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# The long-horned beetles of south Florida (Cerambycidae: Coleoptera): biogeography and relationships with the Bahama Islands and Cuba

Jonathan Browne and Stewart B. Peck

**Abstract:** South Florida is a floral and faunal transition zone between the Nearctic region and the West Indian part of the Neotropical region. Ninety-one species of Cerambycidae are known from the south Florida mainland and 53 species of Cerambycidae from the Florida Keys. The cerambycid fauna of south Florida is about equally of Neotropical (53%) and Nearctic origin (47%). Since the Florida Keys were entirely submerged several times in the Pliocene and Pleistocene epochs, the present cerambycid fauna is predominantly the result of late Pleistocene – Holocene overland dispersal from south-central Florida and overwater dispersal from the West Indies (Bahama Islands and Cuba). Species–area and species–distance relationships for the islands form significant regression lines as predicted by the equilibrium theory of island biogeography. The presence of a “distance effect” is surprising, since it is usually considered that only during the past 10 000 years has the southern tip of the Florida peninsula been fragmented into the present-day islands of the Keys by a rising sea level. An alternative geological scenario, supported by this study, suggests that the present islands of the Keys have appeared as the sea level fell only within the past 6000 years, and the fauna is a more recently derived one.

**Résumé :** Le sud de la Floride constitue une zone de transition florale et faunique entre la région néarctique et la partie antillaise de la région néotropicale. Quarante-vingt onze espèces de Cerambycidae habitent la partie continentale du sud de la Floride et 53 espèces habitent les Keys. La faune de cérambycides du sud de la Floride est à moitié d'origine néotropicale (53%) et à moitié d'origine néarctique (47%). Comme les Keys ont été entièrement submergées au Pliocène et au Pléistocène, la faune actuelle est surtout le résultat de la dispersion, au Pléistocène tardif – Holocène, de la faune du centre-sud de la Floride par voie de terre, et de la faune antillaise (archipel des Bahamas et Cuba) par voie de mer. Les relations espèce–surface et espèce–distance dans les îles donnent lieu à des droites de régression significatives, confirmant les prédictions de la théorie de l'équilibre de la biogéographie insulaire. L'existence d'un « effet de distance » est étonnante puisqu'il est généralement admis que la fragmentation en îlots, les Keys, par la montée du niveau d'eau dans le sud de la péninsule ne remonte qu'à 10 000 ans. Un autre scénario géologique possible, appuyé par les résultats de cette étude, suppose que les Keys telles qu'on les connaît aujourd'hui ne sont apparues qu'au cours des derniers 6000 ans avec la baisse du niveau d'eau, et la faune est donc une faune dérivée plus récente. [Traduit par la Rédaction]

## Introduction

Florida is a peninsula oriented north–south between latitudes 25°30' and 24°30'N and longitudes 80°30' and 81°45'W. Its southern tip lies just north of the Tropic of Cancer. Southern subtropical Florida is generally considered to be the area south of Lake Okeechobee. Dade and Monroe counties are the most southerly of the seven counties that make up southern Florida, and together these two counties constitute the southern tip of Florida, including the Florida Keys. The Keys are low-lying islands extending in a gentle arc southwest from Biscayne Bay and eventually trend almost directly west to Key West and the Dry Tortugas (Fig. 1). The Keys have historically been divided into two groups, the Upper Keys (from Key Largo south to Key Vaca or Pigeon Key) and the Lower Keys (from Ohio and Bahia Honda Keys

to Key West and the Dry Tortugas). The Upper Keys are wetter and more temperate and the Lower Keys drier and more tropical.

The climate of south Florida is subtropical, with a distinct fall, winter, spring, and summer (Tomlinson 1980). The major difference is not so much in temperature as in rainfall, with a wet period extending from May through October and a dry period from November to March. The Florida Keys receive considerably less precipitation than does the south Florida mainland (154 cm at Miami, 116 cm at Tavernier, Key Largo, in the Upper Keys, and 99 cm at Key West) and as a result they are drier and also more exposed to salt spray. Although the Lower Keys receive less precipitation than the Upper Keys, they trap and hold more fresh water because of their oolite bedrock.

South Florida is considered to be mainly West Indian in vegetational cover (Long and Lakela 1971; Tomlinson 1980), with six vegetational types predominant: mangroves, pine-lands, tropical hardwood hammocks, coastal scrub, cypress domes, and sawgrass wetlands (Tomlinson 1980).

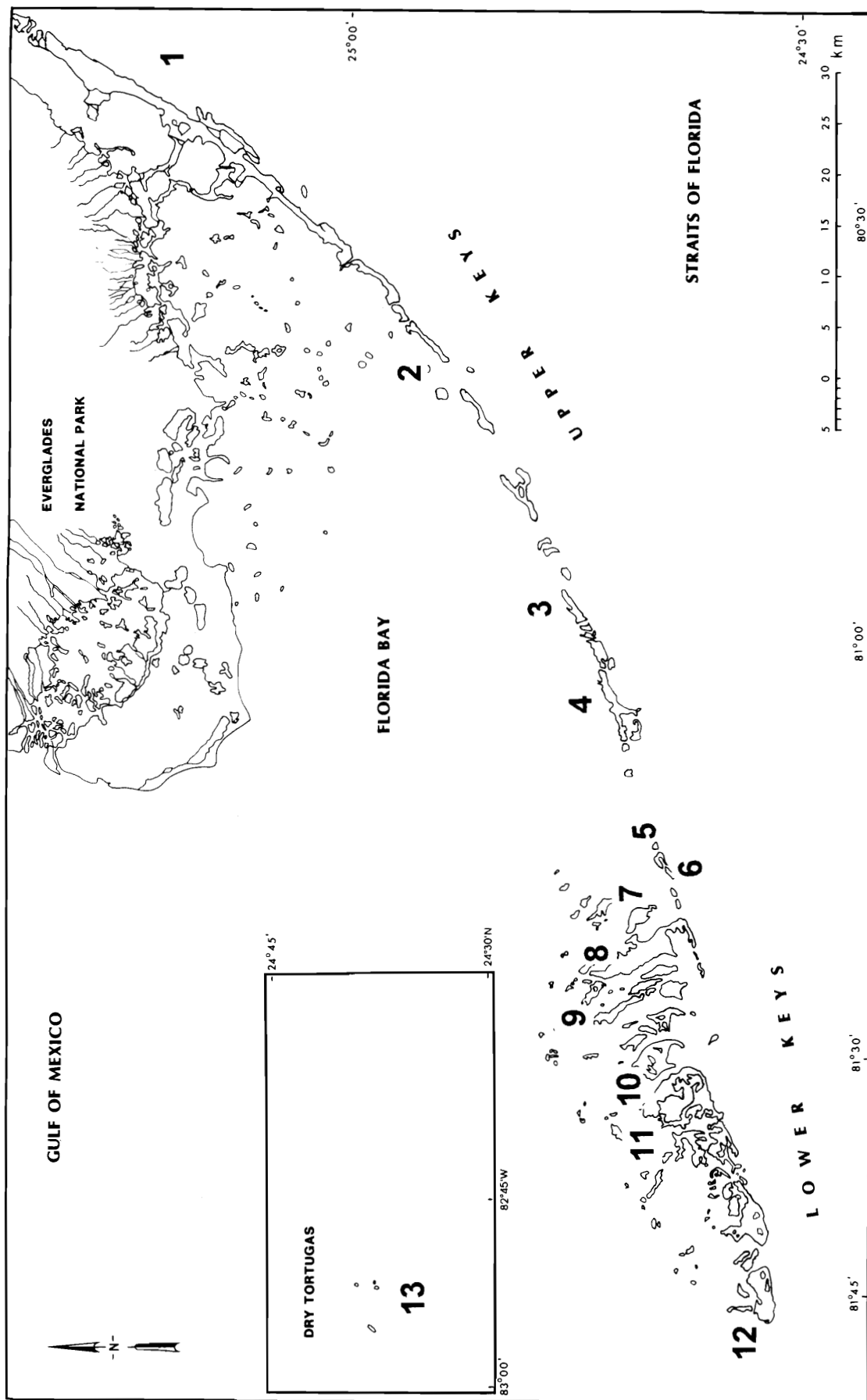
During the Sangamon interglacial stage, about 100 000 years before present (YBP), the sea level was much higher than it is today and no emergent land existed in what is

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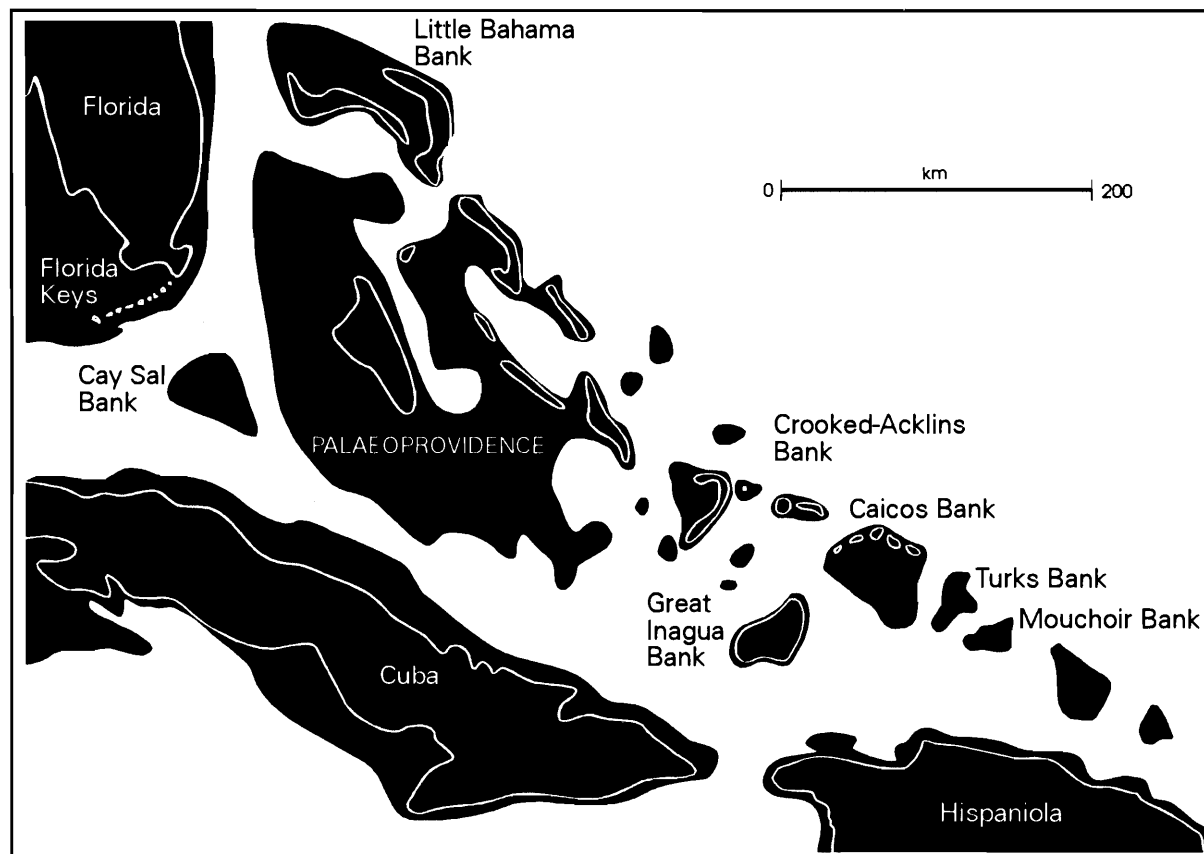
J. Browne and S.B. Peck.<sup>1</sup> Department of Biology, Carleton University, Ottawa, ON K1S 5B6, Canada.

<sup>1</sup> Author to whom all correspondence should be addressed (e-mail: AG658@FreeNet.Carleton.Ca).

**Fig. 1.** Map of south mainland Florida and the Florida Keys. The numbers refer to the main sampling sites, listed in Tables 2 and 3. 1, Key Largo; 2, Matecumbe Key; 3, Fat Deer Key; 4, Key Vaca; 5, Ohio Key; 6, Bahia Honda Key; 7, No Name Key; 8, Big Pine Key; 9, Torch Keys; 10, Cudjoe Key; 11, Sugarloaf Key; 12, Key West; 13, Dry Tortugas.



**Fig. 2.** Map of the major islands of the northern Caribbean, showing the probable increased extent of land area during Pleistocene glacial stage low sea levels. Water barriers were less significant to the dispersal of terrestrial organisms during these times. The white outlines show the present continent and island margins (after Campbell 1981).



now southern Florida and the Bahama Islands. During the Wisconsin glacial stage, about 80 000 – 10 000 YBP, the sea level was much lower than today and all of southern Florida and the Florida Keys were exposed as a much larger and continuous shelf of the southeastern tip of the North American continent. At that time the land area of the islands of the northern Caribbean, including Cuba, the Bahama Islands, and the Yucatan peninsula, was more extensive and the separating water gaps were narrower (Campbell 1981) (Fig. 2).

There are two alternative interpretations of the sea level history and island size of the Keys in the Recent (or Holocene Epoch, the past 10 000 years). The first is that during the past 10 000 years, the sea has risen only to the present level, to partially inundate the margins of the Florida peninsula, creating an extensively flooded landscape composed mainly of marine and freshwater wetlands, and the Florida Keys as a land-bridge island chain (Peck and Howden 1985). Thus, the recent history of the islands is one of an accelerating decrease in size. The second view, less well known, is that from 6000 to 4700 YBP, the sea level rose to about 4 m above present (Fairbridge 1990). This re-submerged most of south Florida and the Keys. Since then the sea level has fallen and risen again to +3, +2, and +0.3 m. This second view of recent sea level implies that the Keys are indeed very young islands which have changed size frequently and that the present terrestrial flora and fauna have only been established very recently.

The Cerambycidae (long-horned beetles) is the sixth largest family of beetles in North America, with more than 290 genera and 1100 species (Borror et al. 1989). Adult Cerambycidae are characteristically elongate, subcylindrical beetles with long antennae and fully developed hind wings. Adult members of the North American fauna vary greatly in size, ranging from 3 mm to more than 70 mm, and display an equal variation in colour, from drab ground-dwelling slow-moving forms to brightly coloured swift-flying forms (Borror et al. 1989). Although the family varies in morphology, it is rather uniform in its biology. All cerambycids are plant feeders. Most larvae eat the solid tissues of various plants, usually wood, although some feed on roots or bore into twigs. Larvae generally feed in the wood of trees or shrubs that may be living, dead and dry, or rotten. Pupation occurs in wood or under bark. Although some adults do not feed, most feed on flowers, leaves, pine needles and cones, sap, fruit, roots, and fungi (Borror et al. 1989).

The Cerambycidae is one of the best known families of North American beetles, in terms of both taxonomy and detailed distribution. We use this family to (i) explore the patterns of species transition from north to south Florida, through the islands of the Keys, and to and from Cuba and the Bahama Islands, the most likely sources of the Neotropical component of the Florida fauna, and (ii) test species–area and species–distance relationships using the equilibrium theory of island biogeography.

## General predictions

In an introductory paper on the insect fauna of southern Florida, Peck (1989) made a number of generalizations that address a variety of topics and help focus our treatment of the southern Florida Cerambycidae. Of interest here are the following hypotheses:

**Species diversity:** (1) The insect fauna is comparatively rich in numbers of species in spite of the small land area of southern Florida. (2) More species occur on the mainland of southern Florida than on the Florida Keys because of the greater habitat diversity, greater area, and more equable climate of the former.

**Speciation patterns and endemism:** (3) Few (or no) species are endemic to southern Florida. The area is geologically young and has been open to dispersal of species rather than a site of geographic isolation resulting in speciation.

**Origin and biogeographic relationships:** (4) Based on the predominantly Neotropical (Caribbean) origin of the flora, a large component of the insect fauna has also come to southern Florida via overwater dispersal from tropical America; a smaller component has come from the north, overland, from elsewhere in the United States.

## Materials and methods

### Sampling methods and identification

A list of south Florida Cerambycidae (Tables 1 and 2) was extracted from Linsley (1961–1972), Chemsak and Linsley (1982), and Chemsak et al. (1992). Additional records are from the Florida State Collection of Arthropods, Florida Division of Plant Industry, Gainesville. These were supplemented by extensive field collections (about 10 000 specimens) made by S.B.P. between 1984 and 1992 using Malaise – flight-intercept traps, blacklighting, and beating and sweeping. Data on Andros Island, Bahama Islands, were collected by J.B. in 1987 (Browne et al. 1993).

Identifications were made using keys in Linsley (1961–1972) and Chemsak and Linsley (1982). Specimens are in the authors' collections or deposited as vouchers in the Canadian National Museum of Nature, Ottawa.

### Distributions

Distributions of species in south Florida are based on Linsley (1961–1972), Chemsak and Linsley (1982), and Chemsak et al. (1992) augmented with locality records of specimens examined in the aforementioned collections (Tables 1 and 2). Distributions elsewhere within and outside of Florida are based on Browne et al. (1993), Chemsak et al. (1992), Monné and Giesbert (1993), Peck and Thomas (1996), and Zayas (1975).

### Species–area and species–distance relationships on the Florida Keys

These were calculated using the least-squares linear regression method. This assumes that the data follow a normal distribution. Each data set was tested using the untransformed model ( $x$  versus  $y$ ), power function ( $\log_{10}x$  versus  $\log_{10}y$ ), and exponential function ( $x$  versus  $\log_{10}y$ ; after Connor and McCoy 1979). The data were deemed to be normalized when the points in the scatterplot were judged to be evenly distributed around the line. Casewise plots of standardized residuals were employed to determine whether a linear regression function fit the data. Island areas and distances from the source (south Florida mainland) were calculated from U.S. Geological Survey 1:24 000 scale maps and National Oceanic and Atmospheric Administration 1:40 000 scale charts (Table 3).

## Faunal affinity and similarity indices

It is normally desirable to investigate the biogeography of a group for which the evolutionary (phylogenetic) relationships have been postulated. Unfortunately, no cladistic analysis of Nearctic, Neotropical, or Caribbean Cerambycidae is known to us. However, the species are well documented in terms of distribution (see Hovore et al. 1987; Chemsak et al. 1992; Browne et al. 1993). Therefore, to determine faunal affinities, known distributions were analysed by a species aggregate method (after Hovore et al. 1987), with the affinity of each species determined by analysing the distribution of the species most likely to be related. For example, if species A has a distribution that includes Florida, the Bahama Islands, and Cuba, and the species most likely to be related to it, species B, is found throughout North America north of Mexico, it would be assumed that species A is of Nearctic origin. An explicit assumption is that a concentration of species in a genus in a single faunal region suggests that the region represents an ancestral home ('centre of origin') of the genus (after Hovore et al. 1987).

The similarity index used here, Simpson's faunal similarity index, is defined as the number of species the two regions have in common divided by the total number of species in the two regions (Simpson 1947). Since the number of endemics is a reflection not of regional relationship but rather of local isolation, the endemic species were removed before the similarity indices were calculated (after Slater 1988).

Similarity indices were used in this study to test whether the cerambycid faunas of (i) the south Florida mainland and (ii) the Florida Keys are primarily a subset of Neotropical (Caribbean) or Nearctic faunas (Tables 4 and 5).

## Results and discussion

### Island biogeography

#### Species–area relationships

The best fitting model of the species–area relationship was the power function that yields a line with the equation  $y = 0.2864x + 0.9202$  (Fig. 3). The regression line shows that for these data the relationship between species number and island area is significant ( $r = 0.9036$ ) as predicted by the equilibrium theory of island biogeography (MacArthur and Wilson 1967). Similar patterns have been found for both scavenging Scarabaeoidea (Peck and Howden 1985) and Curculionidae (Anderson and Peck 1994) on the Florida Keys.

#### Equilibrium number

The evidence for an equilibrium number of cerambycid species on the Florida Keys is unclear. It cannot be said with certainty whether the islands have reached equilibrium, since there are two contradictory sea-level scenarios.

In the first, with a rising post-Pleistocene sea level (and steadily contracting island areas), the Florida Keys were recently an integral part of the south Florida mainland (Fig. 2). This broader region, so fully exposed for many thousands of years, may have reached equilibrium, but the subsequent rising of the post-Pleistocene sea level reduced the areas to their present extent, which may have resulted in a decrease (relaxation) in the equilibrium number.

In the second scenario, with a falling but fluctuating sea level (repeated contraction and expansion of island areas), the Keys were nearly or completely submerged from about 6000 to 4700 years ago (Fairbridge 1990). Thus, the flora and fauna of the Florida Keys have been established only relatively recently. Since then, the sea level, and island

**Table 1.** Checklist and general distribution of established native south Florida Cerambycidae (only those known from Dade and Monroe counties).

		Nearctic				Florida					Neotropical				
		Southwest	Southeast	Central	Northeast	Endemic <sup>a</sup>	Keys	South mainland	Central	North	Bahamas	Cuba	Other Caribbean <sup>b</sup>	Mexico	Central America
Prioninae															
1.	<i>Archodontes melanopus</i> (Linnaeus)	x	x					x	x	x					
2.	<i>Stenodontes chevrolati</i> Gahan						x	x			x	x			
3.	<i>Stenodontes dasytomus</i> (Say)	x	x				x	x	x	x				x	
4.	<i>Derobrachus brevicollis</i> Serville		x					x	x	x					
5.	<i>Prionus pocularis</i> (Dalman)		x	x	x			x	x	x					
6.	<i>Derancistrus rugosus</i> (Gahan)						x				x	x			
7.	<i>Derancistrus scabrosus</i> (Gahan)						x				x	x			
Aseminae															
8.	<i>Arhopalus rusticus</i> (Linnaeus)	x	x	x	x		x	x	x	x	x		x	x	x
Cerambycinae															
9.	<i>Smodicum cucujiforme</i> (Say)		x	x	x			x	x	x					
10.	<i>Methia pusilla</i> (Newman)		x				x	x	x	x					
11.	<i>Oeme rigida</i> (Say)		x	x	x			x	x	x					
12.	<i>Eburia cinereopilosa</i> Fisher						x					x			
13.	<i>Eburia distincta</i> Haldeman		x				x	x	x	x	x				
14.	<i>Eburia quadrigeminata</i> (Say)		x	x	x			x	x	x					
15.	<i>Eburia stigma</i> (Olivier)						x	x			x	x	x	x	x
16.	<i>Eburia stroheckeri</i> Knull					E	x	x							
17.	<i>Knulliana cincta</i> (Drury)		x		x		x	x	x	x	x	x	x	x	
18.	<i>Trachyderes mandibularis</i> (Serville)	x					x								
19.	<i>Aneflomorpha delongi</i> (Champlain & Knull)					E		x	x						
Cerambycinae															
20.	<i>Anelaphus cinereum</i> Olivier						x	x			x	x	x		
21.	<i>Anelaphus inermis</i> (Newman)		x				x	x	x	x	x		x	x	x
22.	<i>Anelaphus moestus pinorum</i> (Casey)	x	x		x			x	x	x				x	
23.	<i>Anelaphus paralellus</i> (Newman)		x	x	x			x	x	x					
24.	<i>Anelaphus spurcus</i> (LeConte)		x				x	x	x	x				x	
25.	<i>Anelaphus villosus</i> (Fabricius)	x	x	x	x			x	x	x		x			
26.	<i>Curtomerus fasciatus</i> (Fisher)							x				x			
27.	<i>Curtomerus flavus</i> (Fabricius)						x	x			x	x	x	x	x
28.	<i>Elaphidion clavis</i> Linsley		x				x	x	x	x					
29.	<i>Elaphidion cryptum</i> Linsley						x	x	x		x				
30.	<i>Elaphidion irroratum</i> (Linnaeus)						x	x			x	x	x	x	x
31.	<i>Elaphidion knulli</i> Linsley					E		x							
32.	<i>Elaphidion mucronatum</i> (Say)		x	x	x		x	x	x	x					
33.	<i>Enaphalodes atomarius</i> (Drury)	x	x	x	x			x	x	x				x	x
34.	<i>Enaphalodes hispicornis</i> (Linnaeus)	x	x	x	x			x	x	x				x	
35.	<i>Enaphalodes rufulum</i> (Haldeman)		x	x	x			x	x	x	x				
36.	<i>Linsleyonides albomaculatus</i> (Champlain & Knull)						x	x			x	x			
37.	<i>Nesostizocera floridana</i> (Linsley)					E		x							
38.	<i>Parelaphidion mutatum</i> (Gahan)						x				x	x			
39.	<i>Psyrassa pertenuis</i> (Casey)		x		x		x	x	x	x					
40.	<i>Romulus globosus</i> Knull							x	x	x					
41.	<i>Heterachthes ebenus</i> Newman				x		x	x	x	x	x	x	x	x	x
42.	<i>Heterachthes quadrimaculatus</i> Haldeman		x	x	x			x	x	x					
43.	<i>Heterachthes ssablensis</i> Blatchley					E	x	x							
44.	<i>Plectomerus dentipes</i> (Olivier)		x				x	x	x	x	x	x			
45.	<i>Obrium maculatum</i> (Olivier)	x	x	x	x		x	x	x	x				x	x

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**Table 1** (concluded).

	Nearctic				Florida					Neotropical				
	Southwest	Southeast	Central	Northeast	Endemic <sup>a</sup>	Keys	South mainland	Central	North	Bahamas	Cuba	Other Caribbean <sup>b</sup>	Mexico	Central America
<b>Cerambycinae</b>														
46. <i>Plinthocoelium suaveolens</i> (Linnaeus)		x				x	x	x	x					
47. <i>Semanotus ligneus</i> (Fabricius)		x	x	x			x	x	x					
48. <i>Euryscelis saturalis</i> (Olivier)						x	x			x	x	x		
49. <i>Neoclytus cordifer</i> (Klug)		x				x	x	x	x	x	x			
50. <i>Neoclytus scutellaris</i> (Olivier)		x		x			x	x	x					
51. <i>Placosternus difficilis</i> (Chevrolat)	x	x				x	x	x	x	x	x	x	x	
52. <i>Xylotrechus sagittatus sagittatus</i> (Germar)	x	x	x	x			x	x	x					x
53. <i>Heterops dimidiata</i> Chevrolat						x				x	x			
54. <i>Osmopleura chamaeropsis</i> (Horn)		x					x	x	x					
55. <i>Zagymnus clerinus</i> (LeConte)		x					x	x	x					
56. <i>Ancylocera bicolor</i> (Olivier)		x				x	x	x	x					
<b>Lepturinae</b>														
57. <i>Strangalia luteicornis</i> (Fabricius)		x	x	x			x	x	x					
58. <i>Strangalia strigosa</i> Newman					E		x	x	x					
59. <i>Typocerus zebra</i> (Olivier)		x	x	x		x	x	x	x					
<b>Lamiinae</b>														
60. <i>Monochamus carolinensis</i> (Olivier)		x	x	x			x	x	x					
61. <i>Monochamus titillator</i> (Fabricius)		x	x	x			x	x	x	x	x			
62. <i>Ecyrus dasycerus</i> Say		x	x	x	e	x	x	x	x				x	
63. <i>Ecyrus hirtipes</i> Gahan						x				x	x	x		
64. <i>Eupogonius annulicornis</i> Fisher						x					x			
65. <i>Eupogonius tomentosus</i> (Haldeman)		x		x			x	x	x					
66. <i>Ataxia crypta</i> (Say)		x	x	x		x	x	x	x				x	
67. <i>Ataxia falli</i> Breuning					E	x	x							
<b>Lamiinae</b>														
68. <i>Ataxia spinicauda</i> Schaeffer						x				x	x	x		
69. <i>Lysimena fuscata</i> Haldeman	x	x	x	x			x	x	x	x	x	x	x	x
70. <i>Oncideres cingulata</i> (Say)		x	x	x		x	x	x	x				x	
71. <i>Hippopsis lemniscata</i> (Fabricius)		x		x		x	x						x	x
72. <i>Spalacopsis filum</i> (Klug)					e	x	x	x		x	x	x		
73. <i>Spalacopsis stolata</i> Newman					E	x	x	x	x					
74. <i>Spalacopsis suffusa</i> Newman					E		x	x	x					
75. <i>Aegomorphus modestus</i> (Gyllenhal)		x	x	x			x	x	x	x				
76. <i>Parmenonta thomasi</i> Linsley & Chemsak					E		x							
77. <i>Alcidion umbraticum</i> Jacquelin du Val						x	x			x	x	x		
78. <i>Astylopus arcuatus</i> (LeConte)					E		x	x	x					
79. <i>Astylopus perplexus</i> Haldeman					E	x	x							
80. <i>Lagocheirus araneiformis</i> (Linnaeus)						x	x			x	x	x		
81. <i>Leptostylopsis albofasciatus</i> (Fisher)							x				x			
82. <i>Leptostylopsis argentatus</i> (Jacquelin du Val)						x	x			x	x	x		
83. <i>Leptostylopsis planidorsus</i> (LeConte)		x				x	x							
84. <i>Leptostylopsis terraecolor</i> (Horn)					E	x	x							
85. <i>Leptostylus transversus</i> (Gyllenhal)	x	x	x		e	x	x	x	x					
86. <i>Acanthocinus obsoletus</i> (Olivier)		x		x			x	x	x					
87. <i>Nyssodrysina haldemani</i> (LeConte)		x		x			x	x	x				x	x
88. <i>Liopinus schwarzi</i> (Hamilton)		x				x	x	x	x					
89. <i>Styloleptus biustus</i> (LeConte)		x				x	x	x	x	x	x			
90. <i>Urgleptes foveatocollis</i> (Hamilton)		x				x	x	x	x					
91. <i>Hemierana suturalis</i> (Linell)		x	x				x	x	x					

<sup>a</sup>E, seemingly endemic species; e, seemingly endemic subspecies.

<sup>b</sup>Turks and Caicos Islands, Jamaica, Hispaniola, Leeward Islands, Lesser Antilles, and Trinidad and Tobago.

**Table 2.** Distribution of established native Cerambycidae among the principal islands of the Florida Keys.

		Upper Keys				Lower Keys						
	Endemic <sup>a</sup>	Key Largo	Matecumbe Key	Fat Deer Key	Key Vaca	No Name Key	Big Pine Key	Torch Keys	Cudjoe Key	Sugarloaf Key	Key West	Dry Tortugas
Prioninae												
1. <i>Stenodontes chevrolati</i> Gahan		x	x				x			x	x	
2. <i>Stenodontes dasytomus</i> (Say)		x										
3. <i>Derancistrus rugosus</i> (Gahan)		x										
4. <i>Derancistrus scabrosus</i> (Gahan)		x			x						x	
Aseminae												
5. <i>Arhopalus rusticus</i> (Linnaeus)							x					
Cerambycinae												
6. <i>Methia pusilla</i> (Newman)		x	x	x	x	x	x	x	x	x	x	x
7. <i>Eburia cinereopilosa</i> Fisher					x							
8. <i>Eburia distincta</i> Haldeman		x										
9. <i>Eburia stigma</i> (Olivier)		x	x	x		x	x	x		x	x	
10. <i>Eburia stroheckeri</i> Knull	E	x			x	x		x			x	
11. <i>Anelaphus cinereum</i> Olivier		x		x	x	x	x	x	x	x	x	
12. <i>Anelaphus inermis</i> (Newman)		x	x	x	x	x	x	x	x	x	x	x
13. <i>Anelaphus spurcus</i> (LeConte)		x	x		x							
14. <i>Knulliana cincta</i> (Drury)		x	x	x			x	x			x	
15. <i>Trachyderes mandibularis</i> (Serville)							x				x	
16. <i>Curtomerus flavus</i> (Fabricius)		x	x			x		x	x	x	x	
17. <i>Elaphidion clavis</i> Linsley											x	
18. <i>Elaphidion cryptum</i> Linsley		x	x			x		x			x	
19. <i>Elaphidion irroratum</i> (Linnaeus)		x	x	x	x	x	x	x			x	x
20. <i>Elaphidion mucronatum</i> (Say)		x				x					x	
21. <i>Linsleyonides albomaculatus</i> (Champlain & Knull)		x										
22. <i>Parelaphidion mutatum</i> (Gahan)											x	
23. <i>Psyrassa pertenuis</i> (Casey)		x	x			x	x	x	x	x	x	
24. <i>Heterachthes ebenus</i> Newman		x					x					
Cerambycinae												
25. <i>Plectomerus dentipes</i> (Olivier)		x	x	x	x		x	x	x			
26. <i>Obrium maculatum</i> (Olivier)		x										
27. <i>Plinthocoelium suaveolens</i> (Linnaeus)												x
28. <i>Euryscelis suturalis</i> (Olivier)		x	x	x	x	x	x					
29. <i>Neoclytus cordifer</i> (Klug)		x	x	x	x	x	x	x	x	x	x	
30. <i>Placosternus difficilis</i> (Chevrolat)		x			x						x	
31. <i>Heterops dimidiata</i> Chevrolat		x										
32. <i>Ancylocera bicolor</i> (Olivier)				x	x							
Lepturinae												
33. <i>Typocerus zebra</i> (Olivier)		?	?	?	?	?	?	?	?	?	?	?
Laminae												
34. <i>Ecyrus dasycerus</i> (Say)	e	x										x
35. <i>Ecyrus hirtipes</i> Gahan		x					x					
36. <i>Ataxia crypta</i> (Say)		x										
37. <i>Ataxia falli</i> Breuning	E	x		x	x		x					
38. <i>Ataxia spinicauda</i> Schaeffer		x										
39. <i>Eupogonius annulicornis</i> Fisher		x										
40. <i>Oncideres cingulata</i> (Say)		x										
41. <i>Hippopsis lemniscata</i> (Fabricius)		x	x		x		x	x			x	
42. <i>Spalacopsis filum</i> (Klug)	e	x	x			x	x				x	
43. <i>Spalacopsis stolata</i> Newman	E	x					x				x	
44. <i>Alcidion umbraticum</i> Jacquelin du Val		x										



**Table 2** (concluded).

		Upper Keys					Lower Keys					
	Endemic <sup>a</sup>	Key Largo	Matecumbe Key	Fat Deer Key	Key Vaca	No Name Key	Big Pine Key	Torch Keys	Cudjoe Key	Sugarloaf Key	Key West	Dry Tortugas
45. <i>Astylopus perplexus</i> Haldeman		x										
46. <i>Lagocheirus araneiformis</i> (Linnaeus)		x										
47. <i>Leptostylopsis argentatus</i> (Jacquelin du Val)							x	x				
48. <i>Leptostylopsis planidorsus</i> (LeConte)		x				x	x					
Lamiinae												
49. <i>Leptostylopsis terraecolor</i> (Horn)	E	x	x	x			x	x	x	x		
50. <i>Leptostylus transversus</i> (Gyllenhal)	e	x				x						
51. <i>Liopinus schwarzi</i> (Hamilton)		x										
52. <i>Styloleptus biustus</i> (LeConte) *		x				x	x	x			x	
53. <i>Urgleptes foveatocollis</i> (Hamilton)		x					x			x		
Total species	4	44	16	12	15	16	24	16	8	10	24	3

**Note:** A question mark indicates that the locality is not known.  
<sup>a</sup>E, seemingly endemic species; e, seemingly endemic subspecies.

**Table 3.** Numbers of cerambycid species with the areas of the islands and their distance from the south Florida mainland.

Island	Area (km <sup>2</sup> )	Distance <sup>a</sup> (km)	No. of species
Florida	149 913		213
South Florida	5 080		91
Upper Keys			
Key Largo	55.1	13	44
Matecumbe Key	4.3	32	16
Fat Deer Key	3.7	66	12
Key Vaca	2.9	72	15
Lower Keys			
No Name Key	3.1	76	16
Big Pine Key	17.1	79	24
Big Torch Key	2.3	88	16
Cudjoe Key	9.2	95	8
Sugarloaf Key	10.2	100	10
Key West	11.9	121	24
Dry Tortugas	0.9	131	3

<sup>a</sup>Measured from the point on the south Florida mainland closest to Key Largo along the axis of the island chain.

areas, have fluctuated greatly, and as recently as 600 years ago. The relative youth of the land area caused by the fluctuating sea level suggests that the equilibrium numbers in the flora and fauna have yet to be reached. Our biological data, through the presence of a distance effect (see below), support the fluctuating sea level scenario.

*Saturation species number*

The slope *z* value of the species saturation line (Fig. 3; 0.2864) is toward the middle of ranges typically found for island faunas (0.20–0.35; Peck and Howden 1985). Similar

slope values were reported for some scavenging scarabaeoid beetles in the Florida Keys (0.385; Peck and Howden 1985) and cerambycids of the Bahama Islands (0.32; Browne et al. 1993). Although the slope has often been touted by many authors as an index of island isolation, Abbott (1983) concluded that it has no unique biological meaning. However, it may not be merely coincidental that the slope values of the Florida Keys and Bahama Island cerambycids are virtually the same; the two islands have the same Holocene geological history and have had similar faunal influences.

Several of the islands have very high species numbers and consequently are above the regression line (Fig. 3). However, oversaturation is not unarguably demonstrated. These high numbers are from islands that are either urban centres or have been more intensively sampled in the past.

Conversely, many of the other islands appear to be unsaturated (Fig. 3). This is probably a reflection of inadequate sampling and extinction through widespread urbanization and human population pressures. We predict that with additional sampling efforts, many of the undisturbed islands will exhibit higher species numbers.

*Species–distance relationships*

The relationship was significant between the number of Florida Keys cerambycid species and distance from the faunal source area (assumed to be the south Florida mainland;  $y = -0.1995x + 32.9160$ ,  $r = 0.6341$ ; Fig. 4) according to the predictions of the equilibrium theory of island biogeography (MacArthur and Wilson 1967).

This would be surprising if the Florida Keys have a simple history of being a land-bridge chain of islands that were once part of the south Florida mainland (Fig. 2). The Keys region, if it was exposed as a single land mass for many thousands of years, likely formerly contained many, if not all, of the species now found on the south Florida mainland. If this is indeed the case, then a distance effect should not be detectable.

**Table 4.** Distribution of native species of Cerambycidae in southern Florida.

	South Florida	Florida Keys
Keys and (or) south Florida	21	45
Nearctic region	7	5
Neotropical region	86	90
Nearctic + Neotropical regions	7	5
Keys and (or) south + central Florida	3	4
Nearctic region	100	100
Neotropical region	0	0
Nearctic + Neotropical regions	0	0
Keys and (or) south and central + north Florida	76	51
Nearctic region	73	58
Neotropical region	10	42
Nearctic + Neotropical regions	17	0
Total	100	100
Nearctic region	57	32
Neotropical region	28	66
Nearctic + Neotropical regions	15	2

**Note:** Thirteen apparently endemic species are not included. All values are percentages.

**Table 5.** Similarity indices of native species of south Florida and West Indian Cerambycidae.

	South Florida	Bahamas	Cuba
Florida Keys	83	57	53
South Florida		51	31
Bahamas			83

**Note:** Thirteen apparently endemic species are not included. All values are percentages.

A second possibility, the peninsula effect, may also explain the apparent distance effect. South Florida lies at the southern extent of the ranges of most Nearctic insect species and the northern extent of the ranges of most Neotropical insect species. This explains the tapering off of Nearctic and Neotropical cerambycid species numbers in a north–south and south–north direction, respectively (Table 4 in part; J. Browne and S.B. Peck, unpublished data). However, this process should not be confused with a strict peninsula effect, which Means and Simberloff (1987) failed to detect with the Florida herpetofauna. In the authors’ opinion, the peninsula effect does not contribute to the observed distance effect.

The distance effect is more understandable if the islands are young (repeatedly reemergent in the last 6000 years) and have only recently (within the 6000 years since the +4 m sea level) been colonized by means of overwater dispersal. This third possibility is favoured by the authors.

Diversity

Species richness

The cerambycid fauna of the entire state of Florida has 116 genera and 214 species (Peck and Thomas 1996). For comparison, MacRae (1993) lists 108 cerambycid genera and 216 species in Missouri, a region much more temperate than Florida. The state of Georgia, with the uplands of the southern Appalachian mountains, has 257 species (Skillman 1993).

South Florida contains 91 species in 58 genera (Table 1).

Seventeen genera are represented in the region by more than one native species. Eight genera contain 32 species (35% of the fauna; species numbers are given in parentheses): *Anelaphus* (6), *Eburia* (5), *Elaphidion* (5), *Enaphalodes* (3), *Heterachthes* (3), *Ataxia* (3), *Spalacopsis* (3), and *Leptostylopsis* (4).

Browne et al. (1993) recorded 63 species and 40 genera in the subtropical Bahama Islands, an area similar in size, latitude, and topography to south Florida.

The diversity of a local flora has both a direct and indirect relationship with local insect diversity (Peck 1989). This is particularly true for phytophages and may explain the much higher cerambycid species diversity in Missouri. MacRae (1993) reported that cerambycid species diversity in Missouri is much higher in regions with many woody plant species, such as the Ozark Mountains, than regions with only herbaceous plant species, such as the savannah of the Osage Plains. Although some cerambycid species use herbaceous plants, most use woody plants. It is expected, and borne out, that woody plant diversity is low in south Florida (130 tree species; Long and Lakela 1971; Tomlinson 1980) and the Bahama Islands (120 tree species; Patterson and Stevenson 1977). In other Caribbean regions where woody plant diversity is much higher, the cerambycid fauna is correspondingly more diverse. Zayas (1975) lists 245 cerambycid species from Cuba; more than 150 of these are endemic. This staggeringly rich and highly endemic fauna is likely due to a combination of many factors, such as topography and climate, but Cuban woody plant diversity (350–500 species) is obviously one of the most important.

The south Florida cerambycid fauna, therefore, is seemingly no richer than faunas in other areas of similar size, climate, latitude, and especially total habitat diversity.

Range patterns

Several significant range disjunctions were found for cerambycid species occurring in the Florida Keys (Table 2): *Stenodontes dasytomus*, *Derancistrus rugosus*, *Eburia cinereopilosa*, *E. distincta*, *Anelaphus spurcus*, *Linsleyonides albomacu-*

Fig. 3. Three models of least-squares linear regression of cerambycid species against island area: untransformed (A), exponential (B), and power (C).

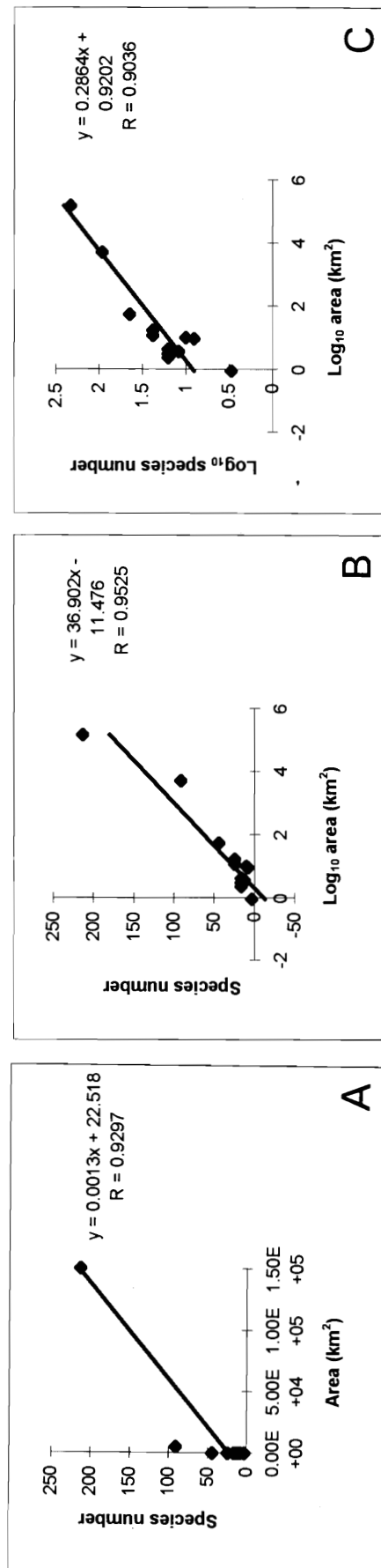
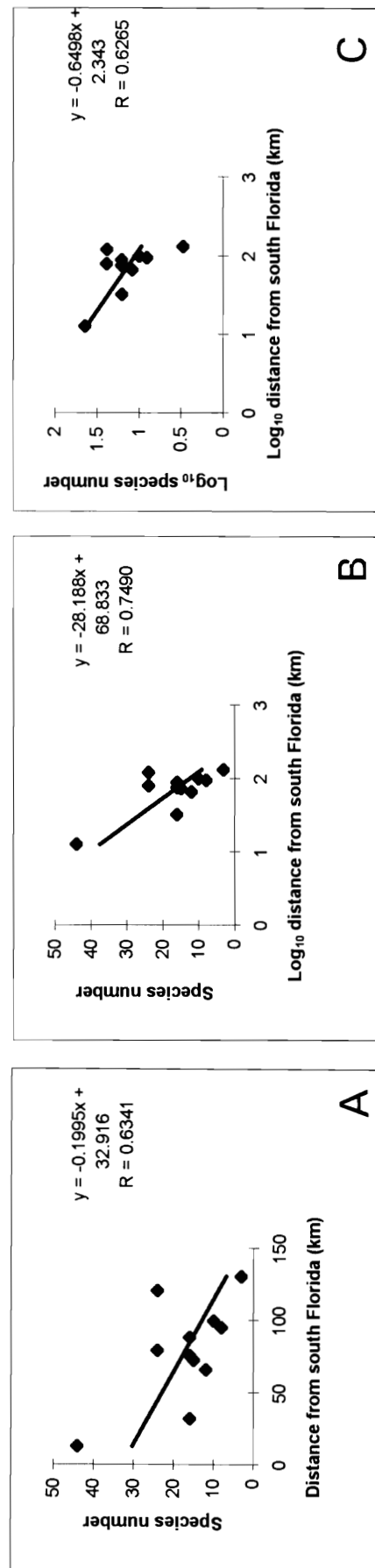


Fig. 4. Three models of least-squares linear regression of cerambycid species against distance from the source region, here assumed to be south mainland Florida: untransformed (A), exponential (B), and power (C).



*latus*, *Obrium maculatum*, *Heterops dimidiata*, *Ancylocera bicolor*, *Ataxia crypta*, *A. spinicauda*, *Eupogonius annulicornis*, *Oncideres cingulata*, *Alcidion umbraticum*, *Astylopus perplexus*, *Lagocheirus araneiformis stroheckeri*, and *Liopinus schwarzi* seemingly occur only in the Upper Keys, while *Arhopalus rusticus nubilus*, *Trachyderes mandibularis*, *Elaphidion clavis*, *Parelaphidion mutatum*, *Plinthocoelium suaveolens*, *Hylotrupes bajalus*, and *Leptostylopsis argentatus* seemingly occur only in the Lower Keys. These range disjunctions may reflect varying abilities to adapt to the different environmental conditions that occur on the south Florida mainland and Upper Keys (wetter, more temperate) and Lower Keys (drier, more subtropical). If this is true, the ranges of species restricted to the Upper Keys would be more likely to include more northern than southern locations, and the opposite would be true for species restricted to the Lower Keys. However, not only is this not borne out by the data, but nearly all of the species found on the Florida Keys are found also on the south Florida mainland. Thus, these range disjunctions are probably artefacts of insufficient sampling, even though the sampling has been more intensive and extensive than for any other beetle family.

More interesting are the ranges of species restricted either to the south Florida mainland or to the Florida Keys (Table 1). Eight species, *Derancistrus rugosus*, *D. scabrosus*, *Eburia cinereopilosa*, *Parelaphidion mutatum*, *Heterops dimidiata*, *Ecyrus hirtipes*, *E. annulicornis*, and *Ata spinicauda*, live on the Keys and in the Caribbean islands but are absent from the mainland. A single exception, *Trachyderes mandibularis*, occurs elsewhere (Mexico and southwestern U.S.A.). Therefore, it appears that species restricted in the U.S.A. to the Florida Keys have been unable to expand their ranges into the more temperate mainland (Table 4).

Forty-seven species are absent from the Keys but are recorded from the mainland. Of these, 24 are found elsewhere in the Nearctic region, 8 occur elsewhere in the Neotropical region, 7 are common to both regions, and 7 appear to be endemic to Florida.

An entire subfamily, the Lepturinae, is virtually absent from south Florida. Only three species, *Strangalia luteicornis*, *S. strigosa*, and *Typocerus zebra*, occur on the south Florida mainland, while *T. zebra* is also recorded from the Keys. This predominantly Holarctic subfamily appears to have a southward decrease in species numbers. Lepturines are absent from the Caribbean islands and it is likely that hosts are lacking (J.A. Chemsak, personal communication).

A single species, *Smodicum cucujiforme*, occurring only in South America and the eastern, southeastern, and southern U.S.A., either displays a relictual distribution or is an introduction.

## Endemism, speciation, and extinction

### Endemism

Thirteen south Florida cerambycid species (14.3% of the fauna) (Table 1) are seemingly endemic, a proportion similar to that reported for weevils (16%; Anderson and Peck 1994) and Orthoptera (18%; Peck et al. 1992). This is in contrast to much lower endemism in other south Florida groups such as some scarabaeoid beetles (3%; Peck and Howden 1985), bark beetles (4%; Atkinson and Peck 1994), and trees (0.7%; Tomlinson 1980).

In contrast, 25.5% of the cerambycid fauna of the Bahama Islands is apparently endemic (Browne et al. 1993), a proportion larger than in the south Florida fauna. Since south Florida and the Bahama Islands have a similar late Pleistocene – Holocene geological history (see above), vegetation types, and climate, other factors must be involved that have resulted in a higher level of endemism in the Bahama Islands. In the authors' opinion, one of these factors is the length of time for which land has been emergent, and thus available for colonization and speciation.

If the sea level has only risen during the past 10 000 years and has not exceeded the present level, then the periods of time during which south Florida and the Bahama Islands have been emergent are equal, and it would be expected that the levels of endemism would be about the same. If the sea level had fluctuated over the past 6000–4700 years and levels were higher than at present, then south Florida would have been completely (or nearly completely) flooded. However, some regions of the Bahama Islands, such as northern Andros Island, are much higher than south Florida and would have remained emergent throughout the period of higher sea level and could have served as refugia. This would have resulted in a greater level of endemism in the Bahama Islands. Our biological data support the fluctuating sea level scenario. Other Caribbean islands or archipelagos display a much higher level of endemism (for comparison see Nichols 1988; Ramos 1988; Peck 1989), but this too is likely to be associated, at least in part, with the period of time during which these regions have been emergent.

The proportion of endemics in each of the five cerambycid subfamilies differs between south Florida and the Bahama Islands. Of the 13 south Florida endemics (species and subspecies), the largest proportion is in the subfamily Lamiinae (53.8%), followed by Cerambycinae (38.5%) and Lepturinae (7.7%). No endemic Prioninae are present. Of the 16 Bahama Island endemics the largest proportion is in the Cerambycinae (75%) followed by the Lamiinae (19%) and Prioninae (6%) (Browne et al. 1993; no Lepturinae are found in the Bahama Islands). This is likely to be a reflection of varying adaptive capabilities of colonizers that became established in each region. That is, something has seemingly favoured the establishment and subsequent speciation of colonizing Lamiinae in south Florida and Cerambycinae in the Bahama Islands.

### Speciation

Because the south Florida region has become emergent only recently (since the Sangamon interglacial stage), we do not believe that these seemingly endemic 13 species evolved in situ in south Florida, but that they originated elsewhere and have now come to occupy south Florida.

Vicariant events may have played an important role in the formation of the endemic cerambycid faunas of both south Florida and the Bahama Islands. A rising sea level, which resulted in the island fragmentation of the Florida shelf and the Bahama platform, was an important mechanism of vicariant isolation, possibly leading to speciation. Since we do not accept that speciation occurred on the present islands (see above), it must have been on islands in earlier cycles of high sea level in central Florida (Deyrup 1990) or somewhere in the Caribbean (Cuba or Hispaniola).

More than half of the endemic species (8) of south Florida

have ranges that do not extend outside the West Indian vegetation zone. In other words they are restricted to south Florida and appear to have ancestors that have colonized south Florida from the West Indies. Therefore, it appears that the ranges of these endemic species are regulated mainly by the presence or absence of the subtropical host plants, which are in turn controlled by the 54°F January isotherm. This finding contrasts with the low endemism of some south Florida scavenging scarabaeoids (Trogidae, Scarabaeinae, and Aphodiinae) whose ranges seem to be controlled by the presence or absence of mammal dung, their main food source (Peck and Howden 1985). We predict that the distribution pattern of generalist predators, such as carabid beetles, will be like that of scavengers. However, we also predict that examination of herbivorous scarabaeoids will yield a pattern similar to those in the cerambycids.

The remaining 5 endemic cerambycid species have ranges that include both the West Indian vegetation zone and the temperate vegetation zone. We are unable to suggest whether the ancestors of these species colonized Florida from the Nearctic region or the West Indies, and what conditions regulate the ranges of these endemic species.

### Extinctions

Two processes have led to the extinction of cerambycids in the Florida Keys in the Holocene. The first is a rising or fluctuating post-Pleistocene sea level, which reduced Pleistocene island areas and, we believe, led to a decrease in the total number of cerambycid species through natural local extinctions. The second, and now more important, process is habitat destruction through widespread human development of residential and commercial zones. A similar conclusion was drawn concerning the apparent undersaturation of some of the scarabaeoid fauna on some of the Florida Keys (Peck and Howden 1985) and the cerambycid fauna of the Bahama Islands (Browne et al. 1993).

### Origins and biogeographic relationships

The geographical history of the south Florida Cerambycidae is a difficult problem to address, both because south Florida has experienced several cycles of submergence and emergence and because its diverse fauna has many Nearctic as well as Neotropical elements, while its flora is primarily Neotropical (Long and Lakela 1971; Tomlinson 1980).

The greatest obstacle to reconstructing the historical biogeography of the cerambycid fauna is the lack of cladistic analyses. Since this most valuable tool is not available for determining patterns of phyletic and geographic relationships, an analysis of the relative importance of dispersal versus vicariance events and colonization routes is not possible. Therefore, as noted above, we are forced to use less powerful methods, such as species aggregate analysis and similarity indices, to construct a scenario of the historical dynamics of the assembly of the south Florida cerambycid fauna.

### Vicariance or dispersal?

We think that both vicariance and dispersal events have strongly influenced the distribution patterns of south Florida, and also West Indian, cerambycids, especially because of sea level dynamics. Clearly, a large proportion of species dispersed via the temperate and subtropical land routes. These well-documented dispersal routes were used by many animal

groups (Webb 1990). However, dispersal across water barriers is a much more strongly debated process, disputed by many pattern cladists.

The geological evidence suggests that distributional patterns in south Florida must have been the result of either dispersal or vicariance events in the past 70 000 years. Vicariance may have occurred during the mid-Oligocene (30 million YBP), the time of the most recent possible land connection between the West Indies and south Florida (Donnelly 1988). This was before many extant insect taxa evolved much, and before the Sangamon Interglacial (0.12–0.07 million YBP), when a higher sea level led to inundation of all south Florida and the Bahama Islands. Since there is no evidence of a recent Bahama Islands – Florida, Cuba–Florida, or Cuba – Bahama Islands land bridge (Donnelly 1988), indirect evidence strongly suggests that late Pleistocene – Holocene overwater dispersal occurred commonly, when possible, in either the past 70 000 or 4000 years. Vicariance may have been a very important mechanism both in the development of the early Florida cerambycid fauna, which subsequently invaded the Keys, and in isolation leading to speciation, especially when central Florida was a set of islands during times of high sea level in the Tertiary and Pleistocene (Deyrup 1990).

Although insects frequently disperse across water barriers (for a review see Peck 1994a, 1994b), no direct evidence is available that cerambycids fly over water with any frequency, even though they are known to be strong and active fliers. Passive dispersal (adults by wind and adults and larvae by sea currents as floating or rafting propagules in wood; see Fig. 5) may account for most, if not all, of the immigration of Neotropical (West Indian) long-horned beetles into south Florida and the Bahama Islands from West Indian sources (see Browne et al. 1993).

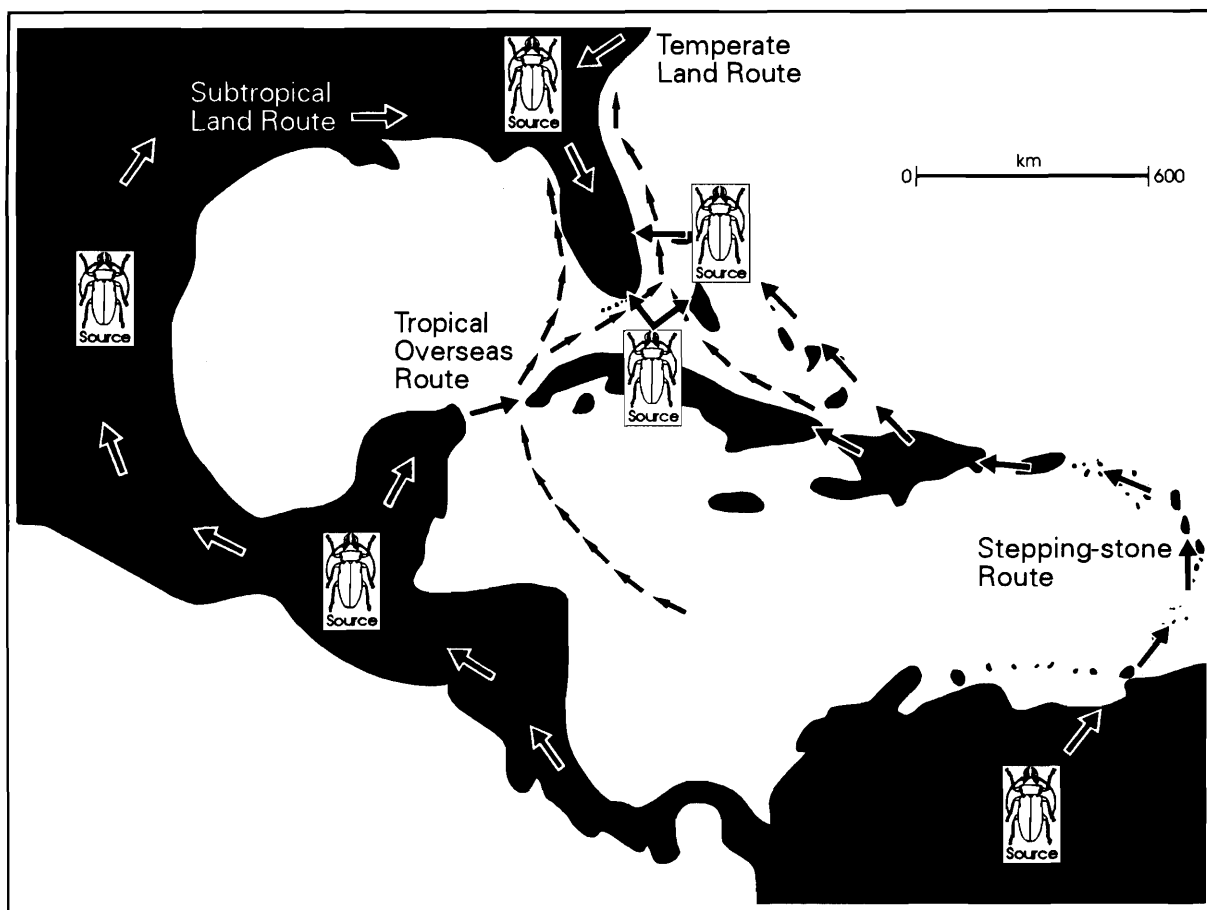
The most compelling direct evidence for overwater dispersal is found in genera and species that have distributions restricted to south Florida and one or more of the Caribbean islands. Three genera, *Elaphidion*, *Spalacopsis*, and *Leptostylopsis*, with species restricted to south Florida, Texas, and the Caribbean are thought to have originated in Caribbean islands (Hovore et al. 1987). Several cerambycid species found only in south Florida, Cuba, and (or) the Bahama Islands are *Stenodontes chevrolati*, *Derancistrus scabrosus*, *Anelaphus cinereum*, *Parelaphion mutatum*, and *Euryscelis suturalis*. These species must have crossed water barriers after speciation to attain their present ranges.

A second example, perhaps less compelling, is the south Florida endemic species whose ancestors dispersed before speciation. Based on the distributions of the putative sister-species of 14 cerambycid species endemic to south Florida, 85% of these have generic roots in the Neotropical region. Of these, 77% have dispersed most recently from the Caribbean, while only 23% have dispersed most recently by an overland route through the Gulf Coast Nearctic region.

The previous examples illustrate that in the absence of evidence for land bridges between south Florida and any of the West Indian islands, overwater dispersal must have occurred.

These findings are not surprising, since overwater dispersal in the Caribbean basin has been well demonstrated (or is the most parsimonious explanation) in many groups, such as trees (Tomlinson 1980), lygaeid bugs (Slater 1988), Hemiptera in general (Ramos 1988), ants (Wilson 1988), and

**Fig. 5.** Map illustrating the four main dispersal routes from source areas to the south Florida mainland and the Florida Keys. The small arrows indicate prevalent sea-surface currents.



butterflies (Scott 1972). The Bahamian cerambycid fauna (and all other terrestrial biotas) is predominantly the result of late Pleistocene – Holocene overwater dispersal from Cuba, Hispaniola, and south Florida (Browne et al. 1993). Increased colonization from Cuba was likely a result of the lower sea level, which greatly decreased the size of the water gap between the two regions (Fig. 2).

#### *Affinities and origin of south Florida Cerambycidae*

**Genera:** Most (80%) south Florida cerambycid genera are clearly Neotropical in origin, while a smaller number (20%) are probably Nearctic in origin. Although this classification is based on species aggregate analysis, it is supported by a similar pattern for the cerambycids of the Bahama Islands (Browne et al. 1993) and south Texas (Hovore et al. 1987) and trees in south Florida (88% Neotropical and 12% Nearctic; Tomlinson 1980).

Five (10%) of the south Florida cerambycid genera are clearly of Caribbean origin. Most species of *Elaphidion*, *Linsleyonides*, *Euryscelis*, *Spalacopsis*, and *Leptostylopsis* occur exclusively in Caribbean islands. Many other Neotropical genera are likely to have originated in the Caribbean, but until a rigorous cladistic analysis is performed it will be difficult to identify them.

**Species:** Similarity indices of species show regional relationships indicating a very different pattern from that of the genera.

The cerambycid fauna of the south Florida mainland, including the Keys, is nearly equally a subset of the Neotropical (53%) and Nearctic fauna (47%) (Table 4). The Florida Keys fauna has a much larger Neotropical (West Indian) component (66%) and a smaller Nearctic component (32%) (Table 4). This is in contrast to the fauna of the Bahama Islands, which is primarily Neotropical, composed of a subset of the Cuban, and secondarily the Hispaniolan, faunas (Browne et al. 1993).

In addition, both the south Florida mainland and Keys faunas are almost equally composed of elements from the Bahama Islands (51 and 57%, respectively), but disproportionately composed of elements from Cuba (31 and 53%, respectively) (Table 5). The reasons for this are complex. Cerambycid species that occur in the Florida Keys are less likely to occur in the central and northern mainland regions of Florida, since they are primarily of Neotropical origins. Species that occur on the south Florida mainland but not in the Florida Keys are more likely to occur in the central and northern mainland regions, since these are primarily of Nearctic stock. This suggests a disparity, perhaps in climate or food plants, between the Keys and the mainland. Likewise the Florida Keys and the south Florida mainland are not equidistant from Cuba: a larger component of Cuban species has succeeded in becoming established in the more geographically closer Keys than on the mainland. The ceram-

bycid fauna of the Bahama Islands, a region more similar to Cuba in climate, has 83% similarity with that of Cuba.

#### *Dispersal routes*

Since more of the south Florida cerambycid genera evolved in the Neotropical region (south and central Mexico, Central America, South America, and the Caribbean) and secondarily in the Nearctic region, four probable dispersal routes from these possible sources were likely followed in total or in part: (1) a tropical overseas route to Florida via the Yucatan peninsula to Cuba and then to Florida; (2) a subtropical land route via the Gulf Coastal States; (3) a stepping-stone route via the Lesser Antilles to Cuba, the Bahama Islands, and Florida; and (4) a temperate-zone land route.

These four routes are illustrated in Fig. 5 and have been discussed by Browne et al. (1993). Of particular interest to us here is the colonization of south Florida from Cuba and the Bahama Islands.

It has already been established that overwater dispersal between south Florida, the Bahama Islands, and Cuba has occurred for a large part of the fauna, and that Cuba is the most likely recent source of cerambycid colonizers, owing to the recent emergence of south Florida and the Bahama Islands. The species and genera included in this category most likely originated in the Neotropical region and dispersed to Cuba along the tropical overseas route via the Yucatan Peninsula, or via the Lesser Antilles and Greater Antilles, employing the stepping-stone route. South Florida and the Bahama Islands are at the northernmost limit of the Caribbean basin, directly in the path of storms, prevailing winds, and the Gulf Stream, which favour a northerly dispersal of insects (Fig. 5). Therefore, the most likely direction of overwater dispersal of airborne or seaborne propagules was directly from Cuba or via the Bahama Islands to south Florida. Although Browne et al. (1993) reported that overwater dispersal and establishment on the Bahama Islands from south Florida occurred for only a very small part of the fauna, the possibility remains that some south Florida species may have colonized first Cuba and secondarily the Bahama Islands.

Reinforcing these general patterns is that of the tree species in south Florida, which originated in the tropics and dispersed north via a tropical overseas route (Tomlinson 1980). Similar patterns have been reported for other south Florida insects (Peck 1989), halictid bees (Eickwort 1988), *Platynus* carabid beetles (Liebherr 1988), scaritine carabid beetles (Nichols 1988), homopteran bugs (Ramos 1988), lygaeid bugs (Slater 1988), ants (Wilson 1988), and amblypygians (Browne 1992).

The cerambycid assemblage of the Florida Keys, with 66% Neotropical–Caribbean and 32% Nearctic affinities, contrasts markedly with the south Florida assemblage of the mainland, which exhibits 28% Neotropical and 57% Nearctic affinities (Nearctic or Neotropical affinity could not be definitively assigned to the remaining 15%) (Table 4). The data suggest that the Florida Keys are more West Indian in nature than the south Florida mainland. In the Keys, establishment by West Indian colonizers has been more successful than that of Nearctic colonizers, despite the much narrower water barrier between the south Florida mainland and the Florida Keys than between the Florida Keys and Cuba or the Bahama Islands. Therefore, the Keys have been populated primarily

by island-based (Caribbean) taxa; invasions occur not only from continents to islands; they also occur from larger islands to smaller islands.

One question remains, however. Why is there not an even higher proportion of Cuban species in south Florida, as there is in the Bahama Islands? We suggest that the answer lies in a combination of two factors: (1) the water gap between Cuba and Florida is significant, though relatively small; and (2) the open avenue of peninsular Florida allowed extensive insect movement from the Nearctic north.

The second has seemingly been more important in allowing abundant access by northern species that were able to occupy most of the available subtropical “niches” in the West Indian vegetation of south Florida. That is, the earlier presence of Nearctic species has somehow limited later colonization by Neotropical species in the predominantly Neotropical vegetation.

#### **Summary**

South Florida represents a transition zone between the Nearctic and Neotropical regions. While the woody flora of south Florida is predominantly Caribbean in origin, the cerambycid fauna is nearly equally of Neotropical (53%) and Nearctic (47%) origin. Since south Florida became emergent, colonizers have employed a combination of overwater and overland dispersal, from Neotropical and Nearctic sources, along the following four routes: (1) a temperate-zone land route; (2) a tropical overseas route; (3) a subtropical land route; and (4) a stepping-stone route.

The south Florida cerambycid fauna is no richer than that of other comparable regions. This may be explained by the relative youth of the region: south Florida has been emergent, and available for colonization, for only the past 10 000 or 6000–4700 years (our cerambycid data support the latter period). The south Florida mainland has been emergent for a longer period of time than the Keys, and this is reflected in the disparity in species richness between the two regions (47 species recorded from the mainland are absent from the Keys). Furthermore, the level of endemism, 14.3% of the south Florida cerambycid fauna, is higher than predicted. However, this level of endemism is much lower than that of the fauna of the Bahama Islands (25.5%), a region of comparable climate, vegetation, and recent geological history.

The biological data do not support the traditional view that the sea level rose steadily from a glacial low (contraction of island area), 10 000 YBP, to its present high. Rather, the data on cerambycids support the hypothesis that the sea level has fluctuated greatly over the past 6000–4700 years, completely submerging the low-lying Keys, but allowing more elevated regions of the Bahama Islands and the south Florida mainland to serve as refugia, preserving species richness.

The surprising presence of a “distance effect” in the Keys also refutes the traditional view of a steadily rising sea level. If this were true, these island assemblages would have been in equilibrium and no distance effect would be detectable. This is not so. Based on our cerambycid data it is far more parsimonious to suggest that the Keys are recently emergent and have been available for colonization during the past 6000–4700 years.

Our support of the fluctuating sea level scenario and rejection of the traditional view of a steadily rising sea level have

important implications for biogeographical studies of south Florida, and suggest that colonization, extinction, and speciation in this region are far more dynamic processes than biologists had earlier thought. Additional evidence from other groups of south Florida taxa should be pursued in order to clarify these findings.

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## References

- Abbott, I. 1983. The meaning of  $z$  in species/area regression and the study of species turnover in island biogeography. *Oikos*, **41**: 385–390.
- Anderson, R.S., and Peck, S.B. 1994. Origin and biogeography of the weevils of southern Florida (Coleoptera: Curculionidae). *Can. Entomol.* **126**: 819–839.
- Atkinson, T.H., and Peck, S.B. 1994. Annotated checklist of the bark and ambrosia beetles (Coleoptera: Platypodidae and Scolytidae) of tropical southern Florida. *Fla. Entomol.* **77**: 313–329.
- Borror, D.J., Triplehorn, C.A., and Johnson, N.F. 1989. An introduction to the study of insects. Saunders College Publishing, Philadelphia.
- Browne, D.J. 1992. Phryniidae (Amblypygi) from Andros Island, Bahamas, with notes on distribution patterns, recent origin and allometry. *J. Arachnol.* **20**: 13–20.
- Browne, D.J., Peck, S.B., and Ivie, M.A. 1993. The longhorn beetles (Coleoptera: Cerambycidae) of the Bahama Islands with an analysis of species–area relationships, distribution patterns, origin of the fauna and an annotated species list. *Trop. Zool.* **6**: 27–53.
- Campbell, D.G. 1981. The ephemeral islands: a natural history of the Bahamas. MacMillan Education Ltd., Hong Kong.
- Chemsak, J.A., and Linsley, E.G. 1982. Checklist of Cerambycidae and Disteniidae of North America, Central America and the West Indies (Coleoptera). Plexus Publishing, Garden City, N.J.
- Chemsak, J.A., Linsley, E.G., and Noguera, F.A. 1992. Listados faunísticos de México. II. Los Cerambycidae y Disteniidae de Norteamérica, Centroamérica y las Indias Occidentales (Coleoptera). Universidad Nacional Autónoma de México, México.
- Connor, E.F., and McCoy, E.D. 1979. The statistics and biology of the species–area relationship. *Am. Nat.* **113**: 791–833.
- Deyrup, M. 1990. Footprints in the sands of time. *Fla. Entomol.* **73**: 529–538.
- Donnelly, T.W. 1988. Geological constraints on Caribbean biogeography. In *Zoogeography of Caribbean insects*. Edited by J.K. Liebherr. Cornell University Press, Ithaca, N.Y. pp. 15–37.
- Eickwort, G.C. 1988. Distribution patterns and biology of West Indian sweat bees (Hymenoptera: Halictidae). In *Zoogeography of Caribbean insects*. Edited by J.K. Liebherr. Cornell University Press, Ithaca, N.Y. pp. 231–254.
- Fairbridge, R.W. 1990. The Holocene sea-level record in south Florida. In *Environments of south Florida: present and past*. Vol. II. Edited by P.J. Gleason. Miami Geological Society, Coral Gables, Florida. pp. 427–435.
- Hovore, F.T., Penrose, R.L., and Neck, R.W. 1987. The Cerambycidae, or longhorned beetles, of southern Texas: a faunal survey (Coleoptera). *Proc. Calif. Acad. Sci.* **44**: 283–334.
- Liebherr, J.K. 1988. Biogeographic patterns of West Indian *Platynus* carabid beetles (Coleoptera). In *Zoogeography of Caribbean insects*. Edited by J.K. Liebherr. Cornell University Press, Ithaca, N.Y. pp. 121–153.
- Linsley, E.G. 1961–1972. Cerambycidae of North America. Parts 1–6. University of California Press, Berkeley.
- Long, R.W., and Lakela, O. 1971. A flora of tropical Florida: a manual of the seed plants and ferns of southern peninsular Florida. University of Miami Press, Coral Gables.
- MacArthur, R.M., and Wilson, E.O. 1967. The theory of island biogeography. *Monogr. Popul. Biol.* No. 1.
- MacRae, T.C. 1993. Annotated checklist of the longhorned beetles (Cerambycidae and Disteniidae) occurring in Missouri. *Insecta Mundi*, **7**: 223–252.
- Means, D.B., and Simberloff, D. 1987. The peninsula effect: habitat correlated species decline in Florida herpetofauna. *J. Biogeogr.* **14**: 551–568.
- Monné, M.A., and Giesbert, E.F. 1993. Checklist of Cerambycidae and Disteniidae (Coleoptera) of the western hemisphere. Wolfsgarden Books, Los Angeles.
- Nichols, S.W. 1988. Kaleidoscopic biogeography of West Indian Scaratinae (Coleoptera: Carabidae). In *Zoogeography of Caribbean insects*. Edited by J.K. Liebherr. Cornell University Press, Ithaca, N.Y. pp. 71–121.
- Patterson, J., and Stevenson, G. 1977. Native trees of the Bahamas. Bahamas National Trust, Nassau.
- Peck, S.B. 1989. A survey of insects in the Florida Keys: post-Pleistocene land-bridge islands: introduction. *Fla. Entomol.* **72**: 603–612.
- Peck, S.B. 1994a. Aerial dispersal of insects between and to islands in the Galápagos Archipelago, Ecuador. *Ann. Entomol. Soc. Am.* **87**: 218–224.
- Peck, S.B. 1994b. Sea-surface (pleuston) transport of insects between islands in the Galápagos Archipelago, Ecuador. *Ann. Entomol. Soc. Am.* **87**: 576–582.
- Peck, S.B., and Howden, H.F. 1985. Biogeography of scavenging scarab beetles in the Florida Keys: post-Pleistocene land-bridge islands. *Can. J. Zool.* **63**: 2730–2737.
- Peck, S.B., and Thomas, M.C. 1996. Arthropods of Florida and neighbouring land areas: a distributional checklist of the beetles (Coleoptera) of Florida. Vol. 16. Florida Department of Agriculture and Consumer Services, Gainesville.
- Peck, S.B., Walker, T.J., and Capinera, J.L. 1992. Distributional review of the Orthoptera of Florida. *Fla. Entomol.* **75**: 329–342.
- Ramos, J.A. 1988. Zoogeography of the auchenorrhynchous Homoptera of the Greater Antilles (Hemiptera). In *Zoogeography of Caribbean insects*. Edited by J.K. Liebherr. Cornell University Press, Ithaca, N.Y. pp. 61–71.
- Scott, J.A. 1972. Biogeography of Antillean butterflies. *Biotropica*, **4**: 32–45.
- Simpson, R.W. 1947. Holoarctic mammalian faunas and continental



- relationships during the Cenozoic. *Bull. Geol. Soc. Am.* **58**: 613–688.
- Skillman, F.W., Jr. 1993. New records of Georgia Cerambycidae (Coleoptera: Cerambycidae). *Insecta Mundi*, **7**: 210.
- Slater, J.A. 1988. Zoogeography of West Indian Lygaeidae (Hemiptera). *In Zoogeography of Caribbean insects. Edited by J.K. Liebherr*. Cornell University Press, Ithaca, N.Y. pp. 38–61.
- Tomlinson, P.B. 1980. The biology of trees native to tropical Florida. Harvard University Press, Cambridge, Mass.
- Webb, S.D. 1990. Historical biogeography. *In Ecosystems of Florida. Edited by R.L. Myers and J.J. Ewel*. University of Central Florida, Orlando. pp. 70–100.
- Wilson, E.O. 1988. The biogeography of the West Indian ants (Hymenoptera: Formicidae). *In Zoogeography of Caribbean insects. Edited by J.K. Liebherr*. Cornell University Press, Ithaca, N.Y. pp. 214–231.
- Zayas, F.D. 1975. Revision de la familia Cerambycidae (Coleoptera, Phytophagoidea). Academia de Ciencias de Cuba, Havana.