COMPARATIVE BIOLOGY OF TEMPERATE AND SUBTROPICAL BARK AND AMBROSIA BEETLES (COLEOPTERA: SCOLYTIDAE, PLATYPODIDAE) IN INDIANA AND FLORIDA

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ABSTRACT

Bark and ambrosia beetles were compared from two intensively studied sites. The Indiana site produced 58 species, the Florida site 57 species; 17 species occurred at both sites. Much greater plant host diversity at the Indiana site seems balanced by more favorable climate at the Florida site. There are more exotic species at the Florida site. Different patterns in feeding habits and mating habits of the beetles are related to the climate and history of the sites in complex ways. A list of the species and their habits is included.

It may be assumed that the fauna of two sites will differ if there are differing climatic, biotic, and historical influences in these sites. Faunal comparisons between sites are useful if they can distinguish among these influences. The bark and ambrosia beetles are well suited to faunal comparisons because their biology and taxonomy have been under study for many years, culminating in Wood's monograph on the bark and ambrosia beetles of North and Central America (1982). Previous studies of biogeography of these beetles (Beaver 1979; Atkinson and Equihua 1986a, 1986b) have lead to some major insights with respect to trends in species diversity, resource use, and mating systems. The present study attempts to relate these characteristics to particular biogeographical influences in two small study areas.

MATERIALS AND METHODS

The two sites are the town of West Lafayette (WL), Tippecanoe County, in north-central Indiana, and Archbold Biological Station (ABS), Lake Placid, Highlands County, in south-central Florida. Intensive inventories of scolytids were conducted in 1978–81 (WL) and 1982–85 (ABS). Malaise traps, window traps, and light traps were used in both areas. Inspection of promising host material was found to be the most productive collecting method.

SITE DESCRIPTIONS

The climate of WL is typical of continental temperate regions. Winters are cold, with temperatures below 0°C for many days at a time. Summers are hot and humid, with temperatures over 25°C during the day and often during the night as well. The ABS is in a transitional zone between warm temperate and subtropical zones of Florida. Winters are

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mild and dry, with temperatures during some years falling below 0°C, but only for a few hours at a time. Sheltered microhabitats are frost-free. Summers are warm and humid, like those of WL, but longer by 2-3 months.

In their biotic characteristics the two sites are generally similar in that they both include upland and lowland habitats, natural and disturbed habitats, open and densely wooded habitats. The natural habitats of WL include areas of mixed deciduous upland and lowland forest, found primarily in Happy Hollow Park and the Purdue University Arboretum. Disturbed habitats include landscaped areas with a rich variety of native and exotic trees. We found 25 genera of native trees and large woody shrubs, and eight genera of abundant exotic trees and shrubs. The ABS includes sandhill and scrub habitats in various states of maturity, flatwoods, bayheads, and seasonal ponds. Plantings of exotic trees, mostly oaks and fruit trees, exist in two areas of the ABS. The vegetation of the ABS contains 13 genera of native trees and shrubs and five genera of abundant exotics (Abrahamson et al. 1984)

Both areas have undergone climatic changes over the last few thousand years. WL is in a glaciated portion of Indiana and was presumably denuded during the Pleistocene. The diverse deciduous forests of the area are probably the result of a massive invasion from the unglaciated southern portion of the state. Peninsular Florida during the Pleistocene was considerably drier and cooler than at present (Watts 1983). The native vegetation of the ABS combines species of the temperate Southeast, the West Indies, and endemic species of xeric scrub. Despite its conglomerate origin, the flora of the ABS is relatively depauperate. The hot climate and xeric conditions seem to limit temperate species, while freezing temperatures, however brief, exclude many West Indian species found farther south on the peninsula. The area is not easily accessible to organisms from any area having a similar climate.

RESULTS AND DISCUSSION

The Appendix provides a combined list of species with their feeding habits, degree of host specificity, mating habits, and hosts.

Total numbers of species found at each site were similar: WL 58; ABS 57. Previous studies (Beaver 1979, Wood 1982) suggested that species diversity in scolytids increases toward the tropics. This does not seem to occur as one proceeds to subtropical Florida, probably because of the biotic isolation and depauperate flora mentioned above. Relative to plant diversity, however, the ABS fauna is remarkably diverse. Since an equal number of species is maintained on about half the diversity of hosts, it appears that the diversity of tropical scolytids may depend more on the warm climate than on the floral diversity of the tropics.

One would expect the ABS to be a haven for a greater number of exotics than WL because of Florida's many seaports and because its isolation may have resulted in unoccupied ecological niches. Since there were no early surveys of bark and ambrosia beetles, it is difficult to determine whether widespread Neotropical species were imported by man. We know of no historical documentation or establishment and range extension of any Neotropical species in the U.S. Although it is probable that some U.S. species of Xyleborus and Hypothenemus are exotic, as suggested by Wood (1982), it is just as likely that the majority were able to disperse across the Caribbean by "island-hopping," or around the Gulf of Mexico from Mesoamerica. Species with Old World origins are incontrovertable exotics; Wood (1982) has provided a list of such species. There are 12 Old World species at the ABS and eight in WL, 21% and 14% of the fauna respectively.

The ABS has a similar proportion of exotic Formicidae: 21 out of 103 species are exotic (Deyrup and Trager 1986). These numbers of exotics are not manifestations of some widely applicable "20% rule" in south central Florida, since unpublished surveys of several groups at the ABS (Scarabaeidae, Mutillidae, Apoide, Symphyta, butterflies) suggested that 20% is an extraordinarily high proportion of exotics. Neither ants nor bark beetles seem well adapted for dispersal over open sea. A study of insects taken on oil-drilling rigs in the Gulf of Mexico (Sparks et al 1986) produced only one specimen of a bark or ambrosia beetle and no ants among the 177 species and thousands of specimens of insects captured. South Florida habitats were therefore not saturated with naturally immigrating species of bark and ambrosia beetles from the tropics. On the other hand, both ants and the inbred polygynous scolytids are particularly effective colonizers once transported to a new habitat. In these groups, mating between sibling offspring of a single fertilized female is practical, if not obligatory. Inbred polygynous bark and ambrosia beetles establish family groups in which a female produces several to many females and only one or a few males, which mate with their sisters before the latter disperse to new hosts (Wood 1982, Kirkendall 1983). Of the Old World exotics at the ABS, 11 out of 12 are inbred polygynous. Even in WL, where there are generally fewer inbred polygynous species, five of the eight exotics have this mating system.

Good evidence exists for geographical trends in feeding habits of scolytoids. In general, in temperate climates there is a much higher proportion of phloeophagous (inner bark or phloem-feeding) species, and in the tropics there is a higher proportion of xylomy-cetophagous (feeding on ecto-symbiotic fungi) species (Beaver 1979). At a dry tropical site in western Mexico, however, Atkinson and Equihua (1986a) found that 57 out of 96 species were phloeophagous. The WL and ABS sites seem to show the more typical patterns of reduced phloeophagy and increased xylomycetophagy from north to south (Table 1). The percentage of phloeophagous species in WL (53.5%) was much lower than that in California (85%) and France (80%), the other temperate areas cited by Beaver (1979). The incidence of phloeophagy at the ABS (32.7%) was more similar to that of tropical areas treated by Beaver (1979: 11.6% in West Malaysia, 30.4% in Fiji) and

Atkinson and Equihua (1986a: 26.5% in southeastern Mexico).

Xylomycetophagous species were more numerous at both sites than in the much larger scolytid and platypodid faunas of California, France (Beaver 1979), or the dry tropical site in Mexico (Atkinson and Equihua 1986b). The percentage of ambrosia beetles in WL fauna (24.1%) is more comparable to that of Korea (36.6%, Choo 1983). The number and proportion of xylomycetophagous species is very high in humid tropical areas such as West Malaysia, Fiji (Beaver 1979), southeastern Mexico (Atkinson and Equihua 1986a), and Zambia (Beaver and Loyttyniemi 1985). While xylomycetophagy is at its peak in the humid tropics, it is also frequent in humid temperate areas. Mediterranean climates, as in France and California, appear even more inimical to this group than a climate with very cold winters but warm, humid summers.

The incidence of xylophagous (wood-feeding), myelophagous (pith-feeding), and spermatophagous (seed-feeding) species is usually also lower in temperate areas (Beaver 1979). The proportion of myelophagous species at the ABS is very high (21.8%). The only area with a comparable representation of this guild is dry tropical forest in Mexico (Atkinson and Equihua 1986b: 13.1%). In both areas, most of these species are polyphagous, inbred polygynous species of the tribe Cryphalini (Hypothenemus, Cryptocarenus). For reasons which are unclear, these species seem to be very numerous (both in terms of individuals as well as species) in areas with warm, seasonally dry climates.

Xylophagy and spermatophagy is infrequent at both study sites.

Beaver (1979) noted that tropical scolytids tend to be less host specific than temperate species. In large part this reflects the strong association between feeding habits and degree of specificity. In general, phloem-feeding species are highly specific, while ambrosia beetles and pith and wood-feeding species are usually polyphagous (Table 1; Beaver 1979; Atkinson and Equihua 1986a, 1986b). Phloeophagous species tend to be monophagous or oligophagous, probably because they deal with the specialized compounds concentrated in the inner bark. Most of the differences in overall degree of specificity between WL and ABS can be explained by the differences in the relative frequency of species with different feeding habits. In addition to this trend, Beaver (1979) suggested that the plant diversity of tropical forests is so great that there is an insufficient resource base to support monophagous species. This explanation cannot be applied to our study sites, as plant diversity is much greater in WL, the more northern, temperate site. Another factor explaining the high proportion of polyphagy at the ABS is that many of the

Table 1. Cross tabulation of feeding habits and degree of host specificity for bark and ambrosia beetles in West Lafayette, Indiana, and Archbold Biological Station, Florida.

Feeding		Total				
Habit	Monophagy	Oligophagy	Polyphagy	Unknown	No.	%
West Lafayette						
Phloeophagy	25	3	3	· -	31	53.5
Xylomycetophagy	1	10 <u></u>	12	1	14	24.1
Xylophagy	1		4		5	8.6
Myelophagy			4	3 -30	4	6.9
Mycetophagy	<u></u>	10 <u></u>	4 2	<u>-</u>	2	3.4
Spermatophagy	1				1	1.7
Herbiphagy	-	1	2 	6 7 - 0 .	1	1.7
Total No. spp.	28	4	25	1	58	
%ª	48.3	6.9	43.9			
Archbold Biological S	tation					
Phloeophagy	14	1	3	-	18	32.7
Xylomycetophagy	4	e 	14	3	18	32.7
Xylophagy	1	1	1	3 <u> </u>	3	5.4
Myelophagy	1	2. 	11		12	21.8
Mycetophagy	-		2	89	2	3.6
Spermatophagy	2	76 <u>1.16</u>	<u> </u>	9 <u></u>	2	3.6
Herbiphagy		_			_	-
Unknown	2 2	69 	3 	2	2	
Total No. spp.	22	2	31	2	57	
%c	40.0	3.6	56.4		5.4	

^aPercentage based on 57 species with known degree of host specificity.

polyphagous species are known or suspected exotics, whose polyphagy may be partly responsible for their establishment.

Host plant use by host specific species differs markedly between the two sites, particularly with respect to conifers and broadleaf trees. In WL 10 out of 32 monophagous and oligophagous species (most of which are phloeophagous), are in conifers; at ABS 16 out of 24 are in conifers. In WL the lower number of species in conifers may be explained by a historical factor; although conifers in plantings now occur throughout Indiana, they were originally confined to the northern and southern extremes of the state. Of the 24 species of phloeophagous species in Indiana conifers, only eight have made their way to the center of the state (Deyrup 1981). In a very local sense, conifers and associated host-specific scolytids could be considered exotics in WL. In central Florida some species associated with hardwoods in Indiana are absent because their hosts are also absent, but others appear to be absent due to other factors. In Indiana there are 14 species of phloeophagous scolytids which attack hardwoods of the genera Carya, Rhus, Fraxinus, Morus, Celtis, and Prunus; these scolytids are not found in central Florida even though trees of these genera are present. Ten of these beetles are found in northern Florida (Wood 1982, Deyrup and Atkinson 1987), but only one occurs as far south as central Florida. These beetles do not apear to be replaced by a greater density of other bark-feeders such as cerambycids and buprestids. It is normal to find large areas of unconsumed phloem in recently killed material. Temperate hardwood species become increasingly patchily distributed from north to south in peninsular Florida. This may make it more difficult for some host-specific bark beetles associated with these trees to maintain their populations.

^bPercentage based on 55 species with known feeding habits.

ePercentage based on 55 species with known degree of host specificity.

Another explanation is that the absence of these species in central Florida may be due to climatic factors.

In summary, biotic, climatic, and historical factors affect scolytid fauna at the two sites in various ways. A biotic factor, the diversity of hosts, accounts for the richness of phloeophagous scolytid fauna in WL, even in the absence of native conifers. Climatic and historical factors foster a partially exotic assemblage of species at the ABS; these factors, combined with a rich fauna in native pines, allow the ABS fauna to approach the diversity of WL, even though there are fewer potential host species. A climatic factor seems to repress southern expansion of certain phloeophagous species in hardwoods, although dispersion of host trees may also be involved. Xylomycetophagous species in both sites appear to be favored by the warm humid summers. Monophagy and oligophagy are dominent in WL and notably reduced at the ABS, due to the southern reduction of phloeophagous species (which tend to be monophagous) and the incursion of tropical polyphagous species.

ACKNOWLEDGMENTS

We thank Dr. R. A. Beaver, University of the South Pacific, Fiji; Dr. S. L. Wood, Brigham Young University, Utah; and the staff of the Archbold Biological Station for their useful comments on early drafts of this paper.

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APPENDIX

Combined lists of species from both areas. Column headings: WL, West Lafayette; ABS, Archbold Biological Station; FH, Feeding Habits; SP, Host Specificity; MS, Mating System. Feeding habits follow categories defined in text: ph, phloeophagy; xm, xylomycetophagy; xy, xylophagy; my, myelophagy, mcy mycetophagy; sp, spermatophagy; he, herbiphagy; ?, unknown. Mating systems follow categories defined by Kirkendall (1983): mg, monogyny; bg, bigyny; hp, harem polygyny; ip, inbred polygyny; th, thelotoky; ?, unknown. Degrees of specificity are defined as monophagy (mo), restriction to a single genus of host plant; oligophagy (ol), restriction to hosts of a single family; polyphagy (po), common use of hosts in unrelated families.

	Location					
Name	WL	ABS	FH	SP	MS	Hosts, Comments
PLATYPODIDAE						
Platypus compositus Say	-	+	xm	po	mg	Hardwoods
Platypus flavicornis (Fabricius)	-	+	xm	mo	mg	Pinus spp.
Platypus parallelus (Fabricius)	-	+	xm	po	mg	Extremely polyphagous
SCOLYTIDAE						
Hylesininae						
Hylastini						
Hylastes exilis Chapuis	-	+	ph	mo	mg	Pinus spp.
Hylastes salebrosus Eichhoff		+	ph	mo	mg	Pinus spp.
Hylastes tenuis Eichhoff	+	200	ph	mo	mg	Pinus spp.
Hylesinini			85			2.5
Hylastinus obscurus (Marsham)	+	-	he	ol	mg	Leguminous perennial forbs
Hylesinus aculeatus Say	+	-	ph	mo	mg	Fraxinus spp.
Hylesinus criddlei (Swaine)	+	-	ph	mo	mg	Fraxinus spp.
Hylesinus fasciatus LeConte	+	1000	ph	mo	mg	Fraxinus spp.
Hylesinus pruinosus Eichhoff	+	-	ph	mo	mg	Fraxinus spp.
Tomicini						
Dendroctonus terebrans (Olivier)	100	+	ph	mo	mg	Pinus spp.
Hylurgopinus rufipes (Eichhoff)	+	-	ph	mo	mg	Ulmus spp.
Bothrosternini						
Cnesinus strigicollis (LeConte)	6736	+	my	po	mg	
Pagiocerus frontalis (Fabricius)	-	+	sp	mo	mg	Locally mo in Persea seeds
Phloeotribini						
Phloeotribus dentifrons (Blackman)	+	-	mo	mo	mg	Celtis spp.
Phloeotribus frontalis (Olivier)	+	_	ph	mo	mg	Morus spp.
Phloeotribus liminaris (Harris)	+	125	ph	mo	mg	Prunus spp.
Phloeosinini						
Chramesus chapuisi LeConte	+	_	ph	mo	-	Celtis spp.
Chramesus hicoriae LeConte	+		ph	mo	mg	Carya spp.
Phloeosinus dentatus (Say)	+	-	ph	mo	mg	Locally mo in Juniperus spp.
Polygraphini						**************************************
Carphoborus bifurcus Eichhoff	-	+	ph	mo	hp	Pinus spp.

	Location					
Name	WL	ABS	FH	SP	MS	Hosts, Comments
SCOLYTIDAE (Continued)						
Scolytinae						
Scolytini						
Scolytus mali (Bechstein)	+	223	ph	ol	mg	Rosaceae, Ulmus
Scolytus multistriatus (Marsham)	+	(100 1)	ph		mg	Ulmus spp.
Scolytus muticus Say	+	-	ph	ol	mg	Celtis spp., Gleditsia
Scolytus quadrispinosus Say	+	420	ph	mo	-	Carya spp., Greansa
Micracini	35		pii	mo	me	carya app.
Hylocurus binodatus Wood	+	_	хy	mo	bg	Carya
Hylocurus langstoni (Blackman)	_	+	XY	ol	hp	Locally on Morus
Hylocurus rudis LeConte	+		XY	po	bg	Hardwoods
Micracis suturalis LeConte	+	-		55.55	_	Hardwoods
Micracis suntrans LeConte Micracis swainei Blackman	T	+	хy	po	bg	
		200	ху	po	bg	Hardwoods, at ABS mo in Salix
Micracisella nanula (LeConte)	§-	+	my	po	mg	Hardwoods
Pseudothysanoes lecontei Blackman	+		ph	po	bg	Carya, Quercus
Pseudothysanoes rigidus (LeConte)	+	7	ph	mo	bg	Tilia
Thysanoes fimbricornis LeConte	+	+	xy	po	bg	Hardwoods
Ipini						
Ips avulsus (Eichhoff)	-	+	ph	mo	hp	Pinus spp.
Ips calligraphus (Germar)	10	+	ph	mo	hp	Pinus spp.
Ips grandicollis (Eichhoff)	+	+	ph	mo	hp	Pinus spp.
Orthotomicus caelatus (Eichhoff)	+	+	ph	ol	hp	Pinus, Larix, Picea; mo at ABS in Pinu
Pityogenes hopkinsi Swaine	+	4	ph	mo	hp	Pinus
Dryocoetini			1			
Coccotrypes distinctus (Motscholsky)	_	+	sp	mo	in	At ABS mo in Saba
Dryocoetes granicollis (LeConte)	+		ph	mo	0.000	Picea
Lymantor decipiens (LeConte)	+	 8	myc	ро	mg	Fungus in hardwood
Crypturgini			9	F	0	
Crypturgus alutaceus Schwarz	35_	+	ph	mo	mg	Pinus spp.
Xyloternini		8.	P.,		6	· mas spp.
Xyloterinus politus (Say)	+	-	xm	ро	mg	Hardwoods
Xyleborini (Gay)			Ain	ро	mg	Hardwoods
Ambrosiodmus devexulus (Wood)		+	xm	po	ip	Hardwoods
Ambrosiodmus lecontei Hopkins	_	+	xm	po	ip	Hardwoods and pine
Premnobius cavipennis Eichhoff	S2_	+		100000		Highly polyphagous
Xyleborinus saxeseni (Ratzeburg)	+	+	xm	po	ip	Highly polyphagous
Xyleborinus saxesem (Ratzeburg) Xyleborus affinus Eichhoff	+	+	xm xm	po	ip	
Xyleborus celsus Eichhoff	+	+	2003	po	ip	Highly polyphagous Carya spp.
200 (4 5) 2 (1	+	_	xm	mo	ip	Carya spp. Hardwoods
Xyleborus dispar (Fabricius)			xm	po	ip	
Xyleborus ferrugineus (Fabricius)	+	+	xm	po	ip	Highly polyphagous
Xyleborus obesus LeConte	+		xm	po	ip	Hardwoods
Xyleborus planicollis Zimmermann	+	750	xm	?	ip	Hosts unknown, presumed xm, ip
Xyleborus pubescens Zimmermann	-	+	xm	mo	ip	Pinus spp.
Xyleborus sayi (Hopkins)	+	PRES.	xm	po	ip	Hardwoods
Xyleborus volvulus (Fabricius)	35-	+	xm	po	ip	Highly polyphagous
Xyleborus xylographus (Say)	+		xm	po	ip	Hardwoods

	Location					
Name	WL	ABS	FH	SP	MS	Hosts, Comments
COLYTIDAE (Continued)						
Xylosandrus compactus (Eichhoff)	_	+	xm	po	ip	Hardwoods
Xylosandrus crassiusculus (Motschulsky)	220	+	xm	po	ip	Hardwoods
Xylosandrus germanus (Blandford)	+	100	xm	po	ip	Highly polyphagous
Cryphalini				3.	250	20 1200 1120 IV
Cryptocarenus seriatus Eggers		+	my	po	ip	Hardwoods
Hypocryphalus mangiferae (Stebbing)	-	+	ph	mo	mg	Mangifera indica
Hypothenemus birmanus (Eichhoff)	-	+	my	po	ip	
Hypothenemus brunneus (Hopkins)		+	my	po	ip	
Hypothenemus californicus Hopkins	-	+	ph	po	ip	
Hypothenemus columbi Hopkins	_	+	ph	po	ip	
Hypothenemus crudiae (Panzer)		+	my	po	ip	
Hypothenemus dissimilis (Zimmermann)	+	+	my	po	ip	
Hypothenemus eruditus Westwood	+	+	ph	po	ip	
Hypothenemus interstitialis (Hopkins)	+	+	my	ро	ip	
Hypothenemus javanus (Eggers)	-	+	my	po	ip	
Hypothenemus miles (LeConte)	-	+	?	?	ip	Galleries and hosts unknown
Hypothenemus rotundicollis (Eichhoff)	+	600	my	po	ip	
Hypothenemus seriatus (Eichhoff)	+	+	my	po	ip	
Hypothenemus sp.	_	_	my	po	?	In Cestrum and Palafoxia
Trischidias atoma (Hopkins)	+	+	myc	po	ip	
Trischidias exigua Wood	200	+	myc	po	ip	In Carya, Quercus
Trischidias sp.	1000	+	?	?	?	Specimen in flight tra
Corthylini: Pityophthorina						
Conophthorus coniperda (Schwarz)	+	77 <u>-</u>	sp	mo	mg	Pinus strobus
Pityoborus comatus (Zimmermann)	-	+	xm	mo	mg	Pinus spp.
Pityophthorus annecteus LeConte	-	+	ph	mo	hp	Pinus spp.
Pityophthorus confusus Blandford	-	+	ph	mo	hp	Pinus spp.
Pityophthorus crinalis Blackman	+	85 87	ph	mo	hp	Rhus
Pityophthorus lautus Eichhoff	+	-	ph	po	hp	In several hardwoods may be a species complex
Pityophthorus opaculus LeConte	+	-	ph	mo	hp	In WL mo in Picea
Pityophthorus pinivorus Bright	-	+	ph	mo	hp	Pinus
Pityophthorus puberulus (LeConte)	+	D=88	ph	po	th	In WL mo in Pinus
Pityophthorus pulicarius (Zimmermann)	-	+	my	mo	hp	Pinus spp.
Pityophthorus sp. nr. virilis Blackman Pseudopityophthorus asperulus	+		ph	mo	hp	Rhus
(LeConte)	+	+	ph	mo	mg	Quercus spp.
Pseudopityophthorus minutissimus			p=100000		•	ox 5 a 10 a 11 a 15 a 15 a 15 a 15 a 15 a
(Zimmermann)	+	+	ph	mo	mg	Quercus spp.
Corthylini: Corthylina			40		0	250
Corthylus spinifer Schwarz	3 <u>-2</u>	+	xm	po	mg	Hardwoods
Corthylus punctatissimus (Zimmermann)	+	===	xm	ро	mg	Hardwoods
Monarthrum fasciatum (Say)	+	+	xm	po	hp	Hardwoods
MORALI IN AM INSCIALAM (SAY)			50000000			Hardwoods