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Why Are There So Few Insect Predators of Nuts of American Beech *(Fagus Grandifolia)?*

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WHY ARE THERE SO FEW INSECT PREDATORS OF NUTS OF AMERICAN BEECH (*FAGUS GRANDIFOLIA*)?

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ABSTRACT

American beech, *Fagus grandifolia* Ehrh., is a common nut-bearing tree of eastern North America. Compared to other North American nut-bearing tree species of comparable geographic range, the nut-infesting insect fauna of American beech is species-poor: only the filbertworn, *Cydia latiferreana* (Wlsm.) (Lepidoptera: Tortricidae), infests nuts of American beech. Why are there so few insect predators of nuts of American beech? Using data from published studies, I explore two hypotheses that may help to explain the species-poor nut-infesting insect fauna of American beech. First, might chemical defense of beechnuts, and/or low nutritional value, restrict the number of insect predators that can exploit this food resource (unprofitable resource hypothesis)? Second, may spatial and temporal variability of beechnut mast crops limit colonization by nut-infesting insects because of the unpredictability of the resource (unpredictable resource hypothesis)? I found no strong evidence to suggest that chemical defense or low nutritional value was associated with the species-poor nut-infesting insect fauna of American beech. Yearly variability in nut crop size alone did not explain the low species richness of American beech compared to other tree species. Instead, I suggest that spatial and temporal unpredictability in production of sound versus incomplete beechnuts was an effective filter that limited colonization of beechnuts by insects. Moreover, the lone insect species able to successfully colonize beechnuts, *C. latiferreana*, is well adapted to resource unpredictability. Unlike specialist insect species that infest nuts of only 1 or 2 North American tree genera, *C. latiferreana* has a relatively broad host range and its mobile larvae can relocate to new resources when faced with food shortages.

Considerable attention has focused on the biogeographic relationships of herbivorous insects and their host plants, especially on factors that affect accumulation of leaf-feeding insects by plants in ecological and evolutionary time (Strong, Jr. 1974, 1979, Blaustein et al. 1983, McCoy and Rey 1983, Strong, Jr. et al. 1984). Research has shown that accrual of leaf-feeding insects by plants is influenced by several factors including plant geographic range, architecture, and toxicity (Strong, Jr. et al. 1984 and references therein).

Little studied in a biogeographic context, fruits and seeds of plants may also support diverse communities of insects (Winston 1956, Andersen and New 1987). Evidence suggests that accrual of fruit- and seed-eating insects by plants is influenced by factors similar to those that affect accumulation of leaf-feeding insects. For example, Andersen and New (1987) found that host plant phylogeny and fruit morphology were important correlates of the distribution and abundance of seed-eating insects of fruits of Australian *Eucalyptus*, *Leptospermum*, and *Casuarina*.

American beech, *Fagus grandifolia* Ehrh., a common tree species of eastern North America, is a member of the Fagaceae, a nut-bearing woody plant family whose fruits are extensively used as food by animals, especially insects

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(Martin et al. 1951, Marquis et al. 1976, Williams 1989). However, compared to other nut-bearing tree species in North America, the nut-infesting insect fauna of American beech is decidedly species-poor (Williams 1989). Only one species, *Cydia latiferreana* (Wlsm.) (Lepidoptera: Tortricidae), the filbertworm, infests nuts of American beech. In contrast, the nut-infesting insect faunas of most other North American tree genera of comparable geographic range are substantially more species-rich (Table 1, Williams 1989), particularly the major fagaceous genera, *Quercus* (oaks) and *Castanea* (chestnuts, chinkapins) (plant nomenclature follows Gleason and Cronquist 1991). Similarly, nuts of European beech, *Fagus silvatica* L., are infested only by *Cydia fagiglandana* Zeller, a European relative of the filbertworm (Watt 1923, Nielsen 1977, Jensen 1985, Nilsson 1985).

Why are there so few insect predators of nuts of American beech? Using data from published studies, I explore two hypotheses that may help explain the species-poor nut-infesting insect fauna of American beech. First, might chemical defense of beechnuts, and/or low nutritional value, restrict the number of insect predators that can exploit this food resource (non-profitable resource hypothesis)? In particular, tannins, common chemical constituents of nuts of many fagaceous species, can influence feeding preferences in animals (Smallwood and Peters 1986) and can bind with proteins in the digestive tract, rendering them indigestible (Martin and Martin 1982). Second, may spatial and temporal variability of beechnut mast crops limit colonization by nut-infesting insects because of the unpredictability of the resource (unpredictable resource hypothesis)? Masting, the synchronous production of seed crops at irregular intervals (Silvertown 1980, Sork et al. 1993, Kelly 1994, Kelly and Sork 2002), has been shown to influence the population dynamics of seed predators and associated species (e.g., Ostfeld et al. 1996, McShea 2000) and may influence the risk of post-dispersal predation to seeds and fruits (Silvertown 1980).

MATERIALS AND METHODS

Chemical data to test the non-profitable resource hypothesis were summarized from a range of studies (Table 2) and focused on four main nut defense/nutritional parameters (concentrations of tannin, crude fat, crude protein, and crude carbohydrate) expressed on a percent dry weight basis. Chemical data were summarized for eight nut-bearing tree species in each of three taxonomic groups (white oaks, subgenus *Lepidobalanus*; red oaks, subgenus *Erythrobalanus*; and hickories, Juglandaceae) that occur within the range of American beech and for which adequate data were available. Using data from individual species, means were calculated for each chemical parameter by nut tree taxonomic group. When multiple values for a chemical parameter were available for a tree species, they were averaged and the species mean was used in calculating the taxonomic group mean. In instances where the concentration of a chemical constituent was listed as trace or negligible, a default value of 0.1% was used in the analysis.

I used both univariate and multivariate statistical approaches to analyze nut defense/nutritional data. Univariate tests allowed me to explore potential differences in single nut defense/nutritional parameters between American beech and the three taxonomic groups of nut trees as described above. Univariate one sample *t*-tests ($\alpha \leq 0.05$) were used to explore differences in nut chemistry between American beech and each of the three taxonomic groups of trees. Multivariate principal components analysis (PCA) was used to examine the relationship of the suite of nut nutritional and chemical defense parameters across tree species and not just single factors as in univariate tests. One sample *t*-tests were done using SYSTAT version 7.0 (Wilkinson 1997). PCA was done using MVSP version 3.14 (Kovach 2000).

Data to test the unpredictable resource hypothesis were obtained from a ten-year American beech mast crop study conducted by Gysel (1971) in southern

Table 1. Species richness of North American nut-infesting insect species by plant family and genus (compiled from Williams 1989). *Castanopsis* and *Lithocarpus* are much more restricted in range than the other nut tree genera (both are confined to a narrow coastal band of California, Oregon and Washington, USA) but are included for comparative purposes.

	Number of species by insect order				Number of species by host taxon	
Host plant family/genus	**Coleoptera**	**Diptera**	**Lepidoptera**	**Hymenoptera**	**Genus**	**Family**
Betulaceae						
Corylus L.	2	0	1	0	3	3
Fagaceae						
Castanea Mill.	5	0	2	0	7	76
Castanopsis (D.Don) Sprach	1	0	1	0	2	
Fagus L.	0	0	1	0	1	
Lithocarpus Blume	1	0	1	0	2	
Quercus L.	24	2	4	34	64	
Juglandaceae						
Carya Nutt.	3	1	3	0	7	16
Juglans L.	2	4	3	0	9	
Total by insect order	38	7	16	34	95	

Table 2. Chemical and mast frequency data for selected nuts of North American nut-bearing trees expressed on a percent dry weight basis. Superscripts refer to references from which data were obtained[a] (range of values recorded across studies appear in parentheses). Data on mast crop frequency (mast) is from Schopmeyer (1974) and is presented as a range. For tannin concentration in *Fagus grandifolia* and Juglandaceae, a dashed line indicates that a negligible amount (< 0.5%) was detected. NA = data not available; crude carb. = crude carbohydrate.

Taxon	Tannin (%)	Crude fat (%)	Crude protein (%)	Crude carb. (%)	Mast (years)
Fagus grandifolia Ehrh.	---	10.6[5]	7.8[5]	6.5[5]	2-8
Fagaceae: *Lepidobalanus*					
Quercus alba L.	4.5 (3.3-5.6)[1,13]	5.7 (2.9-8.8)[1,3,7,8,13]	5.7 (4.6-7.3)[1,3,8,13]	46.6[3]	4-10
Q. bicolor Willd.	2.1[6]	2.9[8]	4.4[6,8]	NA	3-5
Q. lyrata Walt.	0.6[6]	0.9[8]	4.5 (4.4-4.6)[6,8]	49.8[5]	3-4
Q. macrocarpa Michx.	2.0 (0.7-3.2)[6,12]	6.7 (4.8-9.8)[5,7,13]	4.4 (3.9-4.9)[5,6,12]	45.9[5]	2-3
Q. muehlenbergii Engelm.	4.7[12]	6.4 (6.1-6.6)[3,12]	4.6 (4.4-4.8)[3,12]	34.5[3]	NA
Q. prinoides Willd.	4.4[1]	6.3[1]	7.6[1]	NA	NA
Q. prinus L.	9.3 (8.1-10.4)[1,13]	6.8 (3.3-10.1)[1,2,10,13]	6.3 (5.8-6.9)[1,2,10,13]	NA	2-3
Q. stellata Wangenh.	3.7 (0.9-6.5)[6,12]	5.9 (5.2-6.7)[2,3,8,12]	5.5 (3.8-6.8)[2,3,6,8,12]	37.9[3]	2-3
Mean ± 1 SE	**3.9 ± 0.9**	**5.2 ± 0.8**	**5.4 ± 0.4**	**42.9 ± 2.9**	
Fagaceae: *Erythrobalanus*					
Quercus falcata Michx.	8.7[6]	18.4 (15.6-22.7)[2,5,8]	5.8 (4.2-7.0)[2,5,6,8]	40.4 (23.0-57.7)[2,5]	1-2
Q. ilicifolia Wangenh.	1.3[1]	19.7 (19.4-20.0)[1,2]	8.2 (6.1-10.3)[1,2]	NA	NA
Q. marilandica Muenchh.	7[6]	10.7[2]	6.6 (6.3-6.9)[2,6]	NA	NA
Q. nigra L.	8.8[6]	20.7 (20.3-21.1)[3,8]	4.7 (3.8-5.4)[3,6,8]	25.8[3]	1-2
Q. palustris Muenchh.	9.3[12]	13.6 (11.7-15.4)[5,12]	5.0 (3.8-6.1)[5,12]	45.4[5]	1-2
Q. phellos L.	7.2[6]	19.8 (19.6-20.0)[3,8]	5.5 (5.2-5.9)[3,6,8]	31.2[3]	1
Q. rubra L.	11.5 (9.8-13.0)[1,10,12]	19.0 (14.0-23.0)[1,8,12,13]	5.9 (4.9-6.6)[1,8,12,13]	NA	3-5
Q. velutina Lam.	16.5[12]	15.3 (13.0-17.5)[8,12]	5.9 (5.7-6.0)[8,12]	NA	2-3
Mean ± 1 SE	**9.9 ± 1.2**	**17.2 ± 1.3**	**6.0 ± 0.4**	**34.1 ± 5.9**	

Table 2. Continued.

Taxon	Tannin (%)	Crude fat (%)	Crude protein (%)	Crude carb. (%)	Mast (years)
Juglandaceae					
Carya aquatica					
(Michx. F.) Nutt.	---	32.0[9]	10.2[9]	54.2[9]	1-2
C. cordiformis					
(Wangenh.) K. Koch	---	39.6 (30.8-48.3)[5,9]	5.4 (3.3-7.5)[5,9]	29.2 (17.1-41.3)[5,9]	3-5
C. floridana Sarg.	---	34.3[11]	9.6[11]	45.3[11]	NA
C. illinoensis					
(Wangenh.) K. Koch	---	32.9[3]	9.3[3]	13.3[3]	1-2
C. laciniosa					
(Michx. F.) Loudon	---	8.7[3]	1.5[3]	13.8[3]	1-2
C. myristiciformis					
(Michx. F.) Nutt	.---	15.2[3]	5.8[3]	16.1[3]	2-3
C. ovata (Mill.) K. Koch	0.5[1]	33.4 (29.3-37.4)[3,7,9]	10.8 (5.9-13.3)[1,3,9]	10.9 (8.8-13.0)[1,3]	1-3
C. tomentosa (Poir.) Nutt	.---	20.0[5]	3.7[5]	12.7[5]	2-3
Mean ± 1 SE	**---**	**27.0 ± 3.9**	**7.0 ± 1.2**	**24.4 ± 5.9**	

[a]References include: [1]Waino and Forbes (1941), [2]King and McClure (1944), [3]Bonner (1971), [4]Burns and Viers (1973), [5]Bonner (1974), [6]Ofcarcik and Burns (1971), [7]Smith and Follmer (1972), [8]Short (1976), [9]Halls (1977), [10]Smallwood and Peters (1986), [11]Abrahamson and Abrahamson (1989), [12]Briggs and Smith (1989), [13]Servello and Kirkpatrick (1989).

Michigan, USA, and a six-year study conducted by Leak (1993) in the White Mountains of New Hampshire, USA. I lumped Gysel's (1971) and Leak's (1993) nut condition classes - sound (i.e., non-infested or damaged), insect-infested, and vertebrate-damaged - into a single class, available mast, for analysis. Neither Gysel (1971) nor Leak (1993) identified the specific insect species infesting beechnuts at their study site. However, their descriptions of frass-filled nuts, characteristic of nut-infesting lepidopterans, strongly implicate *C. latiferreana* (e.g., Winston 1956, Gibson 1971). Moreover, Graber and Leak (1992), in a related study in New Hampshire, identified *C. latiferreana* as the sole insect predator of beech nuts. Pearson product-moment correlation ($\alpha \leq 0.05$) with Bonferroni correction was used to examine the relationships of insect-infestation and vertebrate damage to beechnuts with available mast across years. Percentage data were arcsin transformed prior to analysis to ensure normality (Zar 1996). Correlation analysis was done using SYSTAT version 7.0 (Wilkinson 1997).

RESULTS

Results from univariate statistical tests suggest that nuts of American beech were more similar in tannin concentration and nutritional value to nuts of the hickory group than to those of either the white oak or red oak groups (Tables 2 and 3). Beechnuts were significantly lower in crude fat and crude carbohydrate concentrations than hickory nuts but did not differ significantly in tannin or crude protein concentrations (Table 3). Beechnuts had significantly higher crude fat and protein concentrations than acorns of the white oak group but were significantly lower in tannin and crude carbohydrate concentrations (Table 3). Beechnuts had a significantly higher concentration of crude protein than red oak acorns but were significantly lower in tannin, crude fat, and crude carbohydrate concentrations (Table 3). Overall, beechnuts were consistently lower in crude carbohydrate concentration, generally lower in crude fat and tannin concentrations, and generally higher in crude protein concentration, than nuts of the white oak, red oak, and hickory species groups examined in this study.

PCA showed a clear separation of most hickory species from white and red oak species largely on the basis of crude fat, crude protein and tannin content of nuts (Fig. 1). Red and white oak species groups were separated from each other in ordination space mostly on the basis of high tannin content (red oaks) and high carbohydrate content (white oaks). Principal components axis 2 accounted for 41.6% of the variance in the data matrix and separated nuts of species on a gradient from high tannin concentration to high crude fat and high crude protein percentages (Table 4). Principal components axis 1 accounted for 30.7% of the variance in the data matrix and separated nuts of species on a gradient from high tannin to high crude carbohydrate percentages. Together the two principal components axes accounted for 72.3% of the variance in the data matrix. American beech clustered in the middle of ordination space (Fig. 1) suggesting that it is intermediate in the suite of the four nut nutrition and defense parameters considered in this study.

American beech exhibited the second greatest variation in frequency of mast production of any of the nut tree species examined (Table 2). Gysel (1971) observed a large mast crop of viable beechnuts only once in ten years and crop failures twice (Fig. 2). Sound nuts comprised less than 10% of the total beechnut crop for 7 of 10 years (mean = 15.2 ± 5.0% SE, range = 2.4 to 47.5%). Incomplete, nonviable nuts comprised more than 20% of the annual production for nine years (mean = 43.5 ± 7.6% SE, range = 23.5 to 87.7%). Yearly variance in nut crops (65%), and variance among individual trees (30%), accounted for most of the variation in beechnut crop production during Gysel's (1971) study. In contrast, Leak (1993) found that sound nuts comprised an average of 80% (± 2.5 SE) of the annual production during his six-year-study with no nut crop failures.

Table 3. Comparison of chemical constituents of nuts of American beech (AB) with those of the white oak (WO), red oak (RO), and hickory (HK) species groups. Significant differences ($P \leq 0.05$, one sample t-test) between groups are denoted by < and >; non-significance is denoted by =.

Tannin (%)	Crude fat (%)	Crude protein (%)	Crude carbohydrate (%)
AB < WO	AB > WO	AB > WO	AB < WO
($P = 0.005$, df =7, $t = 4.11$)	($P < 0.0001$, df =7, $t = -7.15$)	($P = 0.001$, df =7, $t = -5.99$)	($P = 0.005$, df =7, $t = 12.65$)
AB < RO	AB < RO	AB > RO	AB < RO
($P < 0.0001$, df =7, $t = 8.39$)	($P = 0.001$, df =7, $t = 5.20$)	($P = 0.002$, df =7, $t = -4.84$)	($P = 0.007$, df =3, $t = 6.61$)
AB = HK	AB < HK	AB = HK	AB < HK
($P = 0.5$, df =7, $t = 0.73$)	($P = 0.004$, df =7, $t = 4.25$)	($P = 0.6$, df =7, $t = -0.63$)	($P = 0.019$, df =7, $t = 3.02$)

Table 4. Results of principal components analysis (PCA) for nut nutritional and chemical defense parameters.

PCA variable loadings	Axis 1	Axis 2
% Tannin content	-0.360	-0.574
% Crude fat	0.666	-0.183
% Crude protein	0.625	-0.354
% Crude carbohydrates	0.191	0.716
Eigenvalues	1.663	1.229
Percent variance explained	41.57	30.72

Insect damage to beechnut crops in Gysel's (1971) study ranged from 1.2 to 23.3% (mean = 10.7 ± 2.5% SE). Vertebrate damage to beechnut crops was greater than insect damage, and ranged from 0.6 (crop failure year) to 46.2% of the total crop (mean = 27.8 ± 5.6% SE). Both insect infestation ($r = 0.82$, df = 1, $P = 0.004$) and vertebrate damage ($r = 0.94$, df = 1, $P \leq 0.0001$) were significantly and positively correlated with available beechnut mast across study years. However, during the two peak years of sound beechnut production, insect damage was low (3.9% and 7.6% of the total crop; Figure 2).

Insect damage to beechnut crops in Leak's (1993) study ranged from 16.0 to 100% (mean = 62.0 ± 12.0 % SE). Vertebrate damage to beechnut crops was less than insect damage, and ranged from 0 (an apparent outbreak year in which insects destroyed the whole nut crop) to 20.0% of the total crop (mean = 8.5 ± 2.7% SE). Both insect infestation ($r = 0.85$, df = 1, $P = 0.034$) and vertebrate damage ($r = 0.85$, df = 1, $P \leq 0.031$) were significantly and positively correlated with available beechnut mast across study years.

DISCUSSION

I found no strong evidence to suggest that chemical defense or low nutritional value was associated with the species-poor nut-infesting insect fauna of American beech. In contrast, beechnuts appear to be a quality food resource for nut-feeding insects, having good protein content and negligible levels of tannins.

Masting, a complicated phenomenon influenced by weather, past reproductive events and root carbohydrate reserves (Matthews 1955, Sork et al. 1993, Piovesan and Adams 2001, Kelly and Sork 2002), is widespread in the Fagaceae, particularly among oaks (e.g., Downs and McQuilken 1944, McShea 2000, Table 2). As in American beech, nut crop failure is not uncommon in oaks (Downs and McQuilken 1944, Sork et al. 1993, McShea 2000), thus year-to-year variability in nut crop size alone does not explain the great difference in species richness of the nut-infesting insect fauna between these two taxa. In contrast, American beech and hickories, somewhat similar in nut tannin content and nutritional value, differ greatly in mast periodicity (Nixon et al. 1980, Sork 1983; Table 1). Hickory nuts, produced at relatively frequent intervals across years, may be a more predictable, easily colonized food resource for insects than are nutritionally comparable but temporally variable beechnuts.

I suggest that the great variability in production of sound versus incomplete beechnuts both within crops and across years as noted by Gysel (1971; Fig. 1) and others (Ward 1961, Dix and Skrentny, Jr. 1965, Stalter 1982, Johnson and Adkisson 1985) has restricted colonization of nuts of American beech by insects and limited accrual of species. An incomplete beechnut lacks endosperm and

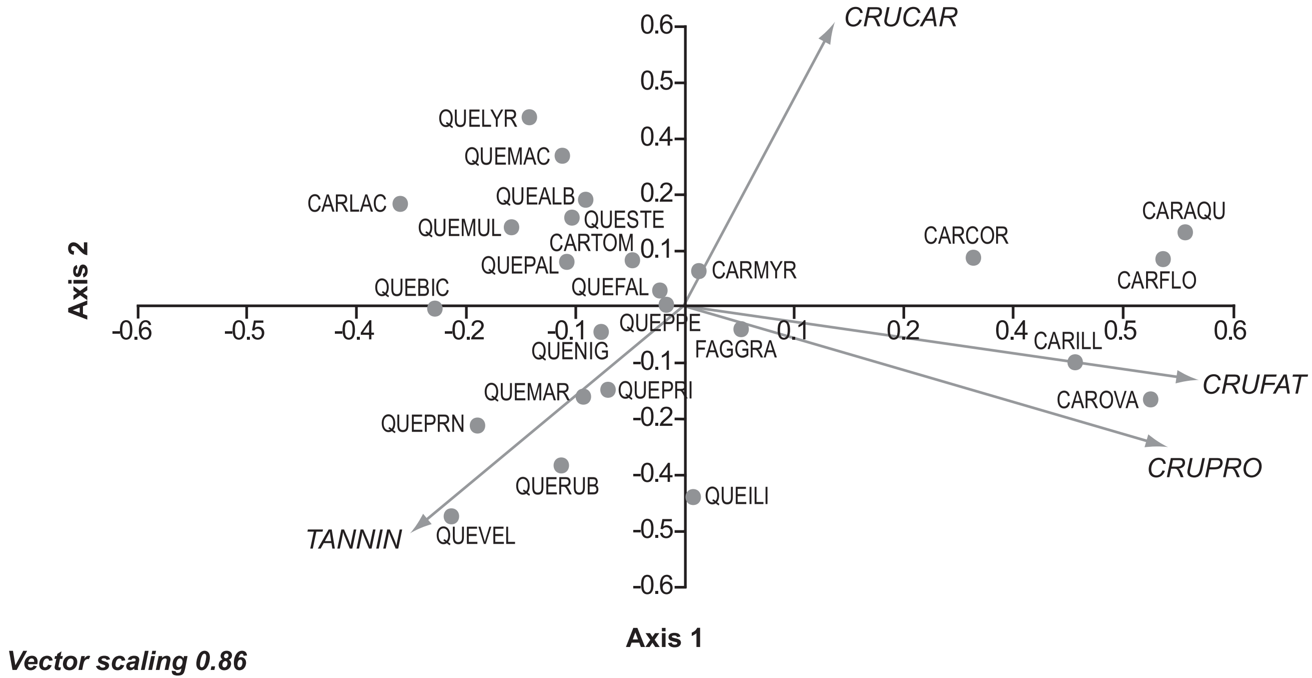

Figure 1. Principal components biplot for nut defense/nutritional characters by tree species. Species are from Table 2 and are coded by the first three letters of the genus and the first three letters of the specific epithet. Lines are vectors of nut defense/nutritional parameters associated with principal components axes. CRUCAR = crude carbohydrate concentration, CRUFAT = crude fat concentration, CRUPRO = crude protein concentration, TANNIN = tannin concentration.

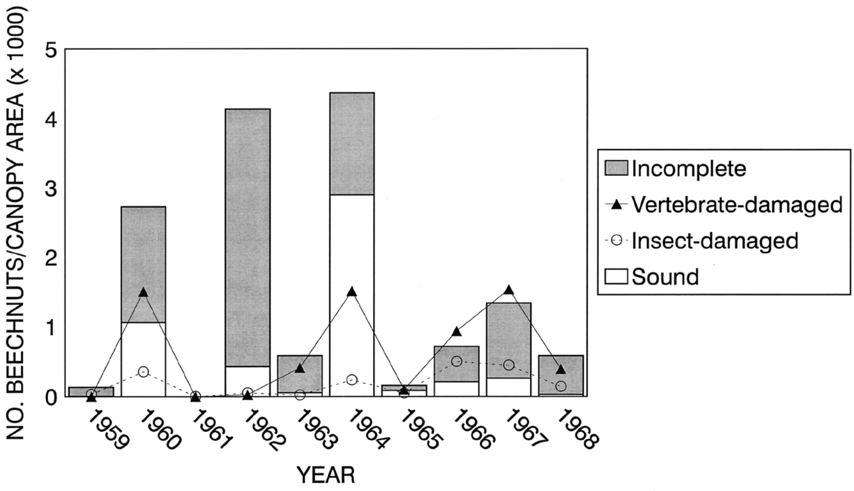

Figure 2. Mean annual production of sound, incomplete, vertebrate-damaged, and insect-infested nuts of American beech per 100 ft^2 (9.3 m^2) of crown collection area in Michigan, USA. Data are from a ten-year mast crop study conducted by Gysel (1971). Data were collected from 20 trees in 2 woodlots for 2 years and 30 trees in three woodlots for 8 years.

an embryo, but has a fully developed pericarp and is morphologically similar to sound nuts (Gysel 1971). Incomplete nuts are also produced by European beech (Matthews 1955, Hilton and Packham 1986). Oaks also produce incomplete or abortive nuts, but these generally comprise less of the total crop than incomplete beechnuts and are small and deformed in appearance compared to sound nuts (Downs and McQuilken 1944, Sork et al. 1983). Vertebrates, such as blue jays, *Cyanocitta cristata* (L.), can discriminate between sound and incomplete beechnuts and preferentially select sound nuts for feeding and caching (Johnson and Adkisson 1985), presumably by tactile and visual means as in other corvids (e.g., Ligon and Martin 1974). However unlike vertebrates, nut-infesting insects may be limited in their ability to find sound beechnuts in a large crop of incomplete nuts or they may be unable to distinguish between sound and incomplete nuts (e.g., Hall et al. 1979, Butkewich et al. 1987, Desouhant 1998, Stamps and Linit 2002). Adult nut insects may select incomplete beechnuts that cannot provide the energy needed for larval growth and development or alternatively, they may expose themselves to increased predation risk when searching tree canopies for spatially dispersed, numerically rare, sound beechnuts.

The life history of *C. latiferreana* provides further evidence that variability in beechnut crops may have restricted development of a diverse nut insect fauna on American beech. Compared to most primary nut insects (i.e., those capable of entering nuts through their own feeding or oviposition holes, Winston 1956), *C. latiferreana* feeds on a broad range of hosts, including nuts of 19 tree and shrub species in 6 genera and 3 families as well as the fleshy fruits of other woody plants (Dohanian 1940, Williams 1989). Other insect species, like *Conotrachelus* and *Curculio* acorn weevils, are nut specialists whose hosts are typically confined to 1 or 2 genera in a single family (Williams 1989). A broad host range is a means by which *C. latiferreana* can cope with unpredictable beechnut resources by switching to alternate, more abundant food resources when necessary. Moreover, larvae of *C. latiferreana*, unlike those of most other nut-feeding insects, have some mobility and can relocate to different nuts when faced with diminished food resources (Winston 1956, Gibson 1971).

It is interesting to speculate why other North American nut-infesting insect species besides *C. latiferreana* apparently failed to develop generalist feeding strategies under the selective pressure of masting. Perhaps phylogenetic constraints in the plasticity of certain morphological, physiological or behavioral traits limited the development of generalist feeding strategies in the other nut-infesting taxa. A second possibility is that *C. latiferreana* may be a superior competitor that eliminated other nut-feeding species through competitive exclusion. Finally, perhaps *C. latiferreana* had a limited pool of natural enemies to limit is population size and allow for coexistence of other generalist nut-feeding insect species.

It is also important to consider the competitive effects of other nut-consuming animals on beechnut resources and their potential influence on the accrual of a diverse nut insect fauna. Beechnuts are widely used as food by many species of North American vertebrates including several species of tree squirrels (*Sciurus, Tamiasciurus*), blue jay, *C.cristata* , wild turkey, *Meleagris gallopavo* (L.), ruffed grouse, *Bonasa umbellatus* (L.), white-tailed deer (*Odocoileus virginianus* Zimmermann), black bear (*Ursus americanus* Pallas), and other birds and mammals (Martin et al. 1951, Nixon et al. 1968, Halls 1977, Johnson and Adkisson 1985, Webb 1986). Gysel (1971) and others (Graber and Leak 1992, Leak 1993) have noted that sound beechnuts fallen beneath trees were quickly consumed or removed by vertebrates and very few nuts survived more than two to three weeks. Likewise, harvest of beechnuts from beech canopies by blue jays can be extensive (Johnson and Adkisson 1985). Selective harvest by vertebrates would further reduce the number of sound beechnuts available to insects and increase the probability that insects within nuts themselves may fall prey to vertebrates. Vertebrate nut predators like the white-footed mouse (*Peromyscus leucopus* Rafinesque) and grey squirrel (*Sciurus carolinensis*) generally cannot discriminate between non-infested and insect-infested nuts and will feed on either (Semel and Andersen 1988, Weckerly et al. 1989). It should be noted that contemporary nut harvests by vertebrates are nowhere near the magnitude of historic harvests by massive flocks of the extinct passenger pigeon, *Ectopistes migratorius* (L.), for which beechnuts were a preferred food (Schorger 1955, Webb 1986, Ellsworth and McComb 2003). Whether competition for beechnut resources with passenger pigeons influenced the composition of the present-day nut insect fauna of American beech can only be speculated.

Based on the arguments outlined above, I suggest that spatial and temporal unpredictability of the nut crop of American beech was an effective filter limiting colonization of beechnuts by insects and the accrual of a diverse insect fauna. The lone insect species able to successfully colonize beechnuts, *C. latiferreana*, has a relatively broad host range that buffers it from resource unpredictability, unlike specialist insect species that infest nuts of few hosts. Given the parallels between European beech and American beech in mast frequency, production of incomplete nuts, and a species-poor nut insect fauna dominated by *Cydia* species (Matthews 1955, Nielsen 1977, Jensen 1985, Nilsson 1985, Hilton and Packham 1986, Piovesan and Adams 2001), I also suggest that unpredictability of beechnut resources helped to shape the composition of the nut insect fauna of European beech.

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