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Lichens, Sun, and Fire: A Search for an Embiid-Environment Connection in Australia (Order Embiidina: Australembiidae and Notoligotomidae)

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Lichens, Sun, and Fire: A Search for an Embiid-Environment Connection in Australia (Order Embiidina: Australembiidae and Notoligotomidae)

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ABSTRACT   This investigation is the first to quantify the degree of habitat specialization for any species within the little-known order Embiidina. The lichen and plant communities found in the habitats of two sympatric species, one living on lichens encrusted on granite and another feeding in leaf litter, were characterized using a process of ordination and cluster analysis. Differences among 40 samples and their relationships to environmental factors were probed statistically using Spearman's coefficient of rank correlations generated by comparing rank similarity matrices of the census sites. The lichen eater, *Notoligotoma hardyi* (Friederichs), was more abundant in areas with strong southern exposures and was associated with higher lichen abundance. They preferentially grazed on particular lichens, the first indication that an embiid shows specialization in feeding. The detritivore, *Australembia incompta* Ross, was closely associated with particular plant communities, especially those less susceptible to fire. Their colonies were more common in rockier, coastal areas and less abundant in grasslands and habitats dominated by *Eucalyptus*. Insight into ecological variation within the order can guide further exploration of other traits (such as silk structure and function and primitive social behavior) in this rarely studied group of insects.

KEY WORDS   webspinners, insect ecology, ordination, detritivore

TO THE CASUAL OBSERVER, the embiids (Order Embiidina) seem to be a fairly homogeneous group. Their elongate, flexible body form is remarkably conserved, apparently because of constraints imposed by the tight confines of the silken tubes and domiciles in which all embiids live (Ross 2000). Moreover, it seems that the various species lack specialization in their diet, because all species tested to date can be successfully reared on a diet of leaf litter and lettuce (Ross 2000). On closer examination, however, it is clear that species do differ in important ways. In some species, the females are solitary, whereas in others, they are colonial (see references in Edgerly 1997, Edgerly et al. 2002). In addition, taxonomists who have collected embiids have noted that species seem to exhibit distinct patterns of habitat use (Kusnezov 1904, Mills 1932, Ling 1934–1935, Callan 1952, Ross 2000). If embiids do differ in habitat use, these differences may be critical to understanding why species differ in the degree of colonial behavior. Similarly, choice of microhabitat may partly explain the ability of embiids to survive in a wide range of habitat conditions, from arid and hot to humid and warm. Unfortunately, such hypotheses cannot yet be examined because habitat use has never previously been quantified for any species of embiid.

In this study, we have adapted methods from research on habitat specialization in other animals to examine the habitat preferences of embiids.

To determine ecological correlates, we quantified a number of environmental variables on Magnetic Island (Queensland, Australia) where two species overlap: *Notoligotoma hardyi* (Friederichs) (Notoligotomidae) and *Australembia incompta* Ross (Australembiidae) (Ross 1963). Our preliminary survey of the island showed that the former lives on surfaces of rocks where they feed on lichens, while the latter lives in leaf litter as detritivores. This is consistent with the observations of Ross (2000) of similar habitat separation by notoligotomids and australembiids in Queensland. In a search for habitat characteristics specific to each species, we sampled sites that ranged in quality and quantity of the foods on which the embiids seemed to depend and that ranged in thermal stress, potentially extreme in some locations on the island. To achieve a range of samples with replication, gradient-directed transects (known as gradsects; e.g., Austin and Heyligers 1989, Bullock 1996) were chosen to include 40 samples varying in the accumulation of annual solar radiation.

We investigated the range of habitats for the two embiids by applying two distinct, but complementary, statistical approaches. In the first, we used classification and ordination techniques to examine patterns

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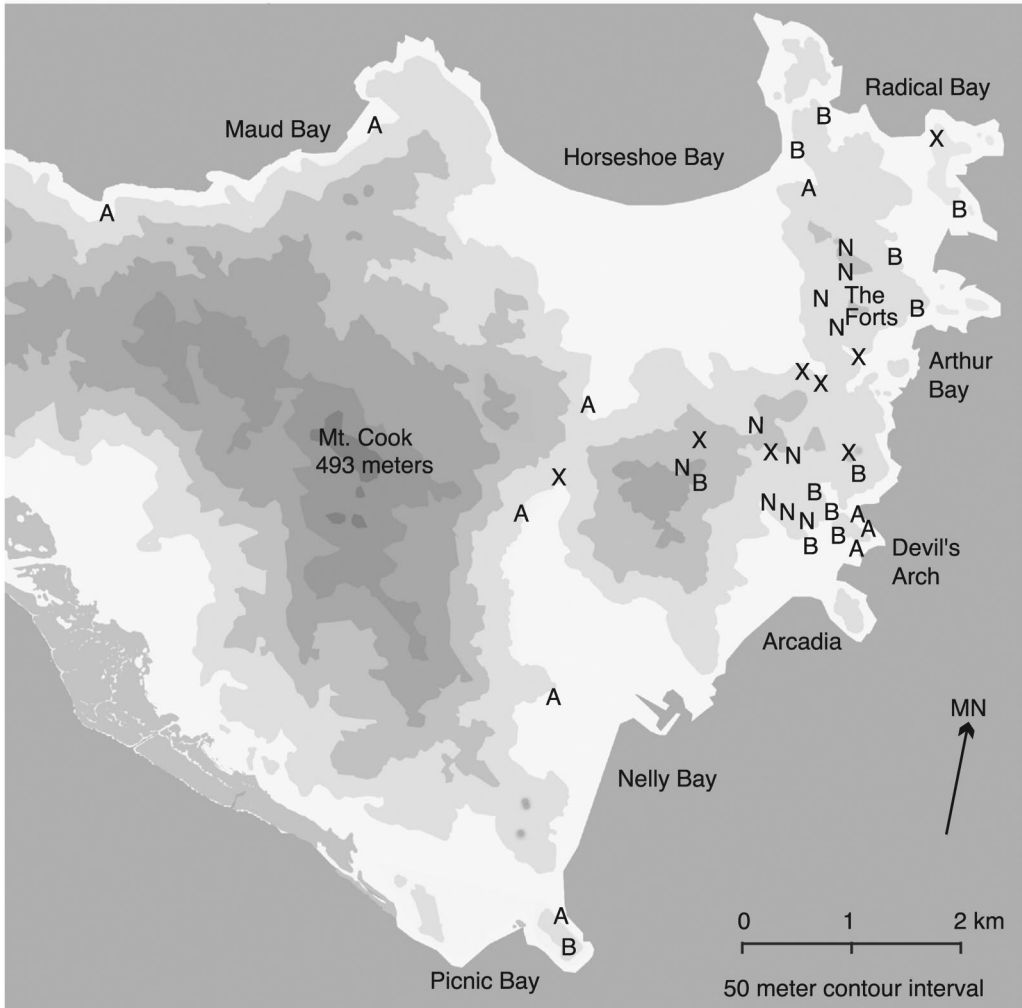
Magnetic Island, Queensland, Australia

Fig. 1. Map showing the section of Magnetic Island (Queensland, Australia) where census sites were located. Each census site ($n = 40$) is indicated by a letter: B, sites with both embiid species; N, sites with just *N. hardyi*; A, sites with just *A. incompta*; X, sites with neither species. Contour lines show 50-m increments in altitude, with higher altitude shown in darker tones. A white border outlines the island against the ocean, shown in dark gray. Drawing is based on Sunmap 8259-14.

and assemblages of species within the ecological communities in our samples. We sought to describe the communities of lichens or plants and to identify environmental factors that shape these communities. Such approaches are typical for studies that explore habitat selection and that seek variables that might explain the differences between species (e.g., Ludwig and Reynolds 1988, Bergemann and Largent 2000, Ihl and Klein 2001). After sorting the samples based on similarity, we asked whether the distribution of either embiid reflected the variation in the communities most closely related to their distinct food resources (lichens for one, leaves for the other). The second statistical approach, stepwise multiple regression, was used to identify key environmental variables that might predict abundance of the embiids.

Materials and Methods

Location. Magnetic Island (147°50' E, 19°08' S) is located 10 km northeast of the North Queensland city of Townsville. The rugged, granitic island is ≈5,184 ha in area and has numerous valleys and gullies, rising to its highest peak of 493 m (Fig. 1). The region experiences subtropical weather, with warm, dry winters and hot, wet summers. The mean annual rainfall is ≈1,196 mm. Mean maximum temperature in the warmest month (January) is 31°C, whereas the coolest month (July) experiences a mean daily minimum of 13.6°C (Sandercoe 1990). The dominant vegetation types include mixed eucalyptus woodland, vine forest along the coast and in gullies, and semideciduous woodlands. Also present are grasslands with sparse

trees, hoop pine (Araucariaceae) forests, littoral scrub, low vine forests among boulders, and mixed low coastal forests. The form of the local vegetation is influenced by disturbance as well as by microclimates. Sandercoe (1990) identified clearing, fire, introduced plants and feral animals, and cyclones as disturbance factors. *Acacia* shrublands, dominated by *A. leptostachya*, occur at sites disturbed by fires or cyclones.

Sampling Design. Gradsects were laid onto a topographic map (Sunmap 8259-14, 1997) of the island as parallel lines in a SE-NW direction, following the direction of the dominant winds. Sites were chosen along these lines to match with one of the following criteria: sites had to be on peaks (with two samples taken at each peak, one NW and the other SE), on slopes at varying altitudes facing NW or SE, or in gullies. In this order, such sites should vary from high levels of solar radiation (NW exposures) to lower levels (gullies and SE exposures). To be included, sites also had to be within walking distance of local roads or trails or accessible by boat. To increase the variability in frequency of disturbance, sites were also selected to range from close to far from the coast. The 40 sites (Fig. 1) were chosen before fieldwork to avoid unintended bias. Once a site was located in the field with aid of a topographic map and compass, a concerted effort was made to find colonies of *N. hardyi* on the rocks in the area. If embiids were present, the census plot was situated to include their colonies in the sample to avoid false negatives.

A pilot survey in February 2001 of habitat characteristics was conducted on four circular plots of 10 m radius located on a 50-m contour encircling the peak called Devil's Arch (Fig. 1). Each plot was chosen to center on a compass point (N, E, S, or W) along the 50-m contour. Each was evaluated for characteristics typically quantified in studies that characterize environmental features. Inspection of these data suggested that the following characteristics would be useful for quantifying the distinctiveness of each site: the angle of the slope estimated by eye, canopy cover (see Cox 1996 for scale used), height of the tallest trees, percent cover of ground by grasses, and number of rocks in three size categories (small, 0.1–0.5 m; medium, >0.5–1.0 m; large, >1.0 m). The number of trees recorded was split into four categories based on diameter at breast height (1.0–5.0; >5.0–10; >10–20; >20 cm), hereafter designated, respectively, as saplings or small, medium, and large trees.

Cryptogams (lichens, moss, and cyanobacteria) growing on granite boulders were sampled at each site by a random selection process. Preliminary analysis showed that sampling eight rocks in detail yielded the same information as sampling four; therefore, in our final scheme, only four large boulders at each census site were sampled. In addition, the boulders (>1 m in at least one dimension) were from the four compass directions (N, E, S, W) from the center of the plot. Percent cover of lichens, moss, and cyanobacteria (called "lichens" from this point on because 20 of the 23 cryptogams recorded were lichens) was estimated for each boulder. The boulder was measured to de-

termine approximate area of substrate available. Lichen cover for each site was calculated as the average cover by each species of lichen for the four boulders. A majority of the lichen specimens were sent to J. A. Elix of Australian National University for identification. A few rare lichens, mosses, and algae were not identified.

Identification of common plants was based on a Magnetic Island field guide by Jackes (1997). Vegetation type was confirmed after plants were identified in the field by cross-referencing a detailed vegetation map of the island (Sandercoe 1990). For all 40 sites, the vegetation types identified on site matched those predicted by Sandercoe's map, despite the 19-yr time lag between this study and the year Sandercoe collected her data. Other information was measured using the topographic map including altitude, distance (km) from the nearest coast, and distance (km) from the SE coast (the direction of the prevailing tradewinds). James Moloney of James Cook University evaluated a Geographic Information System (GIS) raster map of Magnetic Island for us using the program ArcView Spatial Analyst (2001). His analysis generated a relative score that represented insolation at a site based on two positions of the sun. One position was the sun in the northern sky at 70° above the horizon, and the other position was the same height but in the southern sky, simulating winter and summer, respectively. ArcView takes into account the shading imposed by the topography of the island for each sample site. For our purposes, sites were assigned scores such that higher numbers indicated brighter conditions. To compute an annual score for a site, the score for insolation when the sun was north was multiplied by 0.82 and added to the score from the south sun that was multiplied by 0.18. The fractions represent approximately how much time the sun is north or south of the island during the year. Total radiation score was used only in univariate analyses, whereas the separate scores for a northern sun and southern sun were used in the multivariate analyses. Finally, park rangers were consulted to determine the years since the most recent fire for each site. Fires can greatly alter the plant community through death of trees or changing light regimens and soil. Leaf litter and lichens, food for the embiids, might also be destroyed or damaged.

All rocks at each site were closely inspected, and all colonies of *N. hardyi* on the rocks were counted. A colony is a distinct patch of silk, with associated silk foraging trails. The silk contrasts with the background and is conspicuous to the eye. In contrast, quantification of *A. incompta* populations was based on a random sampling technique designed to explore the more secretive inhabitants of leaf litter. Each of the four rocks selected for evaluation of lichen cover was also sampled for *A. incompta*. Litter along each rockface was inspected for the presence of the colonies, obvious because of their use of silk in stitching leaves together. To score the relative abundance of this embiid, the number of positive samples as a proportion of the total number of samples was computed for each site.

Statistical Analysis. No two variables were found to correlate strongly with each other; therefore, all variables described in the methods were included in the analysis. The angular transformation was used on all proportional data, including percent cover of rocks by lichens, cover by grass, and proportion of samples with *A. incompta.* Because units varied from one variable to the next, the environmental data were normalized, and Euclidean distances were computed between samples as a measure of similarity. The lichen scores were moderately transformed using the square root to allow rare lichens to exert more influence on the calculation of similarity. Similarly, the fourth root was applied to counts of *N. hardyi* colonies because they ranged from 0 to 82, with the exception of one sample of 440.

JMP IN statistics (Sall et al. 2001, SAS Institute 2001) was used for stepwise multiple regression analyses and analysis of variance (ANOVA); all community-level multivariate analyses were conducted with an ecological analysis program called Primer-E (Clarke and Warwick 2001). Primer-E provides a framework for detecting community pattern through cluster analysis, for determining the species responsible for the sample groupings, and for linking the community patterns to environmental variables (Clarke 1993). Marine ecologists have often used Primer-E to seek environmental variables that may drive community structure (see references in Clarke and Warwick 2001). We probed our data in a similar manner to determine whether continuous variables or discrete categories were useful for defining the environments for the two embiids. Our operational rule for identifying informative habitat characteristics was to search for the categorization of samples that most closely correlated with the presence of each embiid species.

The general statistical methods of Primer-E used in our analysis are shown in Fig. 2. Bray-Curtis similarity matrices, which are useful for community data with numerous zeros, were used to compare the 40 census sites and to probe for influential environmental variables. The biota matrices for this analysis were based on either plant species (presence/absence) or lichen species (percent cover). BIO-ENV of Primer-E takes two similarity matrices (one for the biota and one for environmental variables) and applies forward- and backward-stepping phases to determine the best fitting combinations (based on r_s, Spearman's coefficient of correlation) of the environmental variables to match the Bray-Curtis similarity matrices for the biota (Fig. 2A). The BIO-ENV algorithm, which resembles stepwise multiple regression, proceeds until no further improvement in the correlation value is possible by adding any single variable. The stopping criterion for the stepping phase was set to find the best five variables at a correlation of 0.95; 10 iterations were run with random starting points. Before conducting BIO-ENV, another process called BVSTEP was employed to determine which environmental variables or lichen species were most influential in the two sets of data. This process allowed deletion of variables and species that did not influence the ordination pro-

cess and allowed us to pare down the large data sets. Four of the 23 lichens were removed from further analysis because ordination of sites (using nonmetric multidimensional scaling) with all lichens was almost identical to that with only 19 ($r_s = 0.94$). The four deleted lichens were rarely seen in the 40 census plots. A similar procedure examining the environmental variables did not identify variables that could be removed.

We also sought to determine if the biota formed identifiable assemblages and how these assemblages related to the presence of either embiid species. Cluster analysis was used to classify the sites based on percent similarity for plants or lichens. Such an inspection of similarity of sites based on biota might reveal qualities of the long-term nature of each habitat that could be missed by an assessment of the environmental variables that we selected to measure. Cluster analysis (using group-average linking) was conducted on the Bray-Curtis similarity matrices to allow identification of assemblages of lichens or plants based on percentage similarity (Fig. 2B). Cluster analysis reveals the degree to which samples resemble each other for certain traits, in this case, species.

We were also interested in determining if knowledge of the embiids might lead to a similar sorting of samples as did knowledge of environmental variables and other biota. Clarke and Green (1988) developed a technique for comparing rank similarity matrices that underlie the classification of samples, as represented in the schematic shown in Fig. 2B. For our study, we statistically compared the classification of samples based on presence/absence of the embiid to that based on the relevant food source (plants or lichens) and/or on environmental factors. For this nonparametric test, called ANOSIM, the null hypothesis states that there are no differences in community composition at sites with or without the embiids (Fig. 2B). The test statistic (R) gives a measure of how similar sites with the embiids are to sites without them. We evaluated a series of models using the ANOSIM test in a search for an embiid-environment match by comparing resulting significance levels, with a criterion of significance of $\alpha < 0.05$. The models used to generate similarity matrices that were compared with embiid presence/absence matrices were as follows: Environmental Variables model, which included all environmental variables measured in the field census; Lichen–Environment model, which included variables identified by the BIO-ENV algorithm as influencing the lichen community (solar radiation score of the south sun, distance from nearest coast and from SE coast, years since last fire, number of rocks [0.5–1 m], number of saplings and medium trees, percent cover by grass, and height of tallest tree); Lichen Species model, which was based on the percent cover of each lichen species at each site; Environment and Lichen Indices model, which included all environmental variables plus general indices describing the lichen community (species richness, species diversity, percent cover by lichens, and cover by cyanobacteria); Plant–Environment model, which included environmental

Fig. 2. Graphical summary of the statistical techniques provided by Primer-E used for ordination and clustering of census sites. (**A**) BIO-ENV procedure for determining the degree of correlation between biota and environmental variables. Boxes with rows and columns marked off as lines represent data arrays derived from the census; triangles enclosing a few black circles represent triangular similarity matrices where each circle represents the numerical ranked similarity score for a pair of census sites. (**B**) Depiction of the relationship between Bray-Curtis similarity matrices, SIMPER (an analysis of each species' contribution to dissimilarity), cluster analysis, nonmetric multidimensional scaling (labeled as 2D MDS), and the ANOSIM test. Illustrations are redrawn with permission from Clarke and Warwick (2001).

variables identified by BIO-ENV as correlating with the distribution of plant communities (slope, distance from the nearest coast and from the SE coast, years since last fire, number of rocks between 0.5–1.0 and >1.0 m); and Plant Species model, which was based on presence/absence of plant species (gleaned from the plant list and map of Sandercoe 1990) for each plant community encountered. The vegetation map showed that the 40 sites potentially supported 289 species of plants. Use of the map and a plant species list reduces the variability between the real census sites because, for the analysis, we assumed that all sites with the same designation on the vegetation map contained identical plant species. The models identified by ANOSIM as being correlated to the embiid presence/absence matrix were used to construct a two-dimensional MDS ordination map of the 40 samples (Fig. 2B). In each case, the stress values of the resulting ordinations were <0.2, implying that the two-dimensional pictures are potentially useful for interpreting the (dis)similarity among sites (Clarke and Warwick 2001).

A further analysis of the Bray-Curtis lichen matrix was used to determine which lichens characterized samples with and without the lichen-eater, *N. hardyi*. This Primer-E operation, called SIMPER, orders each species by their average contribution to the total average dissimilarity between all pairs of intergroup samples (Fig. 2B). Because we did not have abundance data for plant species, we did not use this analysis for *A. incompta*.

To determine if *N. hardyi* has preferences for particular lichens as food, a study site with many embiid colonies was selected near Arcadia (40 m altitude). The center point for the site faced SSE on a slope that also faced that direction. Eight rocks were randomly selected with the sample stratified by compass direction. For each rock, all colonies and an adjacent ruler were digitally photographed. Percent cover of lichens on the entire rock was estimated by eye. In the following descriptions, some lichens will be denoted by genus name only if the species was undescribed or unidentifiable or by an operational name that we made up if no identification was made.

The area of lichens covered by embiid silk was quantified using Photoshop (Adobe, San Jose, CA). Because silk is a thin covering, the lichens or blue-green algae could be seen through it and quantified. Photoshop has a tool for selecting an area of interest in a photograph and determining the proportion of the entire image that is taken up by that specific area. In this manner, the area of lichen covered by silk could be selected and quantified. After developing this method in the field, we discovered a reference describing an automated technique for applying Photoshop to analysis of lichen abundance (McCarthy and Zaniewski 2001), corroborating the efficacy of applying this software as a tool. The area of rock covered by lichens was compared with the area covered by embiid silk. Because the embiids spin silk to cover their feeding zones, we assumed that the coverage by silk reflects their choice of food. A χ^2 test was used to test whether embiids selected their food randomly from that available.

Results

Using Environmental Measures to Characterize Habitats. The 40 census sites were selected to represent a range from potentially heat-stressed, exposed sites to those in wetter, forested areas in gullies. ANOVA revealed that the sites differed in annual solar radiation scores computed using ArcView, with southern exposures showing the lowest scores (SE peaks and SE slopes) and sites exposed to the north showing the highest (NW slopes, gullies, and NW peaks; Fig. 3A; north sun: $F = 6.03$; df = 4, 35; $P < 0.001$; south sun: $F = 2.83$; df = 4, 35; $P = 0.04$; annual sun: $F = 6.03$; df = 4, 35; $P < 0.001$). Solar radiation scores from each site are not directly related to each other (north to south, total to north, etc.) because each site has a unique combination of exposures to the north and south. Topography greatly affects this relationship. For example, sites closest to the north coast were flatter and were not shaded during the summer or winter months, whereas sites near the peaks experienced shade at different times depending on direction of slope. Given these complications, one cannot predict how much solar radiation a site would experience overall just by knowing its exposure during part of the year.

Gullies, often located along creeks, were the most densely forested, as reflected in the higher number of small trees found there (Fig. 3B; $F = 3.74$; df = 4, 35; $P = 0.01$). Abundance for each of the two embiids did not differ significantly with respect to site types (Fig. 3C: $F = 1.9$; df = 4, 35; $P = 0.13$ and Fig. 3D: $F = 0.56$; df = 4, 35; $P = 0.64$). The two species showed distinct distributions with overlap: 8 sites had neither, 12 had both, 10 had only *N. hardyi,* and 10 had only *A. incompta* (Fig. 1).

Habitat Characteristics and *N. hardyi.* Stepwise multiple regression (with a stepping criterion of probability to enter of 0.25 and probability to leave of 0.15) identified lichen cover and 3 of the 17 environmental variables as yielding the best regression model using the available information to predict abundance of *N. hardyi* ($F = 6.9$; df = 4, 35; $P < 0.001$; $r^2 = 0.38$; Table 1). The environmental variables related to *N. hardyi* abundance were degree of southern exposure, number of large boulders, and number of saplings. If *N. hardyi* is evaluated as a function of just these environmental variables (ignoring lichens), r^2 drops to 0.24 ($F = 3.4$; df = 4, 35; $P = 0.01$). An inspection of how the cryptogams responded to the solar radiation scores showed that lichens (excluding cyanobacteria) decreased (Fig. 4; $F = 10.4$; df = 1, 38; $P = 0.003$; $r^2 = 0.19$), whereas cyanobacteria increased ($F = 4.7$; df = 1, 38; $P = 0.04$; $r^2 = 0.09$) as a function of total sun. The other measurements for solar radiation (north and south sun) were not significantly related to the cryptogams.

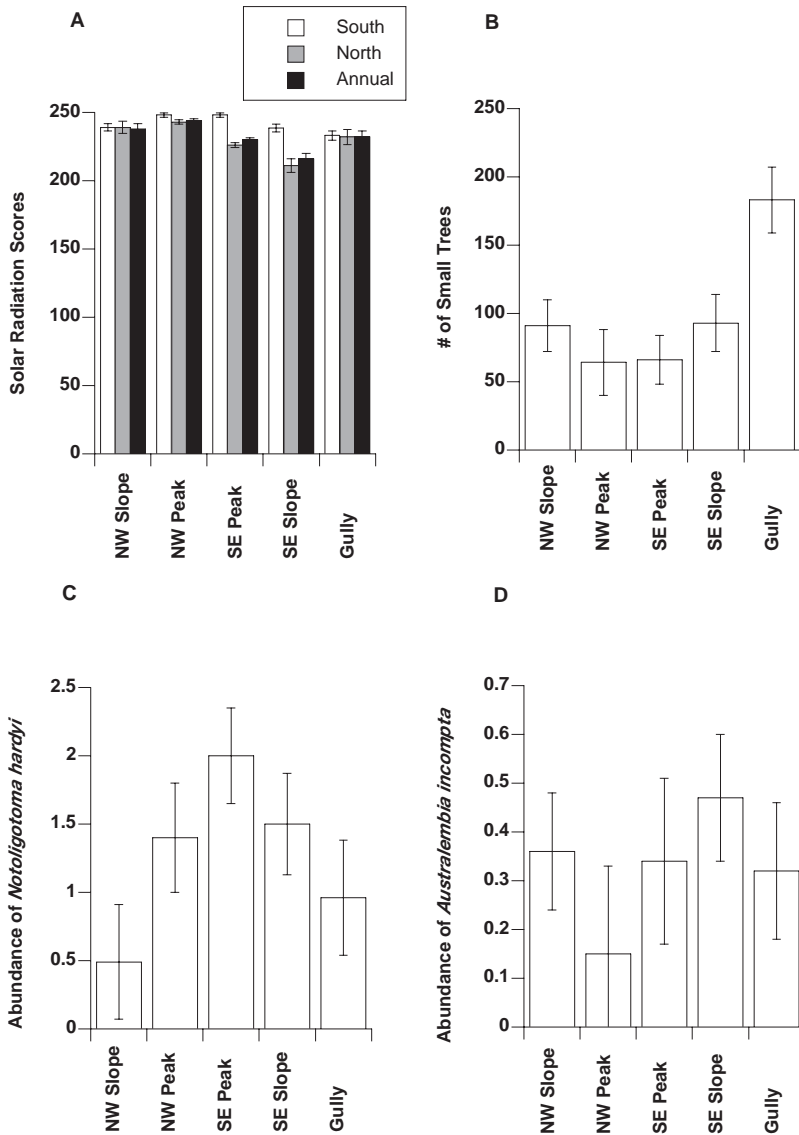Results of the six ANOSIM tests yielded similar information about the environment–*N. hardyi* con-

Fig. 3. Characteristics of census sites divided into categories: slopes (facing NW, $n = 12$; facing SE, $n = 10$), peaks (SE peak, $n = 5$; NW peak, $n = 5$), and gully ($n = 8$). Data are plotted as means, with error bars showing SE. (A) Sun scores for the different site types. (B) Number of small trees as a function of site type. Abundance of (C) *N. hardyi* and (D) *A.* as a function of site type.

nection. Sorting census sites using the Environment and Lichen Indices model was most similar ($P = 0.002$) to using the matrix based on presence/absence of *N. hardyi* (Table 2). In contrast, using the Lichen Species model ($P = 0.07$) did not yield a significant match. Therefore, environmental data plus general characterization of the lichen resource is more useful for identifying the embiid's habitat requirements than knowledge of particular lichen species or of just the environmental variables ($P = 0.02$).

An ordination plot based on a Bray-Curtis similarity matrix of sites using the Environment and Lichen Indices data reveals that a clustering of census sites to some degree reflects our original categorization of

sites (north-facing slopes, south-facing slopes, peaks, and gullies; Fig. 5). When the relative abundance of *N. hardyi* is superimposed onto the ordination map, a trend appears; sites in the center support the most colonies. Moving away from the center takes one out of the apparent niche of this animal. Sites with a northern exposure, mostly to the left of the ordination map, were the least likely (25%), and peaks, generally clustered in the center, were most likely (90%) to support colonies. Depicted in small oval panels placed around the ordination map are the variables detected by stepwise multiple regression as being related to the abundance of the embiid. The sites are variable for these traits, but trends appear; sites more likely to have

Table 1. Stepwise multiple regression results relating abundance of *N. hardyi*, tested as a function of 17 environmental variables plus cover by various cryptograms, and *A. incompta*, tested as a function of environmental variables

Source	Estimate	F	P
Notoligotoma hardyi			
($r^2 = 0.38$; $F_{4,35}$)			
Intercept	−12.64		
Lichen cover	2.66	10.6	0.003
Sun from south	0.05	10.2	0.003
Saplings	−0.004	3.43	0.07
Large rocks	0.007	1.78	0.19
Australembia incompta			
($r^2 = 0.40$; $F_{6,39}$)			
Intercept	−2.42		
Sun from south	0.016	7.18	0.01
Altitude	−0.002	5.11	0.03
Small rocks	0.002	6.02	0.02
Sun from north	−0.004	2.18	0.15
Distance from coast	−0.07	0.72	0.40
Distance from SE coast	0.043	0.79	0.38

Table 2. Test statistic (*R* value) of ANOSIM test comparing a matrix of similarity for 40 field samples based on the presence or absence of each embiid species to rank similarity matrices of the samples based on a variety of abiotic and biotic measurements

Data used in MDS plots (Stress value of 2-D plot)	*N. hardyi* (R)	*A. incompta* (R)
Environmental variables model (0.2)	0.098[a]	0.16[b]
Lichen-Environment model (0.19)	0.093[a]	0.043
Lichen Species model (0.16)	0.06	0.08[a]
Environment and Lichen Indices model (0.2)	0.126[b]	0.047
Plant-Environment model (0.15)	0.06	0.05
Plant Species model (0.01)	0.048	0.21[b]

[a] Significant at $\alpha < 0.05$.
[b] Significant at $\alpha < 0.01$.
See Fig. 2B for graphical illustration of the ANOSIM technique and the text for details on sources of data for each model.
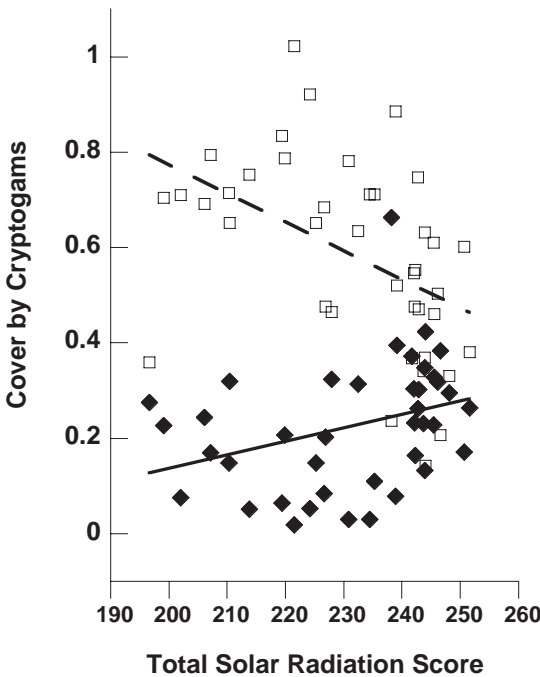
embiids tended to have a stronger southern exposure, a moderate number of large rocks and saplings, and moderate lichen cover. Also depicted is cover by the lichens detected by SIMPER analysis (see below) as being more common where the embiid was (dubbed "lichens associated with the embiid") and where the embiid was not (moss and red film). Having lush lichens does not necessarily mean the embiids are present, as evidenced by the high level of lichen cover

Fig. 4. Cover by lichens (open squares; dashed line) and cyanobacteria (solid diamonds; solid line) as a function of total solar radiation. Proportion cover of rocks by the cryptograms was transformed by the angular transformation before analysis and is plotted in that form.

in sites positioned to the right of the ordination map, away from the apparent hotspot for the embiid. In contrast, scant lichen cover does correlate with the absence of the embiid, as seen for sites on the left of the ordination. Sites categorized as north-facing slopes were especially likely to have little lichen cover and no embiids.

The contribution each lichen species made in explaining the similarity between sites with and without *N. hardyi* (Table 3) was computed using SIMPER (Fig. 2B). The overall average dissimilarity between sites was 54.55. Five rare lichens were omitted from the Table 3 because they contributed <3.5% each to the differences between sites. Two fairly common species (*Pertusaria hypoxantha* Malma and cyanobacteria) were also omitted because they were not identified by SIMPER as of significance in explaining differences between sites. Fourteen species, including lichens ($n = 12$), moss ($n = 1$), and an unidentified red film ($n = 1$), explained 92% of the variation between the sites with and without the embiid. This high number of species needed to sort sites reflects the complexity of the photosynthetic community encrusted on the granite boulders on the island and the lack of an exact match between the embiid and any one species. Moss and red film were more abundant in sites without the embiid. The embiid was most closely matched to the lichen, *B. substellulans*.

Notoligotoma hardyi displayed a feeding preference for particular lichens (Fig. 6; $\chi^2 = 66.8$; df = 8; critical value at α of 0.05 = 15.5). Silk covered more of two of the nine possibilities than expected by chance and was less well developed on the other seven choices than expected by chance. *B. substellulans* accumulated the most silk (3,604 cm^2) at the site, two times more than expected by chance alone (1,574 cm^2).

Habitat Characteristics and *A. incompta*. Stepwise multiple regression identified both solar radiation scores, altitude, number of small rocks, and distance from the coast as forming the best fit model for predicting *A. incompta* (Table 1; $F = 8.01$; df = 6, 38; $P <$
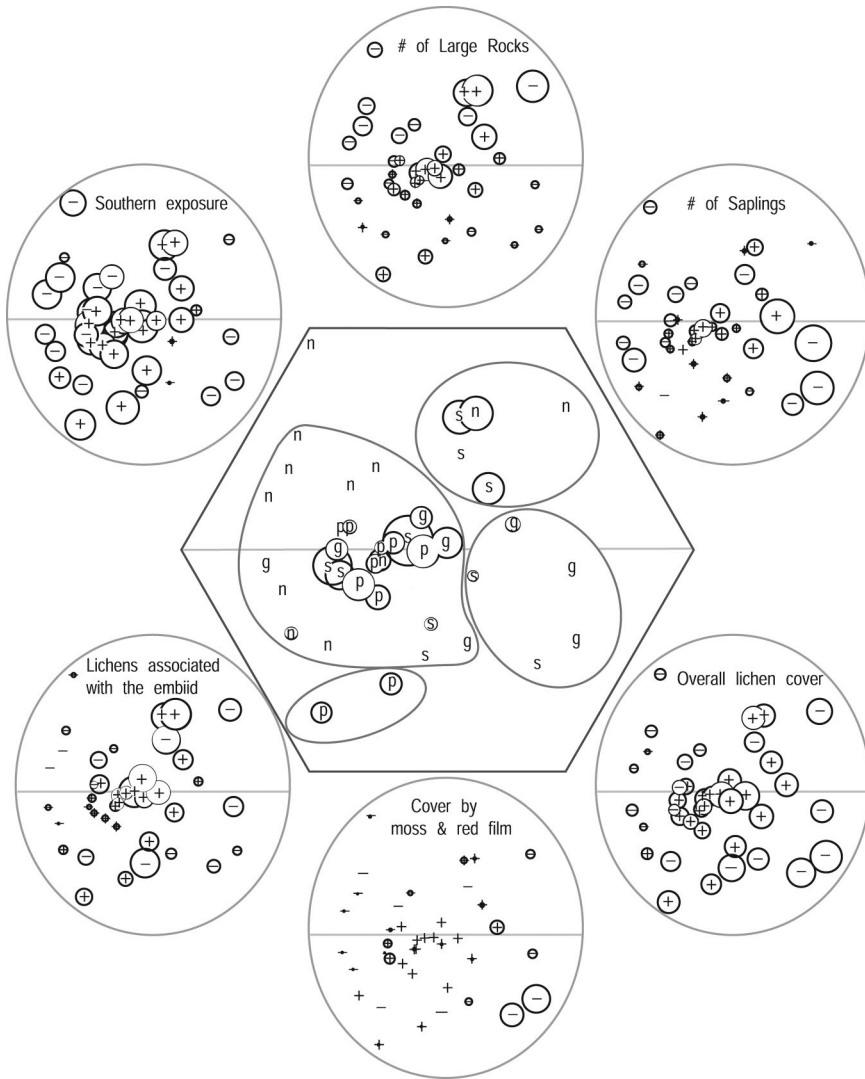
Fig. 5. Relationship between the presence and abundance of *N. hardyi* and the Environment and Lichen Indices model. The central hexagon shows a nonmetric MDS ordination (stress value = 0.2) of the 40 census sites, where the letters indicate type of site: n, north-facing slope; s, south-facing slope; p, peak; g, gully. The embiid abundance data were not used in the construction of the ordination map but rather were added to the illustration to allow for comparison. The size of the bubble (open black circles) surrounding each letter represents the relative abundance of the embiid at the site. If no bubble appears, the species was absent. Cluster analysis based on Euclidean distance was used to determine clusters (minimum distance of six) within the plot. The pale gray lines encircling four groups of samples represent the clusters. Each of the six ovals ringing the outside of the hexagon shows informative environmental variables superimposed onto the ordination of the Environment and Lichen Indices model. Symbols represent each census site as either having (+) the embiid or not (−); the sizes of the bubbles reflect the relative number, percent cover, or intensity of the variable named within the oval. The pale gray line on each graph acts as a guideline.

0.001; $r^2 = 0.40$). The ANOSIM tests were significant when the similarity matrix based on presence/absence of *A. incompta* was compared with three of the habitat similarity matrices: the Environmental Variables model ($P = 0.002$), the Lichen Species model ($P = 0.03$), and the Plant Species model ($P = 0.005$). The model that generated the lowest *P* value in the ANO-SIM test (Environmental Variables model) was used to produce a nonmetric MDS map of the census sites

(Fig. 7). Sites with *A. incompta* tend to be central and slightly below center on the ordination. Sites with the embiid tended to be closer to the coast, rockier, and at lower altitude. The solar radiation scores, identified by the regression analysis as important for the embiid, are not shown because they did not reveal obvious patterns for sorting census sites. Grasslands and *Eucalyptus* woodlands are shifted to the left on the map, in the direction away from the coast, higher altitude,

Table 3. Dissimilarity between 40 sites based on cryptogams on granite boulders (see text for details); underlined numbers indicate where the autotroph was more abundant, either in sites with or without *N. hardyi*

| Cryptogams growing on rocks at sites	Average abundance with *N. hardyi*	Average abundance without *N. hardyi*	Contribution to dissimilarity of sites (%)	Cumulative contribution (%)
Buellia substellulans Zahlbr.	<u>3.07</u>	2.42	15.69	15.69
A reddish film[a]	1.07	<u>1.66</u>	12.44	28.13
Pyxine consocians Vainio	<u>1.07</u>	0.99	11.07	39.20
Buellia sp. (olive color)[b]	<u>1.20</u>	0.73	10.76	49.88
Caloplaca leptozona (Nyl.) Zahlbr.	<u>1.05</u>	0.71	8.28	58.16
Australiaena streimannii Matzer, Mayrhofer and Elix	<u>0.43</u>	0.22	4.93	63.09
Moss[a]	0.30	<u>0.41</u>	4.34	67.43
Parmotrema queenslandense Elix	<u>0.44</u>	0.19	4.30	71.73
Peltula clavata (Kremp.) Wetmore	<u>0.44</u>	0.09	4.06	75.79

[a] Not identified.
[b] An undescribed species.

and recently burned. These plant communities did not support many colonies of *A. incompta.*

The Plant Species model is the simplest of the models evaluated with ANOSIM because it assumes each sample is one of seven types. This model strongly correlated, as mentioned above, with the presence/absence matrix of the leaf-litter embiid *A. incompta* but was not related to the lichenivore. Cluster analysis of the census sites defined by the presence and absence of plant species generated two major groupings: (1) grassland with sparse trees, *Eucalyptus* woodland, and *Acacia* shrubland; and (2) vine forest, low vine forest, coastal forest, and semideciduous woodland (Fig. 8). Eighty percent of sites ($n = 20$) in one well-defined cluster had the webspinner, whereas only 30% of sites ($n = 20$) in the other cluster did.

Discussion

Process of Embiid-Environment Matching. This investigation involving two distinct, complementary statistical approaches identified elements of habitat specialization for two sympatric species of embiids. In general, ordination and the analysis of similarity matrices revealed a level of association among biota (plants, lichens, or embiids) and environmental factors that shape those associations, and the regression analyses identified distinct habitat requirements for each embiid species. The analyses largely corroborated one another. We now address the following question: did our investigation yield the answer to the question of how embiids fit into their environment?

By applying statistical procedures of Primer-E, we systematically winnowed the large number of variables into smaller sets to search for species-specific habitat characteristics for the embiids. This process evaluated underlying environmental factors that may influence the quality and diversity of primary producers (such as lichens and plants), which are the food resources for the embiids. The process also asked the questions as to whether embiid populations reflect underlying distributions of lichens or plants or whether they are affected by environmental factors in a distinct manner. Overall, the statistical results sug-
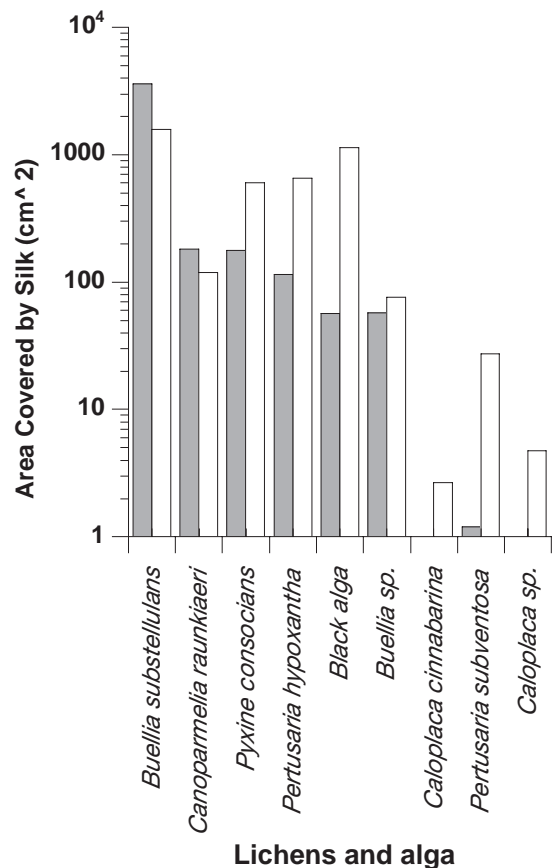
Fig. 6. χ^2 results for field observations of preference by *N. hardyi* for lichens ($n = 8$ species) and a black alga ($n = 1$ species). Area covered by silk is shown as expected values (open bars), based on the availability of the potential food resource on the rocks, compared with observed values (shaded bars), based on area covered by embiid silk. Eight rocks were surveyed at one location near Arcadia on Magnetic Island. The y-axis is a log scale to allow presentation of the full range of values. As such, comparing the heights of the bars can be misleading. For example, the difference between observed and expected for *B. substellulans* is more than twofold even though the heights of the bars appear almost the same.
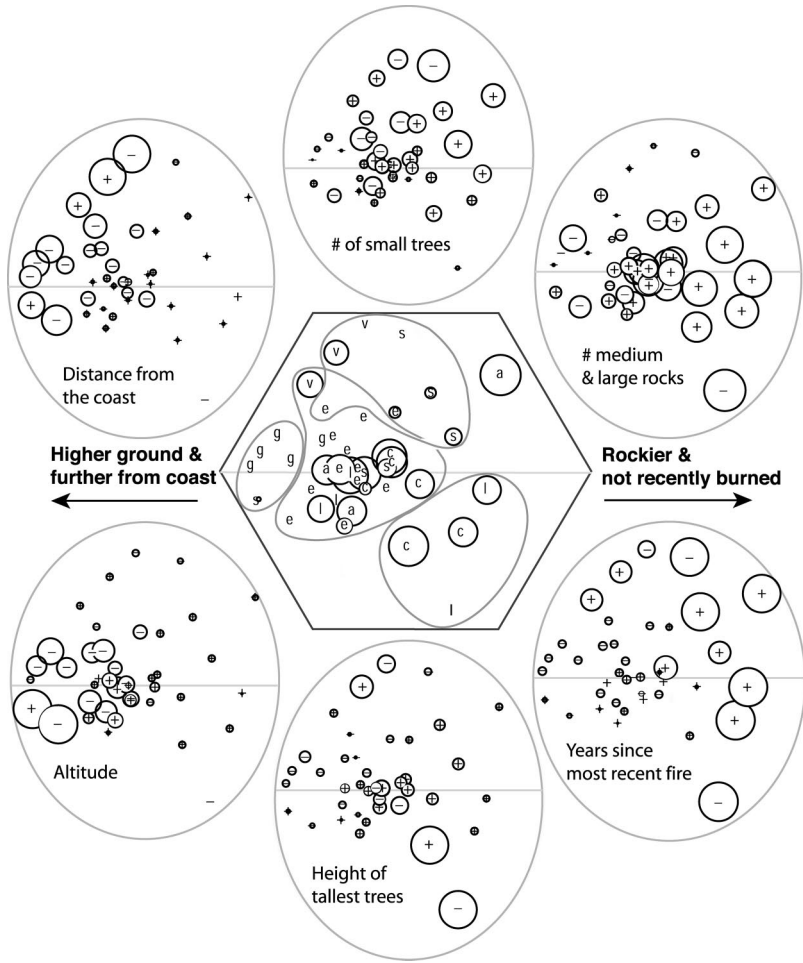
Fig. 7. Relationship between the presence and abundance of *A. incompta* and the Environmental Variables model. See Fig. 5 for explanation of the symbolism in the illustration. The central hexagon shows the nonmetric MDS ordination (stress value = 0.2) of the 40 census sites, where the letters indicate vegetation types at each site: a, *Acacia* shrubland; c, coastal forest; e, *Eucalyptus* woodland; g, grassland with sparse trees; l, low vine forest; s, semideciduous forest; v, vine forest. Cluster analysis based on Euclidean distance was used to determine clusters (minimum distance of six) within the plot.

gest that habitat specialization can be inferred for each embiid species despite the moderate degree of overlap between the ranges of the two species (30% of the 40 sites had both species).

Interpretation of results will be proposed below for each embiid species on Magnetic Island. Of cautionary note is the recognition that some embiids vary their microhabitat choice depending on climatic conditions. For example, *Oligotoma saundersii* (Westwood) (Oligotomidae) lives under rocks in dry regions and on tree bark in humid areas (Ling 1934–1935). On Magnetic Island, no such variability appeared, presumably because the climate is relatively consistent across the small island. *N. hardyi* was always found in association with lichens. They were commonly seen on rock faces and within rock crevices and were also found, although rarely, on tree bark that supported lichens. *A. incompta* was only found in leaf litter, even in sites where the litter hugged granite boulders festooned with *N. hardyi* colonies.
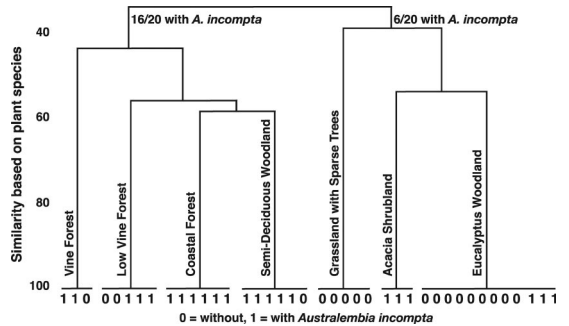

Fig. 8. Cluster analysis based on presence/absence of plant species for seven vegetation types discovered at 40 census sites on Magnetic Island. The dendrogram is the result of hierarchical clustering (using group-average linking) based on a Bray-Curtis similarity matrix. The 40 census sites are coded to show whether *A. incompta* was found at a site (1) or not (0).

Notoligotoma hardyi. Not only does *N. hardyi* feed on lichens, but its presence can also be linked to environmental factors that seem to affect lichen abundance and quality. The food resource for *N. hardyi* is diverse; they were seen feeding on many species of lichen. Perhaps this is why a relationship between the embiid and a model based only on lichen species diversity (Lichen Species model) was not enough to understand the embiid's distribution. *N. hardyi* thrives, however, on certain lichens; *B. substellulans* are most notable. This lichen stood out as preferred in the observational field study of embiid feeding behavior and was highlighted by the SIMPER analysis as being the most significant lichen in explaining differences between sites with and without the embiid.

Notoligotoma hardyi colonies were rare in places with less lichen cover, which was the variable identified by stepwise multiple regression model as among the most significant for predicting their abundance. Lichen cover was also important in sorting census sites by nonmetric MDS ordination (Fig. 5). *N. hardyi* were rarely seen in sites with strong northern exposure, a characteristic that relates to low lichen availability and possibly to stressful conditions during hotter months. Analysis of single variables corroborates these observations; *N. hardyi* abundance was positively related to lichen cover but negatively related to an increase in cyanobacteria found encrusted on granite even in very exposed sites. This autotroph was typical of all sites, almost always on the tops of the rocks. In exposed locations, even the sides of the boulders were stained black by its presence. It seems possible that cyanobacteria is an inadequate food source for the embiid and/or that the rock surfaces where it thrives (and most lichens disappear) are too hot. Temperatures of such rocks recorded for a separate study of heat stress often reached 50°C in May 2001—25°C hotter than the ambient air temperature (unpublished data). These temperatures will likely kill most insects, and yet, it wasn't even the hottest time of the year.

At the other extreme in habitat type, forested gullies displayed high scores for annual solar radiation, but their location along creek beds provided the water and humidity necessary for development of thick vine forests. Lichens at these sites tended to be dull in color, as reflected in the operational names we gave them in the field (such as brown, drab, pale green). Perhaps an indicator of shade, mosses, and the unidentified red film, although generally rare, were most common in the forested sites. Many lichens in more open areas contrasted more with the background (such as chartreuse, orange, and white). Embiids were more common where the lichens were more colorful, but it is not known if the pigments affected the quality of lichens as food.

In summary, the positive correlation between *N. hardyi* abundance and a strong southern exposure and the negative relationship between lichen cover and total solar radiation suggests that the association between the two life forms and their environment is complicated by light and heat. *N. hardyi* colonies facing south may experience less sun and heat overall because the sun shines from north of the island most of the time. Other features of the environment are clearly affecting the habitat, because knowing the intensity of the sun when in the north did not allow us to predict the abundance of the embiid. Perhaps because lichens were influenced by sun in a different manner from that of the embiid, multiple lines of evidence are more informative for understanding the insect's habitat. As such, by characterizing the lichen associations with ecological indices (diversity, richness, and cover) and by adding such information to a multivariate model, we sharpened our ability to predict embiid abundance beyond just knowing environmental measures. Correlation cannot identify cause and effect, but we feel we have identified important factors related to embiid habitat selection. These factors seem closely related to food quality and to solar radiation.

Australembia incompta. *Australembia incompta* abundance is related to features of terrain (rockiness) and topography (exposure to the sun, altitude, and distance from the coast) and to fire history (see below). Support for this interpretation comes from the stepwise multiple regression model and their apparent association with particular plant communities, as highlighted in the cluster analysis of plant species.

Overall, *A. incompta* habitat seems defined by traits that relate to fire ecology. Relevant factors range from aspects of terrain to plant community structure. *A. incompta* was more likely to be present in sites not recently burned, with a denser canopy and more trees, less grass, more rocks, and closer to the coast. These traits are consistent with the supposition that the leaf litter embiid survives better in areas that are less prone to fires, such as those with large boulders that can provide refuge between boulders where leaf litter accumulates and flames cannot reach. Finding less grass and more trees is also consistent with the notion that this embiid is more abundant in areas not recently burned. Not only might fire kill the embiids, but the fire-prone sites, typified by fewer understory trees and more grass, may not provide enough leaf litter to support populations of *A. incompta.* This might be true even if they did rapidly recolonize after a fire, as the majority of detritivores were shown to do in a 4-yr study of another fire-prone region of Australia (Abbott 1984).

The two vegetative types with the fewest *A. incompta* colonies are known to be fire prone (*Eucalyptus* woodland and grassland with sparse trees) (Gill et al. 1990, Williams et al. 1999), a finding that is consistent with the contention that fire hinders the development of embiid populations. These two plant communities share many plant species, as reflected by their degree of similarity as shown by cluster analysis (Fig. 8). Grasslands may mark areas of recent fires and are also more vulnerable because flammable grasses, which can perpetuate cycles of fire in Australia, often invade (Gill et al. 1990).

Another possible cause of low populations of *A. incompta* in these habitats is the quality of leaf litter. *Eucalyptus* was not unique to these two habitats, but

it was dominant. *Eucalyptus* may not be as palatable as other species, such as kapok (*Cochlospermum gillivraei*), a deciduous tree common to the other forested habitats on the island. Crumpled, dead kapok leaves were often occupied by numerous *A. incompta;* the presence of these leaves may have allowed populations to build up in habitats such as the semideciduous woodland. Despite their strong oils and toughness, *Eucalyptus* leaves were also used by *A. incompta* as food and as dwelling places (unpublished observation). Ross (2000) reported that species of the family Australembiidae feed almost exclusively on layered, dead *Eucalyptus* leaf litter. Although this was not the case for many *A. incompta* on Magnetic Island, some colonies were found within *Eucalyptus* leaves that they stitched together with silk, suggesting that such leaf litter is appropriate food and shelter. Therefore, it is more likely that other factors, such as fire or low humidity, may be inhibiting their populations in *Eucalyptus*-dominated habitats on the island.

Other testable hypotheses emerge from an inspection of results. For example, distance from the coast may affect moisture in the air. Being at the coast may allow the embiids to better cope with the combination of heat and lack of humidity during the dry season. Higher altitude sites, especially the peaks, supported fewer *A. incompta:* 7 of 10 peaks had none. Ridges are known to be drier (and more prone to fire) than lowlands in the tropical zone where the island is situated (Gill et al. 1990). At this point, it is not possible to identify a single cause of their distribution: whether it is heat because of exposure to the sun, leaf litter quality, or fire history. All of these factors are probably related, and hence, the most parsimonious solution at this time for defining *A. incompta* habitat is a multivariate model based on environmental traits that generally relate to the distribution of plant species on the island and to topography.

Conclusion

Of all the insect orders, embiids are among the least studied, perhaps because of their secretive nature. They are especially cryptic in temperate and subtropical regions, where they often reside beneath rocks or within litter. On Magnetic Island, the lichenivore was actually conspicuous, because its presence was marked by copious silk spun on the large boulders that form a major part of the landscape. Such conspicuousness afforded us the opportunity to evaluate questions of habitat selection, the first study of its kind for the order Embiidina. We suggest that *N. hardyi* may be one of the easiest insects to survey in the field. We were able to quantify abundance merely by looking at the surfaces of large boulders and by tallying up the distinct patches of silk. As such, we did not need nets, traps, or black light to conduct this survey.

Ours is not the first study of lichen-eaters. A diversity of animals feed on lichens, including bark lice (Turner and Broadhead 1974), mites (e.g., Materna 2000), chironomid larvae (Delettre 2000), caterpillars (Sigal 1984, Callaghan 1992), snails (Baur et al. 1994),

flying squirrels (Zabel and Waters 1997), and reindeer (Ihl and Klein 2001; see Gerson and Seaward 1977 for a review of lichen–invertebrate associations). Recently, lichens in colder climes have attracted the attention of ecologists (e.g., Pintado et al. 2001); one such author investigated the association between communities of lichens and mites (e.g., Colloff 1988). Environmental variables, such as distance from the coast and altitude, found to influence lichens also seemed to influence mite communities. This study contrasted with ours because lichens supported many sympatric species of mites, whereas we located only one lichen-feeding embiid on Magnetic Island.

A study of lichens that is similar to ours in intent and in method was recently conducted on reindeer and muskoxen in Alaska (Ihl and Klein 2001). As for the Magnetic Island embiids, these two ungulates overlapped in their ranges. Ihl and Klein employed a multivariate analysis to evaluate the match between the habitat and the two species. They identified influential factors: lichen cover was positively related to both animal populations. Their populations were also affected by quality of snow and cover by graminoids. Ihl and Klein are seeking ways of improving techniques for wildlife management by understanding the dynamics of natural resources. Our ultimate goal, in contrast, is to tie behavioral and physiological traits of embiid species to their distinct habitats. We hope to establish an ecological context for such features as adaptation to heat, colony composition and maternal care, the evolution of winglessness in males, and silk, which varies in amino acid composition from species to species (unpublished data). To achieve this goal, we plan to apply the field and statistical methods developed during this project to other habitats.

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