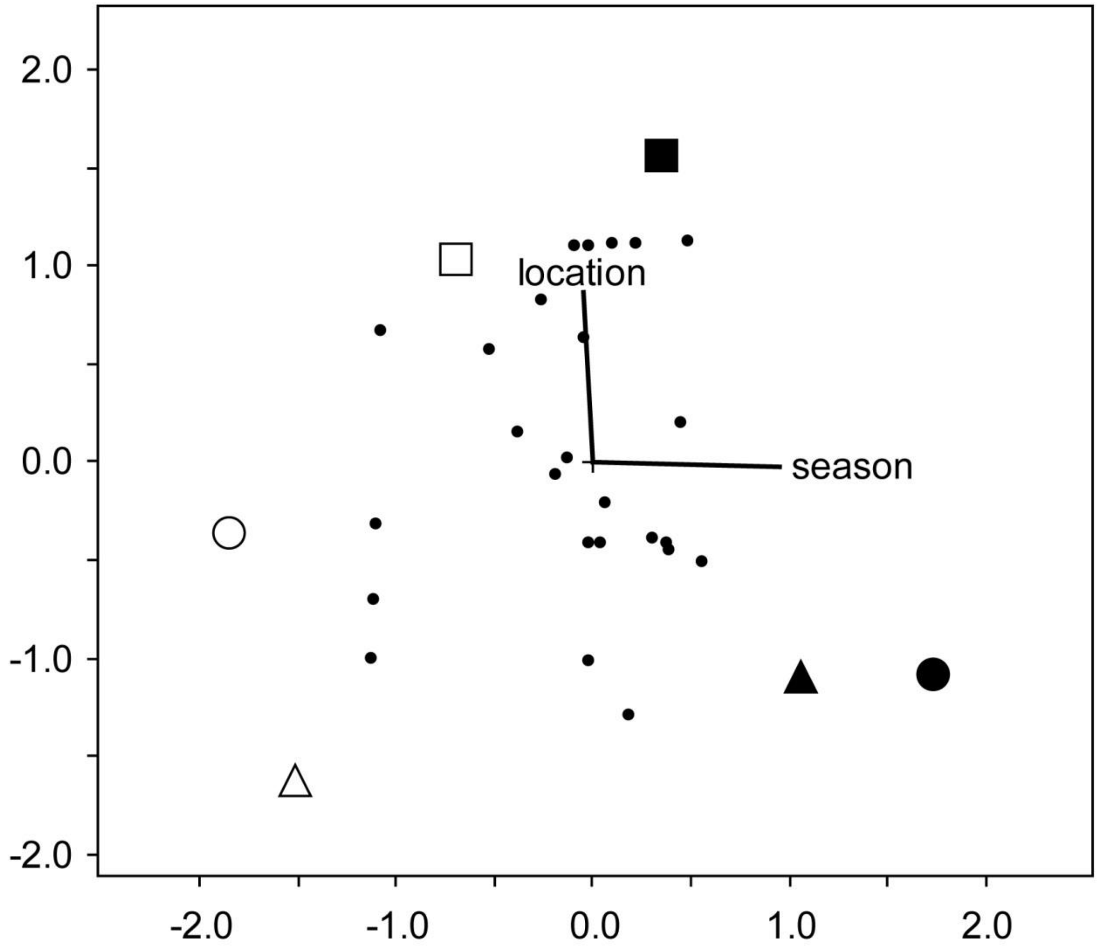


Figure 3.7: Canonical correspondence analysis for French Guiana (1995, 2007) and Peru 03 shows clear segregation by location and season. Triangle = French Guiana (FG) 1995, Square = Peru 2003, Circle = FG 07. Open = dry, Solid = rainy; Black dots indicate individual weevil species.

Seasonality

In Peru 03, the dry season exhibited greater species richness and abundance than the rainy season (dry season: 2099 individuals in 52 species; rainy season: 830 individuals in 42 species) (G = 568.438, $p < 0.00001$; Table 3.2). All weevil subfamilies, and the two most abundant conoderine genera (*Zygops* and *Piazurus*), emerged in higher numbers from branches cut during the dry season (Figs. 3.8, 3.9). In FG 07, the rainy season had both the highest weevil species richness and abundance (dry season: 83 individuals in 11 species; rainy season: 1173 individuals in 19 species) (Appendix 3). All weevil subfamilies and the two most abundant conoderine genera (*Piazurus* and *Copturomorpha*) emerged in greater numbers from branches cut during the rainy season (Figs. 3.8, 3.9). *Pseudopinarus* and *Zygops* were represented by fewer individuals, but emerged in greater abundance from branches cut during the dry season (Fig. 3.8). FG 95 differed in that both cryptorhynchines and conoderines were better represented in branches cut during the dry season (Figs. 3.8, 3.9).

In Peru 03, six of the fifteen weevil species represented by 10 or more individuals were classified as dry season specialists, while none were classified as rainy season specialists, and the remaining nine species were season generalists (Appendix 3). In FG 07, eight of the ten species represented by 10 or more individuals were classified as rainy season specialists, one species as a dry season specialist, and only one as a season generalist (Appendix 3). One weevil species, *Piazurus incommodus*, was classified as dry season specialist in Peru, but was a rainy season specialist in French Guiana (Appendix 3). None of these species, however, exhibited statistically significant indicator values for either season or location.

Table 3.2: G-test for season in Peru 03 indicates that saproxylic weevils emerged disproportionately from branches cut during the dry season.

Season	**Sample *N*[1]**	**Ind. Obs.[2]**	**Ind. Exp.[3]**	**Ratio obs./exp.[4]**	**df**	***G***	***p***
Dry	1	2099	1464.5	1.43	1	568.438	< 0.00001
Rainy	1	830	1464.5	0.56			

[1] Ratio of branch sections. [2] Number of individuals reared by season. [3] Number of individuals expected to be reared each season. [4] Ratio of individuals observed to expected.

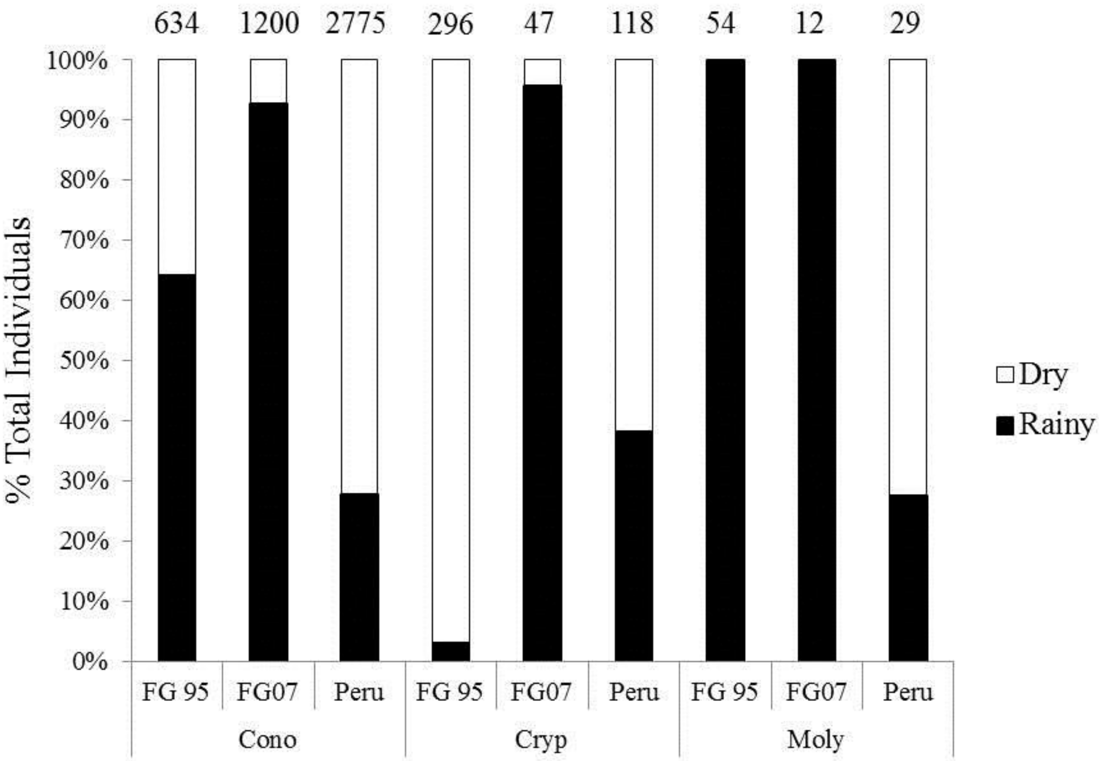


Figure 3.8: In Peru, weevils were more abundant in dry season branches. Percentages were generated separately by subfamily; total *N* individuals are indicated above columns. Cono = Conoderinae, Cryp = Cryptorhynchinae, and Moly = Molytinae.

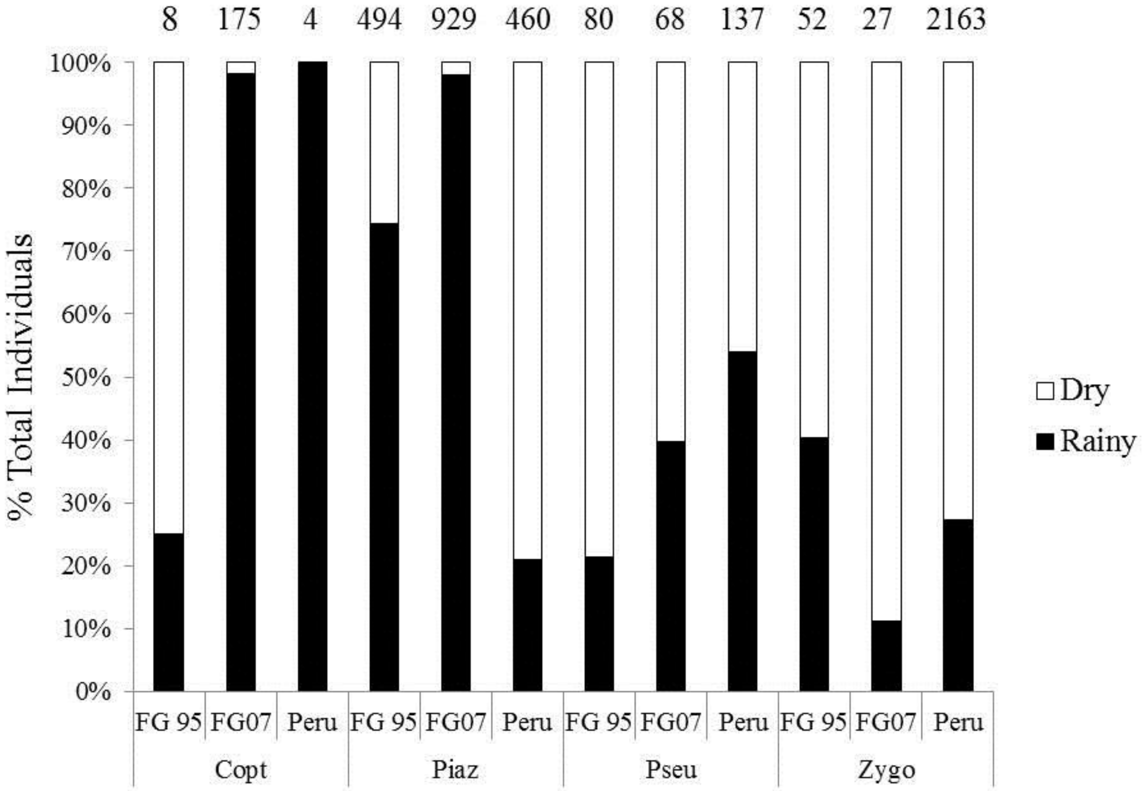


Figure 3.9: Within the subfamily Conoderinae, weevils in the genera *Zygops* and *Pseudopinarus* appear to be more drought-tolerant. Percentages were generated separately by genus; total *N* individuals are indicated above columns. Copt = *Copturomorpha*, Piaz = *Piazurus*, Pseu = *Pseudopinarus*, and Zygo = *Zygops*.

Host Association

In both Peru 03 and French Guiana 2007, *Eschweilera coriacea* yielded the greatest weevil abundance (Peru 03: AD = 377, BE = 625, CM = 12, EC = 1773, ET = 188, GA = 142; FG 07: EC = 934, GH = 57, LP= 271) (Fig. 3.10; Appendix 2). In Peru 03, the difference between numbers of weevils collected among hosts was significantly higher than can be explained by variation among number of branches sampled (G = 2175.21, df = 5, $p < 0.00001$; Table 3.3). In Peru 03, the conoderine weevil genus *Zygops* emerged in greater numbers from EC. Conoderine weevils were reared with the second highest abundance from BE. In FG 07, *Piazurus* yielded the greatest abundance from EC, while *Zygops* species richness and abundance was low from all hosts (Appendix 2).

In Peru 03, only 20% of the 15 species with ten or more individuals were classified as specialists associated with a particular host species; one on EC, one on GA, one on BE; the remaining twelve species had broader host ranges (Appendix 2). In FG 07, 70% of the ten species with ten or more individuals were classified as specialists associated preferentially with a particular host species; four on EC, one on GH, two on LP, and the remaining three species collected from both EC and LP (Appendix 2). The two-way cluster analysis for Peru 03 shows that of the two taxa that form a polytomy with trees in the *Bertholletia* clade, *Allantoma decandra* clusters with the *Bertholletia* clade. *Couratari macrosperma* tends to cluster with the basal species *Gustavia augusta* (which yielded very few weevils other than *Pseudopinarus cerastes*). *Eschweilera coriacea* (both seasons) and *B. excelsa* (dry season) formed a cluster associated with particularly high weevil species richness; colonization of *Eschweilera tessmannii, A. decandra, C. macrosperma*, and *G. augusta* was more sporadic (Fig. 3.11).

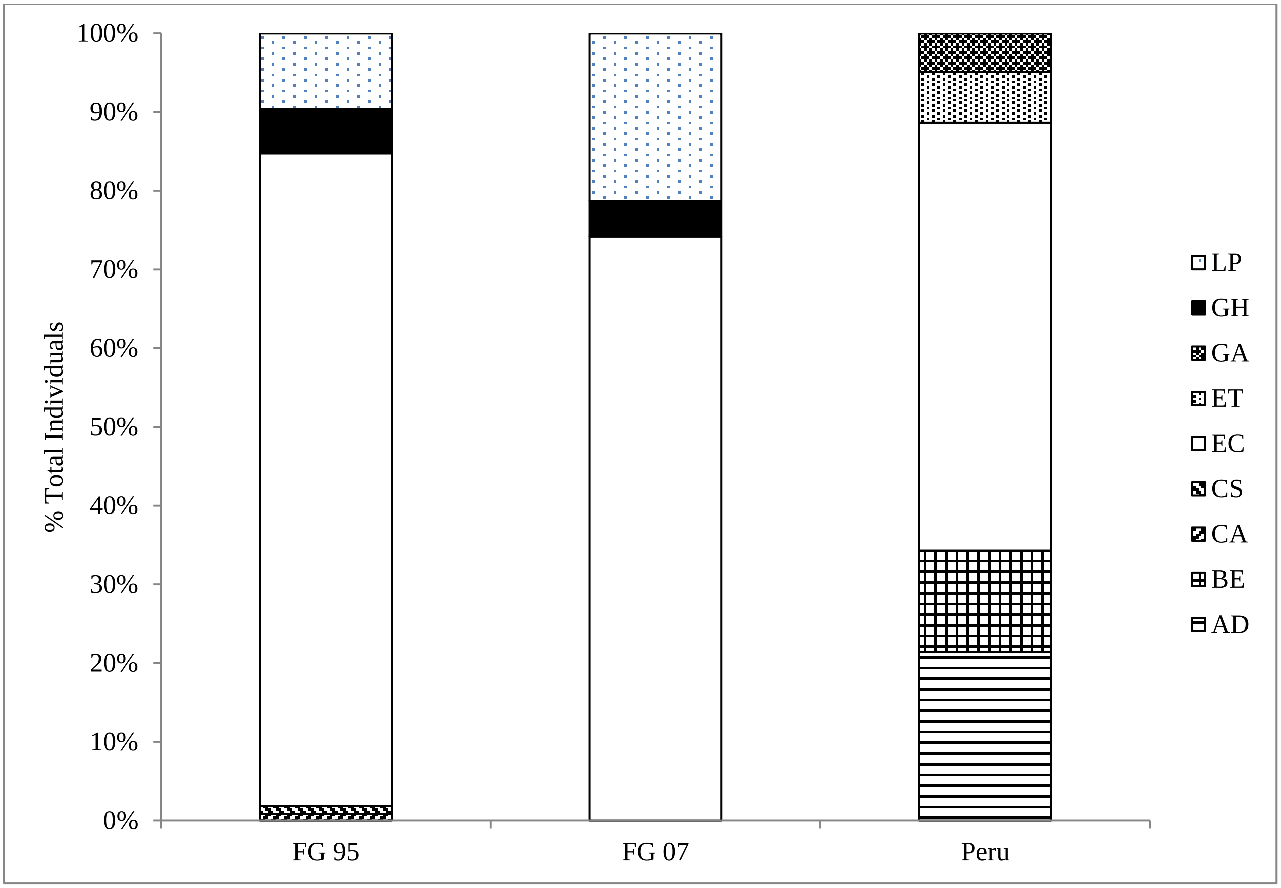


Figure 3.10: Host associations for Peru and French Guiana shows most weevils were reared from *Eschweilera coriacea*. AD = *Allantoma decandra*, BE = *Bertholletia excelsa*, CS = *Couratari stellata*, CM = *Couratari macrosperma*, CA = *Corythophora amapaensis*, EC = *Eschweilera coriacea*, ET = *Eschweilera tessmannii*, GA = *Gustavia augusta*, and GH = *Gustavia hexapetala*.

Table 3.3: G-test for host in Peru 03 indicates weevils emerged disproportionately from *Eschweilera coriacea*.

Host Genus	**Sample *N*[1]**	**Ind. Obs.[2]**	**Ind. Exp.[3]**	**Ratio obs./exp.[4]**	**df**	***G***	***p***
Allantoma decandra	4	377	558	0.68	5	2715.21	< 0.00001
Bertholletia excelsa	4	625	558	1.12			
Couratari macrosperma	1	12	139	0.09			
E. coriacea	4	1587	558	2.84			
E. tessmannii	4	187	558	0.33			
Gustavia augusta	4	142	558	0.25			

[1]Number of branch sections. [2]Number of individuals reared by branch. [3]Number of individuals expected to be reared by branch. [4]Ratio of individuals observed to expected.

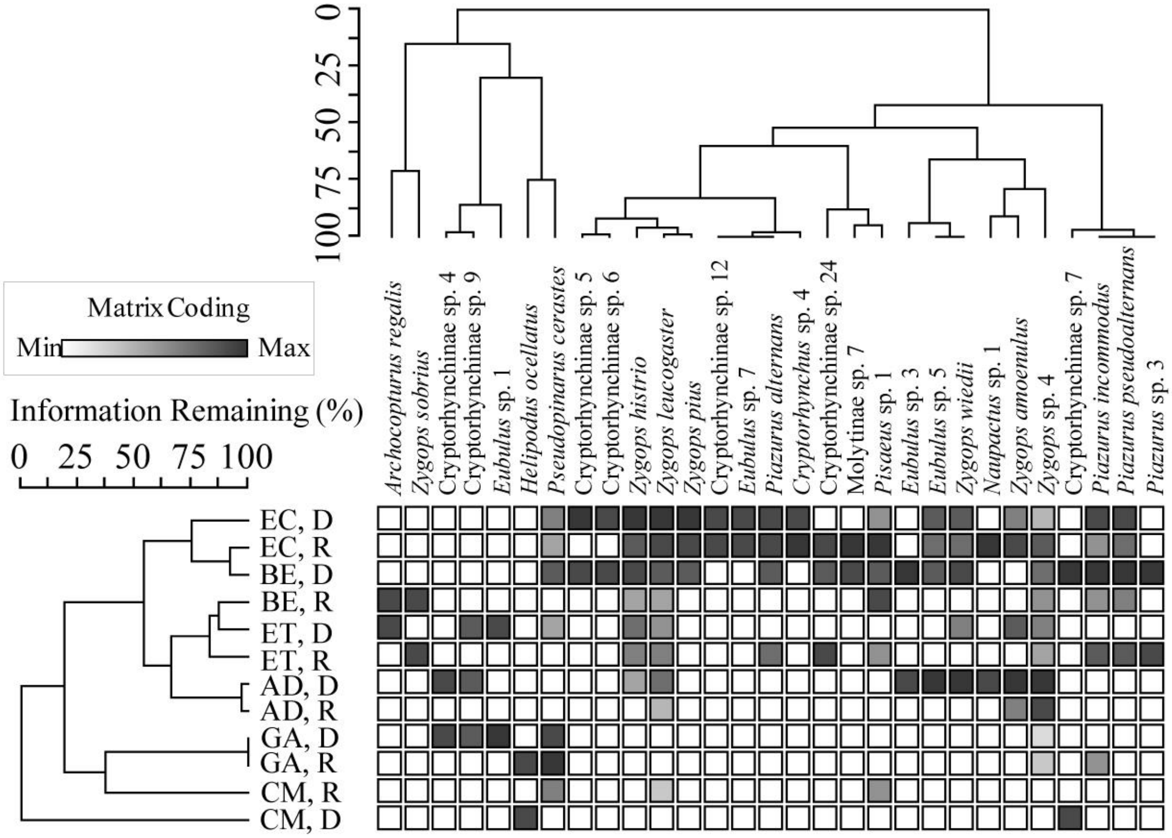


Figure 3.11: Two-way cluster analysis for Peru 03 indicates that weevils favor the *Bertholletia* clade. AD = *Allantoma decandra*, BE = *Bertholletia excelsa*, CM = *Couratari macrosperma*, EC = *Eschweilera coriacea*, ET = *Eschweilera tessmannii*, and GA = *Gustavia augusta*; D = dry, R = rainy.

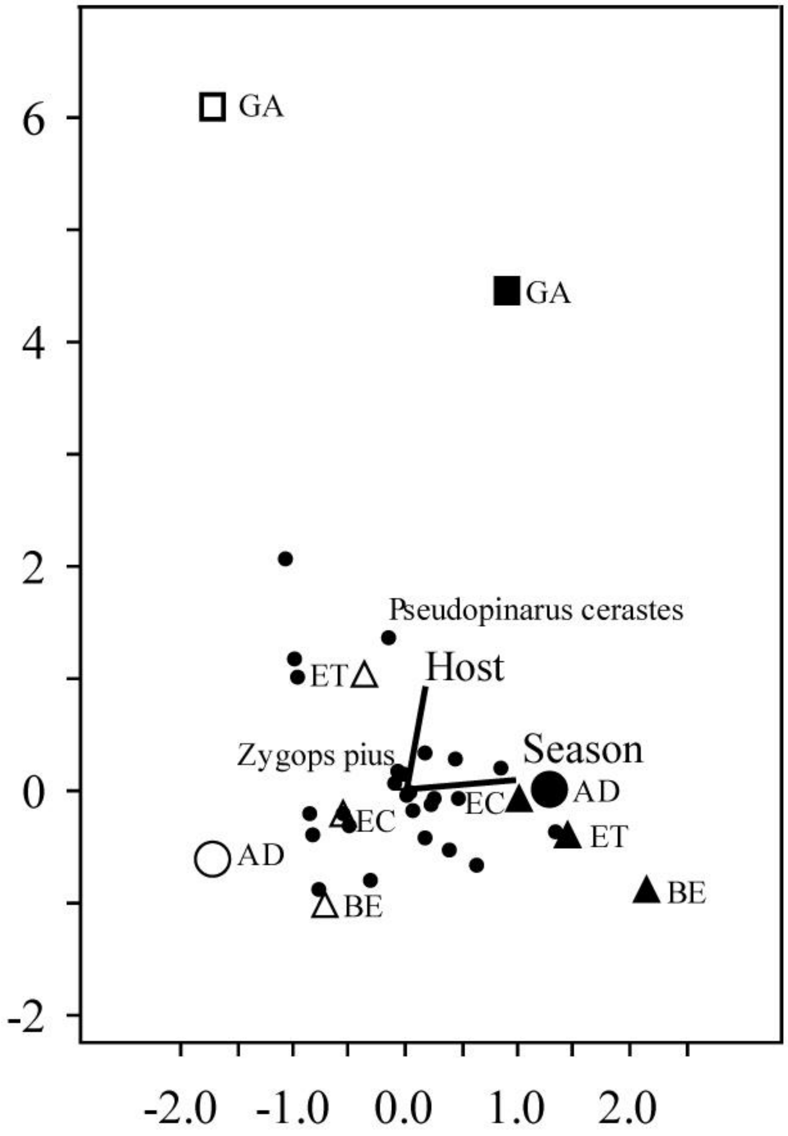


Figure 3.12: Canonical correspondence analysis for Peru 03 shows clear segregation by host and season. AD = *Allantoma decandra*, BE = *Bertholletia excelsa*, CM = *Couratari macrosperma*, EC = *Eschweilera coriacea*, ET = *Eschweilera tessmannii*, and GA = *Gustavia augusta*; open = dry, solid = rainy; black dots indicate individual species; Square = *Gustavia augusta*, circle = part of polytomy with *Bertholletia* clade, triangle = member of *Bertholletia* clade. Named species are those considered to be host specialists: *Pseudopinarus cerastes* on GA, *Zygops pius* on EC.

Bertholletia excelsa and ET yielded weevils that were not reared from EC, but the species that were reared most consistently from BE were also reared from EC. In spite of the apparent preference for EC, there were no weevil species (in either Peru 03 or FG 07) with significant indicator values for EC, while one species had a statistically significant indicator value for the genus *Gustavia* (*Pseudopinarus cerastes*, $p = 0.004$) and one species for *A. decandra* (*Zygops* sp. 4, $p = 0.028$).

In Peru 03, the cumulative variance explained by the three CCA axes was 51.5% (axis 1: 16.2 %, axis 2: 7.9 %, axis: 27.4 %), suggesting a moderate correlation between host and season and weevil abundance (total inertia = 1.3113; cumulative explained inertia = 0.676; Fig. 3.12). The remaining variance was unexplained (48.5%). The correlation between species and environment was not statistically significant ($p = 0.842$). *Gustavia augusta* (rainy and dry) shows clear separation from other host species. Samples from the rainy and dry season form distinct clusters.

Discussion

Diversity

The high species richness in plants and vertebrates that has been documented in southeast Peru (ter Steege *et al*., 2006; Bass *et al.*, 2010) appears to extend to saproxylic weevils associated with the Brazil nut family. Peru had nearly twice the species richness of the two French Guiana studies combined. High species richness in Peru can likely be attributed to topographic and climatic heterogeneity as well as to variation in levels of disturbance by humans (Morrone, 2006; ter Steege *et al*., 2006; Bass *et al.*, 2010; FAO, 2010). The most abundant weevil species, in the subfamily Conoderinae, were reared at both sites. The consistent presence of a cohort of conoderine weevils in such disjunct forests, particularly species of the genera *Piazurus* and *Zygops*, argues for a long, stable association with the Brazil nut family. However, the Peru site yielded more singletons which may not be associated with the Brazil nut family. An association could be confirmed with data from a more taxonomically diverse plant sample, as exists for Neotropical cerambycid beetles (Tavakilian *et al.*, 1997).

Weevil abundance was also greater in Peru than in French Guiana. The two French Guiana studies cumulatively yielded only 77% of the abundance found in Peru, even though similar volumes of wood were sampled in FG 95 and Peru 03. The FG 07 study included fewer samples than either of the previous studies, but focused on the most densely colonized host species from FG 95. The high weevil abundance in Peru may be due to the nutrients available in the younger soils in western Amazonia and the resulting increase in plant productivity and wood biomass (ter Steege *et al.*, 2006; Quesada, *et al*., 2011); thus increasing the availability of food sources and rearing substrate for saproxylic beetles that feed on moribund wood.

Species turnover between Peru and French Guiana was high, with only 16% of wood-boring weevil species shared between the two localities. The vast geographic distance and gradient in plant productivity between the two sites likely had a major effect on species richness and turnover at each site because even short distances can strongly influence wood-boring beetle species composition (Ødegaard, 2006). While species turnover was high between the two sites, the shared species were the most abundant species at each locality. Shared species emerged in the largest numbers from members of the *Bertholletia* clade, with the highest abundance from *E. coriacea*, a host species that is widely distributed across the Neotropics and was sampled at both sites.

Niche Breadth

Seasonal differences in weevil composition were detected in between localities. French Guiana (2007) had higher weevil species richness and abundance from branches cut during the rainy season, consistent with the hypothesis that saproxylic weevils are strongly moisture dependent. Peru, on the other hand, the higher weevil species richness and abundance from branches cut during the dry season. In Peru, the most abundant species collected in the dry season consisted primarily of conoderines from the genus *Zygops*. *Zygops* is characterized by species that appear to be diurnal because they have bright or contrasting colors, and may be better adapted to drier conditions. The conoderine genus that was most abundant in French Guiana was *Piazurus,* which includes relatively small species with cryptic coloration that may be more moisture dependent. Precipitation patterns differed at the two sites which may have influenced colonization. Although mean annual rainfall was similar, the periodicity was different and might be more evenly distributed in Peru (Fig. 3.13). Additionally, the greatest difference between dry and rainy season colonization was found in the FG 07 project. In the FG 95 and Peru 03 projects, the dry season branches were exposed to beetles until the rainy season branches were prepared, and therefore were exposed to beetles at the onset of the rainy season. In the FG 07 project the dry season branches were collected and caged prior to the onset of the rainy season, and this may well have resulted in the documentation of more extreme weevil seasonality.

Consistent associations of weevil species with particular hosts across time and distance can yield important information on host preference. In both French Guiana and Peru, the majority of the weevils were reared from host trees belonging to the derived *Bertholletia* clade,

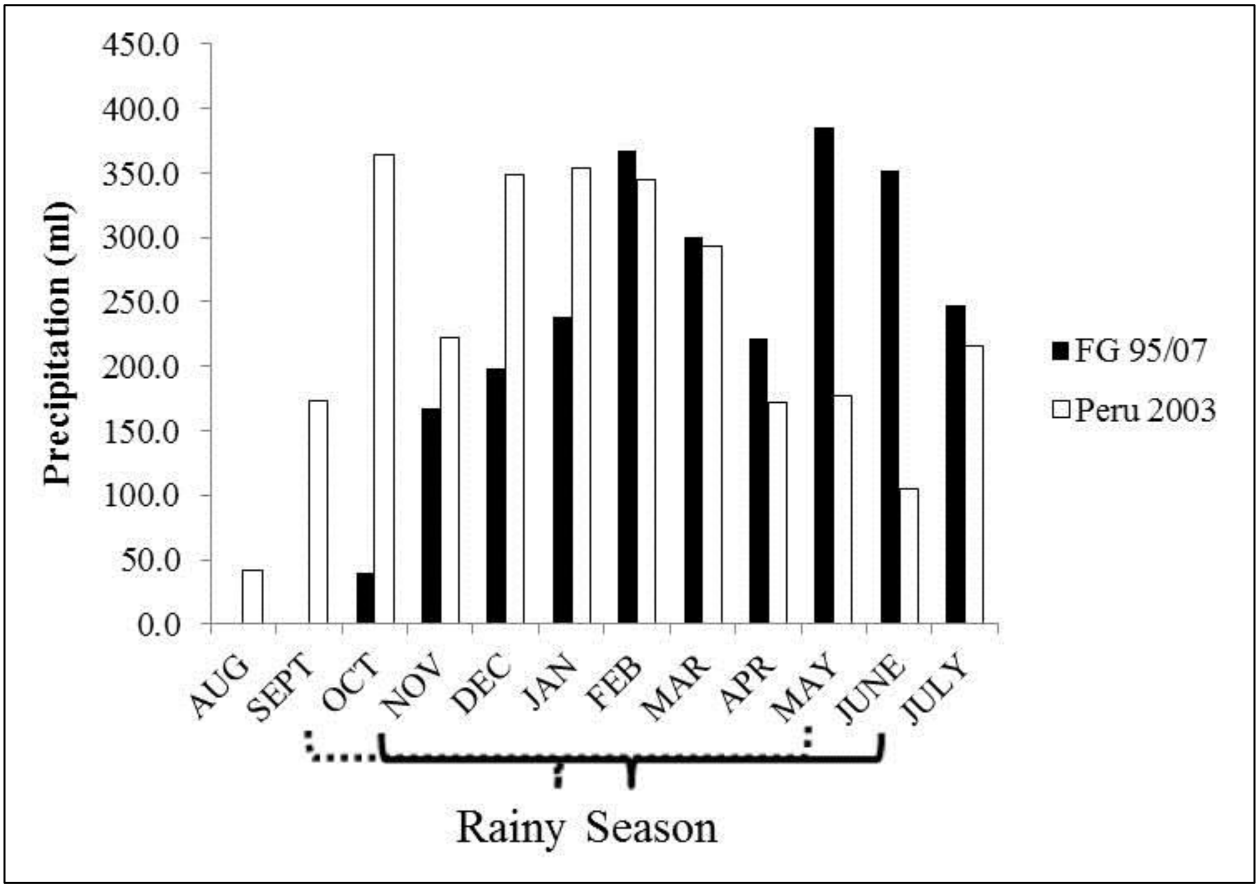


Figure 3.13: Precipitation in French Guiana (1995 / 2007) and Peru (2003). Dashed line = Peru rainy season; solid line = French Guiana rainy season. French Guiana data were averaged over the two study years, but data were missing for Aug and Sept. FG 2007 data adapted from Lee, 2010; FG 1995 data from Berkov, unpublished, and Peru 2003 from CICRA (2005-2012).

which includes most Neotropical species (Huang, 2010). There was a consistent preferential association with *Eschweilera coriacea* (EC), which has a widespread geographic distribution and tends to be locally abundant (Mori *et al*., 2010 onward).

Conservation implications

South American rainforests are expected to experience increased temperatures and decreased precipitation over the next century causing shifts in host phenology or geographical distribution (Lewinsohn *et al*., 2005) severely impacting species that rely on them to survive and reproduce. Lecythidaceae is currently restricted to moist tropical habitats (Mori *et al.*, 2010onward) and has relatively higher diversity in French Guiana than in Peru (ter Steege *et al*., 2009).Under current climate prediction models, northeast Amazon, including the Guiana shield are expected to experience increasingly long dry seasons and reduced humidity. These changes are expected to have a detrimental effect on host populations and limit their ranges. One Lecythidaceae species, *Lecythis poiteaui*, is limited in range to the northeast Amazon and Guiana shield. As the climate changes its home range would be expected to shrink, putting both the tree species and any weevil species that rely upon it, at risk of extinction. In both localities, hosts with restricted geographic distributions were seemingly used as supplemental hosts by weevil species.

In Peru, moisture appears to be more evenly distributed throughout the year, thus decreasing insect susceptibility to drought. Dramatic differences in periodicity and drought potential can lead to extreme variation in precipitation between locations and even between years in the same location. The southeast Amazon, including southeast Peru, is expected to be less impacted by climate change with only a mild to moderate projected decrease in annual moisture

(Miles *et al*., 2004). This minimal climate change will aid in the retention of weevil species diversity in the Neotropics. While Lecythidaceae thrives in old growth habitats, the favored host species of Neotropical wood-boring weevils, *Eschweilera coriacea,* has a wide geographical distribution (Mori, *et al*., 2010 onward) and seems adaptable to the effects of variation in seasonality. This host species might provide a refuge for many of the saproxylic species associated with the Brazil nut family as forests become increasing fragmented and stressed. Although much conservation emphasis is currently placed upon endemic species that are most threatened by deforestation and global change, geographically widespread species such as *E. coriacea* are probably in the best position to conserve species interactions and, as keystone species, should have an important place at the conservation table.

CHAPTER 4

Resource Partitioning in Saproxylic Beetles (Coleoptera: Cerambycidae, Curculionidae) in French Guiana, and Potential Effects of Global Climate Change

Abstract

Over the next century, greenhouse gas levels are expected to continue to increase, driving increases in temperature and decreases in rainfall. High levels of CO_2 may help the trees in tropical forests withstand a drought-induced decrease in photosynthetic efficiency; however, their fitness might be negatively impacted by the loss of saproxylic arthropods that facilitate the return of nutrients to the soil from dead wood. This rearing study examines resource partitioning in Neotropical saproxylic cerambycid and curculionid beetles. I hypothesized that curculionids and cerambycids would be associated with trees in the *Bertholletia* clade. I also hypothesized that small bodied curculionid species would be preferentially associated with the rainy season, ground stratum branches while larger bodied cerambycids would be associated with drier substrates. ANOVAs were conducted to determine if beetle abundance and species richness was proportional between hosts. A G-test for goodness of fit was conducted to determine whether weevil abundance was proportional between seasons. Community structure was examined through multivariate analyses (two-way cluster, canonical correspondence, and indicator species). Beetles in the cerambycid subfamily Cerambycinae were most abundant at canopy stratum during the dry season, while beetles in the subfamily Lamiinae were most abundant at ground stratum during the dry season and at canopy stratum during the rainy season. Small-bodied weevils (Conoderinae), as well as bark and ambrosia beetles (Platypodinae and Scolytinae), were most abundant during the rainy season, with conoderines and platypodines best represented at ground stratum. As the tropics become warmer and dryer, Cerambycinae are expected to thrive, while Lamiinae may adapt to drying conditions by shifting from canopy to ground stratum. Neotropical weevils (Conoderinae) and bark/Ambrosia beetles (Scolytinae and

Platypodinae) appear to be strongly moisture-dependent, and increased drought would probably lead to population declines.

Introduction

Global surface temperatures have increased 0.6º C during the past century, primarily due to increases in greenhouse gases (Lewis *et al.,* 2004), e.g. methane, tropospheric ozone, and carbon dioxide. Of these three, carbon dioxide (CO_2) has the farthest reaching effect, over both time and distance. The effects of ozone, while causing physical damage to plants through acidifying precipitation and decreased growth due to lower photosynthetic rates, are localized to areas of increased urbanization and industrialization (Lewis *et al.,* 2004). Methane is actually a stronger greenhouse gas than CO_2, but it only has a chemical lifetime of about a decade before it oxidizes into CO_2. On the other hand, carbon dioxide can persist in the atmosphere for thousands to hundreds of thousands of years (Archer *et al*., 2009). Global levels of CO_2 are the highest they have been during the last 20 million years, and are expected to increase over the coming century (Lewis *et al.,* 2004).

In the tropics, temperatures have increased approximately 0.26º C per decade since the mid-1970s (Malhi & Wright, 2004). Even small increases in temperature can affect tropical rainforests by increasing rates of biological processes, e.g. photosynthesis and decomposition. However, at temperatures above the optimum for photosynthesis (35 - 45º C), the amount of carbon sequestered decreases as rates of plant growth and forest litter decomposition slow down (Lewis *et al.,* 2004). In addition to increases in temperature, higher levels of CO_2 are contributing to increased drought frequency and severity as well as overall decreases in precipitation. A pantropical decrease in precipitation of one percent per decade has been occurring since the 1970s (Lewis *et al*., 2004). Amazonia is expected to experience particularly extreme reductions in rainfall over the next century, with a projected rainfall deficit of up to 3 ml per day in the hardest hit areas (Cox *et al*., 2004). Eastern Amazonia may experience a greater than 20% decline in rainfall over the next century (Nepstad *et al*., 2008). Amazonian precipitation deficits could potentially reduce the number of broadleaf trees by as much as 80% (Cox *et al*., 2004); further reducing rainfall and humidity as well as increasing temperatures, dry season severity, and tree mortality (Laurance & Williamson, 2001).

Trees in tropical rainforests may have means of mitigating the damaging effects of increased temperature and decreased precipitation. At higher levels of CO_2, trees are better able to withstand the detrimental effects of increased temperature (Lewis *et al.*, 2004). Water-use efficiency is improved by regulation of stomatal aperture, which decreases transpiration. Although this would normally restrict access to carbon dioxide, higher levels of CO_2 could lessen this effect. Short-term photosynthetic gains may allow the trees to put on greater mass and grow taller; however, such responses are also limited by the amount of nutrients present in the soil (Lewis *et al.*, 2004).

Forest arthropods, especially saproxylic insects, facilitate the return of nutrients from dead plants to the soil. Saproxylic species are those associated with dead wood—or with the fungi or microorganisms associated with dead wood—as well as their parasitoids and predators (Grove and Stork, 1999). They include representatives from all orders, with beetles (Coleoptera) accounting for the largest proportion (Grove, 2002). Saproxylic beetle larvae develop within or under bark, forming tunnels or galleries that are later colonized by other animals or microorganisms. While wood decomposition is primarily due to the activity of fungi and microorganisms, it is facilitated by the saproxylic insects that initiate wood fragmentation and deposit microbe-laden frass (Schowalter *et al.*, 1992; Calderon & Berkov, 2012).

The first insects to colonize moribund and dead wood are wood-boring beetles including Cerambycidae and some members of the Curculionidae subfamilies Conoderinae, Scolytinae and Platypodinae (weevils, bark, and ambrosia beetles) (Madoff & Bakke, 1995; Jacobs *et al*, 2007). Saproxylic beetles are expected to be sensitive to both environmental disturbance and forest alterations. Increases in temperature or decreases in precipitation would adversely affect the smaller saproxylic beetles if they, like many other insects, have a limited ability to tolerate drought (Addo-Bediako *et al*, 2001). Diverse studies suggest that many saproxylic beetles require a mesic environment. In Tanzania, saproxylic beetles were most abundant during the rainy season, and the largest insect catches occurred at times of higher precipitation (Madoffe and Bakke, 1995). In Panama, curculionids (including saproxylic species) showed sharp peaks in abundance at the beginning of the rainy season (Wolda *et al*, 1999). Ødegaard (2006) collected almost twice as many saproxylic beetles, including Cerambycidae and some Curculionidae (Conoderinae, Scolytinae, and Platypodinae), in a Panamanian wet forest as in a tropical dry forest, while the dry forest harbored more flower-visiting curculionids (Ødegaard, 2006). Conoderines had the lowest turnover between the two forest types while cerambycids had the highest turnover (Ødegaard, 2006), suggesting some cerambyicids may be better able to tolerate drought. In relatively dry Neotropical forests in Mexico (annual precipitation: ~800 ml), adults of most cerambycid species were active during the rainy season (Toledo *et al.*, 2002); while in French Guiana adults of most species were active during the short dry season (Tavakilian *et al.*, 1997).

Some saproxylic beetles show marked vertical stratification, apparently in response to differences in forest microclimate (Lee, 2010). Ødegaard (2004) reported that, in Panama, there was high turnover in saproxylic beetle species between canopy and understory. In North Queensland, Australia, a four-year study found that, while 72% of beetle species were found in both strata, cerambycids, curculionids, and platypodinae were all slightly more abundant at the canopy level; however, scolytine beetles were most abundant at the ground level (Stork and Grimbacher, 2006). In French Guiana, Lee (2010) demonstrated that cerambycid species which appeared to be season and stratum generalists actually made a seasonal shift in stratum: from ground stratum in the dry season to canopy stratum in the rainy season. They apparently avoided both the hottest, driest microhabitat (canopy stratum in the dry season) and a moisture-saturated microhabitat (ground stratum in the rainy season).

Host plant breadth will affect the ability of saproxylic beetles to respond to both inter-annual variability in climate and long-term shifts in climate. If host ranges are broad, saproxylic beetles will be better able to track appropriate climatic conditions via migration. If host ranges are excessively narrow, insects that already depend on a patchily distributed substrate might have increased difficulty locating appropriate hosts—and their fates will be inevitably linked to the fate of the host species. In Tavakilian *et al.*'s (1997) study of cerambyicids reared from felled trees in French Guiana, host plant specialists outnumbered generalists by approximately 3:1, but most specialists were associated with a particular plant genus or family. In New Guinea, ambrosia beetles (Platypodinae and some Scolytinae) that transport, cultivate, and feed on symbiotic fungi had broad host ranges, while scolytines that feed on bark rather than fungi were—like cerambycids in French Guiana—specialists associated with congeneric or confamilial host plants (Hulcr *et al.*, 2007). Conoderine weevils are a poorly known group, and comparative data from taxonomically diverse studies are lacking. Among conoderines associated with the Brazil nut family in French Guiana, when three host species were sampled, almost 64% emerged from a single host (Fassbender, Chapter 2).

The purpose of this study was to assess niche preferences of, and resource partitioning among, saproxylic beetles (Cerambycidae: Cerambycinae and Lamiinae; Curculionidae: Conoderinae, Platypodinae, and Scolytinae) that feed on trees in the Brazil nut family, an iconic family of Neotropical moist forests. Cerambycidae and Curculionidae (Fig. 4.1) are part of a radiation of plant-feeding beetles including >86,000 species (Cerambycidae: 35,000; Curculionidae: 51,000) (Lawrence & Newton, 1982; Oberprieler *et al*., 2007). More than 1400 cerambycid species have been documented thus far in French Guiana (Tavakilian *et al*., 1997; Berkov & Tavakilian, 1999). The larvae bore into wood and roots, where they tunnel and form galleries as they feed directly on host plant tissue (Turnbow and Thomas, 2002). Two subfamilies, Cerambycinae and Lamiinae, are particularly well represented in the Neotropics (Tavakilian *et al*., 1997; Berkov & Tavakilian. 1999). Conoderinae is a curculionid weevil subfamily that consists of 1500 species. Conoderines, which are abundant in the tropics, are usually found on moribund or dead wood and leaves. The larvae develop in dead wood, leaf petioles, as leaf miners, or in seeds (Kojima and Lyal, 2002). Like other weevils, conoderines use an elongated rostrum to dig oviposition pits, into which they lay eggs. The oviposition pits enable larvae to burrow into the larval rearing substrate, thus avoiding predators and adverse weather conditions (Anderson, 1995). Bark and ambrosia beetles, included in the curculionid subfamilies Platypodinae and Scolytinae, cumulatively include 7500 species (Farrell *et al*., 2001). Bark beetles (some Scolytinae) feed directly on host plant tissue, whereas ambrosia beetles (Platypodinae and some Scolytinae) feed on symbiotic fungi they transport and cultivate (Hulcr *et al*, 2007).

Because these groups of saproxylic beetles represent a broad range of body sizes and feeding strategies, they probably exploit the local environment in different ways. I hypothesized that small-bodied weevils, bark beetles, and ambrosia beetles would be more diverse and abundant at ground stratum during the rainy season, while larger-bodied cerambycids would be more abundant and diverse during the dry season. Additionally, I expected cerambycid species to exhibit greater host specificity than curculionids, especially when compared to ambrosia beetles. Data collected in this relatively undisturbed forest were used to assess species richness, host specificity, and seasonality; these will make it possible to detect changes as forest dynamics change as well as to make predictions about the potential responses of different cohorts of saproxylic beetles to climate change.

Materials and Methods

Study Site

The study took place in Les Eaux Claires (3° 37-39’N, 53° 12-13’W), a homestead located approximately 7 km north of Saul, French Guiana. The area is located 200 - 400 m above sea level and has well-drained soils. The primary dry season occurs from July to November. The rainy season then begins and lasts through June, often interrupted by a short dry period in March or April. Cumulative rainfall over the course of the study (26 August 2007 to 31 July 2008) was 2894.7 ml (Lee, 2010). During the period of this study, dry season daily mean temperatures ranged from 24 to 25° C, while rainy season daily mean temperatures ranged from 22 to 23° C.

Study System

Host trees were members of the Brazil nut family (Lecythidaceae), which has a pantropical distribution and is abundant in the new world tropics (Mori *et al*., 1997). Two host species were investigated: *Eschweilera coriacea* (DC.) S.A. Mori and *Lecythis poiteaui* Berg. These species are particularly abundant at the study site, and both were heavily colonized by both cerambycids and curculionids during a previous rearing study (Berkov and Tavakilian, 1999; Fassbender Chapter 2). *Eschweilera coriacea* is a canopy species widely distributed throughout Amazonia, while *L. poiteaui* is an emergent species with a more restricted distribution in French Guiana, Surinam, and northern Amazonia east of Manaus (Mori *et al*., 2010).

Branch Sampling

Eight trees were sampled: *Eschweilera coriacea* (EC; $N = 4$) and *Lecythis poiteaui* (LP; $N = 4$). These same individuals were sampled and vouchered during a previous experiment in 1995 (Berkov and Tavakilian, 1999). Bait branches were cut during the dry season (26 - 28 August 2007) and the rainy season (17 - 20 January 2008). During each sampling period, one branch was severed from each tree. One thick section (~8 cm x 65 cm) was hung from the canopy as canopy bait, with the remainder of the branch left on the ground as ground bait. Branches were left in the field for approximately three months and then retrieved. Three thick sections (~8 cm x 65 cm) and six thin sections (~2 cm x 65 cm) were cut from each ground branch. Branch sections were placed into rearing cages constructed from No-see-um insect netting. For each host tree there were three such cages: 1) thick canopy; 2) thick ground; and 3) thin ground (Fig. 4.2). Rearing cages were monitored each day, and beetles collected through

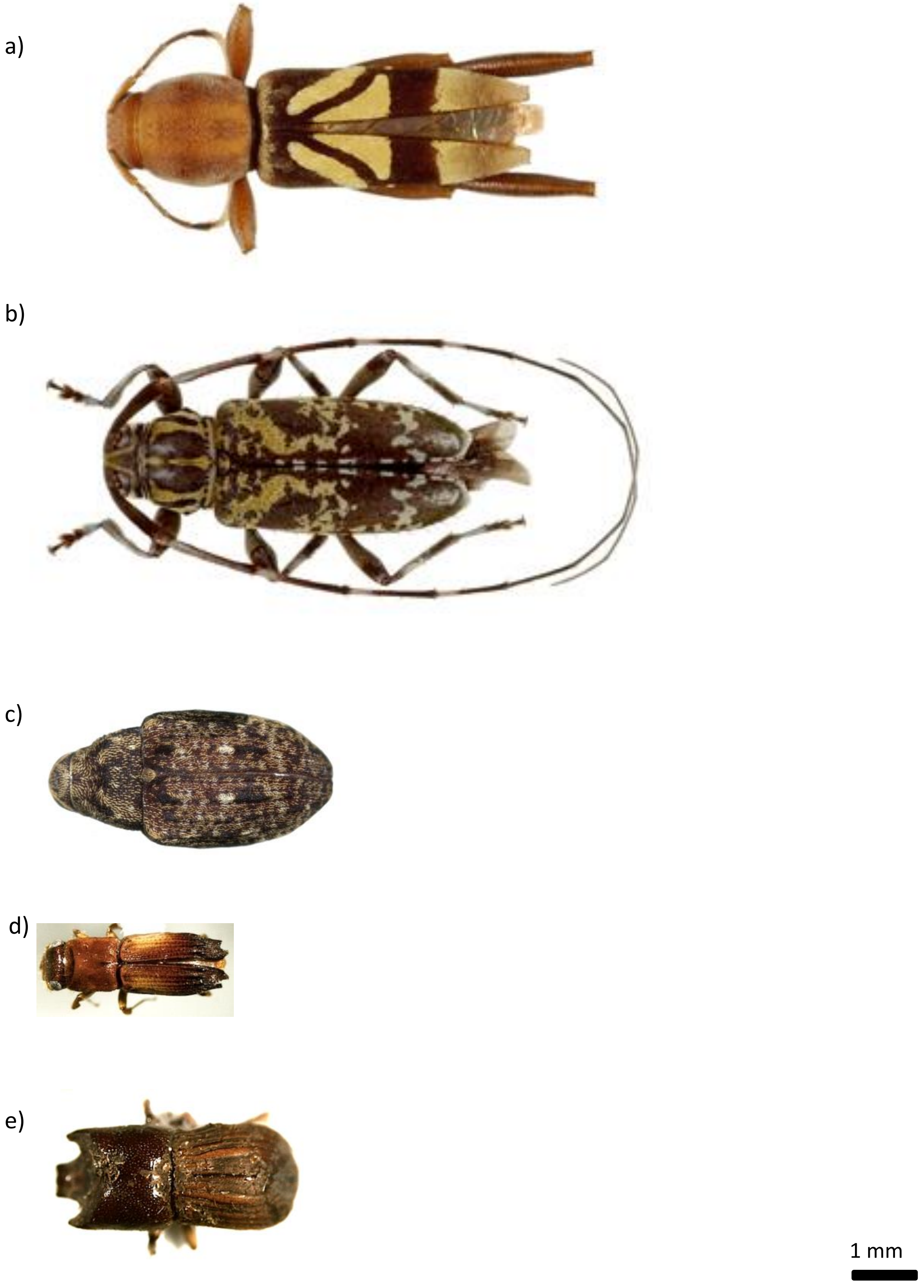


Figure 4.1: Exemplars of subfamilies. (a) Cerambycinae, (b) Lamiinae, (c) Conoderinae, (d) Platypodinae, (e) Scolytinae. Scale: 1.3 cm = 1 mm.

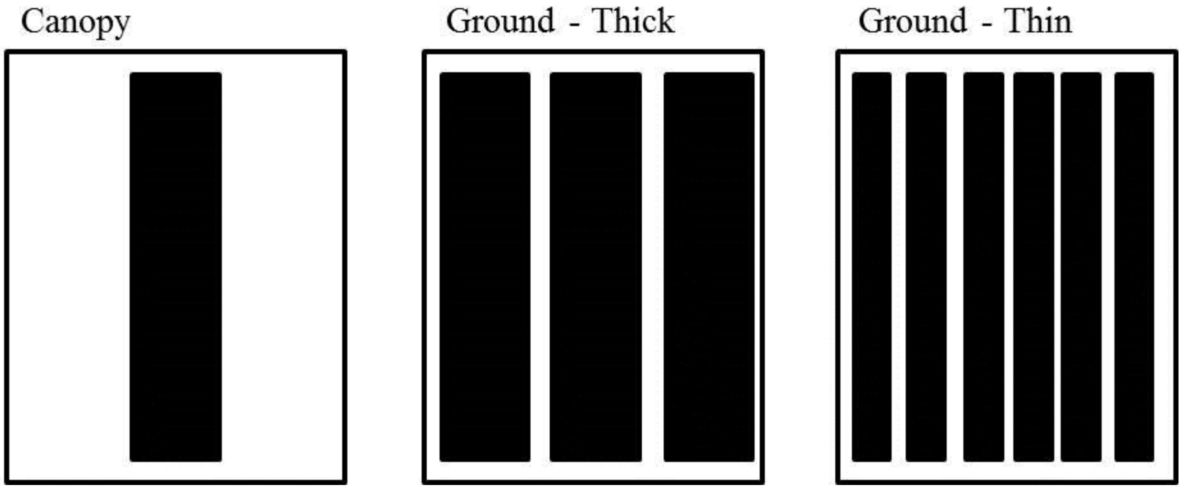


Figure 4.2: Branch number and quantity per rearing cage: branch length: ~ 65 cm, branch width: thick ~ 8 cm, thin ~ 2 cm.

August 2008. The beetles were given a preliminary identification in the field and preserved in 100% ethanol. Specimens were transported to City College of New York for final identification. Cerambycid species were identified by Amy Berkov, using a reference collection of specimens previously identified by Gérald Tavakilian; conoderine weevil species were identified by Charles O'Brien (Green Valley, AZ) or by comparing specimens to those in a reference collection previously identified by him, and scolytine and platypodine species were identified by Sarah M. Smith (Michigan State University).

Data Analysis

EstimateS 8.2 (Colwell, 2005) was used to generate species accumulation curves to compare overall species richness and sampling efficiency among the main subfamilies of saproxylic beetles. Each sample consisted of host tree species (EC or LP), season (dry or rainy), stratum (canopy or ground), and branch size; S_{obs} Mao Tau was used to generate species accumulation curves. Chao 1 species richness estimates and confidence intervals were calculated to assess species diversity by subfamily, and inverse Simpson's index (1 / D) was calculated to assess sample diversity. For the latter, samples consisted of specimens sorted by host tree, season, stratum, and branch diameter. Evenness ($E_{1/D}$) was calculated:

$$\frac{1/D}{S}$$

where 1/D = inverse Simpson's and S = species richness (Magurran, 2004).

Seasonality and Stratification

To compare abundance and species richness by season, species accumulation curves were generated for the five subfamilies during the dry and rainy season. A goodness of fit (G) test

(Sokal and Rohlf, 1995; McDonald, 2009) was conducted to determine if seasonal differences in stratification were due to differences in the number of bait branches available at different strata (for each tree, *N* = 3 at ground stratum, and *N* = 1 at canopy stratum). Thin branches were not included in the G-test because they yielded few specimens.

Host Association

To compare species richness by host plant, data from all five subfamilies were combined and used to generated species accumulation curves for each host / stratum combination. Separate analyses were conducted for dry and rainy season. ANOVAs were performed using JMP (JMP, 1989 – 2007) to determine if beetle subfamilies were disproportionately associated with a particular host tree species. ANOVAs were performed on both abundance (*N* individuals per subfamily) and species richness data (*N* species per subfamily) of beetles collected from each host per season.

Subfamily Niches

To visualize resource partitioning among beetle subfamilies, for each subfamily the number of individual beetles reared per branch from a particular host, stratum, and season combination was calculated. Because each branch was represented by three ground sections and a single canopy section, ground branch abundance was divided by three. Thin branches were excluded because they yielded insufficient data. PC-ORD was used to perform a two-way cluster analysis to assess the consistency of beetle host and season preferences across potential host tree individuals. Subfamily datasets were sorted by host, individual tree, and season. Raw abundance data were analyzed using the group linkage method and Sorenson’s distance measure.

To visualize the distribution of saproxylic species in relation to host tree and season, canonical correspondence analysis (CCA) was performed on a dataset including host species, individual host tree, and season. Abundance data were transformed by log x+1 before analysis. Axis scores were standardized by Hill's (1979) method and scaled to optimize representation of explanatory variables. The statistical significance of the correlation between species and environment was evaluated using a Monte Carlo permutation test (998 permutations) where p = (1 + no. permutations > observed)/ (1 + no. permutations).

Niche Classifications of Saproxylic Species

To assess specialization among individual beetle species, a beetle species was considered a specialist if 90% or more individuals were collected from a single host, season, stratum, or branch diameter (Novotny & Basset, 2005; Wardhaugh *et al.*, 2012). Species represented by fewer than 10 individuals were excluded from specialist classification due to insufficient data, and classifications are considered tentative when sample sizes were small. Indicator species analysis, in PC-ORD (McCune & Mefford, 2011), was used to determine if any species were statistically significant indicators for a particular host tree or season. Data were first relativized (general relativization) to decrease influence of extremes in absolute abundance. Then the Dufrêne and Legendre (1997) method was used on a dataset that included host species, individual host tree, and season. Significance was determined with a Monte Carlo test of the significance of maximum indicator values, where p = (1 + number of runs > observed) / (1 + number of randomized runs). Only species represented in more than one sample were included in PC-ORD analyses. To further assess predictive value of beetle occurrence, species reared in

2007 were compared with those reared in the 1995 study to determine the percent total species reared from *E. coriacea* or *L. poiteaui* during both experiments (Berkov and Tavakilian 1999).

Results

The study yielded 4485 beetles in 64 species (Table 4.1; Fig. 4.3), including 2593 curculionids in 42 species, and 1790 cerambycids in 22 species. Curculionids were represented by 1143 conoderines in 13 species, 1064 platypodines in 9 species, and 486 scolytines in 20 species; cerambycids were represented by 1614 lamiines in 18 species, and 176 cerambycines in 4 species. The curculionid subfamily Scolytinae had the greatest species richness, but abundance was relatively low. Conoderinae and Platypodinae were similar in abundance, but Conoderinae had slightly higher species richness. The cerambycid subfamily Lamiinae was most abundant and second in terms of species richness, while the cerambycid subfamily Cerambycinae was lowest in both abundance and species richness (Table 4.1; Fig. 4.3). Twelve saproxylic species were represented by >100 individuals and made up 77% of the total abundance (Appendix 4); these included two species of Cerambycinae, four species of Lamiinae, four species of Conoderinae, and two species of Platypodinae.

For all subfamilies, species richness was close to, but under, the lower confidence interval for the Chao 1 species richness estimator (Table 4.1). Species accumulation in Scolytinae did not reach an asymptote, which suggests that additional sampling effort would be productive. Lamiinae, Conoderinae, and Platypodinae are approaching an asymptote, and Cerambycinae appears to have reached an asymptote, which suggests that additional sampling effort might be less productive (Fig. 4.3). Conoderinae and Lamiinae had the highest inverse Simpson's values (1/D = 4.34 and 4.33, respectively; Table 4.1) showing that they were the most

Table 4.1: Species diversity measures indicated that Conoderinae and Lamiinae are the most diverse subfamilies.

Family	Subfamily	*N* Species	*N* Individuals	Chao 1[1]	Chao 1 C I[2]	1 / D[3]	$E_{1/D}$[4]
Cerambycidae	Cerambycinae	4	176	3.94	3.94 – 3.94	1.42	0.355
	Lamiinae	18	1614	24	18.94 – 56.42	4.33	0.241
Curculionidae	Conoderinae	13	1143	15	13.18 – 35.13	4.34	0.334
	Platypodinae	9	1066	10	9.07 - 22.95	2.53	0.281
	Scolytinae	20	486	22	21.06 – 32.06	3.15	0.158

[1]Chao 1 = Chao 1 richness estimator; [2]Chao 1 CI = Chao 1 Confidence interval; [3]1 / D = reciprocal Simpson's index; [4]$E_{1/D}$ = Evenness.

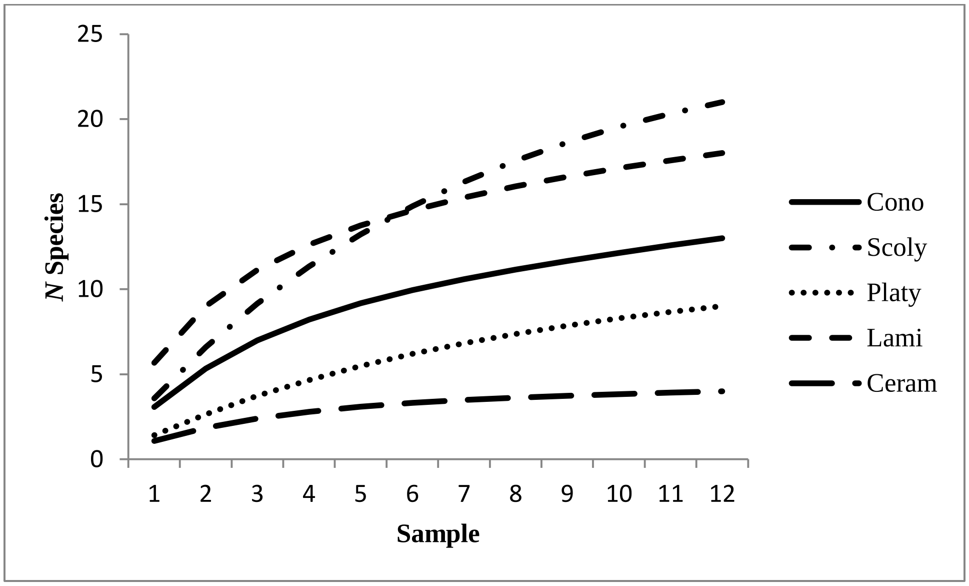


Figure 4.3: Species accumulation by subfamily shows that Scolytinae had the greatest overall species richness. Cera = Cerambycinae, Lami = Lamiinae, Cono = Conoderinae, Platy = Platypodinae, and Scoly = Scolytinae.

diverse. Scolytinae had the lowest evenness indicating that abundance was not evenly distributed among species ($E_{1/D}$ = 0.158), whereas Cerambycinae had the highest.

Seasonality and Stratification

Saproxylic beetle subfamilies were distinctly seasonal. Bait branches cut during the dry season yielded predominantly cerambycids (Figs. 4.4a and 4.4b; Appendix 4): the subfamily Lamiinae had the greatest species richness (N = 16) and abundance (N = 968); Cerambycinae had low species richness (N = 4) but was second in abundance (N = 174). Curculionids were poorly represented: Conoderinae had relatively high species richness (N = 8), but abundance was low (N = 54). Only one individual bark beetle (a scolytine) emerged from a dry season bait branch (Appendix 4).

Bait branches cut during the rainy season yielded both curculionids and cerambycids in the subfamily Lamiinae (Figs. 4.4c and 4.4d; Appendix 4). The curculionid subfamilies Conoderinae (weevils) and Platypodinae (ambrosia beetles) were highest in abundance (N = 1089 and 1066, respectively) but were represented by relatively few species (N = 10 and 9, respectively). Scolytinae (bark and ambrosia beetles) had the highest species richness (N = 20) but the lowest abundance (N = 485). The cerambycid subfamily Lamiinae was intermediate in both species richness and abundance (N = 14 and N = 646, respectively) (Figs. 4.4c and 4.4d; Appendix 4).

The distributions of saproxylic beetle subfamilies were not only seasonal, but also stratified, and it was not an artifact of resource availability (Table 4.2, Fig.4.5). Cerambycids in the subfamily Cerambycinae emerged almost exclusively from branches cut during the dry

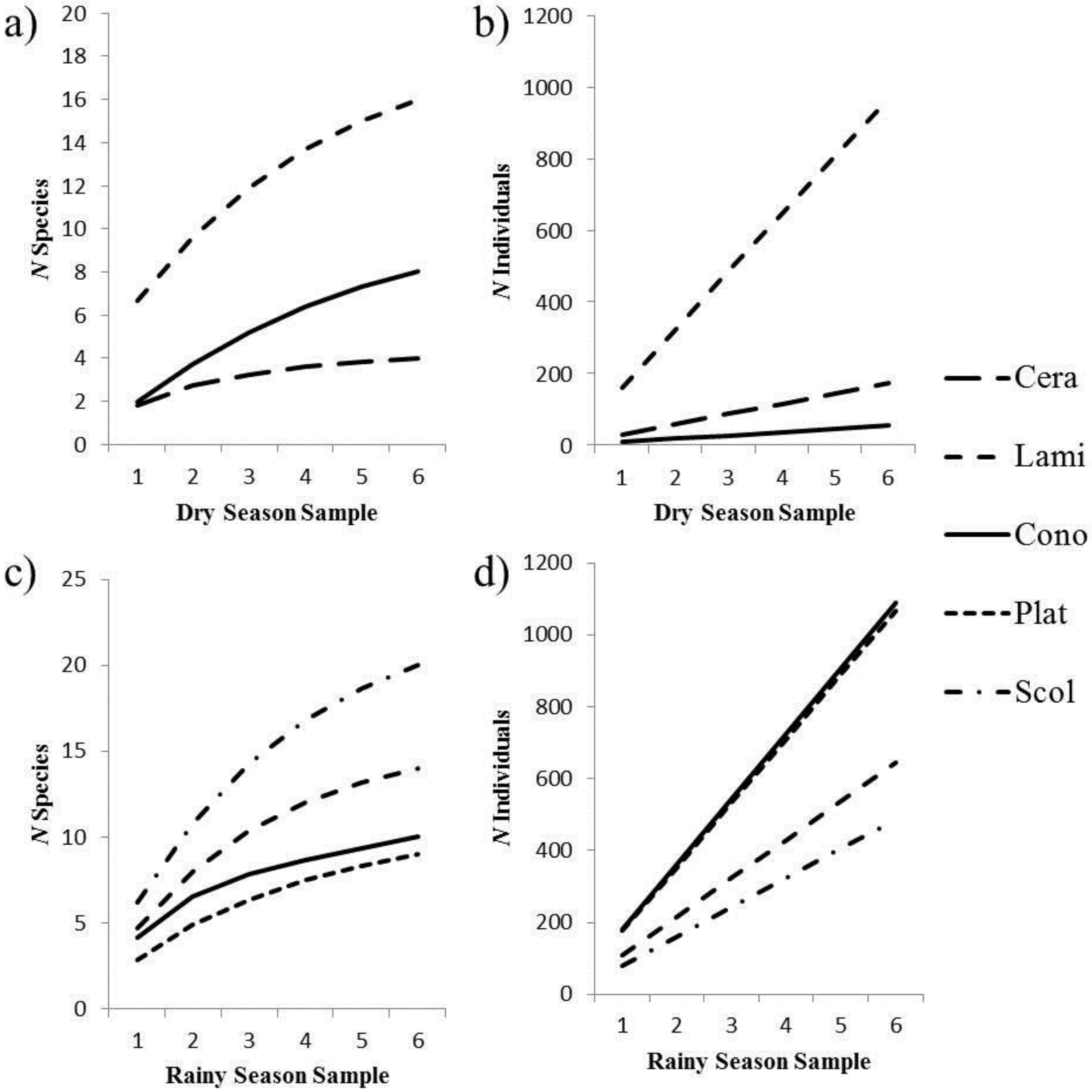


Figure 4.4: Dry season species accumulation (a) and abundance (b) show that branch samples produced lamiines, conoderines, and cerambycines, and rainy season species accumulation (c) and abundance (d) show that branch samples produced scolytines, platypodines, conoderines, and lamiines. Cera = Cerambycinae, Lami = Lamiinae, Cono = Conoderinae, Platy = Platypodinae, and Scoly = Scolytinae.

Table 4.2. G-test for abiotic factors indicates significant differences in beetle abundance between strata and season.

Subfamily	Season	Stratum	N^1 Branches	Ind.^{2} Obs.	Ind.^{3} Exp.	Ratio^4 Obs/Exp	df	G	*p*
Cerambycinae	Dry	Canopy	8	83	20	4.15	3	256.45	< 0.00001
		Ground	24	77	61	1.26			
	Rainy	Canopy	8	1	20	0.05			
		Ground	24	1	61	0.02			
Lamiinae	Dry	Canopy	8	146	182	0.80	3	1378.15	< 0.00001
		Ground	24	735	546	1.35			
	Rainy	Canopy	8	543	182	2.98			
		Ground	24	32	546	0.06			
Conoderinae	Dry	Canopy	8	7	119	0.06	3	940.47	< 0.00001
		Ground	24	44	357	0.12			
	Rainy	Canopy	8	177	119	1.49			
		Ground	24	724	357	2.03			
Platypodinae	Dry	Canopy	8	0	133	0	3	1570.93	< 0.00001
		Ground	24	0	398	0			
	Rainy	Canopy	8	135	133	1.02			
		Ground	24	927	398	2.33			
Scolytinae	Dry	Canopy	8	0	59	0	3	647.99	< 0.00001
		Ground	24	1	177	0.01			
	Rainy	Canopy	8	146	59	2.47			
		Ground	24	324	177	1.83			

[1] Number of branch sections. [2] Number of individuals reared from branches. [3] Number of individuals expected to be reared from branches. [4] Ratio of observed to expected individuals.

season, and were disproportionately abundant in canopy stratum branches (G = 256.45, df = 3, p < 0.00001). Cerambycids in the subfamily Lamiinae emerged from bait branches at both strata during the dry season, but during the rainy season emerged preferentially from canopy stratum branches (G = 1378.5, df = 3, p < 0.00001). Curculionids in the subfamilies Conoderinae and Platypodinae emerged in greatest abundance from ground stratum branches cut during the rainy season (Conoderinae: G = 940.47, df = 3, *p* < 0.00001; Platypodinae: G = 1570.93, df = 3, *p* < 0.00001). Curculionids in the subfamily Scolytinae also emerged preferentially from branches cut during the rainy season, but were more abundant in the canopy (G = 647.99, df = 3, *p* < 0.00001).

Host association

Bait branches cut from *E. coriacea* had higher species richness than those cut from *L. poiteaui*, particularly during the rainy season (Figs. 4.5a and 4.5b) and at canopy stratum, where up to 24 species could co-occur in a single EC branch section (data not shown). During the dry season, ground stratum EC branches had the highest species richness. The bait branches with the lowest species richness were the *L. poiteaui* canopy branches, a pattern that was consistent in both the dry and rainy season. Differences in beetle host associations were not an artifact of resource availability (Table 4.3, Fig. 4.6). Conoderinae emerged with significantly higher number from EC (F (3, 12) = 4.836; *p* = 0.020) and Cerambycinae emerged in significantly higher numbers from LP (F (3, 12) = 15.560; *p* < 0.0001); none of the other subfamilies showed significantly different abundance between host species (Table 4.3; Appendix 4). However, each subfamily showed significantly different species richness between host species (Table 4.3).

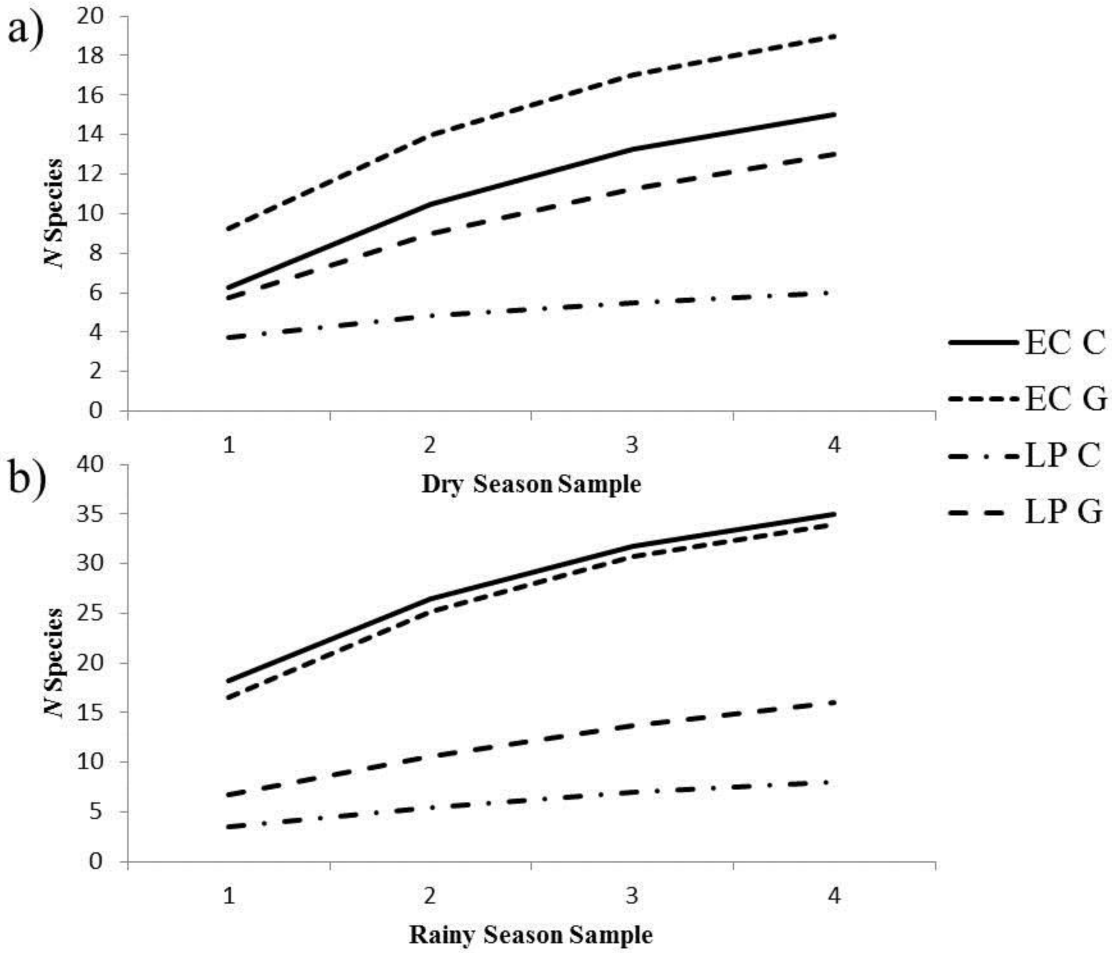


Figure 4.5: Species accumulation by host and stratum indicates that *E. coriacea* had the greatest species richness in both dry (a) and rainy (b) seasons. EC = *Eschweilera coriacea*, LP = *Lecythis poiteaui*; C = canopy, G = ground.

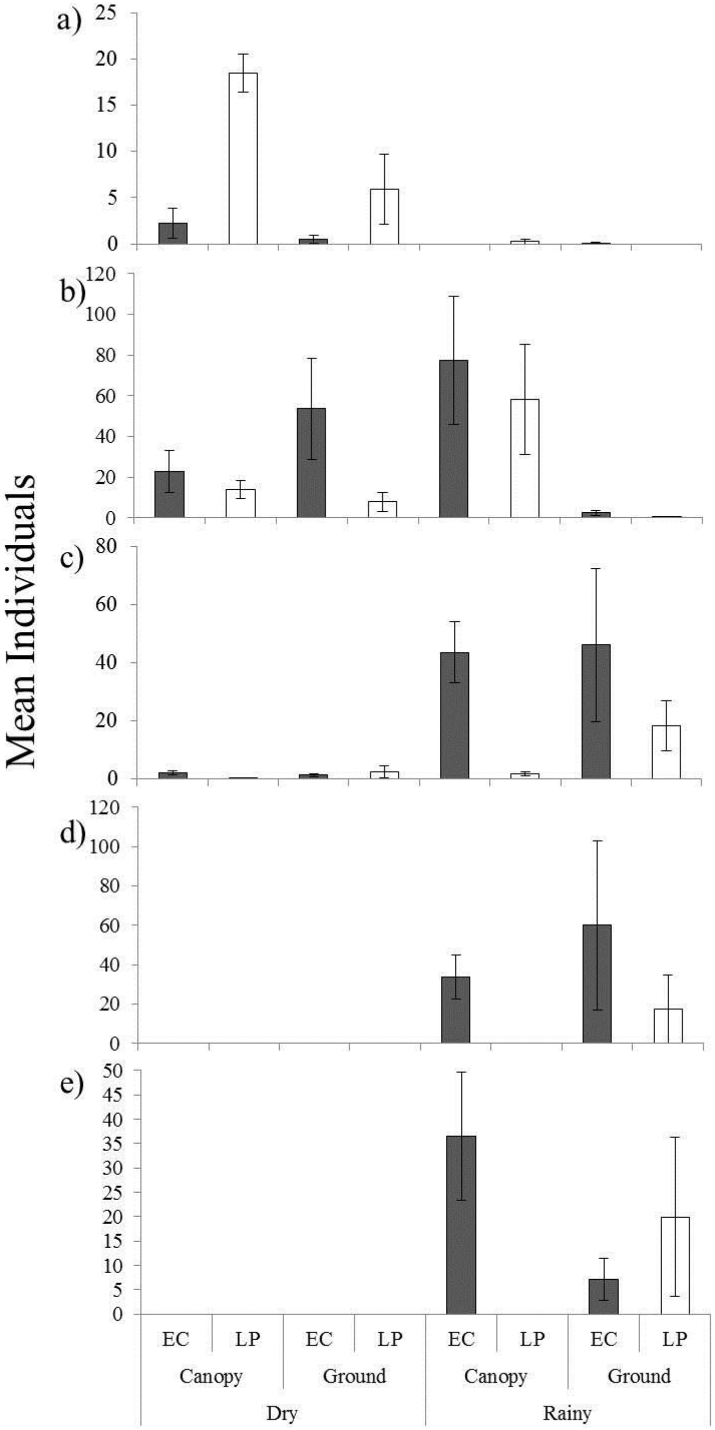


Figure 4.6: Mean and standard error for individuals collected per host at each stratum per season by subfamily. a) Cerambycinae, b) Lamiinae, c) Conoderinae, d) Platypodinae, and e) Scolytinae. Filled bar = *Eschweilera coriacea* (EC), unfilled bar = *Lecythis poiteaui* (LP).

Table 4.3: ANOVA showed only Cerambycinae and Conoderinae had significant variation in abundance between host and season whereas all subfamilies had significant variation in species richness.

	Partition					
	EC Dry[1,2,3]	LP Dry[1,2.3]	EC Rainy[1,2,3]	LP Rainy[1,2,3]	F value	*p* value
Abundance						
Cerambycinae	4.25 +/- 6.5	39.2 +/- 18	0.25 +/- 0.5	0.25 +/- 0.5	15.560[4]	< 0.0001
Lamiinae	202 +/- 184	39.8 +/- 28.5	102 +/- 50.2	59.5 +/- 54.9	2.091[4]	0.155
Conoderinae	6 +/- 4.4	7.5 +/- 12.5	222 +/- 182	50.2 +/- 38.1	4.836[4]	0.020
Platypodinae	0 +/- 0	0 +/- 0	214 +/- 266	52 +/- 103	2.023[4]	0.164
Scolytinae	0.25 +/- 0.5	0 +/- 0	59.8 +/- 43.8	61.5 +/- 96.7	1.733[4]	0.213
All Subfamilies	170 +/- 358	69.4 +/- 81.8	479 +/- 388	179 +/- 101	2.115[5]	0.138
Species Richness						
Cerambycinae	1 +/- 0.0	1.75 +/- 0.5	0.25 +/- 0.5	0.25 +/- 0.5	11.000[4]	0.001
Lamiinae	8.25 +/- 4.57	4 +/- 0.816	8.75 +/- 2.06	2.75 +/- 0.957	5.417[4]	0.014
Conoderinae	2.75 +/- 1.71	1.5 +/- 1.91	6.25 +/- 0.957	3.25 +/- 0.957	7.713[4]	0.004
Platypodinae	0 +/- 0	0 +/- 0	4.25 +/- 2.75	0.5 +/- 1	7.874[4]	0.004
Scolytinae	0.25 +/- 0.5	0 +/- 0	8.75 +/- 5.85	2.5 +/- 1.73	7.084[4]	0.005
All Subfamilies	9.60 +/- 13.8	6 +/- 6.36	22.6 +/- 14.2	7.40 +/- 5.5	2.493[5]	0.097

[1]EC = *Eschweilera coriacea*, LP = *Lecythis poiteaui*; [2]D = dry season, R = rainy season; [3]mean +/- standard deviation; [4]DF = (3, 12); [5]DF = (3, 16).

Cerambycinae species richness was highest on LP whereas EC branches yielded greater species richness for the remaining subfamilies (Appendix 4).

Subfamily Niches

Cerambycids in the subfamily Cerambycinae were collected most consistently from LP dry season branches and were most abundant at canopy stratum (Fig. 4.6). Cerambycids in the subfamily Lamiinae occupied the greatest breadth of niches, but during the rainy season were conspicuously absent from thick ground stratum branches. All curculionids were most abundant in branches cut during the rainy season, but were conspicuously absent from LP canopy stratum. The two-way cluster analysis indicates that these patterns were consistent among individual trees: Lamiines and conoderines occupied the broadest range of niches, but conoderines were most abundant in rainy season branches (Fig. 4.7). Although Cerambycinae were represented by relatively few species and individuals, they consistently colonized dry season branches, especially LP. The bark beetles, Platypodinae and Scolytinae were reared almost exclusively from branches cut during the rainy season, but colonized both hosts.

The canonical correspondence analysis showed clear segregation of saproxylic beetle species by both host and season (Fig. 4.8; note that the CCA was a single analysis, but results are shown by subfamily for clarity). Total inertia was 2.1058, with 46.4% of variance explained by the environmental variables of host and season, and the remaining variance unexplained. The correlation between species and environmental variables was statistically significant ($p = 0.001$). The highest density of saproxylic species was found in a cluster around EC rainy season samples. This cluster included species representing all subfamilies, with the exception of Cerambycinae. Some species of Conoderinae and Scolytinae were partially or predominantly associated with LP

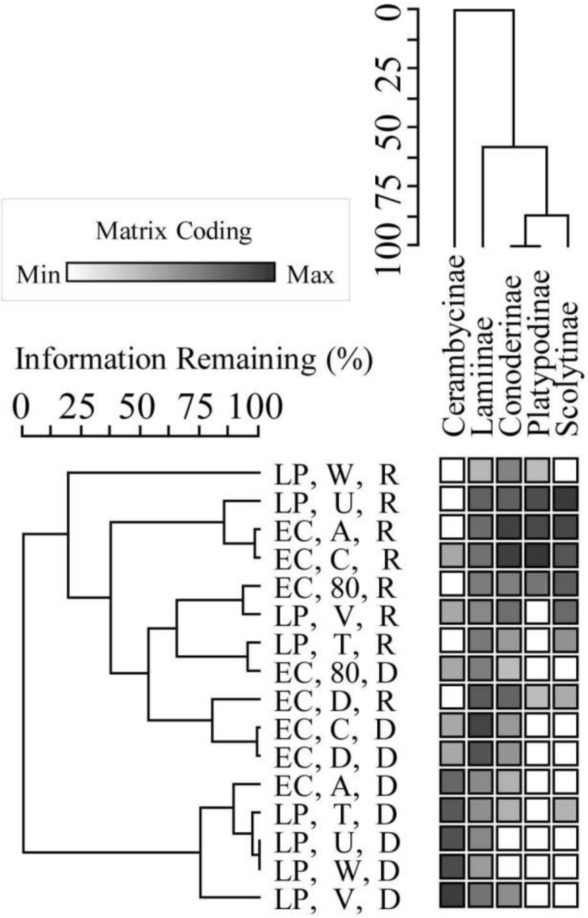


Figure 4.7: Niche breadth and consistency of association among five saproxylic subfamilies.

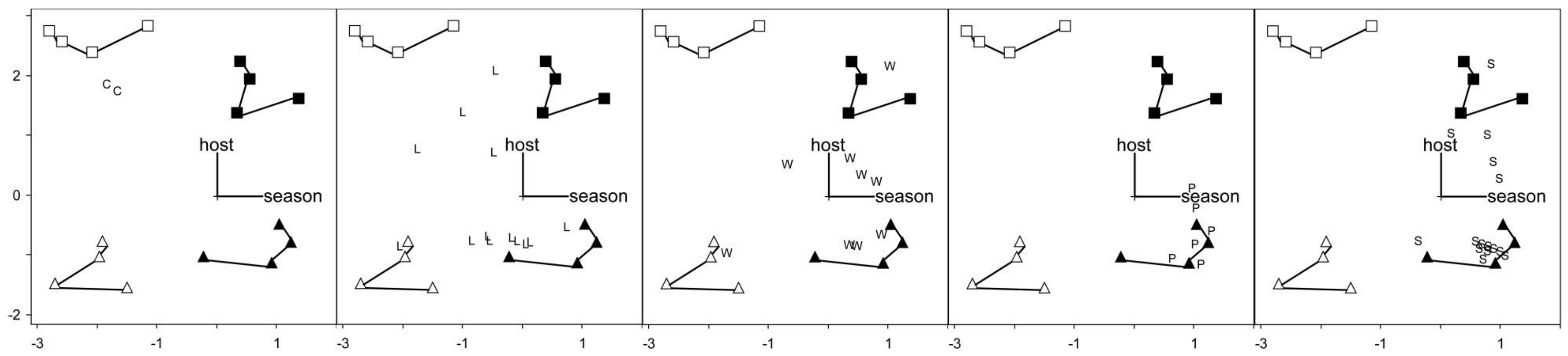


Figure 4.8: Canonical correspondence analysis by host and season. Triangle = *Eschweilera coriacea*, Square = *Lecythis poiteaui*; White = dry, Black = rainy; C = Cerambycinae, L = Lamiinae, W = Conoderinae, P = Platypodinae, and S = Scolytinae.

rainy season samples. Lamiinae and a couple of species of Conoderinae graded into the dry season, but only species in the subfamily Cerambycinae clustered near the LP dry season samples.

Niche Classifications of Saproxylic Species

A total of 36 beetle species had an abundance of 10 or more individuals. Of these 36 species, 26 (72%) were classified as seasonal specialists; five as dry season specialists, and twenty-one as rainy season specialists (Appendix 4). Dry season specialists include: *E. sulphureosignata*, *M. triangularis*, and *P. pubescens* (Cerambycinae); *N. mutilatus* (Lamiinae); and *Z. pius* (Conoderinae). Two cerambycid species had statistically significant indicator values for the dry season: *P. pubescens* ($p = 0.006$) (Cerambycinae) and *N. mutilatus* ($p=0.042$) (Lamiinae). Rainy season specialists include: *Acanthocinini* sp. 50 (Lamiinae); *Copturomorpha* sp.1, *P. alternans*, *P. incommodus, P. pseudoalternans, Piazurus* sp. 2, and *Piazurus* sp. 3 (Conoderinae); Platypodinae spp. 3, 4, 5, 8, 9, and 12; and *Amphicranus* sp. 17, *Monarthrum* spp. 6, 16, 18, and 32, *Xyleborus spathipennis*, *Xyleborus* sp. 14, and *Xyleborus* sp. 19 (Scolytinae). Five curculionid species had statistically significant indicator values for the rainy season: *P. alternans* ($p = 0.023$, *P. incommodus* ($p = 0.0004$), and *P. pseudoalternans* ($p = 0.003$) (Conoderinae); *Xyleborus* sp. 19 ($p = 0.022$) (Scolytinae); and Platypodinae sp.4 ($p = 0.027$).

Twenty-three of the 36 species (64%) with 10 or more individuals were classified as stratum specialists (Appendix 4). There were ten canopy specialists (including three lamiines, one conoderine, and four scolytines) and thirteen ground specialists (including one cerambycine, one lamiine, four conoderines, two platypodines, and two scolytines). Although several species appeared to be preferentially associated with thin branches cut during the rainy season, only one, a lamiine, was classified as a thin branch specialist (Appendix 4). Twenty-eight species (80%) were classified as specialists associated with thick branches, including one cerambycine, eight lamiines, five conoderines, six platypodines, and eight scolytines.

Twenty-six of the 36 beetle species (72%) represented by 10 or more individuals were classified as specialists preferentially associated with either EC or LP (Appendix 4). Five were associated with *Lecythis poiteaui*, including two cerambycines, two lamiines, and one conoderine. Only one lamiine, *N. altissimus*, had a statistically significant indicator value for *L. poiteaui* (*p* = 0.0004). Twenty-one were associated with *Eschweilera coriacea*, including one cerambycine, eight lamiines, three conoderines, four platypodines, and five scolytines. Six lamiines and two conoderines had statistically significant indicator values for *E. coriacea*. These include the lamiines *O. leucostigma* (*p* = 0.023), *O. simplex* (*p* = 0.002), *Ozineus* sp. 1 (*p* = 0.007), *P. anceps* (*p* = 0.002), *P. crassimana* ‘unicolor’ (*p* = 0.023), and *X. elaineae* (*p* = 0.001), and the conoderines *Copturomorpha* sp. 1 (*p* = 0.004) and *Piazurus* sp. 3 (*p* = 0.007). The cerambycid subfamily Lamiinae and the curculionid subfamily Conoderinae had the lowest species turnover (58% and 56% were reared in both 1995 and 2007, respectively). The cerambycid subfamily Cerambycinae and the curculionid subfamily Platypodinae had intermediate levels of turnover, with 29% and 28% reared in both experiments. Scolytinae had the highest species turnover, with only 17% of the species reared in both 1995 and 2007 (Table 4.4). Species reared in both studies were often among the most abundant species reared in 2007 (Appendix 4), and are considered core associates with a high level of predictive value.

Table 4.4: Saproxylic species reared from *E. coriacea* and *L. poiteaui* in both 1995 and 2007

Subfamily	95 only	07 only	Shared	Total	% Total Shared
Cerambycinae	3	2	2	7	29
Lamiinae	8	3	15	26	58
Conoderinae	3	4	9	16	56
Platypodinae	16	2	7	25	28
Scolytinae	22	13	7	42	17

Discussion

In the tropics, decreased precipitation and increased temperature during the dry season increases the potential for desiccation in smaller insects (Kaspari, 1993; Addo-Bediako *et al*., 2001). The results in this study were consistent with the hypothesis that curculionids, which are usually smaller than cerambycids and therefore have a higher surface area: volume ratio, should be more susceptible to desiccation and therefore be more abundant and diverse in the rainy season. Although several curculionid species emerged from microhabitats where maximum temperatures reached approximately 27° C (Lee, 2010), the majority of conoderines, platypodines, and the scolytine *Xyleborus spathipennis* were most abundant when temperatures seldom exceeded 25° C and relative humidity levels seldom dropped below 100% (Lee, 2010). It is not currently possible to separate moisture-dependence due to body size from the moisture-dependence inherent in the nutritional dependence that some curculionids have on fungi (Wood, 1982; Ødegaard, 2006).

Cerambycids in the subfamily Cerambycinae were most tolerant of heat and drought. The subfamily was represented by relatively few species and individuals, but was most abundant in microhabitats where maximum temperatures could exceed 34° C and relative humidity levels typically dropped to 50-60% (Lee, 2010). Cerambycids in the subfamily Lamiinae were more abundant and slightly more species rich in microhabitats were that were characterized by intermediate temperatures. Although resource partitioning among these saproxylic beetles might appear to be the result of competitive exclusion, it seems unlikely that curculionids would exclude the larger cerambycids from the cool, moist branches at ground stratum in the rainy season. Both groups are early visitors to bait branches (Berkov, pers. comm.) and, since cerambycid larvae are sometimes facultative predators of bark beetle larvae (Dodds *et al*., 2001), it is unlikely that curculionids “capture” the resource.

Cerambycid colonization should not be inhibited by the moderate temperatures of the forest understory, but might be challenged by the constant high humidity, which probably results in substrate saturation. Cerambycids lay their eggs in crevices or slits in the bark, and first instar larvae must further penetrate the bark to reach their optimal feeding zones near the cambium. Hanks *et al*. (1999) demonstrated that when bark moisture content was above a critical threshold (60%), *Phoracantha semipunctata* larvae did not reach the cambium, and failed to grow or pupate. If pore spaces in the bark fill with moisture, there may not be sufficient oxygen to support larval development. In this study, when cerambycids did colonize ground stratum rainy season branches, they were usually associated with the thinner secondary branches (Appendix 4). Thinner branches have thinner bark (Paine *et al*., 2010), which might present less of a barrier.

Humid microhabitats were, however, accessible to most curculionids—perhaps because adults successfully breech the barrier. Conoderines have an elongated rostrum that they use to form oviposition pits. Eggs are placed into these pits; thus, upon hatching, the larvae have only a short distance to burrow before reaching food (Anderson, 1995). Platypodine and scolytine adults bore through the outer bark to form egg galleries in the phloem-cambium area (bark beetles) or the xylem (ambrosia beetles) (Rabaglia, 2002), and sometimes create special ventilation holes (Caird, 1935).

The larvae of wood- and bark-boring beetles that attack moribund wood are concealed feeders that often lack legs, therefore they cannot escape suboptimal environmental conditions and may be particularly vulnerable to global change. Host breadth, coupled with migratory capabilities, will determine their long-term success in tracking suitable substrates that—even without forest fragmentation—are patchily distributed resources (Novotny *et al.*, 2007). In this study, cerambycid species were expected to exhibit greater host specificity than curculionids; especially when compared to species that feed directly on ambrosia or on fungal-infested wood. Eighty percent of the cerambycids were considered specialists associated with either EC or LP, and while only 47% were reared with enough consistency that they were considered indicator species, 80% were reared from the same host(s) in 1995. Sixty-two percent of the curculionids were considered specialists associated with either EC of LP, but < 10% were reared with enough consistency that they were considered indicator species. Nevertheless, 71% were reared from Lecythidaceae in 1995. I expected the Platypodinae, which feed on ambrosia fungus, to have the lowest host specificity and the highest turnover, but this was not the case. The Scolytinae, some of which feed on fungus, actually had much higher turnover, and the most abundant scolytine species (*Xyleborus spathipennis, N* = 238) has a wide geographic distribution, and is associated with several unrelated plant families (Cognato, 2008). Co-occurrence over time (or space) cannot automatically be used as a proxy for host specificity because generalists also can have consistent associations (Gómez *et al*, 2010). On the other hand, indicator species analysis substantially underestimates the predictive value in the rearing data, as shown by the appearance of many species in both 1995 and 2007.

Conservation Implications

In this study, canopy stratum during the dry season did not offer optimal conditions for most saproxylic beetles; the only subfamily that emerged in abundance was the Cerambycinae. Cerambycine adults are often diurnal, brightly colored, and feed (and mate) on flowers (Linsley, 1959). Should the climate in French Guiana become warmer and dryer, it would probably favor the Cerambycinae, which, in this study, were represented by few individuals and species. Furthermore, two of the three species represented by at least 10 individuals have host records from alternate plant families, and therefore are not strict Lecythidaceae specialists (Tavakilian *et al.*, 1997; Monné, 2001). Although climate change has been invoked as an explanation for bark beetle outbreaks in temperate biomes (Choi, 2011), in the tropical rain forests of French Guiana the bark and ambrosia beetles appear to be highly moisture dependent, perhaps due to their dependence on fungi. While they might enjoy short-lived population increases as stressed trees die, they would ultimately be severely challenged by warmer, dryer conditions. Temperate species are expected to track their hosts via latitudinal migration (Choi, 2011), but options might be limited for bark and ambrosia beetles associated with the Brazil nut family, due to its restricted geographic distribution in the moist tropics. The challenge of host location might, however, be mitigated in fungus-feeders because their host ranges appear to be broad (Wood, 1982; Hulcr *et al.*, 2007), which would provide a greater opportunity to track optimal climate via migration.

Lamiinae and Conoderinae were the subfamilies of saproxylic beetles that were most consistently associated with the Brazil nut family. They colonized most available trees, they were the only subfamilies in which species were both sufficiently abundant and frequent to have significant indicator values, they had the lowest turnover between 1995 and 2007, and the species that were reared in both studies accounted for much of the total abundance. Although comparative data from a taxonomically diverse sample of plants are still needed to assess host specificity for the Conoderinae, the dominant species in this study are consistently associated with suitable host branches over both space and time (Fassbender, Chapter 2; Berkov, unpubl. data). Currently, the lamiines appear to select drier microhabitats, and the conoderines moister microhabitats. If the climate in French Guiana becomes warmer and dryer, it is possible that lamiines would no longer be excluded from ground stratum branches during the rainy season. A shift to colonize branches on the ground would put lamiines into direct competition with the conoderines, with potential negative fitness outcomes for both subfamilies, and possible impacts on nutrient cycling.

Tropical forests are often carbon sinks during the rainy season and carbon neutral during the dry season (Bonan, 2008). At times of drought, rainforests lose their carbon sink status through tree growth inhibition, and can even increase atmospheric carbon through burning and forest dieback (Nepstad *et al*., 2004; Bonan, 2008). As CO_2 levels increase, drought conditions are expected to become more common in rainforests. A short-term increase in photosynthetic rate is expected in tropical forests as carbon dioxide levels increase. Additionally, the effects of decreased moisture may be mitigated in tropical tree species by increased water use efficiency (Lewis *et al*, 2004). However, these adaptations disappear when nitrogen and phosphorus are limited (Bazzaz, 1990). The process by which these nutrients are returned to the soil from dead wood begins with saproxylic insect species. Prior to bark penetration by primary colonizers (wood-boring, bark, and ambrosia beetles), the fungi and bacteria of decay are unable to pass through the outer bark of the dead tree (Schowalter *et al*., 1992). Increases in global temperatures and decreases precipitation rates resulting from increased CO_2 levels (Lewis *et al*., 2004) are likely to have a detrimental effect on some saproxylic beetle species in tropical regions. The loss of these wood-boring saproxylic beetle species will make it more difficult for tropical trees to adapt to climate change by decreasing nutrient availability, potentially affecting the long term viability of tropical forest habitats.

CHAPTER 5

Discussion

The studies in this evaluated the diversity and niche breadth of wood-boring weevils (excluding the subfamilies Platypodinae and Scolytinae) over time (French Guiana 1995, 2007) and across distance (French Guiana and Peru 03), and resource partitioning among weevils and other saproxylic beetles (French Guiana 1995, 2007). By examining their seasonal and microhabitat preferences, it can be inferred how they might respond should their moist forest habitats experience longer dry seasons and less precipitation.

This is the first rearing study concentrating on saproxylic weevils. One of the major impediments to work with tropical insects is the sheer volume of material that is collected. Rearing studies reduce the abundance and diversity of such material relative to mass sampling studies, and presumably reduce the ratio of noise to signal. Nevertheless, during one year in French Guiana, 5177 specimens in five curculionid and cerambycid subfamilies were collected from just sixteen branches cut from two host species—with up to 39 beetle species emerging from a single branch. Although most species have been seen by specialists, 33% of the weevils collected during these rearing studies have only been identified to genus with an additional 44% identified only to morphospecies. This is consistent with Tavakilian's (1997) cerambycid study in which 40% of the species reared had not been described. The unnamed weevils collected during these studies may represent species completely unknown to science.

Diversity, Host Association, and Seasonality Over Time

The guild of saproxylic weevils associated with the Brazil nut family includes species in the subfamily Conoderinae, Cryptorhynchinae, and Molytinae, but in the two rearing studies in French Guiana (1995, 2007), ten conoderine species accounted for 83% of the specimens. Only 33% of the weevil species overall, but 56% of the conoderines, were reared in both 1995 and

2007. The cerambycid subfamily Lamiinae also had comparatively low species turnover (58% were reared in both studies), while species turnover in the bark and ambrosia beetles, and cerambycid subfamily Cerambycinae, were substantially higher (with only 17-29% of the species reared in both studies). The weevil subfamily Conoderinae and the cerambycid subfamily Lamiinae both include cryptic species that are probably well adapted to the high moisture levels that currently characterize central French Guiana. They each include numerous species that seem to have stable associations with the Brazil nut family—a family restricted to moist lowland forests.

Most saproxylic weevils were reared from tree species belonging to the large *Bertholletia* clade. Within this clade, the preferred host was the geographically widespread and locally abundant tree species *Eschweilera coriacea*. A widespread geographic distribution does not automatically predict weevil preference. Both species of the basal genus *Gustavia* are widely distributed, and yet yielded few weevils (although there is one conoderine species, *Pseudopinarus cerastes*, that emerges preferentially from *Gustavia*).

Weevil seasonality varied more than host association. In FG 07, 93% of the weevils were reared from branches cut during the rainy season, consistent with the hypothesis that smaller insects would be particularly vulnerable to desiccation. In 1995, almost half of weevils (48%) were reared from branches cut during the dry season. Some of the 1995 dry season diversity was due to the presence of several species in the subfamily Cryptorhynchinae, which may be more drought tolerant. There was also increased abundance in the conoderine genus *Piazurus*, which appears to be moisture dependent, but this might be explained by the rearing protocol. In 1995 the dry season branches were exposed through the beginning of the rainy season, when adults may be particularly active, while in 2007 the dry season branches were collected approximately six weeks earlier. Inter-annual variability in precipitation may also affect seasonal patterns of activity.

Diversity, Host Association, and Seasonality Across Distance

There was a major shift in species richness between localities (French Guiana and Peru). French Guiana had only 52% of the species richness of Peru, with only 18 species shared between localities. Species turnover was therefore high, but the species reared at both sites accounted for much of the abundance. The reciprocal Simpson's index yielded identical estimates of diversity for the two localities, but this is probably due the low evenness of the Peru samples. With its environmental heterogeneity, relatively fertile soils, and resulting high productivity, Peru had higher weevil species richness and abundance than French Guiana, but that abundance was not evenly distributed among the species. In French Guiana, where the environment is less heterogeneous, forests are much older, and productivity lower, species richness and abundance were comparatively low, and abundance was more evenly distributed. Similar trends are found among tree and vertebrate species: e.g. birds and mammals. Overall, species richness of these organisms is higher in southwest Amazonia than in the northeast (ter Steege *et al.*, 2006).

In Peru, weevils also showed a consistent association with host tree species within the *Bertholletia* clade. Because this association persists in such widely separated forests it may reflect a long and stable association between insect and plant, but additional sampling from a taxonomically diverse plant sample is needed. Unlike French Guiana, weevils were more diverse and abundant in branches cut during the dry season, perhaps due to the dominance of species in the conoderine genus *Zygops*, which appear to be diurnal, may be relatively drought tolerant, and were poorly represented in French Guiana.

Resource Partitioning Among Weevils, Bark & Ambrosia Beetles, and Cerambycids

In the FG 07 study, conoderine weevils were analyzed along with the other abundant subfamilies of saproxylic beetles: bark and ambrosia beetles (Scolytinae and Platypodinae) and cerambycids (Cerambycinae and Lamiinae). The most diverse subfamilies were Conoderinae and Lamiinae. Resource use was similar across the curculionid subfamilies, but differed dramatically from that of the cerambycids. While conoderines, platypodines, and lamiines were preferentially associated with the host species *E. coriacea*, saproxylic beetles may combat the detrimental effects of competition through different seasonal or stratum preferences. Conoderine weevils primarily colonized branches at the ground stratum during the rainy season. Their main competitors for these branches were the platypodines and some scolytines, whose larvae are relatively small (less than 4 mm) and often feed on fungi rather than host plant tissue. The remaining scolytines, as well as the lamiines (Cerambycidae), were collected at the canopy stratum during the rainy season, experiencing little competition with weevil larvae. Cerambycines were relatively uncommon, were collected from the warmest, driest microhabitat, (canopy stratum during the dry season), and therefore would not be expected to compete with weevils for resources. These results were not consistent with stratum preferences in North Queensland, Australia. Stork and Grimbacher (2006) found cerambycids, curculionids, and platypodines to be more abundant in the canopy and the scolytines more abundant at the ground stratum. Within each group there are probably lineages that are better adapted to drought (such as cerambycines, or conoderines in the genus *Zygops*), or more dependent on moisture (such as lamiines, or conoderines in the genus *Piazurus*). Their ratios are likely to differ from locality to locality, depending on local conditions. The French Guiana site receives abundant moisture in most months of the year, and is surrounded by large expanses of primary moist forest; these may define the seasonal behavior of local insect communities.

Conclusions

Saproxylic wood-boring beetle larvae are excellent model organisms with which to evaluate the effects of global climate change. They spend their larval period inside a single host until they undergo metamorphosis to become adults. Should the conditions of the wood they inhabit become inhospitable, they are unable to migrate to a more suitable habitat. If the conditions become too harsh (*e.g.*, temperature too high or not enough moisture in the wood), the larvae will likely die. Saproxylic species associated with the Brazil nut family will be especially important indicators of global change, because the trees themselves are restricted to moist lowland forests, and, like other large-seeded species, do not appear to thrive in secondary forests. As climates in the Neotropics become hotter and drier, saproxylic beetles must adapt to these changes or they will not survive. Beetles that appear to be drought tolerant (cerambycines and weevils in the conoderine genus *Zygops*) would be expected to thrive, probably at the expense of the moisture dependent groups.

If Southwest Amazonia retains its tropical rainforests, they should be able to maintain their surprisingly high species richness over time, because the forests are already relatively heterogeneous, and the region is not predicted to experience dramatic climate change (Miles *et al*., 2004). Northeast Amazonia, on the other hand, may not be able to maintain its current level of curculionid diversity because it is expected to experience dramatic drops in precipitation and moisture over the next century, and much of its curculionid fauna appears to be more moisture dependent. As temperatures increase and precipitation decreases or becomes less evenly distributed, the data collected in these studies will serve as a foundation to investigate the impact of climate change on these ecologically important saproxylic beetles. It may be possible to monitor the strength of the effects of climate change on a forest habitat before the tree communities themselves manifest any signs of distress by examining species composition, diversity, and resource partitioning among saproxylic wood-boring beetles.

Appendix 1: The number of individuals of wood-boring weevils reared from trees in the Brazil nut family (Lecythidaceae) in French Guiana in 1995 and 2007.

		Host[1,2,3]					Season[1,2,4]		2007[1,2]	
Species	***N***	**CA (95/07)**	**CS (95/07)**	**EC (95/07)**	**GH (95/07)**	**LP (95/07)**	**1995 (D / R)**	**2007 (D / R)**	**Stratum[5] (C / G)**	**Diameter[6] (L /S)**
Conoderinae										
Copturomorpha sp. 1	183	0 / ---	0 / ---	8 / **175**[*]	0 / 0	0 / 0	6 / 2	3 / **172**	4 / **171**	25 / 150
Piazurus alternans Kirsch	116	0 / ---	0 / ---	**24 / 89**	0 / 0	1 / 2	0 / **25**	0 / **91**	44 / 47	**85** / 6
Piazurus incommodus Boheman	616	0 / ---	0 / ---	**293** / 195	0 / 0	34 / 94	97 / 230	6 / **283**	0 / **289**	**279** / 10
Piazurus phlesus (Fabricius)	1	0 / ---	0 / ---	0 / 0	0 / 0	1 / 0	1 / 0	0 / 0	---	---
Piazurus pseudoalternans Hustache	495	7 / ---	0 / ---	63 / 302	0 / 2	21 / 100	27 / 64	9 / **395**	1 / **403**	**387** / 17
Piazurus sp. 2	14	0 / ---	0 / ---	1 / 6	0 / 0	0 / 7	1 / 0	0 / **13**	0 / **13**	11 / 2
Piazurus sp. 3	181	0 / ---	0 / ---	**49 / 132**[*]	0 / 0	0 / 0	1 / **48**	4 / **128**	**124** / 8	**130** / 2
Pseudopinarus cerastes (Fabricius)	107	1 / ---	9 / ---	0 / 0	40 / **55**[*]	2 / 0	**49** / 3	33 / 22	3 / **52**	45 / 10
Pseudopinarus sp. 1	20	0 / ---	0 / ---	0 / 0	0 / 0	**17** / 3	8 / 9	0 / 3	3 / 0	3 / 0
Pseudopinarus sp. 2	13	0 / ---	0 / ---	**11** / 2	0 / 0	0 / 0	6 / 5	0 / 2	0 / 2	0 / 2
Pseudopinarus sp. 3	8	0 / ---	0 / ---	0 / 8	0 / 0	0 / 0	0 / 0	8 / 0	6 / 2	6 / 2
Zygops histrio Boheman	45	0 / ---	0 / ---	26 / 3	0 / 0	14 / 2	27 / 13	2 / 3	3 / 2	5 / 0
Zygops leucogaster Desbrochers	7	0 / ---	0 / ---	7 / 0	0 / 0	0 / 0	1 / 6	0 / 0	---	---
Zygops pius Boheman	21	0 / ---	0 / ---	0 / 0	0 / 0	0 / **21**	0 / 0	**21** / 0	0 / **21**	**21** / 0
Zygops rufitorquis (Champion)	1	0 / ---	0 / ---	0 / 0	0 / 0	0 / 1	0 / 0	1 / 0	0 / 1	0 / 1
Zygops sanctus (Fabricius)	1	0 / ---	0 / ---	0 / 0	0 / 0	1 / 0	1 / 0	0 / 0	---	---
Zygops wiedii (Germar)	4	0 / ---	0 / ---	1 / 0	0 / 0	3 / 0	2 / 2	0 / 0	---	---
Conoderinae sp. 1	1	0 / ---	0 / ---	0 / 0	0 / 0	0 / 1	0 / 0	0 / 1	0 / 1	1 / 0
Cryptorhynchinae										
Cophes sp. 1	32	0 / ---	0 / ---	0 / 0	0 / 0	0 / **32**	0 / 0	0 / **32**	0 / **32**	**32** / 0
Cryptorhynchus sp. 1	1	0 / ---	1 / --	0 / 0	0 / 0	0 / 0	1 / 0	0 / 0	---	---

Species	*N*	Host[1,2,3]					Season[1,2,4]		2007[1,2]	
		CA (95/07)	CS (95/07)	EC (95/07)	GH (95/07)	LP (95/07)	1995 (D / R)	2007 (D / R)	Stratum[5] (C / G)	Diameter[6] (L /S)
Cryptorhynchus sp. 2	1	0 / ---	0 / ---	0 / 0	1 / 0	0 / 0	1 / 0	0 / 0	---	---
Cryptorhynchus sp. 5	1	0 / ---	0 / ---	0 / 0	0 / 0	0 / 1	0 / 0	1 / 0	1 / 0	1 / 0
Eubulus sp. 1	11	0 / ---	0 / ---	0 / 0	**11** / 0	0 / 0	**11** / 0	0 / 0	---	---
Eubulus sp. 2	2	0 / ---	0 / ---	0 / 0	2 / 0	0 / 0	2 / 0	0 / 0	---	---
Eubulus sp. 4	87	0 / ---	0 / ---	**87** / 0	0 / 0	0 / 0	**87** / 0	0 / 0	---	---
Eubulus sp. 5	1	0 / ---	0 / ---	0 / 1	0 / 0	0 / 0	0 / 0	0 / 1	0 / 1	0 / 1
Eubulus sp. 6	1	0 / ---	0 / ---	0 / 1	0 / 0	0 / 0	0 / 0	0 / 1	0 / 1	1 / 0
Pisaeus sp. 1	204	0 / ---	0 / ---	**193 / 11**	0 / 0	0 / 0	**184** / 9	0 / **11**	0 / **11**	**11** / 0
Semnorhynchus sp. 1	2	0 / ---	0 / ---	0 / 1	1 / 0	0 / 0	1 / 0	1 / 0	1 / 0	1 / 0
Dryopthorinae										
Dryophthorinae sp. 1	3	0 / ---	0 / ---	0 / 0	0 / 0	0 / 3	0 / 0	0 / 3	0 / 3	3 / 0
Molytinae										
Heilipodus sp. 6	1	0 / ---	0 / ---	0 / 0	0 / 0	1 / 0	0 / 1	0 / 0	---	---
Microhyus sp. 1	46	0 / ---	0 / ---	**38** / 8	0 / 0	0 / 0	0 / **38**	0 / 8	0 / 8	1 / 7
Microhyus sp. 2	13	0 / ---	0 / ---	**13** / 0	0 / 0	0 / 0	0 / **13**	0 / 0	---	---
Oncorrhinus planatus Fahraeus	2	0 / ---	0 / ---	2 / 0	0 / 0	0 / 0	0 / 2	0 / 0	---	---
Molytinae sp. 1	1	0 / ---	0 / ---	0 / 0	0 / 0	0 / 1	0 / 0	0 / 1	1 / 0	1 / 0
Molytinae sp. 2	3	0 / ---	0 / ---	0 / 0	0 / 0	0 / 3	0 / 0	0 / 3	3 / 0	3 / 0
Incertae sedis										
Genus sp. 1	1	0 / ---	0 / ---	1 / 0	0 / 0	0 / 0	1 / 0	0 / 0	---	---
Genus sp. 2	1	0 / ---	0 / ---	0 / 0	1 / 0	0 / 0	1 / 0	0 / 0	---	---
Total	2248	8 / ---	10 / ---	817 / 934	56 / 57	95 / 271	516 / 470	89 / 1173	194 / 1068	1052 / 89

[1] Species are classified as specialists if 90 % of the specimens with $\geq$ 10 individuals are associated with a single host, season, stratum, or branch diameter; [2] bold = specialist, gen = generalist; [3] CA = *Corythophora amapaensis*, CS = *Couratari stellata*, EC = *Eschweilera coriacea*, LP = *Lecythis poiteaui*, GH= *Gustavia hexapetala*; [4] D = dry, R = rainy; [5] C = canopy, G = ground; [6] L = large, S = small; [*] Indicator Values were statistically significant for host ($p < 0.03$).

Appendix 2: Wood-boring weevils reared from trees in the Brazil nut family (Lecythidaceae) in French Guiana (1995, 2007) and Peru 2003.

	FG 95^{1,2}					FG 07^{1,2}			Peru 03^{1}					
	CA	**CS**	**EC**	**GH**	**LP**	**EC**	**GH**	**LP**	**AD**	**BE**	**CM**	**EC**	**ET**	**GA**
Species	**D/R**	**D/R**	**D/R**	**D/R**	**D/R**	**D/R**	**D/R**	**D/R**	**D/R**	**D/R**	**D/R**	**D/R**	**D/R**	**D/R**
Conoderinae														
Archocoptorus regalis (Boheman)	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 1	0 / 0	0 / 0	1 / 0	0 / 0
Copturomorpha sp. 1	0 / 0	0 / 0	6 / 2	0 / 0	0 / 0	**3 / 172**	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 4	0 / 0	0 / 0
Piazurus alternans Kirsch	0 / 0	0 / 0	**0 / 24**	0 / 0	0 / 1	**0 / 89**	0 / 0	0 / 2	0 / 0	20 / 0	0 / 0	58 / 58	0 / 2	0 / 0
Piazurus incommodus Boheman	0 / 0	0 / 0	**75 / 218**	0 / 0	22 / 12	5 / 190	0 / 0	1 / 93	0 / 0	101 / 0	0 / 0	11 / 2	0 / 6	0 / 2
Piazurus phlesus (Fabricius)	0 / 0	0 / 0	0 / 0	0 / 0	1 / 0	0 / 0	0 / 0	0 / 0	1 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0
Piazurus pseudoalternans Hustache	2 / 5	0 / 0	11 /52	0 / 0	14 / 7	4 / 298	0 / 2	5 / 95	0 / 0	150 / 6	0 / 0	13 / 7	0 / 10	0 / 0
Piazurus sp. 2	0 / 0	0 / 0	1 / 0	0 / 0	0 / 0	0 / 6	0 / 0	0 / 7	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0
Piazurus sp. 3	0 / 0	0 / 0	**1 / 48**	0 / 0	0 / 0	**4 / 128**	0 / 0	0 / 0	0 / 0	10 / 0	0 / 0	0 / 0	0 / 1	0 / 0
Pseudopinarus cerastes (Fabricius)	1 / 0	9 / 0	0 / 0	37 / 3	2 / 0	0 / 0	**33 / 22**	0 / 0	0 / 0	6 / 0	0 / 2	2 / 1	1 / 0	**53 / 71**
Pseudopinarus sp. 1	0 / 0	0 / 0	0 / 0	0 / 0	8 / 9	0 / 0	0 / 0	0 / 3	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0
Pseudopinarus sp. 2	0 / 0	0 / 0	**6 / 5**	0 / 0	0 / 0	0 / 2	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	1 / 0	0 / 0
Pseudopinarus sp. 3	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	8 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0
Zygops amoenulus Champion	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	26 / 2	0 / 0	0 / 0	2 / 19	5 / 0	0 / 0
Zygops buffo Gyllenhal	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 4	0 / 0
Zygops histrio Boheman	0 / 0	0 / 0	13 / 13	0 / 0	14 / 0	0 / 3	0 / 0	2 / 0	1 / 0	66 / 1	0 / 0	130 / 61	21 / 16	0 / 0
Zygops leucogaster Desbrochers	0 / 0	0 / 0	1 / 6	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	95 / 4	116 / 9	0 / 2	844 / 213	12 / 36	0 / 0
Zygops pius Boheman	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	**21 / 0**	0 / 0	2 / 0	0 / 0	**17 / 8**	0 / 0	0 / 0
Zygops rufitorquis (Champion)	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	1 / 0	0 / 0	0 / 0	0 / 0	5 / 0	0 / 0	0 / 0
Zygops sanctus (Fabricius)	0 / 0	0 / 0	0 / 0	0 / 0	1 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0
Zygops sobrius (Gyllenhal)	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 1	0 / 0	0 / 0	0 / 1	0 / 0
Zygops wiedii (Germar)	0 / 0	0 / 0	0 / 1	0 / 0	2 / 1	0 / 0	0 / 0	0 / 0	10 / 0	7 / 0	0 / 0	4 / 2	1 / 0	0 / 0
Zygops sp. 4	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	110 / 97	46 / 24	0 / 0	9 / 73	42 / 16	1 / 2
Conoderinae sp. 1	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 1	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0
Conoderinae sp. 2	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	2 / 0	0 / 0	0 / 0	0 / 0	0 / 0
Conoderinae sp. 3	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	1 / 0	0 / 0	0 / 0	0 / 0	0 / 0

Conoderinae sp. 4	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 1	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0
Conoderinae sp. 5	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 1	0 / 0
Conoderinae sp. 7	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 1	0 / 0	0 / 0	0 / 0	0 / 0
Conoderinae sp. 8	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 2	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0
Total	3 / 5	9 / 0	114 / 369	37 / 3	64 / 30	24 / 888	33 / 24	30 /201	243 / 106	527 / 43	0 / 4	1095 / 448	84 / 94	54 / 75
Cryptorhynchinae														
Apteromechus sp. 1	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 1	0 / 0	0 / 0
Cophes sp. 1	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	**0 / 32**	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0
Cryptorhynchus sp. 1	0 / 0	1 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0
Cryptorhynchus sp. 2	0 / 0	0 / 0	0 / 0	1 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0
Cryptorhynchus sp. 4	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	1 / 2	0 / 0	0 / 0
Cryptorhynchus sp. 5	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	1 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0
Eubulus sp. 1	0 / 0	0 / 0	0 / 0	**11 / 0**	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	1 / 0	2 / 0
Eubulus sp. 2	0 / 0	0 / 0	0 / 0	2 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0
Eubulus sp. 3	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	7 / 0	8 / 0	0 / 0	0 / 0	0 / 0	0 / 0
Eubulus sp. 4	0 / 0	0 / 0	**87 / 0**	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0
Eubulus sp. 5	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 1	0 / 0	0 / 0	4 / 0	2 / 0	0 / 0	2 / 1	0 / 0	0 / 0
Eubulus sp. 6	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 1	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0
Eubulus sp. 7	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	1 / 1	0 / 0	0 / 0
Pisaeus sp. 1	0 / 0	0 / 0	**184 / 9**	0 / 0	0 / 0	**0 / 11**	0 / 0	0 / 0	0 / 0	9 / 10	0 / 1	1 / 15	0 / 1	0 / 0
Semnoryhchus sp. 1	0 / 0	0 / 0	0 / 0	1 / 0	0 / 0	1 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0
Cryptorhynchinae sp. 2	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	1 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0
Cryptorhynchinae sp. 3	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	1 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0
Cryptorhynchinae sp. 4	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	1 / 0	0 / 0	0 / 0	0 / 0	0 / 0	1 / 0
Cryptorhynchinae sp. 5	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	2 / 0	0 / 0	4 / 0	0 / 0	0 / 0
Cryptorhynchinae sp. 6	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	1 / 0	0 / 0	1 / 0	0 / 0	0 / 0
Cryptorhynchinae sp. 7	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	3 / 0	1 / 0	0 / 0	0 / 0	0 / 0
Cryptorhynchinae sp. 8	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	1 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0
Cryptorhynchinae sp. 9	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	1 / 0	0 / 0	0 / 0	0 / 0	1 / 0	1 / 0
Cryptorhynchinae sp. 10	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	1 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0
Cryptorhynchinae sp. 11	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	1 / 0	0 / 0	0 / 0	0 / 0
Cryptorhynchinae sp. 12	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	1 / 0	0 / 0	0 / 0	0 / 0
Cryptorhynchinae sp. 13	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	1 / 0	0 / 0	0 / 0	0 / 0
Cryptorhynchinae sp. 14	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	3 / 0	0 / 0

Cryptorhynchinae sp. 15	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	1 / 0	0 / 0
Cryptorhynchinae sp. 16	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	5 / 0
Cryptorhynchinae sp. 17	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	1 / 0
Cryptorhynchinae sp. 18	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 1	0 / 0	0 / 0	0 / 0	0 / 0
Cryptorhynchinae sp. 19	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 1	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0
Cryptorhynchinae sp. 20	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 1	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0
Cryptorhynchinae sp. 21	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 2	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0
Cryptorhynchinae sp. 22	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 1	0 / 0	0 / 0	0 / 0
Cryptorhynchinae sp. 23	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 1	0 / 0	0 / 0
Cryptorhynchinae sp. 24	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	1 / 0	0 / 0	0 / 3	0 / 3	0 / 0
Total	0 / 0	1 / 0	271 / 9	15 / 0	0 / 0	1 / 13	0 / 0	1 / 32	17 / 4	26/ 11	4 / 2	10 / 24	6 / 4	10 / 0
Dryophthorine														
Rhinostomus barbirostris Fabricius	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	1 / 0	0 / 0	0 / 0	0 / 0
Dryophthorine sp. 1	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 3	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0
Total	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 3	0 / 0	0 / 0	1 / 0	0 / 0	0 / 0	0 / 0
Entiminae														
Naupactus sp. 1	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	1 / 0	0 / 0	0 / 0	0 / 2	0 / 0	0 / 0
Pronecops sp. 1	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 1	0 / 0	0 / 0
Entiminae sp. 1	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 1	0 / 0	0 / 0	0 / 0	0 / 0
Total	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	1 / 0	0 / 1	0 / 0	0 / 3	0 / 0	0 / 0
Molytinae														
Helipodus sp. 1	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	3 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0
Helipodus sp. 2	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	1 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0
Helipodus sp. 4	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 1	0 / 0	0 / 0
Helipodus sp. 5	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 1
Helipodus sp. 6	0 / 0	0 / 0	0 / 0	0 / 0	0 / 1	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0
Helipodus sp. 7	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	1 / 0	0 / 0	0 / 0	0 / 1
Microhyus sp. 1	0 / 0	0 / 0	**0 / 38**	0 / 0	0 / 0	0 / 8	0 / 0	0 / 0	0 / 0	**10 / 0**	0 / 0	0 / 0	0 / 0	0 / 0
Microhyus sp. 2	0 / 0	0 / 0	**0 / 13**	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0
Oncorhinus planatus Fahreaus	0 / 0	0 / 0	0 / 2	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0
Molytinae sp 1	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 1	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0
Molytinae sp 2	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 3	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0
Molytinae sp. 3	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	1 / 0	0 / 0	0 / 0	0 / 0	0 / 0
Molytinae sp. 4	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	1 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0
Molytinae sp. 5	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	1 / 0

Molytinae sp. 6	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 1	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0
Molytinae sp. 7	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	2 / 0	0 / 0	0 / 3	0 / 0	0 / 0
Molytinae sp. 8	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 1	0 / 0	0 / 0
Molytinae sp. 9	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	1 / 0	0 / 0	0 / 0	0 / 0	0 / 0
Total	0 / 0	0 / 0	0 / 53	0 / 0	0 / 1	0 / 8	0 / 0	0 / 4	5 / 1	14 / 0	0 / 0	0 / 5	0 / 0	1 / 2
Incertae Sedis														
Genus sp. 7	0 / 0	0 / 0	1 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0
Genus sp. 8	0 / 0	0 / 0	0 / 0	1 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0
Genus sp. 10	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 1	0 / 0	0 / 0	0 / 0	0 / 0
Total	0 / 0	0 / 0	1 / 0	1 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 1	0 / 0	0 / 0	0 / 0	0 / 0
Overall Total	3 / 5	10 / 0	386 / 431	53 / 3	64 / 31	25 / 909	33 / 24	31 / 240	266 / 111	567 / 58	6 / 6	1105 / 480	90 / 98	65 / 77

[1] Species are classified as specialists if 90% or more of the specimens with ≥ 10 individuals associated with a single host or season; bold = host specialist; AD = *Allantoma decandra*, BE = *Bertholletia excelsa*, CS = *Couratari stellata*, CM = *Couratari macrosperma*, CA = *Corythophora amapaensis*, EC = *Eschweilera coriacea*, ET = *Eschweilera tessmannii*, GA = *Gustavia augusta*, and GH = *Gustavia hexapetala*; D = dry, R = rainy; [2] FG = French Guiana.

Appendix 3: Wood-boring weevils reared by season (Lecythidaceae) in French Guiana (1995, 2007) and Peru 2003.

	FG 95[1,2]		**FG 07[1,2]**		**Peru 03[1]**	
Species	**Dry**	**Rainy**	**Dry**	**Rainy**	**Dry**	**Rainy**
Conoderinae						
Archocoptorus regalis (Boheman)	0	0	0	0	1	1
Copturomorpha sp. 1	6	2	3	**172**	0	4
Piazurus alternans Kirsch	0	**25**	0	**91**	78	60
Piazurus incommodus Boheman	97	230	6	**283**	**112**	12
Piazurus phlesus (Fabricius)	1	0	0	0	1	0
Piazurus pseudoalternans Hustache	27	64	9	**395**	163	23
Piazurus sp. 2	1	0	0	13	0	0
Piazurus sp. 3	1	**48**	4	**128**	10	1
Pseudopinarus cerastes (Fabricius)	**49**	3	33	22	62	74
Pseudopinarus sp. 1	8	9	0	3	0	0
Pseudopinarus sp. 2	6	5	0	2	1	0
Pseudopinarus sp. 3	0	0	8	0	0	0
Zygops amoenulus Champion	0	0	0	0	33	21
Zygops buffo Gyllenhal	0	0	0	0	0	4
Zygops histrio Boheman	27	13	2	3	218	78
Zygops leucogaster Desbrochers	1	6	0	0	1067	264
Zygops pius Boheman	0	0	**21**	0	19	8
Zygops rufitorquis (Champion)	0	0	1	0	5	0
Zygops sanctus (Fabricius)	1	0	0	0	0	0
Zygops sobrius (Gyllenhal)	0	0	0	0	0	2
Zygops wiedii (Germar)	2	2	0	0	**22**	2
Zygops sp. 4	0	0	0	0	208	212
Conoderinae sp. 1	0	0	0	1	0	0
Conoderinae sp. 2	0	0	0	1	2	0
Conoderinae sp. 3	0	0	0	0	1	0
Conoderinae sp. 4	0	0	0	0	0	1
Conoderinae sp. 5	0	0	0	0	0	1
Conoderinae sp. 7	0	0	0	0	0	1
Conoderinae sp. 8	0	0	0	0	0	2
Total	227	407	87	1113	2003	772
Cryptorhynchinae						
Apteromechus sp. 1	0	0	0	0	0	1
Cophes sp. 1	0	0	0	**32**	0	0
Cryptorhynchus sp. 1	1	0	0	0	0	0
Cryptorhynchus sp. 2	1	0	0	0	0	0
Cryptorhynchus sp. 4	0	0	0	0	1	2
Cryptorhynchus sp. 5	0	0	1	0	0	0
Eubulus sp. 1	**11**	0	0	0	3	0
Eubulus sp. 2	2	0	0	0	0	0
Eubulus sp. 3	0	0	0	0	**15**	0
Eubulus sp. 4	**87**	0	0	0	0	0
Eubulus sp. 5	0	0	0	1	8	1
Eubulus sp. 6	0	0	0	1	0	0

Eubulus sp. 7	0	0	0	0	1	1
Pisaeus sp. 1	**184**	9	0	**11**	10	27
Semnoryhchus sp. 1	1	0	1	0	0	0
Cryptorhynchinae sp. 2	0	0	0	0	1	0
Cryptorhynchinae sp. 3	0	0	0	0	1	0
Cryptorhynchinae sp. 4	0	0	0	0	2	0
Cryptorhynchinae sp. 5	0	0	0	0	6	0
Cryptorhynchinae sp. 6	0	0	0	0	2	0
Cryptorhynchinae sp. 7	0	0	0	0	4	0
Cryptorhynchinae sp. 8	0	0	0	0	1	0
Cryptorhynchinae sp. 9	0	0	0	0	3	0
Cryptorhynchinae sp. 10	0	0	0	0	1	0
Cryptorhynchinae sp. 11	0	0	0	0	1	0
Cryptorhynchinae sp. 12	0	0	0	0	1	0
Cryptorhynchinae sp. 13	0	0	0	0	1	0
Cryptorhynchinae sp. 14	0	0	0	0	3	0
Cryptorhynchinae sp. 15	0	0	0	0	1	0
Cryptorhynchinae sp. 16	0	0	0	0	5	0
Cryptorhynchinae sp. 17	0	0	0	0	1	0
Cryptorhynchinae sp. 18	0	0	0	0	0	1
Cryptorhynchinae sp. 19	0	0	0	0	0	1
Cryptorhynchinae sp. 20	0	0	0	0	0	1
Cryptorhynchinae sp. 21	0	0	0	0	0	2
Cryptorhynchinae sp. 22	0	0	0	0	0	1
Cryptorhynchinae sp. 23	0	0	0	0	0	1
Cryptorhynchinae sp. 24	0	0	0	0	1	6
Total	287	9	2	45	73	45
Dryophthorine						
Rhinostomus barbirostris Fabricius	0	0	0	0	1	0
Dryophthorine sp. 1	0	0	0	3	0	0
Total	0	0	0	3	1	0
Entiminae						
Naupactus sp. 1	0	0	0	0	1	2
Pronecops sp. 1	0	0	0	0	0	1
Entiminae sp. 1	0	0	0	0	0	1
Total	0	0	0	0	1	4
Molytinae						
Helipodus sp. 1	0	0	0	0	3	0
Helipodus sp. 2	0	0	0	0	1	0
Helipodus sp. 4	0	0	0	0	0	1
Helipodus sp. 5	0	0	0	0	0	1
Helipodus sp. 6	0	1	0	0	0	0
Helipodus sp. 7	0	0	0	0	1	1
Microhyus sp. 1	0	**38**	0	8	**10**	0
Microhyus sp. 2	0	**13**	0	0	0	0
Oncorhinus planatus Fahreaus	0	2	0	0	0	0
Molytinae sp 1	0	0	0	1	0	0
Molytinae sp 2	0	0	0	3	0	0
Molytinae sp. 3	0	0	0	0	1	0
Molytinae sp. 4	0	0	0	0	1	0

Molytinae sp. 5	0	0	0	0	1	0
Molytinae sp. 6	0	0	0	0	0	1
Molytinae sp. 7	0	0	0	0	2	3
Molytinae sp. 8	0	0	0	0	0	1
Molytinae sp. 9	0	0	0	0	1	0
Total	0	54	0	12	21	8
Incertae Sedis						
Genus sp. 7	1	0	0	0	0	0
Genus sp. 8	1	0	0	0	0	0
Genus sp. 10	0	0	0	0	0	1
Total	2	0	0	0	0	1
Overall Total	516	470	89	1173	2099	830

[1] Species are classified as specialists if 90% or more of the specimens with ≥ 10 individuals associated with a single host or season; bold = host specialist; [2] FG = French Guiana.

Appendix 4. Wood-boring beetles reared from trees in the Brazil nut family (Lecythidaceae) in French Guiana in 2007.

	EC^{1,2,3}		LP^{1,2,3}		Season^{1,2}		Stratum^{1,2}		Branch Diameter^{1,2}	
Species	Dry	Rainy	Dry	Rainy	Dry	Rainy	Canopy	Ground	Thick	Thin
Cerambycidae: Cerambycinae										
Eburodacrys sulphureosignata (Erichson)	**14**	**0**	0	0	**14**	0	7	7	12	2
Mecometopus triangularis (Laporte & Gory)	0	1	**13**	**0**	**13**	1	0	**14**	8	6
Periboem pubescens (Oliver)	3	0	**143**	**1**	**146**	1	76	71	**141**	6
Pseudoeriphus sp. 1	0	0	1	0	1	0	1	0	1	0
Total	17	1	157	1	174	2	84	92	162	14
Cerambycidae: Lamiinae										
Neobaryssinus altissimus Berkov & Monne	1	0	**44**	**120**	45	120	**160**	5	**165**	0
Neoeutrypanus mutilatus (Germar)	18	0	7	2	**25**	2	19	8	24	3
Neoeutrypanus nobilus (Bates)	5	0	0	0	5	0	5	0	5	0
Oedopeza leucostigma Bates	**24**	**26**	0	0	24	26	19	31	**50**	0
Oreodera simplex Bates	**40**	**12**	0	0	40	12	2	**50**	37	15
Ozineus sp. 1	**27**	**58**	0	0	27	58	8	77	16	69
Palame anceps (Bates)	**607**	**97**	0	1	607	98	137	568	**673**	32
Palame crassimana Bates 'bicolor'	17	2	**96**	**76**	113	78	86	105	**181**	10
Palame crassimana Bates 'olivaceous'	0	23	0	1	0	24	**24**	0	24	0
Palame crassimana Bates 'unicolor'	**23**	**95**	0	0	23	95	**110**	9	**118**	0
Palame mimetica Monne ‘runt’	16	31	11	38	27	69	76	20	**92**	4
Pseudosparna sp. 1	1	2	0	0	1	2	2	1	2	1
Xenofrea magdalenae Néouze & Tavakilian	1	0	0	0	1	0	1	0	1	0
Xenofrea rogueti Néouze &	0	1	0	0	0	1	0	1	1	0

Tavakilian										
Xylergates elaineae Gilmour	**26**	**39**	0	0	26	39	40	25	**65**	0
Xylergates pulcher Lane	1	0	0	0	1	0	0	1	1	0
Acanthocinini sp. 50	**2**	**22**	0	0	2	**22**	0	24	0	**24**
Acanthocinini sp. 51	0	0	1	0	1	0	0	1	1	0
Total	809	408	159	238	968	646	689	925	1456	158
Curculionidae: Conoderinae										
Copturomorpha sp. 1	**3**	**172**	0	0	3	**172**	4	**171**	25	150
Piazurus alternans Kirsch	**0**	**89**	0	2	0	**91**	44	47	**85**	6
Piazurus incommodus Boheman	5	190	1	93	6	**283**	0	289	279	10
Piazurus pseudoalternans Hustache	4	298	5	95	9	**393**	0	**402**	**386**	16
Piazurus sp. 2	0	6	0	7	0	**13**	0	**13**	11	2
Piazurus sp. 3	**4**	**128**	0	0	4	**128**	**124**	8	**130**	2
Pseudopinarus sp. 1	0	0	0	3	0	3	3	0	3	0
Pseudopinarus sp. 2	0	2	0	0	0	2	0	2	0	2
Pseudopinarus sp. 3	8	0	0	0	8	0	6	2	6	2
Zygops histrio Boheman	0	3	2	0	2	3	3	2	5	0
Zygops pius Boheman	0	0	**21**	**0**	**21**	0	0	**21**	**21**	0
Zygops rufitorquis (Champion)	0	0	1	0	1	0	0	1	0	1
Conoderinae sp. 1	0	0	0	1	0	1	0	1	1	0
Total	24	888	30	201	54	1089	184	959	952	191
Curculionidae: Platypodinae										
Platypodinae sp 1	0	0	0	1	0	1	0	1	1	0
Platypodinae sp 2	0	1	0	0	0	1	1	0	1	0
Platypodinae sp 3	**0**	**43**	0	0	0	**43**	5	38	**43**	0
Platypodinae sp 4	0	351	0	83	0	**434**	62	372	**433**	1
Platypodinae sp 5	0	383	0	124	0	**507**	6	**501**	**507**	0
Platypodinae sp 8	**0**	**31**	0	0	0	**31**	31	0	**31**	0
Platypodinae sp 9	**0**	**13**	0	0	0	**13**	0	**13**	**13**	0
Platypodinae sp 12	**0**	**31**	0	0	0	**31**	30	1	**31**	0

Platypodinae sp 13	0	5	0	0	0	5	0	5	2	3
Total	0	858	0	208	0	1066	135	931	1062	4
Curculionidae: Scolytinae										
Amphicranus sp.17	**0**	**43**	0	0	0	**43**	**42**	1	**42**	1
Coptoborus neosphenos Wood & Bright	0	6	0	0	0	6	1	5	1	5
Metacorthylus sp. 11	0	3	0	0	0	3	3	0	3	0
Microcorthylus sp. 30	0	1	0	0	0	1	1	0	1	0
Monarthrum sp. 6	**0**	**12**	0	0	0	**12**	**11**	1	**12**	0
Monarthrum sp. 16	**0**	**11**	0	0	0	**11**	6	5	**11**	0
Monarthrum sp. 18	**0**	**44**	0	0	0	**44**	**42**	2	**44**	0
Monarthrum sp. 32	**0**	**13**	0	0	0	**13**	**12**	1	**12**	1
Monarthrum sp. 36	0	0	0	1	0	1	0	1	1	0
Phelloterus cf *atrocis* Wood	0	5	0	0	0	5	5	0	5	0
Theoborus cf *coartatus* Wood & Bright	0	0	0	2	0	2	0	2	1	1
Theoborus sp. 3	0	0	0	6	0	6	0	6	0	6
Xyleborinus saginatus Wood	0	3	0	0	0	3	3	0	3	0
Xyleborus spathipennis Eichhoff	0	47	0	191	0	**238**	1	**237**	**237**	1
Xyleborus sp. 1	0	2	1	2	1	4	2	3	5	0
Xyleborus sp. 13	0	3	0	0	0	3	0	3	3	0
Xyleborus sp. 14	0	9	0	37	0	**46**	4	**42**	**46**	0
Xyleborus sp. 19	0	30	0	7	0	**37**	9	28	**37**	0
Xyleborus sp. 28	0	2	0	0	0	2	0	2	2	0
Xyleborus sp. 29	0	5	0	0	0	5	4	1	5	0
Total	0	239	1	246	1	485	146	340	471	15
Overall Total	850	2394	347	894	1197	3288	1238	3247	4103	382

[1] Species are classified as specialists if 90% or more of the specimens with ≥ 10 individuals associated with a single host, season, stratum, or branch diameter; [2] bold = specialist; [3] EC = *Eschweilera coriacea*, LP = *Lecythis poiteaui*.

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