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1	Functional traits of indigenous and exotic ground-dwelling arthropods show
2	contrasting responses to land-use change in an oceanic island, Terceira, Azores
3	François Rigal ^{1,2*} , Pedro Cardoso ^{1,3} , Jorge M. Lobo ⁴ , Kostas A. Triantis ^{1,5} , Robert J.
4	Whittaker ^{6,7} , Isabel R. Amorim ¹ and Paulo A.V. Borges ¹
5	¹ cE3c – Centre for Ecology, Evolution and Environmental Changes / Azorean
6	Biodiversity Group and Universidade dos Açores - Departamento de Ciências e
7	Engenharia do Ambiente, 9700-042 Angra do Heroísmo, Açores, Portugal
8	² CNRS-Université de Pau et des Pays de l'Adour, Institut des Sciences Analytiques et
9	de Physico-Chimie pour l'Environnement et les Materiaux, MIRA, Environment and
10	Microbiology Team, UMR 5254, BP 1155, 64013 Pau Cedex, France
11	³ Finnish Museum of Natural History, University of Helsinki, Helsinki, Finland.
12	⁴ Departament of Biogeography and Global Change, Museo Nacional de Ciencias
13	Naturales (CSIC), Madrid, Spain
14	⁵ Department of Ecology and Taxonomy, Faculty of Biology, National and
15	Kapodistrian University of Athens, Athens GR-15784, Greece
16	⁶ Conservation Biogeography and Macroecology Programme, School of Geography
17	and the Environment, University of Oxford, South Parks Road, Oxford, OX1 3QY,
18	United Kingdom
19	⁷ Center for Macroecology, Evolution and Climate, Department of Biology, University
20	of Copenhagen, Universitetsparken 15, DK-2100 Copenhagen Ø, Denmark
21	
22	*Corresponding author: François Rigal, email: francois.rigal@univ-pau.fr
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27 ABSTRACT

28 Aim Land-use change typically goes hand-in-hand with the introduction of exotic

29 species, which mingle with indigenous species to form novel assemblages. Here we

30 compare the functional structure of indigenous and exotic elements of ground-

31 dwelling arthropod assemblages across four land-uses of varying management

32 intensity.

33 Location Terceira Island (Azores, North Atlantic).

34 Methods We used pitfall traps to sample arthropods in 36 sites across the four land-35 uses and collated traits related to dispersal ability, body size and resource-use. For 36 both indigenous and exotic species, we examined the impact of land-uses on trait 37 diversity and tested for the existence of non-random assembly processes using null 38 models. We analysed differences in trait composition among land-uses for both 39 indigenous and exotic species with multivariate analyses. We used point-biserial 40 correlations to identity traits significantly correlated with specific land-uses for each 41 element.

42 **Results** We recorded 86 indigenous and 116 exotic arthropod species. Under high 43 intensity land-use, both indigenous and exotic elements showed significant trait 44 clustering. Trait composition strongly shifted across land-uses, with indigenous and 45 exotic species being functionally dissimilar in all land-uses. Large-bodied herbivores 46 dominated exotic species in low intensity land-uses, while small-bodied spiders 47 dominated exotics in high intensity land-uses. In contrast, with increasing land-use 48 intensity, indigenous species changed from functionally diverse to being dominated 49 by piercing and cutting herbivores.

50 Main conclusions Our study revealed two main findings: first, in high intensity land51 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

57 INTRODUCTION

58 Land-use change is inducing profound changes in biodiversity patterns throughout the 59 world (Mooney & Hobbs, 2000; Newbold et al., 2015). Different species may be 60 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 61 62 community assembly processes and ecosystem functioning, special attention has been 63 given to the consequences of the loss of indigenous species for functional diversity 64 (FD) (Diaz, Fargione, Chapin & Tilman, 2006; Flynn et al., 2009; Brown et al., 2013; 65 Forrest, Thorp, Kremen & Williams, 2015). Land-use changes frequently promote the 66 establishment of exotic species, often generating an increase in overall species richness at particular scales of analysis (Sax, Gaines & Brown, 2002). However, the 67 68 role of exotic species in driving changes in FD in the context of land-use changes 69 remains understudied (Vilà et al., 2011). Particularly, it remains unclear how land-use 70 change shapes functional trait structure of exotic species and to what extent exotic 71 species could contribute to the provision and maintenance of ecosystem functions in 72 agricultural landscape (Rodgers & Parker, 2003; Didham, Tylianakis, Gemmell, Rand 73 & Ewers, 2007; Hobbs, Sayre & Gupta, 2008). 74 Many exotic species are known to be particularly successful in anthropogenic 75 habitats. Exotic species can possess functional traits that are not present in the 76 indigenous community, allowing them to occupy new ecological opportunities

provided by land-conversion and transformation (Mayfield & Levine, 2010). In

78 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,

81 2012). As land-use change intensifies, both indigenous and exotic species may,

82	however, be filtered out towards a restricted set of functional strategies due to
83	stressful environmental conditions (Tecco, Díaz, Cabido & Urcelay, 2010). This may
84	lead to functional homogenization whereby exotic and indigenous species fulfill
85	similar functional roles (Olden & Rooney, 2006; Drenovsky et al., 2012).
86	Arthropods are the most diverse group of organisms and form also a great part of the
87	exotic fauna worldwide (Kenis et al., 2009). Several studies have reported lower
88	indigenous arthropod species richness and abundance in agricultural land-uses than in
89	more natural habitats (Hendrickx et al., 2007, Attwood, Maron, House & Zammit,
90	2008), while exotic arthropods generally benefit from agricultural landscapes (Grez,
91	Rand, Zaviezo & Castillo-Serey, 2013). Although arthropods provide numerous
92	ecosystem services, including pollination, regulation of herbivorous pests and
93	decomposition (Losey & Vaughn, 2006; Isaacs, Tuell, Fiedler, Gardiner & Landis,
94	2009), there has been relatively little trait-based analysis of these functions compared
95	to plants or vertebrates (Kenis et al., 2009; Diekotter, Wamser, Wolters & Birkhofer,
96	2010). Moreover, we are unaware of any studies examining how traits of indigenous
97	and exotic arthropods change in communities sampled across contrasting land-use
98	types.
99	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,
- 110 Simons, Weisser & Gossner, 2016).

111 Specifically, we first hypothesized that both indigenous and exotic species, analysed

separately, should show increased trait clustering in high intensity land-uses (H1).

113 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)

115 (Flynn et al., 2009). Our second hypothesis was that exotic species should show trait

116 dissimilarities when compared to co-occurring indigenous species under low and high

117 intensity land-uses (H2). The rationale is that, under low intensity land-uses (e.g.

118 native forest), exotic species exhibiting novel functional traits are favoured in

119 exploiting the vacant niches offered by the non-saturated nature of insular and/or

120 impoverished indigenous assemblages in Terceira (Whittaker et al., 2014). In contrast,

121 under high-intensity land-uses, exotic species have a competitive advantage for

122 resource exploitation and establishment space over the indigenous species (Grigulis,

123 Sheppard, Ash & Groves, 2001; Saar, de Bello, Pärtel & Helm, 2017).

124 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.,

126 2009; Meijer, Whittaker & Borges, 2011; Florencio, Cardoso, Lobo, Azevedo &

127 Borges, 2013; Florencio, Lobo, Cardoso, Almeida-Neto & Borges, 2015; Florencio et

al. 2016; Rigal, Whittaker, Triantis & Borges, 2013), and by focusing on traits allows

129 for stronger inferences on the functional processes that might control the respective

130 role of indigenous and exotic species in community assembly in the Azores.

131

132 **METHODS**

133 Study area

The Azores (37° to 40° N; 25° to 31° W) is one of the world's most isolated 134 135 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 136 137 colonization, around AD 1440, the Azorean archipelago was almost entirely forest-138 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 139 140 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 141 plantation of forests of exotic species was incentivized during the 1950s in areas 142 143 unsuitable for cattle grazing, thus promoting additional deforestation of natural forest 144 habitat. Thus, in < 600 years, 95% of the original native forest has been destroyed (Gaspar, Borges & Gaston, 2008). 145 146 Our study was conducted on Terceira Island (402 km², 3.52 Ma), on which the native 147 forest is restricted to 23 km², about 6% of its original area (Triantis et al., 2010 and references herein). The non-urban landscape of Terceira is dominated by four major 148 149 habitats: (i) native forests, (ii) exotic forests (Cryptomeria japonica and Eucalyptus 150 globulus monoculture plantations, monocultures and mixed forest of the invasive 151 *Pittosporum undulatum*); (iii) semi-natural pastures (mid- and high- elevation pastures 152 maintaining some indigenous plants) subject to short-term cattle grazing activity and 153 low inputs of fertilizers and (iv) intensively managed pastures subject to intensive 154 cattle grazing and high inputs of fertilizers (See Appendix S1 and Table S1.1 in 155 Supporting Information for detailed features of the land-uses). The four land-uses

156 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

Nine sampling sites were established in each of the four land-use types (total = 36), 164 165 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 other and 0.73 Km apart (0.13–3.8) from the edge of the sampled land-use type (Table 167 168 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 are those considered to have colonized via human mediation, many of which having a 178 179 cosmopolitan distribution (Borges et al., 2010 and see Appendix S1 for furthers 180 details in species classification).

181 All analyses were conducted using the transect (i.e. set of 30 pitfall traps) as the unit182 of analysis.

183

184 Traits characterization

For all arthropod species, we collated body size, dispersal abilities and a set of 185 functional traits related to resource-use (Table 1). Apart from body size, which was 186 187 measured on the individuals sampled in this study, traits were collected from an extensive literature search, including manuscripts with the first descriptions of the 188 189 species, first species records for the Azores, brief notes, and ecological studies. 190 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 191 192 was not available. Most of the literature was retrieved from the taxonomic catalogue 193 of the entomological bibliography for the Azores (See Vieira & Borges, 1993 and 194 Borges & Vieira, 1994), with the addition of some recent documentation (Barnard, 195 2011). Functional information was assigned to each species according to the adult characteristics, except for Lepidoptera, where traits were assigned by reference to the 196 197 larvae. For the unidentified morphospecies, we assigned functional traits of the 198 nearest taxonomic resolution (genus, family), except for body size. Species trait 199 assignments, together with the species mean abundances per land-use are given in 200 Appendix S2.

201

202 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

206 performed independently for indigenous and exotic species. To provide context for 207 our trait-based analyses, we first quantify species diversity in each site using species 208 richness and the Simpson index. Due to differences in sampling completeness 209 between sites among the land-uses (See Appendix S3 and Fig. S3.1), we calculated 210 rarefied richness to the lowest sample size (n = 77 individuals) to perform direct 211 comparisons of richness between our four land-uses. Prior to our FD analysis, we 212 built a functional dissimilarity matrix between species using the extension of the Gower's distance metric provided by Pavoine, Vallet, Dufour, Gachet & Daniel 213 214 (2009). To assess clustering of species in trait space per site, we computed the mean 215 pairwise functional distance (MFD), i.e. the averaged functional distance between all 216 pairs of species co-occurring in a site (Webb, Ackerly, McPeek & Donoghue, 2002). 217 To account for abundance distributions within sites and to lower the weight of rare 218 and possibly 'vagrant' species, the distance values were weighted according to the 219 log-transformed species abundance. By construction, MFD is hardly, if at all, 220 sensitive to species richness (Pavoine, Gasc, Bonsall & Mason, 2013). To test 221 whether rarefied species richness, the Simpson index and MPD differ between land-222 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 223 224 models to account for potential spatial structure by estimating the Moran's I spatial 225 autocorrelation index on residuals using latitude and longitude of each sample site. We quantified the effect of land-uses by using Magee's pseudo-R² (Magee, 1990). 226 227 When the overall GLS model was statistically significant, the Tukey's post hoc test 228 was used to identify statistically significant pairwise differences between land-uses. 229 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

231 site to a random distribution under the null hypothesis of no association between landuses and traits (Cornwell & Ackerly, 2009). We then generated 999 null assemblages 232 233 using the Independent Swap algorithm (Gotelli & Graves, 1996), which reshuffles the 234 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 235 236 expectation for each site, we computed the standardized effect size (SES) using the 237 formula SES_{MFD} = (MFD_{obs} - μ_{null})/ σ_{null} where MFD_{obs} is the observed MFD value at a 238 given site, μ_{null} , the mean MFD of the simulated communities, and σ_{null} the associated 239 standard deviation. Positive SES_{MFD} indicate that species occurring together in a site are less functionally related than expected by chance (functionally overdispersed) 240 241 while negative SES_{MFD} indicate that co-occurring species are more functionally 242 related than expected by chance (functionally clustered). We tested whether SES_{MFD} 243 values for a given land-use presented significant deviations from the null expectation 244 (median=0) using a one-sample Wilcoxon test (Swenson & Enquist, 2009). We also 245 computed GLS for SES_{MFD} in the same way as specified for diversity metrics. 246 Our second set of analyses aimed to test whether exotic and indigenous elements of 247 single ground-dwelling arthropods assemblages differ in their trait composition among land-uses (H2). For each individual site, we began by calculating the 248 249 community-weighted means (CWM) for body size and each trait attribute for both 250 indigenous and exotic species separately. The CWMs express the mean attribute value 251 between species occurring at a site, weighted by the relative abundance of each species (Violle et al., 2007) and was calculated as follows: 252

 $253 \qquad CWM_j = \mathop{\text{a}}\limits_{i=1}^{S} p_i x_{ij}$

254 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 j255 256 for species *i*. Prior to CWM calculation, multi-choice nominal traits and nominal traits 257 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" 258 259 matrices separately for indigenous and exotic species. Based on these matrices, we 260 calculated the Bray-Curtis distance between all pairs of sites and conducted a non-261 parametric permutational multivariate analysis of variance (PerMANOVA; Anderson, 262 2001) to test for difference in trait attributes composition among land-uses. 263 PerMANOVA was performed using permutation tests with 9999 iterations. When the overall PerMANOVA was significant, post-hoc t-tests were performed to identify 264 265 statistically significant pairwise differences between land-uses (Anderson, Gorley & 266 Clarke, 2008). To test for differences between indigenous and exotic species among land-uses, we computed a PerMANOVA to specifically test the interaction between 267 268 species origin (indigenous vs. exotic) and land-uses using a Bray-Curtis distance 269 matrix computed by combining the indigenous and exotics "CWM-by-sites" matrices. 270 Site was set as a random effect. When the interaction term was significant, post-hoc ttests were performed to identify land-uses where trait compositions of indigenous and 271 272 exotic species were significantly different from each other. Results of the 273 PerMANOVAs were visualized using non-metric multidimensional scaling 274 ordinations (NMDS) based on Bray-Curtis distance matrices. 275 Finally, to help the interpretation of our functional trait-based patterns, we conducted 276 an indicator analysis (Dufrêne & Legendre, 1997) to identify the degree of correlations between trait attributes and land-uses for both indigenous and exotic 277 278 species. We then used the point-biserial correlation coefficient (r_{pb} , De Caceres &

Legendre, 2009) to test the correlation between each CWM and the four land-use 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 r_{pb} values by bootstrapping the observed data 9999 times and considered values not 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 (Anderson289 et al., 2008).

290

291 **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.

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

from low to high intensity land-uses (Fig. 1A and Table S4.2), while rarefied exotic

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

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

305 overdispersed in native forest (median SES_{MFD} > 0; Wilcoxon test, P=0.003 and P=306 0.007 respectively, Fig. 1E, F). Indigenous species were significantly functionally 307 clustered in intensively managed pastures (median SES_{MFD} < 0; Wilcoxon test, 308 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 309 310 pastures and intensively managed pastures (median $SES_{MFD} < 0$ Wilcoxon test, P =311 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 312 313 (Wilcoxon test, P = 0.73 and P = 0.12 respectively) 314 Trait composition significantly differed between land-uses for both indigenous and 315 exotic species (PERMANOVA: $R^2 = 0.44$, pseudo-F_{3,32} = 8.518, P < 0.001 and $R^2 =$ 316 0.76, pseudo-F_{3,32} = 33.741, P < 0.001 respectively). Moreover, *post-hoc t* tests 317 revealed that land-uses were significantly different from each other in their trait 318 composition for both indigenous and exotic species (P<0.05, Table S4.3), except 319 between semi-natural and intensively managed pastures for indigenous species (P =320 0.056, Table S4.3 and see Fig. S4.2A and B for the NMDS plots for indigenous and 321 exotic species, respectively). Analyses combining both indigenous and exotic "CWM-by-sites" matrices showed that trait composition differed between indigenous 322 323 and exotic species among land-use types (PERMANOVA, Interaction species origin x 324 land-uses: $R^2 = 0.324$, pseudo-F_{3,64} = 28.317, *P* < 0.001). Moreover, *post-hoc t* tests 325 revealed that indigenous and exotic species were significantly different from each 326 other in their trait composition within all land-uses (P<0.05, Table S4.3). This pattern 327 was clearly evident in the NMDS plot (Fig. 2) showing a clear absence of overlap for 328 each land-use between indigenous and exotic species in the two-dimensional space.

329 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. 330 331 3). For instance, the trait attributes plants (Trait: Type of food), detritus (Type of 332 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 333 334 indigenous species while significantly positive correlations were found for exotic 335 species. In contrast, the attribute plants (Type of food) and piercing and sucking (Mode of ingestion) showed significantly positive correlations with intensive 336 337 managed pastures for indigenous species and significantly negative correlations for 338 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 339 340 size was also negatively correlated with intensively managed pastures. Only the 341 attribute high dispersal ability exhibited a consistent pattern for both indigenous and 342 exotic species, with significantly negative correlations in native and exotic forests and 343 significantly positive correlations in intensive managed pastures.

344

345 **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).

352 Prevalence of trait clustering for both indigenous and exotic species in high
353 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-

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

as the result of biotic interactions, typically competitive exclusion (Webb et al., 2002),

are 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

379 may result predominantly from environmental constraints overpowering the importance of local species interactions (Münkemüller et al., 2013). It is possible that 380 381 different outcomes would be produced if we down-scaled the species pool to a 382 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., 383 competition between predators), whereas our study considers all ecological guilds and 384 385 trophic levels of ground-dwelling arthropods. Therefore, the functional overdispersion 386 observed herein might simply reflect the large range of niches occupied by species in 387 native forest comparatively to the other land-uses.

388

389 Land-use change filtered out indigenous and exotic species towards distinct

390 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.

396 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

399 coleopterans *Hirticollis quadriguttatus* (Anthicidae, native) and *Heteroderes azoricus*

400 (Elateridae, Azorean endemic) (Appendix S2). This finding is consistent with

401 previous studies on Azorean herbivores that have reported a high proportion of

402 generalists in free-living phytophagous insects (Ribeiro et al., 2005). Such patterns

403 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 increase in abundance with habitat loss due to a reduction in specialist predator 408 409 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 establishment of pastures destroy all trees. Also, some Chilopoda species are known 417 418 to display strong preferences for low temperatures and high humidity (conditions encountered in native and exotic forest). Examples include species of Lithobius 419 420 (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)

432 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 433 434 low-intensity land-uses, towards elements dominated mainly by smaller-bodied 435 species, active throughout both day and night, carnivorous, with extra-intestinal 436 digestion and highly dispersive (mostly spider species) in high land-use intensity (Fig. 437 3). Native forest provides abundant resources for herbivorous species, thereby 438 allowing the successful establishment of exotic herbivores. Moreover, since 439 indigenous Azorean communities are largely unsaturated (Borges & Brown, 2004; 440 Whittaker et al., 2014), competition for food is likely to be reduced. Interestingly, the 441 most successful exotic herbivores were two Julidae species, Ommatoiulus moreletii 442 and *Cylindroiulus propinguus*, which possess the largest body size of all arthropods 443 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 444 445 species may have been favoured in establishing populations in native forests. These 446 two Julidae species are also occasionally detritivores (Bailey & Mendonça, 1990), 447 explaining the dominance of this trait within exotic elements in native forest. 448 The directional shift within exotic elements towards small-sized spiders in sites of 449 high intensity land-use was accompanied by a clear pattern of functional redundancy 450 (Fig. 1F). In both semi-natural and intensively managed pastures, small-sized 451 Linyphiidae spiders featured prominently, especially members of the genera *Erigone* 452 (E. autumnalis and E. dentipalpis) and Oedothorax (O. fuscus), both well adapted to 453 grazed pastureland (Wise, 1995 and Appendix S2). Linyphiidae in general, and those

454 genera in particular, are mostly r-selected species, which are tiny ($\approx 2 \text{ mm}$), efficient dispersers, often with multiple generations per year (Bell, Wheater & Cullen, 2001). 455 456 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 Linyphilds could also be due to the wide availability of prey. However, Linyphilds mainly feed on Collembola, 459 460 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 (60% of the current arthropod fauna, Borges et al., 2010), including many species able 473 474 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 highintensity land-uses due to interactions (competition, predation) with exotic species 483 484 (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

Although arthropods play important functional roles in both natural and
anthropogenic habitats (Losey & Vaughn, 2006; Isaacs et al., 2009), 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

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

sos assemblages in both low and high intensity land-uses.

506

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773 SUPPORTING INFORMATION

- Additional Supporting Information may be found online in the sup-porting
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- 776

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783 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 thewriting process.

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789 **BIOSKETCH**

790 François Rigal is an assistant professor at Université de Pau et des Pays de l'Adour.

His research interests include island biogeography, macroecology and functional

recology.

- 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.

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 <i>via</i> 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-R² 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 specie		Functional traits and their associated attributes											Land-uses				
Class	Order	Family	Species	Origin	Body size	Disp	FoodPl	FoodAni	FoodFg	FoodDet	Get	bul	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	IngEDS	1	0	0	0	0	0	1.44
Arachnida	Araneae	Tetragnathidae	Pachygnatha degeeri	Exo	3.38	Hdisp	0	1	0	0	GetLact	IngEDS	0	0	0	0	0	1.33	9.56
Arachnida	Araneae	Theridiidae	Cryptachaea blattea	Exo	3	Hdisp	0	1	0	0	GetLact	IngEDS	0	0	1	0	0.33	0.11	0
Arachnida	Araneae	Theridiidae	Steatoda grossa	Exo	8.25	Hdisp	0	1	0	0	GetLact	IngEDS	0	0	1	0	0.11	0	0
Arachnida	Araneae	Thomisidae	Xysticus nubilus	Exo	7	Hdisp	0	1	0	0	GetLact	IngEDS	1	0	0	0	0	1.00	0.11
Arachnida	Pseudoscorpiones	Chthoniidae	Chthonius ischnocheles	Exo	2	Ldisp	0	1	0	0	GetHact	IngCC	0	0	0	5.11	2.67	0.22	0
Arachnida	Pseudoscorpiones	Chthoniidae	Chthonius tetrachelatus	Exo	1.61	Ldisp	0	1	0	0	GetHact	IngCC	0	0	0	0.44	0.33	0	0
Chilopoda	Scutigeromorpha	Scutigeridae	Scutigera coleoptrata	Exo	12.64	Ldisp	0	1	0	0	GetHact	IngCC	0	0	1	0	0	0	1.67
Diplopoda	Julida	Blaniulidae	Blaniulus guttullatus	Exo	6.83	Ldisp	1	0	0	1	GetHact	IngCC	0	0	1	0	48.56	0	0
Diplopoda	Julida	Blaniulidae	Choneiulus palmatus	Exo	10.43	Ldisp	1	0	0	1	GetHact	IngCC	0	0	1	0.11	0.00	0	0
Diplopoda	Julida	Blaniulidae	Proteroiulus fuscus	Exo	11.28	Ldisp	1	0	0	1	GetHact	IngCC	0	0	1	0	1.44	0	0
Diplopoda	Julida	Julidae	Brachyiulus pusillus	Exo	7.53	Ldisp	1	0	0	1	GetHact	IngCC	0	0	1	0	1.11	0	0
Diplopoda	Julida	Julidae	Cylindroiulus propinquus	Exo	37.44	Ldisp	1	0	0	1	GetHact	IngCC	0	0	1	5.44	0.67	0.11	0
Diplopoda	Julida	Julidae	Ommatoiulus moreletii	Exo	40.04	Ldisp	1	0	0	1	GetHact	IngCC	0	0	1	19.22	19.22	3.67	0.67
Diplopoda	Polydesmida	Paradoxosomatidae	Oxidus gracilis	Exo	16	Ldisp	0	0	0	1	GetHact	IngCC	0	0	1	0	0.11	0.11	0
Diplopoda	Polydesmida	Polydesmidae	Brachydesmus superus	Exo	6.62	Ldisp	0	0	0	1	GetHact	IngCC	0	0	1	0.11	0	0	0
Diplopoda	Polydesmida	Polydesmidae	Polydesmus coriaceus	Exo	25.38	Ldisp	0	0	0	1	GetHact	IngCC	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	IngCC	0	0	0	0	0	0	0.44
Insecta	Coleoptera	Carabidae	Amara aenea	Exo	7	Hdisp	1	1	0	0	GetHact	IngCC	1	0	0	0	0	0.22	6.11
Insecta	Coleoptera	Carabidae	Anisodactylus binotatus	Exo	11	Hdisp	1	1	0	0	GetHact	IngCC	0	0	1	0	0.11	1.22	1.56
Insecta	Coleoptera	Carabidae	Paranchus albipes	Exo	10	Hdisp	0	1	0	0	GetHact	IngCC	0	0	1	4.44	2.00	0	0
Insecta	Coleoptera	Carabidae	Pseudophonus rufipes	Exo	13	Hdisp	1	1	0	0	GetHact	IngCC	0	0	1	0.00	0	0.33	3.33
Insecta	Coleoptera	Carabidae	Pterostichus vernalis	Exo	7	Hdisp	0	1	0	0	GetHact	IngCC	0	0	1	0	0.33	7.67	1.56
Insecta	Coleoptera	Chrysomelidae	Chaetocnema hortensis	Exo	2.01	Hdisp	1	0	0	0	GetHact	IngCC	1	0	0	0	0	0.11	8.89
Insecta	Coleoptera	Chrysomelidae	Epitrix cucumeris	Exo	1.85	Hdisp	1	0	0	0	GetHact	IngCC	1	0	0	0	0	0	0.67
Insecta	Coleoptera	Corylophidae	Sericoderus lateralis	Exo	0.5	Hdisp	0	0	1	0	GetHact	IngCC	1	0	0	0	0	0.11	1.11

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

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

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

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

1 APPENDIX S3. Sampling completeness.

2 We calculated species accumulation curves for each sampling unit (transect; N = 36), using 3 the inventories obtained in their corresponding 30 pitfall traps. We use the number of 4 individuals caught as a measure of survey effort. Species accumulation curves were 5 calculated using 1000 randomizations. The degree of completeness was estimated by 6 calculating the slope at the end of the obtained accumulative curve (i.e. the rate of species 7 addition per individual or the tangent line using the last two points in the species accumulation 8 curves). The slopes so calculated were submitted to a non-parametric Kruskal-Wallis one-way 9 analysis of variance (KW) in order to examine if there were differences in the completeness of 10 the inventories across the four land-uses. KW was followed by Nemenyi-Damico-Wolfe-11 Dunn post-hoc tests (Nemenyi, 1963) to identify statistically significant pairwise differences 12 between land-uses. Analyses were performed within the R programming environment (R 13 Development Core Team 2014) using the package BAT (Cardoso, Rigal & Carvalho. 2015). 14 The results obtained suggest that the completeness values vary according to the land-uses 15 (KW: H=15.569, P= 0.001, Figure S2). Multiple comparisons showed that the statistically 16 significant differences occur between the completeness value of native forests and intensive 17 pastures (Post-hoc test: P= 0.003) and between exotic forest and intensive pastures (Post-18 hoc test: P=0.017); all other multiple comparisons being non-significant.

19



21	Figure S3.1. Box plots displaying the differences between the slope values reflecting
22	completeness in the sampling units (sites) between the four land-uses. Land-use types
23	accompanied by a different letter are significantly different from each other (Post hoc tests; P
24	< 0.05). Land-use types are ranked according to their intensity uses with NAT = native forest,
25	EXO = exotic forest, SEM = semi-natural pastures and INT = intensive managed pastures
26	(See Table S1 for detailed land-use features).
27	
28	References
29	Cardoso, P., Rigal, F., & Carvalho, J. C. (2015). BAT–Biodiversity Assessment Tools, an R
30	package for the measurement and estimation of alpha and beta taxon, phylogenetic
31	and functional diversity. Methods in Ecology and Evolution, 6, 232-236.
32	Nemenyi, P.B. (1963). Distribution-free multiple comparisons. PhD thesis, Princeton
33	University.
34	R Development Core Team (2014). R: A language and environment for statistical computing.
35	R Foundation for Statistical Computing, Vienna, Austria.
36	

37 Appendix S4. Supplementary results.



38

39 Figure S4.1. Box plots displaying difference in Simpson index values between the four land-40 use types for both indigenous (A) and exotic elements (B). The Magee 's pseudo-R² and the P values from the generalized least squares (GLS) models are given on the top right of each 41 42 panel. Land-use types accompanied by a different letter are significantly different (post hoc 43 tests; P < 0.05, see Table S4). Land-use types are ranked according to their intensity uses 44 represented by either indigenous (green) or exotic (grey) gradation, with NAT = Native forest, 45 EXO = exotic forest, SEM = Semi-natural pastures and INT = intensive managed pastures 46 (See Table S1.1 in Appendix S1 for detailed land-use features).



49

50 Figure S4.2. A two-dimensional non-metric multidimensional scaling (NMDS) ordination 51 based on the Bray-Curtis distance measure, applied to the "CWMs x sites" matrix for 52 indigenous (A) and exotic (B) elements. Dots indicate site types (i.e. where assemblages 53 were sampled) while lines delimit the smallest polygon that encloses all elements for a given 54 land-use. The stress value of the NMDS was 0.1 and 0.07 for indigenous and exotics, 55 respectively. The black squares and their associated labels indicate the weighted averages 56 scores of the attributes (i.e. CWMs) in the two-dimensional ordination configuration. Land-use 57 types are ranked according to their intensity uses represented by either green (indigenous) or 58 grey (exotic) gradation with NAT = native forest, EXO = exotic forest, SEM = semi-natural 59 pastures and INT = intensive managed pastures (See Table S1.1 in Appendix S1 for detailed 60 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

65 marked in bold.

	Raw	metrics	Res	iduals
	Ι	Р	Ι	Р
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).

-			Exotio oposioo				
	Indigeno	us species	Exotic	species			
Rarefied species richness	Ζ	Р	Z	Р			
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

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).

Deirwige comparigene between land us	a for indigonous	
Pairwise compansons between land-us		
	t	Р
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	Р
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 exc	otics within land-us	es
	t	Р
NAT	15.396	<0.001
EXO	5.4323	<0.001
SEM	16.301	<0.001