ORIGINAL ARTICLE

The role of human disturbance in island biogeography of arthropods and plants: an information theoretic approach

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ABSTRACT

Aim Recent progress in island biogeography indicates that classical island biogeography alone cannot encapsulate the complex and dynamic nature of island biogeographical processes. Factors such as habitat complexity and connectivity, and in the face of the Anthropocene, human disturbance and invasive species, may influence insular communities. The relative importance of these factors, however, may differ among groups of biota. Here we employed an information theoretic approach to investigate factors likely to explain patterns in species richness and assemblage composition of five different groups of arthropods (ants, beetles, flies, spiders and cockroaches) and native and exotic plants within an insular community.

Location Capricornia Cays located at the southern end of Great Barrier Reef, eastern Australia.

Methods Arthropods were sampled from 14 cays using pitfall and Malaise traps and hand collecting. Plants were comprehensively surveyed on each island. We used univariate and multivariate generalized linear models with a model averaging technique, to calculate summed Akaike weights which quantified the relative importance of predictor variables in explaining variation in species richness and assemblage composition.

Results We found that infestation of the invasive ant *Pheidole megacephala* was negatively correlated with the species richness of ants, beetles and flies. Unlike species richness, only the assemblage composition of ants was related to *P. megacephala* infestation. Assemblage composition of other arthropod groups and plants was related to various factors, including island size (native plants), native plant species richness (beetles, flies and spiders) and presence of human disturbances (exotic plants and cockroaches).

Main conclusions The information theoretic approach proved useful in determining the relative likelihood of factors influencing both univariate and multivariate data of insular fauna and flora. The results demonstrated that human disturbance and proliferation of invasive species can override other biogeographical processes. The relative importance of these factors, however, varied depending on the taxonomic groups studied.

Keywords
Arthropods, Australia, biodiversity, biological invasion, Formicidae, human disturbance, information theory, insects, island biogeography, multi-taxon approach.

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INTRODUCTION

Since the foundational framework of MacArthur & Wilson (1967), substantial developments have been made in island biogeography theory with a plethora of mechanisms having been postulated to explain the structure and dynamics of insular communities (Lomolino *et al.*, 2010). We now understand that MacArthur and Wilson's classical equilibrium theory alone cannot encapsulate the dynamic and complex nature of insular biotas and, as stressed by Lomolino (2000) and other authors (e.g. Hortal *et al.*, 2009; Franzén *et al.*, 2012; Helmus *et al.*, 2014), we must examine not only the size and isolation of islands but other characteristics of the islands and species under consideration.

Subsequent studies have documented the importance of island characteristics, such as habitat complexity (Jonsson *et al.*, 2009) and available energy (Kreft *et al.*, 2008), which may be related to niche dimensions and breadths, and hence the assembly rules of island biotas (Götzenberger *et al.*, 2012). In addition to the isolation of islands from the mainland, connectivity among islands is considered important as organisms may use islands as 'stepping stones' producing nested distributional patterns (Nieminen & Hanski, 1998). Despite the large number of factors that may influence island biotas, there is broad consensus that much of the variation in diversity (particularly species richness) is explained by island size with other factors playing minor roles (see McMaster, 2005; Kalmar & Currie, 2006; Kreft *et al.*, 2008 and references within).

Recent studies have highlighted the influence of human disturbance, such as land use (and consequent habitat loss) and introduction of invasive species, on island biotas. Rizali *et al.* (2010), for example, found that, for ants, human disturbance obscured both alpha and beta diversity patterns predicted by the classical island biogeography factors of island size and isolation. Human disturbance has also been found to influence other groups, including spiders (Cardoso *et al.*, 2010) and plants (Castro *et al.*, 2010). Compared with continental systems, islands are more vulnerable to the introduction of exotic, invasive species, which may have devastating impacts on native species and may completely alter ecosystem functioning. Furthermore, an increase in human visits and transport of goods to islands leads to increased propagule pressure and the likelihood of introduction of invasive species (Lonsdale, 1999; Pyšek & Richardson, 2006). Among invasive species, introduced ants are of particular concern as they have been increasingly reported to devastate communities of native ants as well as other fauna (Wetterer, 2007).

Classical island biogeography theory is 'species neutral' (Hubbell, 2010) – it assumes no ecological distinctions among species, so the likelihood of immigration and extinction events for all species is a function of island size and isolation alone. Species or taxonomic groups, however, often differ in ecological traits, including vagility (Fattorini, 2010), habitat requirements (Kotze *et al.*, 2000) and interspecific interactions (Buckley & Jetz, 2007). These differences in ecological traits may result in non-random responses to island size and isolation, as well as other factors associated with insular systems. As a consequence, it is difficult to make generalizations unless island biogeography is studied using a broad range of taxonomic groups with varying ecological traits within the same insular system. This, however, has not been adequately addressed, as the majority of previous studies have focused upon a particular taxonomic group [e.g. plants (Moody, 2000), spiders (Cardoso *et al.*, 2010), beetles (Qie *et al.*, 2011), ants (Wetterer *et al.*, 2006), birds (Kalmar & Currie, 2006)].

A few studies have investigated island biogeographical patterns of multiple taxonomic groups within the same insular system. Fernández-Palacios & Andersson (1993), for example, found that island isolation had a stronger effect on the species richness of less mobile plants and beetles, compared with that of highly mobile birds and butterflies. Fattorini (2010) found that beta diversity patterns of birds were explained by mainland–island but not inter-island distances, whereas the opposite trend was found for invertebrates. Borges *et al.* (2006) examined arthropods within the Azores and found that the species richness of the endemic species was related to climatic and geomorphological factors, whereas that of exotic species was associated with human disturbances. None of these studies, however, investigated the relative importance of human disturbance and other island characteristics using multiple taxonomic groups.

In investigating factors that potentially drive the alpha and beta diversity of insular systems, ecologists often use a model selection approach (hereafter MSA) to arrive at one or more models that best explain the data (Stephens *et al.*, 2005). Such conventional approaches rely on binary significant or non-significant results and do not allow one to make inferences from multiple explanations (multi-model inference) (Lukacs *et al.*, 2007). This is problematic when data are collected from complex systems where multiple models (or multiple predictor variables) are plausible and/or where little biological information is available to establish a priori hypotheses (Johnson & Omland, 2004).

An information theoretic approach (hereafter ITA) offers a new statistical paradigm in which the relative strength of evidence for individual candidate models is calculated, enabling more robust inferences from the observed data (Burnham & Anderson, 2002). An ITA seeks multiple models that plausibly explain variation in the data, as opposed to a MSA that seeks a single 'best model'. When there are similar levels of support for multiple models, model averaging can be used to quantify the relative importance of individual predictor variables, based upon their cumulative weight of evidence (Akaike weights; see Burnham & Anderson, 2002) across all the candidate models. An ITA has been used for recent ecological studies but only for univariate analyses. This approach can now be applied to multivariate analyses (assemblage composition), using a multivariate generalized linear model developed by Wang *et al.* (2012).

Here we adopt this ITA to investigate which predictor variables most likely explain the species richness and assemblage composition of plants and five groups of arthropods (ants, beetles, flies, spiders and cockroaches) of coral cays in the southern Great Barrier Reef, Australia. We also employed an MSA for the same datasets for comparison. These coral cays vary greatly in size and in the types and degree of human disturbance they have experienced, providing an ideal system to study island biogeography where human disturbance is commonplace.

MATERIALS AND METHODS

Study area

We surveyed 14 vegetated coral sand islets, including 13 islands within the Capricorn and Bunker Groups, located at the southern end of the Great Barrier Reef Marine Park, approximately 80 km east of the town of Gladstone (23°11′–24°07′ S, 151°42′–152°43′ E; see Fig. 1). These islands vary in size from 2.3 to 119.8 ha, but most are under 20 ha. Vegetation of the islands generally consists of *Pisonia grandis* closed-forest in the interior with *Casuarina equisetifolia* open-forest and mixed shrubland of *Argusia argentea*, *Pandanus tectorius* and *Scaevola taccada* around the circumference. The 23 native vegetation communities and five non-native communities found on the cays are described in detail in Neldner *et al.* (2012). Average maximum and minimum temperatures at Heron Island (see Fig. 1) are 29.8 °C and 24.2 °C, respectively, in mid-summer (January), and 21.5 °C and 16.5 °C in mid-winter (July). Average annual rainfall is 1034 mm at Heron Island with February the wettest month (139 mm). Prevailing winds are easterly to south-easterly (Burwell *et al.*, 2010).

All the islands are fully or partially protected as State or Commonwealth reserves, but many are, or have been, subjected to human disturbances (see Appendix S1a in Supporting Information). A notable natural disturbance is outbreaks of scale insects which occurred on some islands in the past 20 years (Olds, 2008). Scale insect outbreaks have been generally associated with very high population densities of the introduced and invasive African big-headed ant, *Pheidole megacephala*. This species is considered one of the world's worst invasive ant species and is firmly entrenched on a number of islands. Although its role in scale insect outbreaks is still unclear (but see Greenslade, 2010), this species is known to cause negative impacts on native ants, and to a lesser extent other invertebrates in Australia and elsewhere (Wetterer, 2007; Burwell *et al.*, 2012).

Arthropod sampling

Relative to its size, three to eight survey sites were established per island (Appendix S1a). Survey sites were located in different habitat types, including *Pisonia* forest, other woody vegetation, open grassland and disturbed areas such as those within or nearby resort and research facilities. On larger islands often two or more sites were located within the same habitat type. Detailed locations of survey sites on each island are provided in Burwell *et al.* (2010). Arthropod sampling was conducted at different times of the year between March 2008 and April 2009 (Appendix S1a). To collect arthropods from various microhabitats, we used multiple sampling techniques including pitfall traps, Malaise traps, and timed day hand collection (see Appendix S2 for more details of sampling protocols).

The five target arthropod groups were identified to family and morphospecies. Where possible, morphospecies were
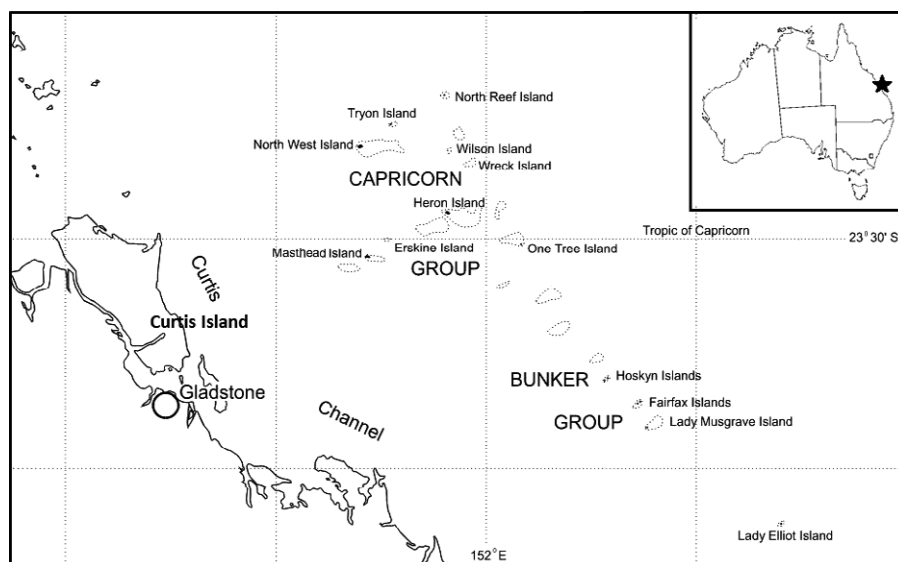

Figure 1 Map of coral cays of the Capricorn and Bunker Group within and around the Capricornia Cays National Park, off the city of Gladstone (marked by a star symbol) located on the central Queensland coast of eastern Australia.

identified to genus and described species (both species and morphospecies are referred to as species hereafter; Appendix S2). Our sampling sufficiency was tested using coverage-based rarefaction curves (Appendix S2).

Vegetation survey

Vegetation of the islands was mapped on the basis of aerial photo-interpretation of 1:4000 scale aerial photographs flown in 2007. Both native and exotic vascular plants of all 14 islands were surveyed between August 2007 and September 2008 by a team from the Queensland Herbarium. Exotic species included plants exotic to the Australian mainland as well as plants native to mainland Australia but transported to the islands by humans and which subsequently established wild populations. Native and exotic plant species richness were recorded for each island, and the spatial distribution of the 23 native vegetation communities, five exotic communities, and sandy and lithified shores were mapped using ArcGIS (Batianoff *et al.*, 2012).

Predictor variables

We generated a total of 34 predictor variables associated with various ecological or geographical factors (Appendix S1b). Predictor variables were grouped into eight classes, each with similar attributes, comprising island biogeography (island size and isolation), vegetation (five predictor variables), infestation by the invasive ant *P. megacephala* (four), temperature (two), rainfall (three), human disturbance (three), connectivity among islands (six) and spatial arrangement of the islands (nine). Scale insect outbreaks were not considered in the analysis as only one island had been recently affected and reliable records of outbreaks were not available for other islands. As sampling was conducted at different times of the year, mean maximum and minimum temperatures and rainfall data were used for the period before and while sampling took place (see Burwell *et al.*, 2010 and Appendix S1b for details).

Data analyses

Analyses focused on inter-island differences in species richness and assemblage composition of the five arthropod groups (ants, beetles, flies, spiders, cockroaches) and plants (native and exotic). Individual islands were therefore treated as replicates ($n = 14$). Arthropod data collected by different methods were combined at each sampling site. Raw abundances were not used due to inherent sampling bias. Arthropod assemblage data were therefore composed of incidence (binary data) or relative frequency of occupancy (as measured by the proportion of the number of survey sites where a given species was collected) on each island. We employed abundance data for pitfall-trapped *P. megacephala* only, which were used as a predictor variable. Consequently *P. megacephala* was excluded from the ant dataset. Plant data were divided into native and exotic species, and only incidence data were used for analyses. Owing to varying sampling intensity per island (three to eight

sites, depending on island size), the species richness of arthropod taxa at each island was rarefied at three sites, using sample-based species rarefaction curves using 999 permutations executed with PRIMER 6 (Clarke & Gorley, 2006). Extrapolation of species richness was not used as reliable estimates could not be derived from the relatively small number of sites (abundance was not used for extrapolation) on some islands. Our measure of species richness, therefore, represents species density given the same sampling intensity ($n = 3$ survey sites) per island (see Appendix S1c for actual and rarefied number of species on each island).

We adopted a model averaging method derived from an ITA (Burnham & Anderson, 2002) to investigate the relative importance of predictor variables in explaining variation in the species richness and assemblage composition of plant and arthropod groups. A number of predictor variables were either log-transformed or arcsine-transformed to improve their normality and homogeneity (Appendix S1b). All variables were then centred and standardized to have a mean of 0 and standard deviation of 1. For plant data, predictor variables associated with plants ('vegetation' class; see Appendix S1b), temperature and rainfall were excluded from analyses.

We reduced the number of predictor variables from 34 to a more manageable 10 by a two-step procedure. First, we made a draftsman plot of all pairwise correlations of predictor variables (Appendix S1d). We focused on correlations within the same variable class and when two variables were found to be highly correlated ($P < 0.05$ and $r > 0.75$), one was discarded. The resultant 22 variables (see Appendix S1b) were reduced to 10 using *marginal tests* available within the *DistLM* routine in PRIMER 6 and PERMANOVA+ add-on software (Anderson *et al.*, 2008). This tested predictor variables individually (i.e. not in combination), and we selected the 10 predictor variables that best explained the variation in the matrix of similarity values (see Appendix S2 for details of the similarity values) based on species richness or assemblage composition. A set of 10 predictor variables was generated separately for species richness and assemblage composition of each of the five arthropod groups and native and exotic plants.

For each response group, we calculated the relative importance of the 10 predictor variables using model averaging based on modified Akaike information criterion (AIC$_c$; Burnham & Anderson, 2002) (see Appendix S2 for more details of model averaging procedures). AIC 'penalizes' over-parameterized models and hence these models with a large number of predictor variables did not attain high Akaike weights. We fitted GLMs to analyse effects of predictors on species richness, and multivariate GLMs developed by Wang *et al.* (2012) to analyse species assemblages. Instead of using an arbitrary cut off value (i.e. based on Δ Akaike between best and other models; Burnham & Anderson, 2002), we included all possible 1024 models to calculate the sum of the Akaike weights for individual predictor variables. We selected 'plausible' predictor variables by testing whether the sum of the Akaike weights of each predictor variable was significantly

greater than the summed Akaike weights obtained from a null distribution of the islands. The null model was generated by permuting islands, as this preserves the species composition and thus species interactions of each island. We compared the observed Akaike weights with those derived from 999 permutations. The R code is provided in Appendix S3.

For comparison, we also employed a more conventional MSA using the same set of 10 predictor variables for each dataset. We used the *DistLM* routine with a stepwise selection procedure based on modified AIC values (Appendix S2).

We also analysed whether the assemblages of arthropods and plants showed nested structures among the 14 islands, using NODF (nestedness based on overlap and decreasing fill; Almeida-Neto *et al.*, 2008) available in ANINHADO software (Appendix S2). Assemblage compositions of arthropods and plants were visually represented by non-metric multi-dimensional scaling (NMDS) ordination using PRIMER 6 based on the Sørensen similarity matrix of assemblages (Appendix S2), with 25 random restarts.

Relationships between the assemblage composition of plants and those of the various groups of arthropods were further analysed using Mantel tests available in the *RELATE* routine of PRIMER 6. We conducted simple Mantel tests that quantified overall similarity of the plant (native or exotic species) and arthropod assemblages by calculating Spearman's rank correlation (ρ) between the two assemblage matrices. Significance levels were calculated using 4999 permutations of the samples.

A permutational *t*-test was conducted to further elucidate the effects of human disturbance on cockroach species richness using the *PERMANOVA* routine (permutational ANOVA in PRIMER 6 and PERMANOVA+ add-on software; Anderson *et al.*, 2008). The cockroach dataset was subdivided into native and exotic species and the species richness of each was analysed separately, using Euclidean distance measures. The presence or absence of human disturbance was used as a fixed factor and the significance level of the disturbance effect was calculated by 4999 unrestricted permutations of the data. We also tested whether infestation with *P. megecephala* caused homogenization of the assemblages of ant species using the *PERMDISP* routine in PRIMER 6 and PERMANOVA+, which tests homogeneity of multivariate dispersions within groups (three levels of *P. megacephala* infestation; see Appendix S2), based on a resemblance matrix (centroids of the Sørensen similarity matrix of ant assemblages) using permutations (Anderson *et al.*, 2008). The *P*-value was calculated using 4999 permutations of the matrix.

RESULTS

We collected a total of 363 species from the five arthropod groups; mostly beetles (141 species), followed by flies (98), spiders (93), ants (23) and cockroaches (8). Although relatively few species were collected, ants were the most abun-

dant of the five groups due to high abundance of *P. megacephala* on some islands. This species accounted for over 85% (88,128 individuals) of the total number of ants collected by pitfall and Malaise traps. Plants were represented by 43 native and 88 exotic species across the 14 islands (Batianoff *et al.*, 2009). Coverage-based rarefaction curves showed that all of the arthropod datasets attained more than 90% sample coverage, suggesting that the majority of the species was represented in our samples (Appendix S1e).

Assemblages of all arthropod groups and exotic plants showed relatively weakly nested structures with NODF values of 50% or less (only native plants showed over 70% NODF; see Appendix S1f). Despite this, all NODF values were highly significant ($P = 0.001$) with the exception of cockroaches ($P = 0.100$) due to the small number of species collected (eight species).

Information theoretic approach

The ITA highlighted up to three 'plausible' predictor variables (i.e. variables with significant Akaike weights) for each dataset (Table 1). Plausible variables included those associated with *P. megacephala* infestation, island biogeography (island size, distance to continent), vegetation (native plant species richness), human disturbance (current or historical presence of resort, presence of frequent human visitation) and spatial configuration of the islands. Variables related to temperature, rainfall and connectivity among islands were not selected in any dataset. For arthropods, the ITA was also used on relative frequency of occupancy data (Appendix S1g), but the results were very similar to those based on incidence in Table 1.

For native plants, island size and, to a lesser extent, their spatial configuration ('X') were significant and most plausible in explaining variation in both species richness and assemblage composition (Table 1). Species richness was positively correlated with island size (Fig. 2a). In the NMDS ordination (Fig. 3a), larger islands (i.e. Lady Elliot, Masthead and North West Islands) tended to cluster, suggesting they have similar native plant assemblages. Smaller islands were scattered around the larger islands on the ordination pane. Patterns in species richness and assemblage composition of exotic plants were primarily driven by the presence of resort facilities. Spatial configuration ('Y^2') was significant, although marginally, for exotic plant richness. Current and historical presence of resort facilities was associated with increased numbers of exotic plant species (Fig. 2b), and the composition of exotic plants was clearly different between islands with and without resorts (Fig. 3b).

The species richness of ants, beetles and flies were significantly negatively correlated with the abundance of *P. megecephala* (Table 1, Figs 4, 5a & 6a). While this was the only plausible predictor variable for ants, beetle and fly richness were significantly and positively associated with other variables including native plant species richness (beetles, Fig. 5b), island size (flies, Fig. 6b) and distance to continent (flies,

Table 1 Summary results of the information theoretic approach (ITA) for species richness and assemblage composition of plants (native and exotic species were analysed separately) and the five arthropod groups among the 14 islands in the southern Great Barrier Reef, Australia. The three explanatory variables (see Appendix S1b for full names and explanations of the abbreviated explanatory variables) which attained the highest summed Akaike weights are shown with *P*-values (significant *P*-values are shown in bold).

		Explanatory variable	Summed Akaike weight	P	Explanatory variable	Summed Akaike weight	P	Explanatory variable	Summed Akaike weight	P
Species richness										
Plants	Native species	**IslandSize**	**0.996**	**0.002**	**X**	**0.854**	**0.040**	DistContinent	0.583	0.069
	Exotic species†	**Resort**	**0.906**	**0.033**	**Y²**	**0.860**	**0.045**	Disturbance	0.781	0.052
Arthropods	Ants	**P.megaAbund**	**0.947**	**0.012**	MaxTemp	0.536	0.094	Y	0.328	0.163
	Beetles	**P.megaAbund**	**0.893**	**0.036**	**NativePlSp**	**0.706**	**0.045**	IslandSize	0.505	0.097
	Flies	**P.megaAbund**	**0.999**	**0.002**	**IslandSize**	**0.999**	**0.002**	**DistContinent**	**0.994**	**0.004**
	Spiders	DistContinent	0.611	0.052	NativePlSp	0.535	0.067	IslandSize	0.497	0.097
	Cockroaches	**HumanVisit**	**0.799**	**0.017**	NoIs30 km	0.375	0.201	P.megaPA	0.307	0.210
Assemblages										
Plants	Native species	**IslandSize**	**0.473**	**0.013**	**X**	**0.327**	**0.038**	NoIs30 km	0.243	0.064
	Exotic species	**Resort**	**0.715**	**0.011**	IslandSize	0.335	0.106	Y²	0.246	0.206
Arthropods	Ants	**P.megaAbund**	**0.453**	**0.010**	**Y**	**0.328**	**0.030**	P.megaPA	0.263	0.064
	Beetles	**NativePlSp**	**0.863**	**0.001**	IslandSize	0.117	0.204	ExoticPlSp	0.106	0.217
	Flies	**NativePlSp**	**0.394**	**0.020**	**DistContinent**	**0.390**	**0.027**	IslandSize	0.229	0.084
	Spiders	**NativePlSp**	**0.395**	**0.017**	**IslandSize**	**0.314**	**0.038**	X × Y	0.127	0.241
	Cockroaches	**HumanVisit**	**0.437**	**0.003**	Disturbance	0.373	0.066	X × Y	0.388	0.088

†Exotic species richness was log-transformed to improve normality of the data.

Fig. 6c). Cockroach species richness, in contrast, was likely to be explained by frequent human visitation, with significantly more exotic species occurring on frequently visited islands (PERMANOVA *P* = 0.002) (Fig. 7) while native species richness did not show significant differences (PERMANOVA *P* = 0.461). No predictor variables were found to be significant for spider species richness.

For ant assemblage composition, abundance of *P. megacephala*, and to a lesser extent, spatial configuration of the islands ('Y') were the most plausible predictor variables (Table 1). NMDS ordinations showed progressive change in ant assemblage composition with increasing *P. megacephala* abundance (Fig. 3c). Homogeneity of dispersion in ant assemblage composition was tested using islands grouped into three levels of *P. megacephala* infestation (see Appendix S1a). There was, however, no significant difference in dispersion among these groups (PERMDISP *P* = 0.298).

Variation in assemblage composition of beetles and flies was best explained by native plant species richness (Table 1, Fig. 3d,e), which was also found to be the most plausible predictor variable for spider assemblages (Fig. 3f). Mantel tests showed that assemblage composition of native plants

was significantly correlated with that of beetles, flies and spiders (Table 2). The correlation coefficient (and the significance level) of spiders, however, was not as strong as that for beetles and flies. Distance to continent and island size also likely explained variation in fly and spider assemblages, respectively (Table 1, Fig. 3e,f). Cockroach assemblage composition, like species richness, was most plausibly explained by the presence of frequent human visitation (Fig. 3g).

Model selection approach

The MSA with stepwise selection procedure chose one to five predictor variables in the 'best' models, with the exception of spider assemblage composition where no variables were selected (Appendix S1h). For most datasets, similar variables were selected by the MSA and ITA, however, for some, spurious results emerged using the MSA. For assemblage composition of native plants, MSA included only a single spatial configuration variable ('X') in the final model. In contrast, ITA also included island size which had a greater summed Akaike weight than that of spatial configuration, suggesting that island size is a more plausible predictor of the composi-

Table 2 Summary results of Mantel tests comparing relationships between plant (native and exotic species) and arthropod assemblage composition of the 14 islands in the southern Great Barrier Reef, Australia. Significant *P*-values are shown in bold.

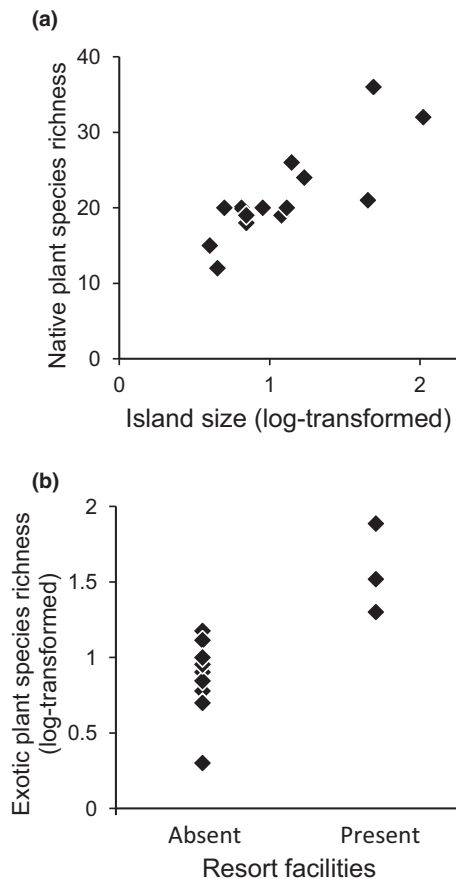|	Ants		Beetles		Flies		Spiders		Cockroaches	
	Rho	*P*	*Rho*	*P*	*Rho*	*P*	*Rho*	*P*	*Rho*	*P*
Native plants	0.20	0.069	0.39	**0.003**	0.42	**<0.001**	0.25	**0.033**	0.13	0.160
Exotic plants	0.08	0.263	0.38	**0.001**	0.33	**0.002**	0.05	0.360	0.05	0.334

Figure 2 Relationships between (a) native plant species richness and island size, and (b) exotic plant species richness on islands with or without current or past presence of resort facilities across the 14 islands in the southern Great Barrier Reef, Australia.

tion of native plants. For fly species richness, stepwise selection included spatial configuration ('X^2') and the total rainfall in the 4 weeks prior to sampling in the final model. This result was, however, heavily influenced by one outlier island (Lady Elliot Island), which not only had the highest fly species richness but was geographically isolated (Fig. 1). When this island was excluded from the analysis, MSA included the same set of predictor variables in the final model as those selected by ITA.

DISCUSSION

Factors affecting the distributions of arthropods and plants

Using an information theoretic approach, we demonstrated that human disturbance and invasive species can override influence of typical island biogeographical processes on small islands. Furthermore, the results support our initial supposition that the relative importance of anthropogenic and biogeographical influences are taxon dependent – different

groups of organisms, with different biologies, were associated with different predictor variables. The apparent negative and overriding relationship between the invasive ant and the fauna of other ants concurs with other studies (e.g. Rizali et al., 2010). This, however, was not the pattern for other groups of arthropods – the impacts of P. megacephala did not fully obscure the influence of island biogeographical processes for beetles and flies, and as for spiders and cockroaches, apparent impacts of P. megacephala were not detected.

Native plants were the only group that followed predictions derived from classical island biogeography. Simple increase in the area of available habitat was strongly and positively correlated with species richness. This species–area relationship is not uncommon for plants – and has been reported from many insular systems worldwide (Kreft et al., 2008). Unlike native plants, exotic plant richness was associated with the presence of resort facilities (current or historical), where increased propagule pressure may have facilitated the naturalization of exotic plants on these islands (Lonsdale, 1999; McMaster, 2005). An increase in exotic plant species is often (but not always) associated with reduced diversity of native plants (Vilà et al., 2011). This, however, was not the case in our study (correlation coefficient between native and exotic plant species richness = 0.48; see Appendix S1d). Batianoff et al. (2009) investigated historical plant records from the cays and found that, despite an increase in exotic species (the number almost doubled over 24 years), the number of native species remained steady with little species turnover. This possibly reflects the resistance of established native communities to exotic species, for example Pisonia closed forest allows limited sunlight to reach the forest floor, and also active weed management by National Park officers, volunteers and resort staff.

The ecological impacts of introduced species, particularly ants, have been documented in many insular systems (New, 2008). Previous studies (see Wetterer, 2007) have documented decreases in the species richness of some arthropod groups in response to increased abundance of P. megacephala. Burwell et al. (2012) examined historical records of ants on one of the cays (One Tree Island) and found that the number of ant species diminished following the introduction of P. megacephala, suggesting that it is likely to be directly responsible for the depauperate ant fauna on infested islands. On heavily infested islands, where P. megacephala was ubiquitous, there were very few species of other ants and they appeared to be completely extirpated on the most heavily infested island (North Reef Island). Many ant species require the same or similar food and nesting resources (Holldobler & Wilson, 1990). It is therefore likely that the numerically dominant P. megacephala outcompetes other ants. This may ultimately result in biotic homogenization on heavily infested islands, although we did not find significant changes in assemblage dispersion among the islands with different levels of P. megecephala infestation.
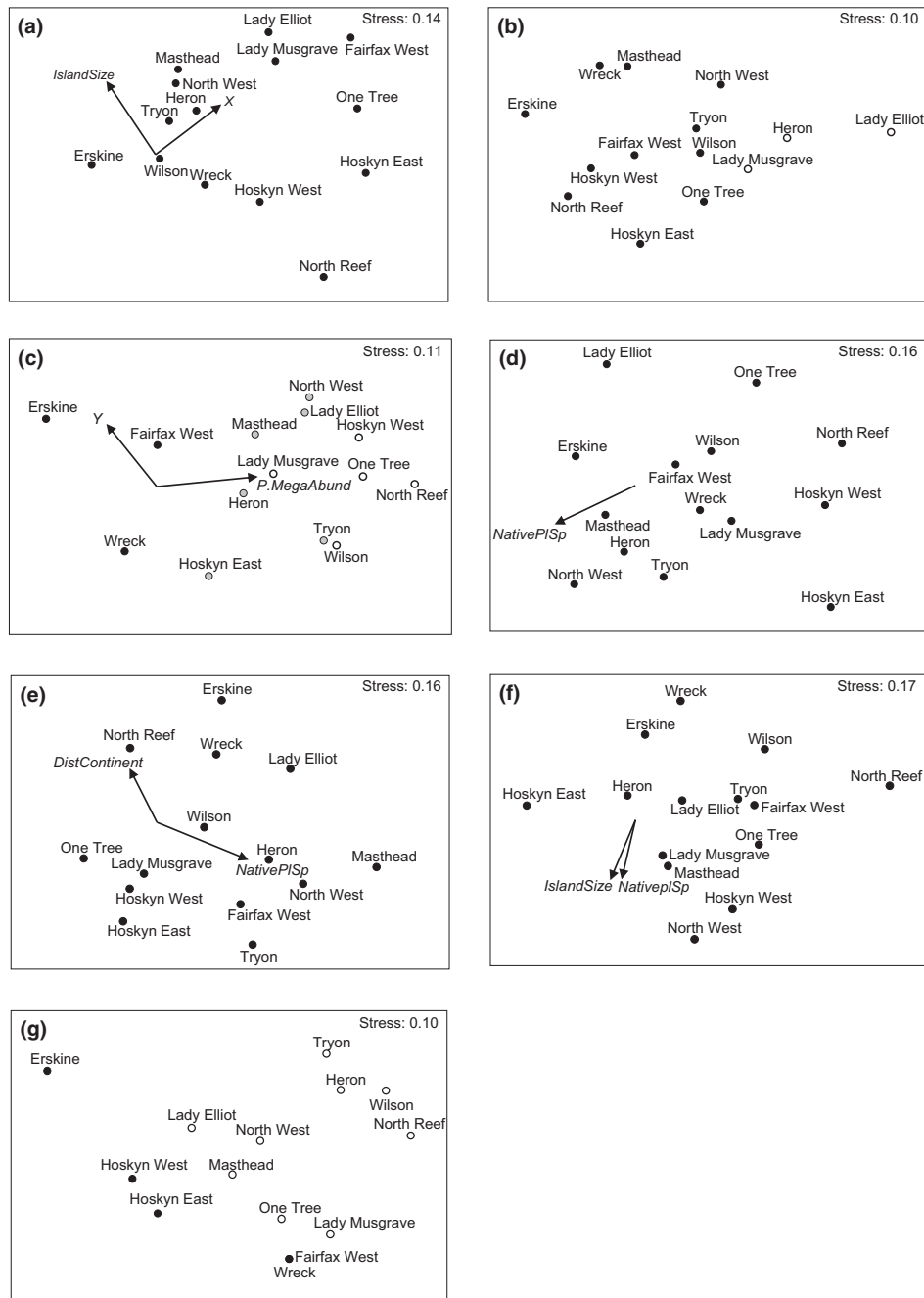
Figure 3 Non-metric multidimensional scaling (NMDS) ordinations of plant and arthropod assemblages across the 14 islands in the southern Great Barrier Reef, Australia (a, native plants; b, exotic plants; c, ants; d, beetles; e, flies; f, spiders; g, cockroaches), each based on Sørensen similarity measures with a single dummy variable (see Appendix S2 for more details). Bi-plot vectors of the predictor variables selected by the information theoretic approach (Table 1) are overlaid on the ordinations. Categorical predictor variables are represented by different plot symbols. For exotic plants, open points represent islands with current or past resort facilities; for ants, black, grey and open points represent islands with level 0, 1, and 2 infestation by *Pheidole megacephala*, respectively (see Appendix S1a); and for cockroaches, open points represent islands with frequent human visitation.

Beetle and fly species richness were also negatively associated with the abundance of *P. megacephala*, perhaps as a result of direct predation and competition. In addition, when *P. megacephla* tend honeydew-producing hemipterans, they exert aggressive behaviour toward their natural enemies such as predatory coccinellids, which may have resulted in reduced diversity and abundance of some arthropods (Wetterer, 2007). However, adverse effects of *P. megacephala* were less apparent on islands with lower levels of infestation (Figs 5a & 6a). Other studies documenting devastating impacts of *P. megacephala* have primarily focused on oceanic islands which often feature endemic species that are generally
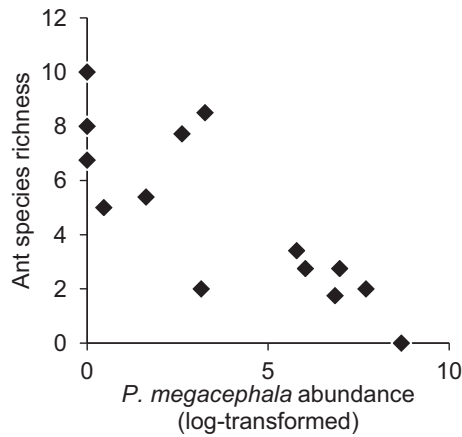
Figure 4 Relationships between ant species richness (all ants minus *Pheidole megacephala*) and average *P. megacephala* abundance across the 14 islands in the southern Great Barrier Reef, Australia.

more vulnerable to invasion by exotic species (Wetterer, 2007). Our insular system, on the other hand, consists of relatively newly established coral cays (c. 4000 years ago; Fairbridge, 1950), and the fauna primarily consists of species that have colonized from the mainland. A lack of 'naïve' endemics may confer some degree of resilience against *P. mega-*

cephala, at least until its abundance reaches a certain threshold.

Unlike species richness, assemblage composition of our focal arthropod groups, with the exception of ants, was not influenced by *P. megacephala* infestation. This suggests that although infestation reduced species richness of some groups, neither biological homogenization nor selective extirpation of certain species occurred. The most plausible predictor of beetle, fly and spider assemblages was native plant species richness. Furthermore, both native and exotic plant assemblages were significantly correlated with those of beetles, flies and, to a lesser extent, spiders (Table 2). These results suggest that differences in the diversity and composition of plants determine the species composition of these arthropod groups, and predictors related to island biogeography played relatively minor roles. Similar studies conducted on 30 lake islands in Sweden also found that plant diversity, and not island size or habitat isolation per se, influenced the density and species richness of invertebrates including spiders and beetles (Jonsson et al., 2009). Plant species composition may influence the composition of beetles and flies through differences in food resources such as nectar, fruits, seeds and foliage. For predatory spiders, changes in plant structural diversity may influence their hunting abilities and the availability of web-building sites. Spiders are also likely to be

Figure 5 Relationships between rarefied beetle species richness and (a) average *Pheidole megacephala* abundance, and (b) native plant species richness across the 14 islands in the southern Great Barrier Reef, Australia. Islands heavily infested by *P. megacephala* (> 5.0 on a logged scale) are shown in open points.
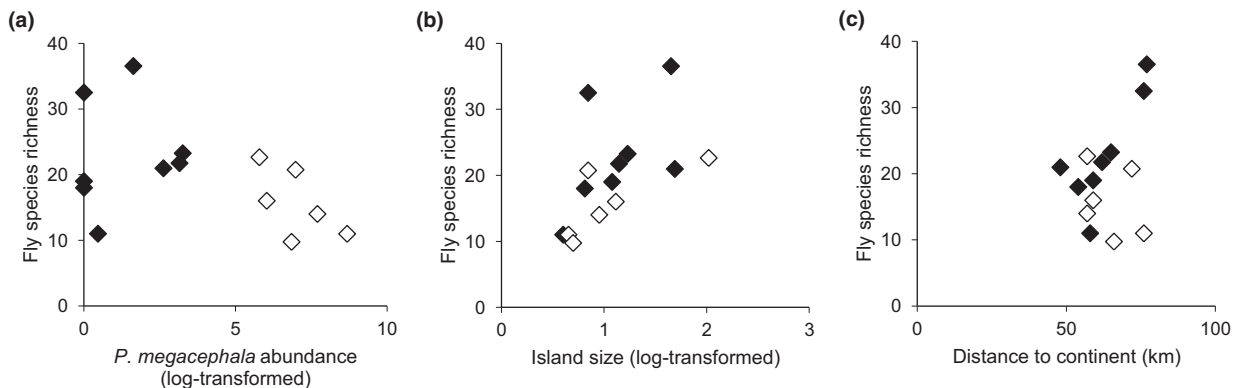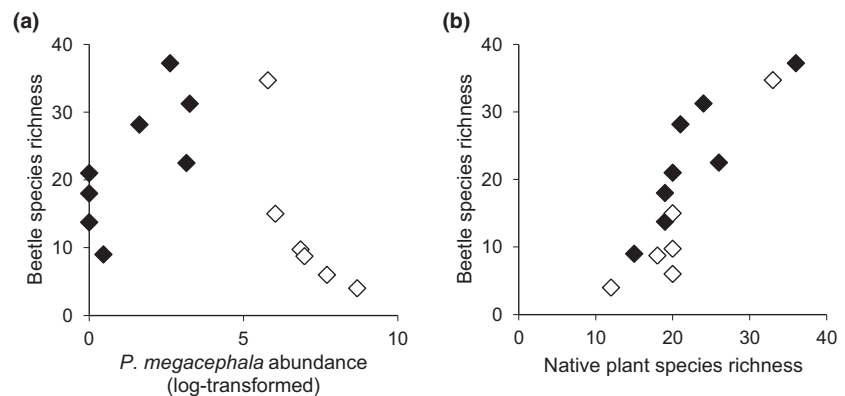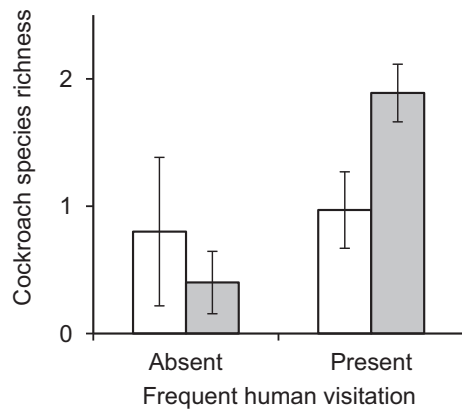

Figure 6 Relationships between rarefied fly species richness and (a) average *Pheidole megacephala* abundance, (b) island size and (c) distance to the nearest continent across the 14 islands in the southern Great Barrier Reef, Australia. Islands heavily infested by *P. megacephala* (> 5.0 on a logged scale) are shown in open points.

Figure 7 Average cockroach species richness (± standard errors) on islands with and without frequent human visitation across the 14 islands in the southern Great Barrier Reef, Australia. Cockroach species are divided into native (open bars) and exotic (closed bars) species.

secondarily influenced by the occurrence of prey species, including beetles and flies.

Cockroaches were the only group whose species richness and assemblage composition were most plausibly explained by frequent human visitation. The species richness of exotic cockroach species was substantially greater on more frequently visited islands (Fig. 7). Detailed analysis (Burwell *et al.*, 2010) further revealed that notably more native cockroaches were caught in Malaise traps than pitfall traps, suggesting that native species are active fliers and can potentially disperse between cays and from the mainland. Exotic species, on the other hand, may depend on passive, human-mediated dispersal. Indeed, the most numerous exotic species on the cays, *Pycnoscelus surinamensis*, is predominantly flightless and requires passive dispersal (Burwell *et al.*, 2010).

The utility of an Information theoretic approach

Our study presents a number of predictor variables that *plausibly* explain variation in both univariate (species richness) and multivariate (assemblage) data. It should be stressed that we are not testing, but rather generating hypotheses that are likely to explain the observed patterns across different taxonomic groups. ITA provides a very useful tool when we do not know the likely factors structuring communities and multiple factors may be involved (Stephens *et al.*, 2005). The results of ITA indicated that multiple factors were likely to drive the species richness and composition of the insular faunas of some taxa.

When there were correlated variables with similar ecological properties, we removed one of them prior to analysis (Appendix S1d). We opted, however, to include correlated, yet ecologically unrelated variables in order to quantify their relative importance. In this instance, there may be several equally plausible alternative models and selecting only the 'best' model using MSA is undesirable. Indeed, for many of our datasets,

differences in AIC values between the best and other models were small (see Akaike weight values in Appendix S1i), suggesting that multiple models were well supported. ITA, for example, selected two variables, island size and one related to spatial configuration ('X'), as plausible predictors of native plant species composition (Table 1). In contrast, MSA chose only the spatial configuration variable and excluded the equally (if not more) plausible and ecologically meaningful variable of island size (Appendix S1h). Similarly, MSA included only a single variable for both beetle and fly composition (native plant species richness) and excluded other equally plausible variables from the final model. One may argue that our results exaggerate the weakness of MSAs as we employed stepwise regression, which is considered one of the poorest selection procedures (Burnham & Anderson, 2014). Several other model selection procedures (e.g. optimal shrinkage applied in ridge regression) and modified model selection methods are available to alleviate the collinearity of predictor variables; however, Dormann *et al.* (2013) demonstrated that none of them fully solve this problem.

Furthermore, MSA is often biased and random variables can be selected when there is collinearity of predictor variables or presence of noise in the data (Flack & Chang, 1987). This is especially true when the number of observations ($n = 14$, in our study) is small relative to the number of predictor variables ($n = 10$) (Dahlgren, 2010). Indeed, this was the case in our study where some apparently spurious variables were selected due to inherent bias in MSA. One notable result was fly species richness where exclusion or inclusion of one island (Lady Elliot Island) changed the predictor variables selected by MSA (Appendix S1h). We therefore argue that model averaging provided unbiased measures of the relative importance of predictor variables (but see Richards, 2005).

CONCLUSIONS

Using the information theoretic approach on both univariate and multivariate datasets, we demonstrate that human disturbance and infestation of invasive species can override the influence of island biogeographical processes. The relative importance of these factors was, however, taxon dependent. We stress the importance of multi-taxon approach in studying island biogeography and in monitoring the impacts of human-disturbance and invasive fauna on insular communities.

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SUPPORTING INFORMATION

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

Appendix S1 Supplementary tables and figures.
Appendix S2 Supplementary methods.
Appendix S3 The R code.

DATA ACCESSIBILITY

The data used for the present study has been deposited in PANGAEA Data Archiving & Publication (http://www.pangaea.de/) (Publication doi:10.1594/PANGAEA.844955).

BIOSKETCH

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