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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Running head: Functional traits of indigenous and exotic arthropods

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 species in low intensity land-uses, while small-bodied spiders dominated exotics 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,

52 exotic species differed in their functional profile from indigenous species in all land-
53 use types. Overall, our results provide new insights into the functional role of exotic
54 species in a land-use context, suggesting that, in agricultural landscape, exotic species
55 may contribute positively to the maintenance of some ecosystem functions.
56

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) (Diaz, Fargione, Chapin & Tilman, 2006; Flynn et al., 2009; Brown et al., 2013; Forrest, Thorp, Kremen & Williams, 2015). Land-use changes frequently promote 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 changes 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 (Rodgers & Parker, 2003; Didham, Tylianakis, Gemmell, Rand & Ewers, 2007; Hobbs, Sayre & Gupta, 2008).

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 changes (e.g. Aslan, Zavaleta, Tershy, Croll & Robichaux, 2012). 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 fulfill similar functional roles (Olden & Rooney, 2006; Drenovsky et al., 2012).

Arthropods are the most diverse group of organisms and form also 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 (Hendrickx et al., 2007, Attwood, Maron, House & Zammit, 2008), 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 (Losey & Vaughn, 2006; Isaacs, Tuell, Fiedler, Gardiner & Landis, 2009), there has been relatively little trait-based analysis of these functions compared to plants or vertebrates (Kenis et al., 2009; Diekotter, Wamser, Wolters & Birkhofer, 2010). 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 of 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 fertilisation (Borges et al., 2006; Cardoso et al., 2009). Indigenous and exotic species have been shown to co-occur at the local scale 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). 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).

This study expands on previous works on the impact of land-use change on arthropod assemblages in the Azores (Borges, Ugland, Dinis & Gaspar, 2008; Cardoso et al., 2009; Meijer, Whittaker & Borges, 2011; Florencio, Cardoso, Lobo, Azevedo & Borges, 2013; Florencio, Lobo, Cardoso, Almeida-Neto & Borges, 2015; Florencio et al. 2016; Rigal, Whittaker, Triantis & Borges, 2013), and by focusing on traits allows for stronger inferences on the functional processes that might control the respective role of indigenous and exotic species in community assembly in the Azores.

METHODS

Study area

The Azores (37° to 40° N; 25° to 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: (i) native forests, (ii) exotic forests (*Cryptomeria japonica* and *Eucalyptus globulus* monoculture plantations, monocultures and mixed forest of the invasive *Pittosporum undulatum*); (iii) 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 (iv) 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

157 forest, (2) exotic forest, (3) semi-natural pasture and (4) intensively managed pasture.
158 Exotic forests were considered as the closest to the native forest since, contrary to
159 pastures, they maintain some of the architectural and microclimatic conditions of the
160 natural forests (Cardoso et al., 2009, Cardoso, Rigal, Fattorini, Terzopoulou &
161 Borges, 2013).
162
163 **Sampling methodology**
164 Nine sampling sites were established in each of the four land-use types (total = 36),
165 distributed across the island without regard to the character of the surrounding land-
166 use matrix. Sampling sites were on average 1.6 Km (range 0.137–3.7) apart from each
167 other and 0.73 Km apart (0.13–3.8) from the edge of the sampled land-use type (Table
168 S1.2 and Fig. S1.1). The ground-dwelling fauna was sampled at each site using 30
169 pitfall traps, spaced 5 m apart, along a 150 m transect. Traps were left in the field for
170 two weeks in the summer months of June, July or September of different years (native
171 forests between 1999 and 2003, and the other habitats in 2008 and 2009). A potential
172 effect of the sampling years on species compositions across sites were discarded by a
173 between-year analysis using additional data (Florencio et al., 2013). The majority of
174 captured arthropods (excluding Crustacea, Collembola, Diplura, Diptera and
175 Hymenoptera) were sorted to species level; the remaining specimens were sorted to
176 morphospecies. All species were classified as indigenous or exotic. Indigenous
177 species comprise Azorean endemics and other native non-endemics. Exotic species
178 are those considered to have colonized via human mediation, many of which having a
179 cosmopolitan distribution (Borges et al., 2010 and see Appendix S1 for furthers
180 details in species classification).

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

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 Vieira & Borges, 1993 and Borges & Vieira, 1994), 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.

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 & Daniel (2009). To assess clustering of species in trait space per site, we computed the mean pairwise functional distance (MFD), i.e. the averaged functional distance between all pairs of species co-occurring in a site (Webb, Ackerly, McPeek & Donoghue, 2002). To account for abundance 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 square 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 by using Magee's pseudo-R^2 (Magee, 1990). When the overall GLS model was statistically significant, the Tukey's *post hoc* test was used to identify statistically significant pairwise differences between land-uses.

To test if 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} indicate that species occurring together in a site are less functionally related than expected by chance (functionally overdispersed) while negative SES_{MFD} indicate 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 arthropods 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 was 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, multi-choice 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 non-parametric permutational multivariate analysis of variance (PerMANOVA; Anderson, 2001) to test for difference in trait attributes composition among land-uses. PerMANOVA was performed using permutation tests with 9999 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 vs. exotic) and land-uses using a Bray-Curtis distance matrix computed by combining the indigenous and exotics “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 non-metric 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}, De Caceres &

279 Legendre, 2009) to test the correlation between each CWM and the four land-use
280 separately using a binary coding for land-uses, with 1 and 0 indicating whether sites
281 belong or not to the land-use under study. We calculated 95% confidence intervals for
282 r_{pb} values by bootstrapping the observed data 9999 times and considered values not
283 overlapping zero as significant.
284 Statistical analyses were implemented within the R programming environment (R
285 Development Core Team 2014) using the packages *vegan* (Oksanen et al., 2013),
286 *picante* (Kembel et al., 2010), *nlme* (Pinheiro, Bates, DebRoy & Sarkar, 2012),
287 *indicspecies* (De Caceres & Legendre, 2009) and *BAT* (Cardoso, Rigal & Carvalho,
288 2015). PERMANOVAs were performed using the software PRIMER v.6 (Anderson
289 et al., 2008).
290
291 **RESULTS**
292 A total of 20,800 soil-arthropod specimens were collected and 202 (morpho) species
293 were identified, representing 20 orders, 76 families and 161 genera. Of the 202
294 species, 86 were considered to be indigenous and 116 to be exotics (Appendix S2).
295 About 13% of the taxa were identified to morphospecies rather than species.
296 No spatial autocorrelation was detected in the residuals of the GLS models (Table
297 S4.1 in Appendix S4). Rarefied indigenous species richness decreased significantly
298 from low to high intensity land-uses (Fig. 1A and Table S4.2), while rarefied exotic
299 species richness increased (Fig. 1B and Table S4.2). Similar trends were observed for
300 the Simpson's index (See Fig. S4.1A, B and Table S4.2). MFD of indigenous species
301 decreased significantly from low to high intensity land-uses (Fig. 1C and Table S4.2).
302 For exotic species, MFD of semi-natural pastures was significantly lower than for
303 other land-use types but no other significant differences occurred (Fig. 1D and Table
304 S4.2). Both indigenous and exotic elements were significantly functionally

overdispersed in native forest (median $SES_{MFD} > 0$; Wilcoxon test, P=0.003 and P = 0.007 respectively, Fig. 1E, F). Indigenous species were significantly functionally clustered in intensively managed pastures (median $SES_{MFD} < 0$; Wilcoxon test, P=0.003, Fig. 1E) but not in semi-natural pastures (Wilcoxon test, P=0.07, Fig. 1E) while exotic species were significantly functionally clustered in both semi-natural pastures and intensively managed pastures (median $SES_{MFD} <0$ Wilcoxon test, P = 0.003 and P = 0.003 respectively, Fig. 1F). Neither indigenous nor exotic species showed significant deviation from the null expectation in exotic forest samples (Wilcoxon test, P = 0.73 and P = 0.12 respectively)

Trait composition significantly differed between land-uses for both indigenous and exotic species (PERMANOVA: $R^2 = 0.44$, pseudo-$F_{3,32} = 8.518$, $P <0.001$ and $R^2 = 0.76$, pseudo-$F_{3,32} = 33.741$, $P <0.001$ 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 ($P<0.05$, Table S4.3), except between semi-natural and intensively managed pastures for indigenous species (P = 0.056, 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 x land-uses: $R^2 = 0.324$, pseudo-$F_{3,64} = 28.317$, $P <0.001$). 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 ($P<0.05$, Table S4.3). This pattern was clearly evident in the NMDS plot (Fig. 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 (Fig. 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.

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).

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

354 Both indigenous and exotic elements were found to display significant trait-clustering
355 in high intensity land-uses, highlighting the fact that species were functionally more
356 similar than expected by chance in those land-uses. Overall, these findings are in
357 accordance with recent trait-based studies claiming that land-use intensification acts
358 as a filter, favouring a limited array of trait combinations (Flynn et al., 2009; Laliberté
359 et al., 2011). Specifically, for arthropods, our results confirm recent observations
360 made in a land-use change context for insect pollinators (Rader, Bartomeus,
361 Tylianakis & Laliberté, 2014), beetles (Birkhofer, Smith, Weisser, Wolters &
362 Gossner, 2015), bees (Forrest et al., 2015) and arthropods as a whole (Simons et al.,
363 2016).
364 For indigenous species, MFD values lower than expected by chance in intensively
365 managed land-uses (Fig. 1E) were coupled with a decline of species diversity,
366 indicating that functions were lost at a higher rate than would be predicted by chance
367 if species were lost randomly (Flynn et al., 2009). In contrast, exotic species richness
368 increased as land-use intensity increased, but this was accompanied by lower than
369 expected MFD values under high intensity land-uses (Fig. 1F). These results reveal a
370 degree of apparent functional redundancy within the exotic element of ground-
371 dwelling arthropod assemblages under high intensity land-uses, with more species
372 executing similar functions.
373 Interestingly, we found significant trait divergence in native forests for both
374 indigenous and exotic species (Fig. 1E-F). Although this pattern is usually interpreted
375 as the result of biotic interactions, typically competitive exclusion (Webb et al., 2002),
376 caution is needed with such an interpretation (de Bello, 2012). Since for the null
377 model analysis, we considered all the species found across the four land-uses as our
378 regional species pool, it is more likely that species distribution across these land-uses

may result predominantly from environmental constraints overpowering the importance of local species interactions (Münkemüller et al., 2013). It is possible that different outcomes would be produced if we down-scaled the species pool to a particular land-use (Münkemüller et al., 2013). 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.

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 land-use intensity. 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 pasture land-uses (Fig. 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 (Olesen,

404 Eskildsen & Venkatasamy, 2002; Kaiser-Bunbury, Traveset & Hansen, 2010) and are
405 usually explained as reflecting the relaxation of interspecific competition as
406 consequence of the young age and the isolation of such islands (Olesen et al., 2002).
407 An alternative and non-exclusive explanation is that some herbivorous species can
408 increase in abundance with habitat loss due to a reduction in specialist predator
409 populations (a top-down effect) (Ryall & Fahrig, 2006). The directional shift towards
410 herbivore-dominated elements was accompanied by a correspondingly low relative
411 abundance of carnivorous species in intensively-managed pastures (Fig. 3). This is in
412 accordance with several previous studies that have reported that high trophic-level
413 arthropod taxa were relatively sensitive to environmental stress (e.g. Holt, 1996,
414 Pearce & Venier, 2006). Web-building spiders in particular, often being dependent on
415 substantial habitat structure and vegetation architecture to anchor their webs (e.g.
416 Samu, Sunderland & Szinetar, 1999), cannot find suitable sites when clear-cutting or
417 establishment of pastures destroy all trees. Also, some Chilopoda species are known
418 to display strong preferences for low temperatures and high humidity (conditions
419 encountered in native and exotic forest). Examples include species of *Lithobius*
420 (Lewis, 2006), one of which, *Lithobius pilicornis pilicornis* (Lithobiidae; native), was
421 found to be abundant in forest but almost absent in pastures (Appendix S2). From a
422 bottom-up perspective, predator populations could have also been indirectly and
423 negatively affected by the decline of their prey populations (Ryall & Fahrig, 2006).
424 We also found a significant correlation between high dispersal ability and high
425 intensity land-uses for indigenous species (Fig. 3). This suggests the hypothesis that
426 pastures act as sinks for forest-associated species, with only the good dispersers being
427 able to colonize them from native forest patches (Borges et al, 2008). Native forest is
428 particularly characterised 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 (Fig. 3). Native forest provides abundant resources for herbivorous species, thereby allowing the successful establishment of exotic herbivores. Moreover, since 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-use was accompanied by a clear pattern of functional redundancy (Fig. 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

454 genera in particular, are mostly *r*-selected species, which are tiny (≈ 2 mm), efficient
455 dispersers, often with multiple generations per year (Bell, Wheater & Cullen, 2001).
456 These features may therefore confer strong advantages in the re-colonization of
457 pasture lands after intensive grazing and mowing (Tscharntke, Klein, Kruess, Steffan-
458 Dewenter & Thies, 2005). The dominance of exotic Linyphiids could also be due to
459 the wide availability of prey. However, Linyphiids mainly feed on Collembola,
460 Diptera and Hymenoptera (Agusti et al., 2003), three orders that were not considered
461 in our study.
462
463 **Potential mechanisms involved in functional structure of both indigenous and**
464 **exotic elements**
465 Our study clearly shows that indigenous and exotic species display opposing
466 functional profiles across land-use types. There could be multiple alternative
467 underlying mechanisms for this pattern. Prior to human colonization, the native forest
468 in the archipelago acted as a filter, selecting species that were able to establish, some
469 of which subsequently speciated in the archipelago. Hence the indigenous species
470 pool did not probably include species pre-adapted to pasturelands and in this regard,
471 generalist herbivores may be the exceptions. However, 600 years of human
472 occupation of the Azores have led to the emergence of a large exotic species pool
473 (60% of the current arthropod fauna, Borges et al., 2010), including many species able
474 to cope with both anthropogenic and native habitats (e.g. Cardoso et al., 2013;
475 Florencio et al., 2016). To some extent it is possible that exotic species simply filled
476 the ecological space not occupied by indigenous species. In low land-use intensity,
477 historical factors and/or the extinction of disturbance-sensitive species (i.e.
478 particularly those of comparatively large body size, Terzopoulou, Rigal, Whittaker,

479 Borges & Triantis, 2015) might have led to ecological niche space being vacated,
480 while it is evident that unoccupied spaces in high land-use intensity were made
481 available for exotics due to the inability of indigenous species to persist in them. It is
482 also likely that some indigenous species have been wiped out, especially from high-
483 intensity land-uses due to interactions (competition, predation) with exotic species
484 (Cardoso, Arnedo, Triantis & Borges, 2010). It is also entirely plausible that some
485 indigenous species may have been driven to extinction without ever having been
486 scientifically documented (e.g. Cardoso et al., 2010).
487
488 **CONCLUSION**
489 Although arthropods play important functional roles in both natural and
490 anthropogenic habitats (Losey & Vaughn, 2006; Isaacs et al., 2009), trait-based
491 studies on arthropod assemblages are scarce and, as far as we are aware, our study is
492 the first to formally assess the impact of land-use changes on the functional trait
493 structure of both indigenous and exotic elements of arthropod assemblages.
494 In Terceira Island, the establishment of novel habitats as a result of human activities
495 has led to the formation of novel biotic assemblages in which indigenous and exotic
496 species co-exist. Our results clearly showed that, within these novel assemblages,
497 exotic species differed in their functional profile from indigenous species, suggesting
498 that exotic species might play important roles in providing and maintaining some key
499 ecosystem functions, particularly in high-intensity land-uses. To what degree these
500 assemblages are self-sustaining and stable remains, however, unknown, emphasizing
501 the need for long-term studies to reliably assess the functional trajectory of those
502 assemblages. Future studies will also need to integrate data on other components of
503 the arthropod communities, such as plant-dweller and sedentary species in order to

504 better understand the functioning and the role of these newly built arthropod
505 assemblages in both low and high intensity land-uses.
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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the sup-porting information tab for this article.

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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.

BIOSKETCH

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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.

796 **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[1]) vs 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 colonisation/re-colonisation.
Type of food	Multi-choice 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[1]) vs 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 micro-scale 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	Multi-choice 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 micro-habitats, which are less favourable for species with day activity.

797 [1] Attributes used in the CWM analysis to avoid collinearity

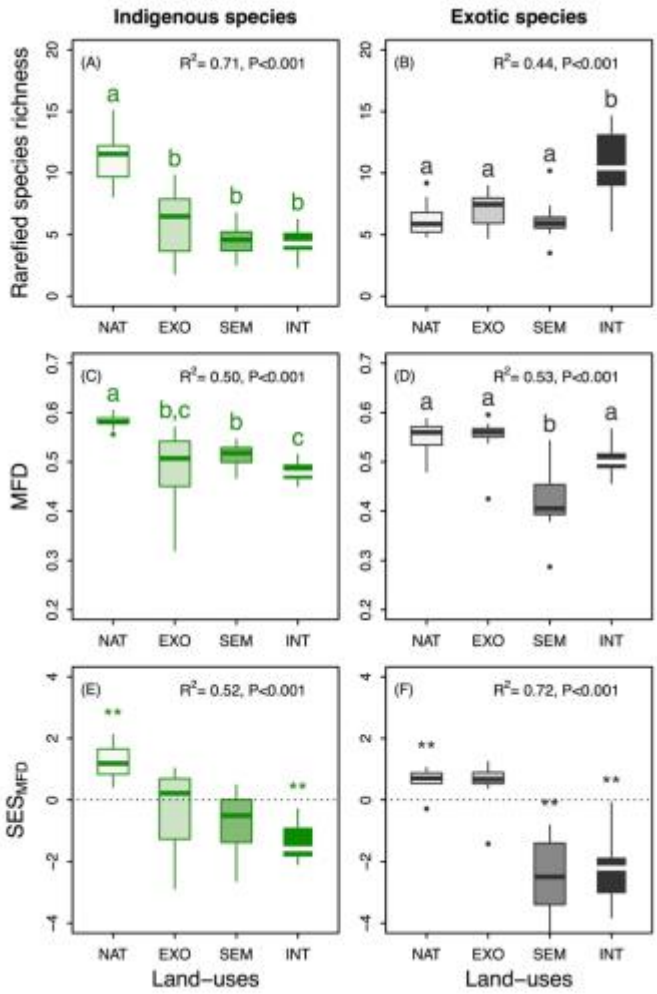

Figure 1. Rarefied species richness (A, B), mean pairwise functional distance **(**MFD) (C, D) and standardized effect sizes of MPD (SES_{MFD}) (E, F) across the four land-use types for both indigenous (A, C, E) and exotic arthropod elements (B, D, F) in Terceira Island. The Magee 's pseudo-R^2 and the *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; $P < 0.05$, see Table S4). For the SES_{MFD} values, asterisks indicate significant deviations from 0 according to the Wilcoxon test with $^{**}P < 0.01$. 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.

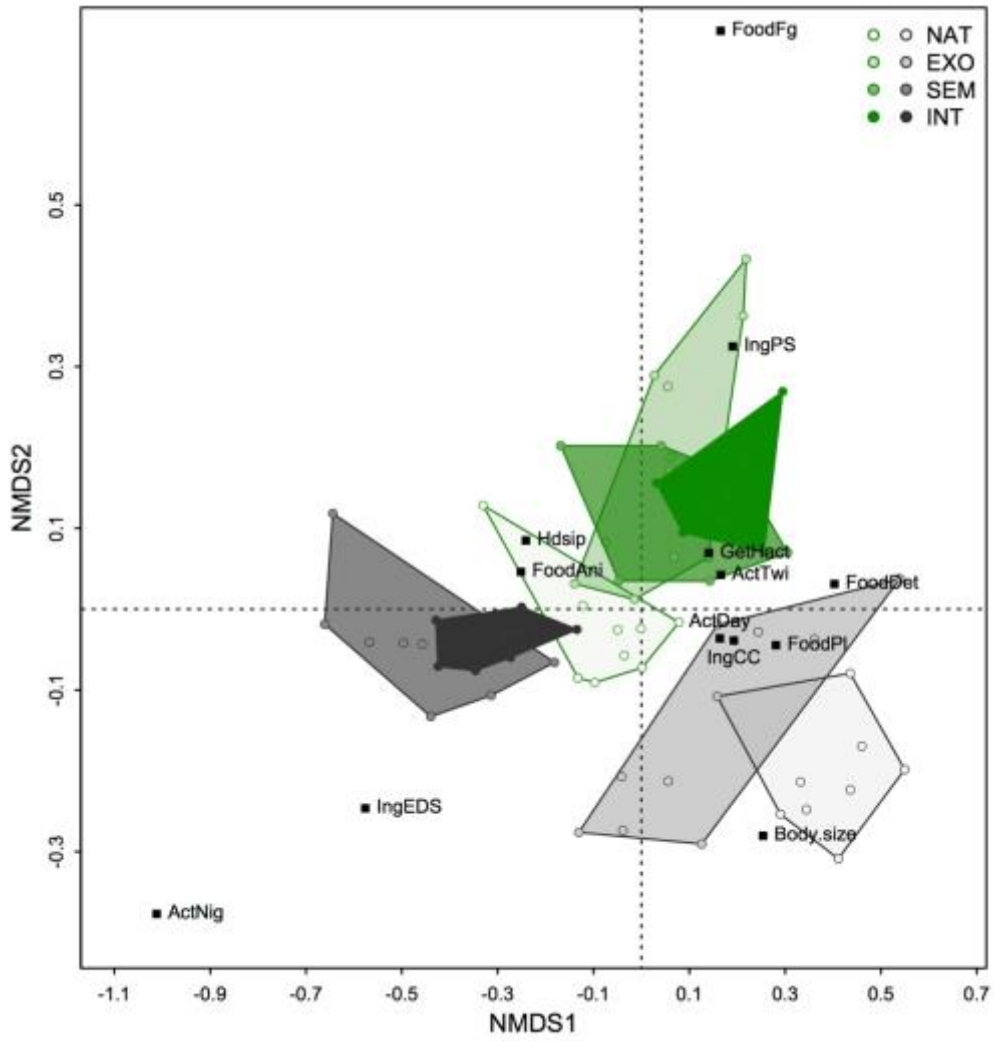

Figure 2. Two-dimensional ordination solution using non-metric multidimensional scaling (NMDS) based on the Bray-Curtis distance computed by combining the "community-weighted mean (CWM) x sites" matrices of indigenous and exotic arthropod elements across the land-use gradient in Terceira island. Dots 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 transformation and use, 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.

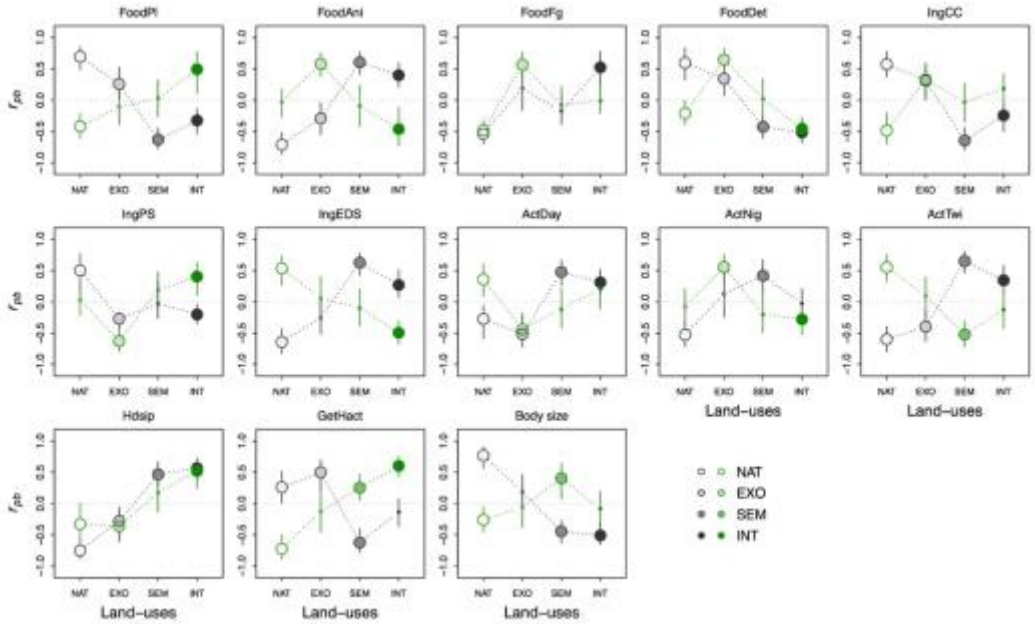

Figure 3. Results of the indicator analysis showing correlations between trait attributes (CWM) and land-uses for both indigenous and exotic arthropod species in Terceira Island. Correlations were computed using point-biserial correlation coefficients (r_{pb}) between CWM and each land-use separately 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 9999. 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 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.

SUPPORTING INFORMATION

Rigal, F., Cardoso, P., Lobo, J.M., Triantis, K.A., Whittaker, R.J., Amorim, I.R. and Borges, P.A.V. Functional traits of indigenous and exotic ground-dwelling arthropods show contrasting responses to land-use change in an oceanic island, Terceira, Azores.

Appendix S1. Sampling details across transects, taxonomical identifications and features of the four land-use types.

Nine sites (our sampling units) were randomly selected in each of the land-uses (n = 36). Detailed features of each land-use are given in Table S1.1 and a land-use distribution map on the Terceira Island is provided in Figure S1 based on the Cartographic information from DROTRH (2008) and Gaspar (2007). Information on spatial distribution of the sampling sites is given in Table S1.2 and in Figure S1.1

The sites in native forests were sampled during summer between 1999 (one site) and 2003 (8 sites) (Borges et al., 2005). Data were collected in the other three habitats during the summer of 2008 (see Cardoso et al., 2009). In each site, a transect of 150 m was set up with of 30 pitfall traps spaced 5 m apart. The pitfall traps were plastic cups with diameters of 42 mm and depths of 78 mm; they were buried in the ground so that the rims of the cups were level with the surface. For each transect, half of the traps were filled with approximately 60 ml of an antifreeze liquid (diluted ethylene glycol), and the other half were filled with the same volume of an attractive Turquin solution made of dark beer, and for each litre of beer, 10 g of chloral hydrate, 5 ml formalin and 5ml glacial acetic acid. The ethylene and Turquin traps were alternated in each transect. Traps were left in the field for 2 weeks. The arthropods collected in the traps were preserved at 70% ethanol for identification in the laboratory at the species level for the taxa Araneae, Opiliones, Pseudoscorpiones, Diplopoda, Chilopoda and Insects (excluding Collembola, Diplura, Diptera and Hymenoptera). Taxonomic identification was performed in two steps: i) trained parataxonomists sorted samples into morphospecies (or RTUs, i.e. recognizable taxonomic units, sensu Oliver & Beattie 1996) using a non-complete reference collection; ii) experienced taxonomists assisted in the identification of the morphospecies: Andrew Polaszek, António Bivar Sousa, Artur Serrano, Arturo Baz, Fernando Ilharco, Henrik Enghoff, Jordi Ribes, José Quartau, Jörg Wunderlich, Mário Boieiro, Ole Karsholt, Richard zur Strassen, Volker Assing, Volker Manhert and Virgílio Vieira.

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). As in some of our previous studies (e.g. Borges et al., 2005, Gaspar, Borges & Gaston, 2008), we dealt with unidentified morphospecies as follows. When other species in the same genus, subfamily or family were present in the archipelago and all belonged to the same colonization category (according to Borges et al.,

2010), the unknown morphospecies were classified similarly. If no information was available, we assumed the species to be native since exotics are usually widespread and easier to identify (Borges et al., 2010).

Table S1.1. Features of land-use types

Land-use (Rank)	Type of disturbance	Disturbance intensity/frequency	Types of vegetation	Complexity of habitats for epigean arthropods
Native forest (1) 	Subject to a very low degree of, or no, human management. In some sites, occurrence of invasive plants with modification of soil cover (decreasing the cover of mosses and ferns)	Generally low, but variable depending on the spread of invasive plant species	*Juniperus brevifolia Laurus azorica, Ilex perado* subsp *azorica*, *Erica azorica*	The evergreen native forest of the Azores is complex in architecture and offers a great variety of substrates for epigean arthropods. Most remnant patches are characterized by a dense tree and shrub cover of small stature.
Exotic forest (2) 	Subject to some human management and sensitivity to wind-storms	Low to medium depending on management type	*Cryptomeria japonica* and *Eucalyptus globulus*	Medium to low if the understory is completely absent.
Semi-natural pastures (3) 	Cattle grazing activity concentrated mainly in spring and particularly in summer. Fertilizers are added in Spring by hand or in some specifically large sites using machinery.	Medium	*Lotus uliginosus* + exotic and native grasses, rushes, sedges and ferns.	Medium, depending on soil characteristics. Some sites can be badly drained, with the formation of "hummocks" as an adaptation of plants to periodic flooding, topographic conditions, cattle trampling or a combination of some of the former together with a fortuitous result of the morphology of some of the dominant species.
Intensive-managed pastures (4) 	Cattle grazing and fertilization. In the summer some sites are used for frequent hay cut or corn production. Fertilizers are added using machinery	High	Poor vascular flora of dominant species, mainly composed of introduced grasses and leguminous forbs	Uniform monocultures with low complexity.

Table S1.2. Information on the spatial distribution of the 36 sites sampled in this study. For each site, the distance to the closest site and the distance from the edge of the sampled land-use type as well as its geographical coordinates (Longitude and Latitude) and the land-use type. Land-use types are ranked according to their intensity uses 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).

Site Code	Distance to the closest site (m)	Distance from the edge of the sampled land-use type (m)	Longitude	Latitude	Land-use types
T-46	783	130	38.73339	-27.28363	NAT
T-57	1818	160	38.75712	-27.3086	NAT
T-7	1243	506	38.73908	-27.29111	NAT
TE-45	2613	677	38.73864	-27.29475	NAT
TE-48	872	168	38.75121	-27.33176	NAT
TE-49	1223	1266	38.74745	-27.31885	NAT
TE-50	3432	905	38.75499	-27.31732	NAT
TY-5	2232	250	38.72592	-27.32619	NAT
TY-6	2039	190	38.75057	-27.33285	NAT
T-25	406	150	38.72638	-27.22258	EXO
T-26	340	180	38.7252	-27.22912	EXO
T-36	733	157	38.73765	-27.13682	EXO
T-37	1818	170	38.74598	-27.1343	EXO
T-62	872	152	38.73981	-27.2657	EXO
T-63	783	150	38.73186	-27.28639	EXO
T-64	3727	140	38.68872	-27.25919	EXO
T-65	765	158	38.76637	-27.2494	EXO
T-66	990	164	38.75594	-27.18915	EXO
T-61	1833	200	38.75454	-27.20551	SEM
T-67	3390	157	38.73399	-27.22935	SEM
T-69	2049	180	38.70443	-27.20951	SEM
T-72	3261	900	38.71488	-27.32124	SEM
T-73	340	935	38.72635	-27.26478	SEM
T-76	2234	150	38.73714	-27.25905	SEM
T-77	137	718	38.70727	-27.23324	SEM
T-78	765	873	38.70962	-27.25162	SEM
T-86	872	329	38.72529	-27.17557	SEM
T-70	2464	1855	38.76603	-27.14744	INT

T-74	1223	2600	38.67475	-27.3074	INT
T-75	2191	1000	38.71507	-27.10464	INT
T-80	406	1487	38.78593	-27.29137	INT
T-81	733	870	38.67444	-27.14455	INT
T-82	3085	695	38.75131	-27.10527	INT
T-83	3594	3800	38.66696	-27.10976	INT
T-87	2191	2900	38.69309	-27.13394	INT
T-90	137	934	38.69633	-27.31322	INT

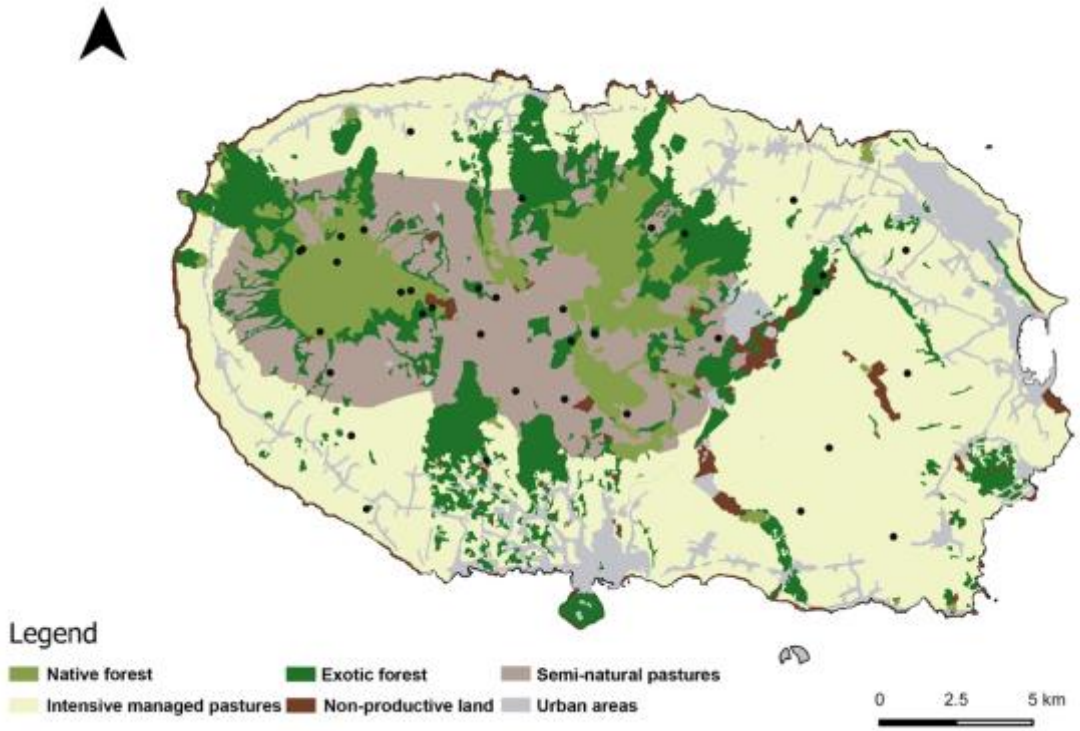

Figure S1.1. Land-use distribution map of Terceira Island with the selected sampling sites. Sampling sites are marked with black dots.

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Appendix S2. Indigenous and exotic species sampled across the four land-uses considered in the study. Species taxonomy, species origin, trait attributes and mean abundance per land-use are given. Traits and their associated attributes are: Body size in (mm); Dispersal abilities (Disp) with; Type of food with Plants (FoodPl); Animals (FoodAni); Fungi (FoodFg); Detritus (FoodDet); Way of getting food (Get) with High active search (GetHact) vs low active search (GetLact); Mode of ingestion (Ing) with Chewing and cutting (IngCC); Piercing and sucking (IngPS); External digestion and sucking (IngEDS) and period of activities with Day (ActDay); Night (ActNig); Twilight (ActTwi). See Table 1 in main text for ecological relevance of the traits. Land-use types are ranked according to their intensity uses with NAT = native forest, EXO = exotic forest, SEM = semi-natural pastures and INT = intensive managed pastures. See Table S1 for detailed land-use features.

Taxonomy and species origin					Functional traits and their associated attributes											Land-uses			
Class	Order	Family	Species	Origin	Body size	Disp	FoodPl	FoodAni	FoodFg	FoodDet	Get	Ing	ActDay	ActTwi	ActNig	NAT	EXO	SEM	INT
Arachnida	Araneae	Agelenidae	*Lycosoides coarctata*	Exo	7	Hdisp	0	1	0	0	GetLact	IngEDS	0	0	0	0	0	0	0.11
Arachnida	Araneae	Dysderidae	*Dysdera crocata*	Exo	13	Ldisp	0	1	0	0	GetHact	IngEDS	0	0	1	1.78	4.67	0	0.89
Arachnida	Araneae	Gnaphosidae	*Zelotes aeneus*	Exo	6	Hdisp	0	1	0	0	GetHact	IngEDS	0	0	1	0.00	0.00	0	3.00
Arachnida	Araneae	Linyphiidae	*Agyneta decora*	Exo	2.75	Hdisp	0	1	0	0	GetLact	IngEDS	0	0	0	0.56	1.78	1.22	0
Arachnida	Araneae	Linyphiidae	*Erigone atra*	Exo	2.4	Hdisp	0	1	0	0	GetLact	IngEDS	0	0	0	0	0.11	7.78	1.00
Arachnida	Araneae	Linyphiidae	*Erigone autumnalis*	Exo	2.2	Hdisp	0	1	0	0	GetLact	IngEDS	0	0	0	0	0.44	8.44	39.89
Arachnida	Araneae	Linyphiidae	*Erigone dentipalpis*	Exo	2.3	Hdisp	0	1	0	0	GetLact	IngEDS	0	0	0	0	0	19.00	56.78
Arachnida	Araneae	Linyphiidae	*Meioneta fuscipalpa*	Exo	1.9	Hdisp	0	1	0	0	GetLact	IngEDS	0	0	0	0	0	0.11	18.67
Arachnida	Araneae	Linyphiidae	*Mermessus bryantae*	Exo	2.2	Hdisp	0	1	0	0	GetLact	IngEDS	0	0	0	0.22	0	2.44	2.89
Arachnida	Araneae	Linyphiidae	*Mermessus fradeorum*	Exo	2.2	Hdisp	0	1	0	0	GetLact	IngEDS	0	0	0	0	0.33	3.78	0.44
Arachnida	Araneae	Linyphiidae	*Microlinyphia johnsoni*	Exo	4	Hdisp	0	1	0	0	GetLact	IngEDS	0	0	0	0	0.11	0	0
Arachnida	Araneae	Linyphiidae	*Oedothorax fuscus*	Exo	2.75	Hdisp	0	1	0	0	GetLact	IngEDS	0	0	0	0	0.67	543.67	489.11
Arachnida	Araneae	Linyphiidae	*Ostearius melanopygius*	Exo	2.3	Hdisp	0	1	0	0	GetLact	IngEDS	0	0	0	0	0	0.56	7.22
Arachnida	Araneae	Linyphiidae	*Pelecopsis parallela*	Exo	1.65	Hdisp	0	1	0	0	GetLact	IngEDS	0	0	0	0	0	0	3.11
Arachnida	Araneae	Linyphiidae	*Prinerigone vagans*	Exo	2.1	Hdisp	0	1	0	0	GetLact	IngEDS	0	0	0	0	0	0.89	6.44
Arachnida	Araneae	Linyphiidae	*Tenuiphantes tenuis*	Exo	2.65	Hdisp	0	1	0	0	GetLact	IngEDS	0	0	0	2.78	8.00	4.78	5.56
Arachnida	Araneae	Mimetidae	*Ero furcata*	Exo	2.88	Ldisp	0	1	0	0	GetLact	IngEDS	0	0	1	0.11	0.67	0	0.11
Arachnida	Araneae	Oecobiidae	*Oecobius navus*	Exo	2	Ldisp	0	1	0	0	GetLact	IngEDS	0	0	0	0.11	0	0	0

Arachnida	Araneae	Salticidae	*Gen. sp.1*	Exo	2.95	Hdisp	0	1	0	0	GetHact	lngEDS	1	0	0	0	0	0	1.44
Arachnida	Araneae	Tetragnathidae	*Pachygnatha degeeri*	Exo	3.38	Hdisp	0	1	0	0	GetLact	lngEDS	0	0	0	0	0	1.33	9.56
Arachnida	Araneae	Theridiidae	*Cryptachaea blattea*	Exo	3	Hdisp	0	1	0	0	GetLact	lngEDS	0	0	1	0	0.33	0.11	0
Arachnida	Araneae	Theridiidae	*Steatoda grossa*	Exo	8.25	Hdisp	0	1	0	0	GetLact	lngEDS	0	0	1	0	0.11	0	0
Arachnida	Araneae	Thomisidae	*Xysticus nubilus*	Exo	7	Hdisp	0	1	0	0	GetLact	lngEDS	1	0	0	0	0	1.00	0.11
Arachnida	Pseudoscorpiones	Chthoniidae	*Chthonius ischnocheles*	Exo	2	Ldisp	0	1	0	0	GetHact	lngCC	0	0	0	5.11	2.67	0.22	0
Arachnida	Pseudoscorpiones	Chthoniidae	*Chthonius tetrachelatus*	Exo	1.61	Ldisp	0	1	0	0	GetHact	lngCC	0	0	0	0.44	0.33	0	0
Chilopoda	Scutigeromorpha	Scutigeridae	*Scutigera coleoptrata*	Exo	12.64	Ldisp	0	1	0	0	GetHact	lngCC	0	0	1	0	0	0	1.67
Diplopoda	Julida	Blaniulidae	*Blaniulus guttullatus*	Exo	6.83	Ldisp	1	0	0	1	GetHact	lngCC	0	0	1	0	48.56	0	0
Diplopoda	Julida	Blaniulidae	*Choneiulus palmatus*	Exo	10.43	Ldisp	1	0	0	1	GetHact	lngCC	0	0	1	0.11	0.00	0	0
Diplopoda	Julida	Blaniulidae	*Proteroiulus fuscus*	Exo	11.28	Ldisp	1	0	0	1	GetHact	lngCC	0	0	1	0	1.44	0	0
Diplopoda	Julida	Julidae	*Brachyiulus pusillus*	Exo	7.53	Ldisp	1	0	0	1	GetHact	lngCC	0	0	1	0	1.11	0	0
Diplopoda	Julida	Julidae	*Cylindroiulus propinquus*	Exo	37.44	Ldisp	1	0	0	1	GetHact	lngCC	0	0	1	5.44	0.67	0.11	0
Diplopoda	Julida	Julidae	*Ommatoiulus moreletii*	Exo	40.04	Ldisp	1	0	0	1	GetHact	lngCC	0	0	1	19.22	19.22	3.67	0.67
Diplopoda	Polydesmida	Paradoxosomatidae	*Oxidus gracilis*	Exo	16	Ldisp	0	0	0	1	GetHact	lngCC	0	0	1	0	0.11	0.11	0
Diplopoda	Polydesmida	Polydesmidae	*Brachydesmus superus*	Exo	6.62	Ldisp	0	0	0	1	GetHact	lngCC	0	0	1	0.11	0	0	0
Diplopoda	Polydesmida	Polydesmidae	*Polydesmus coriaceus*	Exo	25.38	Ldisp	0	0	0	1	GetHact	lngCC	0	0	1	0.78	3.00	0.22	0
Insecta	Coleoptera	Anthicidae	*Gen. sp.2*	Exo	2.63	Hdisp	1	1	1	0	GetHact	lngCC	0	0	0	0	0	0	0.44
Insecta	Coleoptera	Carabidae	*Amara aenea*	Exo	7	Hdisp	1	1	0	0	GetHact	lngCC	1	0	0	0	0	0.22	6.11
Insecta	Coleoptera	Carabidae	*Anisodactylus binotatus*	Exo	11	Hdisp	1	1	0	0	GetHact	lngCC	0	0	1	0	0.11	1.22	1.56
Insecta	Coleoptera	Carabidae	*Paranchus albipes*	Exo	10	Hdisp	0	1	0	0	GetHact	lngCC	0	0	1	4.44	2.00	0	0
Insecta	Coleoptera	Carabidae	*Pseudophonus rufipes*	Exo	13	Hdisp	1	1	0	0	GetHact	lngCC	0	0	1	0.00	0	0.33	3.33
Insecta	Coleoptera	Carabidae	*Pterostichus vernalis*	Exo	7	Hdisp	0	1	0	0	GetHact	lngCC	0	0	1	0	0.33	7.67	1.56
Insecta	Coleoptera	Chrysomelidae	*Chaetocnema hortensis*	Exo	2.01	Hdisp	1	0	0	0	GetHact	lngCC	1	0	0	0	0	0.11	8.89
Insecta	Coleoptera	Chrysomelidae	*Epitrix cucumeris*	Exo	1.85	Hdisp	1	0	0	0	GetHact	lngCC	1	0	0	0	0	0	0.67
Insecta	Coleoptera	Corylophidae	*Sericoderus lateralis*	Exo	0.5	Hdisp	0	0	1	0	GetHact	lngCC	1	0	0	0	0	0.11	1.11

Insecta	Coleoptera	Cryptophagidae	*Cryptophagus sp.1*	Exo	1.44	Hdisp	0	0	1	0	GetHact	lngCC	0	0	0	0	0	0.44	2.78
Insecta	Coleoptera	Cryptophagidae	*Cryptophagus sp.8*	Exo	1.64	Hdisp	0	0	1	0	GetHact	lngCC	0	0	0	0	0	0.11	0.11
Insecta	Coleoptera	Cryptophagidae	*Cryptophagus sp.9*	Exo	2.2	Hdisp	0	0	1	0	GetHact	lngCC	0	0	0	0	0.11	0.11	0.44
Insecta	Coleoptera	Curculionidae	*Coccotrypes carpophagus*	Exo	2	Hdisp	1	0	0	0	GetHact	lngCC	0	0	0	0.11	1.22	0	0
Insecta	Coleoptera	Curculionidae	*Gymnetron pascuorum*	Exo	2.44	Hdisp	1	0	0	0	GetHact	lngCC	1	0	0	0	0	0	0.11
Insecta	Coleoptera	Curculionidae	*Otiorhynchus rugosostriatus*	Exo	11.62	Ldisp	1	0	0	0	GetHact	lngCC	0	0	1	0	0.33	0	0
Insecta	Coleoptera	Curculionidae	*Otiorhynchus sulcatus*	Exo	7	Ldisp	1	0	0	0	GetHact	lngCC	0	0	1	0	0.11	0	0
Insecta	Coleoptera	Curculionidae	*Pantomorus cervinus*	Exo	9.75	Ldisp	1	0	0	0	GetHact	lngCC	0	0	1	0	0	0.11	0
Insecta	Coleoptera	Curculionidae	*Sitona discoideus*	Exo	5.79	Hdisp	1	0	0	0	GetHact	lngCC	0	1	0	0	0	0.44	4.67
Insecta	Coleoptera	Curculionidae	*Sitona puberulus*	Exo	6	Hdisp	1	0	0	0	GetHact	lngCC	0	1	0	0	0	0.11	0
Insecta	Coleoptera	Curculionidae	*Sitona sp.1*	Exo	4.27	Hdisp	1	0	0	0	GetHact	lngCC	0	1	0	0	0	1.56	17.22
Insecta	Coleoptera	Curculionidae	*Sitona sp.3*	Exo	4.74	Hdisp	1	0	0	0	GetHact	lngCC	0	1	0	0	0	3.22	0.22
Insecta	Coleoptera	Curculionidae	*Tychius picirostris*	Exo	2	Hdisp	1	0	0	0	GetHact	lngCC	1	0	0	0	0	0.00	0.56
Insecta	Coleoptera	Curculionidae	*Xyleborinus alni*	Exo	3.14	Hdisp	0	0	1	0	GetHact	lngCC	0	0	0	0	0	0.56	0.22
Insecta	Coleoptera	Dryophthoridae	*Sphenophorus abbreviatus*	Exo	10.45	Ldisp	1	0	0	0	GetHact	lngCC	0	0	0	0	0.11	0.56	1.11
Insecta	Coleoptera	Elateridae	*Aeolus melliculus*	Exo	8	Hdisp	1	0	0	0	GetHact	lngCC	0	0	1	0	0	0	0.78
Insecta	Coleoptera	Elateridae	*Heteroderes vagus*	Exo	6.55	Hdisp	1	0	0	0	GetHact	lngCC	0	0	1	0	0	0	8.22
Insecta	Coleoptera	Hydrophilidae	*Cercyon haemorrhoidalis*	Exo	2	Hdisp	0	0	0	1	GetHact	lngCC	0	0	0	0.22	0	0.11	0
Insecta	Coleoptera	Hydrophilidae	*Cercyon sp.1*	Exo	2.22	Hdisp	0	0	0	1	GetHact	lngCC	0	0	0	0	0	0.11	0
Insecta	Coleoptera	Hydrophilidae	*Cercyon sp.2*	Exo	2.43	Hdisp	0	0	0	1	GetHact	lngCC	0	0	0	0	0	0.11	0
Insecta	Coleoptera	Hydrophilidae	*Sphaeridium bipustulatum*	Exo	4	Hdisp	0	0	0	1	GetHact	lngCC	0	0	0	0	0	0.11	0.22
Insecta	Coleoptera	Mycetophagidae	*Typhaea stercorea*	Exo	2.27	Hdisp	0	0	1	0	GetHact	lngCC	1	0	0	0	0	0	22.44
Insecta	Coleoptera	Nitidulidae	*Carpophilus fumatus*	Exo	3.65	Hdisp	1	0	0	0	GetHact	lngCC	1	0	0	0	0	0.11	0.56
Insecta	Coleoptera	Nitidulidae	*Carpophilus hemipterus*	Exo	3.22	Hdisp	1	0	0	0	GetHact	lngCC	1	0	0	0	0	0	0.11
Insecta	Coleoptera	Nitidulidae	*Carpophilus sp.1*	Exo	2.42	Hdisp	1	0	0	0	GetHact	lngCC	1	0	0	0	0	0.11	0.22
Insecta	Coleoptera	Nitidulidae	*Epuraea biguttata*	Exo	2.98	Hdisp	1	0	1	0	GetHact	lngCC	1	0	0	0	0.78	0.11	0.89

Insecta	Coleoptera	Nitidulidae	*Phenolia limbata*	Exo	5.95	Hdisp	1	0	1	0	GetHact	lngCC	1	0	0	0	12.89	0	0
Insecta	Coleoptera	Nitidulidae	*Stelidota geminata*	Exo	2.17	Hdisp	1	0	0	0	GetHact	lngCC	1	0	0	0.11	12.78	0	0.56
Insecta	Coleoptera	Ptiliidae	*Ptenidium pusillum*	Exo	1	Hdisp	0	0	1	0	GetHact	lngCC	0	0	0	0	0	0.33	0.11
Insecta	Coleoptera	Scarabaeidae	*Gen. sp.1*	Exo	4.19	Hdisp	1	0	0	0	GetHact	lngCC	1	0	0	0	0	0	0.11
Insecta	Coleoptera	Scarabaeidae	*Onthophagus taurus*	Exo	7.82	Hdisp	1	0	0	0	GetHact	lngCC	0	0	0	0	0	0.33	0
Insecta	Coleoptera	Scarabaeidae	*Popillia japonica*	Exo	11	Hdisp	1	0	0	0	GetHact	lngCC	1	0	0	0	0	0.11	0.11
Insecta	Coleoptera	Silvanidae	*Cryptamorpha desjardinsii*	Exo	4	Hdisp	0	0	1	0	GetHact	lngCC	0	0	1	0	0	0	0.11
Insecta	Coleoptera	Staphylinidae	*Aleochara bipustulata*	Exo	3	Hdisp	0	1	0	0	GetHact	lngCC	0	0	1	0.11	0	0.44	2.11
Insecta	Coleoptera	Staphylinidae	*Amischa analis*	Exo	3	Hdisp	0	1	0	0	GetHact	lngCC	0	0	1	0	0	2.56	3.44
Insecta	Coleoptera	Staphylinidae	*Anotylus nitidifrons*	Exo	2	Hdisp	0	1	0	0	GetHact	lngCC	0	0	1	0	22.78	0.33	0.33
Insecta	Coleoptera	Staphylinidae	*Carpelimus corticinus*	Exo	3.02	Hdisp	0	1	0	0	GetHact	lngCC	0	0	1	0.56	0	0	0
Insecta	Coleoptera	Staphylinidae	*Atheta atramentaria*	Exo	3	Hdisp	0	1	0	0	GetHact	lngCC	0	0	1	3.89	0.33	0.00	0
Insecta	Coleoptera	Staphylinidae	*Atheta fungi*	Exo	3	Hdisp	0	1	0	0	GetHact	lngCC	0	0	1	0	0.22	0.00	0.44
Insecta	Coleoptera	Staphylinidae	*Atheta atramentaria*	Exo	3.36	Hdisp	0	1	0	0	GetHact	lngCC	0	0	1	0	0	0.22	0
Insecta	Coleoptera	Staphylinidae	*Cordalia obscura*	Exo	2	Hdisp	0	1	0	0	GetHact	lngCC	0	0	1	0	0	0.89	3.44
Insecta	Coleoptera	Staphylinidae	*Euplectus infirmus*	Exo	1.19	Hdisp	0	1	0	0	GetHact	lngCC	0	0	1	0	0.11	0	0
Insecta	Coleoptera	Staphylinidae	*Gabrius nigritulus*	Exo	5.61	Hdisp	0	1	0	0	GetHact	lngCC	0	0	1	0	0	0.11	0
Insecta	Coleoptera	Staphylinidae	*Gyrohypnus fracticornis*	Exo	8.34	Hdisp	0	1	0	0	GetHact	lngCC	0	0	1	0	0	0	0.33
Insecta	Coleoptera	Staphylinidae	*Oligota parva*	Exo	1	Hdisp	0	1	0	0	GetHact	lngCC	0	0	1	0	0	0.22	0.67
Insecta	Coleoptera	Staphylinidae	*Oxytelus sculptus*	Exo	5	Hdisp	0	1	0	0	GetHact	lngCC	0	0	1	0	0	0	0.11
Insecta	Coleoptera	Staphylinidae	*Philonthus sp.*	Exo	8.15	Hdisp	0	1	0	0	GetHact	lngCC	0	0	1	0	0	0	0.11
Insecta	Coleoptera	Staphylinidae	*Tachyporus chrysomelinus*	Exo	3	Hdisp	0	1	0	0	GetHact	lngCC	0	0	1	0	0	0	0.11
Insecta	Coleoptera	Staphylinidae	*Xantholinus longiventris*	Exo	7	Hdisp	0	1	0	0	GetHact	lngCC	0	0	1	0	0	0.78	1.56
Insecta	Coleoptera	Tenebrionidae	*Blaps lethifera*	Exo	19.17	Ldisp	1	0	0	1	GetHact	lngCC	0	0	1	0	0	0	0.11
Insecta	Dermaptera	Anisolabididae	*Euborellia annulipes*	Exo	14.64	Ldisp	1	1	0	1	GetHact	lngCC	0	0	1	0	0	1.11	1.00
Insecta	Dermaptera	Forficulidae	*Forficula auricularia*	Exo	16	Ldisp	1	1	0	0	GetHact	lngCC	0	0	1	0	0.22	0.56	13.67

Insecta	Hemiptera	Aphididae	*Dysaphis plantaginea*	Exo	2.5	Hdisp	1	0	0	0	GetHact	lngPS	1	0	0	0	0	0.11	0.33
Insecta	Hemiptera	Aphididae	*Rhopalosiphonimus latysiphon*	Exo	1.18	Hdisp	1	0	0	0	GetHact	lngPS	1	0	0	1.44	0	0	0
Insecta	Hemiptera	Aphididae	*Rhopalosiphum oxyacanthae*	Exo	1.7	Hdisp	1	0	0	0	GetHact	lngPS	1	0	0	0.11	0	0.44	0
Insecta	Hemiptera	Aphididae	*Rhopalosiphum rufiabdominalis*	Exo	0.88	Hdisp	1	0	0	0	GetHact	lngPS	1	0	0	0.22	0	0	0
Insecta	Hemiptera	Aphididae	*Uroleucon erigeronense*	Exo	0.92	Hdisp	1	0	0	0	GetHact	lngPS	1	0	0	0.11	0	0	0
Insecta	Lepidoptera	Choreutidae	*Gen. sp.26*	Exo	12.73	Hdisp	1	0	0	0	GetHact	lngCC	1	0	0	0	0.11	0	0
Insecta	Lepidoptera	Choreutidae	*Tebenna micalis*	Exo	10	Hdisp	1	0	0	0	GetHact	lngCC	1	0	0	0	0	0	0.11
Insecta	Lepidoptera	Noctuidae	*Gen. sp.12*	Exo	22	Ldisp	1	0	0	0	GetHact	lngCC	0	0	1	0	0	0.33	0
Insecta	Lepidoptera	Noctuidae	*Gen. sp.13*	Exo	21.62	Hdisp	1	0	0	0	GetHact	lngCC	0	0	1	0	0	0	0.44
Insecta	Lepidoptera	Tineidae	*Oinophila v-flava*	Exo	8.3	Hdisp	1	0	1	0	GetHact	lngCC	0	0	0	0	0	0.11	0
Insecta	Lepidoptera	Tortricidae	*Gen. sp.1*	Exo	16.41	Ldisp	1	0	0	0	GetLact	lngCC	1	0	0	12.33	0.89	1.11	0.11
Insecta	Lepidoptera	Tortricidae	*Gen. sp.3*	Exo	9.41	Ldisp	1	0	0	0	GetLact	lngCC	1	0	0	1.89	0	0	0
Insecta	Lepidoptera	Tortricidae	*Gen. sp.6*	Exo	11.61	Ldisp	1	0	0	0	GetLact	lngCC	1	0	0	3.00	0	0	0
Insecta	Lepidoptera	Tortricidae	*Rhopobota naevana*	Exo	5.57	Hdisp	1	0	0	0	GetLact	lngCC	1	0	0	0.78	0	0	0
Insecta	Orthoptera	Gryllidae	*Eumodicogryllus bordigalensis*	Exo	10.21	Hdisp	1	0	0	0	GetHact	lngCC	0	0	1	0	0.22	0.11	0.22
Insecta	Orthoptera	Gryllidae	*Gryllus bimaculatus*	Exo	32.69	Hdisp	1	1	0	1	GetHact	lngCC	1	0	1	0	0	0.11	17.89
Insecta	Psocoptera	Ectopsocidae	*Ectopsocus briggsi*	Exo	2	Hdisp	1	0	1	0	GetHact	lngCC	0	0	0	0	0.11	0	0
Insecta	Psocoptera	Lachesillidae	*Lachesilla greeni*	Exo	0.93	Hdisp	1	0	1	0	GetHact	lngCC	0	0	0	0	0.11	0	0
Insecta	Thysanoptera	Phlaeothripidae	*Nesothrips propinquus*	Exo	0.76	Hdisp	1	0	0	0	GetHact	lngPS	1	0	0	0	0	0	0.11
Insecta	Thysanoptera	Thripidae	*Aptinothrips rufus*	Exo	1.04	Hdisp	1	0	0	0	GetHact	lngPS	1	0	0	0	0	0.11	0
Arachnida	Araneae	Clubionidae	*Clubiona decora*	Ind	6	Ldisp	0	1	0	0	GetHact	lngEDS	0	0	1	0	0.22	0	0
Arachnida	Araneae	Linyphiidae	*Acorigone acoreensis*	Ind	1.4	Hdisp	0	1	0	0	GetLact	lngEDS	0	0	0	0.44	0	0.11	0
Arachnida	Araneae	Linyphiidae	*Lepthyphantes acoreensis*	Ind	3.25	Hdisp	0	1	0	0	GetLact	lngEDS	0	0	0	1.44	0.33	0	0
Arachnida	Araneae	Linyphiidae	*Palliduphantes schmitzi*	Ind	1.95	Hdisp	0	1	0	0	GetLact	lngEDS	0	0	0	1.78	0.89	1.11	0

Arachnida	Araneae	Linyphiidae	*Porrhomma borgesi*	Ind	2	Hdisp	0	1	0	0	GetLact	lngEDS	0	0	0	0.67	0.22	0	0
Arachnida	Araneae	Linyphiidae	*Tenuiphantes miguelensis*	Ind	2.65	Hdisp	0	1	0	0	GetLact	lngEDS	0	0	0	35.22	13.89	1.00	0
Arachnida	Araneae	Linyphiidae	*Walckenaeria grandis*	Ind	2.3	Hdisp	0	1	0	0	GetLact	lngEDS	0	0	0	0.67	0	0	0
Arachnida	Araneae	Lycosidae	*Pardosa acorensis*	Ind	6	Hdisp	0	1	0	0	GetHact	lngEDS	1	0	0	7.67	7.89	51.44	12.11
Arachnida	Araneae	Pisauridae	*Pisaura acoreensis*	Ind	10.5	Ldisp	0	1	0	0	GetHact	lngEDS	0	0	0	0.67	0	0	0
Arachnida	Araneae	Salticidae	*Neon acoreensis*	Ind	2	Hdisp	0	1	0	0	GetHact	lngEDS	1	0	0	0.11	0	0.11	0
Arachnida	Araneae	Tetragnathidae	*Sancus acoreensis*	Ind	4.05	Hdisp	0	1	0	0	GetLact	lngEDS	0	0	0	0.33	0	0.11	0
Arachnida	Araneae	Theridiidae	*Lasaeola oceanica*	Ind	2	Hdisp	0	1	0	0	GetLact	lngEDS	0	0	1	0.11	0	0	0
Arachnida	Araneae	Theridiidae	*Rugathodes acoreensis*	Ind	1.8	Hdisp	0	1	0	0	GetLact	lngEDS	0	0	1	4.56	0.44	0	0
Arachnida	Araneae	Thomisidae	*Xysticus cor*	Ind	7	Hdisp	0	1	0	0	GetLact	lngEDS	1	0	0	0.89	0	0	0
Arachnida	Opiliones	Phalangiidae	*Homalenotus coriaceus*	Ind	3.82	Ldisp	1	1	1	1	GetHact	lngCC	0	0	1	0	17.89	7.22	0.22
Arachnida	Opiliones	Phalangiidae	*Leiobunum blackwalli*	Ind	6	Hdisp	1	1	1	1	GetHact	lngCC	0	0	1	4.67	32.22	14.78	3.44
Chilopoda	Geophilomorpha	Geophilidae	*Geophilus truncorum*	Ind	13.78	Ldisp	0	1	0	0	GetHact	lngCC	0	0	1	0.67	0.11	0	0
Chilopoda	Lithobiomorpha	Lithobiidae	*Lithobius pilicornis*	Ind	21.83	Ldisp	0	1	0	0	GetHact	lngCC	0	0	1	98.00	34.78	3.44	0.67
Chilopoda	Lithobiomorpha	Lithobiidae	*Lithobius sp.2*	Ind	8.97	Ldisp	0	1	0	0	GetHact	lngCC	0	0	1	0	0	16.11	13.11
Chilopoda	Scolopendromorpha	Cryptopidae	*Cryptops hortensis*	Ind	15.39	Ldisp	0	1	0	0	GetHact	lngCC	0	0	1	0.22	0.11	0.11	0.00
Insecta	Blattaria	Polyphagidae	*Zetha vestita*	Ind	5	Hdisp	0	0	0	1	GetHact	lngCC	1	0	0	0.67	0.56	0	0
Insecta	Coleoptera	Anthicidae	*Hirticollis quadriguttatus*	Ind	2.61	Hdisp	1	1	1	0	GetHact	lngCC	0	0	0	0	0	0	95.22
Insecta	Coleoptera	Carabidae	*Calosoma olivieri*	Ind	23	Hdisp	0	1	0	0	GetHact	lngCC	0	0	1	0	0	0.67	0.78
Insecta	Coleoptera	Carabidae	*Cedrorum azoricus*	Ind	10.71	Ldisp	0	1	0	0	GetHact	lngCC	0	0	1	11.56	0	0	0
Insecta	Coleoptera	Carabidae	*Ocys harpaloides*	Ind	6	Hdisp	0	1	0	0	GetHact	lngCC	0	0	1	0.00	0.89	0	0
Insecta	Coleoptera	Carabidae	*Pterostichus aterrimus*	Ind	9	Hdisp	0	1	0	0	GetHact	lngCC	0	0	1	0.11	0	0	0.11
Insecta	Coleoptera	Carabidae	*Stenolophus teutonus*	Ind	7	Hdisp	0	1	0	0	GetHact	lngCC	0	0	1	0	0	0	0.11
Insecta	Coleoptera	Carabidae	*Trechus terrabravensis*	Ind	1.12	Ldisp	0	1	0	0	GetHact	lngCC	0	0	1	0.33	0	0	0
Insecta	Coleoptera	Chrysomelidae	*Chrysolina bankii*	Ind	11.78	Hdisp	1	0	0	0	GetHact	lngCC	1	0	0	0	0	0.11	0
Insecta	Coleoptera	Chrysomelidae	*Psylliodes marcidus*	Ind	2.56	Hdisp	1	0	0	0	GetHact	lngCC	1	0	0	0	0	0.11	1.33

Insecta	Coleoptera	Coccinellidae	*Scymnus interruptus*	Ind	2	Hdisp	0	1	0	0	GetHact	IngCC	1	0	0	0	0	0	0.11
Insecta	Coleoptera	Curculionidae	*Drouetius borgesi*	Ind	8.12	Ldisp	1	0	0	0	GetHact	IngCC	0	0	1	6.33	0.11	0	0
Insecta	Coleoptera	Elateridae	*Alestrus dolosus*	Ind	5.01	Hdisp	1	0	0	0	GetHact	IngCC	0	0	1	0.22	0	0	0.00
Insecta	Coleoptera	Elateridae	*Heteroderes azoricus*	Ind	7.65	Hdisp	1	0	0	0	GetHact	IngCC	0	0	1	0	0	0	58.56
Insecta	Coleoptera	Laemophloeidae	*Placonotus sp.1*	Ind	2.37	Hdisp	1	0	1	0	GetHact	IngCC	0	0	0	0	0	0.11	0.11
Insecta	Coleoptera	Phalacridae	*Gen. sp.2*	Ind	1.34	Hdisp	1	0	1	0	GetHact	IngCC	1	0	0	0	0	0.22	0.33
Insecta	Coleoptera	Scraptiidae	*Anaspis proteus*	Ind	2	Hdisp	1	0	0	0	GetHact	IngCC	1	0	0	0	0.11	0	0
Insecta	Coleoptera	Staphylinidae	*Aloconota sulcifrons*	Ind	2.74	Hdisp	0	1	0	0	GetHact	IngCC	0	0	1	1.67	0	0.00	0.00
Insecta	Coleoptera	Staphylinidae	*Astenus lyonessius*	Ind	4	Hdisp	0	1	0	0	GetHact	IngCC	0	0	1	0	0	0.11	0.33
Insecta	Coleoptera	Staphylinidae	*Carpelimus corticinus*	Ind	3	Hdisp	0	1	0	0	GetHact	IngCC	0	0	1	0.11	0	0.11	0
Insecta	Coleoptera	Staphylinidae	*Habrocerus capillaricornis*	Ind	3.55	Hdisp	0	1	0	0	GetHact	IngCC	0	0	1	0.11	0	0	0
Insecta	Coleoptera	Staphylinidae	*Ocypus aethiops*	Ind	9	Hdisp	0	1	0	1	GetHact	IngCC	0	0	1	11.78	3.00	5.44	0
Insecta	Coleoptera	Staphylinidae	*Ocypus olens*	Ind	17	Hdisp	0	1	0	1	GetHact	IngCC	0	0	1	0	0.67	3.44	3.33
Insecta	Coleoptera	Staphylinidae	*Phloeonomus punctipennis*	Ind	2.3	Hdisp	0	1	0	0	GetHact	IngCC	0	0	1	0	0.11	0	0
Insecta	Coleoptera	Staphylinidae	*Proteinus atomarius*	Ind	1.52	Hdisp	0	1	0	0	GetHact	IngCC	0	0	1	0.22	0.11	0	0
Insecta	Coleoptera	Staphylinidae	*Pseudoplectus perplexus*	Ind	0.92	Hdisp	0	1	0	0	GetHact	IngCC	0	0	1	0	0	0.11	0
Insecta	Coleoptera	Staphylinidae	*Quedius curtipennis*	Ind	11	Hdisp	0	1	0	0	GetHact	IngCC	0	0	1	0	0	0.33	0
Insecta	Coleoptera	Staphylinidae	*Quedius simplicifrons*	Ind	11	Hdisp	0	1	0	0	GetHact	IngCC	0	0	1	0	0	0.44	0.33
Insecta	Coleoptera	Staphylinidae	*Rugilus orbiculatus*	Ind	4	Hdisp	0	1	0	0	GetHact	IngCC	0	0	1	0	0	3.22	3.67
Insecta	Coleoptera	Staphylinidae	*Scopaeus portai*	Ind	1.72	Hdisp	0	1	0	0	GetHact	IngCC	0	0	1	0	0	0.11	0
Insecta	Coleoptera	Staphylinidae	*Coproporus pulchellus*	Ind	3.36	Hdisp	0	1	0	0	GetHact	IngCC	0	0	1	0	0.11	0	0
Insecta	Coleoptera	Zopheridae	*Tarphius azoricus*	Ind	2.84	Ldisp	0	0	1	0	GetHact	IngCC	0	0	0	0	0.11	0	0
Insecta	Hemiptera	Aphididae	*Acyrthosiphon pisum*	Ind	0.63	Hdisp	1	0	0	0	GetHact	IngPS	1	0	0	0	0	0.22	0.11
Insecta	Hemiptera	Cicadellidae	*Anoscopus albifrons*	Ind	4	Hdisp	1	0	0	0	GetHact	IngPS	1	0	0	0.22	1.22	6.00	2.44
Insecta	Hemiptera	Cicadellidae	*Aphrodes hamiltoni*	Ind	2.31	Hdisp	1	0	0	0	GetHact	IngPS	1	0	0	8.00	0.33	0.11	0
Insecta	Hemiptera	Cicadellidae	*Euscelidius variegatus*	Ind	3.56	Hdisp	1	0	0	0	GetHact	IngPS	1	0	0	0	0	0.44	10.11

Insecta	Hemiptera	Cixiidae	*Cixius azoterceirae*	Ind	5	Hdisp	1	0	0	0	GetHact	IngPS	1	0	0	1.67	0	0	0
Insecta	Hemiptera	Cydnidae	*Geotomus punctulatus*	Ind	4.61	Hdisp	1	0	0	0	GetHact	IngPS	0	0	0	0	0	0	0.11
Insecta	Hemiptera	Delphacidae	*Megamelodes quadrimaculatus*	Ind	3	Hdisp	1	0	0	0	GetHact	IngPS	1	0	0	3.44	0.11	0	0
Insecta	Hemiptera	Delphacidae	*Muellerianella sp.1*	Ind	3.02	Hdisp	1	0	0	0	GetHact	IngPS	1	0	0	0	0	0	0.22
Insecta	Hemiptera	Flatidae	*Cyphopterum adcendens*	Ind	5	Hdisp	1	0	0	0	GetHact	IngPS	1	0	0	0.22	0	0.11	0
Insecta	Hemiptera	Lachnidae	*Cinara juniperi*	Ind	1.34	Hdisp	1	0	0	0	GetHact	IngPS	1	0	0	0.44	0	0	0
Insecta	Hemiptera	Lygaeidae	*Nysius atlantidum*	Ind	3.34	Hdisp	1	0	0	0	GetHact	IngPS	1	0	0	0	0	0	0.78
Insecta	Hemiptera	Lygaeidae	*Scolopostethus decoratus*	Ind	0.48	Hdisp	1	0	0	0	GetHact	IngPS	1	0	0	0	0	0.11	0.11
Insecta	Hemiptera	Nabidae	*Nabis pseudoferus*	Ind	9	Hdisp	0	1	0	0	GetHact	IngPS	1	0	0	0	0	2.00	3.22
Insecta	Hemiptera	Saldidae	*Saldula palustris*	Ind	4.5	Hdisp	0	1	0	0	GetHact	IngPS	0	0	1	0	0	0.11	0
Insecta	Hemiptera	Tingidae	*Acalypta parvula*	Ind	1.86	Hdisp	1	0	0	0	GetHact	IngPS	1	0	0	0	0	0.44	0
Insecta	Lepidoptera	Crambidae	*Gen. sp.21*	Ind	8.57	Ldisp	1	0	0	0	GetHact	IngCC	1	0	0	0.11	0	0	0
Insecta	Lepidoptera	Crambidae	*Gen. sp.1*	Ind	1.54	Ldisp	1	0	0	0	GetHact	IngCC	0	0	1	2.11	0	0	0
Insecta	Lepidoptera	Crambidae	*Scoparia coecimaculalis*	Ind	25.4	Hdisp	1	0	0	0	GetHact	IngCC	0	0	1	0.44	0.11	0.11	0
Insecta	Lepidoptera	Crambidae	*Scoparia semiamplalis*	Ind	6	Hdisp	1	0	0	0	GetHact	IngCC	0	0	1	0.11	0	0	0
Insecta	Lepidoptera	Geometridae	*Ascotis fortunata*	Ind	14.12	Ldisp	1	0	0	0	GetHact	IngCC	1	0	0	0.11	0	0	0
Insecta	Lepidoptera	Geometridae	*Cyclophora azorensis*	Ind	13	Ldisp	1	0	0	0	GetHact	IngCC	1	0	0	0.33	0	0	0
Insecta	Lepidoptera	Noctuidae	*Agrotis sp.1*	Ind	34	Ldisp	1	0	0	0	GetHact	IngCC	0	0	1	0	0	0.11	0
Insecta	Lepidoptera	Noctuidae	*Gen. sp.1*	Ind	28	Hdisp	1	0	0	0	GetHact	IngCC	0	0	1	0	0	0.11	0
Insecta	Lepidoptera	Noctuidae	*Gen. sp.14*	Ind	18.77	Hdisp	1	0	0	0	GetHact	IngCC	0	0	1	0	0	0.11	0
Insecta	Lepidoptera	Noctuidae	*Gen. sp.5*	Ind	15.96	Ldisp	1	0	0	0	GetHact	IngCC	0	0	1	0	0	0.11	0
Insecta	Lepidoptera	Noctuidae	*Mythimna unipuncta*	Ind	21.01	Hdisp	1	0	0	0	GetHact	IngCC	0	0	1	0.11	0.44	11.89	5.33
Insecta	Lepidoptera	Noctuidae	*Noctua pronuba*	Ind	24.96	Hdisp	1	0	0	0	GetLact	IngCC	0	0	0	0	0	0.11	0
Insecta	Lepidoptera	Noctuidae	*Phlogophora interrupta*	Ind	40	Ldisp	1	0	0	0	GetHact	IngCC	0	0	1	0	0.11	0.56	0.67
Insecta	Lepidoptera	Yponomeutidae	*Argyresthia atlanticella*	Ind	3.44	Hdisp	1	0	0	0	GetLact	IngCC	1	0	0	4.56	0.78	0.33	0

Insecta	Microcoryphia	Machilidae	*Trigoniophthalmus borgesi*	Ind	14.11	Ldisp	0	0	1	0	GetHact	IngCC	0	1	0	0.56	0	0	0
Insecta	Psocoptera	Ectopsocidae	*Ectopsocus strauchi*	Ind	1.44	Hdisp	1	0	1	0	GetHact	IngCC	0	0	0	0	0.22	0	0
Insecta	Thysanoptera	Phlaeothripidae	*Hoplothrips corticis*	Ind	2.76	Hdisp	0	0	1	0	GetHact	IngPS	1	0	0	0.11	0.22	0.22	0
Insecta	Trichoptera	Limnephilidae	*Limnephilus atlanticus*	Ind	9.14	Hdisp	0	1	0	1	GetHact	IngCC	0	0	0	1.67	0	0	0
Symphyla	Symphyla	Scutigerellidae	*Scutigerella immaculata*	Ind	3.89	Ldisp	1	0	0	0	GetHact	IngCC	0	0	0	0	0.11	0	0

APPENDIX S3. Sampling completeness.

We calculated species accumulation curves for each sampling unit (transect; N = 36), using the inventories obtained in their corresponding 30 pitfall traps. We use the number of individuals caught as a measure of survey effort. Species accumulation curves were calculated using 1000 randomizations. The degree of completeness was estimated by calculating the slope at the end of the obtained accumulative curve (i.e. the rate of species addition per individual or the tangent line using the last two points in the species accumulation curves). The slopes so calculated were submitted to a non-parametric Kruskal-Wallis one-way analysis of variance (KW) in order to examine if there were differences in the completeness of the inventories across the four land-uses. KW was followed by Nemenyi–Damico–Wolfe–Dunn *post-hoc* tests (Nemenyi, 1963) to identify statistically significant pairwise differences between land-uses. Analyses were performed within the R programming environment (R Development Core Team 2014) using the package *BAT* (Cardoso, Rigal & Carvalho. 2015). The results obtained suggest that the completeness values vary according to the land-uses (KW: H=15.569, P= 0.001, Figure S2). Multiple comparisons showed that the statistically significant differences occur between the completeness value of native forests and intensive pastures (*Post-hoc* test: P= 0.003) and between exotic forest and intensive pastures (*Post-hoc* test*:* P=0.017); all other multiple comparisons being non-significant.

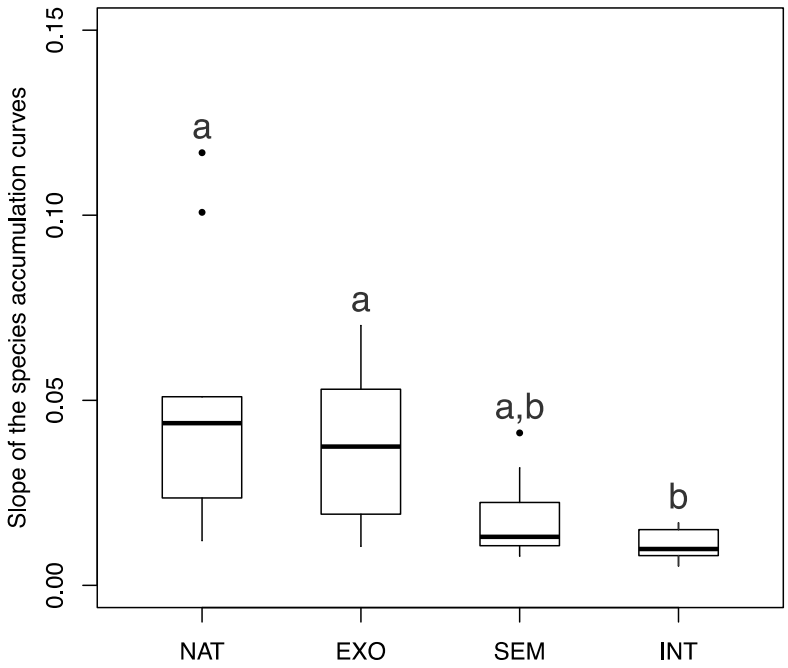

Figure S3.1. Box plots displaying the differences between the slope values reflecting completeness in the sampling units (sites) between the four land-uses. Land-use types accompanied by a different letter are significantly different from each other (*Post hoc* tests; $P < 0.05$). Land-use types are ranked according to their intensity uses with NAT = native forest, EXO = exotic forest, SEM = semi-natural pastures and INT = intensive managed pastures (See Table S1 for detailed land-use features).

References

Cardoso, P., Rigal, F., & Carvalho, J. C. (2015). BAT–Biodiversity Assessment Tools, an R package for the measurement and estimation of alpha and beta taxon, phylogenetic and functional diversity. *Methods in Ecology and Evolution*, **6**, 232-236.

Nemenyi, P.B. (1963). Distribution-free multiple comparisons. PhD thesis, Princeton University.

R Development Core Team (2014). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria.

Appendix S4. Supplementary results.

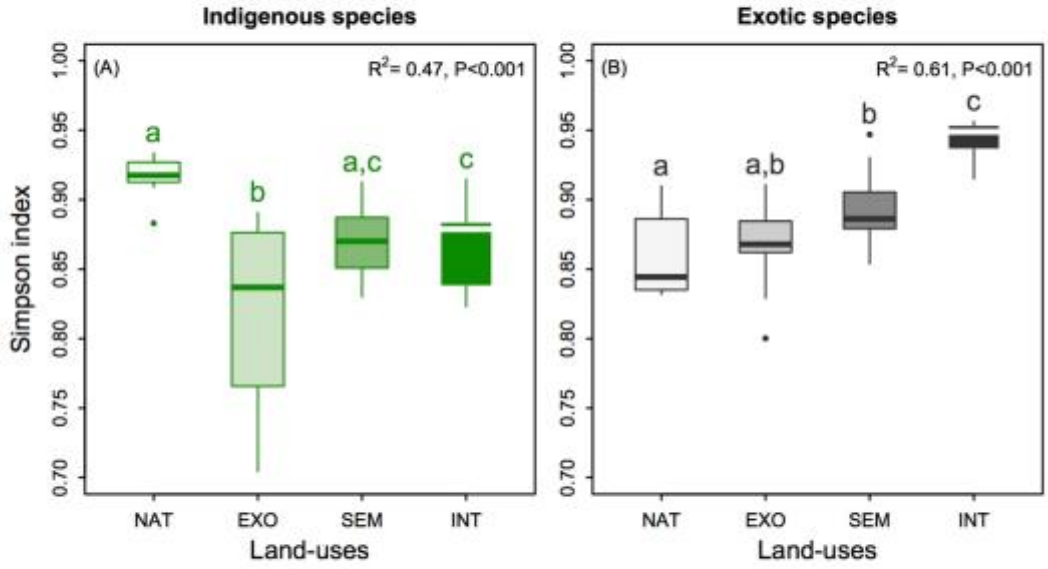

Figure S4.1. Box plots displaying difference in Simpson index values between the four land-use types for both indigenous (A) and exotic elements (B). The Magee 's pseudo-R^2 and the *P* values from the generalized least squares (GLS) models are given on the top right of each panel. Land-use types accompanied by a different letter are significantly different (*post hoc* tests; P < 0.05, see Table S4). Land-use types are ranked according to their intensity uses 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).

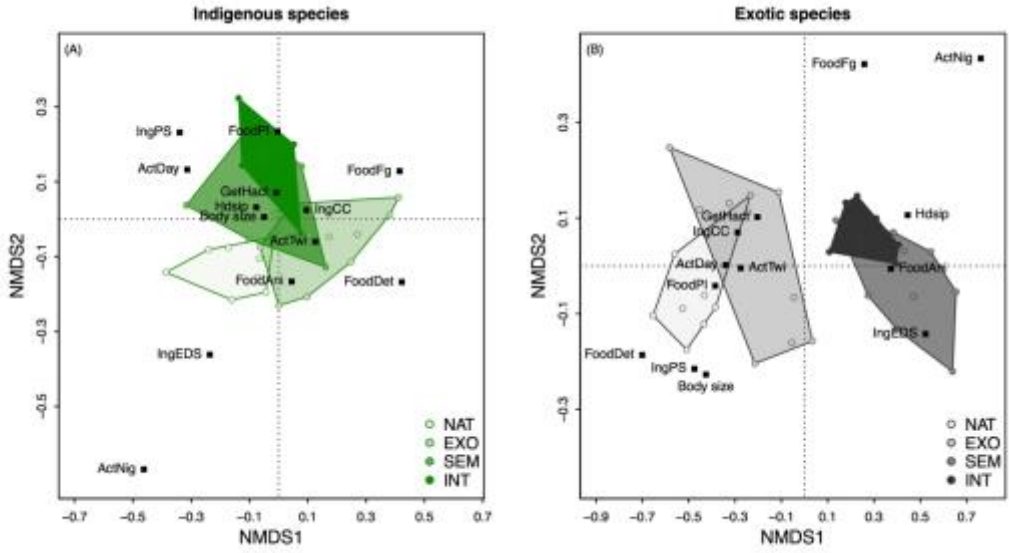

Figure S4.2. A two-dimensional non-metric multidimensional scaling (NMDS) ordination based on the Bray-Curtis distance measure, applied to the "CWMs x sites" matrix for indigenous (A) and exotic (B) elements. Dots indicate site types (i.e. where assemblages were sampled) while lines delimit the smallest polygon that encloses all elements for a given land-use. The stress value of the NMDS was 0.1 and 0.07 for indigenous and exotics, respectively. The black squares and their associated labels indicate the weighted averages scores of the attributes (i.e. CWMs) in the two-dimensional ordination configuration. Land-use types are ranked according to their intensity uses represented by either green (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 detailed land-use features).

Table S4.1. Moran's *I* values and their associated *P* values for both the raw diversity metrics and the corresponding residuals from the generalized linear square models (GLS) with land-use type as a factor for both indigenous and exotic arthropod species. Significant results are marked in bold.

	Raw metrics		Residuals	
	I	*P*	*I*	*P*
Indigenous species				
Rarefied species richness	0.192	**<0.001**	-0.064	0.472
Simpson index	0.153	**<0.001**	0.063	0.054
MFD	0.214	**<0.001**	0.013	0.334
SES_{MFD}	0.133	**0.001**	-0.046	0.723
Exotic species				
Rarefied species richness	0.028	0.239	-0.054	0.593
Simpson index	0.116	**0.003**	-0.051	0.642
MFD	-0.028	0.988	-0.059	0.519
SES_{MFD}	0.072	**0.043**	-0.033	0.923

Table S4.2. Results of the Tukey *post hoc* tests performed when the generalized least square (GLS) models were significant. Results are given for each diversity metric and for both indigenous and exotic arthropod species. The statistic *z* and its associated *P* values are given. Land-use types are ranked according to their intensity uses with NAT = native forest, EXO = exotic forest, SEM = semi-natural pastures and INT = intensive managed pastures. Significant results are marked in bold (See Table S1.1 in Appendix S1 for detailed land-use features).

		Indigenous species		Exotic species	
Rarefied species richness		*z*	*P*	*z*	*P*
	NAT - EXO	5.809	**<0.001**	-0.668	0.909
	NAT - SEM	-7.386	**<0.001**	-0.100	1.000
	NAT - INT	7.663	**<0.001**	-4.230	**<0.001**
	EXO - SEM	-1.577	0.392	-0.768	0.869
	EXO - INT	-1.707	0.248	3.562	**0.002**
	SEM - INT	0.277	0.993	-4.330	**<0.001**
Simpson index					
	NAT - EXO	5.397	**<0.001**	-0.438	0.972
	NAT - SEM	-2.403	0.077	2.815	**0.025**
	NAT - INT	2.598	**0.046**	-6.403	**<0.001**
	EXO - SEM	2.994	**0.014**	2.377	0.082
	EXO - INT	2.799	**0.027**	5.965	**<0.001**
	SEM - INT	0.195	0.997	-3.588	**0.002**
MFD					
	NAT - EXO	4.697	**<0.001**	0.082	1.000
	NAT - SEM	-3.501	**0.003**	-5.233	**<0.001**
	NAT - INT	5.091	**<0.001**	2.036	0.175
	EXO - SEM	1.196	0.629	-5.151	**<0.001**
	EXO - INT	-0.394	0.979	-1.954	0.206
	SEM - INT	1.590	0.385	-3.197	**0.008**
SES_{MFD}					
	NAT - EXO	2.435	0.071	0.170	0.998
	NAT - SEM	-3.334	**0.005**	-6.712	**<0.001**
	NAT - INT	5.765	**<0.001**	6.262	**<0.001**

EXO - SEM	-0.899	0.805	-6.542	**<0.001**
EXO - INT	-3.330	0.005	-6.092	**<0.001**
SEM - INT	2.431	0.071	-0.450	0.970

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Table S4.3. Results of the post hoc *t* tests performed for significant PERMANOVAs. The post hoc *t* tests were performed to highlight which land-uses differ between each other in their trait's attributes compositions. Analysis were performed for both indigenous and exotic arthropod elements separately. The post hoc *t* tests were also performed within each land-use type to highlight differences in trait's attributes compositions between indigenous and exotic arthropod elements. The statistic *t* and its associated *P* values are given. Land-use types are ranked according to their intensity uses with NAT = native forest, EXO = exotic forest, SEM = semi-natural pastures and INT = intensive managed pastures. Significant results are marked in bold (See Table S1.1 in Appendix S1 for detailed land-use features).

Pairwise comparisons between land-uses for indigenous		
	t	P
NAT - EXO	3.382	**<0.001**
NAT - SEM	2.697	**<0.001**
NAT - INT	4.044	**<0.001**
EXO - SEM	2.210	**0.012**
EXO - INT	3.457	**<0.001**
SEM - INT	1.567	0.056
Pairwise comparisons between land-uses for exotics		
	t	P
NAT - EXO	2.423	**0.004**
NAT - SEM	9.595	**<0.001**
NAT - INT	9.480	**<0.001**
EXO - SEM	5.247	**<0.001**
EXO - INT	4.477	**<0.001**
SEM - INT	2.702	**0.004**
Comparisons between indigenous and exotics within land-uses		
	t	P
NAT	15.396	**<0.001**
EXO	5.4323	**<0.001**
SEM	16.301	**<0.001**
INT	22.494	**<0.001**