Biol Invasions
https://doi.org/10.1007/s10530-020-02368-5

ORIGINAL PAPER

Functional segregation of resource-use strategies of native and invasive plants across Mediterranean biome communities

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Received: 24 May 2020 / Accepted: 19 September 2020

Abstract Functional segregation among species in a community depends on their mean trait values (i.e. functional distinctiveness), and the range of trait attributes exhibited by each species (i.e. functional diversity). Previous evidence suggests that invasive plants tend to display traits related to a more acquisitive resource-use strategy than natives. However, the contribution of intraspecific trait variation to functional diversity has received little attention in community ecology, and might provide interesting information about community processes. In this study, we used eight plant traits related to carbon and nutrient acquisition of coexisting dominant native and invasive plants in eight communities across the Mediterranean-climate biome to determine sources of functional segregation between native and invasive species. We found three major axes of functional variation, related to leaf economics, resource-use efficiency, and plant height. Invasive species across communities had leaf traits related to an acquisitive resource-use strategy in contrast to native species, whereas differences in the second and third axes were community dependent. Invasive species were more functionally diverse than native species across the dataset and in four out of the

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Electronic supplementary material The online version of this article (https://doi.org/10.1007/s10530-020-02368-5) contains supplementary material, which is available to authorized users.

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eight communities. Intraspecific variance accounted for 11%–27% of total trait variation and was on average greater in invasive species, and especially important in the axis related to resource use efficiency. These results, although dependent on the trait and community considered, offer interesting insights to the sources of functional trait diversity of native and invasive species within communities, indicating that intraspecific variation might not be equally distributed between native and invasive species.

Keywords Functional diversity · Functional strategies · Intraspecific variance · Invasive plants · Leaf economics spectrum · Plant life form

Introduction

Functional segregation among species in a community depends on the mean difference between their trait values, which represents their functional distinctiveness; and the range of trait values exhibited by each species, which contributes to functional diversity (Violle and Jiang 2009; Hulme and Bernard-Verdier 2018). High functional distinctiveness allows invasive species to establish in the recipient community by minimizing interspecific competition (MacDougall et al. 2009; Cadotte et al. 2018; Divíšek et al. 2018; de la Riva et al. 2019). Previous evidence suggests that invasive species tend to display traits related to fast return on investments of nutrients, such as higher specific leaf area or lower tissue construction costs, than native congeners (Pyšek and Richardson 2007), or coexisting natives (Daehler 2003; Ordonez et al. 2010; Funk et al. 2016). This is often the case in Mediterranean habitats, where invasive plants frequently display traits of rapid resource acquisition in comparison with coexisting native species (D'Antonio and Vitousek 1992; Arianoutsou et al. 2013).

Mediterranean regions are frequently dry and low-resource environments where strong abiotic constraints structure trait composition (de la Riva et al. 2018; Michelaki et al. 2019). Thus, functional distinctiveness between native and invasive species might be limited within the environmental constraints of Mediterranean communities (environmental filtering; Cadotte et al. 2018). It has been argued that environmental filtering is important at higher scales, with species from the same biome being functionally similar (Echeverría-Londoño et al. 2018), whereas functional distinctiveness operates at a local scale (Loiola et al. 2018). For instance, plant species adapted to dry habitats, such as the Mediterranean, often show contrasting resource uptake strategies due to opportunistic behaviour with respect to water and nutrient use efficiency (Querejeta et al. 2018; Carvajal et al. 2019). Furthermore, studies have observed invaders with very different functional profiles to establish in Mediterranean habitats (Tecco et al. 2010; de la Riva et al. 2019), suggesting that different mechanisms of invasion might operate.

Functional diversity of a community depends on interspecific and intraspecific trait variance (Violle and Jiang 2009). Intraspecific variance depends on the species and traits under consideration (Albert et al. 2011; Siefert et al. 2015), environmental constraints (i.e. climate and resource availability), and ecological processes operating in each community (Grime and Mackey 2002; Messier et al. 2010; Walters and Gerlach 2013). Because intraspecific trait variance often accounts for a smaller proportion ($\sim$ 25%) of total trait diversity than interspecific variance (Albert et al. 2011; Siefert et al. 2015), it is frequently overlooked in the context of biological invasions (Hulme and Bernard-Verdier 2018; but see Helsen et al. 2020). However, the sources and extent of intraspecific trait variance might differ between native and invasive species within the same community. It has been argued that, whereas native species occupy specific suitable patches within their range (Gallien et al. 2010), invasive plants are often generalist species (Okimura and Mori 2018), able to thrive under diverse ecological constraints (Clavel et al. 2011), and may show greater plasticity than phylogenetically related non-invasive species (Sultan 2001; Funk 2008; Davidson et al. 2011; Martín-Forés et al. 2017). Thus, we might expect that, in a given community, the contribution of intraspecific variance to total trait diversity will be greater in invasive than native species.

To correctly assess the role of intraspecific variance in the functional segregation of native and invasive species, it is necessary to consider two things. First, the relative contribution of intraspecific trait variance to total diversity might largely depend on the observed interspecific variance (de Bello et al. 2011). Thus, a greater contribution of intraspecific trait variance to total diversity of invasive species might just reflect that native species are overall more diverse, i.e. are more different among themselves (have greater interspecific variance). Second, native and invasive species across Mediterranean Regions tend to show contrasting life forms, with invasive species being more frequently annual species in contrast to native perennial species (Arianoutsou et al. 2013; Funk et al. 2016). Therefore, intraspecific trait variance in Mediterranean communities could depend on species' life forms, rather than origin per se. It has been argued that long-lived plant species might show higher intraspecific variation in traits related to leaf morphology due to greater ontogenetic variation (Watson et al. 1995; Sultan 2004), but be more physiologically constrained by costly leaf tissues than ruderal and fast-growing plant species (Maire et al. 2013). It is crucial to assess these considerations to correctly understand functional segregation in trait-space.

Plant performance is rarely determined by a single trait, thus it is necessary to move towards a whole-plant approach by exploring trait covariation along functional axes (Albert et al. 2011; Díaz et al. 2016; Hulme and Bernard-Verdier 2018). There are several axes of trait covariation, such as leaf and water economy, light competition or reproductive effort (Laughlin 2014; Díaz et al. 2016; Prieto et al. 2018). In this regard, the best known axis of plant trait covariation is the leaf economics spectrum (Wright et al. 2004), which represents a trade-off between acquisition and conservation of resources, i.e. quick or slow return of investments. Whereas the acquisitive-end of this spectrum encompasses species with short-lived leaves with high maximum photosynthetic rates and leaf nutrient content, the conservative-end includes species with long-lived leaves and high construction costs. As there are several known axes of trait covariation, it is necessary to use tools that allow to estimate functional segregation considering all functional axes simultaneously such as trait hypervolumes based on kernel density estimation methods (Blonder et al. 2018). Hypervolumes define high-dimensional, non-continuous shapes and permit an accurate quantification of the amount of trait-space occupied by a species (i.e. functional diversity) (Blonder et al. 2018). Hence, hypervolumes may be a useful tool to explore functional segregation between native and invasive species (see Guerin et al. 2019; Helsen et al. 2020).

To test this framework, we analysed native and invasive species' traits data from eight communities across the five Mediterranean-climate regions (Funk et al. 2016). Previous analyses with a focus on single traits showed that invasive species had traits related to faster resource acquisition and use than native species, and that this difference was related to life form (Funk et al. 2016). Here, we aim to understand how native and invasive species segregate in trait-space by exploring the two sources of functional segregation, i.e. functional distinctiveness and diversity. First, we identified the major axes of trait covariation, and determined whether native and invasive species occupy different positions along them (i.e. functional distinctiveness). Second, we compared the functional diversity of native and invasive species, and quantified whether the contribution of intraspecific trait variance to the total functional diversity differs between invasive and native species.

Material and methods

Field data collection

We analysed plant traits of dominant native and invasive species of eight representative communities from five Mediterranean regions collected by Funk et al. (2016, 2017) (Table 1). Particularly, we measured eight traits of leaf morphology, physiology (leaf chemical compounds) and plant size related to plant resource-use and acquisition strategies (Table 2). These traits have been widely studied in the literature because of their importance in community assembly (Tecco et al. 2010; Michelaki et al. 2019; Henn et al. 2019; Helsen et al. 2020). The database included a total of 734 observations: 137 species and four to five replicate plants per species and community (Table A1). Eighteen species were present in more than one community.

Species were classified according to their origin as native or invasive; and according to their life form as annual, herbaceous perennial, or woody. Here "invasive" follows the definition of Richardson et al. (2000), i.e. non-native species with great reproductive potential which become very abundant locally and are able to quickly spread from the area of introduction. The category annual were therophytes, i.e. species that spend the summer in the seed bank mostly grasses and

Table 1 Studied communities and their soil characteristics, mean annual precipitation, management regimes, and number of species grouped by origin and life form

Region	Community	Soil N (g N/100 g soil)	Soil P (mg P/kg soil)	Soil pH	Mean annual rainfall	Grazing	Years since last fire	Number of native species	Number of invasive species	Annual	Herbaceous perennial	Woody	Total
Australia	Banksia woodland	0.05	47.7	5.38	834	Low	> 20	10	8	5	9	4	18
	Coastal banksia woodland	0.06	150.9	5.74	734	Low	> 30	7	6	3	7	3	13
Spain	Coastal grassland	0.05	117.8	7.96	550	High	> 50	20	9	11	10	8	29
California	Serpentine grassland	0.23	30	6.69	760	Low	> 50	23	4	17	6	4	27
	Coastal sage scrub	0.19	628.3	6.58	330	Low	3	14	9	10	6	7	23
South Africa	Acid sands fynbos	0.03	31	4.81	522	Low	10	11	5	3	6	7	16
	Renosterveld	0.29	304	5.75	515	Low	> 50	11	5	5	3	8	16
Chile	Sclerophyll woodland	0.09	1001	7.15	360	Low	> 100	13	5	5	5	8	18

Table 2 Traits considered in this study, abbreviation, units and functional role

Trait	Abb	Units	Significance
Leaf mass per area	LMA	$g \times m^{-2}$	Plant investment in structural leaf tissue. High LMA indicates a conservative resource-use strategy
Mass-based photosynthetic rate	Amass	nmol $CO_2 \times g^{-1} \times s^{-1}$	Photosynthetic rate per leaf mass at saturating light levels
Instantaneous water-use efficiency	WUE	µmol CO_2 × mmol H_2O^{-1}	Ratio between CO_2 assimilation and transpiration
Mass-based leaf nitrogen content	Nmass	mg $N \times g^{-1}$	Amount of nitrogen per leaf mass. Related to plant growth and economics
Photosynthetic nitrogen-use efficiency	PNUE	mmol $CO_2 \times mol^{-1}\ N \times s^{-1}$	Photosynthetic capacity per unit leaf nitrogen
Mass-based leaf phosphorus content	Pmass	mg $P \times g^{-1}$	Amount of phosphorus per leaf mass. Related to plant growth and economics
Photosynthetic phosphorus-use efficiency	PPUE	mmol $CO_2 \times mol^{-1}\ P \times s^{-1}$	Photosynthetic capacity per unit leaf phosphorus
Plant height	Height	cm	Indicates the position of the plant in the vertical light gradient of the community

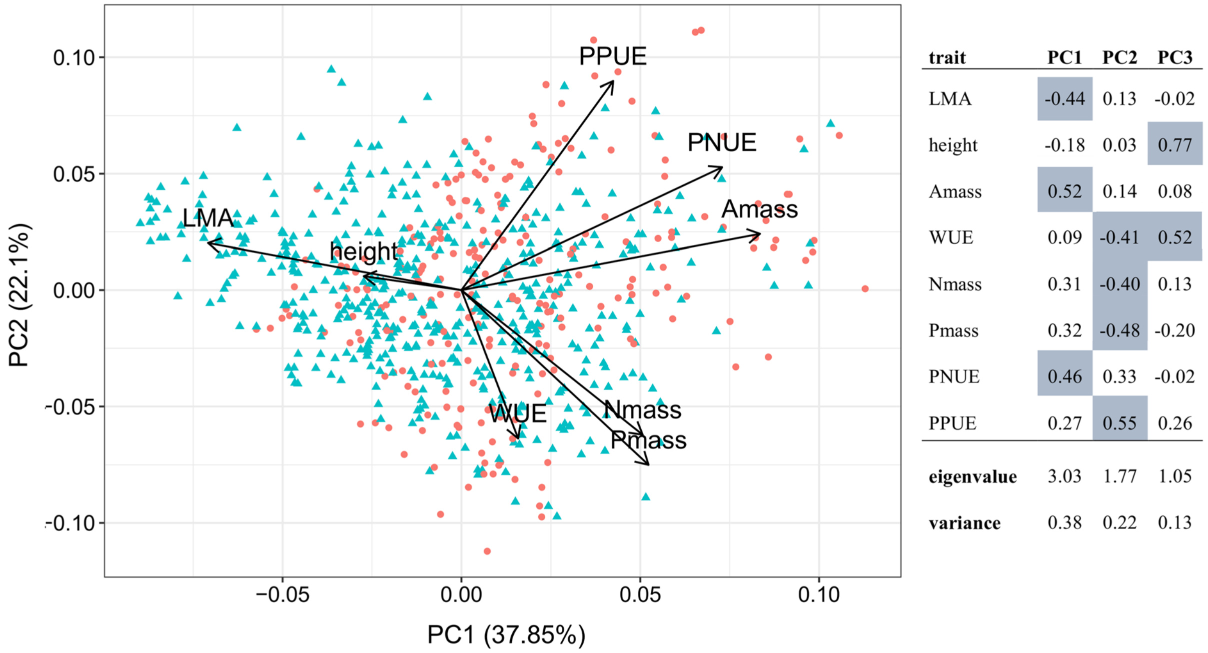
forbs. Herbaceous perennials were plants without lignified stems but with dormant organs below or near the ground. Woody species included shrubs and trees.

Data analyses

First, we ran a principal component analysis (PCA) to identify major axes of trait covariation, and reduce the dataset into fewer functional dimensions (Laughlin 2014). We used the first three principal components for posterior analyses, those with eigenvalues greater than one. Then, we explored the functional distinctiveness between native and invasive species, i.e. if native and invasive species differ in their mean trait values along each principal component. For each principal component, we fitted a linear mixed model for the total dataset with community and species, nested within community, as random effect, and a linear mixed model for each community with species as random effects. We used the Satterthwaite method to approximate degrees of freedom. The residual versus fitted plots revealed that errors were normally distributed and homoscedastic.

Second, to characterize the functional diversity of native and invasive species, we built hypervolumes using a Box kernel density estimation method and Silverman bandwidth estimator (hypervolume package, Blonder et al. 2018). For the trait-space defined by the three principal components, we built several hypervolumes: one for all native species in the dataset, one for all invasive species in the dataset, and one for each group of native and invasive species within each community. We also built hypervolumes to estimate the diversity of the total pool of native and invasive species in each principal component. The units of the hypervolumes are reported as the standard deviations of PCA scores in the first three axes, raised to the power of the number of trait dimensions (SD^3). As hypervolumes depend on species richness, and all communities have more native than invasive species, we created 99 randomized communities where the number of native species was adjusted to the number of invasive species in the community (see invasive species column in Table 2). To compare the functional diversity of native and invasive species across randomized communities, we calculated the mean effect size (Hedges'd) and bias-corrected 95%-bootstrap confidence intervals (effsize package, Torchiano 2018). A mean effect size was considered significantly different from zero when its confidence interval did not bracket zero.

Third, we assessed if the relative contribution of intraspecific variance to total trait diversity (i.e. total variance of a pool of native or invasive species in a given principal component) is greater in invasive than native species. We partitioned the total community



trait	PC1	PC2	PC3
LMA	-0.44	0.13	-0.02
height	-0.18	0.03	0.77
Amass	0.52	0.14	0.08
WUE	0.09	-0.41	0.52
Nmass	0.31	-0.40	0.13
Pmass	0.32	-0.48	-0.20
PNUE	0.46	0.33	-0.02
PPUE	0.27	0.55	0.26
eigenvalue	3.03	1.77	1.05
variance	0.38	0.22	0.13

Fig. 1 Principal Component Analysis (PCA) of eight plant traits from 137 natives (blue triangles) and invasive (red dots) plant species in Mediterranean communities (4–5 replicates per species). The table shows the loadings and variance associated with each principal component with eigenvalues over 1. The most relevant traits of each principal component have been shaded. Traits: LMA: leaf mass per area, Amass: mass-based photosynthetic rate, WUE: instantaneous water use efficiency, Nmass: mass-based leaf nitrogen concentration, Pmass: mass-based leaf phosphorus concentration, PNUE: photosynthetic nitrogen-use efficiency, PPUE: photosynthetic phosphorus-use efficiency, and Height: vegetative plant height

variance into interspecific and intraspecific variance as formulated in Eq. 1 of de Bello et al. (2011), i.e. the extent of trait variation in a community which results from variation between coexisting species and variation among individuals of a species. In this formulation, the contribution of each species to the variance partitioning is identical (de Bello et al. 2011). Then, we divided the absolute intraspecific variance by the total community variance to obtain the relative contribution of intraspecific trait variance to total trait diversity (Siefert et al. 2015). We did this for the total pool of native and invasive species, and native and invasive species within each community.

Finally, we explored whether the functional diversity and the contribution of intraspecific trait variance to total diversity of native and invasive species is related to their life forms. For all three dimensions, and each principal component, we estimated the functional diversity of the total pool of annual, herbaceous perennial and woody species with hypervolumes (Blonder et al. 2018), and compared them by computing Hedges'd and bias-corrected 95%-bootstrap confidence intervals between all groups (effsize package, Torchiano 2018). Then, we partitioned the total trait diversity of each group into interspecific and intraspecific variance (de Bello et al. 2011), and calculated their contributions to total diversity (Siefert et al. 2015). If the relative contribution of intraspecific trait variance of native and invasive species is related to their life forms, then we might expect to observe a similar or greater effect size between annual and perennial species compared to between native and invasive. All statistical analyses were performed, and all figures produced, in the R-3.6.1 statistical platform (R Development Core Team 2019).

Results

Functional strategies of native and invasive species

The first three components of the PCA accumulated 73.11% of the total variance (Fig. 1). The first principal component explained 37.85% of the variance and reflected a coordination between Amass (mass-based photosynthetic rate), LMA (leaf mass per area), and PNUE (photosynthetic nitrogen-use efficiency) (Fig. 1), which is representative of the leaf economics spectrum (Wright et al. 2004). The second principal component explained 22.10% of the variance and reflected a covariation between leaf nutrient concentration, WUE (instantaneous water-use efficiency) and PPUE (photosynthetic phosphorus-use efficiency) and represents the trade-off between water- and phosphorous-use efficiency. The third principal component explained 13.15% of the variance and was linked to plant height and, to a lesser extent, WUE.

Overall, native species occupied the high LMA end of PC1, whereas invasive species occupied the high Amass and PNUE end ($F_{1,157} = 27.04$, $p < 0.001$). Native and invasive species occupied similar positions in PC2 ($F_{1,157} = 0.03$, $p = 0.87$) and PC3 ($F_{1,158} = 0.94$, $p = 0.33$). Within communities, invasive species were significantly displaced towards the high Amass and PNUE end of PC1 in six communities (Fig. 2A). Invasive species in sclerophyll woodland and coastal sage scrub occupied a position of greater PPUE end in PC2 than native species, whereas in acid sands fynbos invasive species occupied a position of greater Nmass (mass-based leaf nitrogen content), Pmass (mass-based leaf phosphorus content) and WUE ($p < 0.05$ in all cases) (Fig. 2B). Native species in sclerophyll woodland were on average taller than invasive species ($F_{1,18} = 5.34$, $p = 0.03$).

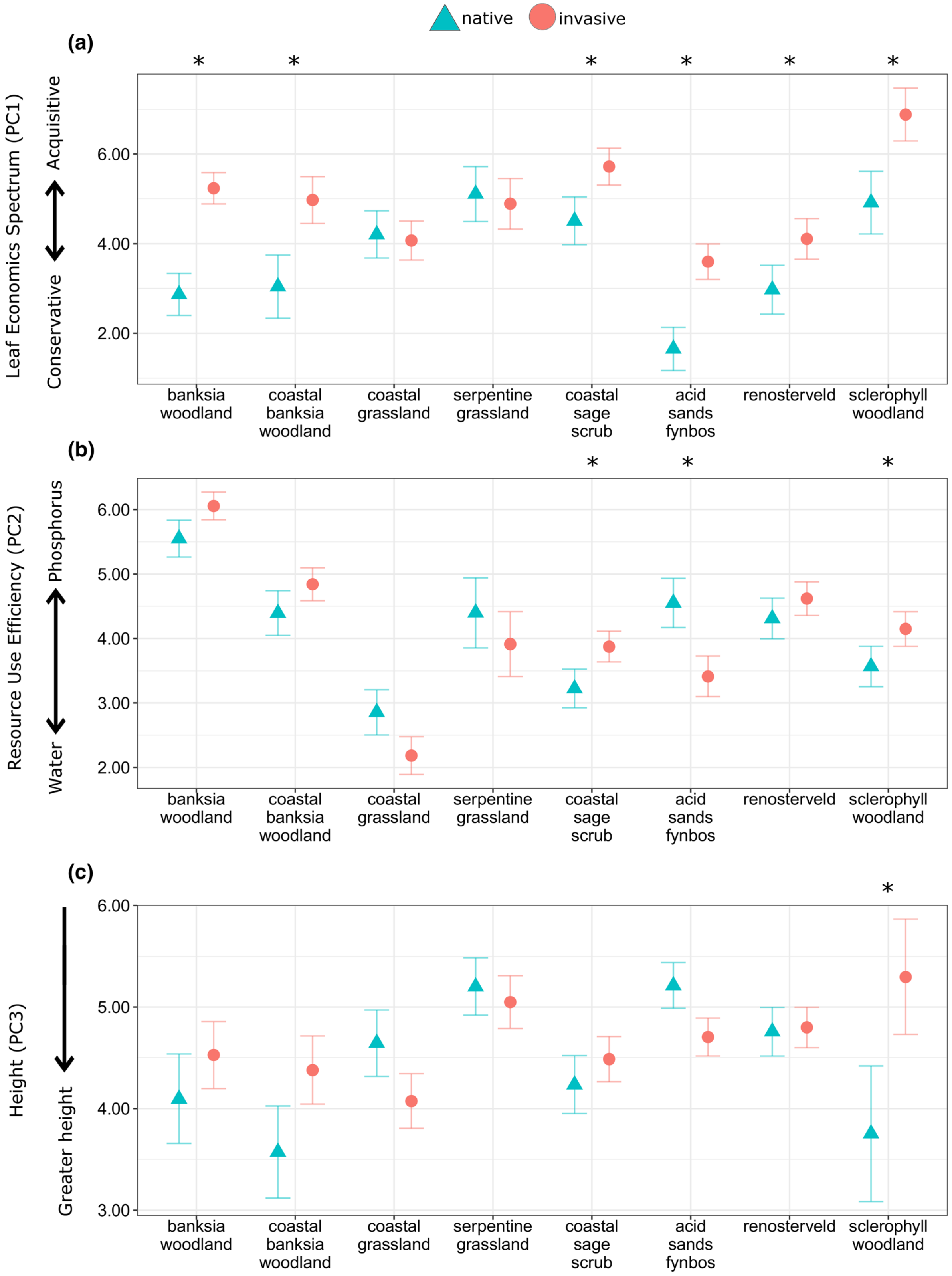
Functional diversity of native and invasive species

Overall, invasive species showed 9.65% greater functional diversity in trait-space respect to natives (natives: 231.28 SD^3 ± 5.8, invasives: 253.6 SD^3 ± 2.3, mean ± standard error). Particularly, invasive species were 26.02% more diverse than native species in PC2 (water and phosphorous use efficiency; nat: 7.84 SD ± 0.09, inv: 9.98 SD ± 0.10), whereas native species showed 4.80% greater functional diversity than invasive species in PC1 (leaf economics spectrum; nat: 10.49 SD ± 0.14, inv: 9.99 SD ± 0.04) and 8.51% in PC3 (height; nat: 7.27 SD ± 0.09, inv: 6.70 SD ± 0.03) (Fig. 3). At the community level, invasive species showed greater functional diversity than natives in serpentine grassland (nat: 50.41 SD^3 ± 5.46, inv: 90.19 SD^3 ± 0.99), coastal sage scrub (nat: 83.16 SD^3 ± 2.33, inv: 108.02 SD^3 ± 0.98), acid sand fynbos (nat: 35.58 SD^3 ± 1.58, inv: 78.16 SD^3 ± 1.34) and renosterveld (nat: 22.41 SD^3 ± 1.23, inv: 28.69 SD^3 ± 0.48) (Fig. 3). Native species showed greater functional diversity than invasive species in banksia woodland (nat: 103.44 SD^3 ± 2.55, inv: 50.58 SD^3 ± 0.66), coastal banksia woodland (nat: 104.94 SD^3 ± 2.75, inv: 78.17 SD^3 ± 1.56) and sclerophyll woodland (nat: 170.20 SD^3 ± 9.25, inv: 79.42 SD^3 ± 1.33). Native and invasive species within coastal grassland were equally diverse (nat: 115.53 SD^3 ± 3.57, inv: 109.14 SD^3 ± 0.45).

Fig. 2 (**a**) Distribution of native (blue triangles) and invasive ▶ (red dots) species along PC1 (leaf economics spectrum) within communities. Greater values of PC1 correspond to the high Amass (mass-based photosynthetic rate) and PNUE (photosynthetic nitrogen-use efficiency) end. (**b**) Distribution of native and invasive species along PC2 (resource use efficiency). Greater values of PC2 correspond to high PPUE (photosynthetic phosphorus-use efficiency). (**c**) Distribution of native and invasive species along PC3 (plant height). Greater values of PC3 correspond to the high height end. Values indicate estimates ± standard error of linear mixed models with species as random effect. Asterisks denote significant differences between native and invasive species for a given community and principal component (p value < 0.05)

The mean relative contribution of intraspecific diversity across the dataset was on average greater in invasive than native species for all principal components (PC1: 25.4% and 10.7%, PC2: 23.9% and 18.5%, PC3: 26.6% and 18.9%). At the community level, the relative contribution of intraspecific variation to PC1 trait diversity was greater for invasive than native species in five communities, and only greater for native species in renosterveld (Fig. 4). The relative contribution of intraspecific variation to PC2 trait diversity was greater for invasive than native species in three communities, and greater for native species in three communities. The relative contribution of intraspecific variation to PC3 trait diversity was greater for invasive than native species in four communities, and greater for native species in two communities.

Overall, woody species (228.3 SD^3 ± 2.9, mean ± standard error) showed 18.05% greater diversity than herbaceous perennial species (193.4 SD^3 ± 3.2) in trait-space, and herbaceous perennial species were 14.85% more diverse than annual species (168.4 SD^3 ± 1.8) (effect sizes in Table A3).


native
invasive
(a)
Leaf Economics Spectrum (PC1)
Conservative
Acquisitive
6.00
4.00
2.00
*
*
*
*
*
*
banksia woodland
coastal banksia woodland
coastal grassland
serpentine grassland
coastal sage scrub
acid sands fynbos
renosterveld
sclerophyll woodland
(b)
Resource Use Efficiency (PC2)
Water
Phosphorus
6.00
5.00
4.00
3.00
2.00
*
*
*
banksia woodland
coastal banksia woodland
coastal grassland
serpentine grassland
coastal sage scrub
acid sands fynbos
renosterveld
sclerophyll woodland
(c)
Height (PC3)
Greater height
6.00
5.00
4.00
3.00
*
banksia woodland
coastal banksia woodland
coastal grassland
serpentine grassland
coastal sage scrub
acid sands fynbos
renosterveld
sclerophyll woodland

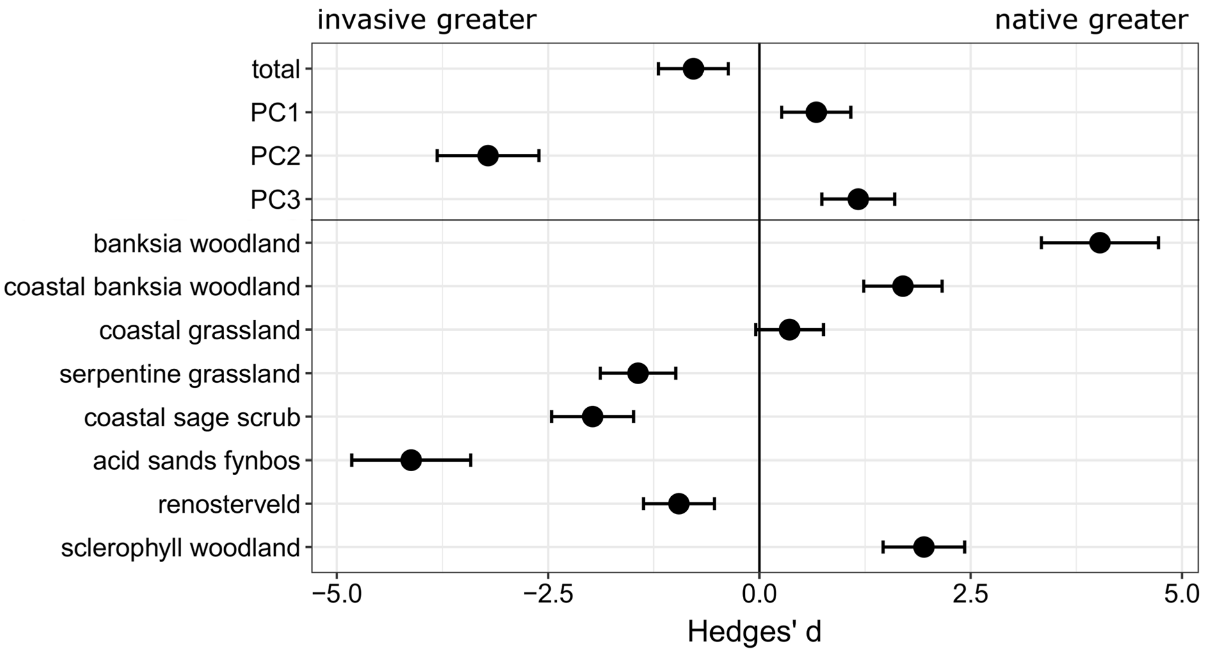


Fig. 3 Mean effect size (Hedges' d) and bias-corrected 95%-bootstrap confidence intervals for differences in the native and invasive species hypervolumes for the total pool of native and invasive species in trait-space, the total pool of native and invasive species in each dimension, and native and invasive species in trait-space within each community. Hypervolume sizes are included in Table A2. Negative mean effect sizes indicate that invasive species had on average greater hypervolume size than natives. A mean effect size is significantly different from zero when its confidence interval does not bracket zero

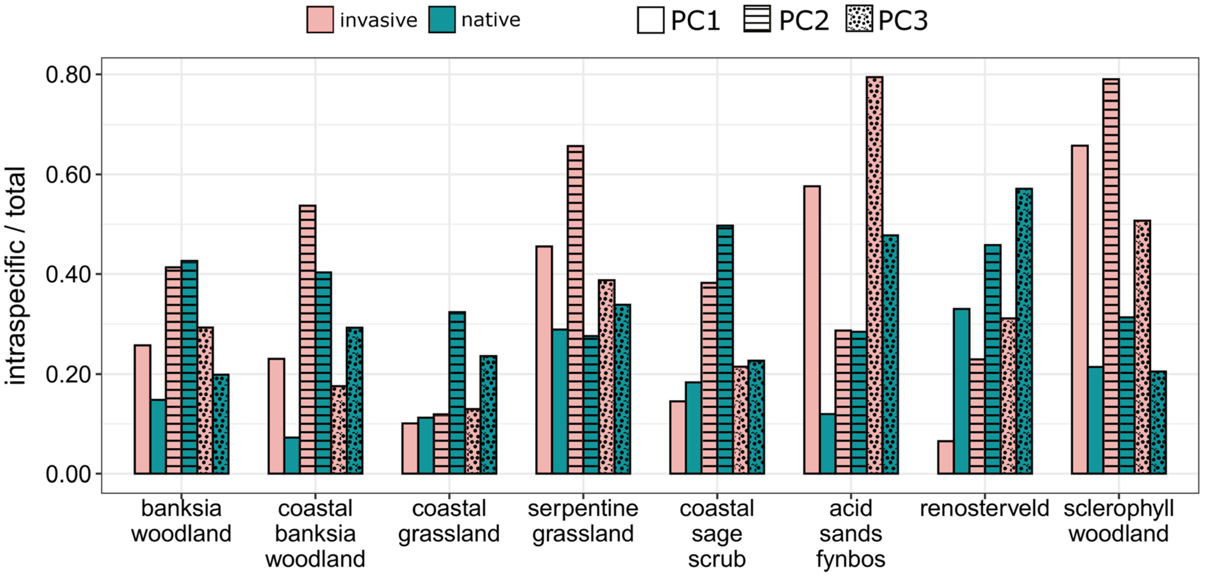


Fig. 4 Relative contribution of intraspecific variance of native and invasive species to total trait diversity for principal components with eigenvalues over one

Herbaceous perennial species (10.8 SD ± 0.1) were significantly more diverse than the other life forms in PC1, whereas annual (8.9 SD ± 0.1) and woody species (8.8 SD ± 0.1) were equally diverse. In PC2, annual species (8.9 SD ± 0.1) were significantly more diverse than the other life forms, whereas woody (8.3 SD ± 0.1) and herbaceous perennial species (8.5 SD ± 0.1) were equally diverse. In PC3, woody species (7.5 SD ± 0.1) were significantly more diverse than herbaceous perennials (5.8 SD ± 0.1), and herbaceous perennials were significantly more diverse than annual species (5.5 SD ± 0.1). In PC1, intraspecific variation accounted for 31.3% of total diversity of annual species, 11.2% for herbaceous perennial species, and 10.5% for woody species. In PC2, intraspecific variation accounted for 27.7% of annual species trait diversity, 29.9% for herbaceous perennial species, and 15.6% for woody species. In PC3, intraspecific variation accounted for 37.0% for annual species trait diversity, 23.2% for herbaceous perennial species, and 19.7% for woody species.

Discussion

Functional strategies of native and invasive species

We found that trait-space was mainly dominated by three axes of trait covariation: leaf economics, water- and phosphorus-use efficiency, and plant height. This supports the idea that certain suites of traits tend to vary together (Laughlin 2014), and plant functioning is constrained to a determined range of viable combinations (Díaz et al. 2016; Lloret et al. 2016). In line with other studies, we found great functional distinctiveness in resource use strategies between invasive species and native species of the recipient community (Pyšek and Richardson 2007; Ordonez et al. 2010; Tecco et al. 2010). These results suggest that contrasting resource use strategies are important in driving the establishment of invasive plants (e.g. Funk et al. 2016; Helsen et al. 2020). In fact, our results confirm previous evidence that the leaf economics spectrum is a main axis of functional differentiation between native and invasive species across Mediterranean communities (Tordoni et al. 2019). That is, the range of trait values displayed by the invasive species is consistent with the 'fast return on investments' end of the leaf economics spectrum not only as a general trend, but also in most of the communities studied separately (significantly different in six of them). These results indicate that higher capacity for the extraction of resources could be an advantageous strategy for invasive species (Daehler 2003; Ordonez et al. 2010; Funk et al. 2016; Henn et al. 2019); especially in habitats with strong abiotic constraints such as those in Mediterranean regions, where native species display conservative resource uptake adaptations (e.g. Lloret et al. 2016; de la Riva et al. 2017).

It is worth noting that we detected water and phosphorous availability as another trait dimension related to resource constraints. Thus, the particular segregation of native and invasive species across these communities might depend also on specific resource limitations within each community. We found functional differences between native and invasive species with respect to this dimension in sclerophyll woodland (Chile), coastal sage scrub (California), and acid sands fynbos (South Africa). Sclerophyll woodland and coastal sage scrub have the lowest mean annual precipitation and the highest soil phosphorus concentration compared to the other Mediterranean communities. In these communities, native species showed higher water-use efficiency and leaf nutrient concentration than invasive species. It is likely that native species, more frequently perennial species, benefit from having a higher stomatal control, and root systems to enhance nutrient uptake than annuals (Pérez-Ramos et al. 2013; Prieto et al. 2018; Tordoni et al. 2019). By contrast, acid sands fynbos is the community with the lowest phosphorus and nitrogen concentration in the soil, and invasive species occupy the high leaf nutrient concentration and WUE end of the spectrum. These results concur with those from studies of Mediterranean grassland species that found higher WUE in invasive species compared to natives (Vaughn et al. 2011). Higher leaf nutrient concentrations in invasive species in our dataset might reflect their fast resource uptake strategy, particularly during periods of high water availability (Pérez-Ramos et al. 2013). Collectively, these results support the idea that trait variation depends on the specific combination of environmental factors and highlights the utility of such studies for predicting plant and community responses in a changing world (Funk et al. 2016).

Disentangling the functional trait diversity of native and invasive species

Overall, our results indicate that dominant invasive species are functionally more diverse than native species across communities and in four out of the eight communities, which indicates that many resource-use profiles might allow species to invade communities (Tecco et al. 2010; de la Riva et al. 2019). That is, contrasting with previous findings (Okimura and Mori 2018), we show that invasive species constitute a functionally diverse pool which contributes to a great proportion of the community trait diversity. As discussed by Loiola et al. (2018), this may reflect that invasive species are creating new functional spaces outside the extant native pool, i.e. excluding functionally similar natives or occupying empty space, or filling empty gaps within the existing space. Yet, our approach does not allow us to identify these underlying mechanisms. Interestingly, although the total pool of perennial species was more diverse in trait-space than annuals, the pool of invasive species (most frequently annuals) was more diverse than natives. The sources of functional diversity for native and invasive species differ: greater diversity in water- and phosphorus-use efficiency for invasives and greater diversity in leaf economics and plant height for natives. In this regard, the higher hypervolumes of invasive species in trait-space support the importance of trait distinctiveness between invasive species and the native community (Helsen et al. 2020).

Overall, in agreement with previous findings (Albert et al. 2011; Siefert et al. 2015), our results indicate intraspecific variance contributed 10.7 to 26.6% of the total functional diversity. On average, the contribution of intraspecific variance was greater in invasive compared to native species. Regarding the dimensions related to leaf economics and plant height, where native species were more diverse than invasive species, the greater contribution of intraspecific variance in invasive species might reflect smaller interspecific differences. Interestingly, we show that annual and woody species were equally diverse in leaf economics traits, but the relative contribution of intraspecific variation was three times greater in annual species, which might reflect that annual species have leaves less structurally and physiologically constrained than woody species (Maire et al. 2013).

With regard to the dimension related to water- and phosphorous-use efficiency, invasive species were overall more diverse than native species and the contribution of intraspecific trait variance was 5.4% greater. This supports the theory that invasive species might be physiologically less constrained in trait-space than their native counterparts (Funk 2008; Valliere 2019). In contrast to native species, invasive species might tend to be generalists that perform well along ecological gradients (Gallien et al. 2010; Clavel et al. 2011). While this might reflect to some extent the dependency between origin and life form, studies of co-occurring annual species have found that invasives do not adhere to the same trade-off between growth and water conservation displayed in natives (Valliere 2019). The contribution of intraspecific trait variation to total diversity was twice as much in annual and herbaceous perennial species than woody species. It is likely due to the fact that herbaceous species are more responsive to microhabitat heterogeneity in water and soil nutrient availability (Chapin et al. 1990; Fernández-Alés et al. 1993). Thus, contrasting structures of inter- and intraspecific trait variance might provide interesting insights about functional responses of native and invasive species operating in different communities (Hulme and Bernard-Verdier 2018), supporting the notion that overlooking intraspecific variation might compromise the ability to correctly infer trait-driven ecological processes (Helsen et al. 2020).

One aspect of our study that warrants further comment is that the above-mentioned patterns were strongly context dependent. In fact, across most communities, intraspecific trait variance was especially important in the second principal component, related to nutrient availability, which is in line with previous evidence highlights how microhabitat heterogeneity might shape leaf attributes (Albert et al. 2010; Jung et al. 2010; Siefert et al. 2015). Invasive species were functionally more diverse than native species in acid sands fynbos and serpentine grassland, in some extent due to greater intraspecific variation. The great diversity of invasive species within these communities, and the substantial contribution of intraspecific variance to this diversity, points to invasive species being generalists with great phenotypic variation (Sultan 2001; Funk 2008; Clavel et al. 2011; Davidson et al. 2011; Martín-Forés et al. 2017), and more phenotypic variation associated with annual and herbaceous perennial species (Maire et al. 2013). In renosterveld and coastal sage scrub, the contribution of intraspecific variance to total diversity was comparable between invasive and native species, and reflected to some extent that invasive species were overall more diverse. By contrast, native species in banksia and sclerophyll woodlands were more functionally diverse than invasive species. Native species in these communities are more frequently woody perennials, much more diverse in plant height than invasive species (more often herbaceous). Hence, functional trait diversity, and the contribution of intra- and interspecific variation to this diversity, varies among communities. The regional species pools are generally the result of the environmental and historical filtering, while some specific adaptations of invasive species allow them to establish successfully at a broad spatial scale with a completely different morpho-physiological profile to the native pool (Loiola et al. 2018).

Conclusions

We applied a multidimensional analysis of plant traits and trait variation to understand the segregation between native and invasive species in trait-space across Mediterranean communities. We found great functional distinctiveness in leaf economic traits and that invasive species can be more functionally diverse than native species. Therefore, our results suggest that invasive species can employ different functional profiles to thrive in recipient communities. In some communities, intraspecific trait variation can contribute a great proportion of functional trait diversity in invasive species, which might reflect evolutionary and life form differences. These results highlight that intraspecific variation might not be equally distributed between native and invasive species, offering interesting insights to species functional trait diversity within communities.

Acknowledgements We thank Rachel Standish, William Stock, and Fernando Valladares for collecting the data.

Author's contribution JGD: Conceptualization, Methodology, Formal analysis, Investigation, Data curation, Writing—original draft, Writing—review and editing. EG: Conceptualization, Methodology, Investigation, Writing—review and editing. JLF: Investigation, Writing—review and editing. MV: Conceptualization, Investigation, Writing—review and editing.

Funding J.G.D. has received financial support through the "la Caixa" INPhINIT Fellowship Grant for Doctoral studies at Spanish Research Centres of Excellence (LCF/BQ/IN17/11620012). J.G.D. and M.V. from EXARBIN (RTI2018-093504-B-I00) project of the Ministerio de Ciencia e Innovación of Spain.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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