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12   Assembling a species-area curve through

13   colonization, speciation and human-

14   mediated introduction

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19   Evan P. Economo[1,2]*, Milan Janda[3,4], Benoit Guénard [5], & Eli Sarnat[1,6]

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23   [1]*Okinawa Institute of Science and Technology Graduate University*

24   *1919-1 Tancha, Onna-son, Okinawa 904-0495, JAPAN*

25   **correspondence: evaneconomo@gmail.com*

26

27   [2]*Department of Ecology & Evolutionary Biology*

28   *University of Michigan*

29

30   *³Biology Center, Czech Academy of Sciences*

31

32   *⁴Cátedras CONACyT, Laboratorio Nacional de Análisis y Síntesis Ecológica, UNAM*

33

34   *⁵School of Biological Sciences, The University of Hong Kong*

35

36   *⁶Antwork Consulting, LLC*

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52   # Abstract

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54   **Aim:** The fundamental biogeographic processes of colonization, speciation and

55   extinction shape island biotas in space and time. On oceanic islands, area and

56   isolation affect these processes and resulting biodiversity patterns. In the

57   Anthropocene, a new human-mediated colonization dynamic is altering insular

58   ecosystems worldwide. Here, we test predictions about the roles of archipelago area

59   and isolation in structuring ant diversity patterns through effects on both natural and

60   anthropogenic biogeographic processes.

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62   **Location:** Tropical Pacific islands.

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Methods: We compiled a comprehensive dataset of ant faunal compositions across tropical Pacific archipelagoes. 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 archipelagoes. The number of colonizing lineages of each archipelago is strongly driven by the isolation of the archipelago. Endemic species are present in large archipelagoes of low and intermediate isolation. The most remote archipelagoes are nearly devoid of endemic lineages and their ant faunas are largely composed of Pacific tramp species and exotics brought from outside the Pacific.

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 archipelagoes. Cladogenesis mediates the isolation effect and increases the area effect through the differential radiation of lineages in large archipelagoes. 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 biogeographic processes can occur to achieve these limits.

Introduction

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

96   *al.*, 2008; Triantis *et al.*, 2012). Since MacArthur and Wilson's theory, many authors

97   have demonstrated that area and isolation can affect species richness through different

98   ecological and evolutionary pathways in addition to colonization and extinction rates,

99   particularly when considering the role of speciation in building island biotas

100 (Whittaker, 1998; Losos & Schluter, 2000). In general, the interplay of colonization,

101 extinction and speciation contribute to species-area and species-isolation relationships

102 that depend strongly on physiographic and biotic factors and vary considerably across

103 different regions and taxonomic groups (Patiño *et al.,* 2014).

104   Here we consider both the natural and anthropogenic processes shaping

105 species-area and species-isolation patterns of ant diversity in the tropical Pacific

106 islands. In particular, extant species richness has been assembled through three

107 processes. First, there is the colonization of islands by lineages from other areas. A

108 longstanding tenet of island biogeography theory is that colonization rates are

109 controlled by isolation, the remoteness of an island or archipelago from potential

110 colonizing sources. This should lead to a decline of colonizing lineages reaching

111 more remote Pacific archipelagoes. Area may have an additional effect on

112 colonization rate, as larger archipelagoes may be correspondingly larger targets for

113 dispersing propagules (Lomolino 1990).

114   Second, cladogenic speciation builds richness from the pool of colonizing

115 lineages. Larger areas may promote speciation (Rosenzweig, 1995; Whittaker, 1998;

116 Losos & Schluter, 2000; Kisel & Barraclough, 2010), while different levels of

117 isolation may depress or promote speciation (Yamaguchi & Iwasa, 2013).

118   Third, against this canvas of natural biogeographic patterns, the modern era

119 has unleashed a new dynamic of human-mediated dispersal and colonization that is

120 rapidly changing the species richness of many islands (Sax *et al.*, 2002; Cassey *et al.*,

121 2005; Gillespie *et al.*, 2008). These can be considered natural experiments in ecology

122 and evolution that can be used to test predictions of island biogeography theory. For

123 example, a recent analysis of Caribbean anoles (Helmus *et al.*, 2014) demonstrated

124 the roles of colonization, speciation, and human-mediated introduction in adding

125 species richness to islands that were otherwise depauperate in species richness.

126 Islands may be depauperate in native richness due to limitations to colonization, for

127 example because they are highly isolated, or due to limitations on speciation. Even

128 when ecological opportunity exists on an island, speciation rates may be limited in

129   small islands because spatial scales of landscapes are too small to allow geographic

130   divergence (Kisel & Barraclough, 2010).

131   Here we consider both the historical and contemporary processes assembling

132   ant faunas in the Pacific islands. Our study taxon, ants, are among Earth's most

133   dominant animal groups (Hölldobler & Wilson, 1990), and understanding the

134   ecological and evolutionary dynamics that assemble ant communities enriches our

135   understanding of terrestrial ecosystems. Ongoing human-mediated ant transfers are

136   unintentional experiments that illuminate the forces regulating ecological

137   communities, and are also major economic and conservation concerns in their own

138   right (McGlynn, 1999; Holway *et al.*, 2002; Lach & Hooper-Bui, 2009). Native ants

139   are a significant component of the threatened, endemic biodiversity of the Pacific

140   islands (Sarnat & Economo, 2012) and exotic ants are a major concern for

141   biodiversity conservation, agriculture and public health in the region (Jourdan, 1997;

142   Le Breton *et al.*, 2003; O'Dowd *et al.*, 2003; Krushelnycky *et al.*, 2005; Lach &

143   Hooper-Bui, 2009).

144   This Pacific ant system is of further interest due to its historical role in the

145   development of biogeographic theory. In a series of papers written a half century ago

146   (Wilson, 1959, 1961; Wilson & Taylor, 1967a, 1967b), E.O. Wilson and colleagues

147   examined some of the first species-area curves and produced several synthetic ideas

148   regarding faunal dynamics – including the *taxon cycle* (Ricklefs & Bermingham,

149   2002; Lomolino & Brown, 2009). In addition, the system partly inspired the

150   equilibrium island biogeography theory (MacArthur & Wilson, 1963, 1967). Wilson

151   argued that across Melanesia there is no apparent effect of isolation on island species

152   richness, and argued that while isolation limits colonization of lineages, this is

153   compensated by greater rates of apparent *in situ* speciation (Wilson, 1959, 1961).

154   Later, in their monographic treatment of Polynesian ant biodiversity, Wilson & Taylor

155   (1967b) interpreted the lack of endemic ants east of Samoa as evidence that ants did

156   not reach the eastern archipelagoes through natural dispersal. The eastern ant faunas,

157   a mix of widespread Pacific species and exotics from outside the Pacific, have

158   generally been thought to be assembled primarily through human introduction

159   (Wilson & Taylor, 1967b; Morrison, 2014).

160   Until recently, however, Pacific ant biogeography had not been revisited, and

161   faunal patterns on a biogeographic scale remain unclear. In studies focusing on

eastern Polynesia, Morrison (1996a, 1996b, 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 dataset, 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 & 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 approximately 1.6 million individual species-occurrence records. The GABI data can be viewed through the web application antmaps.org (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

195   islands within Fiji) for two reasons, a) because within archipelagoes sampling

196   intensity is usually more variable across islands, and b) even if sampling were not an

197   issue, we are comparing patterns of faunal assembly across independent

198   biogeographic units, not landscape scale community processes among islands of a

199   given archipelago. We felt these concerns outweighed the disadvantages of this

200   approach, namely that the judgment of what constitutes an independent biogeographic

201   unit can be subjective in certain cases. Several Pacific archipelagoes, notably

202   including New Caledonia and Vanuatu, are too undersampled to include in our

203   analyses. This left 19 islands and archipelagoes which form the basis of our analysis

204   (Table 1, Figure 1). The full species list and island incidence matrix are archived on

205   dryad (doi xxxx).

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207   **Categorization of species:** The combined fauna of the Pacific archipelagoes

208   (excluding New Guinea, Vanuatu, New Caledonia) totaled 601 species. To facilitate

209   analysis, we categorised these species into four groups based on available evidence of

210   geographic distribution, taxonomy and phylogeny. These were a) *Endemic*: found

211   only on a single island/archipelago, b) *Native*: not endemic to an archipelago but

212   considered native to the Pacific region across its range, c) *Pacific Tramp*: species

213   most likely native to part of the Pacific region, but probably spread by humans to

214   other parts as well, and d) *Exotic:* those native to other biogeographic regions and

215   introduced into the Pacific region through human commerce.

216   While the other categories are straightforward, the status and biogeographic

217   history of Pacific Tramp species is a confounding issue in our understanding of

218   Pacific ant biodiversity (Morrison, 2014). These species are generally derived from

219   Indo-Australian lineages and are widely distributed within but not outside the region,

220   indicating they were not brought from the outside through human commerce after the

221   arrival of Europeans. However, they could be "Palaeo-invasives" spread across the

222   Pacific by early human migrations, and they could have been subsequently spread by

223   commerce after the arrival of Europeans. These species often have ecological

224   characteristics more typical of human-introduced species, such as affinity for

225   disturbed open habitats, and have been documented to be transported by humans

226   during the modern era (Ward *et al.,* 2006). Also, many of them have reached remote

227   areas, such as Hawaii, but it is unlikely this is due to natural dispersal (but see

228 Horrocks *et al.*, 2013). On the other hand, it is also possible that these species are
229 naturally widespread through at least parts of their range. These species have been
230 interpreted as naturally widespread "Stage I" species by Wilson under the taxon cycle
231 hypothesis. Economo & Sarnat (2012) showed that these species had a markedly
232 different habitat distribution than known exotic species in Fiji. In particular, while
233 both groups have affinities for disturbed areas, Pacific Tramp species peak in relative
234 abundance in low-elevation forest. In other taxonomic groups, adaptation to disturbed
235 habitat is known to be associated with wide and expanding ranges, even without the
236 influence of humans. Furthermore, genetic work has supported the notion that at least
237 some of these species are native to the western Pacific (Clouse *et al.,* 2014). Finally,
238 the fact that some of them are transported by humans today (Economo & Sarnat,
239 2012; Ward *et al.,* 2006) does not rule out the possibility that they naturally achieved
240 a large geographic range. Indeed, even if the taxon cycle interpretation is correct, we
241 would expect these species to be good candidates for future human-mediated
242 dispersal, given their commonness, high abundance, and tolerance for disturbed
243 habitats. In summary, these species' ranges reflect some combination of natural
244 dispersal, palaeo-invasion mediated by early human migrations, and dispersal via
245 post-European human commerce. Only future high-resolution population genetic
246 studies and/or palaeoentomological studies will solve the issue definitively.

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

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254

255 **Estimation of colonizing lineage counts:** To separate the roles of colonization and
256 speciation in building species richness, we estimated the number of colonizing
257 lineages that originally seeded the extant faunas of each archipelago (i.e. the number
258 of colonizations that the extant fauna descended from). A very precise dissection of
259 the colonization history requires comprehensive phylogenies of both island and
260 mainland faunas, which are not available for many ant groups in the Pacific.

261   However, some phylogenetic evidence is available, and with taxonomic and

262   biogeographic evidence we are able to put a lower and upper bound on the number of

263   colonizing lineages responsible for each island fauna. We performed all analyses

264   using the upper and lower limits in order to bracket this uncertainty. We found these

265   lower and upper estimates using the following steps. First, the number of putatively

266   monophyletic genera on each archipelago gives an absolute lower bound on the

267   number of colonizing lineages, as only one of the 84 genera in the Pacific is endemic

268   (*Poecilomyrma* in Fiji) and its sister lineage is not in Fiji (Ward *et al.*, 2015). Second,

269   native-but-not-endemic species are assumed to have arrived through colonization to

270   each island, each adding a single lineage to the colonizing lineage count. This leaves

271   cases where an island has multiple congeneric endemic species as the most difficult

272   components of species richness to attribute to either colonization or speciation (e.g.

273   two endemic species of *Pheidole* in Fiji could have descended from either a single

274   colonization followed by *in situ* cladogenesis, or two colonizations followed by

275   anagenetic speciation of each). For this determination, we first used available

276   phylogenetic evidence, notably phylogenies for *Lordomyrma* (Lucky & Sarnat, 2010),

277   *Pheidole* (Sarnat & Moreau 2011; Economo *et al.*, 2015a, 2015b), *Nylanderia* (P.

278   Matos-Maravi, *pers. comm.*), and (one group of) *Camponotus* (Clouse *et al.*, 2015). In

279   a few cases, when there was a well-documented radiation that was morphologically

280   distinct from all other members of the genus in the region and are almost certainly *in*

281   *situ* radiations, we made the assumption that they were monophyletic. When

282   phylogenies or other strong morphological evidence were not available, endemic

283   species were considered to have a lower bound that assumes multiple congeneric

284   endemics on the same island are descended from a single colonist lineage, and an

285   upper bound that assumes that each endemic is derived from an independent

286   colonization (if there are *n* endemics of a genus on an island, the lower bound is one

287   colonization and the upper bound is *n* colonizations for that genus).

288

289   **Statistical Analyses:** We performed a set of regression analyses to estimate the

290   species-area and species-isolation relationships in the Pacific ants. In particular, we

291   sought to disentangle the different processes underlying those patterns by sequentially

292   adding components of species richness that reflect the basic patterns of colonization,

293   speciation, and exotic introduction. First, to estimate the role of colonization, we

294   performed regression on the number of colonizing lineages against area and isolation.

295   Second, we regressed total native richness against area and isolation. The difference

296   between colonizing lineages and total native diversity reflects the outcome of *in situ*

297   cladogenesis. Finally, we regressed native and total richness against area and isolation

298   to represent the current biodiversity patterns across the Pacific. To provide context to

299   the species-area curve patterns in the Pacific, we used richness counts from six large

300   areas for visualization although did not include them in the regressions.

301   We measured isolation as the nearest land point of the island group to the

302   closest large area to the west (New Guinea, Australia, or Asia) using the application

303   Google Earth. Ant dispersal in the Pacific occurs generally in a west-to-east pattern

304   with no documented cases of colonization of the Pacific archipelagoes in this study by

305   New World taxa. The west-to-east colonization pattern of the Pacific is a common

306   finding across groups and is thought to be due to a lack of stepping stones between

307   the New World and the remote Pacific islands (Weigelt & Kreft, 2013). Archipelago

308   areas and maximum elevations were compiled from Wikipedia (www.wikipedia.org).

309   The two main sources of uncertainty in our data were a) the estimates of the

310   colonizing lineage counts and b) the native/exotic status of the Pacific Tramp species.

311   To account for uncertainty in the former, we performed all analyses by either using

312   the lower or upper bound estimates of colonizing lineages, which should bracket the

313   true values. To account for uncertainty of the Pacific Tramp species, we performed

314   analyses assuming either they are all native or assuming they are all exotic, which

315   should also bracket the true values. Thus, in total we performed four permutations of

316   the analyses intended to integrate over the uncertainties in the data.

317   Although there are many biological and physical variables that could

318   potentially affect island diversity patterns, the size of the dataset and collinearity

319   between common predictor variables (e.g. island area and maximum elevation are

320   often correlated) makes simultaneous consideration of a large number of predictor

321   variables difficult. Our main goal is to quantify area and isolation relationships while

322   trying to ensure that other latent variables are not interfering with our inferences.

323   Thus, we consider maximum elevation as an additional potential predictor, and due to

324   the role humans in driving exotic introductions (Roura-Pascual *et al.*, 2016), we also

325   include human population and GDP (PPP) as potential predictors of total (but not

326   native) richness.

327   We log$_{10}$-transformed species/lineage numbers and area values before

328 regression, reflecting the most commonly used power-law form of species-area

329 relationships (Tjørve, 2003, 2009; Triantis *et al.,* 2012). Many authors have extended

330 species area-curves to include additional variables (e.g. Tjørve, 2009; Triantis *et al.*,

331 2003). For trivariate and multivariate regressions, we included log-transformed

332 additional variables without combination variables or interaction terms, which is a

333 common form used in extending the species-area relationship (Tjørve, 2009).

334 Isolation was not log-transformed, following convention in island biogeography (e.g.

335 Weigelt & Kreft, 2013).

336   We used multiple linear regression in a multi-model, information-theoretic

337 framework generally following the procedure described in Grueber *et al.* (2011). The

338 strategy involves evaluating a candidate set of statistical models including different

339 combinations of predictor variables, ranking them based on Akaike's Information

340 Criterion corrected for small sample size (AICc) score, and establishing a final model

341 set of those within a ΔAICc of 4 from the top model. The model scope of the

342 candidate model set was all possible subsets of the full model, but excluding models

343 with pairs of predictor variables that were highly collinear (Spearman's ρ >0.7). The

344 parameters are then averaged across the top model set, weighting models by score.

345 Further details are provided in Appendix S1. Goodness-of-fit was assessed using R^2.

346 We also used bivariate regressions of diversity components on area and isolation

347 individually to estimate the variance explained by each factor. The analyses above

348 were performed in the R computing environment (R Core Team, 2015) using core

349 functions and functions from the 'MuMIn{}' package (Bartoń, 2015).

350

Results

352   Our data compilation found 601 species across the 19 archipelagoes, including

353 151 native, 359 endemic, 36 tramp and 55 exotic species. In general, the model

354 including area and isolation without other variables was the best fit to all components

355 of diversity (Fig. 2, Appendix S1). Only one regression included one of the other

356 variables (elevation) in the top model set, in which it had a very weak effect. Thus,

357 we present the full results of the model averaging in Appendix S1 but focus on area

358 and isolation relationships in the main text.

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

364   Speciation has added species richness to some archipelagoes, but only those
365 that are above ca. 3,500 km^2 and that are not too isolated to receive seed lineages. The
366 influence of speciation peaks in Fiji, which is of intermediate isolation and high area.
367 Total native diversity, which includes both species added through colonization and
368 speciation, is still correlated with both area and isolation. However, the dependency
369 of speciation on area has increased the strength of the species-area relationship (Fig.
370 2, Table 2).

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

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

380

381

Discussion

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

389   Across the Pacific, total ant richness is now strongly correlated with area, and
390 only secondarily correlated with isolation. However, this species-area curve arose
391 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 archipelagoes 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 archipelagoes 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
archipelagoes. The remote archipelagoes 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. Gillespie, 2004; Witter & Carr, 1988), if ant lineages were
able to colonize these archipelagoes 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 geographic and numerical scale of those palaeo-
invasions 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

425   and high dispersal ability. It is certain that after the arrival of Europeans, many new

426   species were subsequently brought into the Pacific from around the world and

427   continue to arrive today (Ward *et al.*, 2006; Krushelnycky *et al.*, 2005). Indeed, rates

428   of exotic ant accumulation on islands globally have been shown to be driven by

429   human-related variables (Roura-Pascual *et al.*, 2016).

430   Regardless of what assumption is made about the native or exotic status of the

431   Pacific Tramp species, the same overall pattern is evident; human-mediated exotic

432   introductions have filled empty regions of the species-area curve while reducing the

433   relative strength of the species-isolation relationship.

434   These results show a striking similarity to other recent results demonstrated in

435   Caribbean lizards (Helmus *et al.*, 2014), indicating there may be common patterns and

436   processes across disparate regions and taxa in both natural and Anthropocene

437   biogeography. Both the patterns exhibited in ants and anoles are consistent with the

438   general idea that island systems have something akin to a carrying capacity of species

439   that may or may not be reached through natural processes (Rabosky & Glor, 2010;

440   Triantis *et al.*, 2015; Valente *et al.*, 2015). This natural deficit leaves open ecological

441   space that can be filled by introduced species. Indeed, it is probably not an accident

442   that Hawaii has the largest deficit of native ants in the Pacific (and probably in the

443   world), and is one of the most invaded areas by ants in the world (McGlynn, 1999;

444   Krushelnycky *et al.*, 2005).

445   Much work remains to investigate the ecological and evolutionary

446   mechanisms behind these patterns. Most importantly, continued research efforts are

447   needed to better document the geographic distributions, evolutionary histories, and

448   ecologies of ant faunas in the Pacific Islands. With such multifaceted data

449   increasingly becoming available, nascent process-based quantitative approaches (e.g.

450   Triantis *et al.*, 2015; Valente *et al.*, 2015; Sukumaran *et al.*, 2016) hold promise for

451   linking aggregate diversity patterns to the biogeographic dynamics that generate them.

452   The Anthropocene has ushered in an unintentional, global-scale,

453   biogeographic transplantation experiment. This has, of course, been an ecological

454   disaster, and nowhere more so than the Pacific islands (McGlynn, 1999; O'Dowd *et*

455   *al.* 2003; Krushelnycky, 2005). Our understanding of natural biogeographic dynamics

456   and evolution after colonization can help us interpret, understand, and predict the

457   future of these human-mediated transfers (Gillespie *et al.*, 2008; Economo & Sarnat,

458 2012; Ricklefs, 2005). In turn, if we ask the right questions, the patterns and dynamics

459 of human mediated invasions can illuminate the ecological factors and processes

460 regulating diversity patterns.

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468

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

643

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

645

646

647   **Data Availability:** The species-list, classification, and species-island incidence

648   matrix are available on Dryad (doi will be added in proof once dryad submission is

649   complete).

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652 **Biosketch:**

653 **Evan P. Economo** is interested in theoretical and empirical approaches to

654 understanding biodiversity patterns and processes in a geographic context. He is

655 particularly fascinated by the ecology, evolution, and biogeography of ants.

656

657 **Author Contributions:** E.P.E., M.J., E.M.S. conceived of the study, all authors

658 contributed and processed the data, E.P.E. analysed the data, E.P.E. led the writing,

659 with input from all co-authors.

660

661 **Editor:** Kostas Triantis

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

Island Group	Area (km^2)	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
Samoan 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

662 **Table 2:** Bivariate and trivariate linear regression statistics for ant species richness

663 and area/isolation of the Pacific archipelagoes. The parameters z and β are the slope

664 of the species area power function and the regression coefficient for Z-scaled

665 isolation, respectively. The high and low estimates of colonizing lineages bound

666 uncertainty in the number of cladogenic speciation events on the islands. Regressions

667 for colonizing lineages and total native richness were performed under the alternate

668 assumption that Pacific Tramp species were native or exotic to the Pacific islands.

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	log10(Area) (bivariate)			Isolation (bivariate)			log10(Area) and Isolation (trivariate)			
	z (SE)	ΔAICc	R^2	β (SE)	ΔAICc	R^2	z (SE)	β (SE)	ΔAICc	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

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683   **Figure Legends**

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685   **Figure 1:** The Pacific island groups included in this study are highlighted.

686   Continental areas, and those archipelagoes lacking sufficient sampling, were excluded

687   from the analyses.

688

689   **Figure 2:** The species-area curves (top row) and species-isolation curves (bottom

690   row) for components of ant richness in Pacific archipelagoes (black dots). The gray

691   dots are large islands (Borneo, Madagascar, New Guinea, Sumatra, Sulawesi, Java,

692   Sri Lanka) not included in our analysis, but included on the plots to provide context

693   for the Pacific SA curve. The black line is a regression on Pacific archipelagoes

694   only, while the grey line is the regression on total richness including the large areas

695   (included on all plots to show how the Pacific line gets closer). The relationships

696   depicted in panels a-f and g-l assume that "Pacific Tramp" species are native or

697   exotic, respectively. These plots use the low estimate of colonizing lineage counts,

698   see supplemental info for the high estimate.

699

700   **Figure 3:** Variance explained by components of species richness by univariate

701   regressions with area, isolation, and multivariate regression of area and isolation. The

702   panels reflect low (a,b) and high (c,d) colonizing lineage counts and assume Pacific

703   Tramps are native (a,c) or exotic (b,d).

120° E 150° E 180° 150° W

Japan

Hawaiian Is.

0   500   1,000
Kilometers
N

20° N

Mariana Is.

20° N

Yap

Philippines

Chuuk

Pohnpei

Marshall Islands

Palau (PA)

0°

0°

New Guinea

Solomon Is.

Tokelau

Cook Islands

Marquesas Is.

Wallis & Futuna

Vanuatu

Samoa

Society Is.

Tuamotu Is.

20° S

New Caledonia

Fiji

Niue

20° S

Australia

Tonga

Austral Is.

Gambier Is.

120° E 150° E 180° 150° W