#### **ORIGINAL PAPER**



# Characterizing arthropod communities and trophic diversity in areas invaded by Australian acacias

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#### Abstract

Plant invasions can modify the composition of native communities through altering diversity and ecosystem functioning. For example, arthropod communities can be influenced by the introduction of invasive plant species, but the impacts of plant invasions on arthropod communities have received little attention. Here, we investigated the diversity and species composition of arthropods in areas with and without invasive plants by comparing native ecosystems and areas invaded by *Acacia dealbata*, *A. longifolia* and *A. melanoxylon* in 18 locations in the northwestern Iberian Peninsula. Yellow sticky traps were placed in branches above ground in randomly selected areas and used to qualify and quantify the number of aerial arthropods. The aim was to assess the impact of invasive *Acacia* on arthropod species in different ecosystems. Our results demonstrate that arthropods are negatively influenced by *Acacia* invasions, reducing the abundance and diversity in invaded areas, which had substantial effects on beta-diversity and trophic levels. Overall, our findings indicate that invasive acacias can alter the species composition by not only reducing abundance and diversity but also altering the different trophic groups of the arthropod assemblages. The physical dominance of *Acacia* invasers alters the co-occurrence of arthropod assemblages, reducing the number of groups and leading to substantial effects on ecosystem dynamics as well as in the trophic diversity. We suggest implementing management strategies to favour the protection of native ecosystems and reduce the impacts of these exotic plants on arthropod biodiversity at the habitat level.

**Keywords** Arthropod diversity · Community structure · Functional diversity · Invasive alien plants · Invasion ecology · Species richness

# Introduction

The anthropogenic introduction of exotic species into new areas has become a global threat to ecosystems worldwide (Kueffer 2017). The movement of introduced plants results

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in new environmental scenarios, where alien plants can occupy a functional space within the range formed by resident species (Loiola et al. 2018). Introduced plants interact with native organisms, and the competition between species determines whether an alien species can establish in a local community (van Kleunen et al. 2018). In this sense, indirect effects amongst introduced and native plants can alter the result of multitrophic interactions at small spatial scales (Harvey et al. 2010). Plant invasions modify the composition of native communities by disrupting biotic interactions (Prior et al. 2015), even causing cascade effects throughout the community (Olden et al. 2004; López-Núñez et al. 2017). Hence, biotic interactions with local communities shape invasion consequences, with important roles for ecological interactions and species composition, and the outcome of new encounters is difficult to predict for many species (van Kleunen et al. 2018).

At present, the problematic of invasive plants has been a preference concern in Europe (European Union 2014;

European Commission 2017). Indeed, Nentwig et al. (2018) have published the "100 worst" invasive species in Europe, which incorporates some plants present in the Iberian Peninsula such as invasive acacias. It is widely known that some Australian Acacia species are one of the most problematic woody exotic group worldwide (Richardson and Rejmánek 2011). In the northwestern Iberian Peninsula, Acacia dealbata, Acacia longifolia and Acacia melanoxy*lon* are widespread around the territory producing a severe impact on native ecosystems (Souza-Alonso et al. 2017). Invasive capacities of those acacias are well documented. They change habitats, leading to a loss of diversity, forming dense monospecific stands that reduce native plant cover and light availability in the understory, and alter ecosystem functioning (Lorenzo et al. 2010; Le Maitre et al. 2011; Lorenzo and Rodríguez-Echeverría 2015; Souza-Alonso et al. 2017). Acacia invasions also can alter the composition of native communities disrupting the biotic interactions, through the accumulation of herbivores and pathogens (Crous et al. 2016; Rodríguez et al. 2019), or changing abiotic characteristics (Rascher et al. 2011; Lorenzo et al. 2017).

Although arthropod assemblages generally are negatively influenced by invasive plants (Bezemer et al. 2014; van Hengstum et al. 2014), not all populations are necessarily equally affected. Impacts on abundance and diversity may vary depending on the taxa group and its functional role in the community (Litt et al. 2014; Clusella-Trullas and Garcia 2017). Introduced plants do not always reduce biodiversity, but produce changes in arthropod composition by replacing some of the native species by biota with traits enabling tolerance to the invaded habitat (Hejda et al. 2017). However, most studies have focused only on a particular assemblage of arthropod species, with few considering many functional and trophic roles of entire arthropod groups (Spafford et al. 2013). Plant invasions can alter the habitat structure leading to substantial effects on ecosystem dynamics, in a way that affects the feeding behaviour through non-trophic mechanisms (Smith-Ramesh 2017).

The response of arthropod diversity to plant invasions can vary across the residence time of introduced plants and invertebrate feeding guilds (Bezemer et al. 2014). Specialist herbivores are often negatively affected by invasive plants (Procheş et al. 2008; Crous et al. 2016). By contrast, introduced plants also promote the expansion of exotic herbivores, favouring the spread of insect pests (Rodríguez et al. 2019). Alien assemblages tend to have higher taxonomic diversity, whereas native assemblages have more specialist species that results in higher functional diversity (Okimura and Mori 2018). Furthermore, behavioural diversity of the insect's functional groups can also be affected by the change in plant species composition, by favouring some behaviours over others (Cordero-Rivera 2017). Introduced plants have substantial negative impacts on primary consumers (McCary



et al. 2016), but also can change the abundances of secondary consumers as parasitoids and predators (Hartley et al. 2010). Some authors have reported that predators may be favoured by the introduced plants (Van der Colff et al. 2015; Gomes et al. 2018). Concerning pollinators, the effects may vary depending on the introduced plant species studied, since they have a variety of species-specific impacts on ecological communities (Davis et al. 2018). Plant invasions can decrease the abundance of specialist pollinators, due to the reduction of native plant biodiversity (Moroń et al. 2009). However, generalist pollinators can be attracted by the flowers of introduced plants, increasing their abundance (Traveset and Richardson 2006; Gillespie and Elle 2018). Instead, detritivore arthropods can rarely benefit from the increase in the amount of organic matter contributed by the introduced plants (Castro-Díez and Alonso 2017), and introduced plants can negatively affect specialized detritivores (Wolkovich et al. 2009), which may have substantial effects on ecosystem functioning.

The arthropod communities are sensitive groups that can be affected by introduced plants, modifying the interactions and changing the environmental scenarios. However, the consequences of invasive plants on arthropod communities have received little attention. The loss of diversity due to invasion of alien acacias is assumed despite almost nothing is known about the effect on arthropod communities. Most studies have only targeted the herbivorous feeding guild, resulting in a loss of important information. Therefore, it is essential to study the direct and indirect effects produced by introduced acacias on the different trophic groups of invaded ecosystems. Here, we investigated the compositional diversity of aerial arthropod species and their trophic role comparing different native ecosystems and areas invaded by Acacia dealbata, Acacia longifolia and Acacia melanoxylon in NW Iberian Peninsula. Since plant invasions can alter the arthropod communities by reducing the taxonomical and functional diversity, we predict (i) a higher abundance and diversity of arthropods in native areas, and that (ii) betadiversity would be reduced in invaded areas due to the lower replacement of species. Additionally, we expect to find that (iii) the trophic groups observed depend closely on the type of ecosystem since in places better conserved there will be greater trophic diversity.

# Materials and methods

#### **Study species**

Acacia dealbata, A. longifolia and A. melanoxylon are the most widespread Australian Acacia species in the NW Iberian Peninsula. These acacias were intentionally introduced in Europe during the first half of the nineteenth century for

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soil stabilization, gardening and forestry (Marchante et al. 2014). Acacia dealbata and A. melanoxylon occur principally in roadsides and mountain areas, and A. longifolia grows largely in Atlantic coastal areas. Both A. dealbata and A. melanoxylon occur more frequently as a tree, while A. longifolia can vary from shrub to small tree. A broad range of Mediterranean biomes are currently endangered by invasive Acacia species, and these invasions are well documented in Chile, France, Italy, New Zealand, Portugal, Spain, and South Africa (Souza-Alonso et al. 2017).

#### Study area

The study was conducted at 18 locations in areas where *Acacia dealbata*, *A. longifolia* and *A. melanoxylon* are prone to invade in the NW Iberian Peninsula (Fig. S1). The area is defined by a Mediterranean sub-humid climate with Atlantic trend, with mean annual temperature values oscillating from 6.7 to 18.0 °C and annual mean precipitation between 600 and 1800 mm (Carballeira et al. 1983). To ensure independence in the arthropod community, locations were separated by at least 500 m. In each study area, dominant plant species and elevation were recorded (Table S1). Sampling was done through the fruiting season (Castroviejo et al. 1999) and coinciding with the peak seasonal presence of most aerial arthropods in the adult form on July 2015.

#### Sampling design

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In each location, four different sampling areas were established: uninvaded areas (without *Acacia*), medium invaded areas (the invasion edge between the native ecosystem and the *Acacia* patch, Rodríguez et al. 2017), highly invaded areas (with Acacia dominant), and the reference areas (native ecosystems without Acacia, at least 500 m apart) (see Fig. 1 for details). Three population replicates of each introduced plant species were surveyed in each location, including mixed pine forest and shrubland for A. dealbata and A. melanoxylon, and coastal pine forest and coastal sand dune for A. longifolia. To qualify and quantify the number of aerial arthropods, a total of 360 yellow sticky traps (10 cm  $\times$  20 cm; two faces) were used and maintained during a week, placing five traps per location in the lower tree canopy (between 0.2 and 2 m above ground) (n = 15). All arthropods in the specific adult life form collected were sorted and assigned to a morphospecies using morphological differences (Oliver and Beattie 1996). Subsequently, each individual was identified to a taxa group (order, family, genus and/ or species) using the help of standard insect guides (Chinery 1997; McGavin 2002; Barrientos 2004). Based on their mouthparts and the predominant feeding behaviour of that particular family/genus/species, arthropods were assigned to functional feeding guilds roughly corresponding to different trophic levels (detritivores, herbivores, nectar feeders, parasitoids and predators).

#### **Statistical analyses**

Species richness was estimated between locations of *A. dealbata*, *A. longifolia* and *A. melanoxylon* that differ in invasive status (uninvaded, medium invaded, highly invaded and reference). To establish sampling representativeness, four non-parametric species estimators (Chao2, Jack 1, Jack 2 and bootstrap) were used, taking into account that most arthropod assemblages usually have rare species (Hortal et al. 2006). Species richness was estimated using the





sticky traps (yellow) are represented. Three population replicates of each introduced plant species (including mixed pine forest and shrubland for *A. dealbata* and *A. melanoxylon*, and coastal pine forest and coastal sand dune for *A. longifolia*) were surveyed in each location

*specpool* function in 'vegan' R package v.2.5-6 (Oksanen et al. 2019). To examine the cumulative and rarefaction number of species, species accumulation curves were used to represent the aggregate species as a function of the studied areas (Gotelli and Colwell 2001), and species diversity was compared between areas using sample-size-based rarefaction and extrapolation (R/E) curves (Chao et al. 2016). Species accumulation curves were computed with the *specaccum* function in 'vegan'. Sample-size-based (R/E) curves were used to quantify three measures of species diversity (Hill numbers) with standardized sample size, including unconditioned 95% CI using the 'iNEXT' R package (Hsieh et al. 2016).

To assess the impacts of invasive acacias on aerial arthropods, Generalized Linear Mixed Models (GLMMs) were used to test the effect of the factors ecosystem (mixed pine forest and shrubland, or coastal pine forest and coastal sand dune) and invasion level (uninvaded, medium invaded, highly invaded and reference) for differences in abundance, species richness and diversity indices (Margalef, Shannon, Simpson and Pielou evenness). Trophic groups were compared between locations using GLMMs to test the effect of the invasion level for differences on abundance and species richness for six feeding guilds and the six most abundant taxonomic groups. To establish statistical comparisons between models, we used the *glmer* function in 'lme4' R package v.1.1-19 (Bates et al. 2015). Models were carried out with species nested within ecosystem type and using location as random effect with Wald Chi-square Method and restricted maximum likelihood (REML), while comparisons between areas were examined using the 'Ismeans' R package (Lenth 2016). Abundance and trophic groups were compared using Poisson distribution and link function  $= \log$ .

To examine beta-diversity differences, a multivariate test for homogeneity of dispersion analyses (PERMDISP) of variations in arthropod species among studied areas was used. Two measures of beta-diversity in this study were assessed (Anderson 2006; Baselga 2010), species turnover (replacement of one species by others among areas of the same acacia species) and nestedness compositional differences between areas with diverse plant invasion status (species richness gain or loss among areas where species lists varies across different invasion level), as well as the total betadiversity. PERMDISP analyses defined the average distance of observation to the geometric centre (centroid) of each predefined group, e.g. arthropods associated with highly invaded areas (Anderson 2006). Significance tests were performed based on a Jaccard's dissimilarity matrix and 999 permutations using the *beta.pair* function in 'betapart' R package (Baselga and Orme 2012). Finally, the species composition between habitats was analysed using a permutational multivariate analysis of variance (PERMANOVA) with the *adonis* function (strata = location) in 'vegan'.

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PERMANOVA was done to test for differences among forest areas invaded by *A. dealbata*, coastal areas invaded by *A. longifolia* and protected areas invaded by *A. melanoxylon*, for the effect of ecosystem (mixed pine forest and shrubland for *A. dealbata* and *A. melanoxylon*, and coastal pine forest and coastal sand dune for *A. longifolia*) and for invasion level (reference, uninvaded, medium invaded and highly invaded), and also taking into account the hierarchical structure of data using location as random effect. All statistical analyses were performed using the software program R (R Development Core Team 2019, v.3.6.1).

# Results

#### Arthropod alpha-diversity

A total of 37,164 individual arthropods were collected from the yellow sticky traps, assigned to 96 families and 181 morphospecies (Tables S2-S4). Species belonged to 17 different taxa groups, of which six orders (Araneae (7 species), Coleoptera (22), Diptera (66), Hemiptera (40), Hymenoptera (18), and Lepidoptera (10)) and six feeding guilds (detritivores (15), herbivores (69), nectar feeders (17), omnivores (12), parasites (17), and predators (51)) were used for the analyses. The remaining taxa were classified into a category named "Other taxa" (11) and included Archaeognatha, Blattodea, Ixodida, Mecoptera, Megaloptera, Neuroptera, Opiliones, Orthoptera, Psocoptera, Thysanoptera and Trombidiformes. Relative abundances of arthropod assemblages varied between the studied areas (Fig. 2). In almost all cases, a slight reduction of Diptera and Other taxa were found at medium and highly invaded areas (Fig. 2), and an especially sensible reduction of Hymenoptera at coastal sand dunes invaded by Acacia longifolia (Fig. 2d). However, the opposite was found for Hemiptera, Lepidoptera (at shrubland invaded by Acacia dealbata, Fig. 2b) and Coleoptera (at coastal sand dunes invaded by A. longifolia, Fig. 2d), that increased in relative abundance simultaneously with the occurrence of the invasive acacias.

Species accumulation curves at areas of *A. dealbata* (Fig. S2A) indicated that sampling effort was sufficient to capture the majority of the species. However, curves at areas of *A. longifolia* were still accumulating species, suggesting that sampling size was a bit small for the estimation (Fig. S2B). For *A. melanoxylon*, mixed pine forest curve was most likely to saturate quickly, while shrubland was still accumulating species (Fig. S2C). Overall, species richness estimators showed that shrubland (at areas of *A. melanoxylon*) and the coastal areas (at areas of *A. longifolia*) had the highest value of observed and estimated species (Table 1). Particularly for *A. dealbata*, the uninvaded and medium invaded areas had on average the highest value of observed and estimated



**Fig. 2** Relative abundances of taxa (order) within each studied area of *Acacia dealbata* in **a** mixed pine forest and **b** shrubland; *Acacia longifolia* in **c** coastal pine forest and **d** coastal sand dune; and *Acacia melanoxylon* in **e** mixed pine forest and **f** shrubland. Abundance of

each taxon was calculated as the percentage of sequences per location for a given arthropod group. The group 'Other taxa' includes grouped orders with lower abundance

species (Table 1). Conversely, the reference areas had the lowest despite having the highest abundance of individuals. For *A. longifolia*, the medium and highly invaded areas had a high number, whereas the reference and uninvaded areas had the lowest (Table 1). For *A. melanoxylon*, the reference areas had a lower value for observed and estimated species (Table 1).

Sample-size-based rarefaction and extrapolation (R/E) curves differ slightly among the all studied areas (Fig. 3), where values close to saturation were found for q = 1 (exponential of the Shannon entropy index), and q = 2 (inverse of the Simpson Concentration Index). For *A. dealbata*, curves suggest that the number of specimens' rates differ at either invasion level areas, where the uninvaded of both ecosystems had higher species diversity estimates (Fig. 3a). Besides, the uninvaded areas overlapped with the

medium invaded areas using the 95% confidence intervals for diversity estimates, when q = 1 at shrubland and q =2 at both ecosystems, whereas the reference and highly invaded areas had lowest values and overlapping (Fig. 3a). For A. longifolia, curves indicated differences between both ecosystems and the invasion levels (Fig. 3b). In the coastal pine forests, the reference areas had higher species diversity estimates when q = 1 and q = 2, while the medium invaded areas had the lowest (Fig. 3b). In coastal sand dunes, the reference, uninvaded and highly invaded areas had higher species diversity estimates and overlap in all cases (Fig. 3b). For A. melanoxylon, the uninvaded, medium and highly invaded areas had higher species diversity estimates and overlap, whereas the medium invaded areas had the lowest at mixed pine forest (Fig. 3c). In shrubland, the uninvaded and medium invaded areas had



**Table 1** Number of collected arthropod species ( $S_{obs}$ ) and individuals as well as the estimated richness of species (calculated by Chao2, Jack 1, Jack 2 and bootstrap species estimators for overall) from three *Acacia* tree species at locations that differ in invasive status (reference, uninvaded, medium invaded and highly invaded)

Areas	S <sub>obs</sub>	Individuals	Chao2 (± SD)	Jack1 (± SD) Jack2	Bootstrap (± SD)
Overall (all combined)	175	37,164	224.60 (18.79)	223.59 (8.25) 248.37	196.74 (4.47)
Overall Acacia dealbata	74	6083	127.55 (40.58)	91.85 (5.06) 106.62	81.39 (2.62)
Mixed pine forest	60	3148	113.10 (40.24)	77.70 (5.40) 92.95	67.12 (2.69)
Reference	27	1114	27.67 (0.95)	29.43 (1.51) 24.59	27.48 (0.79)
Uninvaded	45	915	270.86 (246)	65.53 (7.13) 83.79	53.13 (3.23)
Medium invaded	32	689	35.32 (3.17)	39.47 (2.64) 39.16	36.02 (1.79)
Highly invaded	28	430	46.82 (16.30)	38.27 (3.65) 45.38	32.34 (1.76)
Shrubland	55	2935	73.44 (12.87)	69.75 (5.50) 78.55	61.39 (2.91)
Reference	26	879	26.56 (0.66)	28.40 (1.40) 24.39	26.39 (0.74)
Uninvaded	40	769	66.29 (21.66)	52.13 (5.81) 60.98	45.32 (3.17)
Medium invaded	32	682	39.56 (6.66)	40.40 (3.40) 44.18	35.86 (1.83)
Highly invaded	28	605	30.10 (2.36)	33.60 (2.99) 32.36	31.12 (1.90)
Overall Acacia longifolia	112	14,396	218.66 (49.04)	155.63 (7.82) 190.12	129.53 (3.81)
Coastal pine	85	7965	198.67 (64.95)	118.43 (7.51) 146.55	98.32 (3.56)
Reference	31	1152	31.37 (0.82)	32.87 (1.32) 30.58	32.43 (2.00)
Uninvaded	43	2728	56.07 (9.29)	56.07 (5.03) 62.57	48.93 (2.74)
Medium invaded	49	2848	79.24 (20.40)	65.80 (6.32) 77.38	56.17 (3.17)
Highly invaded	47	1237	71.07 (15.12)	64.73 (6.09) 75.57	54.73 (3.05)
Dune	81	6431	132.69 (27.46)	109.52 (6.12) 129.95	92.95 (3.36)
Reference	31	1373	31.37 (0.81)	32.86 (1.31) 30.57	32.42 (1.78)
Uninvaded	35	1429	50.55 (13.89)	44.33 (4.46) 50.58	38.96 (2.22)
Medium invaded	38	2241	71.71 (24.19)	53.87 (5.28) 65.38	44.55 (2.52)
Highly invaded	43	1388	67.06 (15.12)	60.73 (6.24) 71.56	50.71 (3.04)
Overall Acacia melanoxylon	101	16,685	136.34 (18.09)	128.77 (6.12) 145.57	113.33 (3.29)
Mixed pine forest	52	4819	55.44 (3.45)	58.88 (3.27) 59.00	55.78 (2.17)
Reference	23	1605	23.89 (0.71)	25.78 1.16) 23.58	23.25 (0.79)
Uninvaded	38	1158	42.24 (3.62)	47.33 (5.05) 47.15	42.96 (2.93)
Medium invaded	34	1054	49.55 (13.89)	42.33 (4.67) 49.58	38.01 (2.31)
Highly invaded	35	1002	42.56 (6.66)	43.4 (4.57) 47.18	39.05 (2.96)
Shrubland	88	11,866	117.87 (15.37)	114.55 (6.16) 129.25	99.82 (3.24)
Reference	26	2988	26.45 (0.56)	27.24 (1.12) 26.15	26.32 (1.06)
Uninvaded	50	2458	60.50 (7.14)	64 (5.11) 68.95	56.93 (2.94)
Medium invaded	59	3824	104.17 (28.71)	79.53 (6.30) 94.58	67.72 (3.17)
Highly invaded	47	2596	66.27 (12.63)	62.87 (5.78) 71.97	54.02 (2.89)

higher values, but the reference and high invaded areas had the lowest, even had overlap when q = 2 (Fig. 3c).

GLMMs indicated that the levels of abundance and arthropod diversity (species richness, Margalef, Shannon, Simpson and Pielou evenness) tended to be significantly higher in the reference and uninvaded areas than in the medium and highly invaded areas (Figs. 4, 5; Table 2). For *A. dealbata*, differences were found for the interaction of ecosystem and invasion level in average abundance, as well as for the invasion level of arthropod diversity indices (Table 2). Reference areas of mixed pine forest had the highest abundance, which had about twice more abundance than highly invaded areas (Fig. 4a). Besides, values for the species richness (Fig. 4b), Margalef and Shannon indices (Fig. 5a, b)



were also significantly higher for reference, uninvaded and medium invaded areas, whereas highly invaded areas had higher values for the Simpson and Pielou evenness indices (Fig. 5c, d). For *A. longifolia*, differences were found for the interaction of ecosystems and invasion level in abundance, Margalef, Simpson and Pielou evenness indices (Table 2). Shannon index differed between invasion levels, while differences became not significant for the species richness. The uninvaded and medium invaded areas of coastal pine forest had the highest abundance, with about twice more abundance than the reference and highly invaded areas (Fig. 4a). Reference areas of coastal pine forest had higher values for Margalef, Simpson and Pielou evenness indices than areas with the presence of *A. longifolia* (Fig. 5a, c, d) and had the highest Shannon index for both ecosystems (Fig. 5b). For *A. melanoxylon*, highly significant differences were found for the interaction of ecosystem and invasion level in abundance and arthropod diversity (Table 2). Medium invaded areas of shrubland had significantly higher abundance and species richness (Fig. 4) and the same was found for the Margalef, Shannon, Simpson and Pielou evenness indices (Fig. 5).

#### Arthropod beta-diversity

PERMDISP of differences in areas invaded by acacias revealed a significant beta-diversity response when considering its associated arthropod species between the areas (Table 3). PERMDISP analyses revealed dissimilarity for nestedness between invasion levels and total beta-diversity between ecosystems at locations invaded by A. dealbata (Table 3). Distance to centroid indicated that areas with the presence of A. dealbata had higher average nestedness than reference areas and mixed pine forest had higher total beta-diversity than shrubland (Fig. S3A). However, we did not find differences for species turnover, showing that arthropods turnover is similar among them (Fig. S3A). For A. longifolia, arthropods collected on coastal areas had significantly higher species turnover and total beta-diversity in the coastal pine forest (Fig. S3B). Besides, dissimilarity across the invasion levels was found, which indicated that areas with the presence of A. longifolia had higher average species turnover, nestedness and total beta-diversity than reference areas (Fig. S3B). For A. melanoxylon, significantly higher species turnover and total beta-diversity were found in shrubland than mixed pine forest, and oppositely for nestedness (Fig. S3C). Furthermore, a significant increase of nestedness was found in areas with the presence of A. melanoxylon than reference areas (Fig. S3B). PERMANOVA analyses revealed that arthropod assemblage composition was affected by ecosystem and invasion level of A. dealbata, A. longifolia and A. melanoxylon from all locations combined (Table 4).

#### **Trophic and taxonomic groups**

GLMMs revealed significant differences for the abundance of feeding guilds for the three target acacias, while for species richness significant differences were only found in few trophic groups (Table 5). Particularly for *A. dealbata*, the abundance of all trophic groups was significantly higher on reference and uninvaded areas, while highly invaded areas had the lowest values. Besides, reference and uninvaded areas had a significantly higher species richness for nectar feeders and predators, while highly invaded areas had a significantly higher number of omnivores (Table 5). For *A. longifolia*, a significantly higher abundance was found for nectar feeders, omnivores, parasites and predators in



reference and uninvaded areas, but also higher species richness for nectar feeders. Nevertheless, detritivores occurred in significantly higher abundance in high and medium invaded areas. In medium invaded areas, herbivores had significantly higher abundance and predators had higher species richness (Table 5). For *A. melanoxylon*, reference and uninvaded areas had a significantly higher abundance of nectar feeders, omnivores and parasites, but also reference areas had a significantly higher species richness of herbivores and nectar feeders. Detritivores occurred in significantly higher abundance in high and medium invaded areas. Herbivores had significantly higher abundance in medium invaded areas. Predators had greater abundance in uninvaded and medium invaded areas, while had a significantly higher species richness in medium invaded areas (Table 5).

Within taxonomic groupings, in areas highly invaded by A. dealbata, a significantly lower abundance was found for Diptera, Formicidae, Hymenoptera, Lepidoptera and Other taxa, but also a lower species richness for Diptera, Lepidoptera and ther taxa (Table S5). For A. longifolia, significant differences were found for all taxonomic groups studied (Table S5). Reference and uninvaded areas had a higher abundance for Diptera, Hymenoptera and Other taxa, but also had higher species richness for Hemiptera and Hymenoptera. By contrast, reference areas had the lowest abundance for Araneae, Coleoptera, Formicidae, Hemiptera and Lepidoptera. Highly invaded areas had high values for Diptera, Formicidae and Lepidoptera, while medium invaded areas had a higher number for Araneae and Coleoptera (Table S5). For A. melanoxylon, a significantly higher abundance was found for Coleoptera, Hemiptera, Hymenoptera and Other taxa in highly invaded areas, while Diptera and Formicidae had a significantly highest abundance at uninvaded areas. However, reference areas had significantly lower species richness for Diptera and Hymenoptera but also had significantly higher species richness for Lepidoptera (Table S5).

# Discussion

#### Alpha-diversity

We initially hypothesized that native areas provide a higher abundance and diversity of aerial arthropods. Our results demonstrate that invasive acacias significantly reduce the abundance and species richness at medium and highly invaded areas, and a similar tendency was recorded for diversity indices. By contrast, native areas without acacias tend to have the highest values for species diversity. The present results agree with those obtained in other studies, which showed a negative effect of introduced plants over the arthropod communities (Procheş et al. 2008; Van der

Reference Uninvaded Medium invaded

Highly invaded





# C Acacia melanoxylon





◄Fig. 3 Sample-size-based rarefaction sampling curves with 95% confidence intervals (shaded areas) for the arthropod species richness of a *Acacia dealbata*, b *Acacia longifolia* and c *Acacia melanoxylon*, separately from diversity order: species richness (left panel), Shannon diversity (central panel) and Simpson diversity (right panel)

Colff et al. 2015; Maoela et al. 2016). This might be due to the alteration of ecosystems by invasive acacias, producing a severe impact on native ecosystems (Souza-Alonso et al. 2017). Our results also showed that species estimators and rarefaction curves had a higher estimated species richness at areas affected by the introduced acacias than in the reference native areas far from invasion. This can be explained by our finding of a few rare species that live exclusively in areas with the presence of acacias, which can influence the species estimations due to their low abundance. Introduced plants not only favour the presence of generalist insects but also promote a substantial increase in the number of nonnatives (Rodríguez et al. 2019). Although we tried to catch the major number of taxa using yellow sticky traps, this study has some limitations such as a single sampling event or only using a methodology to measure the aerial arthropods. Most studies have investigated only a limited number of arthropod taxa, with few including the many functional and trophic roles of entire arthropod groups (Spafford et al. 2013). However, our study provides evidence that arthropod alpha-diversity may be affected by acacia invasions. Studies adding more sampling events are needed to confirm that we are not overestimating the alteration of the arthropod communities (e.g. explore long-term sampling intervals).

#### **Beta-diversity**

Sampling introduced plants invading different microhabitats is important to detect impacts on local fauna associated with the presence of alien species (Harvey et al. 2014). It is assumed that the presence of invaders like A. dealbata, A. longifolia and A. melanoxylon will change the presence and distribution of arthropods. Hence, we expect to find that the beta-diversity would be reduced in invaded areas due to the lower replacement of arthropod species. We found that introduced acacias had a significant influence on overall arthropod assemblages. Our results showed that arthropod beta-diversity at locations with acacias was influenced by ecosystem and invasion level, which suggests that the arthropod assemblage composition will be affected differently among distinct ecosystems and invasion levels. In general, the beta-diversity outcome was principally driven by the replacement (species turnover), indicating the importance of the competitive interactions between the arthropod species (Baselga 2010), but also other factors such as environmental characteristics cannot be excluded (Nobis et al. 2016).



**Fig.4** Effect of the ecosystem (mixed pine forest and shrubland, or coastal pine forest and coastal sand dune) and invasion level (reference, uninvaded, medium and highly invaded) for differences in **a** abundance and **b** species richness recorded among locations of *Aca*-

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*cia dealbata, Acacia longifolia* and *Acacia melanoxylon* (n = 15). Model-adjusted least square means values  $\pm$  SE are shown. Different letters indicate statistical significance at  $p \le 0.05$  level using Generalized Linear Mixed Models



Fig. 5 Effect of the ecosystem (mixed pine forest and shrubland, or coastal pine forest and coastal sand dune) and invasion level (reference, uninvaded, medium and highly invaded) for differences in diversity indices, **a** Margalef, **b** Shannon, **c** Simpson and **d** Pielou Evenness recorded among locations of *Acacia dealbata*, *Acacia* 

*longifolia* and *Acacia melanoxylon* (n = 15). Model-adjusted least square means values  $\pm$  SE are shown. Different letters indicate statistical significance at  $p \le 0.05$  level using Generalized Linear Mixed Models

Moreover, differences in the arthropod species composition among ecosystems might be explained due to differences in abiotic and biotic conditions (i.e. soil physicochemical properties, light availability, vegetation cover, etc.), which might modulate the species composition that appears in each ecosystem. For example, understory light is directly conditioned on canopy structure, which additionally regulates the temperature and humidity, changing understory vegetation (Barbier et al. 2008). Additionally, biotic homogenization can modify the overall communities by changing not only



 Table 2 Results from the Generalized Linear Mixed Models (GLMM) to test the effect of the factors ecosystem (pine forest and shrubland, or coastal pine and dune) and invasion level (reference, uninvaded, medium and highly invaded) for differences in abundance,

species richness and diversity indices (Margalef, Shannon, Simpson and Pielou evenness) between the arthropod samples collected in areas invaded by *Acacia dealbata*, *A. longifolia* and *A. melanoxylon* 

Effect	Acacia dealbata			Acacia longifolia			Acacia melanoxylon		
	df	χ <sup>2</sup>	Pr(>Chisq)	df	χ <sup>2</sup>	Pr(>Chisq)	df	χ <sup>2</sup>	Pr(>Chisq)
Abundance									
Ecosystem (ECO)	1, 119	0.239	0.625	1, 120	0.279	0.597	1, 120	13.093	0.001***
Invasion level (IL)	3, 119	382.502	0.001***	3, 120	923.239	0.001***	3, 120	174.575	0.001***
$ECO \times IL$	3, 119	56.173	0.001***	3, 120	657.455	0.001***	3, 120	123.874	0.001***
Species richness									
Ecosystem (ECO)	1, 119	0.102	0.749	1, 120	0.115	0.735	1, 120	7.273	0.007**
Invasion level (IL)	3, 119	17.883	0.001***	3, 120	7.737	0.052	3, 120	5.485	0.139
$ECO \times IL$	3, 119	3.167	0.366	3, 120	1.695	0.638	3, 120	10.324	0.016*
Margalef Index									
Ecosystem (ECO)	1, 119	0.124	0.725	1, 120	0.138	0.710	1, 120	2.655	0.103
Invasion level (IL)	3, 119	15.944	0.002**	3, 120	24.672	0.001***	3, 120	16.417	0.001***
$ECO \times IL$	3, 119	3.283	0.350	3, 120	11.788	0.008**	3, 120	28.549	0.001***
Shannon Index (H')									
Ecosystem (ECO)	1, 119	0.055	0.814	1, 120	3.028	0.082	1, 120	0.919	0.337
Invasion level (IL)	3, 119	23.791	0.001***	3, 120	36.571	0.001***	3, 120	16.663	0.001***
$ECO \times IL$	3, 119	5.903	0.116	3, 120	7.533	0.057	3, 120	38.690	0.001***
Simpson Index (D)									
Ecosystem (ECO)	1, 119	0.170	0.680	1, 120	3.814	0.051	1, 120	0.387	0.534
Invasion level (IL)	3, 119	12.441	0.006**	3, 120	33.371	0.001***	3, 120	19.740	0.001***
$ECO \times IL$	3, 119	3.669	0.299	3, 120	19.455	0.001***	3, 120	14.728	0.002**
Pielou evenness (J)									
Ecosystem (ECO)	1, 119	0.233	0.629	1, 120	3.751	0.053	1, 120	1.684	0.194
Invasion level (IL)	3, 119	39.256	0.001***	3, 120	36.236	0.001***	3, 120	14.782	0.002**
$ECO \times IL$	3, 119	7.673	0.053	3, 120	15.476	0.002**	3, 120	17.523	0.001***

Models were carried out with species nested within ecosystem type and using location as random effect with Wald  $\chi^2$  Method and restricted maximum likelihood (REML). Abundance was calculated using Poisson distribution and link function = log

*df D*egrees of Freedom, *Pr*(> *Chisq*) = *p*-value

Asterisks indicate statistical differences p < 0.05; p < 0.01; p < 0.01; p < 0.01

Values in bold indicate significance at  $p \le 0.05$ 

Table 3Results frommultivariate test forhomogeneity of dispersionanalyses (PERMDISP) ofdifferences in areas invaded by(A) Acacia dealbata, (B) Acacialongifolia and (C) Acaciamelanoxylon. Significance testswere performed based on aJaccard's dissimilarity matrixand 999 permutations using thebeta.pair function of the 'vegan'package in R

PERMDISP	Acacia dealbata			Acacia longifolia			Acacia melanoxylon		
	df	F-value	Pr(>F)	df	F-value	Pr(>F)	df	<i>F</i> -value	Pr(>F)
Species turnover									
Ecosystem	1, 118	3.250	0.084	1, 118	10.43	0.004**	1, 118	26.739	0.001***
Invasion level	3, 116	1.291	0.255	3, 116	5.271	0.002**	3, 116	0.761	0.528
Nestedness									
Ecosystem	1, 118	0.181	0.687	1, 118	2.272	0.138	1, 118	17.102	0.001***
Invasion level	3, 116	3.638	0.014*	3, 116	3.149	0.037*	3, 116	4.144	0.008**
Total beta-divers	sity								
Ecosystem	1, 118	5.819	0.011*	1, 118	12.238	0.002**	1, 118	18.731	0.001***
Invasion level	3, 116	1.684	0.174	3, 116	9.484	0.001***	3, 116	2.875	0.052

df degrees of freedom, Pr(>F) p-value. Number of permutations for each analysis = 999

Asterisks indicate statistical differences \*p < 0.05; \*\*\*p < 0.001

Values in bold indicate significance at  $p \le 0.05$ 



Table 4Results from themultivariate permutationalanalysis (PERMANOVA) ofdifferences in areas invaded by(A) Acacia dealbata, (B) Acacialongifolia and (C) Acaciamelanoxylon

PERMANOVA	df	SS	MS	Pseudo-F	$R^2$	Pr(>F)
(A) Acacia dealbata						
Ecosystem (ECO)	1	0.844	0.844	9.614	0.054	0.001***
Invasion level (IL)	3	3.732	1.244	14.176	0.240	0.001***
$ECO \times IL$	3	1.118	0.371	4.227	0.072	0.001***
Residuals	112	9.827	0.088		0.633	
Total	119	15.515			1.000	
(B) Acacia longifolia						
Ecosystem (ECO)	1	1.234	1.234	10.911	0.054	0.001***
Invasion level (IL)	3	7.703	2.568	22.708	0.339	0.001***
$ECO \times IL$	3	1.123	0.374	3.311	0.049	0.001***
Residuals	112	12.665	0.113		0.557	
Total	119	22.725			1.000	
(C) Acacia melanoxylon						
Ecosystem (ECO)	1	1.757	1.757	20.441	0.097	0.001***
Invasion level (IL)	3	4.712	1.570	18.267	0.260	0.001***
$ECO \times IL$	3	2.005	0.668	7.774	0.111	0.001***
Residuals	112	9.629	0.086		0.532	
Total	119	18.103			1.000	

The PERMANOVA with the *adonis* function (strata = location) in 'vegan' package in R was based on a Bray–Curtis similarity matrix of standardized on log(x + 1)-transformed data

df degrees of freedom, SS sum of squares, MS mean square, Pseudo-F F-statistic, Pr(>F) p-value

Asterisks indicate statistical differences \*\*\*p < 0.001

Values in bold indicate significance at  $p \le 0.05$ 

 Table 5
 Results from the generalized linear mixed models (GLMM) to test the effect of the invasion level (reference, uninvaded, medium and highly invaded) for differences on abundance and species richness for the six most abundant feeding guilds

Feeding guilds	Acacia dealbata			Acacia longifolia			Acacia melanoxylon		
	Mean comp	$\chi^2$	Pr(> Chisq)	Mean comp	χ <sup>2</sup>	Pr(> Chisq)	Mean comp	$\chi^2$	Pr(> Chisq)
Abundance									
Detritivore	RF = MI > UN = HI	46.698	0.001***	$\mathrm{HI}=\mathrm{MI}>\mathrm{UN}>\mathrm{RF}$	156.21	0.001***	HI = MI > RF = UN	172.28	0.001***
Herbivore	RF > UN > MI = HI	369.67	0.001***	$\mathrm{MI} > \mathrm{UN} > \mathrm{HI} > \mathrm{RF}$	1503.5	0.001***	$\mathrm{MI} > \mathrm{RF} > \mathrm{HI} > \mathrm{UN}$	381.57	0.001***
Nectar feeder	$RF \geq UN \geq MI \geq HI$	27.683	0.001***	UN > RF > MI > HI	65.252	0.001***	RF > MI = UN = HI	53.726	0.001***
Omnivore	$\mathrm{UN} \geq \mathrm{MI} \geq \mathrm{RF} \geq \mathrm{HI}$	17.121	0.001***	$\mathrm{RF} > \mathrm{UN} > \mathrm{MI} > \mathrm{HI}$	444.15	0.001***	$\mathrm{MI}=\mathrm{UN}>\mathrm{RF}=\mathrm{HI}$	117.93	0.001***
Parasite	RF = UN = MI > HI	28.985	0.001***	RF = MI = UN > HI	14.007	0.003**	RF > UN > MI = HI	343.71	0.001***
Predator	$\mathrm{UN} > \mathrm{MI} > \mathrm{RF} > \mathrm{HI}$	83.696	0.001***	UN = MI = RF > HI	41.06	0.001***	$\mathrm{UN}=\mathrm{MI}>\mathrm{HI}>\mathrm{RF}$	158.28	0.001***
Species richness									
Detritivore	MI = RF = UN = HI	1.629	0.653	UN = RF = MI = HI	2.236	0.525	MI = HI = UN = RF	3.605	0.307
Herbivore	UN = RF = MI = HI	3.483	0.323	RF = MI = UN = HI	7.776	0.051	$RF = MI \geq UN \geq HI$	9.042	0.029*
Nectar feeder	$RF \geq UN = MI \geq HI$	15.272	0.002**	$\mathrm{UN}=\mathrm{RF}\geq\mathrm{MI}\geq\mathrm{HI}$	15.206	0.002**	RF > MI = HI = UN	15.094	0.002**
Omnivore	$HI \geq MI = UN \geq RF$	8.139	0.043*	RF = MI = UN = HI	4.559	0.207	UN = MI = RF = HI	5.192	0.158
Parasite	RF = UN = MI = HI	0.540	0.910	RF = MI = HI = UN	4.836	0.184	HI = MI = UN = RF	3.975	0.264
Predator	UN = RF = MI > HI	14.349	0.002**	$MI \geq HI = UN \geq RF$	9.166	0.027*	$MI=HI\geq UN\geq RF$	9.91	0.019*

Models were carried out with species nested within ecosystem type and using location as random effect with Wald  $\chi^2$  Method and restricted maximum likelihood (REML). Abundance was compared using Poisson distribution and link function = log

Mean comp. mean comparisons, Pr(> Chisq) p-value

Asterisks indicate statistical differences p < 0.05; p < 0.01; p < 0.01; p < 0.01

Values in bold indicate significance at  $p \le 0.05$ . Invasion levels are ordered with the highest mean on the left and the lowest on the right. RF reference ecosystem habitat type, UN uninvaded, MI medium invaded and HI highly invaded. ' = '' signifies no significant differences, ' > '' signifies that habitats to the left are significantly more abundant/species-rich, "  $\ge$  '' signifies that the first habitat is significantly more abundant/species-rich than the last habitat



species diversity loss but also altering species composition (Olden et al. 2004).

# **Trophic and taxonomic groups**

The combined use of trophic and taxonomic groups is advantageous for a better comprehension of the consequences of plant invasions on ecological processes (Gomes et al. 2018). The expansion of introduced plants can result in a reduction in trophic groups, even if native diversity is maintained (Vellend et al. 2013; Dornelas et al. 2014). Introduced plants tend to have higher arthropod taxonomic diversity, whereas native assemblages have more specialist species that results in higher functional diversity (Okimura and Mori 2018). We predict that the trophic groups observed depend closely on the type of ecosystem since in places better conserved there will be greater trophic diversity. The results show that abundance and species richness of feeding guilds were significantly reduced in areas invaded by the three target acacias. These results agree with some authors, which found that introduced plants can alter the proportion of trophic groups in invaded areas (Moroń et al. 2009; McCary et al. 2016). Particularly in areas invaded by A. dealbata, the abundance of all trophic groups was significantly lower, while species richness was also lower for nectar feeders and predators. Moroń et al. (2009) found that plant invasions can reduce the abundance and species richness of specialist pollinators, altering the entire wild pollinator community. However, this may be the result of the three acacias studied having no flowers during the study. Generalist pollinators can be attracted by the flowers of introduced plants, increasing their abundance (Traveset and Richardson 2006; Gillespie and Elle 2018). Also, introduced plants can have negative impacts on primary consumers, but also can favour the abundances of secondary consumers (Hartley et al. 2010; McCary et al. 2016). Despite introduced plants modification of native habitats, which could affect secondary consumers such as predators, some authors have noted that predators might be favoured by plant invasions (Van der Colff et al. 2015; Dudek et al. 2016; Gomes et al. 2018). For areas invaded by A. longifolia, our results showed a similar tendency. Nevertheless, in areas invaded by A. melanoxylon, detritivores occurred in significantly higher abundance in high and medium invaded areas, which contradicts the study by Castro-Díez and Alonso (2017), where the contribution of the amount of organic matter rarely benefit detritivores. Hence, the effects of introduced plants may negatively affect specialized detritivores (Wolkovich et al. 2009), which might have considerable impacts on ecosystem dynamics.

Some studies focus only on particular arthropod taxa (e.g. van Hengstum et al. 2014), but several groups likely respond differently to the invasive plants (Simao et al. 2010). *Acacia* invasions tend to result in homogenization across

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## Conclusion

Our study highlights that invasive acacias altered the species composition and diversity by not only by a reduction of the abundance and species richness but also by an alteration of the different trophic groups of the arthropod assemblages at invaded areas. Arthropod communities are sensitive groups that can be affected by introduced plants, modifying the interactions and changing the environmental scenarios. Understanding whether introduced species cause ecological harm or benefit over arthropods species at different community levels is crucial, especially if we aim to control and eliminate invasive species or implement common targets of restoration and conservation programmes. This could be key to predict changes in the interactions and functional aspects that occur in nature due to plant invasions. In this sense, further studies may explore long-term modifications produced by invasive plants on arthropod assemblages and the subsequent alteration of ecological networks. The information reported here is important for implementing management strategies to diminish the impacts of these introduced plants on biodiversity at the habitat level.

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