



ORIGINAL  
ARTICLE



# Assembling a species–area curve through colonization, speciation and human-mediated introduction

Evan P. Economo<sup>1,2\*</sup>, Milan Janda<sup>3,4</sup>, Benoit Guénard<sup>5</sup> and Eli Sarnat<sup>1,6</sup>

<sup>1</sup>Okinawa Institute of Science and Technology Graduate University, Onna-son, Okinawa, Japan, <sup>2</sup>Department of Ecology & Evolutionary Biology, University of Michigan, Ann Arbor, MI, USA, <sup>3</sup>Biology Center, Czech Academy of Sciences, Prague, Czech Republic, <sup>4</sup>Cátedras CONACyT, Laboratorio Nacional de Análisis y Síntesis Ecológica, UNAM, Mexico, <sup>5</sup>School of Biological Sciences, The University of Hong Kong, Hong Kong SAR, China, <sup>6</sup>Antwork Consulting, LLC, Davis, CA, USA

## ABSTRACT

**Aim** The fundamental biogeographical processes of colonization, speciation and extinction shape island biotas in space–time. On oceanic islands, area and isolation affect these processes and resulting biodiversity patterns. In the Anthropocene, a new human-mediated colonization dynamic is altering insular ecosystems world-wide. Here, we test predictions about the roles of archipelago area and isolation in structuring ant diversity patterns through effects on both natural and anthropogenic biogeographical processes.

**Location** Tropical Pacific islands.

**Methods** We compiled a comprehensive data set of ant faunal compositions across tropical Pacific archipelagos. Using regression analysis we evaluated the bivariate and interactive effects of area and isolation on the number of colonizing lineages, native species, endemic species, exotic species and total richness in the archipelago.

**Results** There is a strong species–area effect and a much more modest isolation effect on total ant species richness across the Pacific archipelagos. The number of colonizing lineages of each archipelago is strongly driven by the isolation of the archipelago. Endemic species are present in large archipelagos of low and intermediate isolation. The most remote archipelagos are nearly devoid of endemic lineages and their ant faunas are largely composed of Pacific Tramp species and exotics brought from outside the Pacific region.

**Main conclusions** The prominent species–area curve in Pacific ants emerged over time through multiple processes. The colonization of lineages is determined primarily by isolation, with few or no lineages reaching remote archipelagos. Cladogenesis mediates the isolation effect and increases the area effect through the differential radiation of lineages in large archipelagos. In the Anthropocene, the assembly of the species–area relationship has accelerated dramatically through human-mediated colonization. Overall, our results support a view that species–area curves reflect regulating limits on species richness that scale with area, but that multiple biogeographical processes can occur to achieve these limits.

## Keywords

ants, colonization, exotic species, island biogeography, pacific islands, radiation zone, speciation, species–area, species-isolation

\*Correspondence: Okinawa Institute of Science and Technology Graduate University, 1919-1 Tancha, Onna-son, Okinawa 904-0495, Japan. E-mail: evaneconomo@gmail.com

## INTRODUCTION

In their *Equilibrium Theory of Island Biogeography*, MacArthur & Wilson (1963, 1967) highlighted the role of area and isolation in controlling biodiversity patterns

through their effects on colonization–extinction. This began a long history of research focusing on species–area and species-isolation relationships in island biogeography (Rosenzweig, 1995; Whittaker, 1998; Kalmar & Currie, 2006; Kreft *et al.*, 2008; Triantis *et al.*, 2012). Since MacArthur and

Wilson's theory, many authors have demonstrated that area and isolation can affect species richness through different ecological and evolutionary pathways in addition to colonization–extinction rates, particularly when considering the role of speciation in building island biotas (Whittaker, 1998; Losos & Schluter, 2000). In general, the interplay of colonization, extinction and speciation contribute to species–area and species–isolation relationships that depend strongly on physiographic and biotic factors and vary considerably across different regions and taxonomic groups (Patiño *et al.*, 2014).

Here we consider both the natural and anthropogenic processes shaping species–area and species–isolation patterns of ant diversity in the tropical Pacific islands. In particular, extant species richness has been assembled through three processes. First, there is the colonization of islands by lineages from other areas. A long-standing tenet of island biogeography theory is that colonization rates are controlled by isolation, the remoteness of an island or archipelago from potential colonizing sources. This should lead to a decline of colonizing lineages reaching more remote Pacific archipelagos. Area may have an additional effect on colonization rate, as larger archipelagos may be correspondingly larger targets for dispersing propagules (Lomolino, 1990).

Second, cladogenic speciation builds richness from the pool of colonizing lineages. Larger areas may promote speciation (Rosenzweig, 1995; Whittaker, 1998; Losos & Schluter, 2000; Kisel & Barraclough, 2010), while different levels of isolation may depress or promote speciation (Yamaguchi & Iwasa, 2013).

Third, against this canvas of natural biogeographical patterns, the modern era has unleashed a new dynamic of human-mediated dispersal and colonization that is rapidly changing the species richness of many islands (Sax *et al.*, 2002; Cassey *et al.*, 2005; Gillespie *et al.*, 2008). These can be considered natural experiments in ecology and evolution that can be used to test predictions of island biogeography theory. For example, a recent analysis of Caribbean anoles (Helmus *et al.*, 2014) demonstrated the roles of colonization, speciation, and human-mediated introduction in adding species richness to islands that were otherwise depauperate in species richness. Islands may be depauperate in native richness due to limitations to colonization, for example, because they are highly isolated, or due to limitations on speciation. Even when ecological opportunity exists on an island, speciation rates may be limited in small islands because spatial scales of landscapes are too small to allow geographical divergence (Kisel & Barraclough, 2010).

Here we consider both the historical and contemporary processes assembling ant faunas in the Pacific islands. Our study taxon, ants, are among Earth's most dominant animal groups (Hölldobler & Wilson, 1990), and understanding the ecological and evolutionary dynamics that assemble ant communities enriches our understanding of terrestrial ecosystems. Ongoing human-mediated ant transfers are unintentional experiments that illuminate the forces regulating ecological communities, and are also major economic

and conservation concerns in their own right (McGlynn, 1999; Holway *et al.*, 2002; Lach & Hooper-Bui, 2009). Native ants are a significant component of the threatened, endemic biodiversity of the Pacific islands (Sarnat & Economo, 2012) and exotic ants are a major concern for biodiversity conservation, agriculture and public health in the region (Jourdan, 1997; Le Breton *et al.*, 2003; O'Dowd *et al.*, 2003; Krushelnicky *et al.*, 2005; Lach & Hooper-Bui, 2009).

This Pacific ant system is of further interest due to its historical role in the development of biogeographical theory. In a series of papers written a half century ago (Wilson, 1959, 1961; Wilson & Taylor, 1967a,b), E.O. Wilson and colleagues examined some of the first species–area curves and produced several synthetic ideas regarding faunal dynamics – including the *taxon cycle* (Ricklefs & Bermingham, 2002; Lomolino & Brown, 2009). In addition, the system partly inspired the equilibrium island biogeography theory (MacArthur & Wilson, 1963, 1967). Wilson argued that across Melanesia there is no apparent effect of isolation on island species richness, and argued that while isolation limits colonization of lineages, this is compensated by greater rates of apparent *in situ* speciation (Wilson, 1959, 1961). Later, in their monographic treatment of Polynesian ant biodiversity, Wilson & Taylor (1967b) interpreted the lack of endemic ants east of Samoa as evidence that ants did not reach the eastern archipelagos through natural dispersal. The eastern ant faunas, a mix of widespread Pacific species and exotics from outside the Pacific, have generally been thought to be assembled primarily through human introduction (Wilson & Taylor, 1967b; Morrison, 2014).

Until recently, however, Pacific ant biogeography had not been revisited, and faunal patterns on a biogeographical scale remain unclear. In studies focusing on eastern Polynesia, Morrison (1996a,b, 1997) demonstrated the importance of sampling issues when comparing faunal numbers, and his results challenged Wilson's interpretation of species–area patterns and the limited richness of island ant faunas assembled by human introductions compared with faunas assembled through natural processes over millions of years (Wilson & Taylor, 1967a). Recent surveys (Sarnat & Economo, 2012; Sarnat *et al.*, 2013) have also demonstrated the substantial undersampling of island faunas that were previously considered well documented (e.g. Fiji). In general, Wilson and colleagues were working with a very limited data set, a problem that is not ameliorated today, although we now have a clearer idea of what is missing.

In this study we focus on the nature of ant species–area–isolation relationships in the Pacific region, how they have emerged through natural processes, and how they are changing in the modern era. In particular, we test the following hypotheses arising from island biogeography theory: (1) colonization is a major source of species richness, but is limited by distance to source areas, leading to a strong species–isolation effect, (2) speciation is an important process adding species to large–but not small–islands enhancing the species–area relationship, (3) exotic species compensate for richness

deficits left by an isolation-driven lack of colonization or area-driven limits to speciation.

## MATERIALS AND METHODS

### Biodiversity data

Our main source of data was the Global Ant Biodiversity Informatics (GABI) database, a recent effort to compile and curate a comprehensive database on ant species distributions. The database, which combines literature records from over 8500 publications, specimen databases, and museum databases, currently has ~1.6 million individual species-occurrence records. The GABI data can be viewed through the web application [antmaps.org](http://antmaps.org) ([www.antmaps.org](http://www.antmaps.org), Janicki *et al.*, 2016). Of these, ~42,000 records were available from the Pacific islands using the database version from September 2015. We first summarized these data into a checklist for each archipelago. Subsequently, each author independently checked each record for quality and plausibility, making corrections when necessary. In some cases, we supplemented these records with our own unpublished collection records.

We aggregated the data to the archipelago-level (e.g. Fiji but not individual islands within Fiji) for two reasons: (1) because within archipelagos sampling intensity is usually more variable across islands, and (2) even if sampling were not an issue, we are comparing patterns of faunal assembly across independent biogeographical units, not landscape scale community processes among islands of a given archipelago. We felt these concerns outweighed the disadvantages of this approach, namely that the judgment of what constitutes an independent biogeographical unit can be subjective in certain cases. Several Pacific archipelagos, notably including New Caledonia and Vanuatu, are too undersampled to include in our analyses. This left 19 islands and archipelagos which form the basis of our analysis (Table 1, Fig. 1). The full species list and island incidence matrix are archived on dryad ([doi:10.5061/dryad.2f7b2](https://doi.org/10.5061/dryad.2f7b2)).

### Categorization of species

The combined fauna of the Pacific archipelagos (excluding New Guinea, Vanuatu, New Caledonia) totalled 601 species. To facilitate analysis, we categorized these species into four groups based on available evidence of geographical distribution, taxonomy and phylogeny. These were (1) *Endemic*: found only on a single island/archipelago, (2) *Native*: not endemic to an archipelago but considered native to the Pacific region across its range, (3) *Pacific Tramp*: species most likely native to part of the Pacific region, but probably spread by humans to other parts as well, and (4) *Exotic*: those native to other biogeographical regions and introduced into the Pacific region through human commerce.

While the other categories are straightforward, the status and biogeographical history of Pacific Tramp species is a confounding issue in our understanding of Pacific ant

biodiversity (Morrison, 2014). These species are generally derived from Indo-Australian lineages and are widely distributed within but not outside the region, indicating they were not brought from the outside through human commerce after the arrival of Europeans. However, they could be 'Palaeo-invasives' spread across the Pacific by early human migrations, and they could have been subsequently spread by commerce after the arrival of Europeans. These species often have ecological characteristics more typical of human-introduced species, such as affinity for disturbed open habitats, and have been documented to be transported by humans during the modern era (Ward *et al.*, 2006). Also, many of them have reached remote areas, such as Hawaii, but it is unlikely this is due to natural dispersal (but see Horrocks *et al.*, 2013). On the other hand, it is also possible that these species are naturally widespread through at least parts of their range. These species have been interpreted as naturally widespread 'Stage I' species by Wilson under the taxon cycle hypothesis. Economo & Sarnat (2012) showed that these species had a markedly different habitat distribution than known exotic species in Fiji. In particular, while both groups have affinities for disturbed areas, Pacific Tramp species peak in relative abundance in low-elevation forest. In other taxonomic groups, adaptation to disturbed habitat is known to be associated with wide and expanding ranges, even without the influence of humans. Furthermore, genetic work has supported the notion that at least some of these species are native to the western Pacific (Clouse *et al.*, 2015). Finally, the fact that some of them are transported by humans today (Ward *et al.*, 2006; Economo & Sarnat, 2012) does not rule out the possibility that they naturally achieved a large geographical range. Indeed, even if the taxon cycle interpretation is correct, we would expect these species to be good candidates for future human-mediated dispersal, given their commonness, high abundance and tolerance for disturbed habitats. In summary, these species' ranges reflect some combination of natural dispersal, palaeoinvasion mediated by early human migrations, and dispersal via post-European human commerce. Only future high-resolution population genetic studies and/or palaeontomological studies will solve the issue definitively.

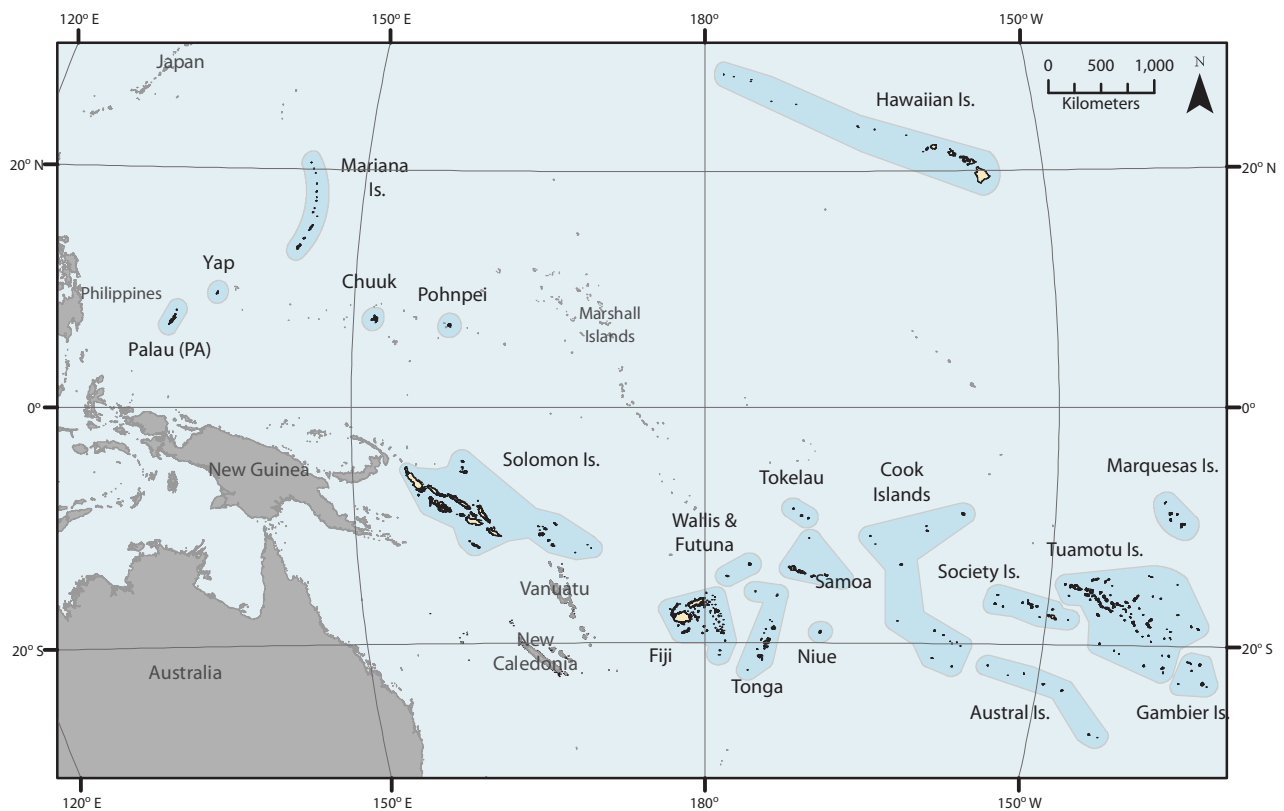
For the purposes of the questions posed in this paper, we need to integrate over this uncertainty in our analysis of the species-area and species-isolation relationships. Practically, Pacific Tramps reflect either additions to species richness due to natural colonization or human introduction. We performed all our analyses both ways by making either assumption (all native or all human-mediated) to evaluate whether any conclusions were sensitive to this uncertainty.

### Estimation of colonizing lineage counts

To separate the roles of colonization and speciation in building species richness, we estimated the number of colonizing lineages that originally seeded the extant faunas of each archipelago (i.e. the number of colonizations that the extant

**Table 1** The Pacific island groups used in this study, with their areas, isolations and components of ant species richness.

Island group	Area (km <sup>2</sup> )	Isolation (km to cont.)	Endemic	Native (not endem.)	Pacific Tramp	Exotic	Total richness
Solomon Islands	28896	640	90	107	28	25	250
Palau	459	829	38	23	24	23	108
Yap	308	1213	4	9	16	17	46
Chuuk	122	1465	0	11	18	15	44
Pohnpei	1048	1802	2	11	21	27	61
Mariana Islands	372	1856	5	15	23	23	66
Fiji	18274	2635	127	12	25	25	189
Samoa Islands	2831	3086	10	9	29	27	75
Tonga	747	3224	6	4	22	22	54
Wallis and Futuna	142	3250	1	4	18	14	37
Niue	260	3850	0	1	16	14	31
Tokelau	12	4102	0	0	14	12	26
Cook Islands	236	4733	0	0	12	16	28
Austral Islands	148	5593	0	2	14	22	38
Society Islands	1590	5709	2	2	22	25	51
Tuamotu Islands	850	6251	0	1	14	19	34
Hawaii	28311	6817	0	0	12	48	60
Gambier Islands	31	7166	0	0	4	16	20
Marquesas Islands	1049	7329	0	1	12	21	34

**Figure 1** The Pacific island groups included in this study are highlighted. Continental areas, and those archipelagos lacking sufficient sampling, were excluded from the analyses.

fauna descended from). A very precise dissection of the colonization history requires comprehensive phylogenies of both island and mainland faunas, which are not available for many ant groups in the Pacific. However, some phylogenetic

evidence is available, and with taxonomic and biogeographical evidence we are able to put a lower and upper bound on the number of colonizing lineages responsible for each island fauna. We performed all analyses using the upper and lower

limits in order to bracket this uncertainty. We found these lower and upper estimates using the following steps. First, the number of putatively monophyletic genera on each archipelago gives an absolute lower bound on the number of colonizing lineages, as only one of the 84 genera in the Pacific is endemic (*Poecilomyrma* in Fiji) and its sister lineage is not in Fiji (Ward *et al.*, 2015). Second, native-but-not-endemic species are assumed to have arrived through colonization to each island, each adding a single lineage to the colonizing lineage count. This leaves cases where an island has multiple congeneric endemic species as the most difficult components of species richness to attribute to either colonization or speciation (e.g. two endemic species of *Pheidole* in Fiji could have descended from either a single colonization followed by *in situ* cladogenesis, or two colonizations followed by anagenetic speciation of each). For this determination, we first used available phylogenetic evidence, notably phylogenies for *Lordomyrma* (Lucky & Sarnat, 2010), *Pheidole* (Sarnat & Moreau, 2011; Economo *et al.*, 2015a,b), *Nylanderia* (P. Matos-Maravi, *pers. comm.*), and (one group of) *Camponotus* (Clouse *et al.*, 2015). In a few cases, when there was a well-documented radiation that was morphologically distinct from all other members of the genus in the region and are almost certainly *in situ* radiations, we made the assumption that they were monophyletic. When phylogenies or other strong morphological evidence were not available, endemic species were considered to have a lower bound that assumes multiple congeneric endemics on the same island are descended from a single colonist lineage, and an upper bound that assumes that each endemic is derived from an independent colonization (if there are  $n$  endemics of a genus on an island, the lower bound is one colonization and the upper bound is  $n$  colonizations for that genus).

### Statistical analyses

We performed a set of regression analyses to estimate the species–area and species–isolation relationships in the Pacific ants. In particular, we sought to disentangle the different processes underlying those patterns by sequentially adding components of species richness that reflect the basic patterns of colonization, speciation and exotic introduction. First, to estimate the role of colonization, we performed regression on the number of colonizing lineages against area and isolation. Second, we regressed total native richness against area and isolation. The difference between colonizing lineages and total native diversity reflects the outcome of *in situ* cladogenesis. Finally, we regressed native and total richness against area and isolation to represent the current biodiversity patterns across the Pacific. To provide context to the species–area curve patterns in the Pacific, we used richness counts from six large areas for visualization although we did not include them in the regressions.

We measured isolation as the nearest land point of the island group to the closest large area to the west (New Guinea, Australia, or Asia) using the application Google Earth.

Ant dispersal in the Pacific occurs generally in a west-to-east pattern with no documented cases of colonization of the Pacific archipelagos in this study by New World taxa. The west-to-east colonization pattern of the Pacific is a common finding across groups and is thought to be due to a lack of stepping stones between the New World and the remote Pacific islands (Weigelt & Krefl, 2013). Archipelago areas and maximum elevations were compiled from Wikipedia ([www.wikipedia.org](http://www.wikipedia.org)).

The two main sources of uncertainty in our data were (1) the estimates of the colonizing lineage counts and (2) the native/exotic status of the Pacific Tramp species. To account for uncertainty in the former, we performed all analyses by either using the lower or upper bound estimates of colonizing lineages, which should bracket the true values. To account for uncertainty of the Pacific Tramp species, we performed analyses assuming either they are all native or assuming they are all exotic, which should also bracket the true values. Thus, in total we performed four permutations of the analyses intended to integrate over the uncertainties in the data.

Although there are many biological and physical variables that could potentially affect island diversity patterns, the size of the data set and collinearity between common predictor variables (e.g. island area and maximum elevation are often correlated) makes simultaneous consideration of a large number of predictor variables difficult. Our main goal is to quantify area and isolation relationships while trying to ensure that other latent variables are not interfering with our inferences. Thus, we consider maximum elevation as an additional potential predictor, and due to the role humans in driving exotic introductions (Roura-Pascual *et al.*, 2016), we also include human population and GDP (PPP) as potential predictors of total (but not native) richness.

We log<sub>10</sub>-transformed species/lineage numbers and area values before regression, reflecting the most commonly used power-law form of species–area relationships (Tjørve, 2003, 2009; Triantis *et al.*, 2012). Many authors have extended species–area curves to include additional variables (e.g. Triantis *et al.*, 2003; Tjørve, 2009). For trivariate and multivariate regressions, we included log-transformed additional variables without combination variables or interaction terms, which is a common form used in extending the species–area relationship (Tjørve, 2009). Isolation was not log-transformed, following convention in island biogeography (e.g. Weigelt & Krefl, 2013).

We used multiple linear regression in a multi-model, information-theoretic framework generally following the procedure described in Grueber *et al.* (2011). The strategy involves evaluating a candidate set of statistical models including different combinations of predictor variables, ranking them based on Akaike's Information Criterion corrected for small sample size (AICc) score, and establishing a final model set of those within a  $\Delta$ AICc of 4 from the top model. The model scope of the candidate model set was all possible subsets of the full model, but excluding models with pairs of

predictor variables that were highly collinear (Spearman's  $\rho > 0.7$ ). The parameters are then averaged across the top model set, weighting models by score. Further details are provided in Appendix S1 (Supporting Information). Goodness-of-fit was assessed using  $R^2$ . We also used bivariate regressions of diversity components on area and isolation individually to estimate the variance explained by each factor. The analyses above were performed in the R computing environment (R Core Team, 2015) using core functions and functions from the 'MuMIn' package (Bartoń, 2015).

## RESULTS

Our data compilation found 601 ant species across the 19 archipelagos, including 151 native, 359 endemic, 36 tramp and 55 exotic species. In general, the model including area and isolation without other variables was the best fit to all components of diversity (Fig. 2, Appendix S1). Only one regression included one of the other variables (elevation) in the top model set, in which it had a very weak effect. Thus, we present the full results of the model averaging in Appendix S1 but focus on area and isolation relationships in the main text.

The number of colonizing lineages on an archipelago was strongly related to area and isolation, with a single model including both variables strongly favoured over other models (Fig. 2, Table 2). Bivariate regressions found that isolation was a better predictor than area for colonizing lineages for the low and high estimates either considering Pacific Tramps as native or exotic (Fig. 2, Table 2).

Speciation has added species richness to some archipelagos, but only those that are above *c.* 3500 km<sup>2</sup> and that are not too isolated to receive seed lineages. The influence of

speciation peaks in Fiji, which is of intermediate isolation and high area. Total native diversity, which includes both species added through colonization and speciation, is still correlated with both area and isolation. However, the dependency of speciation on area has increased the strength of the species–area relationship (Fig. 2, Table 2).

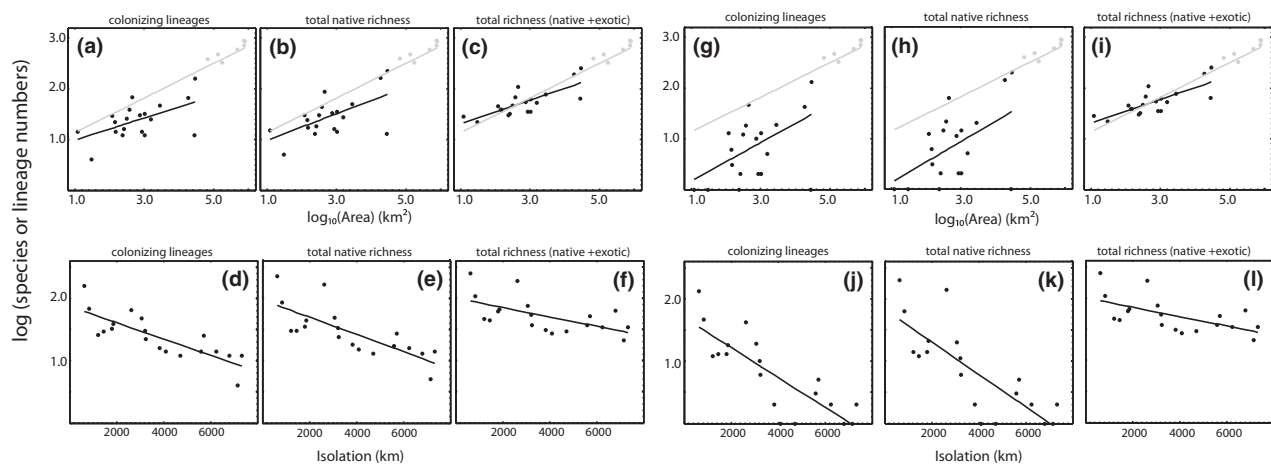
Total richness, which includes both native richness and exotic richness, is also strongly correlated with area and isolation. However, here bivariate regressions showed that area was a stronger predictor of richness than isolation (Fig. 2, Table 2).

Across all permutations of the analysis accounting for data uncertainty, area explains more variance in numbers of native species than colonizing lineages, and more variance in total richness than native richness (Fig. 3). This comes at the expense of variance explained by isolation, which decreases along the same progression. The explanatory power of both variables combined remains high for all components of diversity.

## DISCUSSION

Our results illuminate the ecological and evolutionary processes and biogeographical dynamics shaping native and exotic ant biodiversity across Pacific islands. Although there are uncertainties introduced by gaps in knowledge of the phylogenetic position and introduced status for some species, the variations of the analyses we performed integrating over this uncertainty all point to the same general story about the historical and modern island biogeography in the Pacific islands.

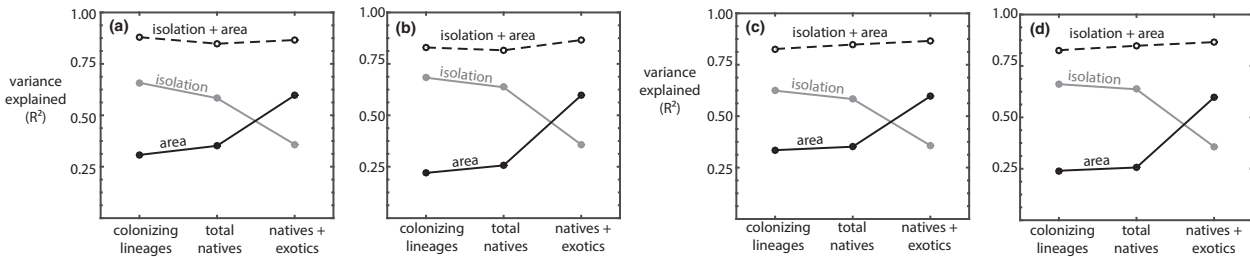
Across the Pacific, total ant richness is now strongly correlated with area, and only secondarily correlated with



**Figure 2** The species–area curves (top row) and species–isolation curves (bottom row) for components of ant richness in Pacific archipelagos (black dots). The grey dots are large islands (Borneo, Madagascar, New Guinea, Sumatra, Sulawesi, Java, Sri Lanka) not included in our analysis, but included on the plots to provide context for the Pacific SA curve. The black line is a regression on Pacific archipelagos only, while the grey line is the regression on total richness including the large areas (included on all plots to show how the Pacific line gets closer). The relationships depicted in panels a–f and g–i assume that ‘Pacific Tramp’ species are native or exotic respectively. These plots use the low estimate of colonizing lineage counts, see supplemental info for the high estimate.

**Table 2** Bivariate and trivariate linear regression statistics for ant species richness and area/isolation of the Pacific archipelagos. The parameters  $z$  and  $\beta$  are the slope of the species–area power function and the regression coefficient for Z-scaled isolation respectively. The high and low estimates of colonizing lineages bound uncertainty in the number of cladogenic speciation events on the islands. Regressions for colonizing lineages and total native richness were performed under the alternate assumption that Pacific Tramp species were native or exotic to the Pacific islands.

	log <sub>10</sub> (Area) (bivariate)			Isolation (bivariate)			log <sub>10</sub> (Area) and Isolation (trivariate)			
	$z$ (SE)	$\Delta$ AICc	$R^2$	$\beta$ (SE)	$\Delta$ AICc	$R^2$	$z$ (SE)	$\beta$ (SE)	$\Delta$ AICc	$R^2$
Colonizing lineages (low estimate, tramps as native)	0.20 (0.07)	29.7	0.27	−0.29 (0.05)	14.4	0.63	0.16 (0.03)	−0.27 (0.03)	0.0	0.86
Colonizing lineages (low estimate, tramps as exotic)	0.32 (0.14)	28.8	0.17	−0.59 (0.09)	9.5	0.70	0.26 (0.06)	−0.56 (0.06)	0.0	0.84
Colonizing lineages (high estimate, tramps as native)	0.23 (0.08)	28.2	0.30	−0.32 (0.06)	17.4	0.60	0.20 (0.04)	−0.30 (0.04)	0.0	0.86
Colonizing lineages (high estimate, tramps as exotic)	0.37 (0.16)	27.4	0.19	−0.63 (0.10)	10.2	0.67	0.30 (0.07)	−0.60 (0.07)	0.0	0.83
Total native richness (tramps as native)	0.25 (0.08)	25.7	0.31	−0.32 (0.06)	16.8	0.57	0.22 (0.04)	−0.30 (0.04)	0.0	0.84
Total native richness (tramps as exotic)	0.38 (0.16)	25.9	0.20	−0.64 (0.11)	10.2	0.65	0.32 (0.08)	−0.60 (0.08)	0.0	0.81
Total species richness	0.22 (0.04)	18.16	0.57	−0.17 (0.06)	26.8	0.32	0.20 (0.03)	−0.15 (0.03)	0.0	0.85



**Figure 3** Variance explained by components of species richness by univariate regressions with area, isolation, and multivariate regression of area and isolation. The panels reflect low (a,b) and high (c,d) colonizing lineage counts and assume Pacific Tramps are native (a,c) or exotic (b,d).

isolation. However, this species–area curve arose through a sequential process of ancient colonization, speciation, and anthropogenic introduction. As predicted by island biogeography theory, the number of colonizing lineages is strongly negatively correlated with isolation, reflecting the difficulty in dispersing across vast water barriers, and positively correlated with area; reflecting the dependency of colonization on area (Lomolino, 1990) and/or the differential attrition of lineages over time due to extinction (MacArthur & Wilson, 1963, 1967).

Even without precise phylogenetic knowledge of all Pacific ant groups, it is possible to deduce the role of speciation in building island species richness. Speciation has a strong influence on archipelagos that are both large enough to facilitate speciation and proximate enough to receive some seed lineages. This strong area-dependency is consistent with the idea that the process of speciation itself is limited by small area, because there may not be enough opportunity for spatial differentiation and divergence within the archipelago (Losos & Schluter, 2000; Kisel & Barraclough, 2010). It is worth noting that compared with some other terrestrial invertebrates such as snails (e.g. Cowie, 1992), ants appear to need a relatively large area

for cladogenic speciation to proceed. As such, speciation is not a predominant factor adding richness across most archipelagos in the Pacific, but becomes a primary factor in relatively large areas such as Fiji. Isolation also limits the contribution of speciation indirectly, because lineages cannot reach isolated archipelagos. The remote archipelagos of Hawaii and French Polynesia would likely be fertile ground for radiation of ant lineages, as they are for many other plant and animal groups (e.g. Witter & Carr, 1988; Gillespie, 2004), if ant lineages were able to colonize these archipelagos more easily without human assistance. This peak of radiation at intermediate isolation is generally consistent with MacArthur–Wilson’s ‘radiation zone’ hypothesis (MacArthur & Wilson, 1967). In the Pacific, the net effect of this area-driven speciation is a tightening of the species–area curve for all native species at the expense of variance explained by isolation.

The role of humans in modern Pacific ant biogeography is perhaps the most complicated. It is likely that pre-European human colonization brought some ant species (e.g. some of the Pacific Tramps) eastward from Asia and through the Pacific islands, as many other taxa accompanied humans during their early migrations through the Pacific. However,

the geographical and numerical scale of those palaeoinvasions is currently unclear. It is also possible that many of these species achieved a large range through at least parts of the Pacific due to disturbance-adapted ecology and high dispersal ability. It is certain that after the arrival of Europeans, many new species were subsequently brought into the Pacific from around the world and continue to arrive today (Krushelnycky *et al.*, 2005; Ward *et al.*, 2006). Indeed, rates of exotic ant accumulation on islands globally have been shown to be driven by human-related variables (Roura-Pascual *et al.*, 2016).

Regardless of what assumption is made about the native or exotic status of the Pacific Tramp species, the same overall pattern is evident; human-mediated exotic introductions have filled empty regions of the species–area curve while reducing the relative strength of the species–isolation relationship.

These results show a striking similarity to other recent results demonstrated in Caribbean lizards (Helmus *et al.*, 2014), indicating there may be common patterns and processes across disparate regions and taxa in both natural and Anthropocene biogeography. Both the patterns exhibited in ants and anoles are consistent with the general idea that island systems have something akin to a carrying capacity of species that may or may not be reached through natural processes (Rabosky & Glor, 2010; Triantis *et al.*, 2015; Valente *et al.*, 2015). This natural deficit leaves open ecological space that can be filled by introduced species. Indeed, it is probably not an accident that Hawaii has the largest deficit of native ants in the Pacific (and probably in the world), and is one of the most invaded areas by ants in the world (McGlynn, 1999; Krushelnycky *et al.*, 2005).

Much work remains to investigate the ecological and evolutionary mechanisms behind these patterns. Most importantly, continued research efforts are needed to better document the geographical distributions, evolutionary histories, and ecologies of ant faunas in the Pacific Islands. With such multifaceted data increasingly becoming available, nascent process-based quantitative approaches (e.g. Triantis *et al.*, 2015; Valente *et al.*, 2015; Sukumaran *et al.*, 2016) hold promise for linking aggregate diversity patterns to the biogeographical dynamics that generate them.

The Anthropocene has ushered in an unintentional, global-scale, biogeographical transplantation experiment. This has, of course, been an ecological disaster, and nowhere more so than the Pacific islands (McGlynn, 1999; O'Dowd *et al.*, 2003; Krushelnycky *et al.*, 2005). Our understanding of natural biogeographical dynamics and evolution after colonization can help us interpret, understand and predict the future of these human-mediated transfers (Ricklefs, 2005; Gillespie *et al.*, 2008; Economo & Sarnat, 2012). In turn, if we ask the right questions, the patterns and dynamics of human-mediated invasions can illuminate the ecological factors and processes regulating diversity patterns.

## ACKNOWLEDGEMENTS

We thank J. Czekanski-Moir, R. Clouse, P. Krushelnycky, D. Ward, G. Alpert, S. Shattuck and M. Borowiec for contributing data, and we thank N. Shankar and K. Dudley for research assistance. EPE, EMS and BG were supported by subsidy funding to OIST. EPE and EMS were supported by a grant from NSF (DEB-1145989), MJ was supported by a grant from the Marie Curie IOF PIOFGA2009-25448 and Czech Science Foundation: P505/12/2467.

## REFERENCES

- Bartoń, K. (2015) MuMIn: Multi-Model Inference. R package version 1.14.0. <http://CRAN.R-project.org/package=MuMIn>
- Cassey, P., Blackburn, T., Duncan, R. & Gaston, K. (2005) Causes of exotic bird establishment across oceanic islands. *Proceedings of the Royal Society B: Biological Sciences*, **272**, 246–251.
- Clouse, R.M., Janda, M., Blanchard, B., Sharma, P., Hoffman, B.D., Andersen, A.N., Czekanski-Moir, J.E., Krushelnycky, P., Rabeling, C., Wilson, E.O., Economo, E.P., Sarnat, E.M., Alpert, G.D. & Wheeler, W.C. (2015) Molecular phylogeny of Indo-Pacific carpenter ants (Hymenoptera: Formicidae, *Camponotus*) reveals waves of dispersal and colonization from diverse source areas. *Cladistics*, **31**, 424–437.
- Cowie, R.H. (1992) Evolution and extinction of Partulidae, endemic Pacific island land snails. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, **335**, 167–191.
- Economo, E.P. & Sarnat, E.M. (2012) Revisiting the ants of Melanesia and the taxon cycle: historical and human-mediated invasions of a tropical archipelago. *The American Naturalist*, **180**, E1–E16.
- Economo, E.P., Klimov, P., Sarnat, E.M., Guénard, B., Weiser, M.D., Lecroq, B. & Knowles, L.L. (2015a) Global phylogenetic structure of the hyperdiverse ant genus *Pheidole* reveals the repeated evolution of macroecological patterns. *Proceedings of the Royal Society of London B: Biological Sciences*, **282**, 20141416.
- Economo, E.P., Sarnat, E.M., Janda, M., Clouse, R., Klimov, P.B., Fischer, G., Blanchard, B.D., Ramirez, L.N., Andersen, A., Berman, M., Guénard, B., Lucky, A., Rabeling, C., Wilson, E.O. & Knowles, L.L. (2015b) Breaking out of biogeographic modules: range expansion and taxon cycles in the hyperdiverse ant genus *Pheidole*. *Journal of Biogeography*, **42**, 2289–2301.
- Gillespie, R. (2004) Community assembly through adaptive radiation in Hawaiian spiders. *Science*, **303**, 356–359.
- Gillespie, R., Claridge, E. & Roderick, G. (2008) Biodiversity dynamics in isolated island communities: interaction between natural and human mediated processes. *Molecular Ecology*, **17**, 45–57.
- Google Earth. Accessed April 2015.



- Grueber, C.E., Nakagawa, S., Laws, R.J. & Jamieson, I.G. (2011) Multimodel inference in ecology and evolution: challenges and solutions. *Journal of Evolutionary Biology*, **24**, 699–711.
- Helmus, M.R., Mahler, D.L. & Losos, J.B. (2014) Island biogeography of the Anthropocene. *Nature*, **513**, 543–546.
- Hölldobler, B. & Wilson, E.O. (1990) *The ants*. Belknap Press of Harvard University Press, Cambridge, Mass.
- Holway, D., Lach, L., Suarez, A., Tsutsui, N. & Case, T. (2002) The causes and consequences of ant invasions. *Annual Review of Ecology and Systematics*, **33**, 181–233.
- Horrocks, M., Marra, M., Baisden, W.T., Flenley, J., Feek, D., Gonzalez Nualart, L., Haoa-Cardinali, S. & Edmunds Gorman, T. (2013) Pollen, phytoliths, arthropods and high-resolution C-14 sampling from Rano Kau, Easter Island: evidence for late Quaternary environments, ant (Formicidae) distributions and human activity. *Journal of Paleolimnology*, **50**, 417–432.
- Janicki, J., Narula, N., Ziegler, M., Guénard, B. & Economo, E.P. (2016) Visualizing and interacting with large-volume biodiversity data using client-server web-mapping applications: the design and implementation of antmaps.org. *Ecological Informatics*, **32**, 185–193.
- Jourdan, H. (1997) Threats on Pacific islands: the spread of the tramp ant *Wasmannia auropunctata* (Hymenoptera: Formicidae). *Pacific Conservation Biology*, **3**, 61–64.
- Kalmar, A. & Currie, D. (2006) A global model of island biogeography. *Global Ecology and Biogeography*, **15**, 72–81.
- Kisel, Y. & Barraclough, T. (2010) Speciation has a spatial scale that depends on levels of gene flow. *The American Naturalist*, **173**, 316–334.
- Kreft, H., Jetz, W., Mutke, J., Kier, G. & Barthlott, W. (2008) Global diversity of island floras from a macroecological perspective. *Ecology Letters*, **11**, 116–127.
- Krushelnicky, P., Loope, L. & Reimer, N. (2005) The ecology, policy, and management of ants in Hawaii. *Proceedings of the Hawaiian Entomological Society*, **37**, 1–25.
- Lach, L. & Hooper-Bui, L. (2009) Consequences of ant invasions. *Ant ecology* (ed. by L. Lach, C. Parr and K. Abbott), pp. 261–286. Oxford University Press, Oxford.
- Le Breton, J., Chazeau, J. & Jourdan, H. (2003) Immediate impacts of invasion by *Wasmannia auropunctata* (Hymenoptera: Formicidae) on native litter ant fauna in a New Caledonian rainforest. *Austral Ecology*, **28**, 204–209.
- Lomolino, M.V. (1990) The target area hypothesis: the influence of island area on immigration rates of non-volant mammals. *Oikos*, **57**, 297–300.
- Lomolino, M.V. & Brown, J.H. (2009) The reticulating phylogeny of island biogeography theory. *Quarterly Review of Biology*, **84**, 357–390.
- Losos, J. & Schluter, D. (2000) Analysis of an evolutionary species-area relationship. *Nature*, **408**, 847–850.
- Lucky, A. & Sarnat, E.M. (2010) Biogeography and diversification of the Pacific ant genus *Lordomyrma* Emery. *Journal of Biogeography*, **37**, 624–634.
- MacArthur, R.H. & Wilson, E.O. (1963) An equilibrium theory of insular zoogeography. *Evolution*, **17**, 373–387.
- MacArthur, R.H. & Wilson, E.O. (1967) *The theory of island biogeography*. Princeton University Press, Princeton, N.J..
- McGlynn, T.P. (1999) The worldwide transfer of ants: geographical distribution and ecological invasions. *Journal of Biogeography*, **26**, 535–548.
- Morrison, L.W. (1996a) Community organization in a recently assembled fauna: the case of Polynesian ants. *Oecologia*, **107**, 243–256.
- Morrison, L.W. (1996b) The ants (Hymenoptera: Formicidae) of Polynesia revisited: species numbers and the importance of sampling intensity. *Ecography*, **19**, 73–84.
- Morrison, L.W. (1997) Polynesian ant (Hymenoptera: Formicidae) species richness and distribution: a regional survey. *Acta Oecologica*, **18**, 685–695.
- Morrison, L.W. (2014) The ants of remote Polynesia revisited. *Insectes Sociaux*, **61**, 217–228.
- O'Dowd, D., Green, P. & Lake, P. (2003) Invasional 'melt-down' on an oceanic island. *Ecology Letters*, **6**, 812–817.
- Patiño, J., Weigelt, P., Guilhaumon, F., Kreft, H., Triantis, K.A., Naranjo-Cigala, A., Solymos, P. & Vanderpoorten, A. (2014) Differences in species-area relationships among the major lineages of land plants: a macroecological perspective. *Global Ecology and Biogeography*, **23**, 1275–1283.
- R Core Team. (2015) *R: a language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. URL <http://www.R-project.org/>.
- Rabosky, D.L. & Glor, R.E. (2010) Equilibrium speciation dynamics in a model adaptive radiation of island lizards. *Proceedings of the National Academy of Sciences USA*, **107**, 22178–22183.
- Ricklefs, R.E. (2005) Taxon cycles: insights from invasive species. *Species invasions. Insights into ecology, evolution, and biogeography* (ed. by Sax, D., Stachowicz, J. & Gaines, S.) pp. 165–199. Sinauer Associates, Sunderland, Massachusetts.
- Ricklefs, R.E. & Bermingham, E. (2002) The concept of the taxon cycle in biogeography. *Global Ecology and Biogeography*, **11**, 353–361.
- Rosenzweig, M. (1995) *Species diversity in space and time*. Cambridge University Press, Cambridge.
- Roura-Pascual, N., Sanders, N.J. & Hui, C. (2016) The distribution and diversity of insular ants: do exotic species play by different rules? *Global Ecology and Biogeography*, **25**, 624–654.
- Sarnat, E.M. & Economo, E.P. (2012) *The ants of Fiji*. University of California Press, Berkeley, California.
- Sarnat, E.M. & Moreau, C.S. (2011) Biogeography and morphological evolution in a Pacific island ant radiation. *Molecular Ecology*, **20**, 115–130.
- Sarnat, E.M., Blanchard, B., Guénard, B., John, F. & Economo, E.P. (2013) Checklist of the ants (Hymenoptera, Formicidae) of the Solomon Islands and a new survey of Makira Island. *ZooKeys*, **257**, 47–88.
- Sax, D.F., Gaines, S.D. & Brown, J.H. (2002) Species invasions exceed extinctions on islands worldwide: a

- comparative study of plants and birds. *The American Naturalist*, **160**, 766–783.
- Sukumaran, J., Economo, E.P. & Knowles, L.L. (2016) Machine learning biogeographic processes from biotic pattern: a trait-driven dispersal and diversification model with model-choice by simulation-trained discriminant analysis of principal components classification. *Systematic Biology*, **65**, 525–545.
- Tjørve, E. (2003) Shapes and functions of species–area curves: a review of possible models. *Journal of Biogeography*, **30**, 827–835.
- Tjørve, E. (2009) Shapes and functions of species–area curves (II): a review of new models and parameterizations. *Journal of Biogeography*, **36**, 1435–1445.
- Triantis, K.A., Mylonas, M., Lika, K. & Vardinoyannis, K. (2003) A model for the species–area–habitat relationship. *Journal of Biogeography*, **30**, 19–27.
- Triantis, K.A., Guilhaumon, F. & Whittaker, R.J. (2012) The island species–area relationship: biology and statistics. *Journal of Biogeography*, **39**, 215–231.
- Triantis, K.A., Economo, E.P., Guilhaumon, F. & Ricklefs, R.E. (2015) Diversity regulation at macro-scales: species richness on oceanic archipelagos. *Global Ecology and Biogeography*, **24**, 594–605.
- Valente, L.M., Phillimore, A.B. & Etienne, R.S. (2015) Equilibrium and non-equilibrium dynamics simultaneously operate in the Galápagos islands. *Ecology Letters*, **18**, 844–852.
- Ward, D.F., Beggs, J.R., Clout, M.N., Harris, R.J. & O'Connor, S. (2006) The diversity and origin of exotic ants arriving in New Zealand via human-mediated dispersal. *Diversity and Distributions*, **12**, 601–609.
- Ward, P.S., Brady, S.G., Fisher, B.L. & Schultz, T.R. (2015) The evolution of myrmicine ants: phylogeny and biogeography of a hyperdiverse ant clade (Hymenoptera: Formicidae). *Systematic Entomology*, **40**, 61–81.
- Weigelt, P. & Kreft, H. (2013) Quantifying island isolation – insights from global patterns of insular plant species richness. *Ecography*, **36**, 417–429.
- Whittaker, R. (1998) *Island biogeography: ecology, evolution, and conservation*. Oxford University Press, Oxford.
- Wilson, E.O. (1959) Adaptive shift and dispersal in a tropical ant fauna. *Evolution*, **13**, 122–144.
- Wilson, E.O. (1961) The nature of the taxon cycle in the melanesian ant fauna. *The American Naturalist*, **95**, 169–193.
- Wilson, E.O. & Taylor, R. (1967a) An estimate of the potential evolutionary increase in species density in the Polynesian ant fauna. *Evolution*, **21**, 1–10.
- Wilson, E.O. & Taylor, R. (1967b) The ants of Polynesia (Hymenoptera: Formicidae). *Pacific Insects Monograph*, **14**, 1–109.
- Witter, M.S. & Carr, G.D. (1988) Adaptive radiation and genetic differentiation in the Hawaiian silversword alliance (Compositae: Madiinae). *Evolution*, **42**, 1278–1287.
- Yamaguchi, R. & Iwasa, Y. (2013) First passage time to allopatric speciation. *Interface Focus*, **3**, 20130026.

## SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

**Appendix S1** Supplemental methods, analysis and figure.

## DATA AVAILABILITY

The species list, classification, and species–island incidence matrix are available on Dryad (doi:10.5061/dryad.2f7b2).

## BIOSKETCH

**Evan P. Economo** is interested in theoretical and empirical approaches to understanding biodiversity patterns and processes in a geographical context. He is particularly fascinated by the ecology, evolution, and biogeography of ants.

Author contributions: E.P.E., M.J., E.M.S. conceived of the study, all authors contributed and processed the data, E.P.E. analysed the data, E.P.E. led the writing, with input from all co-authors.

---

Editor: Kostas Triantis