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Multispecies invasion increases and stabilises function in an understorey plant metacommunity.

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Abstract

Several plant traits have been linked to invasion success in studies involving single alien species or invaded versus non-invaded communities. Less consideration has been given to how traits promoting invasion success relate to invasion gradients of multiple alien species. Additionally, it is not known how patterns of trait-convergence and divergence may correlate with invasion gradients, and what traits are responsible for optimising these patterns. Here, we examine if invasion by multiple alien species is related to changes in community-wide functional traits, and patterns of trait convergence and divergence, across an invasion gradient. We collected field data in Victoria, Australia, on traits previously associated with invasion success from 15 500 m^2 plots. These plots encompassed a range of relative alien cover (~ 4 - 61%) and represented a multispecies invasion gradient. We tested relationships of each trait to the invasion gradient. We also determined trait convergence and divergence patterns across the gradient, using matrix multiplications and regression analysis. Specific leaf area and proportion of annuals significantly increased with the level of invasion. Annual life history and flowering duration maximised trait-convergence, but the two traits had different relationships to the invasion gradient. Specific leaf area, annual life history, leaf dry mass and seed mass maximised trait divergence. Evidence of trait-divergence along the gradient is represented by an increase in functional diversity with invasion level. However, variation in functional diversity was higher in little-invaded communities and stabilised at intermediate and high levels of invasion. Traits (specific leaf area and annual life history) associated with invasion success at a metacommunity scale are traits promoting rapid life cycle completion, and increases in multispecies invasion leads to an increase and consistent level of functional diversity.

Keywords: Annual life history · Functional diversity · Invasion gradient · Metacommunity · Multispecies invasion · Specific leaf area

Introduction

One of plant ecology's central goals is to determine the relative importance of processes governing local community assembly (Weiher et al. 1998). Functional traits are used to examine how assembly processes such as habitat filtering and niche differentiation structure native plant communities (McGill et al. 2006). These assembly processes are known to influence the invasion of native communities by alien species (Daehler 2003). They are also used to explain relationships between species, and between species and the environment, at a metacommunity scale (Logue et al. 2011). Certain traits increase an alien's chances of successfully invading a novel environment (van Kleunen et al. 2010; Dainese and Bragazza 2012). Invasion by multiple alien species exhibiting such traits can also lead to changes in the functional structure and diversity of the invaded community (Castro-Díez et al. 2016). Therefore, identifying community-wide traits associated with invasion and how they relate to assembly processes is important not only to predict likelihood of successful establishment, but also to understand the impact that multiple alien species have on native communities.

Two major, deterministic processes of community assembly are widely recognised to influence community functional structure. First, abiotic habitat conditions cause non-random membership of communities and act as filters that restrict the range of trait values to those that enable persistence under prevailing conditions (Cornwell and Ackerly 2009; Shipley 2010). This 'habitat filtering' leads to functionally-similar species co-occurring in similar environments (Roscher et al. 2013) This clustering of similar trait values along specific environmental or ecological gradients is referred to as trait-convergence (Díaz et al. 1998; Weiher et al. 1998; Pillar et al. 2009). The second process altering community functional structure is niche differentiation (MacArthur and Levins 1967). In contrast to habitat filtering, competition between co-occurring species within sites necessitates the partitioning of limited resources, which reduces interspecific competition and promotes coexistence between functionally dissimilar species (MacArthur and Levins 1967; Silvertown 2004). Niche differentiation generates trait-divergence patterns within the community (Laughlin et al. 2012) characterized by an increase in the range of trait values. However, competition can also exclude species when functionally-distinct traits are linked to competitive dominance (Mayfield and Levine 2010). This must be taken into

account when inferring processes such as competition from patterns of trait-convergence and divergence. Furthermore, these assembly processes are not mutually exclusive, and habitat filtering and niche differentiation can simultaneously influence species assemblages, resulting in communities exhibiting both convergence and divergence (Cornwell and Ackerly 2009). Finally, the size and composition of the species pool can determine variation in trait values within a community, through evolutionary and ecological processes such as selection and dispersal (Vellend 2010).

Assembly processes can also determine whether aliens will converge or diverge in trait values with those of recipient communities. Habitat filtering results in trait-convergence between natives and aliens (Thompson et al. 1995), whereas niche differentiation promotes successful alien establishment when, for example, aliens are better suited to disturbed environments than their native counterparts (Lake and Leishman 2004). If resource conditions in the invaded habitat are poor, aliens may outcompete natives by exhibiting trait values more suited to conserving limited resources, such as long-lived, smaller leaves (Thompson et al. 1995). Conversely, in resource-rich habitats aliens may have traits such as higher specific leaf area (SLA) that allow them to access abundant resources more readily than natives (Leishman et al. 2007). Identifying patterns of trait-convergence and divergence in invaded communities can determine how invasion alters community functional structure, and can reveal which traits of invading aliens are responsible for this change.

Several traits have been linked to successful invasion by aliens. These traits enhance performance (e.g. higher reproductive output and faster growth strategies), giving aliens a competitive advantage over co-occurring natives (Leishman et al. 2007; van Kleunen et al. 2010; Leishman et al. 2014). Arguably the most widely-supported trait characteristic of invasive plant species is SLA. High SLA is strongly correlated with growth-promoting traits such as high relative growth rate and short-lived leaves (Wright and Westoby 1999). Higher SLA has been found among invasive aliens compared to natives in several different habitats (Dainese and Bragazza 2012; Feng and van Kleunen 2016; Marx et al. 2016) and across multiple disturbance and/or resource regimes (Grotkopp et al. 2002; Lake and Leishman 2004). Other traits associated with invasion success and fast growth strategies include short lifespan (annual life history) and flowering duration, the latter of which increases reproductive output by providing higher visitation rates by pollinators and increased overlap between flowering periods and

activities of multiple pollinators (Cadotte and Lovett-Doust 2001; Chrobock et al. 2013; Feng et al. 2016).

Studies determining which traits enable a species to invade have seldom incorporated gradients of multispecies invasion. Most trait-based invasion research, including the use of invasion gradients, focuses on single-species invasions and impacts, or have compared invasive aliens with native congeners (Pyšek and Richardson 2007; Kuebbing et al. 2013; Bansal and Sheley 2016). Those studies that do consider multiple alien species usually involve pairwise comparisons of species, or invaded versus non-invaded communities (Pyšek and Richardson 2007). Invasion, however, is a cumulative process developing along an invasion continuum, with habitats regularly invaded by more than one species over time, and with varying levels of invasion severity (Traveset and Richardson 2011; Campos et al. 2013). Collectively, aliens may exhibit certain trait values that differ from natives and could impact community functional structure and assemblage patterns more severely than the impacts of any single invader (Kuebbing et al. 2013). Examining which traits are divergent or convergent along a multispecies invasion gradient could i) identify what components of community functional structure are altered by multispecies invasion and ii) what consequences this has for functional diversity. Furthermore, investigating community trait similarities and dissimilarities could reveal at what point along the multispecies invasion gradient the greatest shift in patterns of divergence and convergence occurs.

Here, we examine if invasion by multiple alien species is related to changes in community-wide functional traits, and trait-convergence/divergence patterns, across an invasion gradient in a dry forest plant metacommunity. We investigate three key questions: 1) how do community-wide plant traits change with an increase in the level of multispecies plant invasion; 2) do trait patterns in the metacommunity converge or diverge across the invasion gradient and 3) if these patterns are present, which traits contribute most to convergence or divergence? We predict that flowering duration, clonality, proportion of annuals, maximum height, leaf area and SLA will significantly increase as the invasion level increases, while seed mass, leaf dry mass and leaf thickness will decrease (Table 1).

Methods

Study location and multispecies invasion gradient

Chiltern-Mt. Pilot National Park is a 21,560 ha protected area in north-east Victoria, Australia. The park was established in 2002 and contains granitic hills woodlands and box-ironbark forest consisting of open canopies of many native eucalypts (*Eucalyptus*) and a single *Callitris* species. Regional land use around Chiltern-Mt. Pilot historically involved gold mining, forestry and agriculture and has resulted in > 80 % loss of native habitats (Parks Victoria 2008). Subsequent land use and human activity has increased disturbance in the region leading to pressures such as invasive alien species negatively affecting the surviving intact ecosystems (Parks Victoria 2008). While there are few alien tree species within the park, the understorey community has been invaded by many, predominantly herbaceous, aliens.

Fifteen sites were selected for sampling. These sites were spread across the park and ranged in distances of 2.5 to 18 km apart. Sites are 500 m² and divided into 25 subplots each measuring 20 m². The chosen sites represent individual communities within the study system and are henceforth referred to as 'communities'. The fifteen communities collectively represent the metacommunity. Here, we investigate trait changes and patterns of convergence and divergence applied at a metacommunity scale, with communities arranged along the invasion gradient (Pillar et al. 2009).

To determine how traits change across a multispecies invasion gradient, a range of invasion levels was represented across the 15 communities. Relative alien abundance is recommended as an indicator of invasion level as it expresses the contribution that aliens make to a community, is independent of scale and is comparable across ecosystems and regions (Catford et al. 2012). Here we use relative alien cover (%) as a proxy for relative alien abundance. This measure was calculated for each community and used to represent the level of multispecies invasion within that community. Measurements were obtained for the cover (%) of individual understorey species (forbs, graminoids and shrubs ≤ 3 m) in each community. Within each subplot in each community, two 1 m x 1 m quadrats were randomly placed (50 quadrats per community). Percent cover was estimated for every individual species per quadrat, using the following categories: 0 %, < 1 %, 1 %, 2 %, 5 % with subsequent intervals of 5 % from 10 to 100 (Stohlgren 2007). Cover was summed across all 50 quadrats to give a total community cover for each species, as well as a total community cover for all species combined. All alien species were used in defining the invasion gradient in this study (i.e. included in the total alien cover). Aliens

are likely to be situated at different stages of the invasion process due to different introduction times and subsequent lag phases, meaning some aliens may yet significantly impact the invaded community (Catford et al. 2012; Campos et al. 2013). Including all alien species addresses the subjectivity of categorising aliens as invasive (Campos et al. 2013). The multispecies invasion gradient across all 15 communities ranged from 3.92 % to 61.08 % relative alien cover.

Collection of trait data

Data were collected for five field-based traits (1. maximum vegetative height (mm), 2. leaf thickness (mm), 3. leaf area (mm^2), 4. leaf dry mass (mg), 5. SLA (mm^2 mg^{-1})) and four literature-sourced traits (1. flowering duration (months), 2. seed mass (mg), 3. clonal (yes/no), 4. annual life history (proportion of species); Table 1). Traits were selected based on research from prior studies that provide evidence of their link to invasive species (Table 1). Trait data were collected for the most common species in each of the communities (i.e. 85-95 % of total community cover; Pakeman and Quested 2007). Across all 15 communities, a total of 59 plant species were sampled in-field.

Field samples were collected in the austral spring of 2014 and 2015. Maximum plant height measurements were collected *in-situ* for each species per community from the tallest observed individual. Forty leaf samples (four leaves per individual across ten individuals; Pérez-Harguindeguy et al. 2013) were collected for each species in each community to obtain measurements for the four leaf traits. Twenty samples per species in each community were measured for leaf thickness using digital callipers. All leaf samples were scanned using a Canon LiDE210 flatbed scanner and ImageJ software was used to calculate the one-sided area of each leaf. Leaf samples were oven-dried for 72 hours at 70°C then weighed using a microbalance to obtain leaf dry mass. Specific leaf area was calculated by dividing the leaf area of each sample by its leaf dry mass. Seed mass data was collected from the Kew Royal Botanic Gardens Seed Information Database (Royal Botanic Gardens Kew 2017). Life history, clonality and flowering duration data were collated from Walsh and Entwisle (1992-1996) and supplementary literature-based sources.

Statistical analyses

Generalized linear models (Gaussian error distribution with log link function) were used to test relationships between traits and the invasion gradient, with the trait as the response variable. Each trait was analysed separately. Community mean trait values were used and were unweighted by species abundances. Spatial autocorrelation analysis was run for the residuals of each GLM model using global Moran's I (Dormann et al. 2007). No significant spatial autocorrelation was found for any of the traits ($p = \geq 0.05$): i.e. trait data can be regarded as spatially independent. Analyses were performed using R Studio 3.3.1 (R Core Team 2016).

Trait patterns were investigated using three data matrices: matrix **B** containing species described by traits; matrix **W** containing species cover data in each community, and matrix **E** describing communities according to their level of invasion (Pillar et al. 2009). The mean trait value across communities for each species was used for the quantitative traits in matrix **B**. Matrix **W** was standardized so that row totals (communities) = 1. To ensure that the alien species cover data used in Matrix **E** and the cover data used in Matrix **W** were independent, a Pearson's correlation was performed. The correlation was not significant ($r = 0.152$, $p = 0.589$) and the cover data used in each matrix can be treated as independent for the purpose of analysis. The three matrices (**B**, **W** and **E**) form the basis for analysis in the R package "SYNCSA" (Debastiani and Pillar 2012).

Traits were scaled up to metacommunity level separately to measure convergence and divergence. To enable detection of convergence, matrix **T** containing community-weighted mean trait values was created, using the matrix multiplication **T = B'W**. Traits in matrix **T** were standardized due to a combination of binary and quantitative data using different units of measurement. To identify divergence, a matrix **U** was first created with degrees of belonging of species to fuzzy sets defined by the traits in Matrix **B**. This was done using the Gower similarity coefficient which is appropriate for handling different measurement units of traits in matrix **B** (Gower 1971; Podani 1999). Matrix **X** was created using the matrix multiplication **X = U'W**, and describes the composition of the communities in terms of species taken as fuzzy sets. The subsets of traits from matrix **B** that maximised the expression of convergence and divergence related to the invasion gradient in matrix **E** were then identified using an iterative method developed by Pillar and Sosinski (2003).

The matrices **T**, **X** and **E** were used to compute distance matrices of communities ($\mathbf{D}_T$, $\mathbf{D}_X$ and $\mathbf{D}_E$, respectively), that relate both **T** and **X** to **E**. Only the subsets of traits maximising expression of convergence and divergence were used. Relating **T** to **E** involved a matrix correlation $\rho(\mathbf{TE}) = \rho(\mathbf{D}_T; \mathbf{D}_E)$ which measures how congruent community distances based on **T** ($\mathbf{D}_T$) are with community distances based on **E** ($\mathbf{D}_E$), comparable to the correlation in a Mantel test (Pillar et al. 2009). The resulting correlation between $\mathbf{D}_T$ and $\mathbf{D}_E$ is a measure of trait-convergence related to variation along the multispecies invasion gradient. A large $\rho(\mathbf{TE})$ indicates communities sharing trait similarities are also similar in their level of multispecies invasion. Using the same method of matrix correlation for **X** and **E** (i.e. $\rho(\mathbf{XE}) = \rho(\mathbf{D}_X; \mathbf{D}_E)$) reveals both trait-convergence and divergence related to the variation in **E**. To remove the trait-convergence component from $\rho(\mathbf{XE})$ a partial Mantel correlation $\rho(\mathbf{XE.T}) = \rho(\mathbf{D}_X; \mathbf{D}_E)$ is used. This provides a measure of trait-divergence related to the variation in **E** while controlling for the effects of trait-convergence (Pillar et al. 2009). Once values of convergence [$\rho(\mathbf{XE})$] and divergence [$\rho(\mathbf{XE.T})$] were computed, statistical significance was tested against null models of 999 iterations by obtaining a randomly-generated null $\rho(\mathbf{XE})$ and $\rho(\mathbf{XE.T})$.

Because closely-related species are expected to share similar traits with each other than with distantly-related species, it is important to quantify the effects of species' evolutionary history on community patterns (de Bello et al. 2015). Aliens in this system are distantly-related to natives (McGrannachan et al. unpubl.) and this may impact trait patterns along the gradient. Trait phylogenetic signal related to convergence and divergence was measured at the metacommunity level (Pillar and Duarte 2010). The correlation between the phylogenetic structure of the metacommunity and the invasion gradient was also quantified. A phylogenetic tree for the metacommunity (all species with trait measurements across all communities) was created using the APG III phylogeny (Stevens 2001) and Phylomatic (Webb and Donoghue 2005). The branch length adjustment algorithm (BLADJ) in Phylocom was used to assign branch lengths, calibrated in millions of years, to the metacommunity phylogenetic tree (Wikstrom et al. 2001; Webb et al. 2008). A phylogenetic distance matrix based on the branch lengths was then created and standardized (range 0-1). The resulting matrix $\mathbf{S}_F$ was used to scale up the phylogeny to community level using a method analogous to the scaling up of traits to the

234 community level (Pillar et al. 2009; Pillar and Duarte 2010). Matrix **Q** was obtained and standardized
235 with degrees of belonging of species to fuzzy sets defined by the phylogenetic pairwise dissimilarities
236 in matrix $\mathbf{S}_F$. The matrix multiplication **P=W'Q** gives matrix **P** containing the phylogenetic structure
237 of communities after fuzzy-weighting of species abundances by the phylogenetic similarities of species.
238 A distance matrix ($\mathbf{D}_P$) is then computed from **P** and the matrix correlations $\rho(\mathbf{PT}) = \rho(\mathbf{D}_P; \mathbf{D}_T)$ and
239 $\rho(\mathbf{PX.T}) = \rho(\mathbf{D}_P; \mathbf{D}_T.\mathbf{D}_T)$ measure the phylogenetic signal at the metacommunity level related to
240 convergence and divergence, respectively. The strength of the association between the phylogenetic
241 structure of the communities and the invasion gradient was measured by the matrix correlation $\rho(\mathbf{PE})$
242 $= \rho(\mathbf{D}_P; \mathbf{D}_E)$.

243 Upon the identification of convergence and divergence and the subset of traits maximising these
244 patterns, exploratory analysis was performed to interpret results. To interpret patterns of trait-
245 convergence, we performed linear regressions looking at the relationship between community-weighted
246 mean (CWM) trait values from matrix **T** and the invasion gradient. This was done separately for each
247 trait that maximised the expression of trait-convergence. To interpret trait-divergence patterns we first
248 calculated two values of Rao's quadratic entropy (FD_Q) for each community: once using all traits and
249 once using the optimal subset of traits driving divergence. Rao's quadratic entropy gives a measure of
250 functional diversity for each community that is based on species abundances and trait dissimilarities
251 among them (Rao 1982). We used nonlinear regression to explore relationships between FD_Q and the
252 invasion gradient. We also calculated coefficients of variation of mean FD_Q for communities of low (n
253 = 6), intermediate (n = 6) and high (n = 3) levels of invasion to explore variation in FD_Q along the
254 gradient.

255 **Results**

256 *Community-wide trait changes across the invasion gradient*

257 Two of the nine traits were significantly related to the multispecies invasion gradient (Table 2). The
258 proportion of species with an annual life history increased significantly with relative alien cover (p =

0.003, Figure 1). Mean SLA also increased significantly across the multispecies invasion gradient, with high mean SLA found in communities with a high level of invasion (p = 0.003, Figure 1).

Trait-convergence and trait-divergence patterns across the invasion gradient

Both trait-convergence and trait-divergence patterns were significantly related to the multispecies invasion gradient (Table 3). The subset of traits maximising convergence included annual life history and flowering duration (ρ(**TE**) = 0.941, p = < 0.001). There was a significant relationship between annual CWMs and the multispecies invasion gradient (p = < 0.001; Table C1). Communities with higher levels of multispecies invasion supported higher abundances of annual species (Figure 2a). Flowering duration CWMs, however, were found to be non-significant across the invasion gradient (p = 0.669; Figure 2b) despite being one of the traits optimising trait-convergence. Mean flowering duration for aliens was consistently between 4.45 and 5.5 months and for natives between 4.79 and 6.85 months (Figure C1), revealing little difference.

The traits responsible for maximising divergence were leaf dry mass, SLA, seed mass and annual life history (ρ(**XE.T**) = 0.937, p = 0.001). Considering all nine traits, functional diversity (FD_Q) significantly increased with the level of invasion (p = 0.023; Table C1; Figure 2c). This significant pattern remained when considering only those traits maximising divergence (p = 0.004; Table C1; Figure 2d). Variation in functional diversity was greater within little-invaded communities (relative alien cover < 20%) than in communities with intermediate or high invasion levels (Figures 2c, d; 3). Communities with < 20 % relative alien cover had FD_Q ranging from 0.05 – 0.4, while communities with invasion levels greater than 20 % had FD_Q in the range of 0.3 - 0.4 (Figure 2c, d). Functional diversity in communities of intermediate and high invasion had coefficients of variation ranging from 7-12 %, while little-invaded communities had coefficients of variation of 56 % (only optimal traits) and 63 % (all traits; Figure 3a) - equivalent to an eightfold and fivefold increase in variation, respectively.

The correlation between the phylogenetic structure of the communities and the multispecies invasion gradient was non-significant (ρ(**PE**) = 0.096, p = 0.483). Additionally, phylogenetic signal at the metacommunity level was not significant for either trait-convergence or divergence (ρ(**PT**) = 0.171, p

285 = 0.555 and ρ(**PX.T**) = 0.021, p = 0.519, respectively). In other words, phylogenetically-structured
286 assembly patterns are not correlated with patterns of trait-convergence or trait-divergence in this system.

287 **Discussion**

288 As far as we are aware, this study is the first to show that traits previously associated with invasion
289 success, and patterns of trait convergence and divergence, are significantly correlated with a gradient
290 of increasing multispecies invasion. Specifically, the proportion of annual species and SLA increased
291 significantly across the multispecies invasion gradient. Annual life history and flowering duration
292 maximised patterns of trait-convergence in contrasting ways. Annual life history, SLA, leaf dry mass
293 and seed mass maximised trait-divergence. Furthermore, functional diversity increased as multispecies
294 invasion increased, but variation in functional diversity was lower at intermediate and high levels of
295 invasion (> 20 %).

296 *Traits associated with increased multispecies invasion*

297 Studies associating traits to invasion success have predominantly involved pairwise comparisons of
298 aliens and natives, or invaded and uninvaded communities. Here, we have demonstrated that SLA and
299 annual life history are significantly correlated with increases in multispecies invasion of communities.
300 Herbaceous alien annuals such as *Lysimachia arvensis*, *Cerastium glomeratum* and *Sherardia arvensis*,
301 and annual grasses such as *Briza minor*, were characteristic of highly-invaded communities, and were
302 among the species with the highest SLA values in those communities. Invasion success by aliens is
303 often attributed to traits promoting rapid growth and reproduction, particularly in disturbed or
304 temporarily resource-rich environments (Lambdon et al. 2008; Dainese and Bragazza 2012). Such traits
305 include high SLA, which is situated toward the 'fast return' end of the leaf economic spectrum that
306 promotes faster growth and increased photosynthetic rates (Westoby et al. 2002; Wright et al. 2004).
307 Invading aliens have been associated with high SLA across several studies, spanning different
308 functional groups and environmental regions, such as peri-urban bushland and arid shrubland (Lake and
309 Leishman 2004; Dainese and Bragazza 2012). Annual life history is also associated with faster growth
310 rates and has been linked to invasions at global, country, regional and habitat scales (Cadotte and

311 Lovett-Doust 2001; Sutherland 2004; Pyšek et al. 2009; Dainese and Bragazza 2012; Okimura and Mori
312 2018). Mediterranean-type climates such as in our study system are often characterized by annual aliens
313 with high SLA, allowing life cycle completion before the onset of summer drought (Holmes and Rice
314 1996; Garnier et al. 1997). The increase in the proportion of annual species and SLA with invasion level
315 shows that not only dominance by a single invader, but also multispecies invasion, has the potential to
316 significantly alter the functional structure of invaded communities. This in turn may impact ecosystem
317 functioning, supported by the fact that both annual life history and SLA were among the subset of traits
318 maximising patterns of trait-convergence or divergence.

319 The seven remaining traits showed no significant relationship with the invasion gradient. This was
320 particularly surprising for flowering duration because the association between longer flowering periods
321 and invading species is well-supported (Pyšek and Richardson 2007). There are three potential reasons
322 for this. First, the seven traits may be more relevant when conducting analyses between specific species
323 or taxonomic groups, rather than realized communities of species in the field, as shown here. Studies
324 linking these traits with invasion have predominantly tested for trait differences between invasive and
325 native congeners or used pairwise comparisons between invasive aliens and natives (Pyšek and
326 Richardson 2007). Second, processes impacting trait patterns, such as habitat filtering and niche
327 differentiation, differ in strength at different spatial scales and can influence different traits in
328 contrasting ways (Kraft and Ackerly 2010). For example, Hamilton et al. (2005) found smaller seed
329 mass to be significantly correlated with invasion success at regional and continental scales and high
330 SLA at the continental scale only.

331 The third potential reason is that the multispecies invasion gradient is based on the relative alien
332 cover of each community and incorporates alien species that are not considered invasive, even though
333 they have naturalized. Frequently-occurring aliens, such as *Aira elegantissima*, *Hypochaeris spp.* and
334 *L. arvensis*, are classified as non-invasive at both the state and bioregional scale (Adair et al. 2008;
335 Victoria State Government Department of Environment and Primary Industries 2017). Considering all
336 alien species may affect the significance of trait-invasion associations across the gradient by obscuring
337 trait values closely linked to invasive aliens. If this is the case, significant differences between aliens
338 and natives for these traits may occur only when considering highly invasive species, but excluding

339 non-invasive aliens that may still be locally abundant. For this approach, all alien species were included
340 as we are interested in the cumulative effect of multiple alien species on trait patterns across the
341 metacommunity.

342 *Trait-convergence and trait-divergence across the multispecies invasion gradient*

343 Both trait-convergence and divergence were found across the multispecies invasion gradient. This
344 suggests that contrasting mechanisms such as habitat filtering and niche differentiation are influencing
345 community trait patterns along the gradient. These mechanisms are often used to investigate trait
346 patterns in communities and metacommunities (Pillar et al. 2009; Logue et al. 2011). This means that
347 trait-convergence among communities may be observed in one part of the gradient, whereas trait-
348 divergence may occur in another part of the gradient, resulting in both convergence and divergence at
349 the metacommunity scale (Pillar and Duarte 2010; Carlucci et al. 2012). Additionally, the relevance to
350 aliens of mechanisms promoting convergence or divergence may be dependent on the stage of invasion.
351 Convergence may restrict aliens during the establishment stage to those with trait values suited to local
352 conditions (Theoharides and Dukes 2007). Trait-divergence may be more important in enabling aliens
353 to spread throughout the new environment once they are established (Martin and Canham 2010).
354 However, without more detailed information on alien introduction times, and the lag phases which they
355 experience, it is difficult to link convergence/divergence patterns to particular stages of invasion.
356 Trait-convergence can occur when communities in close proximity along the ecological gradient
357 consistently share species with similar trait values, and changes in these traits are associated with the
358 gradient (Pillar et al. 2009). This pattern was evident for annual life history, as communities with similar
359 relative alien cover along the invasion gradient converged toward similar proportions of annual species.
360 In contrast, flowering duration converged along the gradient because all communities contained species
361 with similar flowering periods, regardless of the level of invasion a community experienced. This
362 indicates that annual life history and flowering duration express patterns of convergence in different
363 ways, but their combination maximises the expression of convergence along the invasion gradient.
364 Trait-divergence occurs when turnover in community trait values coincides with changes along the
365 ecological gradient, but the communities consist of species with dissimilar traits (Pillar et al. 2009).

366 Along the invasion gradient, I found trait-divergence to increase with invasion level, as indicated by
367 FD_Q. This increase suggests that aliens collectively exhibit a broader range of trait values than natives.
368 Only one other study that I am aware of (in Mediterranean dune ecosystems) has found invasion by
369 multiple alien species to increase the functional diversity of communities (Marcantonio et al. 2014).
370 The use of the invasion gradient provides a novel insight into the impact of multispecies invasion and
371 identifies the need for more research incorporating gradients of invasion.

372 Annual life history maximised patterns of both trait-convergence and divergence. This is possible
373 when convergence and divergence are represented at different points along the gradient. The proportion
374 of annuals consistently converged between communities with similar invasion levels. Divergence along
375 the same gradient is evident in how the proportion of annuals changes significantly across the entire
376 gradient. Traits such as SLA, plant inclination, leaf shape and leaf resistance have been associated with
377 both convergent and divergent patterns along the same gradients of soil water availability, nitrogen
378 fertilization and grazing intensity (Cornwell and Ackerly 2009; Pillar et al. 2009). Our results support
379 the idea that individual traits are often responsible for influencing trait patterns in opposing ways across
380 ecological gradients.

381 Functional diversity across the invasion gradient was more variable in little-invaded communities
382 than in intermediate- or highly-invaded communities. Rao's quadratic entropy is considered to be
383 independent of species richness in most cases (Götzenberger et al. 2016). However, in this system, FD_Q
384 significantly increased as species richness increased (Figure C2). Despite this, FD_Q increased
385 significantly with invasion level, even when species richness was accounted for. This suggests that trait
386 dissimilarity increases then remains constant in communities that have reached a particular threshold of
387 multispecies invasion (in this case ~ 20 % relative alien cover). Differences in functional diversity
388 between little- and highly-invaded communities stem mostly from variation in functional diversity
389 among little-invaded communities. To our knowledge, the combined increase and stabilisation of
390 functional diversity has not been found in previous studies of plant invasions. The findings here
391 emphasize the need for focus on multispecies invasion studies, in particular studies incorporating
392 invasion gradients, and how they impact metacommunity functional structure.

393 Increased and stabilised functional diversity at intermediate and high invasion levels could indicate
394 the filling of vacant niches by aliens. Rapid increases in functional diversity may be possible if niche
395 dimensionality (i.e. the diversity of niches) in a community is low (Clarke 2013), and would be achieved
396 once the threshold of 20 % relative alien cover is reached. Increased variation in functional diversity in
397 little-invaded communities (<20 %) suggests that these communities have different levels of niche
398 saturation, potentially as a result of environmental heterogeneity or recent disturbances, such as fire
399 (Moles et al. 2012; Clarke 2013). Little-invaded communities with high functional diversity may be
400 more resistant to invasion because empty niches are unavailable to invading aliens (Pokorny et al. 2005;
401 Funk et al. 2008). Little-invaded communities with low functional diversity and vacant niches could
402 experience a rapid increase in functional diversity with further invasions. Niche saturation would be
403 reached at ~ 20 % relative alien cover and subsequent increases in alien cover will not increase
404 functional diversity, but rather maintain it at high diversity. This saturation of functional diversity at
405 intermediate and high levels of invasion may provide some level of resistance to future invaders with
406 similar functional attributes, if there are no vacant niches left to fill.

407 **Conclusions**

408 Growing evidence suggests that traits such as high SLA and annual life history are related to
409 increased invasion success. Our research builds on this evidence by revealing these two traits are
410 characteristic of aliens *in situ* when examined across a multispecies invasion gradient. Specific leaf area
411 and annual life history promote rapid growth and completion of life cycles and this could have
412 implications for ecosystem functioning, such as productivity (Wright et al. 2004; Liao et al. 2008). The
413 correlation of trait-convergence and divergence patterns with the invasion gradient reveals that alien
414 invasion of communities can alter community functional structure in opposing directions (i.e. more or
415 less similar in traits to natives) and that these patterns are driven by traits known to promote invasion.
416 Finding high functional diversity in communities of intermediate and high levels of invasion contrasts
417 with other studies that find invasion by single species to often reduce community functional diversity
418 (Chabrerie et al. 2010; Michelan et al. 2010). With invasion by aliens expected to rise in the future
419 (Hellmann et al. 2008), native communities in many parts of the world may experience increases in

420 functional diversity when invasion by multiple aliens occurs. The use of an invasion gradient in this
421 study therefore provided a novel insight into the impact of multispecies invasion on the functional
422 structure of a metacommunity. More field research focussing on multispecies invasion will help to
423 determine if increased and sustained functional diversity is a common phenomenon in communities
424 containing co-occurring aliens.

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671

672 **Tables**

673 **Table 1.** The traits used and their proposed response mechanisms to multispecies invasion. Positive (+)
674 and negative (-) symbols indicate increases and decreases in species trait values. "Higher invasion"
675 refers to an increase in relative alien cover (%).

Trait	Proposed trait response to multispecies invasion (+/-)	Evidence source of proposed trait response in alien species
Life history (proportion annuals)	Higher proportion of species with annual life history as community invasion increases (+)	Cadotte & Lovett-Doust (2001); Pyšek et al. (2009); Dainese & Bragazza (2012)
Maximum plant height (mm)	Taller species found in communities with higher invasion (+)	Westoby (1998); Feng & van Kleunen (2016)
Flowering duration (months)	Longer flowering duration at sites with higher invasion (+)	Chrobock et al. (2013) ; Bezeng et al. (2015) ; Feng et al. (2016)
Seed mass (mg)	Smaller seeds in communities with higher invasion (-)	Cadotte & Lovett-Doust (2001); Thuiller et al. (2006) ; Schmidt & Drake (2011)
Clonality (proportion species)	Higher proportion of species are clonal in communities with higher invasion (+)	Lake & Leishman (2004); Liu et al. (2006); Shah et al. (2014)
Leaf area (mm^2)	Higher leaf area with an increase in community invasion (+)	Daehler (2003); Liu et al. (2015); Leishman et al. (2014)
Leaf dry mass (mg)	Lower leaf dry mass with higher invasion (-)	Fynn et al. (2009); Matzek (2011)

Leaf thickness (mm)	Lower leaf thickness in communities with higher invasion (-)	Smith et al. (1998); Niinemets (2001); Funk & Throop (2010)
Specific leaf area (SLA) (mm^2 mg^{-1})	Higher SLA in communities with higher invasion (+)	Lake & Leishman (2004); Grotkopp & Rejmánek (2007); Pyšek & Richardson (2007); Marx et al. (2016)

676

677 **Table 2.** Changes in mean trait values across the multispecies invasion gradient. Generalized linear

678 model results (family = Gaussian, link = log).

Trait	Estimate	Std. Error	df	t	p
Annual life history (proportion species)	0.016	0.004	13	3.695	0.003***
Height (mm)	-0.002	0.004	13	-0.51	0.618
Flowering duration (months)	< 0.001	0.001	13	0.254	0.804
Seed mass (mg)	-0.009	0.007	13	-1.245	0.235
Clonal (proportion species)	-0.001	0.002	13	-0.499	0.626
Leaf area (mm^2)	-0.003	0.007	13	-0.358	0.726
Leaf dry mass (mg)	-0.001	0.007	13	-0.205	0.841
Leaf thickness (mm)	-0.001	0.002	13	-0.435	0.671
Specific leaf area ($mm^2\ mg^{-1}$)	0.013	0.004	13	3.564	0.003***

679 Significance codes: ***$p < .001$; **$p < .01$; *$p < .05$

680

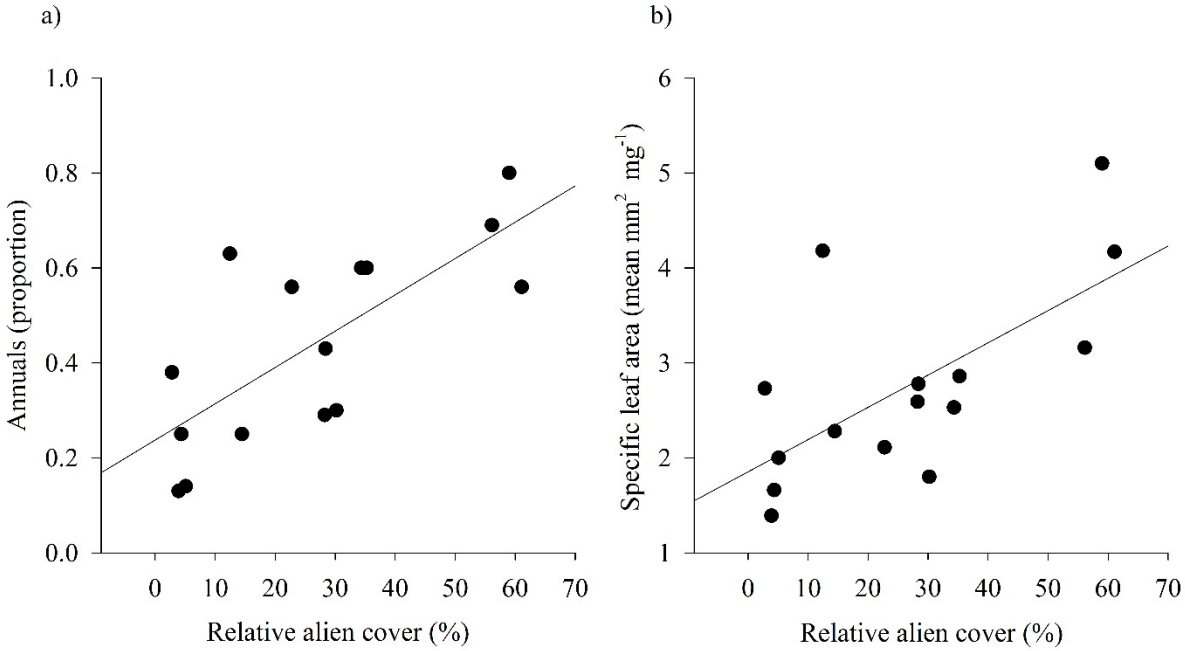
681 **Table 3.** The optimal trait subsets that maximise trait-convergence and trait-divergence along the
682 multispecies invasion gradient.

	Trait-convergence			**Trait-divergence**		
	Optimal Traits	Annual, Flowering duration		**Optimal Traits**	Annual, SLA, Leaf dry mass, Seed mass	
Correlation	**Metric**	**Obs**	***p***	**Correlation**	**Obs**	***p***
Convergence/divergence	ρ(**TE**)	0.941	0.001***	ρ(**XE.T**)	0.937	0.001***
Phylogeny & convergence/divergence	ρ(**PT**)	0.171	0.555	ρ(**PX.T**)	0.021	0.519
Phylogeny & invasion gradient	ρ(**PE**)	0.096	0.483	ρ(**PE**)	0.096	0.493
Phylogenetic signal of species pool	ρ(**FB**)	0.054	0.043*	ρ(**FB**)	0.069	0.066
Convergence/divergence w/o phylogeny effects	ρ(**TE.P**)	0.943	0.001***	ρ(**XE.P**)	0.939	0.001***

683 Significance codes: ***p < .001; **p < .01; *p < .05

684 **Figures**

685



686

687 **Figure 1.** The relationship between relative alien cover and a) proportion of annuals (p = 0.003) and b)
688 specific leaf area (p = 0.003). The p values have been taken from GLM models (Gaussian error
689 distribution with log link function; Table 2).

690

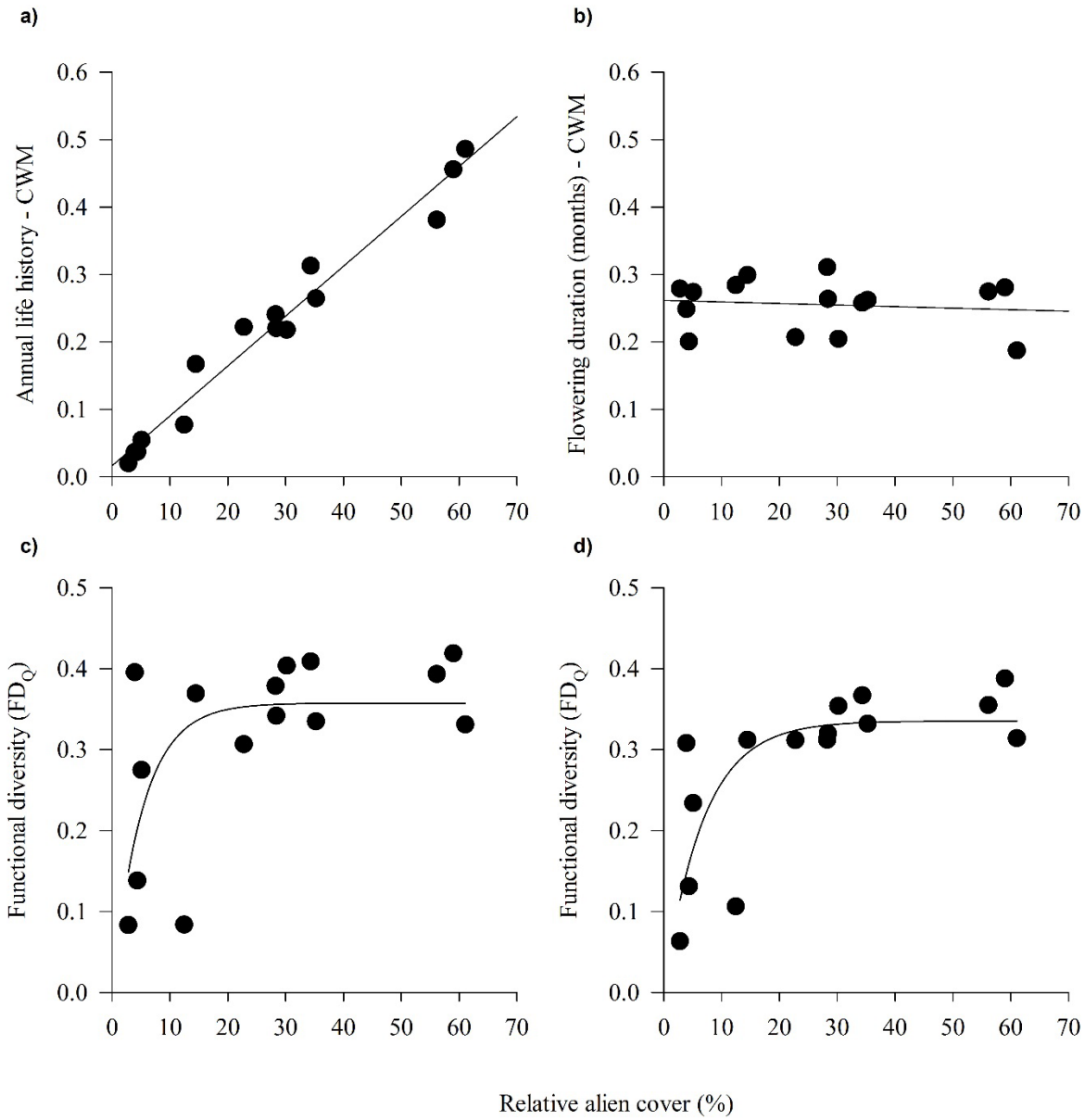


Figure 2. The relationship between relative alien cover and a,b) community-weighted means (CWM), c,d) functional diversity. a) CWM of annual life history (p = < 0.001); b) CWM of flowering duration (p = 0.669); c) functional diversity for all traits (p = 0.026); d) functional diversity for the trait subset maximising divergence (p = 0.005). The p values have been taken from regression models (Table C1).

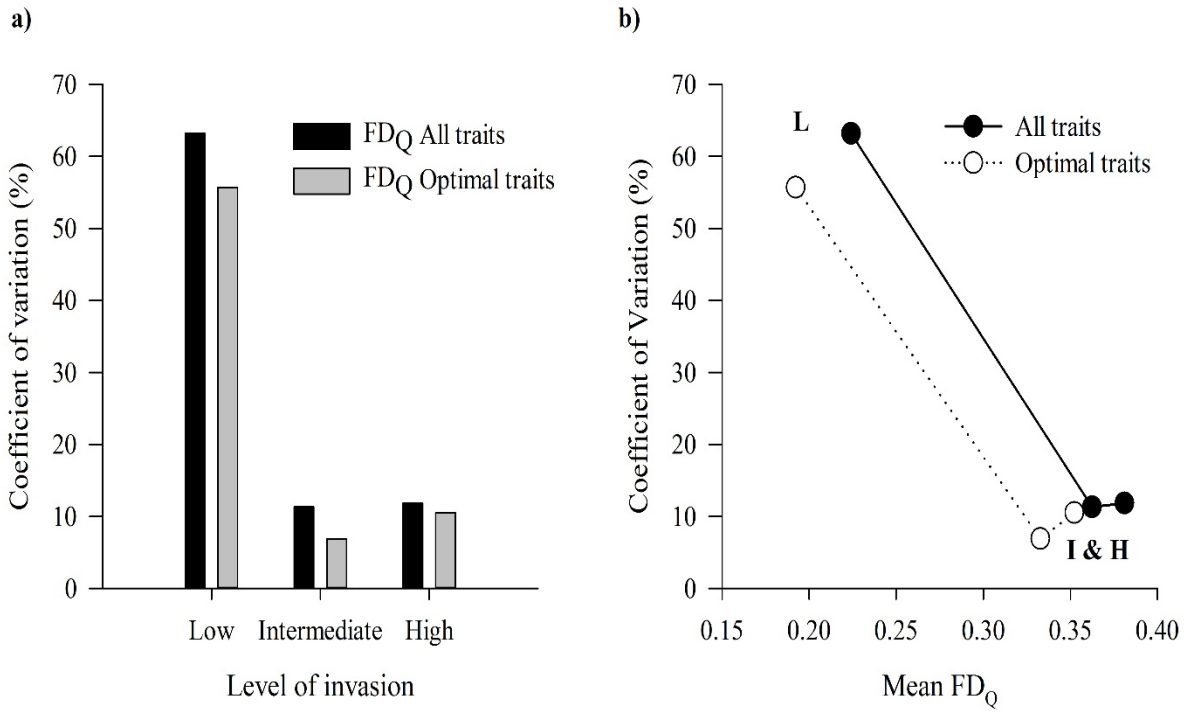


Figure 3. Variation in functional diversity (FD_Q) across the invasion gradient. a) Coefficient of variation for FD_Q across communities of low (n = 6; relative alien cover = < 20 %), intermediate (n = 6; relative alien cover = 20 – 50 %) and high (n = 3; relative alien cover = > 50 %) invasion; b) The relationship between mean FD_Q and the coefficient of variation for FD_Q. L = low invasion levels; I = intermediate invasion levels; H = high invasion levels

704 **Appendix**

705 **Table 1:** Changes across the multispecies invasion gradient of annuals and flowering duration
706 community-weighted means (CWMs), in functional diversity (FD_Q) for all traits and only those traits
707 optimising divergence. Regression model results.

Response Variable	Estimate	Std. Error	df	t value	p value
CWM annuals	0.016	0.012	13	1.321	< 0.001***
CWM flowering duration	-0.000	0.000	13	-0.437	0.669
FD_Q all traits	0.192	0.08	13	2.4	0.031*
FD_Q optimal traits	0.148	0.05	13	2.967	0.011**

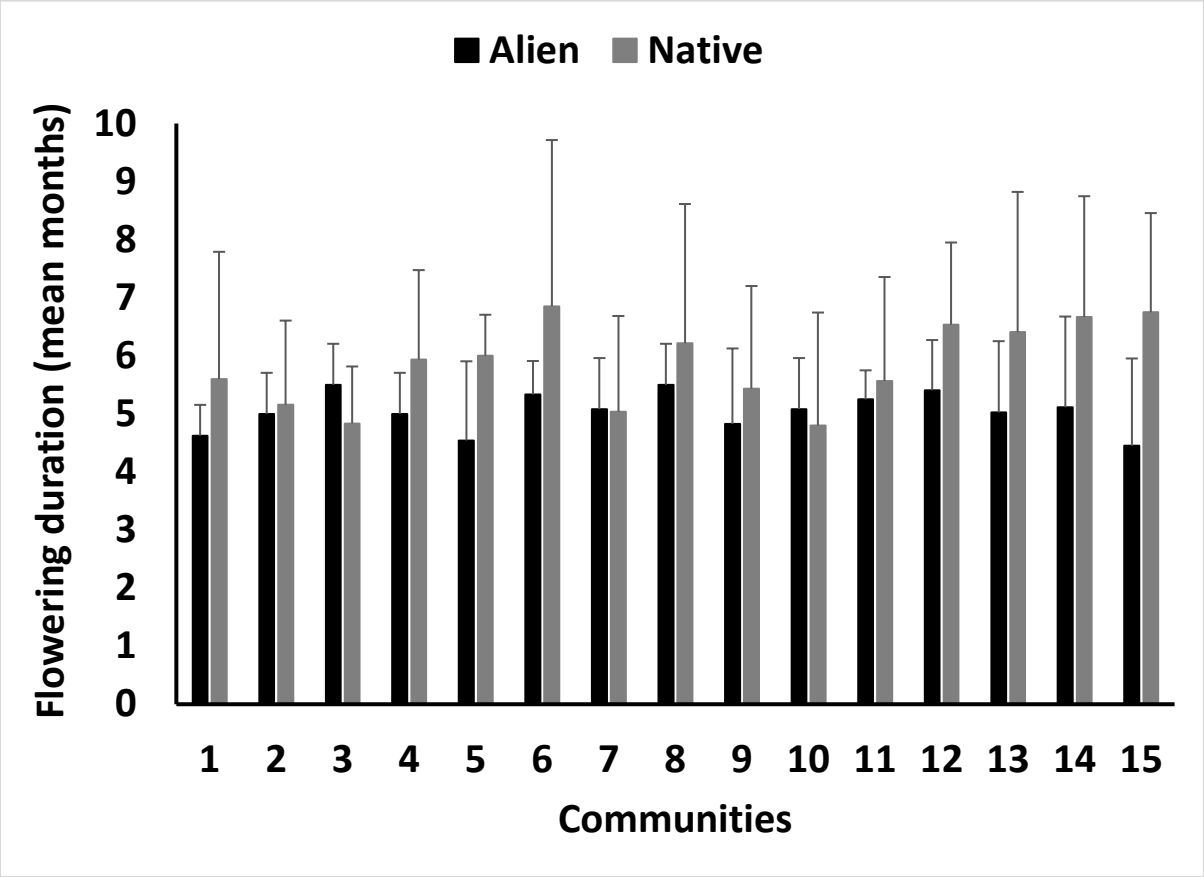
708 Significance codes: ***p < .001; **p < .01; *p < .05

709

710 **Figure 1.** Differences between alien and native species in community mean flowering duration.

711 Communities are sorted from lowest relative alien cover to highest relative alien cover along the *x*

712 axis. Error bars represent standard deviation.



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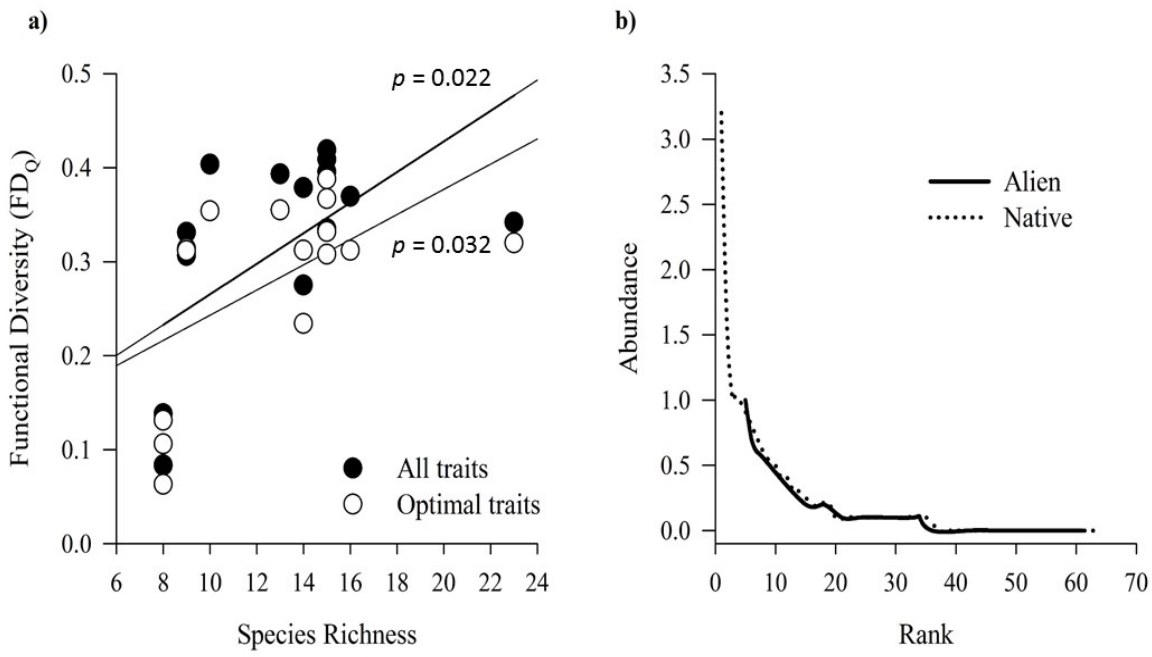
716 **Figure 2:** How species richness and abundance affect functional diversity (FD_Q) across the invasion
717 gradient. a) The relationship between species richness and FD_Q; b) Rank abundance curves for alien
718 and native species within the metacommunity.



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