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1 **Journal: Ecography R2**

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3 **in a fragmented native forest landscape**

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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.

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.

Material and methods

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.

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.*

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 $\Delta AIC_c <=$

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 $\Delta AIC_c <= 2$, 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

Dataset summary

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

Temporal beta-diversity

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

Using multiple-time dissimilarity produced similar results to the pairwise temporal beta-diversity analysis (see Figure S4 in Appendix S3): overall temporal beta-diversity was larger for non-native species than for native species, for all nine plots, and on average the temporal nestedness-dissimilarity component represented a larger proportion of total temporal beta-diversity for native species than for non-native species. One interesting difference was non-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.

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.

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 ΔAIC_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.

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

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).

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

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

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

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

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

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

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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

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

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

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Table 2. Pairwise temporal beta-diversity values for arthropod species sampled in 2013 and 2016 in nine native forest plots on Terceira Island, in the Azores. For each plot, the data are provided for native (Nat) and non-native (Non) species separately. Overall temporal beta-diversity values (Sorensen dissimilarity index) are provided in addition to the temporal turnover (Turn.) and temporal nestedness-dissimilarity (Nest.) components of overall temporal beta-diversity. For the two partition values and the overall temporal beta-diversity value, significance was determined using an FE null model (1000 iterations). For each of the three beta-diversity values, the Z-score (Z) and associated *P*-value (*P*) are provided (see 'Materials and methods'). *P*-values significant at the 0.05 level are highlighted in bold (Plot notation as in Table S1 and Figure S1). The overall temporal beta-diversity differ very slightly from the sum of the turnover and nestedness components in certain plots due to 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	**0.01**
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	**<0.01**	3.64	**<0.01**	-1.08	0.28
4	Nat	0.11	0.08	0.18	-0.36	0.72	-1.58	0.11	-1.96	**0.04**
5	Nat	0.04	0.06	0.10	-2.04	**0.04**	-0.24	0.81	-2.53	**0.01**
6	Nat	0.11	0.18	0.29	-2.68	**0.01**	6.17	**<0.01**	-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	**<0.01**	1.22	0.22	-3.48	**<0.01**
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	**0.01**
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	**<0.01**	11.20	**<0.01**	-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
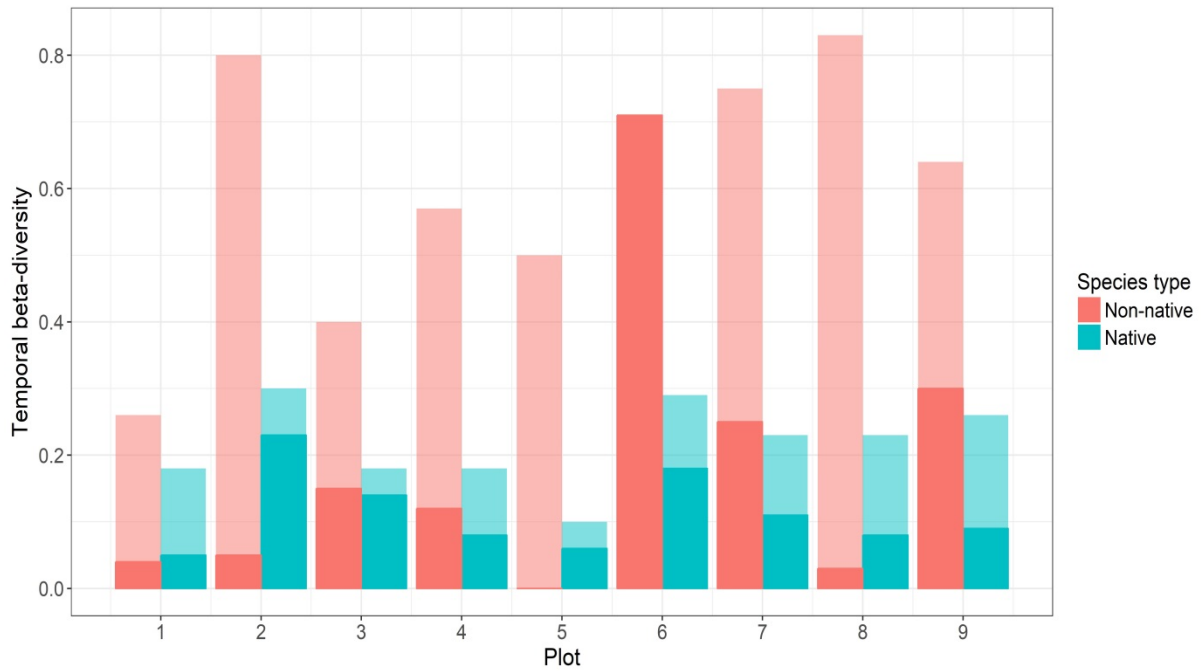
FIGURES

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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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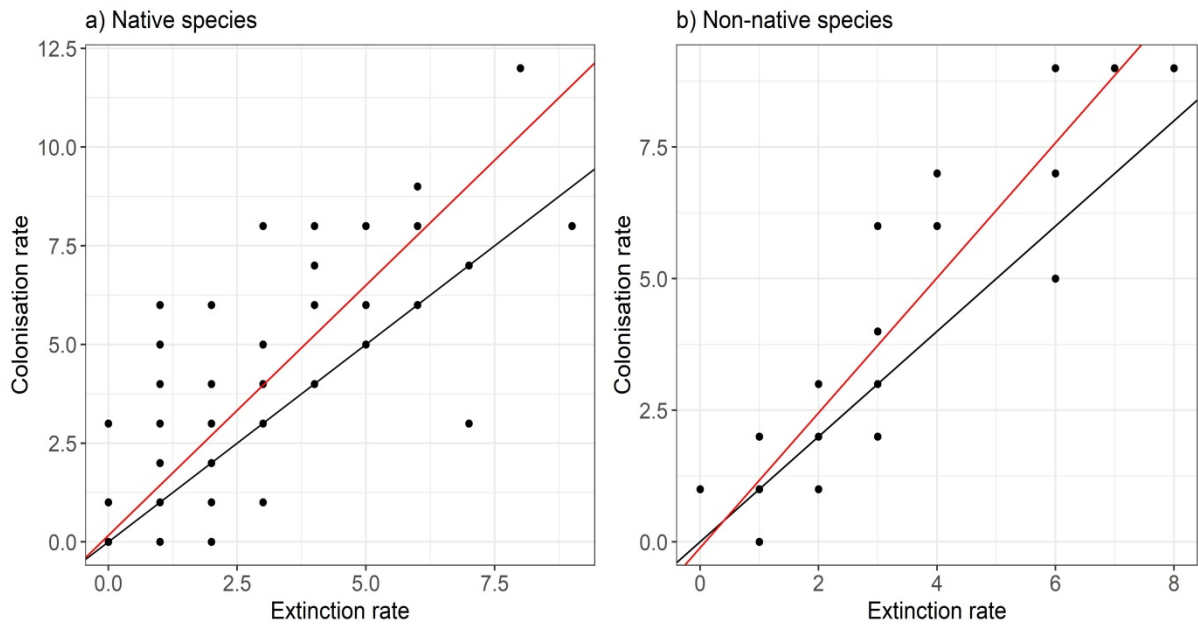
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Figure 2. The relationship between the number of colonisation events and the number of extinction events in native (a) and non-native (b) arthropod species sampled in nine native forest plots on Terceira Island in the Azores. Each plot was sampled 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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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 37º to 40º N
635 latitude and 25º to 3º 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^2 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.

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 15th 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.

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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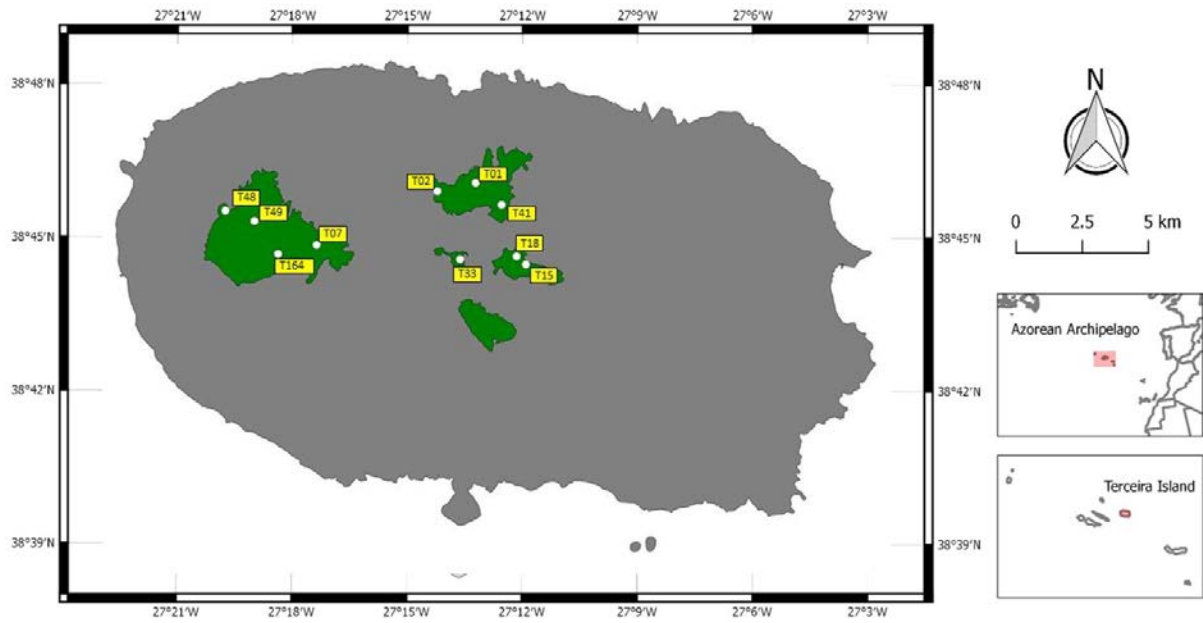
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757 **Plot locations**

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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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Figure S2. Example SLAM trap in a plot within a native forest fragment on Terceira Island
(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**
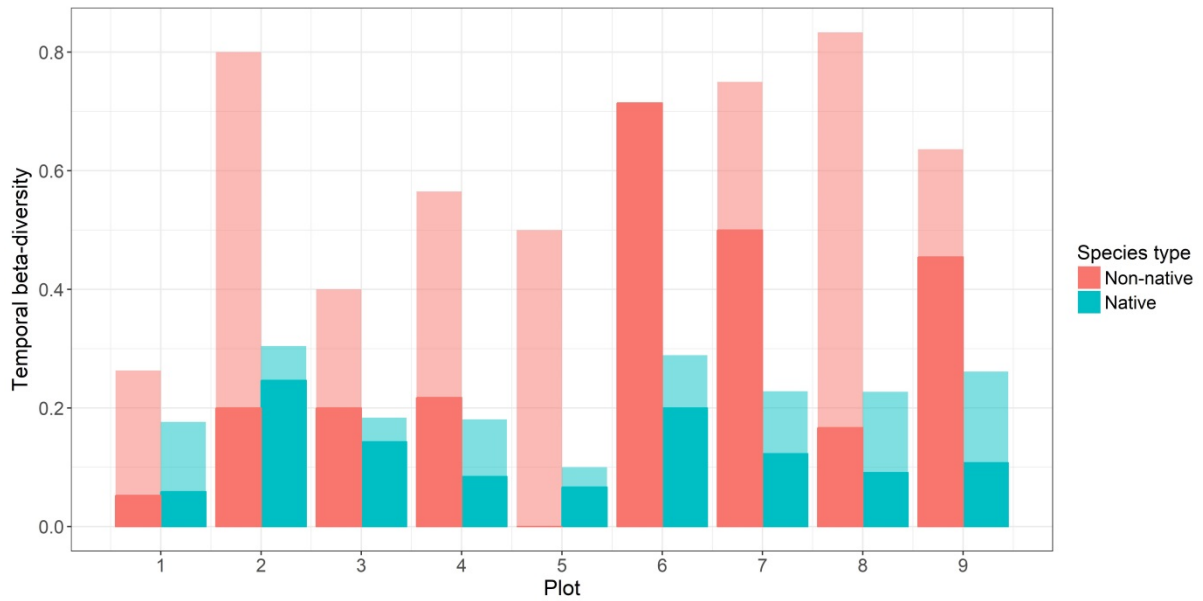
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792 Figure S3. Pairwise temporal beta-diversity values for native and non-native arthropod
793 species across nine plots of native forest on Terceira Island, in the Azores (Plot notation as in
794 Table S1 and Figure S1). For each plot, temporal beta-diversity 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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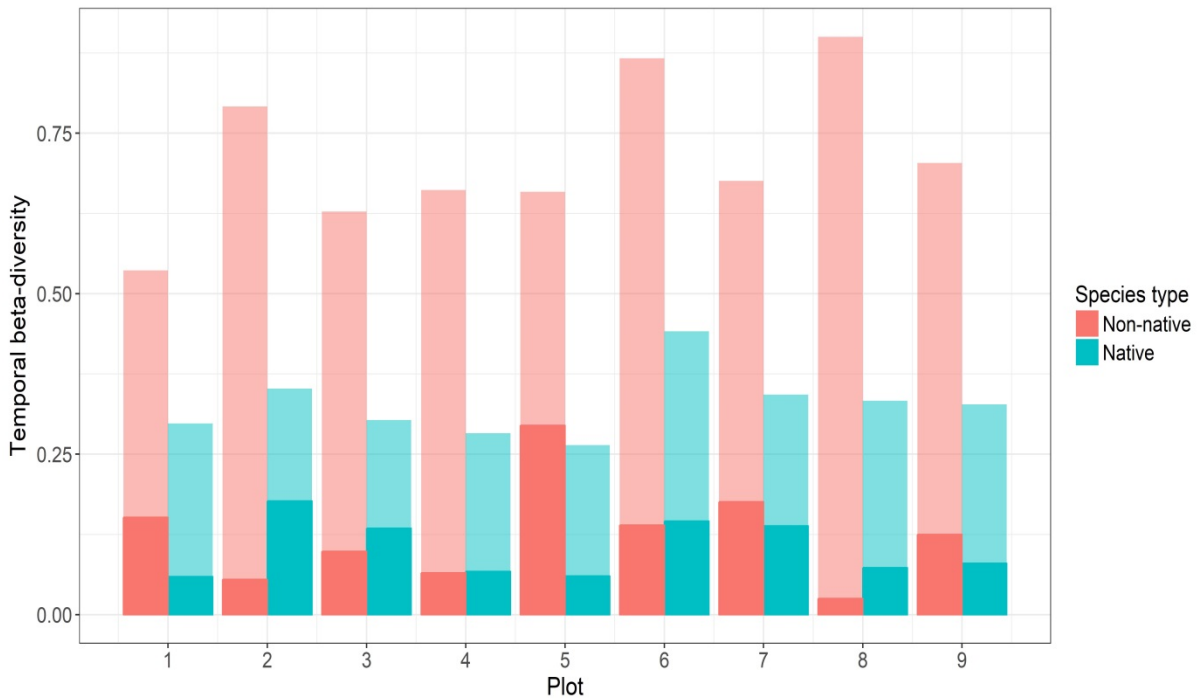**Appendix S3 Multiple-time dissimilarity results**

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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Appendix S4 Sensitivity Analyses Full Results

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