BIODIVERSITY RESEARCH

Functional traits of indigenous and exotic ground-dwelling arthropods show contrasting responses to land-use change in an oceanic island, Terceira, Azores

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Abstract

Aim: Land-use change typically goes hand in hand with the introduction of exotic species, which mingle with indigenous species to form novel assemblages. Here, we compare the functional structure of indigenous and exotic elements of ground-dwelling arthropod assemblages across four land-uses of varying management intensity.

Location: Terceira Island (Azores, North Atlantic).

Methods: We used pitfall traps to sample arthropods in 36 sites across the four land-uses and collated traits related to dispersal ability, body size and resource use. For both indigenous and exotic species, we examined the impact of land-uses on trait diversity and tested for the existence of non-random assembly processes using null models. We analysed differences in trait composition among land-uses for both indigenous and exotic species with multivariate analyses. We used point–biserial correlations to identity traits significantly correlated with specific land-uses for each element.

Results: We recorded 86 indigenous and 116 exotic arthropod species. Under high-intensity land-use, both indigenous and exotic elements showed significant trait clustering. Trait composition strongly shifted across land-uses, with indigenous and exotic species being functionally dissimilar in all land-uses. Large-bodied herbivores dominated exotic elements in low-intensity land-uses, while small-bodied spiders dominated exotic elements in high-intensity land-uses. In contrast, with increasing land-use intensity, indigenous species changed from functionally diverse to being dominated by piercing and cutting herbivores.

Main conclusions: Our study revealed two main findings: first, in high-intensity land-uses, trait clustering characterized both indigenous and exotic elements; second, exotic species differed in their functional profile from indigenous species in all land-use types. Overall, our results provide new insights into the functional role of exotic species in a land-use context, suggesting that, in agricultural landscape, exotic species may contribute positively to the maintenance of some ecosystem functions.

KEYWORDS
arthropods, Azores, community assembly, exotic species, functional diversity, indigenous species

1 | INTRODUCTION

Land-use change is inducing profound changes in biodiversity patterns throughout the world (Mooney & Hobbs, 2000; Newbold et al., 2015). Different species may be more or less sensitive to particular forms of disturbance, depending on their traits (Flynn et al., 2009; Mayfield et al., 2010). Because species' traits influence community assembly processes and ecosystem functioning, special attention has been given to the consequences of the loss of indigenous species for functional diversity (FD) (Brown et al., 2013; Díaz, Fargione, Chapin, & Tilman, 2006; Flynn et al., 2009; Forrest, Thorp, Kremen, & Williams, 2015). Land-use change frequently promotes the establishment of exotic species, often generating an increase in overall species richness at particular scales of analysis (Sax, Gaines, & Brown, 2002). However, the role of exotic species in driving changes in FD in the context of land-use change remains understudied (Vilà et al., 2011). Particularly, it remains unclear how land-use change shapes functional trait structure of exotic species and to what extent exotic species could contribute to the provision and maintenance of ecosystem functions in agricultural landscape (Didham, Tylianakis, Gemmell, Rand, & Ewers, 2007; Hobbs, Sayre, & Gupta, 2008; Rodgers & Parker, 2003).

Many exotic species are known to be particularly successful in anthropogenic habitats. Exotic species can possess functional traits that are not present in the indigenous community, allowing them to occupy new ecological opportunities provided by land conversion and transformation (Mayfield & Levine, 2010). In addition, some exotic species can possess similar functions to indigenous species and may provide ecological "insurance" after the decline of less tolerant indigenous species following land-use change (e.g., Aslan, Zavaleta, Tershy, Croll, & Robichaux, 2014). As land-use change intensifies, both indigenous and exotic species may, however, be filtered out towards a restricted set of functional strategies due to stressful environmental conditions (Tecco, Díaz, Cabido, & Urcelay, 2010). This may lead to functional homogenization whereby exotic and indigenous species fulfil similar functional roles (Drenovsky et al., 2012; Olden & Rooney, 2006).

Arthropods form a great part of the exotic fauna worldwide (Kenis et al., 2009). Several studies have reported lower indigenous arthropod species richness and abundance in agricultural land-uses than in more natural habitats (Attwood, Maron, House, & Zammit, 2008; Hendrickx et al., 2007), while exotic arthropods generally benefit from

agricultural landscapes (Grez, Rand, Zaviezo, & Castillo-Serey, 2013). Although arthropods provide numerous ecosystem services, including pollination, regulation of herbivorous pests and decomposition (Isaacs, Tuell, Fiedler, Gardiner, & Landis, 2009; Losey & Vaughan, 2006), there has been relatively little trait-based analysis of these functions compared to plants or vertebrates (Diekötter, Wamser, Wolters, & Birkhofer, 2010; Kenis et al., 2009). Moreover, we are unaware of any studies examining how traits of indigenous and exotic arthropods change in communities sampled across contrasting land-use types.

In this study, we evaluate and compare the functional trait structure of indigenous and exotic ground-dwelling arthropods across four land-use types of varying management intensity in the oceanic island Terceira (Azores, Portugal). The four land-uses range from pristine native forest patches subject to very low human management to intensively exploited pastures subject to frequent cattle grazing and fertilization (Borges et al., 2006; Cardoso et al., 2009). Indigenous and exotic species have been shown to co-occur at local scales in all four land-uses, permitting comparisons of trait assembly between indigenous and exotic elements of the same assemblages in relation to these contrasting land-uses (Cardoso et al., 2009; Meijer, Whittaker, & Borges, 2011; Rigal, Whittaker, Triantis, & Borges, 2013). Here, we focused on body size, dispersal ability and resource-use traits, all of which are recognized as important ecological traits, especially in a land-use context (Schweiger et al., 2005; Simons, Weisser, & Gossner, 2016).

Specifically, we first hypothesized that both indigenous and exotic species, analysed separately, should show increased trait clustering in high-intensity land-uses (H1). The rationale is that only species with a specific set of traits should persist under intensive and frequent environmental disturbances (i.e., cattle grazing and fertilization) (Flynn et al., 2009). Our second hypothesis was that exotic species should show trait dissimilarities when compared to co-occurring indigenous species under low- and high-intensity land-uses (H2). The rationale is that, under low-intensity land-uses (e.g., native forest), exotic species exhibiting novel functional traits are favoured in exploiting the vacant niches offered by the non-saturated nature of insular and/or impoverished indigenous assemblages in Terceira (Whittaker et al., 2014). In contrast, under high-intensity land-uses, exotic species have a competitive advantage for resource exploitation and establishment space over the indigenous species (Grigulis, Sheppard, Ash, & Groves, 2001; Saar, de Bello, Pärtel, & Helm, 2017).

2 | METHODS

2.1 | Study area

The Azores (37°–40°N; 25°–31°W) is one of the world's most isolated archipelagos. There are nine main islands aligned on a WNW–ESE axis in the Atlantic Ocean. All islands are volcanic and of recent origin. At the time of human colonization, around AD 1440, the Azorean archipelago was almost entirely forest-covered. By *c*. AD 1850, human activities had restricted the native forest to areas above 500 m a.s.l. During the 20th century, the development of an economy based on dairy has led to a further reduction of native forest area, with the clearing of large fragments at mid- and high elevations for pasture development. In addition, the plantation of forests of exotic species was incentivized during the 1950s in areas unsuitable for cattle grazing, thus promoting additional deforestation of natural forest habitat. Thus, in <600 years, 95% of the original native forest has been destroyed (Gaspar, Borges, & Gaston, 2008).

Our study was conducted on Terceira Island (402 km^2, 3.52 Ma), on which the native forest is restricted to 23 km^2, about 6% of its original area (Triantis et al., 2010 and references herein). The non-urban landscape of Terceira is dominated by four major habitats: (1) native forests; (2) exotic forests (*Cryptomeria japonica* and *Eucalyptus globulus* monoculture plantations, monocultures and mixed forest of the invasive *Pittosporum undulatum*); (3) semi-natural pastures (mid- and high-elevation pastures maintaining some indigenous plants) subject to short-term cattle grazing activity and low inputs of fertilizers; and (4) intensively managed pastures subject to intensive cattle grazing and high inputs of fertilizers (see Appendix S1 and Table S1.1 in Supporting Information for detailed features of the land-uses). The four land-uses were ranked in an increasing order, according to their intensity uses with (1) native forest, (2) exotic forest, (3) semi-natural pasture and (4) intensively managed pasture. Exotic forests were considered as the closest to the native forest because, contrary to pastures, they maintain some of the architectural and microclimatic conditions of the natural forests (Cardoso, Rigal, Fattorini, Terzopoulou, & Borges, 2013; Cardoso et al., 2009).

2.2 | Sampling methodology

Nine sampling sites were established in each of the four land-use types (total = 36), distributed across the island without regard to the character of the surrounding land-use matrix. Sampling sites were on average 1.6 km (range 0.137–3.7) apart from each other and 0.73 km apart (0.13–3.8) from the edge of the sampled land-use type (Table S1.2 and Fig. S1.1). The ground-dwelling fauna was sampled at each site using 30 pitfall traps, spaced 5 m apart, along a 150-m transect. Traps were left in the field for 2 weeks in the summer months of June, July or September of different years (native forests between 1999 and 2003 and the other habitats in 2008 and 2009). A potential effect of the sampling years on species compositions across sites was discarded by a between-year analysis using additional data (Florencio, Cardoso, Lobo, Azevedo, & Borges, 2013). The majority of captured arthropods

(excluding Crustacea, Collembola, Diplura, Diptera and Hymenoptera) were sorted to species level; the remaining specimens were sorted to morphospecies. All species were classified as indigenous or exotic. Indigenous species comprise Azorean endemics and other native non-endemics. Exotic species are those considered to have colonized via human mediation, many of which having a cosmopolitan distribution (Borges et al., 2010 and see Appendix S1 for further details in species classification).

All analyses were conducted using the transect (i.e., set of 30 pitfall traps) as the unit of analysis.

2.3 | Traits characterization

For all arthropod species, we collated body size, dispersal abilities and a set of functional traits related to resource use (Table 1). Apart from body size, which was measured on the individuals sampled in this study, traits were collected from an extensive literature search, including manuscripts with the first descriptions of the species, first species records for the Azores, brief notes and ecological studies. Information was also obtained from experts who have identified the specimens or from experts of a given taxonomic group when information for a particular species was not available. Most of the literature was retrieved from the taxonomic catalogue of the entomological bibliography for the Azores (see Borges & Vieira, 1994; Vieira & Borges, 1993), with the addition of some recent documentation (Barnard, 2011). Functional information was assigned to each species according to the adult characteristics, except for Lepidoptera, where traits were assigned by reference to the larvae. For the unidentified morphospecies, we assigned functional traits of the nearest taxonomic resolution (genus, family), except for body size. Species trait assignments, together with the species mean abundances per land-use, are given in Appendix S2.

2.4 | Data analysis

Our first set of analyses aimed to test whether indigenous and exotic elements of ground-dwelling arthropod assemblages each show trait clustering in high land-use intensity (H1). Therefore, unless otherwise stated, all the following analyses were performed independently for indigenous and exotic species. To provide context for our trait-based analyses, we first quantify species diversity in each site using species richness and the Simpson index. Due to differences in sampling completeness between sites among the land-uses (see Appendix S3 and Fig. S3.1), we calculated rarefied richness to the lowest sample size (n = 77 individuals) to perform direct comparisons of richness between our four land-uses. Prior to our FD analysis, we built a functional dissimilarity matrix between species using the extension of the Gower's distance metric provided by Pavoine, Vallet, Dufour, Gachet, and Daniel (2009). To assess clustering of species in trait space per site, we computed the mean pairwise functional distance (MFD), that is the averaged functional distance between all pairs of species co-occurring in a site (Webb, Ackerly, McPeek, & Donoghue, 2002). To account for abundance

TABLE 1 Selection, definition and ecological relevance of the functional traits used in the study

Traits	Data type	Attributes (abbreviations)	Definition	Ecological relevance
Body size	Continuous	Absolute body length in mm	Defined as mean body length measured from up to 10 individuals per species. Males and females were incorporated when clear distinction was available. Measures recorded using digital photography *via* a stereoscopic microscope	Body size is related to many life-history traits such as growth rate, fecundity/clutch size, foraging ability, dispersal and life span
Dispersal abilities	Nominal	High dispersal ability (Hdisp[a]) versus low dispersal ability (Ldisp)	Based on the presence of active wings for coleopteran and Hemipteran, ballooning for spiders and based on descriptions of flying ability for endemics and general guides for the other species. Species subsequently classified as possessing either high or low dispersal ability	Dispersal abilities condition potential colonization/recolonization
Type of food	Multichoice nominal	Plants (FoodPl); Animals (FoodAni); Fungi (FoodFg); Detritus (FoodDet)	Refers to the main food consumed by species during their adult stages except for Lepidoptera, where traits were assigned by reference to the larvae	Species can co-occur in the same site but differ in their feeding strategies and resource use. Feeding guilds can also react differently to land-use changes, such as herbivores being sensitive to change in plant diversity and biomass and predators such as spiders reacting to changes of habitat architecture (Pearce & Venier, 2006; Scherber et al., 2010)
Way of getting food	Nominal	High active search (GetHact[a]) versus low active search (GetLact)	Refers to the mobility of the species in getting their food. Species classified as having active search or low active search such as species with ambush tactics or using traps	Land-use changes can impact the architecture at microscale and reduce potential foraging sites selected by low active search species and affect their feeding opportunities
Mode of ingestion	Nominal	Chewing and cutting (IngCC); Piercing and sucking (IngPS); extra-intestinal digestion and sucking (IngEDS)	Defined as the way nutrients are ingested	Mode of ingestion can be related to host specificity. For instance, land-use changes may alter the kind of plants available and consequently alter the availability of resources for chewing and sucking species
Period of activity	Multichoice nominal	Day (ActDay); Night (ActNig); Twilight (ActTwi)	Classified as species being active during the day, during the twilight or during the night or to a combination of those periods	Species can co-occur in the same sites but have separated temporal niches. Circadian activities also play important roles in species interaction (e.g., prey–predator). Land-use changes may promote high proportion of open microhabitats, which are less favourable for species with day activity

[a]Attributes used in the CWM analysis to avoid collinearity.

distributions within sites and to lower the weight of rare and possibly "vagrant" species, the distance values were weighted according to the log-transformed species abundance. By construction, MFD is hardly, if at all, sensitive to species richness (Pavoine, Gasc, Bonsall, & Mason, 2013). To test whether rarefied species richness, the Simpson index and MPD differ between land-uses, we applied generalized least-squares models (GLS; Pinheiro & Bates, 2000) to account for unequal variances among land-uses. We also tested the ability of the GLS models to account for potential spatial structure by estimating the Moran's I spatial autocorrelation index on residuals using latitude and longitude of each sample site. We quantified the effect of land-uses using Magee's pseudo-R^2 (Magee, 1990). When the overall GLS model was statistically significant, the Tukey post hoc test was used to identify statistically significant pairwise differences between land-uses.

To test whether the MFD was larger (functionally overdispersed) or smaller (functionally clustered) than expected by chance, we compared the observed MFD value in each site to a random distribution under the null hypothesis of no association between land-uses and traits (Cornwell & Ackerly, 2009). We then generated 999 null assemblages using the Independent Swap algorithm (Gotelli & Graves, 1996), which reshuffles the species-by-sites matrices keeping species richness, species frequency and the total abundance of species in the matrix constant. To measure deviation from the null expectation for each site, we computed the standardized effect size (SES) using the formula $SES_{MFD} = (MFD_{obs} - \mu_{null})/\sigma_{null}$ where MFD_{obs} is the observed MFD value at a given site, μ_{null}, the mean MFD of the simulated communities, and σ_{null} the associated standard deviation. Positive SES_{MFD} indicates that species occurring together in a site are less functionally related than expected by chance (functionally overdispersed), while negative SES_{MFD} indicates that co-occurring species are more functionally related than expected by chance (functionally clustered). We tested whether SES_{MFD} values for a given land-use presented significant deviations from the null expectation (median = 0) using a one-sample Wilcoxon test (Swenson & Enquist, 2009). We also computed GLS for SES_{MFD} in the same way as specified for diversity metrics.

Our second set of analyses aimed to test whether exotic and indigenous elements of single ground-dwelling arthropod assemblages differ in their trait composition among land-uses (H2). For each individual site, we began by calculating the community-weighted means (CWM) for body size and each trait attribute for both indigenous and exotic species separately. The CWMs express the mean attribute value between species occurring at a site, weighted by the relative abundance of each species (Violle et al., 2007), and were calculated as follows:

$$CWM_j = \sum_{i=1}^{S} p_i x_{ij}$$

where CWM_j is the community-weighted mean value of trait attribute j, p_i is the relative abundance of species i (i = 1, 2, ..., S), and x_{ij} is the value of trait attribute j for species i. Prior to CWM calculation, multichoice nominal traits and nominal traits were dummy-transformed to as many

binary variables as there were trait attributes and were handled as quantitative variables. This generated new "CWM-by-sites" matrices separately for indigenous and exotic species. Based on these matrices, we calculated the Bray–Curtis distance between all pairs of sites and conducted a nonparametric permutational multivariate analysis of variance (PerMANOVA; Anderson, 2001) to test for difference in trait composition among land-uses. PerMANOVA was performed using permutation tests with 9,999 iterations. When the overall PerMANOVA was significant, post hoc t tests were performed to identify statistically significant pairwise differences between land-uses (Anderson, Gorley, & Clarke, 2008). To test for differences between indigenous and exotic species among land-uses, we computed a PerMANOVA to specifically test the interaction between species origin (indigenous versus exotic) and land-uses using a Bray–Curtis distance matrix computed by combining the indigenous and exotic "CWM-by-sites" matrices. Site was set as a random effect. When the interaction term was significant, post hoc t tests were performed to identify land-uses where trait compositions of indigenous and exotic species were significantly different from each other. Results of the PerMANOVAs were visualized using nonmetric multidimensional scaling ordinations (NMDS) based on Bray–Curtis distance matrices.

Finally, to help the interpretation of our functional trait-based patterns, we conducted an indicator analysis (Dufrêne & Legendre, 1997) to identify the degree of correlations between trait attributes and land-uses for both indigenous and exotic species. We then used the point–biserial correlation coefficient (r_{pb}; Cáceres & Legendre, 2009) to test the correlation between each CWM and the four land-uses separately using a binary coding for land-uses, with 1 and 0 indicating whether sites belong or not to the land-use under study. We calculated 95% confidence intervals for the r_{pb} values by bootstrapping the observed data 9,999 times and considered values not overlapping zero as significant.

Statistical analyses were implemented within the R programming environment (R Development Core Team, 2014) using the packages *vegan* (Oksanen et al., 2013), *picante* (Kembel et al., 2010), *nlme* (Pinheiro, Bates, DebRoy, & Sarkar, 2012), *indicspecies* (Cáceres & Legendre, 2009) and *BAT* (Cardoso, Rigal, & Carvalho, 2015). PERMANOVAs were performed using the software PRIMER v.6 (Anderson et al., 2008).

3 | RESULTS

A total of 20,800 soil-arthropod specimens were collected and 202 (morpho) species were identified, representing 20 orders, 76 families and 161 genera. Of the 202 species, 86 were considered to be indigenous and 116 to be exotics (Appendix S2). About 13% of the taxa were identified to morphospecies rather than species.

No spatial autocorrelation was detected in the residuals of the GLS models (Table S4.1 in Appendix S4). Rarefied indigenous species richness decreased significantly from low- to high-intensity land-uses (Figure 1A and Table S4.2), while rarefied exotic species richness increased (Figure 1B and Table S4.2). Similar trends were observed for the Simpson's index (See Fig. S4.1A,B and Table S4.2). MFD of
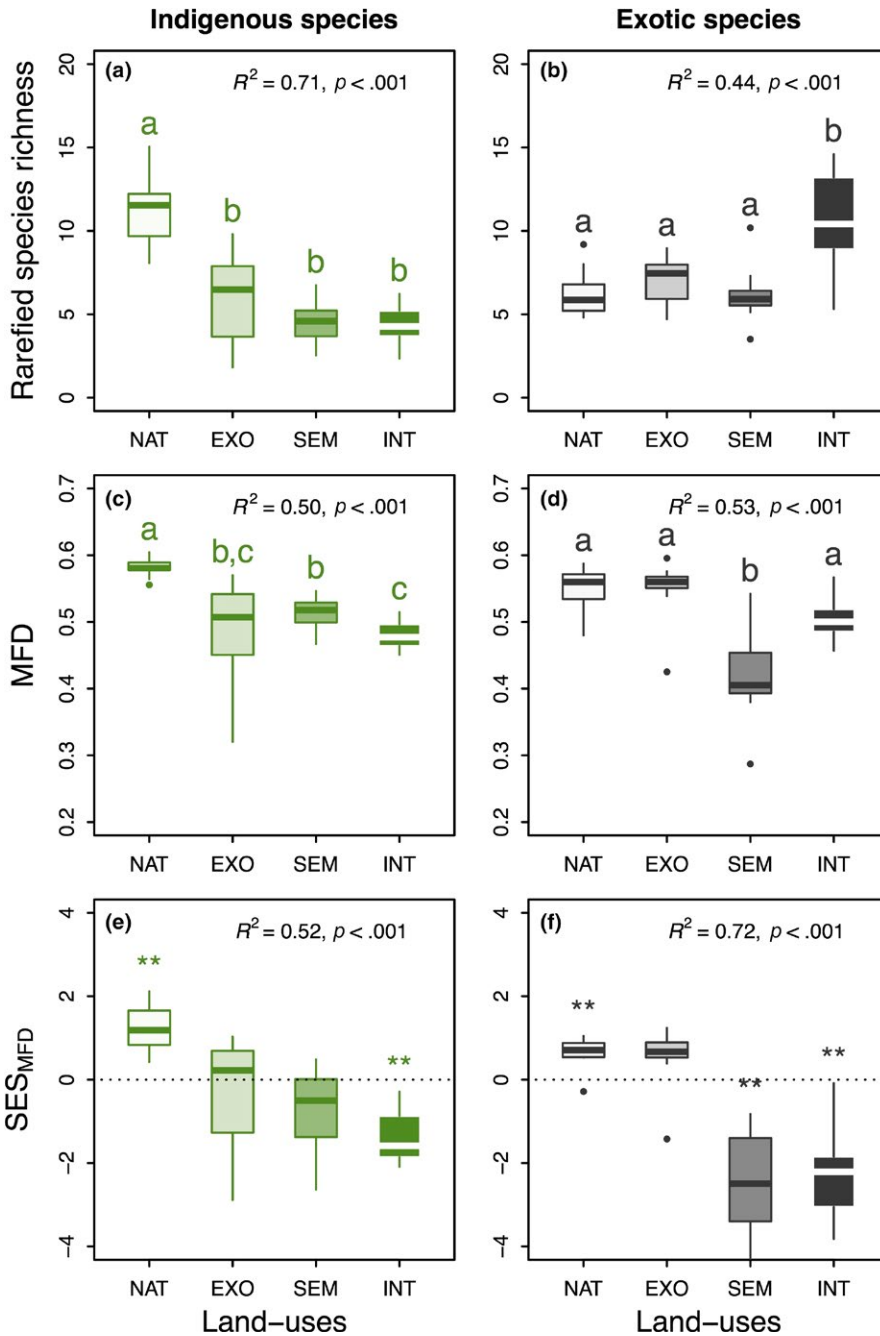
FIGURE 1 Rarefied species richness (a, b), mean pairwise functional distance (MFD) (c, d) and standardized effect sizes of MPD (SES$_{MFD}$) (e, f) across the four land-use types for both indigenous (a, c, e) and exotic arthropod elements (b, d, f) in Terceira Island. The Magee's pseudo-R^2 and the p values from the generalized least-squares (GLS) models are given on the top right of each panel. Land-use types accompanied by a different letter are significantly different from each other (post hoc tests; $p < .05$, see Table S4). For the SES$_{MFD}$ values, asterisks indicate significant deviations from 0 according to the Wilcoxon test with **$p < .01$. For clarity, results of the post hoc tests following the GLS are not given for SES$_{MFD}$ (but see Table S4). Land-use types are ranked according to their intensity of use/transformation, represented by either indigenous (green) or exotic (grey) gradation, with NAT = native forest, EXO = exotic forest, SEM = semi-natural pastures and INT = intensive managed pastures. See Table S1.1 in Appendix S1 for detailed land-use features

indigenous species decreased significantly from low- to high-intensity land-uses (Figure 1C and Table S4.2). For exotic species, MFD of semi-natural pastures was significantly lower than for other land-use types but no other significant differences occurred (Figure 1D and Table S4.2). Both indigenous and exotic elements were significantly functionally overdispersed in native forest (median SES$_{MFD}$ > 0; Wilcoxon test, $p = .003$ and $p = .007$, respectively, Figure 1E,F). Indigenous species were significantly functionally clustered in intensively managed pastures (median SES$_{MFD}$ < 0; Wilcoxon test, $p = .003$, Figure 1E) but not in semi-natural pastures (Wilcoxon test, $p = .07$, Figure 1E), while exotic species were significantly functionally clustered in both semi-natural pastures and intensively managed pastures (median SES$_{MFD}$ < 0 Wilcoxon test, $p = .003$ and $p = .003$, respectively, Figure 1F). Neither

indigenous nor exotic species showed significant deviation from the null expectation in exotic forest samples (Wilcoxon test, $p = .73$ and $p = .12$, respectively).

Trait composition significantly differed between land-uses for both indigenous and exotic species (PERMANOVA: $R^2 = .44$, pseudo-$F_{3,32} = 8.518$, $p < .001$ and $R^2 = 0.76$, pseudo-$F_{3,32} = 33.741$, $p < .001$, respectively). Moreover, post hoc t tests revealed that land-uses were significantly different from each other in their trait composition for both indigenous and exotic species ($p < .05$, Table S4.3), except between semi-natural and intensively managed pastures for indigenous species ($p = .056$, Table S4.3 and see Fig. S4.2A and B for the NMDS plots for indigenous and exotic species, respectively). Analyses combining both indigenous and exotic "CWM-by-sites"

matrices showed that trait composition differed between indigenous and exotic species among land-use types (PERMANOVA, interaction species origin × land-uses: R^2 = .324, pseudo-$F_{3,64}$ = 28.317, p < .001). Moreover, post hoc t tests revealed that indigenous and exotic species were significantly different from each other in their trait composition within all land-uses (p < .05, Table S4.3). This pattern was clearly evident in the NMDS plot (Figure 2) showing a clear absence of overlap for each land-use between indigenous and exotic species in the two-dimensional space.

The point–biserial correlations (r_{pb}) analysis between trait attributes (i.e., CWMs) and land-uses indicated striking differences between indigenous and exotic species (Figure 3). For instance, the trait attributes plants (Trait: type of food), detritus (type of food), chewing and cutting (mode of ingestion), high active search (way of getting food) and body size showed significantly negative correlations with native forest for indigenous species, while significantly positive correlations were found for exotic species. In contrast, the attribute plants (type of food) and piercing and sucking (mode of ingestion) showed significantly positive correlations with intensive managed pastures for indigenous

species and significantly negative correlations for exotic species, while the attributes animals (type of food) and intestinal digestion and sucking (mode of ingestion) showed the opposite pattern. For exotic species, body size was also negatively correlated with intensively managed pastures. Only the attribute high dispersal ability exhibited a consistent pattern for both indigenous and exotic species, with significantly negative correlations in native and exotic forests and significantly positive correlations in intensive managed pastures.

4 | DISCUSSION

Our study revealed two main findings: (1) in high-intensity land-use (semi-natural and intensively managed pastures), trait clustering characterized both indigenous and exotic elements (supporting H1) and (2) indigenous and exotic species were filtered out towards two distinct functional profiles across the four land-use types with both species origin differing in their trait composition in all land-uses (supporting H2).

4.1 | Prevalence of trait clustering for both indigenous and exotic species in high-intensity land-uses

Both indigenous and exotic elements were found to display significant trait clustering in high-intensity land-uses, highlighting the fact that species were functionally more similar than expected by chance in those land-uses. Overall, these findings are in accordance with recent trait-based studies claiming that land-use intensification acts as a filter, favouring a limited array of trait combinations (Flynn et al., 2009; Laliberte et al., 2010). Specifically, for arthropods, our results confirm recent observations made in a land-use change context for insect pollinators (Rader, Bartomeus, Tylianakis, & Laliberté, 2014), beetles (Birkhofer, Smith, Weisser, Wolters, & Gossner, 2015), bees (Forrest et al., 2015) and arthropods as a whole (Simons et al., 2016).

For indigenous species, MFD values lower than expected by chance in intensively managed pastures (Figure 1E) were coupled with a decline of species diversity, indicating that functions were lost at a higher rate than would be predicted by chance if species were lost randomly (Flynn et al., 2009). In contrast, exotic species richness increased as land-use intensity increased, but this was accompanied by lower-than-expected MFD values under high-intensity land-uses (Figure 1F). These results reveal a degree of apparent functional redundancy within the exotic element of ground-dwelling arthropod assemblages under high-intensity land-uses, with more species executing similar functions.

Interestingly, we found significant trait divergence in native forests for both indigenous and exotic species (Figure 1E–F). Although this pattern is usually interpreted as the result of biotic interactions, typically competitive exclusion (Webb et al., 2002), caution is needed with such an interpretation (de Bello, 2012). As for the null model analysis, we considered all the species found across the four land-uses as our regional species pool, it is more likely that species distribution
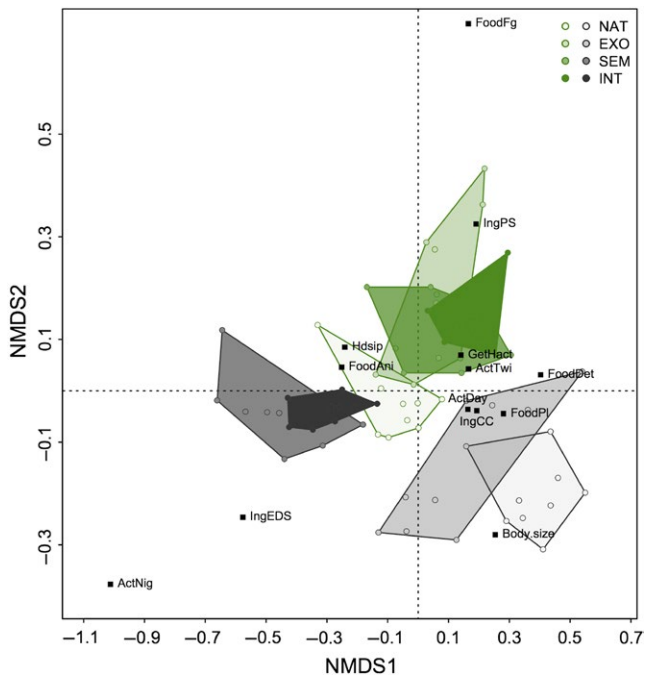

FIGURE 2 Two-dimensional ordination solution using non-metric multidimensional scaling (NMDS) based on the Bray–Curtis distance computed by combining the "community-weighted mean (CWM) × sites" matrices of indigenous and exotic arthropod elements across the land-use gradient in Terceira island. Dots indicate elements, while lines delimit the smallest polygon that encloses all elements for a given land-use. The stress value of NMDS was 0.13. The black squares and their associated labels indicate the weighted mean scores of the attributes (i.e., CWMs) in the two-dimensional ordination configuration. Land-use types are ranked according to their intensity of use/transformation, represented by either green (i.e., indigenous) or grey (exotic) gradation with NAT = native forest, EXO = exotic forest, SEM = semi-natural pastures and INT = intensive managed pastures. See Table S1.1 in Appendix S1 for land-use features and Table 1 for the abbreviations of the trait attributes
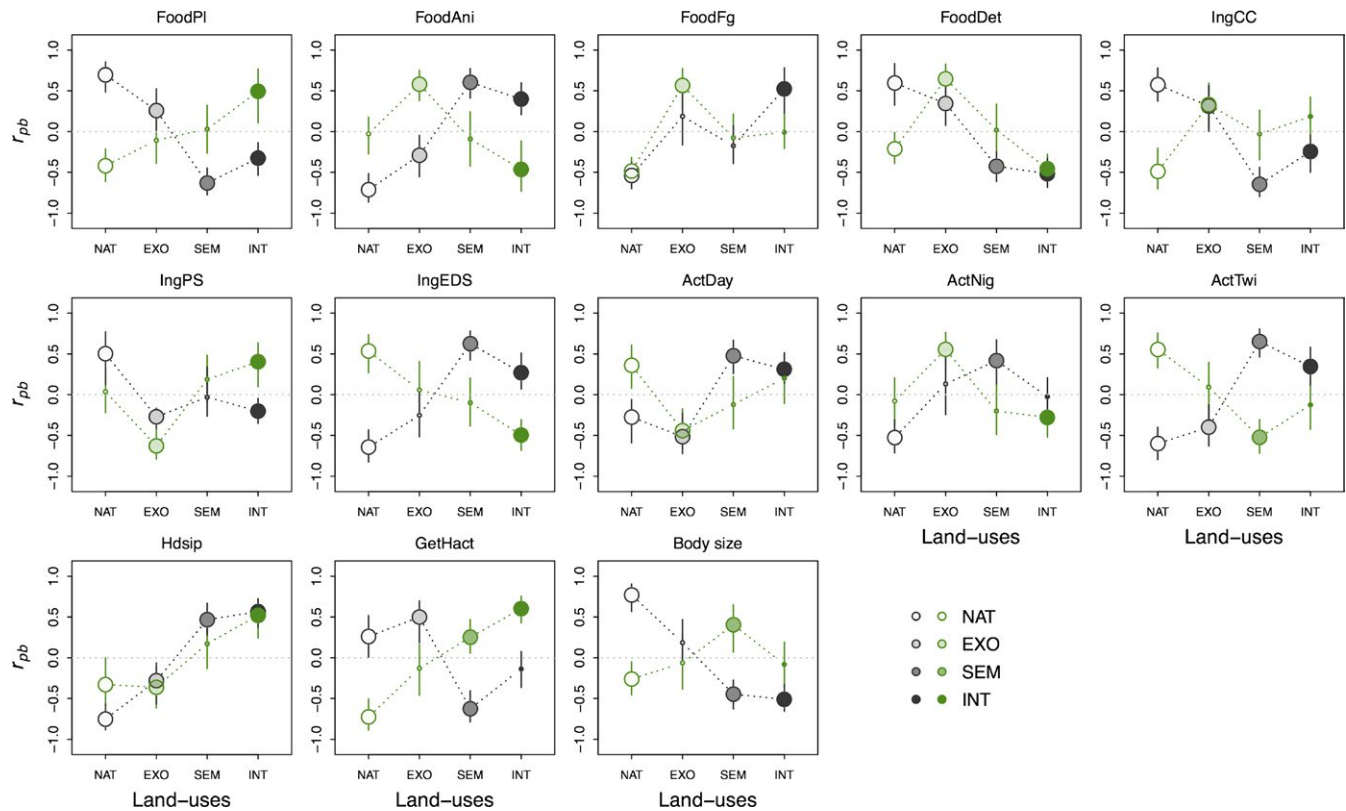
FIGURE 3 Results of the indicator analysis showing correlations between trait attributes (CWM) and land-uses for both indigenous and exotic arthropod species in Terceira Island. Correlations were computed using point–biserial correlation coefficients (r_{pb}) between CWM and each land-use separately using a binary coding for land-uses, with 1 and 0 indicating, respectively, whether sites belong or not to the land-use type indicated. For each r_{pb} value, the 95% confidence interval was calculated by bootstrapping the observed data 9,999. Large dots indicate values not overlapping zero (i.e., significant r_{pb}), while small dots indicate values overlapping zero (i.e., non-significant r_{pb}). Land-use types are ranked according to their intensity of use/transformation, represented by either green (i.e., indigenous) or grey (exotic) gradation, with NAT = native forest, EXO = exotic forest, SEM = semi-natural pastures and INT = intensive managed pastures. See Table S1.1 in Appendix S1 for land-use features and Table 1 for the abbreviations of the trait attributes

across these land-uses may result predominantly from environmental constraints overpowering the importance of local species interactions (Münkemüller et al., 2014). It is possible that different outcomes would be produced if we down-scaled the species pool to a particular land-use (Münkemüller et al., 2014). Moreover, capturing evidence of competitive exclusion would require us to focus on a specific feeding guild (e.g., competition between predators), whereas our study considers all ecological guilds and trophic levels of ground-dwelling arthropods. Therefore, the functional overdispersion observed herein might simply reflect the large range of niches occupied by species in native forest comparatively to the other land-uses.

4.2 | Land-use change filtered out indigenous and exotic species towards distinct functional profiles

We found that trait composition of both indigenous and exotic species differed between land-uses, reflecting a clear shift in the functional space occupation from low to high-intensity land-uses. Moreover, our study reveals that the direction of the effect of land-use change on the trait composition greatly differed between indigenous and exotic species.

Indigenous species shift from functionally diverse elements in low-intensity land-use towards elements dominated mainly by piercing and sucking herbivores in high-intensity land-uses (Figure 3). Examples of the species involved include the coleopterans *Hirticollis quadriguttatus* (Anthicidae, native) and *Heteroderes azoricus* (Elateridae, Azorean endemic) (Appendix S2). This finding is consistent with previous studies on Azorean herbivores that have reported a high proportion of generalists in free-living phytophagous insects (Ribeiro et al., 2005). Such patterns have been observed for other oceanic island guilds of phytophagous insects (Kaiser-Bunbury, Traveset, & Hansen, 2010; Olesen, Eskildsen, & Venkatasamy, 2002) and are usually explained as reflecting the relaxation of interspecific competition as consequence of the young age and the isolation of such islands (Olesen et al., 2002). An alternative and non-exclusive explanation is that some herbivorous species can increase in abundance with habitat loss due to a reduction in specialist predator populations (a top-down effect) (Ryall & Fahrig, 2006). The directional shift towards herbivore-dominated elements was accompanied by a correspondingly low relative abundance of carnivorous species in intensively managed pastures (Figure 3). This is in accordance with several previous studies that have reported that high trophic-level arthropod taxa were relatively sensitive to

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environmental stress (e.g., Holt, 1996; Pearce & Venier, 2006). Web-building spiders in particular, often being dependent on substantial habitat structure and vegetation architecture to anchor their webs (e.g., Samu, Sunderland, & Szinetar, 1999), cannot find suitable sites when clear-cutting or establishment of pastures destroy all trees. Also, some Chilopoda species are known to display strong preferences for low temperatures and high humidity (conditions encountered in native and exotic forest). Examples include species of *Lithobius* (Lewis, 2006), one of which, *Lithobius pilicornis pilicornis* (Lithobiidae; native), was found to be abundant in forest but almost absent in pastures (Appendix S2). From a bottom-up perspective, predator populations could have also been indirectly and negatively affected by the decline of their prey populations (Ryall & Fahrig, 2006). We also found a significant correlation between high dispersal ability and high-intensity land-uses for indigenous species (Figure 3). This suggests the hypothesis that pastures act as sinks for forest-associated species, with only the good dispersers being able to colonize them from native forest patches (Borges, Ugland, Dinis, & Gaspar, 2008). Native forest is particularly characterized by small-bodied indigenous species, reflecting the strong dispersal filter imposed by the remote location of the archipelago. This is particular apparent for indigenous spiders, which have mainly reached the islands by ballooning (Carvalho & Cardoso, 2014).

In contrast to indigenous species, the trait composition of exotic elements shifted from a preponderance of large-bodied, chewing and cutting herbivores and detritivores in low-intensity land-uses, towards elements dominated mainly by smaller-bodied species, active throughout both day and night, carnivorous, with extra-intestinal digestion and highly dispersive (mostly spider species) in high land-use intensity (Figure 3). Native forest provides abundant resources for herbivorous species, thereby allowing the successful establishment of exotic herbivores. Moreover, because indigenous Azorean communities are largely unsaturated (Borges & Brown, 2004; Whittaker et al., 2014), competition for food is likely to be reduced. Interestingly, the most successful exotic herbivores were two Julidae species, *Ommatoiulus moreletii* and *Cylindroiulus propinquus*, which possess the largest body size of all arthropods found in Terceira Island (Appendix S2). Considering that ecological niches for large species have not yet been filled by indigenous species (above), large-sized exotic species may have been favoured in establishing populations in native forests. These two Julidae species are also occasionally detritivores (Bailey & Mendonça, 1990), explaining the dominance of this trait within exotic elements in native forest.

The directional shift within exotic elements towards small-sized spiders in sites of high-intensity land-uses was accompanied by a clear pattern of functional redundancy (Figure 1F). In both semi-natural and intensively managed pastures, small-sized Linyphiidae spiders featured prominently, especially members of the genera *Erigone* (*E. autumnalis* and *E. dentipalpis*) and *Oedothorax* (*O. fuscus*), both well adapted to grazed pastureland (Wise, 1995 and Appendix S2). Linyphiidae in general, and those genera in particular, are mostly *r*-selected species, which are tiny (*c*. 2 mm), efficient dispersers, often with multiple generations per year (Bell, Wheater, & Cullen, 2001). These features may therefore confer strong advantages in the recolonization of pasture lands after intensive grazing and mowing

(Tscharntke, Klein, Kruess, Steffan-Dewenter, & Thies, 2005). The dominance of exotic Linyphiids could also be due to the wide availability of prey. However, Linyphiids mainly feed on Collembola, Diptera and Hymenoptera (Agusti et al., 2003), three orders that were not considered in our study.

4.3 | Potential mechanisms involved in functional structure of both indigenous and exotic elements

Our study clearly shows that indigenous and exotic species display opposing functional profiles across land-use types. There could be multiple alternative underlying mechanisms for this pattern. Prior to human colonization, the native forest in the archipelago acted as a filter, selecting species that were able to establish, some of which subsequently speciated in the archipelago. Hence, the indigenous species pool did not probably include species pre-adapted to pasture-lands, and in this regard, generalist herbivores may be the exceptions. However, 600 years of human occupation of the Azores have led to the emergence of a large exotic species pool (60% of the current arthropod fauna, Borges et al., 2010), including many species able to cope with both anthropogenic and native habitats (e.g., Cardoso et al., 2013; Florencio et al., 2016). To some extent, it is possible that exotic species simply filled the ecological space not occupied by indigenous species. In low-intensity land-uses, historical factors and/or the extinction of disturbance-sensitive species (i.e., particularly those of comparatively large body size, Terzopoulou, Rigal, Whittaker, Borges, & Triantis, 2015) might have led to ecological niche space being vacated, while it is evident that unoccupied spaces in high-intensity land-uses were made available for exotics due to the inability of indigenous species to persist in them. It is also likely that some indigenous species have been wiped out, especially from high-intensity land-uses due to interactions (competition, predation) with exotic species (Cardoso, Arnedo, Triantis, & Borges, 2010). It is also entirely plausible that some indigenous species may have been driven to extinction without ever having been scientifically documented (e.g., Cardoso et al., 2010).

5 | CONCLUSION

Although arthropods play important functional roles in both natural and anthropogenic habitats (Isaacs et al., 2009; Losey & Vaughan, 2006), trait-based studies on arthropod assemblages are scarce and, as far as we are aware, our study is the first to formally assess the impact of land-use changes on the functional trait structure of both indigenous and exotic elements of arthropod assemblages.

In Terceira Island, the establishment of novel habitats as a result of human activities has led to the formation of novel biotic assemblages in which indigenous and exotic species coexist. Our results clearly showed that, within these novel assemblages, exotic species differed in their functional profile from indigenous species, suggesting that exotic species might play important roles in providing and maintaining some key ecosystem functions, particularly in high-intensity

land-uses. To what degree these assemblages are self-sustaining and stable remains, however, unknown, emphasizing the need for long-term studies to reliably assess the functional trajectory of those assemblages. Future studies will also need to integrate data on other components of the arthropod communities, such as plant-dweller and sedentary species in order to better understand the functioning and the role of these newly built arthropod assemblages in both low- and high-intensity land-uses.

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All the authors are interested in understanding the processes that shape Azorean arthropod biodiversity through a range of approaches, including molecular biology, taxonomy, community ecology and biogeography.

Author contributions: F.R., P.C. and P.A.V.B. conceived the ideas. P.A.V.B., P.C. and I.R.A. collected the data; F.R. analysed the data; F.R. led the writing. P.C., P.A.V.B., I.R.A., J.M.L., K.A.T. and R.J.W. provided ideas, critique, revisions and guidance at all steps of the writing process.

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

How to cite this article: Rigal F, Cardoso P, Lobo JM, et al. Functional traits of indigenous and exotic ground-dwelling arthropods show contrasting responses to land-use change in an oceanic island, Terceira, Azores. *Divers Distrib*. 2017;00:1–12. https://doi.org/10.1111/ddi.12655