

# Differential temporal beta-diversity patterns of native and non-native arthropod species in a fragmented native forest landscape

Matthews, Thomas; Sadler, Jonathan; Carvalho, Rui; Nunes, Rui; Borges, Paul A V

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1 **Journal: Ecography R2**

2 **Differential temporal beta-diversity patterns of native and non-native arthropod species**  
3 **in a fragmented native forest landscape**

4

5 Thomas J. Matthews\*<sup>1, 2,3</sup>, Jon Sadler<sup>1</sup>, Rui Carvalho<sup>2</sup>, Rui Nunes<sup>2,4</sup>, Paulo A. V. Borges<sup>2,4,5</sup>

6 <sup>1</sup>GEES (School of Geography, Earth and Environmental Sciences), University of  
7 Birmingham, Birmingham, B15 2TT

8 <sup>2</sup>CE3C – Centre for Ecology, Evolution and Environmental Changes/Azorean Biodiversity  
9 Group and Universidade dos Açores – Depto de Ciências Agrárias Engenharia do Ambiente,  
10 PT-9700-042, Angra do Heroísmo, Açores, Portugal.

11 <sup>3</sup>Birmingham Institute of Forest Research, University of Birmingham, Edgbaston,  
12 Birmingham, B15 2TT, UK

13 <sup>4</sup>IUCN Mid-Atlantic Island Invertebrates Specialist Group

14 <sup>5</sup>IUCN SSC Species Monitoring Specialist Group

15

16 \*Correspondence author. Email: txm676@gmail.com

17 An important factor that hinders the management of non-native species is a general lack of  
18 information regarding the biogeography of non-natives, and, in particular, their rates of  
19 turnover. Here, we address this research gap by analysing differences in temporal beta-  
20 diversity (using both pairwise and multiple-time dissimilarity metrics) between native and  
21 non-native species, using a novel time-series dataset of arthropods sampled in native forest  
22 fragments in the Azores. We use a null model approach to determine whether temporal beta-  
23 diversity was due to deterministic processes or stochastic colonisation and extinction events,  
24 and linear modelling selection to assess the factors driving variation in temporal beta-  
25 diversity between plots. In accordance with our predictions, we found that the temporal beta-  
26 diversity was much greater for non-native species than for native species, and the null model  
27 analyses indicated that the turnover of non-native species was due to stochastic events. No  
28 predictor variables were found to explain the turnover of native or non-native species. We  
29 attribute the greater turnover of non-native species to source-sink processes and the close  
30 proximity of anthropogenic habitats to the fragmented native forest plots sampled in our  
31 study. Thus, our findings point to ways in which the study of turnover can be adapted for  
32 future applications in habitat island systems. The implications of this for biodiversity  
33 conservation and management are significant. The high rate of stochastic turnover of non-  
34 native species indicates that attempts to simply reduce the populations of non-native species

35 *in situ* within native habitats may not be successful. A more efficient management strategy  
36 would be to interrupt source-sink dynamics by improving the harsh boundaries between  
37 native and adjacent anthropogenic habitats.

38 **Keywords:** Invasive species, beta-diversity, turnover, theory of island biogeography for  
39 exotic species, island biogeography, fragmentation, habitat island

## 40 **Introduction**

41 The introduction, spread and establishment of species outside of their native range can result  
42 in substantial changes to natural ecosystems (Mooney and Hobbs 2000, Dyer et al. 2017),  
43 sometimes including the local and/or regional extirpation of native species (Clavero and  
44 García-Berthou 2005, Bellard et al. 2016). Furthermore, the global rate of transfer and mixing  
45 of species between native and non-native ranges does not show any signs of decreasing  
46 (Seebens et al. 2017). We use the term ‘non-native’ throughout this study and we define such  
47 species simply as those that are present in an area outside of their native range as a result of  
48 human actions (Blackburn et al. 2016), which on islands is generally a consequence of  
49 commerce, gardening, agriculture and forestry (Whittaker and Fernández-Palacios 2007).

50 Indeed, the impact of non-native species, and particularly invasive species (a subset of non-  
51 native species), is variable but it does appear to be more acute on islands (Blackburn et al.  
52 2004, Whittaker and Fernández-Palacios 2007, Bellard et al. 2016, but see Sax et al. 2002). A  
53 key component of assessing the impact of non-native species in island systems involves the  
54 development, and testing, of (island) biogeographical theories and models relevant to them  
55 (Pyšek 1998, Blackburn et al. 2008, 2016, Burns 2015). For example, in their fifty  
56 ‘fundamental questions in island biology’, Patiño et al. (2017) recently highlighted that  
57 understanding how the impacts of non-native species differ from those of naturally colonising  
58 species is a key question in their management.

59 Burns (2015) has started this process via a recently introduced extension of MacArthur and  
60 Wilson’s (1967) equilibrium theory of island biogeography (ETIB), which he termed a  
61 ‘theory of island biogeography for exotic species’ (herein, ‘TIBE’). TIBE is a graphical  
62 island biogeographic model that makes a variety of different predictions regarding the species  
63 richness and turnover of native and non-native species (Burns 2015). This was a useful  
64 advance as little is known about the turnover patterns of non-natives. However, the analysis  
65 of turnover dynamics of non-natives has so far only been studied in the context of true

66 islands, i.e. islands surrounded by a matrix of water (Whittaker and Fernández-Palacios 2007,  
67 Burns 2015). In contrast, the knowledge of turnover patterns for non-native species in habitat  
68 islands, i.e. patches of natural habitat surrounded by a matrix of often human dominated  
69 habitats (see Matthews 2015), is lacking. Such knowledge is important as the destruction and  
70 fragmentation of natural habitat is widely recognised as the leading driver of contemporary  
71 species extinctions (e.g. Sala et al. 2000) and also as an important driver of extinction debt  
72 (Triantis et al. 2010). Moreover, there has been an increasing recognition of the synergistic  
73 effects of the different drivers of species loss (e.g. habitat loss, climate change and invasive  
74 species; e.g. Didham et al. 2007, Ferger et al. 2017, Karp et al. 2018). As with true islands,  
75 we predict that the turnover of non-native species will be greater than for native species in  
76 habitat fragments. However, in true islands the matrix (water) can generally be ignored,  
77 whilst in habitat island systems it is possible that the surrounding matrix contributes to  
78 turnover patterns within habitat islands. As many non-native species have strong affinities to  
79 human-dominated habitats, that is, they are generalists or human habitat specialists  
80 (McKinney and Lockwood 1999, Borges et al. 2008, 2010), the presence of non-native  
81 species within habitat islands of native habitat is theorised to be driven by stochastic source-  
82 sink mass effect dynamics as a result of human disturbance (Williamson 1996, Sgarbi and  
83 Melo 2017). Non-native species, which should therefore be less adapted to the conditions  
84 within the sink habitat, should have a higher risk of extinction and turnover (MacArthur and  
85 Wilson 1967). This possibility has not previously been examined in habitat islands.

86 A variety of methods have been employed to analyse turnover in the island literature (e.g.  
87 Russell et al. 1995, Whittaker et al. 2000, Burns 2015), mostly based on the summation of  
88 raw numbers (e.g. number of extinction events). However, another, and arguably more  
89 statistically robust, way of analysing temporal changes in species assemblages uses  
90 dissimilarity indices, which allow researchers to partition out the effect of richness  
91 differences between samples (Baselga 2010, Baselga et al. 2015). One such approach is to  
92 use the framework of temporal beta-diversity. Beta-diversity provides a measure of the  
93 differences in the composition of communities, and is usually calculated in a spatial context,  
94 e.g. to assess how composition changes across a set of sites or along an ecological gradient  
95 (Anderson et al. 2011). Temporal beta-diversity is a similar concept, where beta-diversity is  
96 calculated for the same location at different times, and in conjunction with a suitable null  
97 model the analysis of temporal beta-diversity can be used to determine whether changes in  
98 assemblages across time are due to deterministic processes or stochastic colonisation and

99 extinction events (Baselga et al. 2015). Temporal beta-diversity *sensu stricto* has been much  
100 less studied relative to spatial beta-diversity (but see Baselga et al. 2015, Tonkin et al. 2017).  
101 Beta-diversity can be calculated using a variety of different approaches (see Anderson et al.  
102 2011) and in this study we focus on the use of dissimilarity indices to calculate beta-diversity,  
103 in particular Sørensen dissimilarity. Recent work has partitioned the Sørensen index into  
104 turnover and nestedness-resultant dissimilarity / richness difference components (Baselga  
105 2010, 2012, Carvalho et al. 2012).

106 In this study, we use a unique time-series dataset of arthropods sampled in native forest  
107 fragments over five years in the Azores (see Borges et al. 2017) to investigate the differences  
108 in turnover dynamics of native and non-native species. Using TIBE and past studies on island  
109 theory in habitat islands (e.g. Matthews 2015) as theoretical frameworks, we make two  
110 predictions. First, based on the above points, we predict that temporal beta-diversity will be  
111 greater for non-native species than for native species (Prediction 1). We use a null model  
112 approach to determine whether turnover of species through time was due to deterministic  
113 processes or stochastic colonisation and extinction events, and linear modelling selection to  
114 assess if any factors (i.e. elevation, climate, disturbance) are driving variation in temporal  
115 beta-diversity between plots. Second, as the invasion process is predicted to be on-going (see  
116 Burns 2015, Seebens et al. 2017), based on the TIBE we predict that colonisation rate will be  
117 greater than extinction rate for non-native species, whilst colonisation rate will be roughly  
118 equivalent to extinction rate for native species (Prediction 2).

119 Our dataset is ideal for examining temporal beta-diversity patterns of native and non-native  
120 species in habitat islands as the regular census interval allows us to accurately describe  
121 colonisation and extinction events (and thus turnover), and the Azorean arthropod fauna  
122 contains a high proportion of non-native species (Borges et al. 2010). Confirming or  
123 invalidating these predictions will enable a better understanding of the turnover dynamics of  
124 non-native species in fragmented landscapes and will provide important information to aid in  
125 the conservation of fragmented natural areas impacted by the spread and establishment of  
126 non-native species in currently threatened ecosystems.

## 127 **Material and methods**

### 128 **Study site and data collection**

129 Arthropods were sampled using nine 50m x 50m plots located in four native fragments of  
130 pristine forest on Terceira Island in the Azores. The plots were setup within the  
131 ISLANBIODIV project (Borges et al. 2017; Cicconardi et al. 2017). Arthropods were  
132 sampled using a passive flight interception trap called a SLAM (Sea, Land, and Air Malaise)  
133 trap. The collecting bottles were collected and changed every three months; thus, each sample  
134 covers one season of the year. For the current study, we used data sampled over the years  
135 2012 –2016 (inclusive). The arthropods were grouped by their native and non-native  
136 colonisation strategies. A more comprehensive outline of the study site (including a map) and  
137 the sampling methodology is provided in Appendix S1 in the Supporting Information (see  
138 also Borges et al. 2017).

139 For the climatic data, we used data from the CIELO Model (Azevedo et al. 1999). The  
140 CIELO model is a simple parcel model, based on the transformations experienced by an air  
141 mass ascending a mountain, which simulates the evolution of an air parcel's physical  
142 properties, starting from the sea level. Two Principal Components Analysis (PCA) axes were  
143 calculated using the climatic variables mean annual temperature, annual rainfall and relative  
144 humidity. The PCA was undertaken using the ‘*vegan*’ R package (Oksanen et al. 2013), and  
145 we took the first two axes as they explained ~ 99% of the variance. The first axis (P1)  
146 corresponded to differences in temperature and precipitation, whilst the second axis (P2)  
147 corresponded more to differences in humidity. In addition, we used an ‘index of Disturbance’  
148 developed by Cardoso et al. (2013) for the Azores that models disturbance by considering  
149 landscape configuration and proximity of human-modified habitat to each patch of pristine  
150 native forest (see Appendix S1). We also calculated the elevation of each plot using a digital  
151 elevation model (DEM) for Terceira Island.

152 We pooled the samples within each year to create yearly datasets for each of the nine plots.  
153 Where the same species had been sampled in multiple samples within a single year we  
154 combined records and summed the abundances. We then converted these data into presence-  
155 absence matrices, such that for each of the nine plots we had five presence-absence matrices,  
156 one for each of the five sampling years (2012–2016).

### 157 **Calculating temporal beta-diversity: Prediction 1**

158 To examine whether temporal beta-diversity was greater for non-natives than for natives  
159 (Prediction 1), we used both pairwise and multiple-time temporal beta-diversity frameworks.  
160 First, for each plot we constructed a presence-absence matrix for the pooled 2013 samples

161 (the first full year of sampling, see Appendix S1) and the pooled 2016 samples. We then used  
162 the '*beta.temp*' function in the 'betapart' R package (Baselga et al. 2017) to calculate  
163 partitioned pairwise temporal beta-diversity (Sorensen index) between these two years, and  
164 we stored both partition values (i.e. temporal turnover and temporal nestedness-dissimilarity)  
165 as well as the overall Sorensen's dissimilarity value. This analysis was undertaken separately  
166 for native and non-native species. To determine whether the observed pairwise temporal beta-  
167 diversity and partition values were significantly different from random expectation, we  
168 followed Baselga et al. (2015) and used an FE null model (Ulrich and Gotelli 2007) whereby  
169 row (site species richness) marginal totals were allowed to vary and column (species  
170 incidences) marginal totals are fixed. In this context, the FE null model characterises a  
171 situation whereby species randomly colonise and go extinct at sites, from a common regional  
172 pool (Baselga et al. 2015). This null model was implemented using the 'c0' algorithm in the  
173 'vegan' R package (Oksanen et al. 2013). This null model was used to randomise the 2016  
174 presence/absence matrix, which was then compared to the empirical 2013 presence/absence  
175 matrix, using the '*beta.temp*' function. This process was repeated 1000 times, for both the  
176 native and the non-native species data; the overall dissimilarity value, and the two partition  
177 values, was stored in each instance. Using these null model values, we calculated the Z-  
178 scores for the six metrics (the three temporal beta-diversity metrics, for both the native and  
179 non-native presence/absence matrices). A two-sided *P*-value was also calculated for each Z-  
180 score. To ensure that our results were consistent across the two main beta-diversity  
181 partitioning frameworks, we also calculated temporal beta-diversity and re-ran the above  
182 analyses using the Carvalho partitioning framework (Carvalho et al. 2012), the Sorensen  
183 family of beta-diversity metrics and the BAT R package (Cardoso et al. 2014). The Carvalho  
184 partitioning framework differs from the Baselga framework in that it partitions overall beta-  
185 diversity into turnover and richness difference components, instead of turnover and  
186 nestedness-dissimilarity components.

187 Spatial beta-diversity studies have shown that pairwise beta-diversity metrics and multisite  
188 beta-diversity metrics (i.e. spatial beta-diversity aggregated across multiple sites) can reveal  
189 different patterns (Baselga 2013). Thus, we adapted the '*beta.temp*' function to calculate  
190 partitioned multiple-time dissimilarity, again based on the Sorensen index. This is an  
191 aggregate measure that enables the calculation of temporal beta-diversity across multiple time  
192 periods for the same site. We calculated multiple-time dissimilarity for both native and non-

193 native species for four years (2013 – 2016) and compared the resultant beta-diversity values  
194 with their pairwise counterparts.

## 195 **Calculating turnover: Prediction 2**

196 Following Burns (2015), turnover was calculated as the total number of colonisation and  
197 extinction events across the five years (2012 – 2016). That is, colonisation was considered to  
198 have occurred if a species was not present in a plot in year  $i$ , but was present in year  $i+1$ .  
199 Equally, under this turnover framework, an extinction event was considered to have occurred  
200 if a species was present in a plot in year  $i$ , but not in year  $i+1$ .

201 To test Prediction 2 (that colonisation rate will be greater than extinction rate for non-native  
202 species, but equivalent to extinction rate for native species), we calculated the number of  
203 turnover events for each individual species, across all nine plots. Reduced major axis  
204 regression was then used to determine how colonisation rate varied with extinction rate (see  
205 Burns 2015) as both variables (colonisation and extinction rate) contained random error; in  
206 such cases, standard linear regression underestimates the slope of the relationship. The  
207 regression models were calculated using the ‘lmodel2’ R package (Legendre 2014), and we  
208 used the standard major axis (SMA) method. Models were fitted for native and non-native  
209 species separately. In this analysis, a slope significantly greater than one, or an intercept  
210 significantly greater than zero, would indicate that the colonisation rate exceeded extinction  
211 rate (for either native or non-native species) and thus that the number of native/non-native  
212 species increased in the fragments over the five years, and *vice versa*.

## 213 **Explaining variation in temporal beta-diversity**

214 To determine whether any of our environmental variables explained variation in the turnover  
215 component of temporal beta-diversity, we undertook a model comparison approach using  
216 generalised linear models (GLMs). We used GLMs with the Gaussian family in these  
217 analyses, and normality of the response variables was assessed using the Shapiro-Wilks test  
218 (in both cases the null hypothesis that the response variable was normally distributed could  
219 not be rejected). We ran the model comparison twice, once for each of two response  
220 variables: 1) the pairwise temporal turnover beta-diversity partition values of native species,  
221 and 2) the pairwise temporal turnover beta-diversity partition values of non-native species.  
222 As predictor variables, we started with elevation (log transformed), disturbance (log  
223 transformed) and two climatic PCA axes (P1 and P2). All predictors were standardised to  
224 have a mean of 0 and standard deviation of 1 to enable comparison of the effect sizes.



225 Multicollinearity was assessed using variance inflation factors (VIFs), which resulted in P1  
226 being removed from all subsequent analyses as it was very highly correlated with altitude.  
227 The three remaining predictor variables (elevation, disturbance and P2) all had VIFs under  
228 ten.

229 Using these response and predictor variables, we compared a full set of generalised linear  
230 models (GLMs) within an information theoretic approach (Burnham and Anderson 2002).  
231 For each response variable, a full set of models were compared using Akaike's information  
232 criterion corrected for small sample size ( $AIC_c$ ; see Burnham and Anderson 2002). The  
233 model with the lowest  $AIC_c$  was considered the best model, whilst all models with  $\Delta AIC_c \leq$   
234 2 were considered to have similar support. As our data were sampled using 50 m x 50 m  
235 quadrats nested within fragments, we used a spatial autocovariate within an auto-Gaussian  
236 regression approach to account for the experimental design. First, for each response variable,  
237 we fitted the global model and extracted the residuals. We then created a spatial autocovariate  
238 using the residuals (see Crase et al. 2012) and the 'autocov\_dist' function in the 'spdep' R  
239 package (Bivand 2017). The neighbourhood radius was set to encompass all plots, and we  
240 used the 'inverse' type and row standardised (W) style settings. The spatial autocovariate was  
241 fixed in the model selection. For all models with  $\Delta AIC_c \leq 2$ , we also checked the residuals  
242 for homoscedasticity, and we checked for any remaining spatial autocorrelation in the  
243 residuals using the 'spdep' R package (Bivand 2017), the 'nb2listw' function and row  
244 standardised weights. We also re-ran the model selection analyses using Gaussian mixed  
245 effect models with 'fragment' as a random effect (random intercept); however, the variance  
246 of the random effect was very close to zero in both cases and these results are not discussed  
247 further.

## 248 **Sensitivity analyses**

249 We ran two sensitivity analyses to ensure our results were robust. First, to ensure our  
250 sampling was sufficient we calculated sampling completeness estimates for each year in each  
251 plot using the iNEXT R package (Hill number order  $q = 0$ , Hsieh et al. 2016). Second, we set  
252 up a tenth plot in which we placed three SLAM traps instead of one to determine whether the  
253 use of a single SLAM trap in each of the plots was sufficient to capture the relevant  
254 community properties. A full methodology for each of the sensitivity analyses is provided in  
255 Appendix S1. All analyses were undertaken using R (version 3.4.3, R Core Team 2017).

## 256 **Results**

257 **Dataset summary**

258 Over the five years, we sampled 28,704 arthropod specimens, representing 147 species and  
259 morpho species (no. of native sp. = 89 and no. of non-native sp. = 58), across ten plots (nine  
260 plots were used in the main analysis and a tenth plot was used in the sensitivity tests). Across  
261 the nine plots that formed the main basis of this study, the mean richness (i.e. mean of each  
262 plot across the five years) of species in a plot ranged from 21 to 38 and 3 to 11, for native and  
263 non-native species respectively (Table 1). Mean total abundance (i.e. abundance of all species  
264 in a plot) ranged from 205 to 886 and 4 to 68 for native and non-native species respectively  
265 (Table 1).

266 **Temporal beta-diversity**

267 For all nine plots, overall temporal beta-diversity was larger for non-native species than for  
268 native species (Table 2; Fig. 1), confirming Prediction 1. The temporal turnover component  
269 of overall pairwise beta-diversity was larger than the temporal nestedness-dissimilarity  
270 component for all but one plot for non-native species, and for five of the nine plots for native  
271 species (Fig. 1). For overall temporal beta-diversity, the Z-scores were negative for all but  
272 one plot for native species, whilst Z-scores were both positive and negative for non-native  
273 species (Table 2). Four of the overall pairwise beta Z-scores for native species were  
274 significant, whilst only one of the overall pairwise beta Z-scores for non-native species was  
275 significant (Table 2). The null model results for the pairwise temporal beta-diversity  
276 partitions were similar to the results for the overall pairwise temporal beta-diversity values  
277 (see Table 2). This outcome did not change when the Carvalho pairwise beta-diversity  
278 partitioning framework was used rather than the Baselga approach (see Appendix S2): overall  
279 pairwise beta-diversity and the two partitions were all positively and significantly correlated  
280 between the two approaches (all Pearson's correlation coefficients  $> 0.90$ , and all  $P$ -values  $<$   
281  $0.001$ ), and the same overall picture emerged regardless of the approach used (compare Fig. 1  
282 with Fig. S3 in Appendix S2).

283 Using multiple-time dissimilarity produced similar results to the pairwise temporal beta-  
284 diversity analysis (see Figure S4 in Appendix S3): overall temporal beta-diversity was larger  
285 for non-native species than for native species, for all nine plots, and on average the temporal  
286 nestedness-dissimilarity component represented a larger proportion of total temporal beta-  
287 diversity for native species than for non-native species. One interesting difference was non-  
288 native species in Plot 6 (compare Fig.1 with Fig.S4), whereby the pairwise measure indicated

289 that the nestedness-dissimilarity component represented 100% of overall beta-diversity, but  
290 only 16% using multiple-time dissimilarity.

### 291 **Differences in colonisation and extinction rates**

292 Reduced major axis regression of the number of colonisation events against the number of  
293 extinction events revealed that, contrary to Prediction 2, the slope of the relationship was  
294 significantly greater than one for both native (slope = 1.26; 95% CI = 1.11 – 1.44) and non-  
295 native species (slope = 1.28; 95% CI = 1.16 – 1.42) (Fig. 2), indicating that the colonisation  
296 rate exceeded the extinction rate for both groups. The intercept of the relationship was not  
297 significantly different from zero for either native (intercept = 0.17; 95% CI = -0.22 – 0.51) or  
298 non-native (intercept = -0.11; 95% CI = -0.38 – 0.13) species. The  $R^2$  values for both  
299 regression models were: 0.64 and 0.86 for the native and non-native species models,  
300 respectively.

### 301 **Explaining variation in temporal beta-diversity between plots**

302 When the turnover partition (of overall pairwise temporal beta-diversity) values were used as  
303 the response variables in a set of GLMs, the selection procedure indicated that the only  
304 predictor variable in both the best native and non-native species models was the fixed spatial  
305 autocovariate, and there were no additional models within  $2 \Delta AIC_c$  of either best model. Re-  
306 running the model selection using the turnover component of multiple-time dissimilarity  
307 produced the same overall results.

### 308 **Sensitivity analyses**

309 Sample completeness estimates indicated that our sampling was sufficient: the mean sample  
310 completeness estimate across all years and plots was 0.97 (range = 0.81 to 1.00, the results  
311 for each year and plot are presented in Table S2 in Appendix S4). Using three SLAM traps in  
312 a plot rather than one did not result in substantially different sampled communities according  
313 to various measures of diversity (see Appendix S4).

314

## 315 **Discussion**

316 We have undertaken an evaluation of the differences in temporal beta-diversity patterns  
317 between native and non-native arthropod species across nine native forest plots in the Azores  
318 for which a time series of five years is available (2012 - 2016).

319 **Non-native species have larger rates of temporal beta-diversity than native species in**  
320 **Azorean forest fragments**

321 The results of our temporal beta-diversity analyses (both pairwise and multiple-time  
322 dissimilarity) indicated that, in accordance with Prediction 1, temporal beta-diversity was  
323 considerably greater for non-native species than for native species, across all nine plots. In  
324 addition, with one exception (Plot 6 when using pairwise beta-diversity, Fig. 1), for non-  
325 native species the largest component of temporal beta-diversity was by far the temporal  
326 turnover partition, indicating an actual turnover of species rather than nested patterns in  
327 richness (Baselga partition) or richness differences (Carvalho partition) between years.

328 Burns (2015), in his theory of island biogeography for exotic species (TIBE), attributed  
329 differences in turnover rates between natives and non-natives to standard island  
330 biogeographical variables. However, Burns was focused on true islands. In our study system  
331 of habitat islands, we found that, in regard to overall pairwise temporal beta-diversity for  
332 non-native species, the null model analyses were only significant in one case, and the signs of  
333 the Z-scores varied between the plots (Table 2). These findings, in combination with previous  
334 work in our study system (e.g. Borges et al. 2006, 2008, Florencio et al. 2016), appear to  
335 support the notion that the distribution of non-native arthropods in Azorean native forests is  
336 driven by stochastic processes and occupancy dynamics, possibly due to source-sink  
337 processes (see also Borges et al. 2008). In a study of temporal beta-diversity patterns of birds  
338 in France, Baselga et al. (2015, p.9) also found that temporal changes in assemblages were  
339 not significantly different from a null model and concluded that “the observed changes in  
340 species composition of local bird assemblages might be the consequence of stochastic  
341 processes in which species populations appeared and disappeared from specific localities in a  
342 random-like way.”

343 Many non-native arthropod species in the Azores are adapted to human land-uses (Borges et  
344 al. 2008, Rigal et al. 2018), and thus we would expect there be a large number, and thus high  
345 potential for mass effects (Shmida and Wilson 1985), of non-natives in the disturbed  
346 landscapes surrounding the fragments (see also Borges et al. 2006). The Azores has  
347 undergone substantial land use change since human colonisation of the archipelago (Triantis  
348 et al. 2010), and native forest fragments in the Azores are characterised by hard boundaries,  
349 i.e. there is an abrupt change from native forest habitat to anthropogenic habitat (Borges et al.  
350 2006, 2008). As such, there are likely to be large mass effects and a constant supply of non-

351 native individuals permeating into the native forest where they frequently undergo local  
352 extinction and re-colonisation, leading to high beta-diversity through time. Thus, it seems  
353 likely that is not just the size of the native habitat that underpins the colonisation rate of non-  
354 natives (as in true islands cf. Burns 2015) but also the amount of surrounding anthropogenic  
355 habitat and size of the non-native source pool, which is known to be large in the Azores  
356 (Borges et al. 2010). More detailed studies focusing on the habitat affinities and dispersal  
357 ecology of non-native species are needed to further explore this possibility. Interestingly, our  
358 disturbance metric, that incorporates surrounding land use, was not an important predictor of  
359 non-native temporal beta-diversity in the linear model selection analysis. However, as all of  
360 the native forest fragments on Terceira are surrounded by human land uses, it is likely that  
361 there was simply not enough variation in the disturbance metric between plots.

362 In regards to the processes underpinning temporal beta-diversity patterns of native species,  
363 the results are more equivocal. Overall pairwise temporal beta-diversity was significantly  
364 lower than expected by chance in four of the nine plots for native species, in comparison to  
365 only one of the nine plots for non-native species. This indicates a stronger role for  
366 deterministic processes driving temporal beta-diversity and turnover in native species  
367 assemblages (Baselga et al. 2015). However, as with non-native species, none of our  
368 predictor variables were found to explain variation in the temporal beta-diversity of native  
369 species. The reasons for this finding are unclear but could simply be due to the fact that our  
370 experimental design did not allow us to test for the importance of other biogeographic  
371 variables such as area on turnover (MacArthur & Wilson 1967). Further studies examining  
372 the turnover dynamics of native and non-native species in habitat fragments are needed.

### 373 **Colonization and extinction rates for native and non-native species**

374 Our Prediction 2, that colonisation rate will be greater than extinction rate for non-native  
375 species, whilst colonisation rate will be roughly equivalent to extinction rate for native  
376 species, was not borne out by the data. Whilst we observed that the colonisation rate was  
377 greater than the extinction rate for non-natives, contrary to expectations we found a similar  
378 pattern for native species (Fig. 2). Whilst this finding is expected for non-native species,  
379 these results could imply either that many of the native species in the fragments have high  
380 dispersal ability and are easily able to disperse between plots and fragments, or possibly that  
381 native species have not yet reached equilibrium following substantial habitat loss over the last  
382 few centuries. An alternative explanation is that our sampling did not accurately record all

383 colonisation and extinction events during the study period. Previous work on turnover on  
384 islands has shown that the calculation of turnover rate is sensitive to the grain size of the time  
385 series data analysed (e.g. were samples carried out every year or every ten years) (e.g. Russell  
386 et al. 1995, Whittaker et al. 2000). Considering these issues, inevitably we have not recorded  
387 every true turnover event (i.e. crypto-turnover), and equally, due to sampling error, we have  
388 likely missed individuals in certain instances and thus erroneously recorded turnover events  
389 (i.e. pseudo-turnover). However, sampling was every three months (as opposed to multiple  
390 years in most island studies), and thus a species had to be absent across all the monthly  
391 samples for an extinction event to be classified. We also carried out sensitivity analyses to  
392 ensure our sampling effort was sufficient. As a result, we are confident that our sampling  
393 protocol has generated data of sufficient quality to test our predictions.

#### 394 **Implications for conservation and biodiversity management**

395 Non-native species are thought to be leading drivers of contemporary species extinctions, and  
396 the issue seems particularly acute in true and habitat island systems (Sax and Gaines 2003,  
397 Cardoso et al. 2010, Bellard et al. 2016). However, the biogeography of non-native species is  
398 not well known. Specifically, it is not known whether standard biogeographical theory and  
399 metrics derived from the study of native species can be accurately applied to non-native taxa.  
400 As a result of this uncertainty, a number of recent studies have focused on examining the  
401 differences and similarities between natives and non-natives using classic biogeographical  
402 and ecological patterns, such as the ISAR and the abundance-occupancy relationship (e.g.  
403 Blackburn et al. 2008, Rigal et al. 2013, Burns 2015). The results of our study contribute  
404 towards filling this knowledge gap by showing that it cannot be assumed *a priori* that native  
405 and non-native taxa within the same community are similarly assembled and will follow the  
406 same temporal dynamics.

407 Importantly, our results indicate that it might not be possible to apply simple biogeographical  
408 principles (e.g. Wilson and Willis 1975) when devising non-native species management plans  
409 in fragmented landscapes. Rather, management should be based on the results of  
410 biogeographical and ecological studies explicitly focused on non-native taxa. A corollary of  
411 this statement is that there is an urgent need for additional studies focused on outlining and  
412 testing biogeographical theory in the context of non-native species (Patiño et al. 2017). In the  
413 native forest sampled in our study, the high rate of stochastic turnover of non-native species  
414 that we observed indicates that attempts to simply reduce the populations of non-native

415 species *in situ* within native habitats may not be successful. This is because for many non-  
416 native species the native habitat is likely just a sink, and the constant immigration of  
417 individuals from anthropogenic source habitats in close proximity to the native habitats (i.e.  
418 mass effects) means local extinction of non-natives within the native forest is unlikely to be  
419 permanent. Thus, a more efficient future management strategy and land-use policy will be to  
420 interrupt these source-sink dynamics by improving the harsh boundaries between native  
421 habitat and adjacent anthropogenic habitat, and in the longer term to design and create a more  
422 graded landscape mosaic (Lindenmayer and Fischer 2006) whereby contrasting land uses are  
423 not simply knitted together in an ad hoc fashion. The high turnover of non-native species also  
424 brings into question the ability of non-natives to, amongst other things, replace the functional  
425 roles of extirpated native species (see Whittaker et al. 2014; Rigal et al. 2018) or increase  
426 functional redundancy in fragmented landscapes. Functional diversity studies that focus on  
427 non-native species are often based on static time periods (e.g. a sample from one year) and  
428 their conclusions thus do not account for the fact that many non-native species present in a  
429 patch may simply be ephemeral members of a given community.

430

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444 **Author contributions** – TM designed the analytical study. PB designed the sampling  
445 methodology and collected the data with RC and RN. TM analyzed the data. TM wrote the  
446 manuscript, with the help of JS and PB.

447

448

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566 **Supporting Information**

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

568

569 *Appendix S1.* Additional methodological information, including plot locations and  
 570 environmental data.

571 *Appendix S2.* Pairwise beta-diversity results using the Carvalho partition framework

572 *Appendix S3.* Multiple-time dissimilarity results

573 *Appendix S4.* Sensitivity Analyses Full Results

574

575 **TABLES**

576 Table 1. The mean richness (M. Richness), mean abundance (M. Abundance), and the  
 577 number of colonisation (Colonis.), extinction, and total turnover events of arthropod species  
 578 across nine native forest plots on Terceira Island, in the Azores. For each plot, the data are  
 579 provided for native (Nat) and non-native (Non) species separately. Each plot was sampled  
 580 multiple times across five years and samples were pooled to create five yearly samples (2012  
 581 – 2016). An extinction event was deemed to have occurred if a species was present in year  $i$   
 582 but not in year  $i+1$ , and *vice versa* for a colonisation event (Plot notation as in Table S1 and  
 583 Figure S1).

Plot	Type	M. Richness	M. Abundance	Colonis.	Extinction	Turnover
1	Nat	32.8	790.8	27	24	51
2	Nat	30.2	496.4	28	26	54
3	Nat	25.6	558.0	19	20	39
4	Nat	38.0	885.6	46	20	66
5	Nat	25.0	511.0	36	17	53
6	Nat	21.0	204.6	26	26	52
7	Nat	25.0	272.8	28	21	49
8	Nat	20.6	480.2	21	16	37
9	Nat	30.2	489.4	27	22	49
1	Non	6.8	20.8	17	10	27
2	Non	4.6	9.4	10	11	21
3	Non	4.0	5.6	10	9	19
4	Non	10.8	67.6	31	21	52
5	Non	4.25	11.2	10	8	18
6	Non	3.75	4.4	13	12	25
7	Non	3.2	5.0	8	7	15

8	Non	4.4	8.8	19	14	33
9	Non	5.0	18.2	13	15	28

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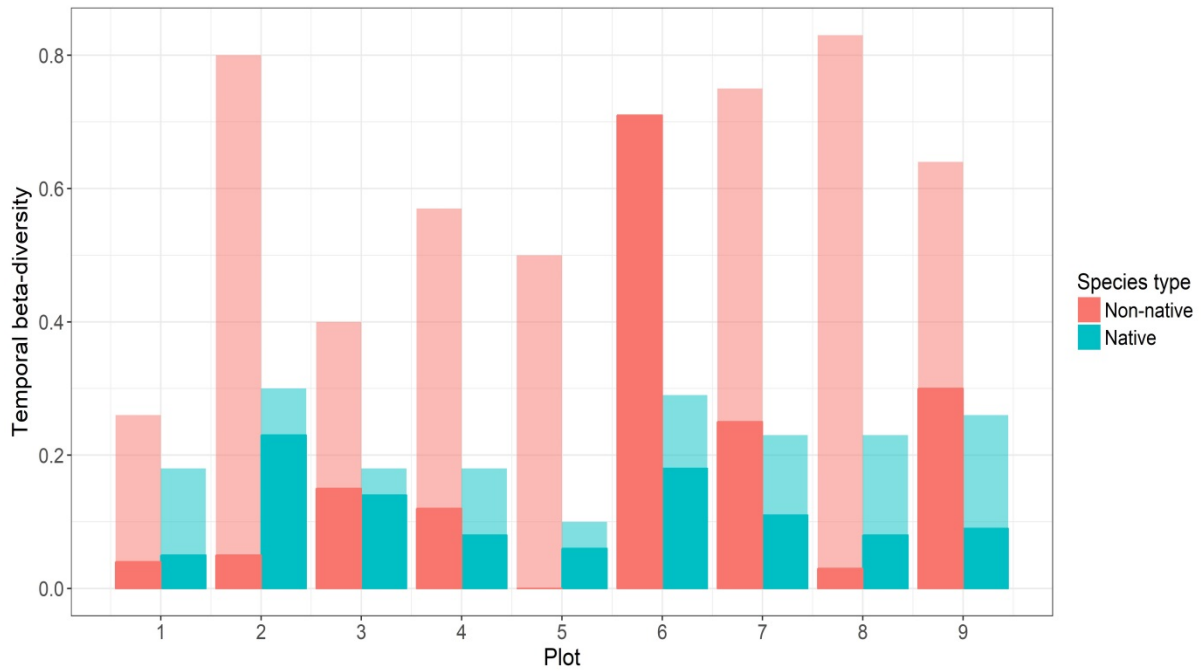
587 Table 2. Pairwise temporal beta-diversity values for arthropod species sampled in 2013 and  
588 2016 in nine native forest plots on Terceira Island, in the Azores. For each plot, the data are  
589 provided for native (Nat) and non-native (Non) species separately. Overall temporal beta-  
590 diversity values (Sorensen dissimilarity index) are provided in addition to the temporal  
591 turnover (Turn.) and temporal nestedness-dissimilarity (Nest.) components of overall  
592 temporal beta-diversity. For the two partition values and the overall temporal beta-diversity  
593 value, significance was determined using an FE null model (1000 iterations). For each of the  
594 three beta-diversity values, the Z-score (Z) and associated P-value (P) are provided (see  
595 ‘Materials and methods’). P-values significant at the 0.05 level are highlighted in bold (Plot  
596 notation as in Table S1 and Figure S1). The overall temporal beta-diversity differ very  
597 slightly from the sum of the turnover and nestedness components in certain plots due to  
598 rounding error.

Plot	Type	Temporal beta-diversity			Turnover		Nestedness		Overall	
		Turn.	Nest.	Overall	Z	P	Z	P	Z	P
1	Nat	0.12	0.05	0.18	-0.94	0.35	-1.48	0.14	-2.49	<b>0.01</b>
2	Nat	0.08	0.23	0.30	-0.85	0.39	0.52	0.60	-0.33	0.74
3	Nat	0.05	0.14	0.18	-2.92	<b>&lt;0.01</b>	3.64	<b>&lt;0.01</b>	-1.08	0.28
4	Nat	0.11	0.08	0.18	-0.36	0.72	-1.58	0.11	-1.96	<b>0.04</b>
5	Nat	0.04	0.06	0.10	-2.04	<b>0.04</b>	-0.24	0.81	-2.53	<b>0.01</b>
6	Nat	0.11	0.18	0.29	-2.68	<b>0.01</b>	6.17	<b>&lt;0.01</b>	-0.1	0.92
7	Nat	0.12	0.11	0.23	-1.00	0.32	0.75	0.45	-0.44	0.66
8	Nat	0.15	0.08	0.23	-3.45	<b>&lt;0.01</b>	1.22	0.22	-3.48	<b>&lt;0.01</b>
9	Nat	0.17	0.09	0.26	0.11	0.91	-0.72	0.47	-0.59	0.56
1	Non	0.22	0.04	0.26	-1.13	0.26	-0.94	0.35	-2.58	<b>0.01</b>
2	Non	0.75	0.05	0.80	1.50	0.13	-0.39	0.70	1.63	0.10
3	Non	0.25	0.15	0.40	-1.52	0.13	0.74	0.46	-1.48	0.14
4	Non	0.44	0.12	0.57	-0.24	0.81	-0.27	0.79	-0.63	0.53
5	Non	0.5	0.00	0.50	0.75	0.45	-1.72	0.08	-0.47	0.64
6	Non	0.00	0.71	0.71	-4.84	<b>&lt;0.01</b>	11.20	<b>&lt;0.01</b>	-0.72	0.47
7	Non	0.5	0.25	0.75	-0.38	0.70	1.73	0.08	0.69	0.49
8	Non	0.8	0.03	0.83	0.02	0.98	0.06	0.95	0.05	0.96
9	Non	0.33	0.3	0.64	-1.06	0.29	1.63	0.10	-0.09	0.92

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Figure 1. Pairwise temporal beta-diversity values for native and non-native arthropod species across nine plots of native forest on Terceira Island, in the Azores. For each plot, temporal beta-diversity was calculated using the pooled 2013 samples and the pooled 2016 samples. For each plot, temporal beta-diversity was calculated separately for native species (blue bars) and non-native species (red bars). The height of each bar corresponds to the overall temporal beta-diversity. Overall temporal beta was also partitioned into nestedness and turnover components using the Baselga partition approach (Baselga et al. 2017). Within each bar, the dark shaded area rising from the x-axis corresponds to the nestedness component of overall temporal beta diversity. Thus, the lighter shaded area within each bar that rises from the dark shaded area corresponds to the turnover component.

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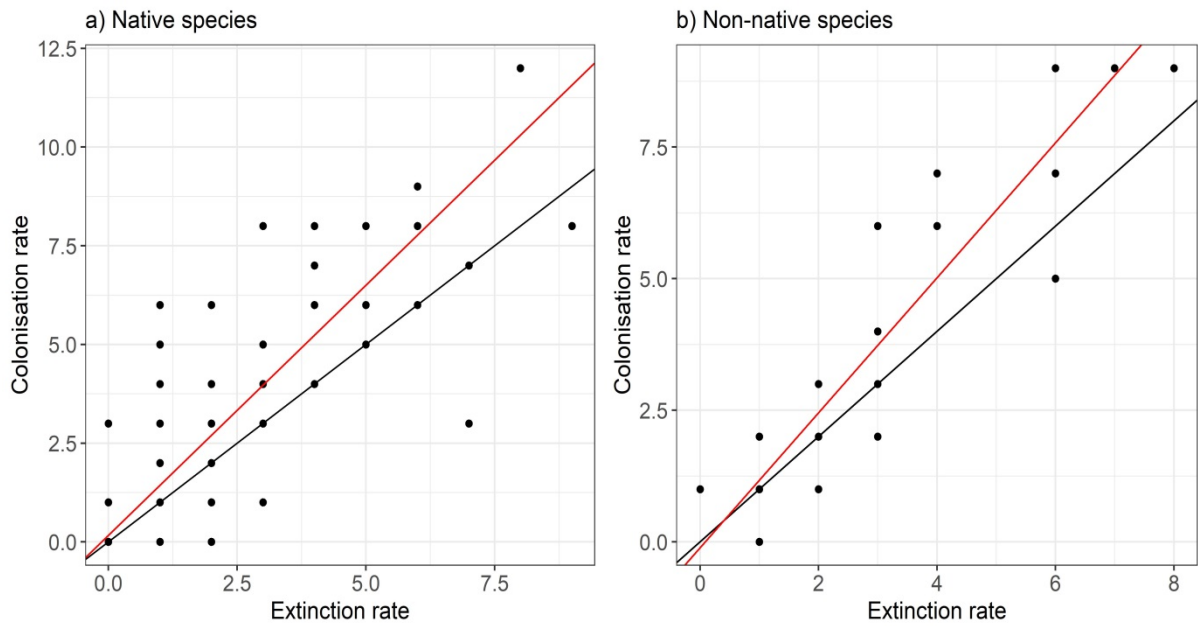
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Figure 2. The relationship between the number of colonisation events and the number of extinction events in native (a) and non-native (b) arthropod species sampled in nine native forest plots on Terceira Island in the Azores. Each plot was sampled multiple times across five years and samples were pooled to create five yearly samples. Turnover was then calculated as the total number of colonisation and extinction events across the five years (see 'Materials and methods'). In (a) and (b), the black line is the isometric line (i.e. intercept of zero and slope of 1) and the red line is the best fit line from reduced major axis regression. In both cases the best fit regression line is significantly greater than one.

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## SUPPORTING INFORMATION

628 Differential temporal beta-diversity patterns of native and non-native arthropod species in a  
629 fragmented native forest landscape

630 Thomas J. Matthews, Jon Sadler, Rui Carvalho, Rui Nunes, Paulo A. V. Borges

631

### 632 **Appendix S1 Additional methodological information**

#### 633 **Study site**

634 The Azorean archipelago is located in the North Atlantic, roughly between 37° to 40° N  
635 latitude and 25° to 3° W longitude. Since human occupation of the islands, there have been  
636 substantial changes in the size and quality of native habitats, mostly due to the creation of  
637 urban areas, agriculture fields, pastures and non-native plantations (Borges et al. 2008,  
638 Triantis et al. 2010). Terceira Island (Fig. 1), a roughly circular island of 402 km<sup>2</sup> area,  
639 contains the largest area of native pristine forests in the Azores (Triantis et al. 2010), with  
640 five main fragments of native forest distributed across four main volcanic polygenetic  
641 complexes.

#### 642 **Data collection**

643 Arthropods were sampled using nine 50m x 50m plots located in four native fragments of  
644 pristine forest on Terceira setup within the ISLANBIODIV project (Cicconardi et al. 2017):  
645 Serra de Santa Bárbara (Plots T07, T48, T49, T164), Biscoito da Ferraria (Plots T01, T02,  
646 T41), Terra Brava (Plot T15) and Galhardo (Plot T33) (see Figure S1, below). Arthropods  
647 were sampled using a passive flight interception trap called a SLAM (Sea, Land, and Air  
648 Malaise) trap. The SLAM traps are approximately 110 x 110 x 110 cm (see Fig. S2 in  
649 Appendix S1), and work by intercepting arthropods on an area of black mesh and funnelling  
650 them into a sampling bottle filled with a killing liquid. Propylene-glycol was used as it  
651 persists for a long time without evaporating, and enables the collection of good quality  
652 specimens for posterior DNA extraction. The collecting bottles were collected and changed  
653 every three months; thus, each sample covers one season of the year. However, due to  
654 logistical challenges and problems with the traps, in a very small number of cases (see Table  
655 S1 in Appendix S1) certain three-month samples were excluded. Further details on the  
656 method can be found in Borges et al. (2017). Samples were sorted and individuals identified  
657 to species level by experienced taxonomists and to morpho species where specific  
658 determinations were not possible. The arthropods were then grouped by their native and non-



659 native colonisation strategies. For the current study, we used data sampled over the years  
660 2012 –2016 (inclusive). Sampling only commenced half way through 2012 (see Table S1,  
661 below) and thus for the temporal beta-diversity analyses we used 2013 as the base year to  
662 ensure that the pairwise comparisons were based on equal samples. However, for the species-  
663 level turnover analyses we used the full dataset as the missing months here are less likely to  
664 affect the results.

665 For the climatic data, we used the CIELO Model (Azevedo et al. 1999). The CIELO model is  
666 a simple parcel model, based on the transformations experienced by an air mass ascending a  
667 mountain, which simulates the evolution of an air parcel's physical properties, starting from  
668 the sea level. CIELO climatic data for the sites were extracted from Borges et al. (2006). In  
669 addition, we used an 'index of Disturbance' developed by Cardoso et al. (2013) for the  
670 Azores that models disturbance by considering landscape configuration and proximity of  
671 human-modified habitat to each patch of pristine native forest. Thus, in this study we  
672 represent anthropogenic disturbance of a plot by explicitly considering landscape  
673 configuration and the amount of neighboring anthropogenic habitats, ranked according to  
674 their level of intensity-use.

### 675 **Species sorting and classification**

676 Parataxonomists sorted samples to orders, and posteriorly to Recognizable Taxonomic Units  
677 (RTUs). One of the authors (PAVB) then identified to species level the RTUs of the  
678 following arthropod orders: Diplopoda (Chordeumatida, Julida), Chilopoda  
679 (Geophilomorpha, Lithobiomorpha, Scolopendromorpha), Arachnida (Araneae, Opiliones,  
680 Pseudoscorpiones) and Insecta (Blattaria, Coleoptera, Hemiptera, Microcoryphia, Neuroptera,  
681 Psocoptera, Thysanoptera, Trichoptera). All material is stored at EDTP—Entomoteca  
682 Dalberto Teixeira Pombo, University of Azores, Angra do Heroísmo, Portugal.

683 Arthropods were grouped into three colonization categories: endemic (i.e. restricted to the  
684 Azores); native non-endemic, i.e. species that arrived naturally to the archipelago but are  
685 present both in the Azorean Islands and elsewhere; and non-native species, i.e., species  
686 whose original distribution range did not include the Azores and that are believed to have  
687 been introduced in the Macaronesian region after human settlement in the 15<sup>th</sup> century. The  
688 non-native status was inferred either from historical records of detected species introductions  
689 or from their current distribution being closely associated with human activity. For  
690 unidentified species, if other species in the same genus, subfamily or family were present in

691 the archipelago and all belonged to the same colonization category (according to Borges et al.  
692 2010), the unknown species were classified similarly. Otherwise, we assumed the species to  
693 be native. For simplicity, endemic and native non-endemic species were grouped and are  
694 termed “native” throughout the text.

### 695 **Sensitivity analyses methodology**

696 To ensure our sampling was sufficient we calculated sampling completeness estimates for  
697 each year in each plot using the iNEXT R package (Hill number order  $q = 0$ , Hsieh et al.  
698 2016).

699 Due to the resources required to sample arthropods in multiple plots every three months over  
700 five years, we only placed one SLAM trap in each plot. To determine whether this was  
701 sufficient to capture the relevant properties (e.g. species composition, distribution of  
702 abundance) of the sampled communities, in 2015 we set up a tenth plot in Terra Brava (Plot  
703 T18), in which we placed three SLAM traps, spaced 30 m apart, and sampled every month.  
704 We constructed three overall assemblage matrices whereby, for each SLAM trap, the data  
705 from the 12 months of 2015 were pooled into one sample. To determine whether community  
706 composition was similar across the three traps, we calculated a number of summary statistics:  
707 1) the number of species in each assemblage, 2) the total abundance of each assemblage, 3)  
708 the proportion of species that were sampled in all three traps (i.e. are present in all three  
709 assemblages), and 4) the distribution of abundance across the species in each assemblage. In  
710 regards to (4), we fitted the gambin species abundance distribution model, using the ‘gambin’  
711 R package and a subsampling procedure to ensure sample sizes were kept consistent (see  
712 Matthews et al. 2014), to the abundances of the species in each assemblage and recorded the  
713 alpha (shape) parameter (Matthews et al. 2014). Finally, to check that spatial species turnover  
714 across the three traps was low, we calculated multisite spatial beta-diversity across the three  
715 assemblages using presence-absence data (*‘beta.multi’* function; Sorensen index) and  
716 abundance data (*‘beta.multi.abund’* function; Bray-Curtis multiple-site dissimilarity), using  
717 the ‘betapart’ R package (Baselga et al. 2017). As most species were found in all three traps,  
718 it was not possible to use a null model approach that constrained the marginal totals. All  
719 analyses were undertaken using R (version 3.4.3, R Core Team 2017).

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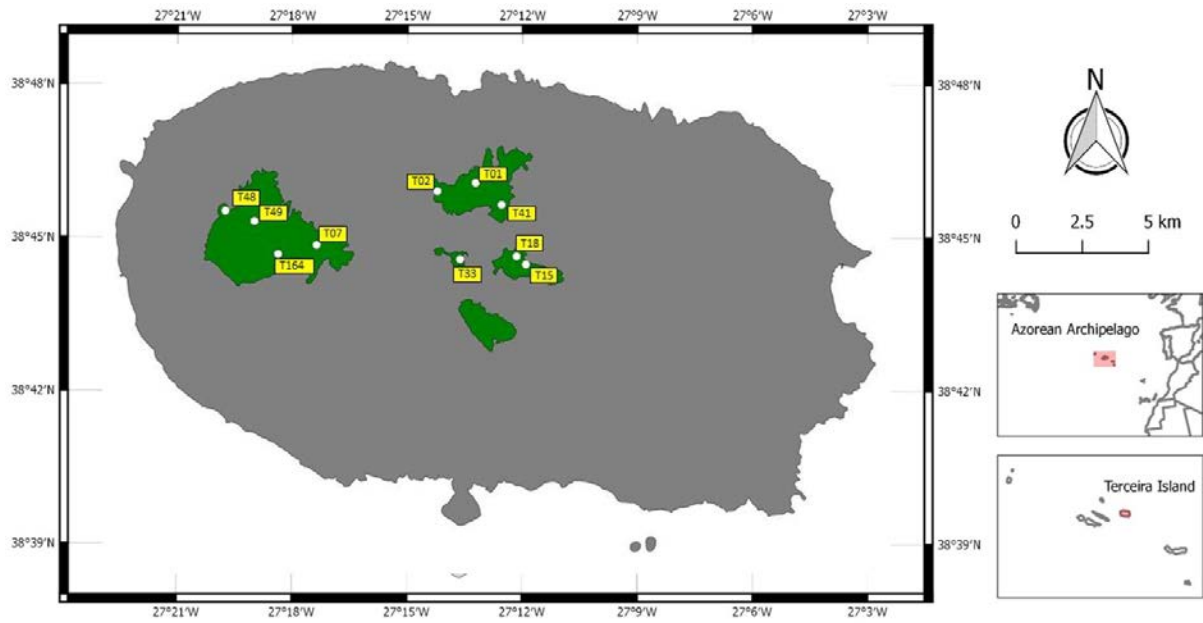
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757 **Plot locations**

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760 Figure S1. A map of the ten sampled 50m x 50m plots and areas of native forest on the island  
761 of Terceira, Azores.

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768 Figure S2. Example SLAM trap in a plot within a native forest fragment on Terceira Island  
769 (Terra-Brava T18), Azores

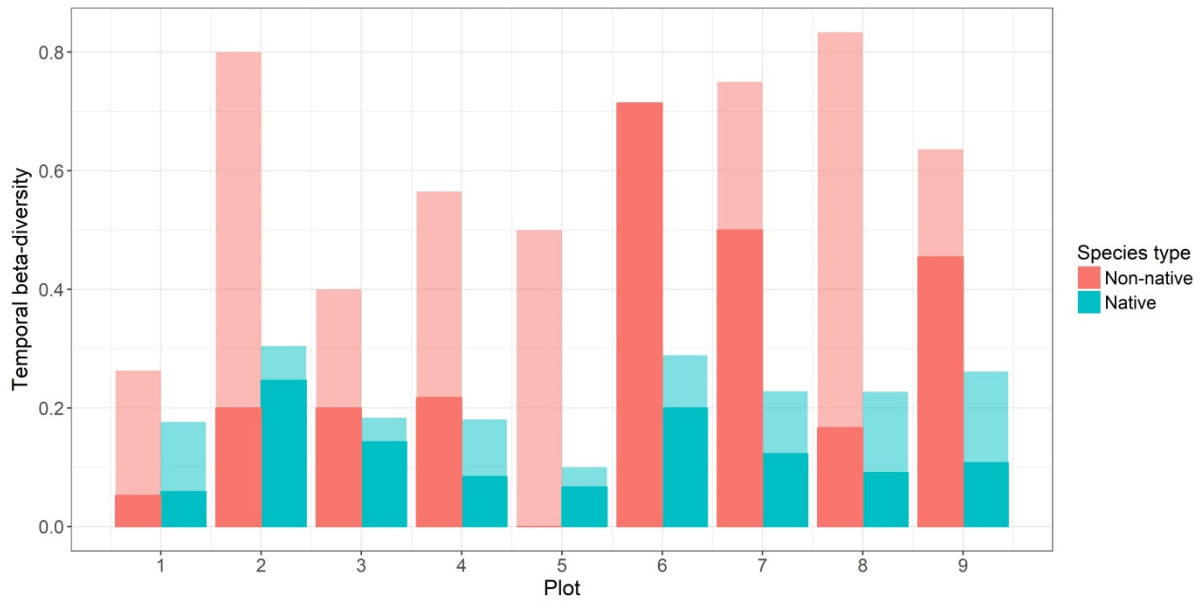
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771 Table S1. Sampling dates for the nine plots across the five years. A '1' indicates that  
 772 sampling was undertaken in this plot during this time period, whilst a '0' indicates that  
 773 sampling was not undertaken during this time period due to either logistical issues or  
 774 problems with the traps. Codes as in Figure S1: 1- TER-NFBF-T-01; 2- TER-NFBF-T-02; 3 -  
 775 TER-NFBF-TP41; 4- TER-NFPG-T-33; 5- TER-NFSB-T-07; 6- TER-NFSB-T164; 7-TER-  
 776 NFSB-TE48; 8- TER-NFSB-TE49; 9- TER-NFTB-T-15,

Plot	2012 Sep.	2012 Dec.	2013 May	2013 Sep.	2013 Dec.	2014 March	2014 June	2014 Sep.	2014 Dec.
1	1	1	1	1	1	1	1	1	1
2	1	1	1	1	1	1	1	1	1
3	1	1	1	1	1	1	1	1	1
4	1	0	1	1	1	1	1	1	1
5	1	0	1	1	1	1	1	1	1
6	1	0	1	1	1	1	1	1	1
7	1	1	1	1	1	1	1	1	1
8	1	1	1	1	1	1	1	1	1
9	1	1	1	1	1	1	1	1	1
Plot	2015 March	2015 Sep.	2015 June	2015 Dec.	2016 March	2016 June	2016 Sep.	2016 Dec.	
1	1	1	1	1	1	1	1	1	
2	1	1	1	0	1	1	1	1	
3	1	1	1	1	1	1	1	1	
4	1	1	1	1	1	1	1	1	
5	1	1	1	1	1	1	1	0	
6	1	0	1	1	1	1	1	1	
7	1	1	1	0	1	1	1	1	
8	1	1	1	1	1	0	1	1	
9	1	1	1	1	1	1	1	1	

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789 **Appendix S2 Temporal beta-diversity results using the Carvalho et al. partition**  
790 **framework**



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792 Figure S3. Pairwise temporal beta-diversity values for native and non-native arthropod  
793 species across nine plots of native forest on Terceira Island, in the Azores (Plot notation as in  
794 Table S1 and Figure S1). For each plot, temporal beta-diversity was calculated using the  
795 pooled 2013 samples and the pooled 2016 samples. For each plot, temporal beta-diversity  
796 was calculated separately for native species (blue bars) and non-native species (red bars). The  
797 height of each bar corresponds to the overall temporal beta-diversity. Overall temporal beta  
798 was also partitioned into richness differences and turnover components using the Carvalho  
799 partition approach (Carvalho et al. 2012). Within each bar, the dark shaded area rising from  
800 the x-axis corresponds to the richness differences component of overall temporal beta  
801 diversity. Thus, the lighter shaded area within each bar that rises from the dark shaded area  
802 corresponds to the turnover component.

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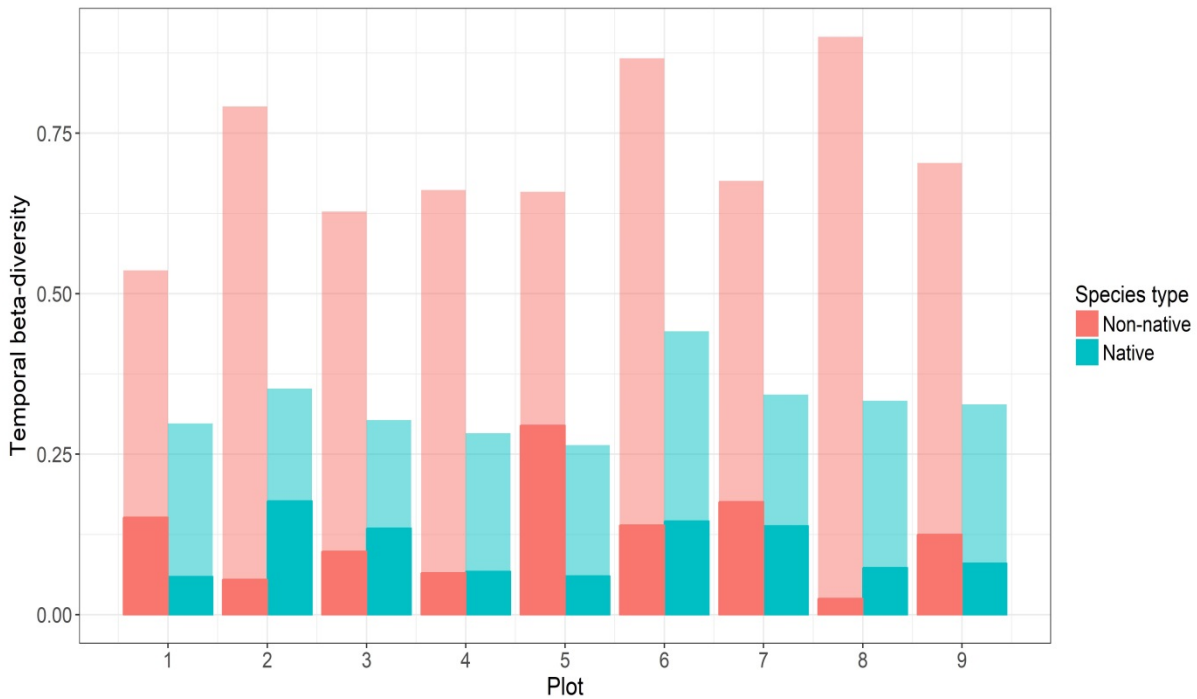


Figure S4. Multiple-time dissimilarity values for native and non-native arthropod species across nine plots of native forest on Terceira Island, in the Azores. For each plot, multiple-time dissimilarity was calculated across four years of data (2013 – 2016). For each plot, temporal beta-diversity was calculated separately for native species (blue bars) and non-native species (red bars). The height of each bar corresponds to the overall multiple-time dissimilarity was. Overall multiple-time dissimilarity was also partitioned into nestedness and turnover components using the Baselga partition approach (Baselga et al. 2017). Within each bar, the dark shaded area rising from the x-axis corresponds to the nestedness component of overall temporal beta diversity. Thus, the lighter shaded area within each bar that rises from the dark shaded area corresponds to the turnover component.



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807 **Appendix S4 Sensitivity Analyses Full Results**

808 Table S2. Sampling coverage estimates for the nine plots across the five years. SC is the  
809 sampling coverage for the observed data, and the LCI and UCI are the 95% lower and upper  
810 confidence intervals, respectively.

SC	LCI	UCI	Plot	Year	SC	LCI	UCI	Plot	Year
0.992	0.987	0.996	1	2012	0.983	0.967	1.000	8	2012
0.986	0.981	0.991	1	2013	0.987	0.981	0.993	8	2013
0.992	0.987	0.997	1	2014	0.989	0.983	0.995	8	2014
0.987	0.982	0.993	1	2015	0.981	0.968	0.993	8	2015
0.986	0.981	0.992	1	2016	0.981	0.970	0.991	8	2016
0.942	0.911	0.974	2	2012	0.979	0.965	0.992	9	2012
0.984	0.977	0.992	2	2013	0.990	0.986	0.995	9	2013
0.985	0.975	0.995	2	2014	0.985	0.976	0.993	9	2014
0.967	0.952	0.981	2	2015	0.976	0.964	0.989	9	2015
0.989	0.983	0.995	2	2016	0.973	0.958	0.987	9	2016
0.970	0.956	0.985	3	2012					
0.990	0.982	0.997	3	2013					
0.996	0.993	1.000	3	2014					
0.972	0.959	0.985	3	2015					
0.985	0.974	0.996	3	2016					
0.918	0.878	0.957	4	2012					
0.991	0.987	0.995	4	2013					
0.991	0.988	0.994	4	2014					
0.979	0.972	0.986	4	2015					
0.985	0.978	0.992	4	2016					
0.810	0.666	0.954	5	2012					
0.994	0.989	0.998	5	2013					
0.989	0.982	0.996	5	2014					
0.984	0.976	0.992	5	2015					
0.988	0.978	0.999	5	2016					
0.902	0.845	0.958	6	2012					
0.954	0.931	0.977	6	2013					
0.968	0.956	0.980	6	2014					
0.965	0.947	0.984	6	2015					
0.966	0.949	0.984	6	2016					
0.983	0.957	1.009	7	2012					
0.977	0.965	0.990	7	2013					
0.985	0.977	0.993	7	2014					
0.963	0.943	0.984	7	2015					
0.910	0.867	0.953	7	2016					

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814 **Using three SLAM traps in a single plot**

815 Using three SLAM traps in a plot rather than one did not result in substantially different  
816 sampled communities. Species richness across the three traps in T18 only ranged 49 – 51  
817 species, whilst abundance varied from 1380 to 1739 individuals per trap. The alpha parameter  
818 of the gambin distribution was relatively constant between the three traps (2.47, 2.44 and  
819 3.69), indicating similar SAD shapes. 58% of the total sampled species ( $n = 38$ ) were present  
820 in all three traps and overall spatial beta-diversity was low based on both presence/absence  
821 data (Sorensen dissimilarity = 0.24) and abundance data (Bray-Curtis multiple-site  
822 dissimilarity = 0.31). Thus, we are confident that our general sampling protocol is sufficient  
823 to obtain representative samples of the arthropod fauna in each plot.

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