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Revisiting the Ants of Melanesia and the Taxon Cycle: Historical and Human-Mediated Invasions of a Tropical Archipelago

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ABSTRACT: Understanding the historical evolution of biotas and the dynamics of contemporary human-mediated species introductions are two central tasks of biology. One hypothesis may address both—the taxon cycle. Taxon cycles are phases of range expansion and contraction coupled to ecological and evolutionary niche shifts. These historical invasion processes resemble human-mediated invasions in pattern and possibly mechanism, but both the existence of historical cycles and the roles of recent introductions are in question. We return to the system that originally inspired the taxon cycle—Melanesian ants—and perform novel tests of the hypothesis. We analyze (i) the habitat distributions of Fiji's entire ant fauna (183 species), (ii) ecological shifts associated with the in situ radiation of Fijian *Pheidole* in a phylogenetic context, and (iii) the ecological structure of a massive exotic ant invasion of the archipelago. Our analyses indicate lineages shift toward primary habitats, higher elevation, rarity, and ecological specialization with increasing level of endemism, consistent with taxon cycle predictions. The marginal habitats that historically formed a dispersal conduit in the Pacific are now mostly replaced by human-modified habitats dominated by a colonization pulse of exotic species. We propose this may represent the first phase of an incipient global cycle of human-mediated colonization, ecological shifts, and diversification.

Keywords: taxon cycle, island biogeography, invasive species, Formicidae, Pacific islands, *Pheidole*, Fiji.

Introduction

Fifty years ago, E. O. Wilson synthesized his work on the Melanesian ant fauna by proposing a hypothesis for biogeographic dynamics in space and time: the taxon cycle (Wilson 1959, 1961). In general terms, taxon cycles arise when the evolution of certain phenotypes and ecological strategies promote phases of range expansion, but large ranges are unstable and fragment into a complex of localized species. This range contraction phase is driven by ecological and evolutionary shifts away from the phenotypes that initially promoted range expansion. Biogeographic dynamics thus follow regular cyclical pathways, and certain phenotypes are channels for dispersal and subsequent diversification.

The hypothesis is notably integrative; it links ecological and evolutionary pattern and process across scales from local communities to biogeographic regions. Wilson's papers stimulated conceptual advances in the field (Brown and Lomolino 1998; Whittaker 1998; Lomolino and Brown 2009), and the idea has been applied usefully to other taxa and geographic areas over the years (Ricklefs and Cox 1972, 1978; Roughgarden and Pacala 1989; Brown and Lomolino 1998; Mayr and Diamond 2001; Ricklefs and Bermingham 2002; Cook et al. 2008; Gillespie et al. 2008). However, it was a later theory—the equilibrium theory of island biogeography (ETIB; MacArthur and Wilson 1963, 1967)—that became the new paradigm for biogeography. The ETIB was much simpler in construction and narrower in scope but had the advantage of a quantitative formulation and was readily testable with available data. The complex story of the taxon cycle was not testable in a convincing way with the data and methods available at the time, even for Wilson's ants (Whittaker 2004). The existence of taxon cycles has been repeatedly questioned over the years (Pregill and Olson 1981; Losos 1992; Ricklefs and Bermingham 2002; Dexter 2010), and today it is a marginal idea in ecology and evolution.

However, in many ways the taxon cycle is more relevant in the modern area of synthesis in biodiversity science. Ecological and evolutionary perspectives are increasingly being integrated across scales of space and time, and ad-

vances in molecular methods, phylogenetics, statistical in-ference, geographical information systems, and the large-scale aggregation of biodiversity data give us new tools for analyzing biodiversity pattern and inferring complex pro-cesses. Additionally, historical taxon cycles resemble con-temporary invasions in pattern and possibly mechanism, raising the possibility that reciprocal insights can be gained from the study of both (Brown and Lomolino 1998; Sax and Brown 2000; Ricklefs and Bermingham 2002; Ricklefs 2005).

Here, for the first time since Wilson's landmark studies, we revisit the ants of Melanesia and test predictions of a historical taxon cycle with one of the most extensive data sets ever compiled for an insular ant fauna. We find the system in the midst of an ongoing massive invasion of exotic ants into the Pacific islands (Wilson and Taylor 1967; McGlynn 1999; Holway et al. 2002). We analyze how both these recent arrivals and the native fauna are orga-nized across the island landscape of the Fijian archipelago.

The Taxon Cycle Hypothesis

A taxon cycle begins when a geographically restricted lin-eage evolves phenotypes or ecological strategies that ini-tiate a phase of range expansion. For Melanesian ants, this involves an adaptive shift from interior primary forest hab-itats to marginal high-disturbance habitats such as coasts and riverbanks in the large diverse "source" areas (i.e., Southeast Asia and New Guinea). Wilson viewed the in-tensity of interspecific competition in the interior forests as occasionally driving a species to make this adaptive shift into marginal habitats. These marginal habitats facilitate oceanic dispersal through rafting and colonization of more remote archipelagoes. Ant phenotypes adapted to open, disturbed habitats possibly include generalized ecological strategies, flexible diet and nesting requirements, or higher thermal tolerance (Wilson 1959, 1961; Torres 1984*a*, 1984*b*).

In the second phase, these expanding species are initially more ecologically successful in novel areas than they were in their source area. They release out of the marginal hab-itats and are more successful than resident endemic spe-cies. Wilson (1959, 1961) proposed this initial success was due to the competitive dominance of species originating in highly diverse source areas over "naive" species that evolved in less diverse areas (i.e., smaller and more remote islands). This leads to a unidirectional flow of lineages from diverse to depauperate geographic areas.

After range expansion and initial ecological success, eco-logical and evolutionary dynamics in the novel area result in a decline phase. The widespread species shifts away from the high-disturbance coastal habitat to the upland interior and evolves towards an endemic syndrome of low pop-ulation density and increased ecological specialization. Wilson (1959, 1961) viewed this decline phase as occurring because selection pressures would adapt the colonizing species to the much larger area of the interior forest, pos-sibly pushed along by competitive pressure from newly arrived expanding taxa in the marginal habitat. As the species shifts away from marginal habitats across the range, gene flow is limited and speciation may transform a single widespread species into many localized endemic allospe-cies. Eventually, the now-endemic lineage may persist and diversify in the interior forest and/or eventually become extinct as it is replaced by the progression of new lineages through the cycle.

Wilson proposed interspecific competition as the driv-ing mechanism behind the cycle, while Ricklefs and Cox (1972) emphasized the role of "vertical" interactions be-tween a species and its predators and pathogens. In this latter view, a species may enter an expanding phase after a coevolutionary escape from natural enemies. The initial success after colonization may be due to further geo-graphic escape from natural enemies and competitors or even the transfer of pathogens from the colonists to the susceptible local fauna. Finally, the decline phase would be explained by the counteradaptation of the local fauna to the now-abundant new arrival. Other variations em-phasizing different mechanisms have appeared in the lit-erature (Roughgarden and Pacala 1989; Taper and Case 1992; Matsuda and Abrams 1994). However, in general the mechanisms driving taxon cycles are not well under-stood, even in the Caribbean bird system where evidence for the taxon cycle pattern is most compelling (Ricklefs and Bermingham 2002).

Despite the conceptual advances contributed by Wil-son's analysis, the evidence for the complex historical sce-nario he described was not strong (Whittaker 2004). His key observation was the differences in community com-position along a disturbance gradient in New Guinea, with marginal habitats composed of widespread species and in-terior habitats composed of endemics (see table 2 and fig. 9 in Wilson 1959). However, the data were generated by unknown spatial and numerical sampling regimes, the ob-served patterns were not statistically significant and could have been driven by the idiosyncrasies of a few species, and the species classified in the subfamily Ponerinae in 1959 are a small fraction of the fauna and are now known to be distributed across the ant phylogeny (Brady et al. 2006; Moreau et al. 2006).

Furthermore, the role of exotic species in the system, a major component of Indo-Pacific ant faunas (Wilson and Taylor 1967; McGlynn 1999), is entirely unknown. Like historical cycles, human-mediated invasions (Elton 1958; Williamson 1996) often involve the geographic spread of species adapted to high disturbance, high connectivity hab-

itats. Like historical cycles, establishment and subsequent ecological success of a new arrival may be a function of local diversity (i.e., " biotic resistance") and/or escape from natural enemies. Furthermore, like natural colonists, introduced species may experience an eventual decline as new waves of invaders arrive or the local fauna adapts to the new arrival.

In the Melanesian ants, there is an opportunity to analyze a potential historical taxon cycle and ongoing human-mediated invasion in the same system. Here we ask two questions focusing on the Fijian archipelago using data generated by a new comprehensive inventory of the fauna (Sarnat and Economo, forthcoming). First, does the native fauna, which has been colonizing the archipelago since the Miocene (Lucky and Sarnat 2010), show evidence of a historical taxon cycle? Second, does this same framework apply to the exotic species brought by Europeans in the last several hundred years—are they simply the next colonization pulse?

Testing the Taxon Cycle

The taxon cycle hypothesis proposed by Wilson and outlined above is a complex narrative with many subcomponents, and it is beyond this or any single study to confirm or reject it in one stroke. Moreover, it is likely that some components of the model are more correct than others. In this study we test predictions for the habitat distributions of the entire ant fauna of the Fiji archipelago. We complement this community-level study with a case study of ecological and evolutionary shifts in one genus, *Pheidole*, in a phylogenetic context. We do not test the assertion that lineage movement is biased from high- to low-diversity systems or in any particular geographic direction.

The taxon cycle predicts that after colonization and over time, ant lineages (i) shift from disturbed to primary forest habitats, (ii) shift from low- to high-elevation habitats, and (iii) decline in commonness. Such shifts should leave a signature in the distribution of species across habitats; increasing levels of endemism should be correlated with the ecological changes described above. We test these predictions with data on the entire ant fauna of the Fijian islands. If species from different endemism classes have contrasting distributions across habitat types in this particular way, the taxon cycle hypothesis will be supported. The taxon cycle will not be supported if habitat distribution is either unrelated to endemism class or if they exhibit one of the many biologically plausible nonrandom patterns that would be inconsistent with the hypothesis. For example, endemics could have the widest habitat distribution and have the highest abundance, perhaps because they are the best adapted to the local environment of Fiji.

Or, under a purely stochastic "neutral" hypothesis (Hubbell 2001), older lineages should on average be more abundant than new arrivals because stochastic extinction will selectively cull species that have not "drifted" to high abundance (Rosindell and Phillimore 2011).

If ecology-endemism correlations are consistent with the taxon cycle, there remains the question of whether they represent phases of a temporal sequence. For example, species adapted to disturbed lowland habitats may have large ranges because those habitats facilitate dispersal, but they do not shift over time into the uplands and eventually acquire the syndromes associated with endemic species (Dexter 2010). In this scenario, ecological niche is conserved, and species colonize interior habitats on islands directly from similar habitats in source areas. Higher-elevation interior species could have restricted ranges simply because dispersal is too limited to maintain gene flow but not limited enough to preclude the occasional colonization event.

Phylogenetic approaches can differentiate between these alternative hypotheses by testing for postcolonization niche shifts and adaptation into high-elevation forest lifestyles. We test this prediction in the Fijian *Pheidole* (20 spp.), for which phylogenetic, ecological, morphological, and behavioral data are available. We synthesize and extend previous work on Fijian *Pheidole* (Sarnat 2008; Sarnat and Moreau 2011; Sarnat and Economo, forthcoming) and interpret it from the perspective of the taxon cycle. Fiji is home to one of the most aberrant, spectacular, and threatened *Pheidole* forms in the world: the *Pheidole roosevelti* group radiation. The taxon cycle predicts this radiation arose in Fiji from generalized ancestors, and trends toward ecological and morphological specialization are associated with in situ habitat shifts, loss of dispersal ability, and declines in density.

Material and Methods

Study System and Biodiversity Data

Over the last several years we have conducted a broad inventory of the Fijian ant fauna. We point-mounted and examined more than 10,000 ant specimens, representative of ~200,000 sorted specimens that remain in alcohol. Our primary source of specimens was our own field expeditions from 2002–2008, including hand collections and litter sifting. Each leaf litter sample constitutes a 200-m transect of 20 1-m^2 samples taken every 10 m and combined into a single "maxi-Winkler" extraction. We also processed 714 malaise trap samples collected during the National Science foundation Fiji Terrestrial Arthropod Survey (Evenhuis and Bickel 2005), each of which represents approximately 2 weeks of trap time. In addition, we processed samples

from canopy fogging and leaf litter conducted by Hilda Waqa (University of the South Pacific) and colleagues and litter sifting conducted by Dave Olsen and the Wildlife Conservation Society. Using the material collected in the surveys and additional material we examined in major collections (U.S. National Museum of Natural History, Harvard Museum of Comparative Zoology), we pursued a comprehensive taxonomic revision of the fauna. To these data, we added records from the extensive hand collections of D. Ward during field expeditions in 2004.

Each specimen was identified to species and analyzed in relation to the regional Indo-Pacific fauna. Undescribed species were assigned geographically consistent temporary codes. The results of this analysis, including a discussion of each species with images, collection records, and distribution maps will be presented in a forthcoming monograph (Sarnat and Economo, forthcoming).

As ants are social organisms, we ignored how many individuals were collected in a sample, and focused on a unique species-sample pair as our unit of data. Together, our sources yielded 6,548 species-sample pairs from 436 localities that could be associated with habitat data. Of these, 1,495 were from hand collections, 1,830 from litter sifting, 3,136 from malaise traps, and 86 from canopy fogging. The sampling spans every major and many of the minor Fijian islands (fig. 1). The resulting data set is notable for its taxonomic completeness; we have habitat distribution data for 177 of the 183 known species in Fiji (the missing six all being endemics collected by early collectors with no habitat data). Both sampling effort and methodologies varied across habitat types (e.g., urban areas were less collected than primary forest; litter sifting is not possible in a city). The statistical analyses described below are designed to mitigate these potential complications.

Species Geographic Classification

The taxon cycle predicts that habitat distribution is correlated with geographic range as a lineage moves through the cycle. While it would be ideal to have each species placed into a phylogenetic context including the massive Indo-Australian source pools, this will not be available in the near future for Fiji's 42 genera. We classified species into broad categories of endemism that (according to this hypothesis) reflect stages of progression through the cycle.

We sorted species into four groups: exotics, widespread natives, endemic allospecies, and deep endemics. We did not use Wilson's "stages" (Wilson 1961) because these classifications have varied in the taxon cycle literature increasing the likelihood of confusion if they are reapplied to ants. (1) Exotics (25 spp.) are species originating outside the Pacific and known to be transported around the globe by human commerce. These presumably reached Fiji after the arrival of Europeans (last 300 years). (2) Widespread natives (26 spp.) are native to the Indo-Australian region and occur broadly and continuously in the Pacific from India, Indonesia, Southeast Asia, or New Guinea to at least Fiji and often further east to Polynesia (these are equivalent to Wilson's "stage I" species). It is possible that some of these species are native to the western Pacific region but were introduced to Fiji by early human migrations or more recent commerce. In one case, a Pacific native, *Iridomyrmex anceps*, was documented to be introduced recently to Fiji (Wilson and Taylor 1967) and thus was classified as
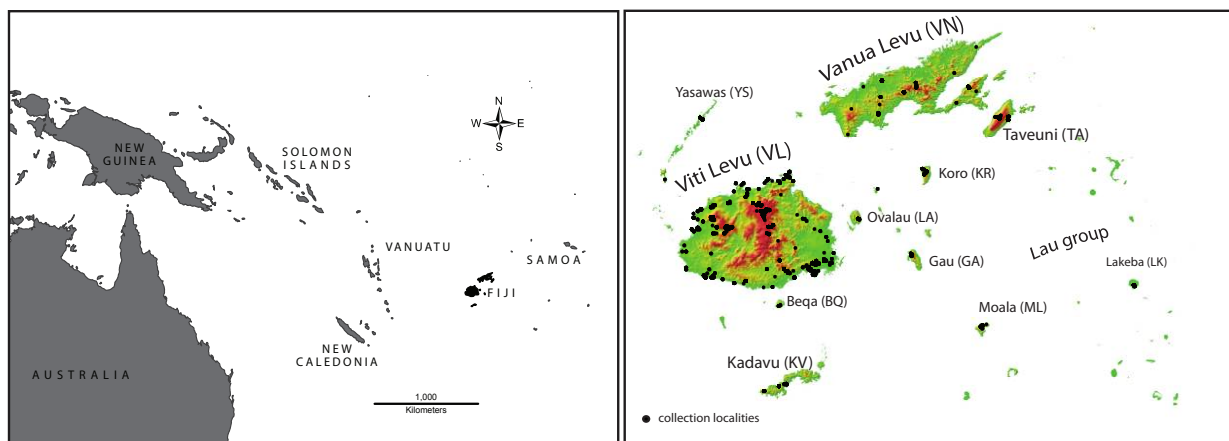

Figure 1: Location of Fiji in the region and a map of sampling localities across the archipelago. Each black dot represents at least one, but up to hundreds of collection events.

exotic. Inferring the arrival dates of all nonendemics to Fiji would require population genetic studies of each species. However, even if some Indo-Australian species have been introduced in the past 3,000 years, as a group they should still have occurred longer in Fiji than exotics (previous 300 years). We address this possibility and implications in the discussion.

We sorted the 121 Fiji endemics into two groups based on their taxonomic relationship to regional faunas. Our main goal was to distinguish between species that are only weakly divergent from relatives elsewhere (and presumably more recent colonists) and those that are strongly differentiated from overseas relatives (presumably older colonists). We classified 24 species as (3) endemic allospecies: taxa differentiated at the species level but are clearly allied to a widely distributed species complex with no evidence of cladogenesis in Fiji. The remaining 97 species were classified as (4) deep endemics: these include 80 endemics that are part of a distinctive endemic Fijian radiation (26 from molecular evidence) and thus are likely the descendants of older colonization events. The other 17 are species are not part of apparent radiations in Fiji but are strongly morphologically divergent from other congeners in the Pacific and could not be associated with other Pacific species groups. Of these four classifications, the distinction between endemic allospecies and deep endemics is the most subjective, but some misclassification among these groups would not be fatal to the analysis. We could have chosen to lump them together into one endemic class and performed the same analysis. Finally, we classified seven species as (5) quasi-endemics: a handful of species that occur in Fiji plus one neighboring archipelago (e.g., Solomon Islands or Samoa). Table A3, available online, lists all species and their classifications.

The taxon cycle predicts that the first four groups represent a sequence of progression through the cycle in Fiji. The fifth group (quasi-endemics) is more difficult to place in this sequence based on geography; they could be remnants of contracting widespread species or incipient expanding species and thus were excluded from the analyses. In lieu of their inclusion, we can report that those five species were among the rarest species in Fiji and were entirely confined to forest habitats.

Habitat Classification

We analyze habitat distributions within the two-dimensional space formed by the two main ecological gradients in Fiji. The first is the gradient in elevation and natural disturbance between the lowland "marginal" coastal forests and high-elevation bryophyte forests at the mountain summits (max. 1,340 m on Viti Levu). The second is a gradient of human disturbance with urban environments and primary forests at the extremes. The position of a locality along the first gradient (elevation) is straightforward. For the second (human disturbance), we assigned collection localities (fig. 1) to one of five coarse-ordered classifications. These categories were based on ecological field notes and if necessary corroborated by satellite imagery. The categories were designed to be intentionally broad in order to minimize subjectivity: (1) port cities (Suva, Lautoka, Nadi, Savusavu): the major urban areas and ports of entry for Fiji; (2) human-dominated landscapes: villages, roadsides, agricultural areas, and pastures; (3) forest edges: localities at the border of native forest with agricultural areas or roads; (4) disturbed forest: habitats retaining a general closed-canopy forest structure but some evidence of disturbance, such as selective logging, planted exotic trees (e.g. mahogany, pine), or evidence of later-stage secondary status; and (5) primary forest: closed canopy forests without observable evidence of recent human or natural disturbance. Specimens not associated with habitat descriptions, a particular problem for the older museum collections, were excluded from the analysis.

Habitat Distribution Analysis

We test the taxon cycle predictions that after lineages colonize Fiji, and as they reach deeper levels of endemism, they (i) shift from disturbed to primary habitats, (ii) shift from low to higher elevations, (iii) decline in commonness. We take two different approaches to characterizing habitat distributions and testing the predictions with our composite data set, the first using regression analysis to model aggregate patterns across the entire fauna and a second using null-model based analysis to compare the positions of individual species along the habitat gradients.

Regression analyses. The aggregated data set consists of species detections across a series of samples and localities. Our first question is whether the composition of species sampled across the four endemism classes (exotic, widespread native, endemic allospecies, deep endemics) changes across the gradients of elevation and human disturbance. In other words, if a single species (or n species) is sampled at a given location, what are the relative probabilities that the species belongs to each class (or the expected proportions of each class in the sample). We treat each species detected as a "trial" associated with one of four multinomial outcomes (the four endemism classes) and use multinomial logistic regression (Trexler and Travis 1993) to model how those relative probabilities (odds) change across classes and gradients. The sampling was diffuse across the landscape but at low intensity in individual sites; thus, detection probability in a sample/locality is a function of both the presence and local abundance of a species. The advantage of using relative probabilities and

not raw counts is they are not sensitive to sampling effort (which varies across localities), and the logistic regression approach accounts for the inherent noise in sampling discrete outcomes. However, the disadvantage is that we can detect changes only in relative, not absolute, collection probabilities, giving us an index of relative prominence. For example, if exotics are more frequently collected in urban environments than endemics, while endemics are more collected in the forest, we would conclude that one class changes relative to the other but cannot say how the absolute probabilities of either class changed. To correct for the fact that different endemism classes have different species numbers in the total fauna, the relative collection probability was divided by the total species number for comparison across groups. While individual species may vary in their conspicuousness to sampling even at the same biological abundance, there is no reason to expect that this variation will be a function of endemism class, each of which represent a phylogenetically, morphologically, and behaviorally diverse group of species.

We performed multinomial logistic regression for relative collection probability using the predictor variables *elevation*, *disturbance*, *elevation*^{2}, *disturbance*^{2}, and *elevation* × *disturbance*, and all simpler models nested within this full model with the constraint that quadratic and interaction terms could be included only if the main effect was included. The higher-order terms allow the model to detect unimodal and other complex distribution patterns if present. Disturbance was coded as an ordinal variable (1 = port city to 5 = primary forest). Good arguments can be made for using either presence-absence in individual samples or at different localities as our unit of data and for including all sampling methods (litter, hand, malaise) or only data from methods that were used in all habitats (hand collections). We performed the regressions using all permutations of these factors and compared results. For the analyses presented in the main text we used all sampling methods, grouped by locality (3,232 occurrence records across 434 sites), but further discussion of sampling issues, statistical design, and results from the other models are presented in the supplemental materials.

Within the larger data set, there is a set of standardized malaise ($n = 617$) and litter samples ($n = 56$) from forest habitats, in which each sample reflects a standardized unit of effort, and the detection of one species does not preclude the detection of another species. Using these data, we can calculate absolute collection probability, in which each endemism class can be modeled separately across the gradient. Here, instead of the relative odds of sampling one class versus another, we model the expected fraction of species in a class that will be detected in a sample/ locality. A separate binomial logistic regression was performed on each endemism class, where each sample re-

flects s successes in n trials if s species of that class were detected out of a total of n species of the class in the entire fauna. Here the model search space included linear and quadratic terms for elevation, allowing for monotonic or unimodal responses to elevation.

Hand collections cover both gradients of elevation and disturbance, while the standardized malaise and litter samples are concentrated in the forest habitats. Thus while we model relative collection probability simultaneously across both gradients and absolute collection probability along elevation in forest habitats only. All regressions were performed in MATLAB in a GLM framework using multinomial or binomial logit links. We used Akaike Information Criterion (AIC) minimizaton for model selection among all subsets of the models described above, including an intercept-only term representing the null hypothesis of no endemism-ecology correlation (but there could still be differences in overall prominence across classes). After selecting the best model for each analysis, confidence intervals for the fitted probabilities were compared to identify regions where endemism classes were significantly different in prominence.

Species-Level Analyses

The regression analyses are designed to test for aggregate community-wide differences in composition among endemism class across the landscape, but obscure variation among individual species. To examine this, we calculated the mean elevation and disturbance score of a species taken over all observations of that species. As these means also depend on the distribution of sampling, we do not interpret them to reflect true centroids of the species distributions. Rather, they are useful for comparing different species in the same data set. High-elevation species should still have a higher mean than low-elevation species, even if those means are both biased in one direction. To account for the fact that different species may be more or less likely to be sampled in different methods, and the sampling from different methodologies is not distributed evenly across the landscape, we generated a null expectation for each species mean and examined deviations from that expectation. We calculated the null expected habitat or elevation mean $\overline{E}_i$ for species i using the formula $\overline{E}_i = \sum_j p_{ij}\overline{E}_j$, where $\overline{E}_j$ is the elevation or habitat mean of all records detected with a given method j and p_{ij} is the fraction of records of species i collected with method j. The deviations of the observed means from expected means were calculated and compared across groups with a one-way ANOVA.
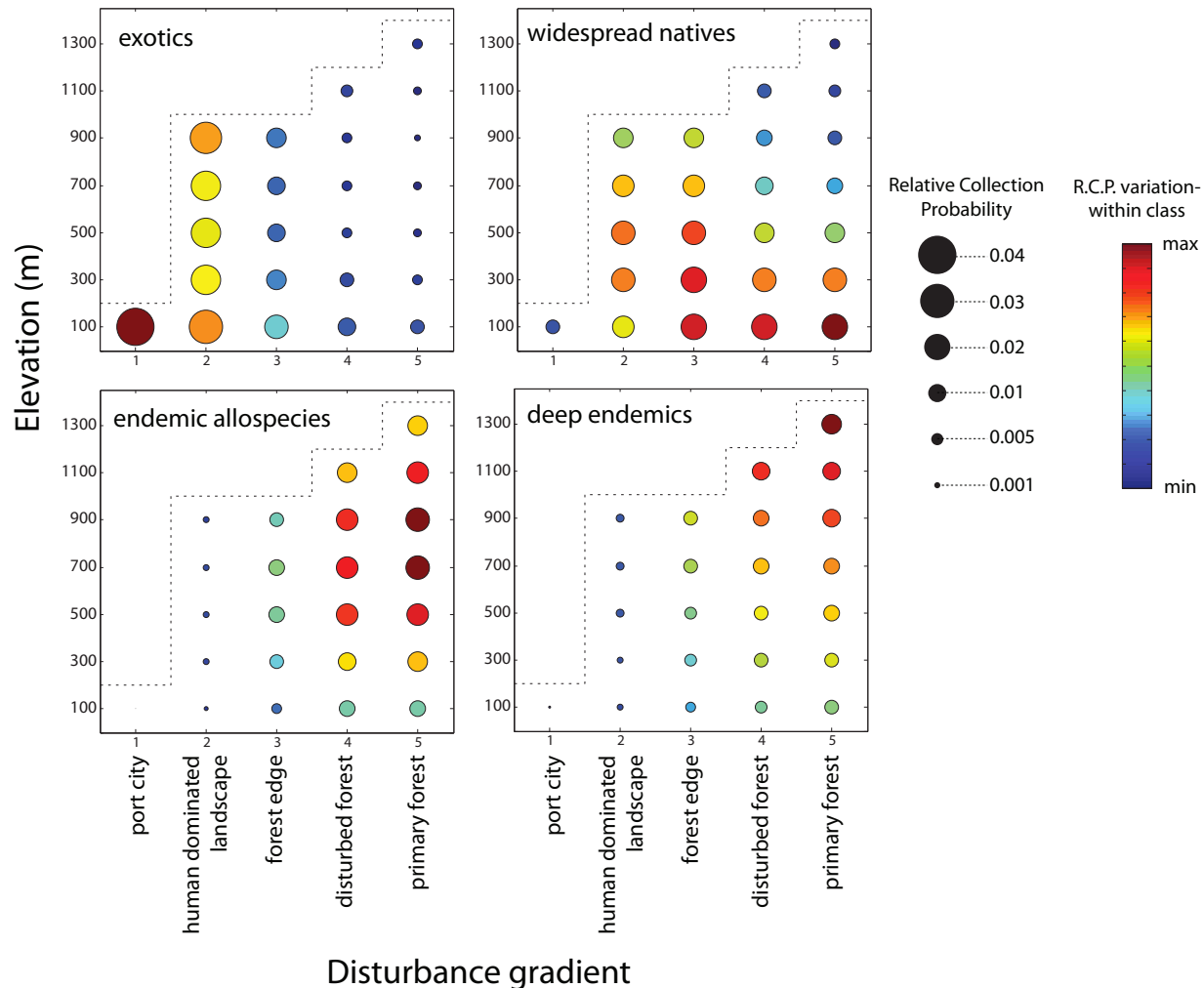
Figure 2: Response surface of the best-fitting multinomial logistic regression model for relative collection probability (RCP) across disturbance and elevation gradients indicates shifts to forest habitat and increasing elevation with increasing levels of endemism. RCP is the probability that a single collection event will detect a species of a given class, divided by the number of species in that class (see text). The size of the dots represents the variation in relative odds across all endemism classes and can be compared across panels, while the color of the dot reflects variation in relative odds within an endemism class. The dashed line reflects the limits of collection data (i.e., there are no high-elevation port cities).

Pheidole *Background and Phylogeny*

We used a molecular phylogeny assembled by Sarnat and Moreau (2011) and ecological data to examine evidence for a postcolonization niche shift in Fijian *Pheidole*. Phylogenetic evidence (Sarnat and Moreau 2011) suggests the Fijian *Pheidole* community assembled through at least six independent colonizations of the archipelago, including the three widespread species (*P. oceanica, P. fervens, P. umbonata*), one introduced by humans (*P. megacephala*), and a lineage represented by a single endemic, *P. onifera* (fig. A4, available online). The phylogeny indicates the rest of

the endemic Fijian *Pheidole* (13 spp.) were derived from a single ancient colonist, although more extensive taxon sampling of the massive source faunas to the west could reveal multiple introductions.

Within the endemic clade, the *Pheidole roosevelti* group has an unusual "spinescent" morphology of pronounced bifurcate propodeal spines and acutely angled mesonotal projections, found only in a few species in Southeast Asian and Indo-Australian *Pheidole* and absent from all extant New World *Pheidole* (Sarnat 2008). One Fijian species (*P. simplispinosa*) represents an "intermediate spinescent" morphology of pronounced but not bifurcate spines and
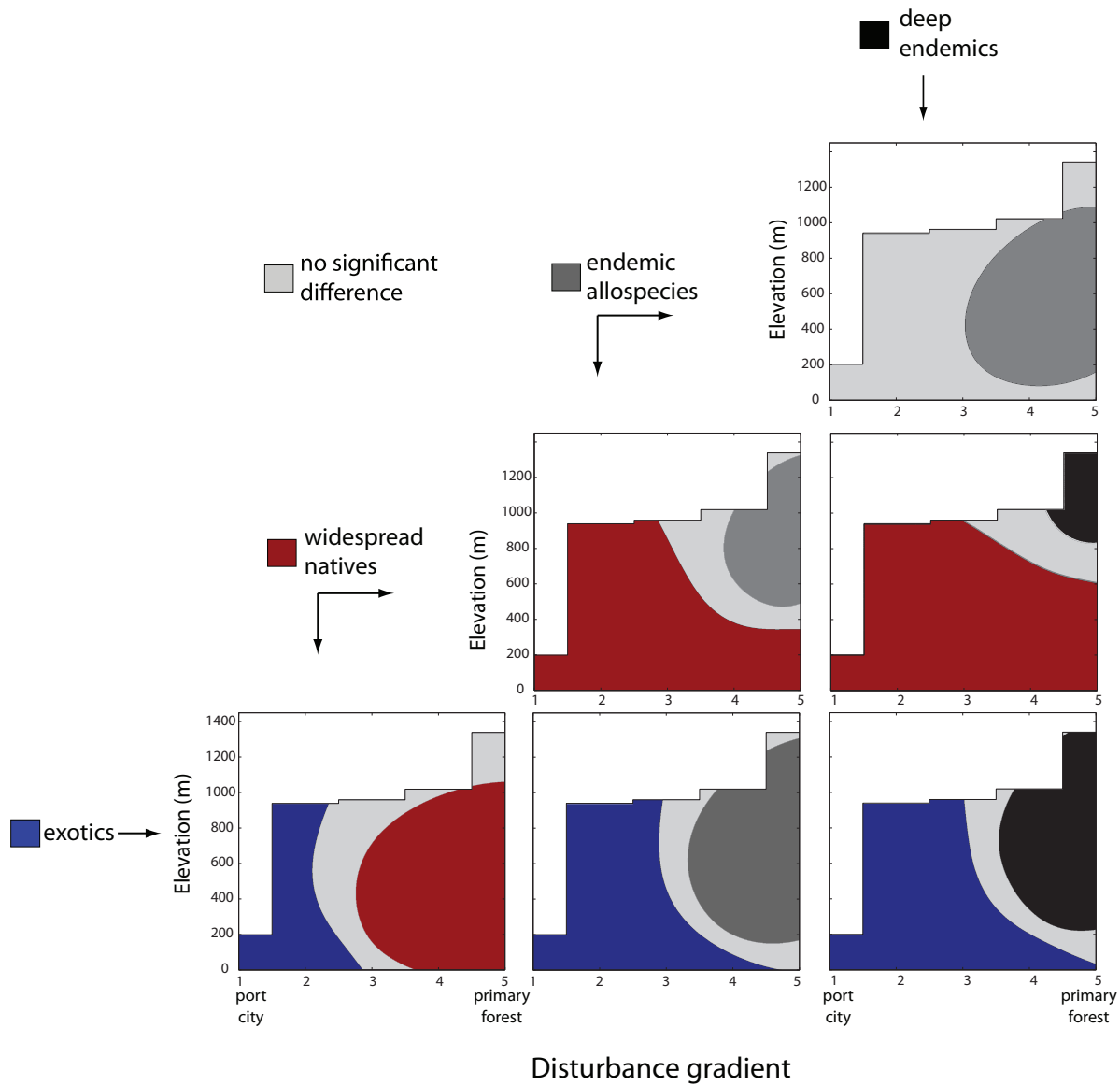
Figure 3: Each panel is a pairwise comparison of two endemism classes, identifying regions in elevation-disturbance space where the relative collection probability of one class is significantly greater (nonoverlap of 95% CI) based on the multinomial regression model visualized in figure 2. The areas shaded with the color of the class indicate that class is greater.

lacking an angled mesonotal projection. Ant spines are thought to be defense mechanisms associated with conspicuous epigaeic foraging, and the *P. roosevelti* group follows this strategy exclusively. The spinescent species in the region were originally grouped based on morphology into one subgenus, *Pheidolecanthinus* (Smith 1865). However, the phylogenetic analysis established that the *P. roosevelti* group evolved convergent spinescence from more generalized ancestors and are distantly related to other spinescent groups in the region. Furthermore, the intermediate *P. simplispinosa* represents a transitional form rather than a secondary loss of spinescence. Species of the *P. knowlesi* group are descended from the same colonization event but retain the ancestral nonspinescent phenotype.

We test the prediction that the in situ evolution of spinescence is associated with a postcolonization shift toward high-elevation primary forest habitats and ecological specialization and more generally that ecological niche is evo-
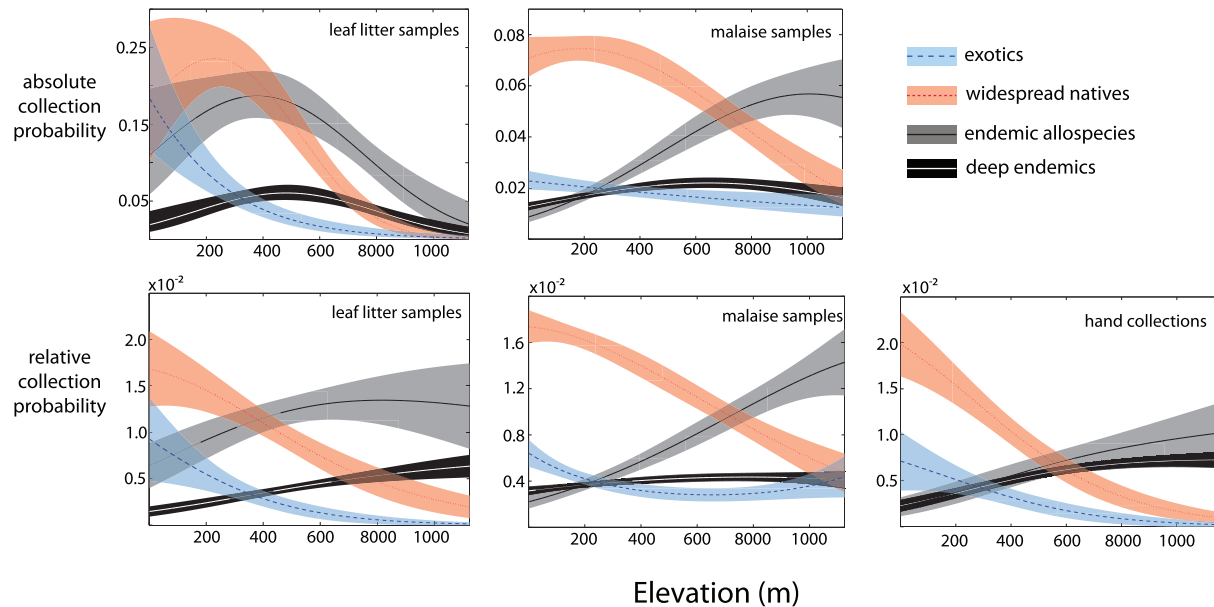
Figure 4: *Top row*, Binomial logistic regression responses for absolute collection probability in standardized malaise and leaf litter samples in forest habitats demonstrate an orderly shift to higher elevations and reduced collection probability with increasing level of endemism. *Bottom row*, Relative collection probability from multinomial regression in the same samples, as well as hand collections. Shaded areas represent 95% CI.

lutionarily labile. We reconstructed states of internal nodes of this clade for elevation mean and disturbance mean using maximum squared-change parsimony for continuous characters, implemented in Mesquite (Maddison 2006). Confidence intervals for the ancestral state were estimated using the PDAP package (Midford et al. 2005). Before reconstructing ancestral states, minor additional analyses of the phylogeny were performed to resolve inconsistencies as described in the appendix.

Results

Ecological Organization of the Fijian Ant Fauna

We identified 183 species of ants (table A3) as occurring in Fiji. Our knowledge of the Melanesian fauna has increased considerably since Wilson's work; in the 1961 paper he listed 58 endemic Fijian species and the number now stands at 129. Of the 183 species, 177 had available habitat data, and 172 remained after removing the five quasi-endemics.

All variations (samples or localities, all methods or only hand collections) of the multinomial logistic regression analysis returned the same general patterns with a few minor differences. We present and discuss the model using all methods across localities in the main text, and results

of the other models in the supplemental materials. The Akaike Information Criterion (AIC) minimizing model (AIC = 2,680, ΔAIC = −0.3, intercepts-only AIC = 3,992) included disturbance, elevation, both square terms, and the interaction term. Coefficients of multinomial regression models can be difficult to interpret directly and we present them in the appendix (table A1, available online). We examined response surfaces of this fitted model over elevation and disturbance in figure 2. Regions of pairwise significant differences (nonoverlap of 95% confidence interval [CI]) between endemism classes are presented in figure 3. As predicted by the taxon cycle, the different endemism classes are ordered in distribution from high to low disturbance (prediction [i]) and from low to high elevation (prediction [ii]). Widespread natives are most prominent in lowland disturbed and primary habitats, consistent with the hypothesis that these habitats facilitate dispersal and colonization. Endemic allospecies are mostly limited to forest habitats and are shifted further upland, while deep endemics are the most confined to high-elevation primary forests and in general have lower a relative collection probability than the other classes (prediction [iii]).

The analysis of absolute collection probability in forest habitats confirmed this pattern under a more standardized sampling regime, a linear or quadratic function of eleva-

The Taxon Cycle in Ants   E11
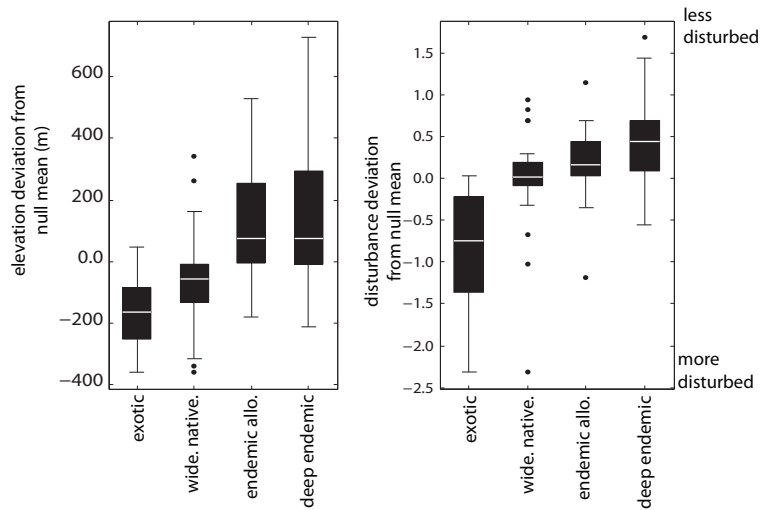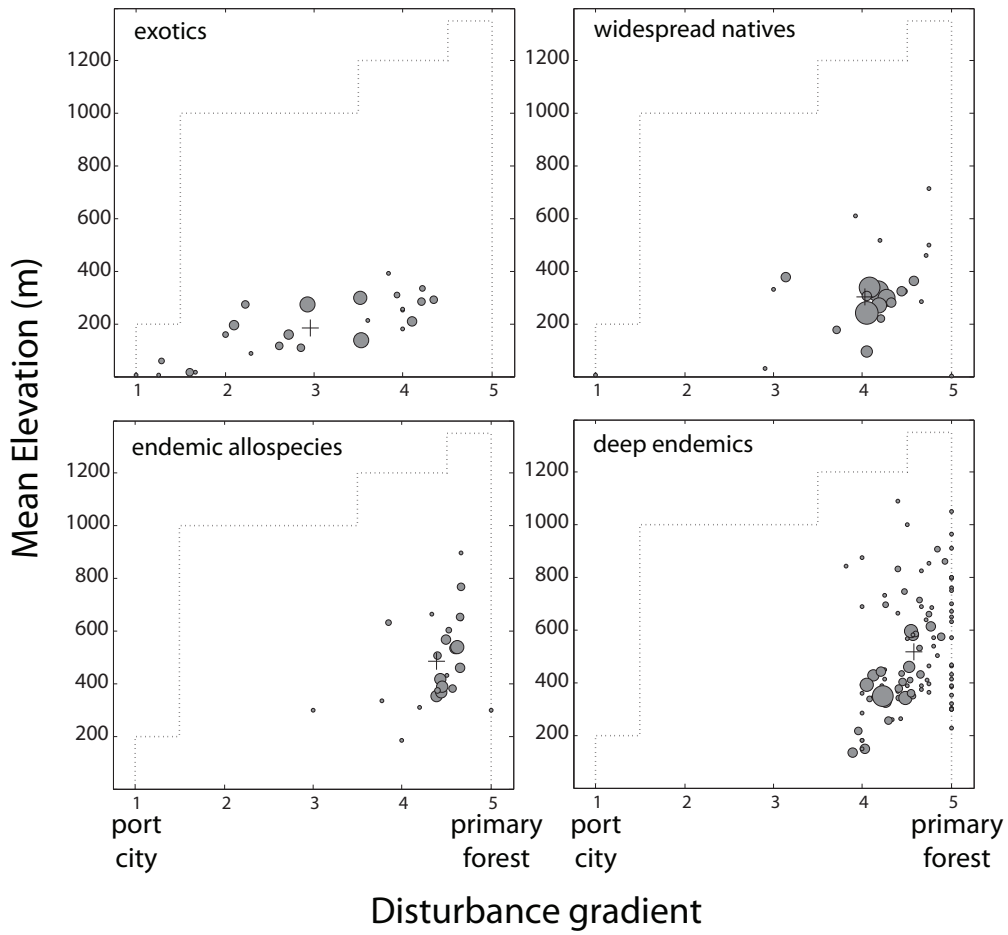
tion was selected over a null model in all cases for both malaise and leaf litter samples. The model shows a decline in absolute collection probability with increasing level of endemism (prediction [ii]), and that deep endemics are generally more rare than the other classes and especially more rare in the lowland forests (prediction [iii]). The coefficients and AIC for each model are reported in the appendix, and the response curves are presented in figure 4. These findings are consistent in both leaf litter and malaise samples, which are biased towards different components of the fauna (ground vs. arboreal species, respectively). There are differences between the two methods on the extent to which ant collection probability decreases on the whole at high elevations. High-elevation leaf-litter samples tend to detect fewer individual ants and species than low-elevation samples, reducing all absolute collection probabilities. While this effect is not as prevalent in malaise samples, relative collection probabilities are similar (fig. 4).

Figure 5 shows the location of elevation and disturbance means for each species, and the distribution of deviations from the species-specific null models. The general picture of habitat shift detected in the regression analysis is confirmed here, but also note individual species exhibit a good deal of variability within class. ANOVAs on the habitat and elevation means were highly significant as a whole (disturbance means: $F_{3,167}) = 35.94$, $P < 10^{-12}$; elevation means: $F_{3,167} = 22.76$, $P < 10^{-11}$). Four of the six pairwise differences were significant after a Tukey-Kramer multiple comparison correction in both elevation (nonsignificant: exotic/widespread native, endemic allospecies/deep endemic) and disturbance (nonsignificant: widespread native /endemic allospecies, endemic allospecies/deep endemic). All of the nonsignificant comparisons were among adjacent endemism classes.

Taken together, these analyses all indicate habitat distributions are related to endemism status in the particular pattern predicted by the taxon cycle, and there is a habitat-endemism correlation in the native fauna. Exotics are most prominent in the new marginal human-dominated habitats, and endemics are almost entirely absent from these areas. Despite the general patterns, there is species level variability within groups that likely reflects both noise in the sampling and analysis and real biological variation.

Ecological Shift and Radiation in Fijian Pheidole

We now look more closely at one component of the Fijian ant fauna, species of the cosmopolitan and hyperdiverse genus *Pheidole* and evaluate whether there is evidence of in situ postcolonization shift in habitat, ecology, and morphology. Consistent with the pattern in the broader fauna, the exotic and widespread native *Pheidole* are found in lower elevation and more disturbed habitats than endemic species. Within the large endemic clade, the spinescent *Pheidole roosevelti* group occurs mainly in high-elevation pristine forests (fig. 6) in contrast to the *Pheidole knowlesi* group species which are commonly found from mid to low elevation in addition to high elevations. We reconstructed the ancestral state of the mean elevation and disturbance score for the endemic Fijian clade including the *roosevelti* and *knowlesi* groups. We do not interpret these values as being reflective of the true state of the original colonist as some degree of niche shift in all descendent species would be expected under a taxon cycle dynamic and ancestral states are constrained to be within the values of all the observed species. However, it does indicate that habitat niches are not conserved postcolonization and supports the hypothesis that the *knowlesi* group species, which retain ancestral morphology, nesting, and foraging habits, are closer to the original ancestral colonist in habitat distribution. Indeed, all the *roosevelti* species except the transitional *Pheidole simplispinosa* fall above the confidence intervals of the ancestral state in either elevation, disturbance, or both, while the *knowlesi* group species are clustered around the ancestral state and all fall within the confidence intervals (fig. 6).

Species of the *P. roosevelti* group have evolved more specialized nesting habits; all exclusively excavate nest chambers in the bare soil with turret entrances. This contrasts with the nonspinescent Fijian *Pheidole*, as the *P. knowlesi* group species are commonly observed nesting under stones, in rotting logs, and in live vegetation. Species of the *P. roosevelti* group are the only Fijian *Pheidole* known to nest exclusively in bare soil or make turret shaped entrances (Sarnat 2008; Sarnat and Economo, forthcoming). *Pheidole simplispinosa*, which exhibits an intermediate morphology, also has intermediate nesting habitats (ground chambers but no turret) and an ecological distribution more typical of the *knowlesi* group (fig. 6).

Within the Fijian archipelago, the *P. roosevelti* group

Figure 5: *A*, Disturbance and elevation means for each species grouped by endemism class. Each dot represents the mean of a species, and size of the dot reflects how many total times the species was observed (a rough indication of commonness). *B*, Deviation of elevation and disturbance means from species-specific null models. White lines indicate medians for a class, boxes represent twenty-fifth and seventy-fifth percentiles, and whiskers enclose 99.3% of the points. ANOVA is highly significant for overall differences in means, but some adjacent classes are not significantly different (see text).
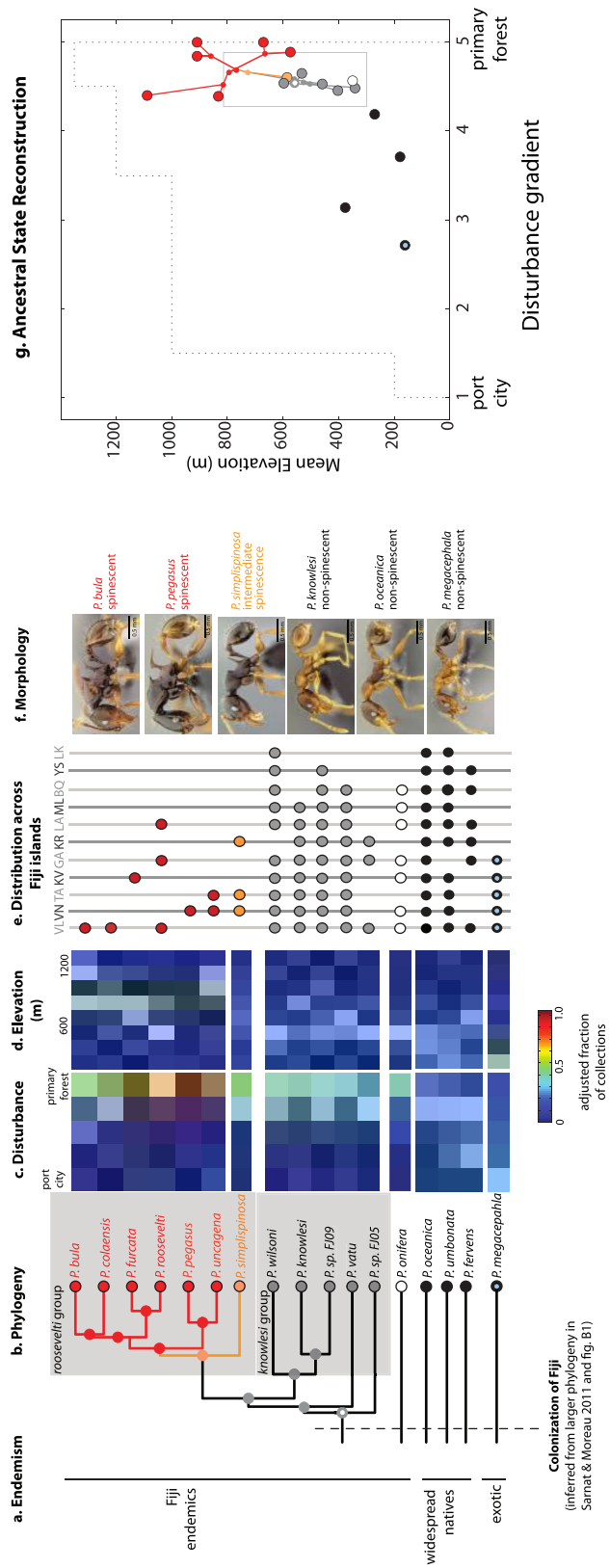
Figure 6: Phylogenetic evidence indicates *Pheidole* lineages have colonized Fiji at least six times (Sarnat and Moreau 2011), and the habitat distributions within the genus echo those in the broader ant community. The morphologically derived *roosevelti* group is associated with forest habitats, high elevations, and confinement to a single island within Fiji. Ancestral state reconstruction indicates a postcolonization habitat shift into high elevations, with the *knowlesi* group retaining ancestral ecological characteristics and morphologies. Dots in panel *g* correspond to terminal nodes (species) and reconstructed ancestral states (internal nodes) of the phylogeny for elevation and habitat means. The box represents 95% CI of the reconstructed ancestral state of the large Fijian endemic clade.

species exhibit the most restricted ranges, with some species restricted to a single mountaintop, others restricted to single islands, and the most widespread restricted to two or three islands. In contrast, species of the *P. knowlesi* group are more widespread across the archipelago, including the small, remote islands of the Lau group (fig. 6). This suggests a loss of dispersal ability concurrent with the ecological and morphological changes.

Taken together, these results support the taxon cycle prediction that habitat niche is not conserved in *Pheidole* after colonization of Fiji, and in situ changes in morphology, nesting, and foraging habits are associated with shifts to high elevation, loss of dispersal ability, and increasing ecological specialization.

Discussion

The Historical Melanesian Taxon Cycle

Our analyses of the Fijian ant fauna are entirely consistent with a historical taxon cycle for Melanesian ants. Ecological distributions across habitats are coupled to geographic distribution on large scales, with increasing endemism associated with increasing confinement inland and upland. This is strong support for at least one component of the taxon cycle; that lowland marginal habitats facilitate dispersal, colonization, and geographic connectivity. Despite the general pattern, there is considerable variability in habitat distribution across species within a class. This variation probably reflects some combination of real biological differences in the evolutionary trajectories of individual lineages and the sampling noise inherent in the course-grained community wide dataset. Future work using more targeted and standardized sampling regimes would better resolve the distribution and abundance of different species on the landscape.

The habitat distributions, island distributions, phylogeny, and morphology of Fijian *Pheidole* indicate that habitat niche is not conserved after colonization. Furthermore, they suggest a preliminary model for the dynamics of ecological shift and evolutionary radiation in the later phases of the taxon cycle. Widespread marginal habitat species colonize Fiji (e.g., *P. megacephala*) and quickly expand across the archipelago (e.g., *P. umbonata*, *P. fervens*, *P. oceanica*). They shift into the low- and midelevation primary forest (e.g., *knowlesi* group) and eventually may acquire specialized morphological adaptations and ecologies as they become increasingly restricted to the high elevations (e.g. *roosevelti* group). The specialized lineage loses dispersal ability to the point where the more modest oceanic barriers within Fiji allow for sequential colonization and speciation among different islands in the archipelago. Note that there is not evidence of a taxon cycle dynamic

within the archipelago of Fiji for *Pheidole*. The data support a single evolution of the high-elevation specialist phenotype in the northern islands followed by sequential colonization and speciation of different islands (Sarnat and Moreau 2011). Radiation is thus associated with ecological decline rather than success and may be the last stage before extinction. Today the species of the *roosevelti* group are among the most threatened in Fiji, confined to mountain peaks with nowhere to go as the climate warms or habitat loss proceeds uphill.

If the *knowlesi* and *roosevelti* groups are indeed derived from a single colonizing species, then this implies the *knowlesi* group retained a more ancestral, generalist ecology while the *roosevelti* group trended toward specialization in the upland habitats. Note that while species of the *knowlesi* group are present in high frequency at the low elevations, several species occur at high elevations and in many cases are more common than members of the *roosevelti* group. An alternative hypothesis is that the *knowlesi* group is derived from one or more recent colonizations and represents an earlier stage in a temporal sequence towards the extreme endemic syndromes exhibited by the *roosevelti* group. The taxon cycle need not progress with clockwork precision. Historical contingencies may promote specialization and radiation in one lineage (e.g., *roosevelti* group), while others remain depauperate or retain ancestral strategies for longer periods of time. Further integrative analyses of *Pheidole* on a broader geographic scale are needed to finely dissect the sequence of colonizations and evolutionary changes as the Fijian community assembled over time.

While both the community-wide habitat distributions and the habitat shift in *Pheidole* are consistent with predictions of the taxon cycle, this analysis represents only an early phase of a thorough evaluation of the hypothesis. There remain biologically plausible alternative explanations for many if not most of these individual patterns. For example, it is possible that the widespread Pacific native species are not part of a historical taxon cycle dynamic; they could be "canoe ants" brought by pre-European human migrations in the Pacific. In this case, we are witnessing the later stages of a human-mediated invasion rather than a snapshot of historical dynamics. This would be interesting as these species show dramatically different patterns than more recent exotics; they are prominent in low-elevation interior forest and are among the most abundant species even in undisturbed habitats. Wilson acknowledged and argued against this possibility, but only molecular phylogeographic analyses of these widespread species can rigorously exclude it.

While the habitat distribution patterns provide a strong indication that dispersal and geographic connectivity are related to habitat affinities, more work is needed to dif-

ferentiate the extent to which ecological niches are conserved over time (i.e., as proposed by Dexter 2010) or whether habitat shifts regularly occur postcolonization (taxon cycle). There is evidence of an in situ niche shift in *Pheidole*, but at most this represents a single example, and it is far from clear that this is the dominant dynamic in the region for either *Pheidole* or Fiji's 42 other ant genera. Phylogenetic studies linked with ecological and morphological data on a regional scale are most critically needed to address this question. If combined with quantitative methods for biogeographic inference (Ronquist and Sanmartin 2011), these could be used to evaluate the interdependency of transitions across geographic, phenotypic, and ecological spaces. Such studies could also evaluate whether lineage movement is biased from high- to low-diversity systems or in any particular geographic direction.

The more general question at stake is the extent to which biogeographic dynamics follow deterministic pathways or are more stochastic and unconstrained. Theories that tend toward the deterministic, such as the taxon cycle, may prove a useful foil to more stochastic theories, such as the ETIB (MacArthur and Wilson 1967) and its conceptual descendants, neutral theories (Hubbell 2001). Our finding that older endemic lineages are less, not more, abundant than new arrivals is inconsistent with predictions arising from initial efforts to apply neutral theory to island biogeography (Rosindell and Phillimore 2011). However, it would probably not require dramatic modifications to the latter theory to make it consistent with the patterns reported in this article. Further theoretical developments from both perspectives integrated with modern tools of biodiversity analysis are needed to address this key question in biology.

The Incipient Global Taxon Cycle

Our data are consistent with the existence of a historical taxon cycle, but what of its present and future? Typical of the region, Fijian landscapes have transformed since human arrival ∼3,000 years ago (Kirch 2000; Anderson 2002). Settlements, agricultural areas, and pastures have mostly replaced the prehuman marginal habitats that historically served as a conduit for dispersal to other archipelagoes. Today there are few places in Fiji where native forest reaches the coast. Although the new human-dominated margins support a few natives and an even smaller number of endemics, they are mostly inhabited by exotics brought from distant continents (figs. 2, 3, 6).

These observations lead us to conclude that the historical dispersal connections across the Pacific are now broken and that the regional Melanesian taxon cycle has been interrupted. A rapid, global colonization pulse is under way (McGlynn 1999; Holway et al. 2002) as a small number of ant species shift into the new "margins"—human-dominated habitats—and spread around the globe through networks of human commerce. It is possible that across the globe, species with the "widespread native" strategy are preadapted to the open, high-disturbance landscapes shaped by humans, and the subset of those that can survive in cargo are spreading out of their native ranges. Fiji is a primary source of ant propagules arriving in New Zealand through trade (Ward et al. 2006), and quarantine data show that this transfer is biased entirely toward widespread native and exotic species. Of species present in Fiji, 76% of exotics (16 spp.) and 37% (10 spp.) of widespread natives have been recorded in New Zealand quarantine, but none of Fiji's 129 endemic species have ever been recorded (compiled from Ward et al. 2006). Likewise, several widespread Pacific natives have recently established populations outside the Indo-Pacific region through human transport (e.g., *Tetramorium pacificum*, *Odontomachus simillimus*, *Pheidole fervens*). We propose that the global pool of "tramp" ants is a mixture of formerly regional expanding species with the generalist stage 1 strategy, filtered by their ability to travel as propagules through human networks.

Future colonists to Fiji are more likely to be species originating from South America and Africa than naturally expanding taxa from New Guinea and Southeast Asia. If these exotics follow trajectories similar to older Pacific colonists, we can expect ecological release and adaptive shift to the interior of the islands, possibly accelerated by new species arriving through human commerce and ultimately applying further pressure on the confined endemic diversity of this biodiversity hotspot. Our data suggest ecological shifts may already be under way as many of the exotics have penetrated the primary forest but at low density (figs. 2–4, 6). It remains to be seen whether this is inconsequential spillover from disturbed areas or the beginnings of adaptive shifts into the primary forest and whether endemic faunas will ultimately be displaced.

If historical taxon cycles do occur, it raises a number of interesting questions about the mechanisms driving different phases of the cycle. Intensive study of human-mediated ant invasions has revealed roles of social organization, reproductive system, genetic population structure, morphology and physiology, climate, and foraging strategy among others, in promoting the spread and ecological success of exotic species (Holway et al. 2002). It is an open question whether any of these same factors promote natural range expansions and invasions in ants. The trajectories of historical invasions, in turn, may provide clues to the futures of contemporary human-mediated range expansions.

Acknowledgments

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Pheidole pegasus. Photograph by Eli Sarnat.