Microbial island biogeography: isolation shapes the life history characteristics but not diversity of root-symbiotic fungal communities

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Microbial island biogeography: isolation shapes the life history characteristics but not diversity of root-symbiotic fungal communities

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Abstract

Island biogeography theory is one of the most influential paradigms in ecology. That island characteristics, including remoteness, can profoundly modulate biological diversity has been borne out by studies of animals and plants. By contrast, the processes influencing microbial diversity in island systems remain largely undetermined. We sequenced arbuscular mycorrhizal (AM) fungal DNA from plant roots collected on 13 islands worldwide and compared AM fungal diversity on islands with existing data from mainland sites. AM fungal communities on islands (even those > 6000 km from the closest mainland) comprised few endemic taxa and were as diverse as mainland communities. Thus, in contrast to patterns recorded among macro-organisms, efficient dispersal appears to outweigh the effects of taxogenesis and extinction in regulating AM fungal diversity on islands. Nonetheless, AM fungal communities on more distant islands comprised a higher proportion of previously-cultured and large-spored taxa, indicating that dispersal may be human-mediated or require tolerance of significant environmental stress, such as exposure to sunlight or high salinity. The processes driving large-scale patterns of microbial diversity are a key consideration for attempts to conserve and restore functioning ecosystems in this era of rapid global change.

Introduction

Islands have figured prominently in the development of ecological theory (e.g., Darwin, 1945; MacArthur and Wilson, 1967; Simberloff and Wilson, 1970). With their theory of island biogeography, MacArthur and Wilson (1967) argued that the equilibrium number of species inhabiting an island or other isolated habitat patch is determined by the balance between immigration and speciation on one hand and emigration and extinction on the other. They also suggested that island characteristics – notably the size of an island and its remoteness from potential source communities (i.e., mainlands) – modulate the importance of these processes, such that a positive species-area relationship leads to higher species richness on large islands, while a negative species-isolation relationship results in lower richness on remote islands. Descriptive and rarely experimental studies have lent empirical support to the theory and have confirmed both species-area and species-isolation relationships (Whittaker and Fernandez-Palacios, 2007). The theory has become one of the most influential ecological paradigms and is central to several applied (e.g. conservation ecology) and theoretical (e.g., metapopulation and metacommunity theories) disciplines (Patiño *et al*., 2017). Moreover, the study of island systems continues to provide new insights into a range of ecological questions, including those related to the process of community assembly (Santos *et al*., 2016).

Most empirical tests of island biogeography theory have focused on animals or plants, and attempts to understand equivalent processes acting on micro-organisms have mainly studied habitat fragmentation at the landscape-level or below (Andrews *et al*., 1987; Mangan *et al*.,

2004; Bell *et al*., 2005; Peay *et al*., 2010). Despite notable work on certain taxonomic groups (e.g. Fungi; Tedersoo *et al*., 2014), information about the large-scale biogeography of micro-organisms is lacking (Bardgett and van der Putten, 2014). One group of micro-organisms whose global biogeography has been relatively well characterised is the arbuscular mycorrhizal (AM) fungi (Öpik *et al*., 2006; Davison *et al*., 2015). AM fungi (subphylum Glomeromycotina; Spatafora *et al*., 2016) live in association with the roots of about 80% of terrestrial plant species, gaining plant-assimilated carbon while supplying their hosts with nutrients (mainly P) and resistance to abiotic stress and pathogens (Smith and Read, 2008). At small scales, the diversity patterns of these essential plant symbionts are influenced by both niche and neutral processes (Lekberg *et al*., 2007; Dumbrell *et al*., 2010), including some degree of dispersal limitation, i.e. an inability of taxa to reach potentially suitable habitats in a given time frame (Davison *et al*., 2016). Nonetheless, AM fungi are found on all continents and many approximately species-level phylogroups (phylogenetically-defined groupings of taxa described by DNA sequences) have been shown to exhibit wide distributions, frequently spanning multiple continents (Davison *et al*., 2015; Savary *et al*., 2018). AM fungi are soil-dwelling organisms and may disperse using spores or by transport of hyphal or colonized root fragments (Smith and Read, 2008). Limited evidence exists for a number of potential dispersal vectors (including wind [Egan *et al*., 2014], invertebrates [Gange *et al*., 1993], mammals [Lekberg *et al*., 2011], birds [Nielsen *et al*., 2016] and water [Harner *et al*., 2011]), but the relative importance of each remains unquantified. It is even unclear whether the wide distributions of AM fungal taxa are the result of incremental small-scale movement or long-distance dispersal events.

93 Evidence from plants indicates that taxon arrival and persistence on isolated islands is
94 correlated with aspects of life history, such as the traits influencing propagule production,
95 dispersal and establishment (Whittaker and Fernandez-Palacios, 2007; Jacquet *et al*., 2017;
96 though see Carvajal-Endara *et al*., 2017). For example, pteridophytes – a group of wind-
97 dispersed plants with very small diaspores – are randomly distributed throughout the Galapagos
98 islands, while the distributions of comparatively larger-seeded plants are correlated with island
99 size and isolation within the archipelago (Adsersen, 1988; Vargas *et al*., 2014). By contrast,
100 assigning life history characteristics to micro-organisms in environmental samples remains
101 extremely challenging (though metagenomic studies represent a promising avenue; Louca *et al*.,
102 2016; Nelson *et al*., 2016), and there have been few attempts to connect micro-organism life
103 history and biogeography (Green *et al*., 2008; Andrew *et al*., 2016; Halbwachs *et al*., 2017).
104
105 Some AM fungal taxa produce spores, but DNA-based surveys of environmental samples have
106 revealed a significant proportion of AM fungal diversity that does not correspond to known
107 sporulating taxa (Öpik and Davison, 2016). While some taxa known only from environmental
108 DNA may yet be shown to produce spores, abundantly sporulating and easily cultured taxa
109 (hereafter 'cultured') are presumed to be relatively efficient dispersers and have been broadly
110 characterised as ruderals (i.e., tolerant of disturbance; van der Heijden, 2008, Ohsowski *et al*.,
111 2014). Among such taxa, certain spore characteristics can also be used to infer a more detailed
112 life history strategy (e.g. spore size). This means that a small number of life history
113 characteristics are available for a fraction of recorded AM fungal diversity, but that alternative

114 traits and methods (e.g. DNA-based) are required for a complete survey of naturally-occurring
115 AM fungal communities.
116
117 All else being equal, smaller fungal propagules are more efficiently transported by wind (Nathan
118 *et al*., 2008; Norros *et al*., 2014). Therefore, if wind is an important dispersal vector for AM
119 fungi, one might expect cultured (i.e., known to be spore-producing) and specifically small-
120 spored AM fungal taxa to predominate on islands. Conversely, among vascular plants and other
121 fungi, large propagules are associated with establishment success in harsh conditions (Westoby
122 *et al*., 2002; Norros *et al*., 2015). This may equally apply to AM fungal spores; for instance, large-
123 spored *Gigaspora* are capable of multiple germinations (Bago *et al*., 1998), and such spores stay
124 viable for several years and through changing environmental conditions (Klironomos *et al*.,
125 2001; Varga *et al*., 2015). In addition, vascular plants may arrive at islands via floating in
126 seawater (Vargas *et al*., 2014, Heleno and Vargas, 2015), in which case the plant propagules are
127 often relatively large (van der Pijl, 1982). If transport in seawater, or other long distance
128 dispersal mechanisms that impose significant stress, are important for AM fungi, large-spored,
129 cultured taxa might be expected to predominate on islands. Finally, the origin of fungal
130 propagules may be an important determinant of island AM fungal life history characteristics.
131 Human-mediated transport might favour cultured taxa since these are known to be associated
132 with anthropogenic habitats (Ohsowski *et al*., 2014).
133
134 We sampled AM fungal communities on oceanic islands worldwide, allowing us to test
135 hypotheses related to AM fungal biogeography and dispersal. We predicted that diversity or

trait responses to island conditions should be most apparent on small or isolated islands, reflecting species-area and species-isolation relationships. Furthermore, we expected that the effects of isolation on the prevalence of culturable taxa and spore size estimates in AM fungal communities should provide evidence about the dispersal characteristics of AM fungi. If AM fungal dispersal is largely conducted through incremental small-scale dispersal events, then island isolation should represent a significant barrier to dispersal and consequently island community composition should be stochastic and characterised by lower diversity and greater endemism than mainland communities. Conversely, if AM fungi are efficient long-distance dispersers, then the taxon pools capable of colonising island and mainland communities should be similar, and endemism should not be particularly pronounced on islands. If small-spored taxa predominate on islands, this might indicate an important role of wind dispersal. However, if large-spored taxa predominate, it might indicate a dispersal or establishment route that requires significant stress tolerance (e.g., seawater transport). Equally, a predominance of cultured AM fungal taxa on islands might indicate that human-mediated transport plays a role.

Materials and Methods

Sampling island AM fungal communities

We collected samples from 13 islands worldwide: in the Arctic Ocean (Svalbard), Baltic Sea (Öland and Saaremaa), Caribbean (Guadeloupe), Pacific Ocean (New Caledonia, Tikehau, Tahiti), Tasman sea (Tasmania), Atlantic Ocean (Iceland, Sal, Santiago) and Mediterranean sea (Mallorca, Crete) (Figure 1; Supplementary Methods and Supplementary Table S1). All islands

158 besides Mallorca, Tasmania and possibly New Caledonia were of oceanic (i.e., volcanic) origin or
159 were submerged following isolation from a continental mainland (Supplementary Methods).
160 This means that vicariance was not a factor in the formation of most of the island AM fungal
161 communities under investigation; rather taxa must have colonised following island formation.
162 We compared island data with an existing global mainland data set, collected and analysed in an
163 identical manner by Davison *et al*. (2015).
164
165 On each island we identified one or two sites in the locally-present ecosystems that were least
166 disturbed by human activities. Following the design used by Davison *et al*. (2015), we sampled
167 two plots at each study site, representing visually homogeneous vegetation and habitat
168 conditions. The plots were approximately 30 x 30 m, and the distance between plots generally
169 ranged between several hundreds of meters and several km. In each plot, we generally selected
170 four locally-abundant arbuscular mycorrhizal (AM) plant species and excavated four randomly-
171 chosen individuals of each plant species (Supplementary Table S1). However, fewer species
172 were sampled on Tikehau and Tahiti, and in these cases more individuals (up to 10 per species)
173 were sampled (Supplementary Table S1). Soil and other material adhering to plant roots was
174 carefully removed by hand. A root sample of approximately 20 cm was wrapped in tissue paper
175 and placed in a plastic bag containing silica gel. A pooled topsoil sample (approximately 500 g)
176 comprising 10 individual samples was collected from all plots except Tasmania. For details of soil
177 chemical analyses and other recorded environmental variables see Supplementary Methods and
178 Table S1.
179

Molecular methods and bioinformatics

We followed the molecular methods and bioinformatics used by Davison *et al*. (2015). A full description of these methods is presented in the Supplementary Methods. Briefly, we amplified AM fungal DNA (partial SSU rRNA gene) from root samples and subjected this to high-throughput (454) sequencing. We used BLAST (Altschul *et al*., 1990) to match (i) the obtained 'island' sequence reads and (ii) the 'mainland' sequencing reads from Davison *et al*. (2015) against known virtual taxa (VT; i.e. phylogroups) from the Maarj*AM* database (Öpik *et al*., 2010; Supplementary Table S2). Using the same classification criteria used to define VT in Maarj*AM*, we then searched for previously unrecorded VT among the reads not matching an existing VT (Supplementary Table S2). We used the Maarj*AM* database to identify those VT that could be associated with an AM fungal morphospecies (i.e., species described on the basis of spore traits from a cultured organism; Supplementary Table S3). VT were defined as 'cultured' if they contained sequences derived from an isolate of known morphospecies identity. For cultured VT we estimated a mean spore diameter based on the spore characteristics of component morphospecies (Supplementary Table S3). Finally we coestimated evolutionary time-scale and phylogeny for all known VT using BEAST (Drummond *et al*., 2012). The phylogeny, VT-morphospecies associations and spore diameter estimates are shown on Figure 2. Sequencing data generated in this study have been submitted to EMBL (study accession PRJEB20015). This includes raw sequencing reads from all runs and a set of representative sequences matched against different VT (where available, 2 sequences per VT from each host plant in each plot; accessions LT828649-LT835058). Sequencing data from Davison *et al*. (2015) used for reanalysis in this study are also available from EMBL (study accession PRJEB9764).

Statistical analysis

We primarily focused on AM fungal diversity and life history characteristics derived from taxon lists (i.e. presence-absence), since the predictions of island biogeography theory mainly relate to the distribution rather than abundance of organisms. However, since organism abundance is expected to influence the functional properties of communities and ecosystems (Grime, 1998), we included several analogous approaches incorporating the relative abundance of VT in samples (estimated from the relative abundance of sequencing reads). We expected these parallel analyses to provide an indication of whether island biogeographic processes were reflected by ecologically relevant changes in community assembly.

For each island and mainland site we estimated local endemism by calculating the number of VT that were recorded at the site and nowhere else. We also calculated an index of VT distribution for each site: the mean number of other sites globally occupied by the VT present.

For further analysis of AM fungal communities on islands and in the mainland set, we pooled the replicates within each host plant species per plot. Based on these plant-species-level community estimates (hereafter referred to as samples) we investigated community diversity, composition and trait characteristics using two modelling approaches: (i) *island biogeography models* (IB) only containing the explanatory variables 'set' (island vs mainland set) or 'island area' and 'island remoteness'; and (ii) *island biogeography and environment models* (IBE) which in addition to IB variables incorporated all available explanatory variables related to soil

chemistry (pH, N, P), altitude and climate (mean annual precipitation [MAP], mean annual temperature [MAT]). The purpose of the IBE models was to test the importance of island biogeographic processes after accounting for measured environmental differences among island and mainland samples. In all analyses besides those describing multivariate community composition, the variable 'island remoteness' was calculated as the Haversine distance (accounting for the curvature of the earth) separating each island from the closest continental coastline. In analyses of composition, each island site was paired with the closest measured mainland site (from Davison *et al*., 2015), and in these cases geographic separation was calculated as the Haversine distance separating the paired sites. This measure was highly correlated with the distance of each island from the closest continent (Pearson's $r = 0.97$, $P < 0.001$), though the rank order of islands changed.

We used PERMANOVA (function *adonis* from R package vegan; Oksanen *et al*., 2016) with Sørensen (abundance-unweighted) and Bray-Curtis (abundance-weighted) distance to estimate compositional differences between island and mainland samples. We also calculated mean pairwise distances between samples from each island and a paired mainland site (the geographically closest mainland site to each island; Supplementary Figure S1). These distances were regressed against island area and the geographic distance separating each island from its paired site. To place the effect of geographic separation on compositional distance in the context of compositional decay over continental land masses, we also included data points corresponding to all pairwise distances (compositional and geographic) between mainland sites within individual continents in the geographic distance analysis. We visualised community

246 composition using non-metric multidimensional scaling (NMDS; function metaMDS from vegan;
247 Sørensen distance, stress = 0.19).
248
249 For all island and mainland samples we calculated VT richness and two diversity estimators that
250 incorporate organism abundance: the asymptotic estimators for exponential Shannon and
251 reciprocal Simpson diversity (Chao *et al*., 2014). We did not generate an extrapolated estimate
252 of richness (Chao), since this estimator is not reliable beyond double the observed sample size
253 and the corresponding sample completeness; by contrast, the abundance-sensitive diversity
254 measures are generally robust in extrapolation to an asymptote (Chao *et al*., 2014). Among the
255 Pacific island samples, where as many as 10 replicates were sampled per host plant species, we
256 randomly selected 4 replicates per host prior to calculating diversity, in order to balance
257 sampling effort with the rest of the data set (Supplementary Table S1).
258
259 We also characterised each sample in terms of certain taxonomic and life history characteristics
260 of its component VT: the proportion of VT in each sample that belonged to the order
261 Glomerales; the phylogenetic diversity (mean pairwise distance; function mpd from R package
262 picante; Kembel *et al*., 2010) of VT present in each sample; the proportion of cultured VT in
263 each sample (i.e., representing cultured morphospecies); and the mean spore diameter of VT in
264 each sample, using those VT for which we had an estimate of this measure. We calculated these
265 taxonomic and life history indices using abundance unweighted (using presence-absence data)
266 and abundance-weighted (using the relative abundance of VT reads in samples) approaches. We
267 used linear or generalised linear mixed models (Bates *et al*., 2015; Pinheiro *et al*., 2016) to

assess how the community parameters (diversity and taxonomic or life history characteristics) differed between island and mainland samples and in relation to island remoteness and area. A detailed description of the modelling and randomization procedures used for inference is presented in the Supplementary Methods.

Results

Taxon distribution and endemism

We recorded 248 AM fungal virtual taxa (VT; i.e., phylogenetically-defined sequence groupings) from plant root samples collected on 13 islands worldwide (Figure 1, Supplementary Tables S1 & S2) and 252 VT from reanalysis of Davison *et al*.'s (2015) global mainland data set (also derived from plant roots and generated using identical field and bioinformatics methods; Supplementary Table S2). 223 VT were recorded from both island and mainland sites, with 25 and 29 VT recorded solely from island and mainland sites, respectively. Of 6 previously unrecorded VT, all were recorded from multiple sites, though the new *Claroideoglomus* VT (IS.Cl1) was only present on the remote atoll of Tikehau in the South Pacific. Island sites were more likely than mainland sites to harbour taxa that were recorded only at a single study site (i.e., endemic within our data set): 33% of island sites contained 1-4 such endemic VT; whereas 11% of mainland sites contained 1 such endemic VT (Wilcoxon Z = 2.09, P = 0.03). Correspondingly, island sites were composed of slightly less well distributed VT than mainland sites (mean ± SE number of other sites occupied by component VT: island sites = 15.4 ± 0.3, mainland sites = 16.4 ± 0.2; $F_{1,51} = 7.06$, P = 0.01).

290

291 *Island vs mainland communities*

292 There was a systematic but minor difference in AM fungal community composition between
293 island and mainland samples, both in models excluding (Island biogeography model; IB) and
294 accounting for (Island biogeography plus environment model; IBE) measured environmental
295 characteristics (PERMANOVA; Sørensen distance, IB model R^2 = 0.01 P = 0.004, IBE model R^2 =
296 0.01 P = 0.005; Figure 2 & Supplementary Figure S2). Models accounting for VT relative
297 abundance indicated a similar pattern (PERMANOVA; Bray-Curtis distance, IB model R^2 = 0.01 P
298 = 0.004; IBE model R^2 = 0.01 P = 0.005). However, island and mainland samples were dominated
299 by the same taxa (Figure 2 & Supplementary Figure S3) and did not differ significantly in any
300 measure of diversity (Figure 3 & Table 1) or in the level of any measured trait connected with
301 taxonomy or life history (Glomerales proportion, mean pairwise genetic distance, proportion of
302 cultured taxa, mean spore diameter; Table 1).

303

304 *Island remoteness and size*

305 Mean compositional distance (Sørensen) between AM fungal communities was positively
306 related to the geographic distance separating them (Figure 4; IB model, $P_{rand} < 0.001$; IBE model,
307 $P_{rand} < 0.001$); and was greater between island and paired mainland sites than between
308 mainland sites an equivalent distance apart (Figure 4; IB model, $P_{rand} < 0.001$; IBE model, $P_{rand} <$
309 0.001). Relationships based on relative abundance (Bray-Curtis distance) were similar
310 (Supplementary Figure S4). Mean compositional distance between paired island and mainland

311 sites did not vary significantly in relation to island area (IB model, P_{rand} = 0.06; IBE model, P_{rand} =
312 0.48).
313
314 No measures of diversity differed significantly in relation to island remoteness or island area
315 (Table 1). However, island remoteness significantly explained the proportion of Glomerales VT
316 in samples (lower on distant islands; IB & IBE models), the unweighted phylogenetic diversity of
317 samples (higher on distant islands; IBE model), the proportion of cultured VT in samples (higher
318 on distant islands; IBE model) and the mean spore diameter of VT in samples (higher on distant
319 islands; IB model; Table 1; Figure 5). Island area explained variation in the proportion of
320 Glomerales VT in samples (lower on large islands; IBE model; Table 1; Supplementary Figure S5).
321 Island remoteness and area both significantly explained the mean spore diameter of VT in
322 samples in abundance-weighted analyses (greater on small and distant islands; Supplementary
323 Table S4; Supplementary Figures S4 & S5).
324
325 **Discussion**
326
327 Here we report a first attempt to measure oceanic island biogeographic patterns in a group of
328 microbial organisms: plant symbiotic AM fungi. We recorded only very minor compositional
329 differences between island and mainland fungal communities and found no evidence of high
330 endemism on islands or significant differences between mainland and island fungal
331 communities in terms of diversity or characteristics reflecting taxonomy and life history.
332 Furthermore, neither island remoteness nor island area significantly explained AM fungal

diversity. These results indicate that isolation does not perceivably restrict immigration or promote endemism as a result of taxogenesis, in island compared with mainland communities, and suggest that long distance dispersal might be effective within this group of organisms. Such a pattern deviates considerably from those typically recorded among macroscopic organisms (Whittaker and Fernandez-Palacios, 2007). Nonetheless, we found that compositional distances between AM fungal communities on islands and paired mainland sites exceeded those observed between mainland sites of equivalent geographic separation. Furthermore, island remoteness was associated with certain taxonomic and life history characteristics that provide clues about AM fungal dispersal and establishment on distant islands.

Few endemic taxa among island AM fungal communities

Some case studies have identified previously unrecorded AM fungal phylogroups or morphospecies from island systems (Koske and Gemma, 1996; Melo *et al*., 2017). Measuring endemism is, however, contingent on the availability of comparative global data, while interpretation is also shaped by the taxonomic resolution of observations (Powell *et al*., 2011; see the Supplementary Methods for a discussion of VT resolution). Using the most comprehensive available comparative data set, we discovered six previously unrecorded AM fungal VT in this analysis, but only one was endemic to a single island (present at both sites on Tikehau, an atoll in the South Pacific Ocean). Furthermore, all taxa that were recorded from a single island site in this analysis had previously been reported from mainland or other island locations (as indicated by their presence in the Maarj*AM* database). Our sampling approach may have overlooked endemic taxa in unsampled areas of study islands or indeed in sampling plots,

355 if the taxa were present at low abundance. Nonetheless, the apparent lack of endemism in
356 island communities – even large or isolated island communities – strongly suggests that the
357 contribution to island diversity of *in situ* taxogenesis (at the level of VT) is low compared with
358 that of immigration. Furthermore, the fact that taxonomic diversity was similar at island and
359 mainland sites indicates that strong immigration is not significantly outweighed by local
360 extinctions on islands.
361
362 Our inference that long distance dispersal of AM fungal VT is relatively efficient, compared with
363 that of many animal and plant species, is not entirely unexpected. A global survey of mainland
364 AM fungal communities indicated that many AM fungal VT have distribution areas
365 encompassing multiple continents, with VT lists exhibiting low turnover at large spatial scales
366 (Davison *et al*., 2015). Furthermore, recent genetic evidence has shown that individual
367 genotypes within the *Rhizophagus irregularis* species group are present on multiple continents
368 (Savary *et al.,* 2018). The diversity and composition of local AM fungal communities on distant
369 oceanic islands presented in this study suggest that the wide distribution of AM fungal VT
370 cannot be explained solely by incremental small-scale dispersal events (i.e., in soil). Rather, long
371 distance dispersal must explain AM fungal presence on islands, and the apparent magnitude of
372 immigration relative to taxogenesis and local extinction suggests that dispersal is relatively
373 efficient rather than occasional.
374
375 *Island remoteness favours certain life history characteristics*

AM fungal communities on distant islands were characterized by relatively high phylogenetic diversity and comprised relatively more spore-forming cultured taxa and taxa from outside of the order Glomerales, even once the environmental characteristics of islands were accounted for. We also found that islands generally harboured somewhat less-well distributed taxa (in terms of the total number of sites occupied) compared with mainland sites, suggesting that the traits allowing taxa to establish on islands do not confer a generally widespread distribution. Furthermore, among cultured taxa we recorded relatively more large-spored AM fungal taxa on distant islands. On one hand, a predominance of large-spored taxa may indicate that the germination and establishment phases are critical stages in the survival of AM fungal spores reaching distant islands, irrespective of the mode of dispersal. There is some evidence that large-spored fungi are characterized by high germinability and establishment (Norros *et al*., 2015) and predominate under resource limitation (Halbwachs *et al*., 2017), but information about the significance of spore size for AM fungal establishment is limited (Marleau *et al*., 2011). Also, it is unclear why the harshness of the local environment should increase with island remoteness. However, in support of this interpretation, the effect of island remoteness on mean spore diameter was apparent in the IB model but not in the IBE model, where measured environmental variables were accounted for. On the other hand, large spores may indicate that conditions during the dispersal process require a high degree of stress tolerance. In the context of dispersal to distant oceanic islands, transport by seawater appears a plausible dispersal mechanism, as AM fungal spores maintain germinability after storage in seawater (Koske *et al*., 1996) though they vary in their tolerance of salinity (Juniper and Abbott, 2006). Among plants, larger diaspores tend to be better able to survive transport in seawater (van der Pijl, 1982).

Analysis of seawater currents suggests that microbial propagules might take less than 10 years to be transported between any two oceanic locations globally (Jönsson and Watson, 2016). Such a time scale suggests that transport in seawater is a process potentially capable of producing the cosmopolitan patterns observed in this organism group, while at the same time highlighting the potential benefit of a stress tolerant dispersal strategy. Though AM fungal sequences have been detected from ocean water (Li *et al.,* 2018), direct empirical evidence with respect to transport of fungal spores in seawater is lacking.

An alternative explanation for the high diversity of island AM fungal communities and for some of the characteristics exhibited by AM fungal communities on distant islands is that they reflect the role of human-mediated transport. Human activities are believed to have transported some AM fungi over long distances (Rosendahl *et al*., 2009). Although the actual means and rates of human-mediated dispersal are not known, humans may preferentially facilitate dispersal of cultured taxa, simply because these occur disproportionately in disturbed systems, including agricultural settings (Ohsowski *et al*., 2014), and produce relatively abundant propagules. Though not directly recorded, human transport is believed to have led highly similar genetic lineages of another soil organism group, Collembola, to occur on several continental landmasses and remote islands worldwide (Cicconardi *et al*., 2017).

We recorded relatively more non-Glomerales taxa and greater phylogenetic diversity on distant islands. Case studies have suggested that disturbed habitats tend to be characterized by a relatively low proportion of Glomeraceae (Moora *et al*., 2014), which may again reflect

favouring of stress tolerance. However, these results and evidence from elsewhere (Lekberg *et al*., 2011; Klironomos *et al*., 2001; Veresoglou *et al*., 2013) demonstrate that trait-environment relationships must be considered in light of the phylogenetic conservatism in traits considered for analysis. In this analysis, cultured VT are more likely to belong to non-Glomerales clades and spore size is also conserved at a lower taxonomic level within the cultured set. Such patterns mean that observed trait-environment relationships might be a proxy for responses attributable to other conserved traits (de Bello *et al*., 2015).

Area effects may operate at smaller scales

Recorded AM fungal community characteristics did not vary as much in relation to island area as they did in relation to island remoteness. A similarly weak effect of area has been reported at a smaller scale from remnant forest patches in an agricultural landscape (Grilli *et al*., 2015). We see multiple reasons why island area was generally not associated with characteristics of AM fungal communities. First, it is possible that our measures of local diversity did not adequately capture particular island biogeographic processes. For instance, a measure of whole-island gamma diversity might be more sensitive to processes (immigration, taxogenesis, extinction) that define island taxon pools, but which are modulated by local conditions in determining the alpha diversity of samples. Second, island area is expected to determine the rate of stochastic local extinction (Whittaker and Fernandez-Palacios, 2007). Our results might therefore indicate that either island diversity is not importantly limited by extinction or that this process operates at a scale below the range of island sizes in our study (e.g. well below 1 km^2). A related point to note is that our study incorporated a relatively small number of islands located over a vast area

(essentially global). By collecting a geographically widespread set of samples we were able to conduct a general test of the effects of isolation *per se*. However, this generality may have come at the expense of some power to detect relationships between diversity and island characteristics (compared with studying multiple islands in a single archipelago). While we accounted for important environmental variables in our analyses, it is to be expected that the variable physical, climatic and biogeographic context of such a widespread set of islands (Weigelt *et al*., 2013) introduces noise into area-diversity and isolation-diversity relationships. For similar reasons, a degree of caution must be exercised when interpreting the relationships we identified, since our explanatory variables (island vs mainland, island area, island remoteness) could have been confounded with other unmeasured variables.

Covariation in mutualist responses to isolation?

Different AM fungal communities are known to differentially affect plant performance (Williams *et al*., 2011; Uibopuu *et al*., 2012), and there is evidence of differences in effect between Glomerales vs non-Glomerales AM fungal taxa and between taxa characterised as cultured vs uncultured or large- vs small-spored (Hoeksema *et al*., 2010; Koch *et al*., 2017). Equally, the presence and density of suitable host plants may limit the establishment of certain AM fungal taxa (passenger hypothesis; Hart *et al*., 2001). Thus, it is possible that the dispersal characteristics of either symbiont community have shaped the functional attributes of both plant and AM fungal communities on islands. Our results suggest that dispersal limitation of AM fungi to distant islands is likely to be slight overall. So, it is perhaps more plausible that over-representation of ruderal plant species with small propagules (efficient-dispersers) has favoured

464 the establishment of ruderal, large-spored (efficient disperser) AM fungal taxa on islands.
465 Nonetheless, if AM fungal taxa represent the more efficient group of dispersers, the early and
466 efficient arrival of ruderal AM fungal taxa to islands may have had an effect on colonizing plants
467 in the past (driver hypothesis; Hart *et al*., 2001).
468
469 *Conclusion*
470 Our results provide a first indication of the oceanic island biogeographic processes influencing a
471 microbial organism group. The island biogeography of AM fungi is characterised by efficient
472 dispersal outweighing potential effects of endemism and extinction. Nonetheless, we found that
473 remote island AM fungal communities are functionally distinct due to their high phylogenetic
474 diversity and relative predominance of cultured taxa from non-Glomerales clades and those
475 exhibiting relatively large spores. These characteristics suggest that stress tolerance is an
476 important trait that either reflects the origin of colonising taxa (e.g., anthropogenic systems) or
477 facilitates dispersal and establishment in the abiotic and biotic conditions associated with island
478 systems.
479
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481
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487

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Figure 1. Map of study island and mainland sites used for comparison. Island sites sampled in this study are shown by red symbols. Mainland sites from Davison *et al*. (*2015*) are shown by black symbols; large symbols indicate those mainland sites that were closest to an island site and were paired in certain analyses (see Figure S1).

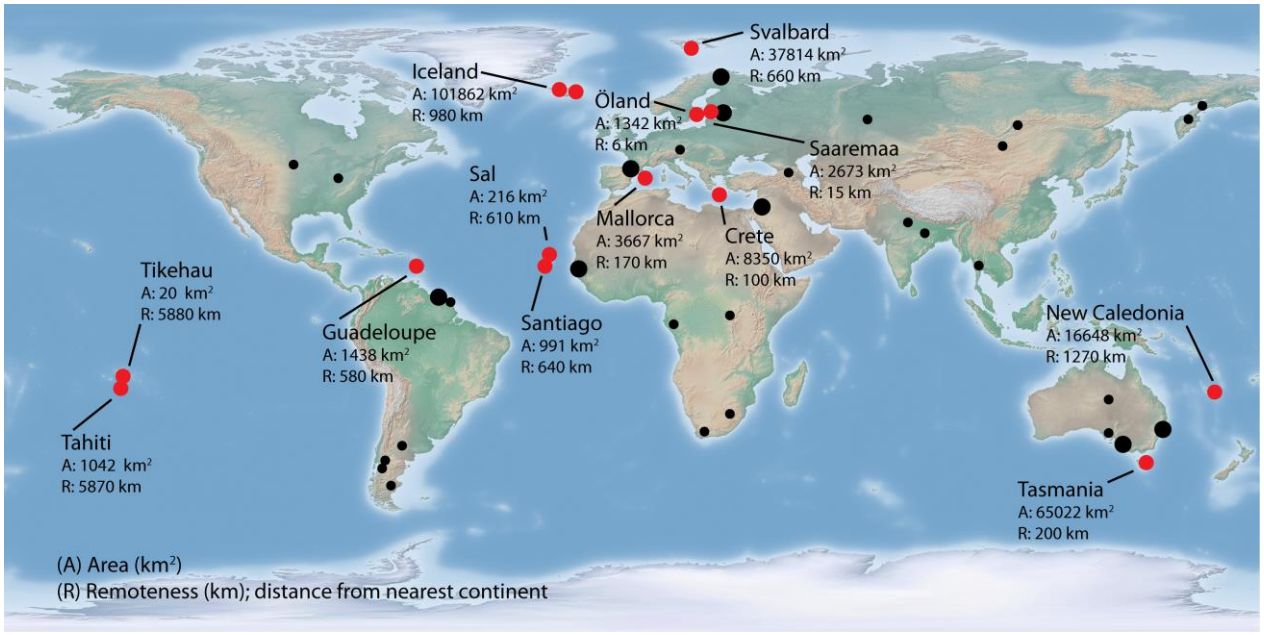


Figure 2 Bayesian phylogeny of Glomeromycotina virtual taxa (VT; SSU rRNA gene sequences). The relative abundance of reads derived from each VT is shown for mainland and island sites collectively and for each island separately (i.e. symbol areas sum to 1 within each column). Islands are ordered by increasing remoteness. Blue symbols indicate islands of oceanic origin; green symbols indicate islands of continental origin. VT containing sequences from known morphospecies (cultured) are indicated by an open symbol. A mean estimate of spore diameter could be calculated for some cultured VT (shown in barplot in right-hand panel).

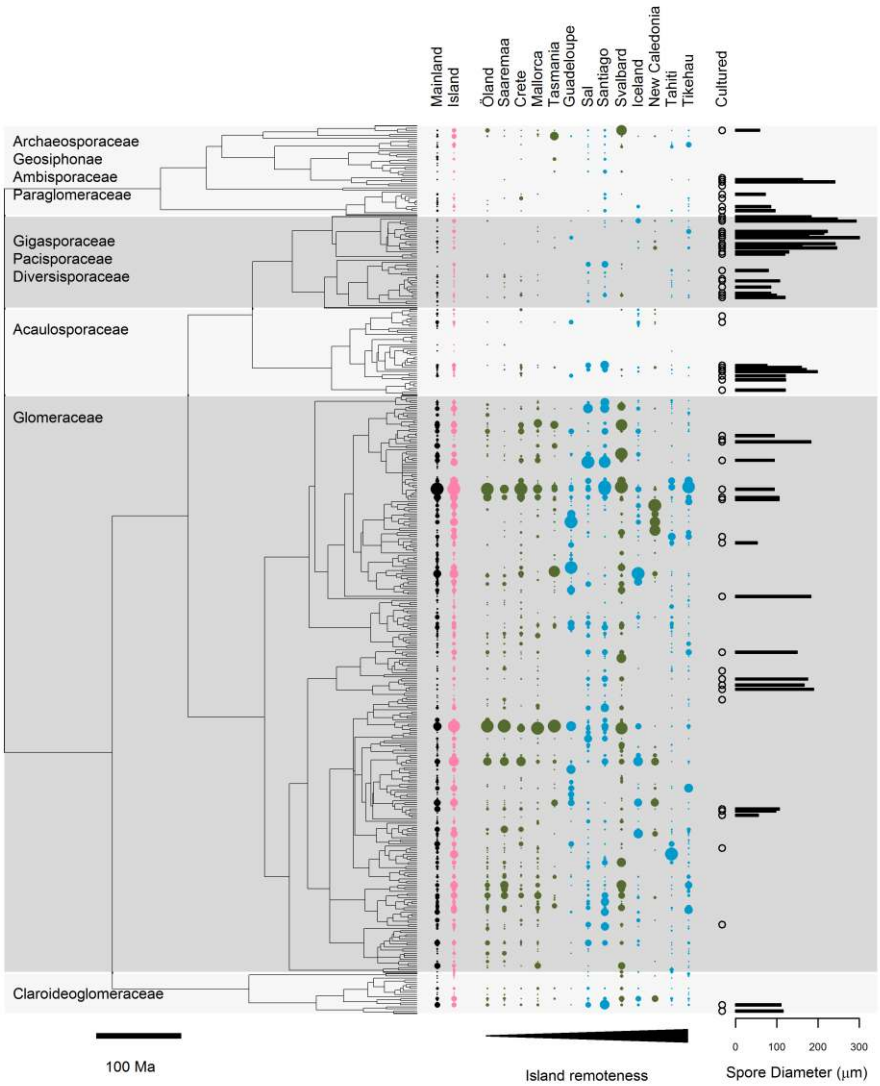


Figure 3 Estimates of diversity in island and mainland arbuscular mycorrhizal fungal communities. Three different diversity metrics are presented: a) raw richness; and the asymptotic estimators for b) exponential Shannon diversity; and c) reciprocal Simpson diversity. The violin plots show the distribution of diversity values (filled curves); as well as the median value (white point), quartiles (black bar) and range (whiskers). Diversity was measured at the level of host plant species per plot (i.e. pooling up to 4 individual samples).

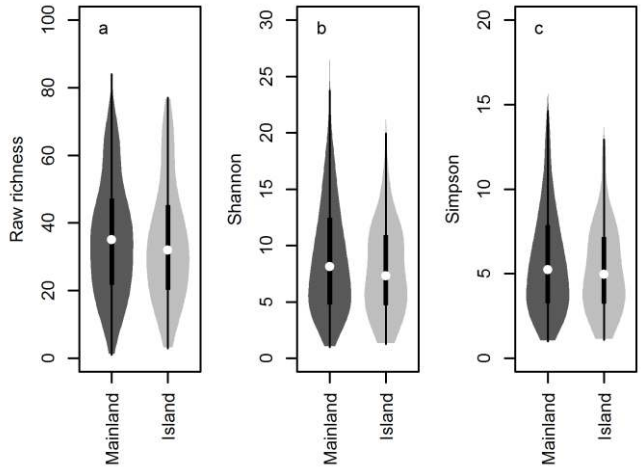


Figure 4. Mean compositional distance (Sørensen) between root-associated AM fungal communities as a function of the geographic distance (Haversine; natural log km) separating them. Points represent community pairs: islands and paired mainland sites (i.e. the geographically closest mainland site; large blue or green points) or pairs of mainland sites within the same continent (small grey points). a) island biogeography (IB) model not accounting for environmental characteristics; b) island biogeography and environment (IBE) model accounting for environmental characteristics. Separate regression lines are shown for island-mainland (solid) and mainland-mainland (dashed) points. Compositional distances in the IBE model were calculated among the residuals of a distance-based redundancy analysis model against measured environmental variables. Blue symbols indicate islands of oceanic origin; green symbols indicate islands of continental origin.

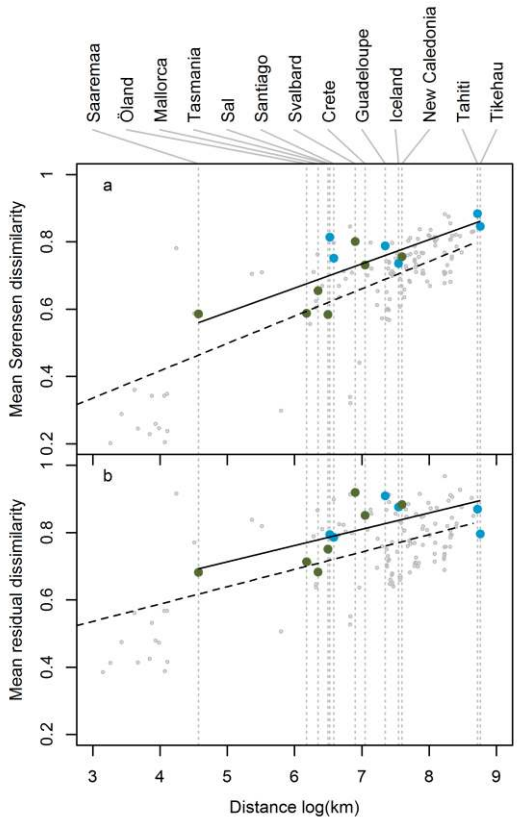
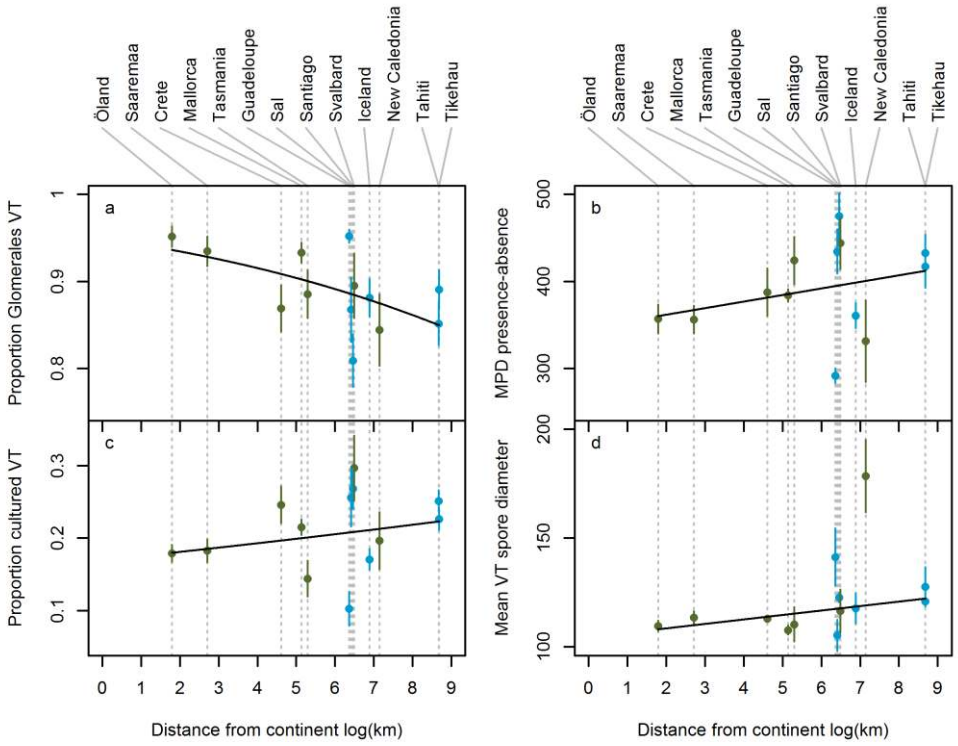


Figure 5. Relationship between island remoteness (natural log Haversine distance in km from the closest mainland) and several (abundance-unweighted) taxonomic and life history characteristics of plant root-associated AM fungal communities: a) the mean proportion of Glomerales VT, b) the mean pairwise phylogenetic distance (MPD) between VT, c) the proportion of cultured VT, and d) the mean spore diameter of VT. Lines show predicted values from island biogeography (IB) generalised linear mixed models. Blue symbols indicate islands of oceanic origin; green symbols indicate islands of continental origin. VT – virtual taxa (phylogenetically-defined DNA-based taxa).



690 Table 1 The effects of island vs mainland location (Set; upper section) and island characteristics (Area, Remoteness;
691 lower section) on characteristics of AM fungal communities worldwide. Island biogeography models (IB model) test
692 the effect of Set or Area and Remoteness in isolation; while island biogeography and environment models (IBE
693 model) do so after accounting for the effects of environmental and climatic variables. Fixed effect coefficients (b ±
694 SE), test statistics (F with Kenward-Roger estimated degrees of freedom or χ^2) and statistical significance from
695 linear or generalised linear mixed models are presented. ** P < 0.01 * P < 0.05 . P< 0.1 (P < 0.05 in bold). The effect
696 of each variable is tested after accounting for all other variables (Type II). MAT – mean annual temperature; MAP –
697 mean annual precipitation; MPD – mean pairwise phylogenetic distance; N –Nitrogen; P – Phosphorus. Shannon
698 and Simpson are asymptotic estimators of the exponential Shannon and reciprocal Simpson diversity indices. All
699 environmental variables were scaled (by one standard deviation) and island area and remoteness were log
700 transformed prior to inclusion in models.
701
702

	Diversity metrics			Taxonomic and life history characteristics			
	Richness	Shannon	Simpson	Glomerales proportion	MPD	Proportion cultured	Spore size
Island vs mainland							
IB model							
Set (island)	b = -2.23 ± 4.70 $F_{1,49.7}$ = 0.22	b = -1.76 ± 1.12 $F_{1,48.5}$ = 2.49	b = -0.70 ± 0.57 $F_{1,47.2}$ = 1.50	b = -0.23 ± 0.15 χ^2 = 2.24	b = 13.7 ± 15.4 $F_{1,48.1}$ = 0.78	b = 0.003 ± 0.08 χ^2 = 0.002	b = 5.98 ± 4.30 $F_{1,47.3}$ = 1.93
IB ENV model							
Set (island)	b = 1.26 ± 4.66 $F_{1,45.8}$ = 0.07	b = -1.49 ± 1.03 $F_{1,41.1}$ = 2.07	b = -0.82 ± 0.55 $F_{1,39.2}$ = 2.27	b = -0.29 ± 0.17 χ^2 = 2.84 .	b = 26.3 ± 18.4 $F_{1,43.0}$ = 2.05	b = 0.01 ± 0.10 χ^2 = 0.02	b = 6.7 ± 5.11 $F_{1,41.6}$ = 1.69
pH	b = 2.64 ± 1.82 $F_{1,87.1}$ = 2.03	**b = 1.86 ± 0.48 $F_{1,65.7}$ = 14.94**	**b = 1.03 ± 0.27 $F_{1,59.5}$ = 14.7**	**b = 0.16 ± 0.08 χ^2 = 4.21 ***	b = -8.7 ± 7.9 $F_{1,75.5}$ = 1.19	b = 0.04 ± 0.04 χ^2 = 1.00	b = -3.90 ± 2.29 $F_{1,68.5}$ = 2.80 .
P	**b = 4.45 ± 1.62 $F_{1,89.4}$ = 7.22 ****	b = 0.47 ± 0.42 $F_{1,63.9}$ = 1.21	b = 0.26 ± 0.24 $F_{1,56.9}$ = 1.16	b = -0.05 ± 0.07 χ^2 = 0.52	b = 12.0 ± 7.0 $F_{1,75.3}$ = 2.84 .	b = 0.03 ± 0.04 χ^2 = 0.85	b = -0.52 ± 2.04 $F_{1,67.5}$ = 0.06
N	b = 2.55 ± 1.48 $F_{1,89.5}$ = 2.85 .	b = 0.48 ± 0.42 $F_{1,78.3}$ = 1.25	b = 0.35 ± 0.24 $F_{1,69.8}$ = 2.04	b = 0.05 ± 0.07 χ^2 = 0.48	b = -0.7 ± 6.7 $F_{1,75.3}$ = 0.01	b = 0.01 ± 0.04 χ^2 = 0.08	b = 1.29 ± 1.99 $F_{1,81.6}$ = 0.41
MAT	b = 3.89 ± 2.14 $F_{1,52.5}$ = 3.30 .	b = 0.39 ± 0.50 $F_{1,50.0}$ = 0.60	b = 0.27 ± 0.27 $F_{1,49.0}$ = 0.33	b = -0.02 ± 0.08 χ^2 = 0.07	b = 1.41 ± 8.6 $F_{1,51.0}$ = 0.03	b = -0.02 ± 0.04 χ^2 = 0.29	b = 3.81 ± 2.42 $F_{1,49.6}$ = 2.45
MAP	b = -0.85 ± 2.21 $F_{1,51.0}$ = 0.15	b = 0.47 ± 0.51 $F_{1,46.8}$ = 0.84	b = 0.17 ± 0.27 $F_{1,44.3}$ = 0.37	b = -0.01 ± 0.09 χ^2 = 0.01	b = -11.9 ± 8.8 $F_{1,48.4}$ = 1.80	b = -0.05 ± 0.04 χ^2 = 1.48	b = 0.12 ± 2.48 $F_{1,46.0}$ = 0.002
Altitude	**b = 5.66 ± 2.15 $F_{1,54.3}$ = 6.86 ***	**b = 1.82 ± 0.50 $F_{1,50.7}$ = 13.17**	b = 0.80 ± 0.27 $F_{1,49.7}$ = 8.39	b = 0.07 ± 0.08 χ^2 = 0.77	b = 1.30 ± 8.7 $F_{1,52.2}$ = 0.02	b = 0.02 ± 0.04 χ^2 = 0.30	b = -1.34 ± 2.46 $F_{1,51.2}$ = 0.29
Island characteristics							
IB model							
Area	b = -3.72 ± 1.83 $F_{1,9,1}$ = 4.07	b = -0.71 ± 0.27 $F_{1,3.4}$ = 5.28	b = -0.45 ± 0.14 $F_{1,3.6}$ = 7.40	b = -0.05 ± 0.04 χ^2 = 1.27	b = -2.8 ± 6.7 $F_{1,9.3}$ = 0.18	b = -0.03 ± 0.03 χ^2 = 0.08	b = -1.08 ± 0.81 $F_{1,10}$ = 1.80
Remoteness	b = -1.61 ± 2.21 $F_{1,9,1}$ = 0.53	b = -0.70 ± 0.36 $F_{1,8.8}$ = 3.31	b = -0.43 ± 0.19 $F_{1,8.8}$ = 4.37	**b = -0.15 ± 0.05 χ^2 = 8.70 ****	b = 6.91 ± 7.9 $F_{1,10.0}$ = 0.77	b = 0.03 ± 0.04 χ^2 = 0.08	**b = 1.91 ± 0.61 $F_{1,10}$ = 9.91 ****
IB ENV model							
Area	b = -3.34 ± 3.38 $F_{1,13.0}$ = 0.85	b = -0.74 ± 0.56 $F_{1,9.6}$ = 1.50	b = -0.60 ± 0.29 $F_{1,9.1}$ = 3.56	**b = -0.14 ± 0.07 χ^2 = 4.67 ***	b = -7.0 ± 8.7 $F_{1,9,12}$ = 0.55	b = 0.03 ± 0.05 χ^2 = 0.33	b = -1.56 ± 1.63 $F_{1,10}$ = 0.93
Remoteness	b = -1.48 ± 2.99 $F_{1,13.0}$ = 0.21	b = -0.39 ± 0.44 $F_{1,8.4}$ = 0.74	b = -0.23 ± 0.22 $F_{1,8.9}$ = 0.92	**b = -0.18 ± 0.04 χ^2 = 15.93 ****	**b = 18.7 ± 6.6 $F_{1,8.85}$ = 7.00 ***	**b = 0.10 ± 0.04 χ^2 = 8.04 ****	b = 0.32 ± 0.78 $F_{1,10}$ = 0.16
pH	b = -2.41 ± 3.58 $F_{1,15.4}$ = 0.26	b = 0.82 ± 0.97 $F_{1,18.6}$ = 0.54	b = 0.37 ± 0.57 $F_{1,13.7}$ = 0.28	b = 0.16 ± 0.12 χ^2 = 1.64	b = -8.5 ± 16.7 $F_{1,14.2}$ = 0.17	b = 0.18 ± 0.11 χ^2 = 2.79 .	b = -2.71 ± 3.73 $F_{1,11}$ = 0.52 **
P	b = 4.97 ± 2.26 $F_{1,18.8}$ = 3.17	b = -0.79 ± 0.70 $F_{1,24.5}$ = 0.98	b = -0.42 ± 0.43 $F_{1,20.3}$ = 0.67	b = -0.15 ± 0.10 χ^2 = 2.34	b = 11.3 ± 12.6 $F_{1,20.8}$ = 0.57	b = 0.09 ± 0.08 χ^2 = 1.24	b = 2.81 ± 2.83 $F_{1,11}$ = 0.99 *
N	b = -3.60 ± 1.91 $F_{1,14.3}$ = 3.27	b = 1.01 ± 0.61 $F_{1,18.9}$ = 2.34	b = 0.74 ± 0.42 $F_{1,23.3}$ = 2.59	b = -0.03 ± 0.10 χ^2 = 0.10	b = 9.3 ± 12.0 $F_{1,23.0}$ = 0.50	b = 0.04 ± 0.08 χ^2 = 0.20	b = -0.88 ± 2.34 $F_{1,11}$ = 0.14
MAT	b = 0.90 ± 7.82 $F_{1,12.1}$ = 0.01	b = 0.05 ± 1.35 $F_{1,11.6}$ = 0.001	b = -0.25 ± 0.72 $F_{1,11.8}$ = 0.11	**b = -0.35 ± 0.17 χ^2 = 4.41 ***	b = -9.8 ± 21.1 $F_{1,11.7}$ = 0.19	b = -0.01 ± 0.14 χ^2 = 0.01	b = -0.59 ± 5.13 $F_{1,11}$ = 0.01 **
MAP	b = 0.90 ± 5.09 $F_{1,2.4}$ = 0.002	b = -0.28 ± 1.13 $F_{1,16.7}$ = 0.05	b = -0.11 ± 0.66 $F_{1,17.6}$ = 0.02	**b = 0.36 ± 0.15 χ^2 = 5.52 ***	**b = -53.4 ± 19.4 $F_{1,17.8}$ = 5.65 ***	b = -0.15 ± 0.13 χ^2 = 1.38	b = 4.60 ± 4.29 $F_{1,11}$ = 1.15
Altitude	b = 1.92 ± 4.40 $F_{1,4.8}$ = 0.09	b = 1.22 ± 1.18 $F_{1,14.5}$ = 0.71	b = 1.13 ± 0.65 $F_{1,10.9}$ = 1.90	b = 0.24 ± 0.14 χ^2 = 3.02	b = 7.9 ± 19.0 $F_{1,11.2}$ = 0.11	b = 0.09 ± 0.12 χ^2 = 0.51	b = 2.80 ± 4.71 $F_{1,11}$ = 0.35