Original article

Integration of non-indigenous species within the interspecific abundance–occupancy relationship

François Rigal [a,*], Robert J. Whittaker [b,c], Kostas A. Triantis [a,b,d], Paulo A.V. Borges [a]

[a] Azorean Biodiversity Group, (CITA-A) and Platform for Ecological and Environmental Research (PEER), Universidade dos Açores, Departamento de Ciências Agrárias, Rua Capitão João d'Ávila, São Pedro, 9700-042 Angra do Heroísmo, Terceira, Portugal
[b] Conservation Biogeography and Macroecology Programme, Oxford University Centre for the Environment, South Parks Road, Oxford OX1 3QY, UK
[c] Center for Macroecology, Evolution and Climate, Department of Biology, University of Copenhagen, Universitetsparken 15, DK-2100 Copenhagen Ø, Denmark
[d] Department of Ecology and Taxonomy, Faculty of Biology, National and Kapodistrian University of Athens, Athens GR-15784, Greece

ARTICLE INFO

ABSTRACT

There is a broad consensus that habitat disturbance and introduction of non-indigenous species may dramatically modify community structure, particularly in insular ecosystems. However, it is less clear whether emergent macroecological patterns are similarly affected. The positive interspecific abundance–occupancy relationship (IAOR) is one of the most pervasive macroecological patterns, yet has rarely been analyzed for oceanic island assemblages. We use an extensive dataset for arthropods from six islands within the Azorean archipelago to test: (1) whether indigenous and non-indigenous species are distributed differently within the IAOR; and (2) to the extent that they are, can differences can be attributed to two indices of disturbance. We implemented modeling averaged methods using five of the most common IAOR models to derive an averaged IAOR fit for each island. After testing if species colonization status (indigenous versus non-indigenous) may explain the residuals of the IAOR, we identified true negative and positive outliers and tested the effect of colonization status on the likelihood of a species being a positive or negative outlier. We found that the indigenous and non-indigenous species are randomly distributed on both sides of the overall IAOR. Only for Flores Island, were non-indigenous species more aggregated than indigenous species. We were unable to detect a meaningful relationship between deviation from the IAOR and disturbance, despite the undoubted impact of both severe habitat loss and non-indigenous species on these oceanic islands. Our results show that the non-indigenous species have been integrated alongside indigenous species in the contemporary Azorean arthropod communities such that they are mostly undetectable by the study of the IAOR.

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1. Introduction

The introduction of non-indigenous species and the destruction of habitat, separately and in combination, are disturbing native communities on a global scale (Hoekstra et al., 2004; Westphal et al., 2008). These impacts are particularly severe on oceanic islands (Gillespie and Roderick, 2002; Whittaker and Fernández-Palacios, 2007). However, despite considerable research effort, many aspects of the impact of species introductions and habitat destruction on oceanic ecosystems remain poorly understood (Mooney and Cleland, 2001; McNatty et al., 2009).

One of the most important and ubiquitous patterns in macroecology is the positive interspecific abundance–occupancy relationship (IAOR) (Hanski, 1982; Brown, 1984; Gaston and Lawton, 1990). For a specific species assemblage, the IAOR is the relationship between the mean local abundance for each species and the proportion of sites they occupy. This pattern has been documented for a wide variety of taxa and ecosystems (Gaston et al., 2000; Blackburn et al., 2006) yet remains poorly studied in oceanic islands (but see Gaston et al., 2006). The influence of non-indigenous species on such relationships is also poorly understood (Holt and Gaston, 2003). If non-indigenous species fall within the same IAOR together with the indigenous species, this would imply that indigenous and non-indigenous species have been assimilated in a common macroecological outcome (Gaston et al., 2006). On the other hand, if non-indigenous species are predominantly outliers

* Corresponding author.
E-mail address: rigal@uac.pt (F. Rigal).

Table 1
Characteristics and sampling effort for the six Azorean islands included in the analyses, together with epigean arthropod species numbers within each distributional category collected in the field, and two measures of disturbance. For the island characteristics and the sampling, A is area of remaining native forest (m²), NFtot the total number of fragments, NFl the number of large fragments, NFm the number of medium size fragments, NFs the number of small fragments and Ns the total number of sampled sites (transects). For the number of species collected, values in the parentheses indicate the numbers species which were identified only to morphospecies. For disturbance, PRF is the percentage of remnant forest area relatively to the size of the island, and QI is a habitat quality index (See Materials and methods for the details of the calculation) and SE is its associated standard error.

Islands	Island characteristics and sampling					Species numbers collected					Disturbance		
	A	NFtot	NFl	NFm	NFs	Ns	Total	Indigenous	Non-indigenous	Endemic	Native	PRF	QI	SE
Terceira	2345	5	2	2	1	28	126 (18)	73 (7)	53 (11)	32 (2)	41 (5)	5.84	12.892	0.515
Flores	1571	2	1	1	0	12	105 (13)	59 (6)	46 (7)	26 (3)	33 (3)	11.06	12.416	1.196
Pico	952	3	1	2	0	16	97 (13)	62 (5)	35 (8)	30 (2)	32 (3)	2.2	13.062	0.432
São Miguel	331	3	0	1	2	12	112 (9)	66 (5)	46 (4)	29 (5)	37 (0)	0.52	8.75	0.551
São Jorge	293	2	0	2	0	8	65 (7)	44 (4)	21 (3)	21 (0)	23 (4)	1.19	10.125	0.875
Faial	226	2	0	1	1	8	84 (7)	46 (3)	38 (4)	12 (0)	34 (3)	1.31	7.125	0.61

from the IAOR this would suggest that they are using the ecological space in a rather distinctive way.

The impact of disturbance on the form of the IAOR is also poorly known. Among the few studies dedicated to this issue, Gaston and Warren (1997) found no significant differences in the intercept, slope and coefficients of determination of the positive IAOR whatever the intensity of disturbance they imposed on microcosm communities of protists. More recently Webb et al. (2007) showed that habitat modifications increased the scatter (i.e. a decline in the strength of the IOAR) in the positive IAOR through time for British birds, while Buckley and Freckleton (2010) found a stable IAOR through a 25-year period for vascular plants in New Zealand tussock grasslands that have undergone environmental changes. These studies suggest two propositions: (1) whether or not the strength of the IOAR is affected by a perturbation, the relationship remains strongly and significantly positive; and (2) the stability of the IAOR is mainly due to a broad organizing process, in which species may differ in their relative abundance and occupancy according to the strength of the disturbance. This in turn implies that the disturbance merely rearranges the species assemblages without necessarily greatly changing the emergent macro-ecological pattern (but see discussion in Gaston and Warren, 1997).

In the last 600 years the Azorean archipelago has suffered large scale deforestation and human encroachment, causing an unprecedented disturbance and reduction of the native habitat (Gaspar et al., 2008; Triantis et al., 2010). As a result, the archipelago has lost >95% of the original native forest and the current biota is dominated by non-indigenous species (e.g. 80% of the flora (Shaefer, 2003)); 60% of the arthropods (Borges et al., 2005b).

A previous study by Gaston et al. (2006) analyzed the IAOR for Azorean arthropods, exploring the performance of a particular IAOR model (the trivariate negative binomial of He and Gaston, 2003) at three spatial scales: the largest forest fragment of the island of Terceira, the whole island Terceira, and the whole archipelago. It was shown that when the fauna was divided into three groups: native but non-endemic, endemic, and non-indigenous species, each group lay on the same IAOR regardless of the spatial extents considered.

The degree of disturbance varies markedly between islands in the Azores, with some, such as Terceira Island, retaining relatively large and pristine native forest fragments while, at the other extreme, some having entirely lost their native forest (Gaspar et al., 2011).

In this study, we extend the work of Gaston et al. (2006) by (1) evaluating individually five additional islands varying in the extent of remaining native forest cover from 0.5% to 11% of the original forest, from which soil arthropod communities have been surveyed using standardized methods (Borges et al., 2005a; Gaspar et al., 2008) and (2) implementing an alternative statistical approach based on modeling averaged methods. Here, we classified species

into two main different colonization categories: indigenous (including native but non-endemic species plus endemic species) and non-indigenous species (anthropogenic introductions, i.e. exotic species).

The introduction of non-indigenous species and ecosystem disturbance is known to have caused profound ecological change on many oceanic islands (Gillespie and Roderick, 2002; Gillespie et al., 2008), including the Azores (e.g. Borges et al., 2006; Cardoso et al., 2009). Given that, we test: (1) whether the absence of difference between indigenous and non-indigenous species in the IAOR space (which is expected based on Gaston et al., 2006) is consistent across islands regardless of their degree of forest disturbance and (2) if differences are detected, whether they could be related to the extent of forest disturbance that has occurred. As we are examining co-occurring species within a single IAOR, we test for differences in the residual variations around the relationship between indigenous versus non-indigenous species and we do so according to the extent of habitat transformation ('disturbance'), based on two different assessments of disturbance level (details below).

2. Materials and methods

2.1. Study area

The Azores is one of the world's most isolated archipelagos. Located in the North Atlantic (37–40° N, 25–31° W), it is made up of nine islands aligned on a West/North-west to East/South-east axis (Flores and Corvo to the west, Faial, Pico, São Jorge, Terceira and Graciosa in the center and São Miguel and Santa Maria to the east). Maximum geological ages of the islands range from 250,000 yr BP for Pico to 8.12 Ma for Santa Maria. Native forest in the Azores is characterized by an association of evergreen shrub and tree species ("Laurisilva" Borges et al., 2005a). Documents from the 15th century suggest that native vegetation in which Laurisilva was a dominant type of forest almost completely covered all of the islands until the point when the first human settlements were established. Clearing for wood, agriculture and pasture has markedly reduced the native forests, which are now largely restricted to high and steep areas (Gaspar et al., 2008). The introductions of exotic species started very early during human land-use changes almost 600 years ago, since the Portuguese settlers brought plants from all parts of the world, and especially from mainland Portugal, South America and Africa.

2.2. Data collection

Eighty-four sites (transects) in 17 native forest fragments distributed on six islands were sampled between 1999 and 2003

(Table 1). Eight sites were surveyed in large fragments (area > 1000 ha) in order to encompass potential area-related variability (e.g. between edge and core sites) and four in medium (100 ha < area < 1000 ha) and small fragments (area < 100 ha). The islands Graciosa and Corvo now lack native forest altogether and so they were excluded from the study. Santa Maria was also excluded as it has just a single small fragment of native forest (area = 9 ha; 4 sites), which does not allow an accurate measure of occupancy at the island scale. Thus, the islands selected were Terceira, Flores, Pico, São Miguel, São Jorge and Faial. The number of sites sampled in each island was calculated so as to be proportional to the area of remaining native forest (Spearman rank correlation $r_s = 0.88$, $p = 0.02$).

At each site, epigean soil fauna were captured using 30 pitfall traps (diameter = 42 mm; depth = 80 mm) equally spaced along transects of 150 m length. The traps were half-filled with 60 ml of solution, alternating from trap to trap between diluted ethylene glycol (anti-freeze liquid) and a general attractive solution (Turquin, 1973). They were left in the field for two weeks in the summer of different years (see Borges et al., 2005a). The majority of arthropods was identified at the species level and a small minority (17%) to morphospecies. All species were classified as indigenous or non-indigenous (Table 1 and Table S1). When it was not possible to obtain a firm species identification, the colonization status was determined using the following criteria: archipelago endemic if it belonged to a genus composed of only endemic taxa in the archipelago; non-indigenous if it belonged to a family mainly composed of non-indigenous species in the archipelago; native in all cases for which there were no reliable data.

2.3. Measures of disturbance

We estimated island disturbance in two ways. First, values were assigned for each island based on the current area of native forest determined by digital aerial photography (Gaspar et al., 2008) and expressed as the percentage of the island area occupied by remnant forest (Table 1). Second, for each of the 84 sampled sites, we calculated a habitat quality index based on six factors (Cardoso et al., 2007): (1) area of the fragment in which the site was included, (2) distance of the site to the edge of the fragment, (3) human encroachment in fragment, (4) dominance of introduced plants, (5) presence of grazing cattle, and (6) abundance of human paths that cross the native forest. We know from previous work that these six factors may have significant impacts on the soil arthropod community. Each factor was evaluated per sampling site using a semi-quantitative scale with four points ranging from three, for no influence, to 0, for a high influence (See Tables S2–S4 for more details). The index is the sum of the values for each factor. The higher the index value, the higher the habitat quality of the site.

Based on these values, we calculated the mean and the standard error to obtain one habitat quality index value per island (Table 1).

2.4. IAOR modeling

The sampling unit considered for this study was the individual site (the set of 30 pitfall traps along one transect). The mean abundance of species per island was computed as the abundance averaged over all sites, and occupancy as the number of sites where the species occurred divided by the total number of sites. We treat occupancy as the response variable and mean abundance as the predictor, which is likely the more prevalent direction of causality (Gaston, 2003). Since our goal is to seek for potential signal in the deviations of the IAOR between indigenous and non-indigenous arthropods species, we adopted a statistical method combining both fit optimization and examination of residuals. This method takes its lead from non-linear modeling methods. However, it is noteworthy to notice that there are no particular methods that warrant primacy in disentangling the mechanisms underlying IAOR, and other statistical procedures may be envisaged (e.g. Holt and Gaston, 2003; Verberk et al., 2010). To obtain the most accurate deviation measures (i.e. residual values) from the overall community IAOR of species in each of the two categories (indigenous versus non-indigenous), we applied a model averaging procedure (Burnham and Anderson, 2002). We justify the choice of this procedure by the fact that, in preliminary analyses, we did not find strong support for a single model (i.e. the islands supported several models with a similar strength). In such cases, a multimodel inference procedure is recommended as a means to determine a robust final fit (Burnham and Anderson, 2002), and particularly in our case, to estimate non-model dependant deviations from the predicted values. Eight commonly used IAOR models were extracted from the literature: the Poisson model (PM: Wright, 1991), the negative binomial (NBD: He and Gaston, 2000), the improved NDB (INBD: see Hui et al., 2009), the trivariate negative binomial distribution model (TNBD: He and Gaston, 2003), the exponential model (EXP: Nachman, 1981), the metapopulation model (MTP: Hanski and Gyllenberg, 1997), the power model (PW: Leitner and Rosenzweig, 1997) and the local−regional population model (LRPM: Freckleton et al., 2005). Of these, the following three models were evaluated but then excluded from further analyses: the PM provided extremely poor fit to the data; the PW and LRPM both produced values of predicted occupancy superior to 1 (i.e. both PW and LRPM are non-asymptotic models). Thus, five models (NBD, INBD, TNBD, EXP and MTP), which provided good fits to the data, were selected in order to define a consensus IAOR for each island (Table 2).

Each of these five models was fitted by minimizing the residual sum of squares in non-linear regressions using the Nelder and Mead (1965) optimization algorithm. We then discriminated among the five models within a model selection framework (Burnham and Anderson, 2002) using the Akaike information criterion (AIC). To account for a potential source of bias, we used the AICc corrected for small sample size (Sugiura, 1978). The lower the AICc, the better a model explains the data. AICc weights (w_i hereafter), normalized across the set of models so that they sum to one, were used to evaluate the relative likelihood of each of the five IAOR models. AIC and BIC (Bayesian Information Criterion) weights were also computed for comparisons. We then computed a model averaging inference considering the average weights of model predictions with respect to the w_i in order to build an averaged IAOR fit. We therefore evaluated goodness-of-fit for the averaged models by R^2 values using the formula of Kvålseth (1985), which is designed to compute goodness-of-fit for non-linear regression models. The formula is $R^2 = 1 - [\sum (y_i - \hat{y}_i)^2 / \sum (y_i - \bar{y}_i)^2]$ where

Table 2
The five models used to fit the interspecific abundance–occupancy relationship (IAOR). p is occupancy, μ abundance, σ^2 the variance of abundance and k, c, b, α, β, are constants. See references in the Materials and methods.

Name	Formula
Negative binomial distribution model (NBD)	$p = 1 - \left(1 + \frac{\mu}{k}\right)^{-k}$
Improved negative binomial distribution model (INBD)	$p = 1 - (c \times \mu^{b-1})^{\mu/(1-c\mu^{b-1})}$
Trivariate negative binomial distribution model (TNBD)	$p = 1 - \left(\frac{\sigma^2}{\mu}\right)^{-\mu 2/(\sigma^2 - \mu)}$
Exponential model (EXP)	$p = 1 - e^{\alpha\mu^\beta}$
Metapopulation model (MTP)	$p = 1 - \left(\frac{1}{1 + \alpha\mu^\beta}\right)$

y_i is the observed value of occupancy, $\hat{y}_i$ is the fitted value, and $\bar{y}_i$ is the mean of the observed values.

2.5. Phylogenetic effects

It may reasonably be assumed that closely related species are on average more likely to display similar traits than less closely related species, raising issues of independence of data points in statistical analyses. Unfortunately, no phylogeny is available for our data. Furthermore, a part of the taxonomic information is still missing for the genera and, for some morphospecies, for the family. Given these limitations, to test for phylogenetic dependence within our data we constructed a similarity matrix using only species for which complete taxonomical information is available. We then used a phylogenetic generalized linear model (pglm) to incorporate the taxonomic similarity matrix into a model per island with abundance and occupancy (both log transformed) (see also Webb et al., 2009). To be more specific, we tested the maximum likelihood value of λ, which varies between 0 when evolution of a trait (here, the macroecological traits abundance and occupancy) is independent of phylogeny and 1 when evolution of the trait is consistent with a Brownian model of evolution (Freckleton et al., 2002). For the six islands, λ was significantly different from 1 but not significantly different from 0, meaning an absence of phylogenetic effect in the relationship between abundance and occupancy. This is unsurprising, as the lack of phylogenetic signal in abundance and occupancy seems to be rather a common observation (Webb and Gaston, 2005). Because our method and pglm are not strictly based on the same statistical framework, we thus used the taxonomical levels Class and Order as hierarchical nested random effects in the following mixed models for the IAORs outliers.

2.6. Analysis of the residuals

We investigated the residuals from the IAOR in two different ways. Note that the use of residuals as data is still controversial (For a critique, see Freckleton, 2009) but no specific method has been proposed yet to explore deviations when non-linear multimodel inference is considered. Then, we first test if the colonization status may explain the residuals from the underlying IAOR. Second, to distinguish true negative and positive outliers for indigenous and non-indigenous species, we estimated a confidence interval (CI) using a non-parametric bootstrapping procedure (See Materials and methods S1 for more details). This method allows model selection and parameter estimation uncertainties to be taken into account (Guilhaumon et al., 2008). For each island, we define negative and positive outliers as those lying respectively above the upper limit and below the lower limit of the 95% confidence interval. We tested for the effect of categories on the likelihood of a species being a positive or negative outlier using a binomial generalized linear model. Following the procedure proposed by Poulin et al. (2011), three sets of analyses were performed: first, in which species were classified as either being positive (coded 1) or negative (coded 0) outliers; second, in which species were classified as either being a positive (coded 1) outlier, or not (coded 0); and third, in which species were classified as either being a negative (coded 1) outlier, or not (coded 0). We tested for the effect of colonization categories by fitting linear mixed models (LMMs) for the IAOR residuals and generalized linear mixed models (GLMMs) with binomial errors and logit link for the analysis of the outliers with, in each case, Class and Order set as nested random effects to control for phylogenetic dependence in the models. The effect of categories was tested against a null model including only the random effects by the likelihood ratio method using the χ^2 distribution for the estimation of significance.

Table 3
Results of the model selection among the five IAOR models for indigenous and non-indigenous epigean arthropod species in each Azorean island. The model abbreviations (columns names) are explained in the text and in Table 2. The values correspond to model weights w_i based on the AICc (Akaike Information Criterion corrected for small sample size). AICc weights w_i correspond to the probabilities of each model providing the best fit to the data. The percentage of the variance explained (R^2) by the averaged multimodel model is also given. The averaged multimodel model is the new predicted values derived from the weights of each model prediction with respect to the AICc weights w_i.

Islands	w_i NDB	w_i INDB	w_i TNDB	w_i EXP	w_i MTP	R^2
Terceira	0	0.413	0	0.587	0	0.898
Flores	0.005	0.412	0	0.325	0.257	0.837
Pico	0	0.419	0	0.564	0.017	0.873
São Miguel	0.001	0.458	0	0.374	0.167	0.894
São Jorge	0.158	0.335	0	0.307	0.201	0.824
Faial	0.003	0.329	0	0.636	0.032	0.697

In addition, we re-ran the analyses (i.e. LMMs/GLMMs for residuals and the outliers) having partitioned the indigenous species into endemics and other native species. This new analysis did not provide any additional insights and therefore, in the following sections, only the results with two categories (indigenous and non-indigenous) are shown. For all the analyses involving probabilistic statistics, the significance level was set at 5%. All the statistical analyses conducted in this study were implemented within the R programming environment (R Development Core Team, 2009). Mixed models were implemented using the packages lme4 (Bates and Maechler, 2010) and nlme (Pinheiro et al., 2009). To test the phylogenetic effect, we used the function pglmEstLambda from the R package CAIC (Orme et al., 2009).

3. Results

3.1. Descriptive statistics and quality index

A total of 10,020 arthropod specimens distributed amongst 19 orders, at least 90 families (including 2 non-identified), 205 genera (including 20 non-identified) and representing 253 species (including 45 morphospecies) was collected. Of these species, 141 were considered to be indigenous (59 Azorean endemics and 82 native to the Azores) and 102 non-indigenous (Table 1 and see Table S1). On average, indigenous species represented $60.4 \pm 5\%$ of the total number of species collected per island while non-indigenous species constituted the remaining $39.6 \pm 5\%$. There was a significant difference in the proportion of indigenous and non-indigenous species between the six islands ($\chi^2 = 14.47$, df $= 5$, $p = 0.012$). The habitat quality index was not significantly higher for islands with larger areas or percentages of remaining native forest (Spearman rank correlation: $r_s = 0.77$; $p = 0.1$ and $r_s = 0.6$; $p = 0.24$ respectively).

3.2. Model selection and multimodel inference

The results of the model selection are given in Table 3 and the averaged multimodel fits are presented in Fig. 1. Here, we report weights based on the AICc statistic but similar results were also obtained with AIC and BIC (data not shown). Each of the five models used in this study explain a high percentage of the variance of the IAOR for each of the six islands (See R^2 values per model for the six islands in Table S5). We did not find strong support ($w_i < 0.9$; Burnham and Anderson, 2002) for any of the models. Nonetheless, the EXP and INDB models best supported the data (mean $w_i > 0.3$) for the six islands, while NBD and TNBD failed for all the islands (with the exception of a weak fit for São Jorge with NDB $w_i > 0.15$).
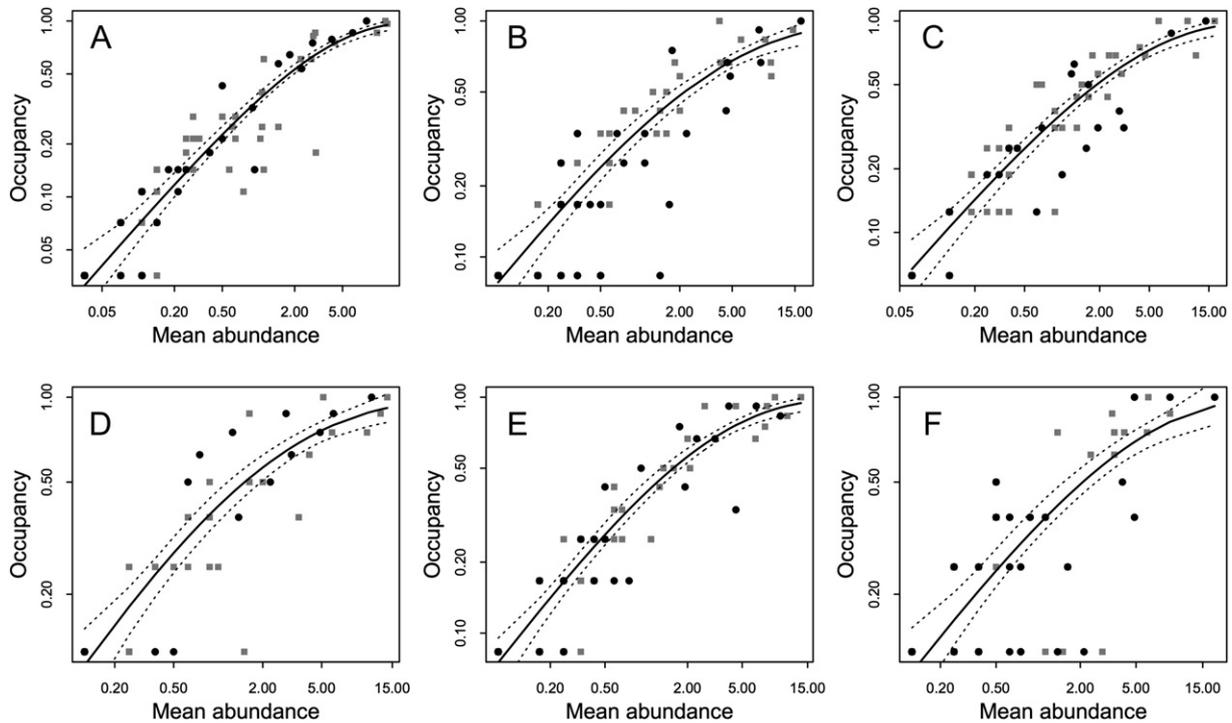
Fig. 1. The interspecific abundance–occupancy relationship of the epigean soil arthropod community for each Azorean island. Figures are presented using a log–log scale. A = Terceira; B = Flores; C = Pico; D = São Miguel; E = São Jorge; F = Faial. The solid smooth curves are the averaged multimodel models and the broken lines indicate the 95% confidence interval. The correspondence of the symbols is: ▪ = Indigenous and ● = Non-indigenous species.

For the six islands, the averaged multimodel explained a high percentage of the variance (Table 3).

3.3. Analysis of the residuals

Results of the LMMs between residuals of the IAOR and colonization categories revealed no significant differences between indigenous and non-indigenous except for the island of Flores. Whether looking for positive versus negative, positive versus non-positive, or negative versus non-negative outliers, the GLMMs did not show any significant results, except also for Flores Island where

Table 4
Results of the linear mixed models (LMMs) and generalized linear mixed models (GLMMs), testing the effect of categories (i.e. indigenous and non-indigenous) on the residuals of the IAOR and the likelihood of epigean arthropod species being a positive or negative outlier for each Azorean island. Species identified as positive and negative outliers are those lying respectively above the upper limit and below the lower limit of the 95% confidence interval. For each model, Class and Order were set as nested random effects to control for phylogenetic dependence. The effect of the categories was tested by the likelihood ratio method using the χ^2 distribution for the estimation of significance. df = degrees of freedom. The log ratio LR of the likelihood ratio test and its associated p-value are given. Significant p-values are in bold.

Island	LMMs for residuals		GLMMs for the outliers					
			POS versus NEG		POS versus non-POS		NEG versus non-NEG	
	LR χ^2 on 1 df	p	LR χ^2 on 1 df	p	LR χ^2 on 1 df	p	LR χ^2 on 1 df	p
Terceira	1.235	0.266	0.006	0.933	0.74	0.389	0.494	0.482
Flores	**6.348**	**0.011**	**7.146**	**0.007**	**5.624**	**0.017**	**5.181**	**0.022**
Pico	3.295	0.069	0.908	0.340	2.366	0.124	0	0.99
São Miguel	0.285	0.593	0.131	0.716	1.117	0.290	0.331	0.565
São Jorge	2.288	0.130	2.054	0.151	2.009	0.157	0.724	0.394
Faial	1.062	0.302	0.758	0.383	0.432	0.510	1.078	0.299

the colonization categories had a significant effect on the likelihood of a species displaying a positive or negative deviation (Table 4). Inspection of the parameters estimated by the model for Flores Island showed for all four sets of analyses that species with negative deviation were significantly more likely to belong to the non-indigenous subset.

4. Discussion

Our analyses show that indigenous and non-indigenous species are generally randomly distributed on both sides of the overall IAOR. Furthermore, the analysis of occupancy and mean abundance independently did not show difference between indigenous and non-indigenous species in the six islands studied. Thus, the roles of indigenous and non-indigenous species within the community dynamics seem to be very similar regardless of the characteristics of the remaining native forest. Our results corroborate those of Gaston et al. (2006), wherein native but non-endemic, endemic and non-indigenous species lie on the same IAOR for the three spatial scales considered: the larger native forest fragment in Terceira Island, the entire Terceira Island and the whole Azorean archipelago.

A single significant pattern of aggregation for non-indigenous species was found in Flores Island. Although the correlation between disturbance and the distribution of the outliers was not demonstrated statistically, the deviance of Flores from the overall pattern may have something to do with this island having the highest percentage of remnant native forest cover, although we note that the quality index for Flores, if averaged at the island level was not the highest observed (Table 1). At best then, the Flores result provides limited support for the existence of a disturbance signal in these data.

Overall, the apparent assimilation of indigenous and non-indigenous species within the IAOR has to be understood as an

outcome of the destruction and fragmentation of Azorean forests in combination with the introduction of non-native species, with these processes occurring in concert since human colonization began 600 years ago. Recent centuries have seen the dramatic reduction of the Azorean native forest, to around 3% of the total area of the archipelago by the end of the 20th century (Gaspar et al., 2008; Triantis et al., 2010). Most of the habitats surrounding native fragments have undergone important land-use changes and anthropogenic disturbance and hence are dominated by non-indigenous species (Borges et al., 2006; Cardoso et al., 2009). Although some endemic and native species may survive in exotic forest or semi-natural pastures (Cardoso et al., 2009; Meijer et al., 2011), habitat fragmentation clearly acts as an isolating factor for most of the indigenous arthropod populations (Borges et al., 2006). Disturbed landscapes offer good habitat for many non-indigenous species, providing source populations that may migrate into the native forests (e.g. Cardoso et al., 2009).

In addition, the indigenous Azorean arthropod fauna is relatively species poor: a consequence of the young age and the isolation of these islands (Borges and Hortal, 2009; Triantis et al., 2011), which in combination has resulted in unsaturated local communities (Borges and Brown, 2004; Ribeiro et al., 2005). Unsaturated local communities are thought to offer greater opportunities for exotic species to invade, especially when the natural habitat is highly disturbed (Gillespie et al., 2008). Thus, the observed distribution of indigenous and non-indigenous species along the overall IAOR may be the consequence of historical factors (i.e. unsaturated communities) commonly reported for remote islands and contemporary factors (e.g. anthropogenic changes, fragmentation of native forest), which combined, have resulted in a community where indigenous and non-indigenous species occur at any rank. An alternative view is simply that the origin of a species has no bearing on the place a species achieves in the IAOR and that the explanation offered cannot be easily distinguished from a simple null hypothesis; thus further studies on oceanic biotas are required to disentangle this issue.

Investigation of the position of species within the IAOR space documented herein may, however, lead to a more accurate estimation of species particularly at risk of extinction (Gaston et al., 2000) and also serves to highlight those non-indigenous species that dominate these communities. As mentioned by Lawton (1993), the existence of a positive IAOR implies that species face "double jeopardy", meaning that local abundance and occupancy may contribute independently or together to the extinction risk of a species. Here, low local abundance may increase the likelihood of stochastic extinction of indigenous species that are unable to establish viable populations outside the remaining native forest patches. Also, a contracted spatial range may increase the likelihood that these indigenous arthropod populations will simultaneously undergo abiotic and biotic environmental stress such as deforestation and encroachment by human activities. Examples of species restricted in both abundance and occupancy in this way include the endangered endemic forest specialist beetles *Alestrus dolosus* in Pico island (included in the IUCN Red list: http://www.iucnredlist.org/apps/redlist/details/157633/0) and *Phloestiba azorica* in Terceira Island. In contrast, the introduced milliped *Ommatoiulus moreletti*, has become the dominant species among epigean soil arthropod communities, both in terms of abundance and occupancy, within the native forest of Faial, Pico, Flores and São Jorge islands.

The positive IAOR appears to be almost ubiquitous and the mechanisms underlying it are not exclusive (Gaston et al., 1997; Hartley, 1998). Several authors have previously advocated explicitly considering deviations amongst species within IAOR space rather than focusing simply on the strength of the IAOR itself (Cowley et al., 2001; Holt and Gaston, 2003; Buckley and Freckleton, 2010). However, incorporating model uncertainty into studies of such deviations can lead to dramatically different conclusions compared with studies based on only a single model (cf. Guilhaumon et al., 2008). Our model selection protocol includes five of the most commonly used models for describing the IAOR and reveals a substantial level of model uncertainty. For the five islands, no single model was clearly better than the others (See w_i in Table 3). Note that the NBD and TNBD models previously tested for the soil arthropod data of Terceira Island (Gaston et al., 2006) accounted either for low or null support (w_i) for the IAOR in each island. Ecological mechanistic assessments for the models are difficult to make (He et al., 2002) and our study does not address this issue.

5. Conclusion

Our work shows an absence of linkage between indigenous/non-indigenous status and species position in the IAOR space for the great majority of studied islands. In essence, via this particular emergent macroecological pattern, indigenous and non-indigenous species are largely undistinguishable. This is despite the fact that some non-indigenous species have become highly abundant and widespread and may have replaced the roles of particular indigenous species in the functional ecology of the system.

Acknowledgments

Appendix A. Supplementary material

Supplementary material related to this article can be found online at http://dx.doi.org/10.1016/j.actao.2013.02.003.

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