

Traits of neighbouring plants and space limitation determine intraspecific trait variability in semi-arid shrublands

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Summary

1. Understanding how intraspecific trait variability (ITV) responds to both abiotic and biotic constraints is crucial to predict how individuals are assembled in plant communities, and how they will be impacted by ongoing global environmental change.
2. Three key functional traits [plant height, leaf area (LA) and specific leaf area (SLA)] were assessed to quantify the range of ITV of four dominant plant species along a rainfall gradient in semi-arid Mediterranean shrublands. Variance partitioning and confirmatory multilevel path analyses were used to assess the direct and indirect effects of rainfall, space limitation (crowding) and neighbouring plant traits on ITV.
3. The direct effect of the local neighbourhood on the trait values of subordinate individuals was as strong as the effect of rainfall. The indirect effect of rainfall, however, mediated by the effect of the local neighbourhood on the trait values of subordinate individuals, was weak. Rainfall decreased the height and SLA of subordinate individuals, but increased their LA. Neighbouring plant traits were just as strong predictors as crowding in explaining changes in ITV.
4. *Synthesis.* Our study provides a framework to disentangle the direct effects of abiotic factors and their indirect effects on ITV mediated by the local neighbourhood. Our results highlight that abiotic and biotic constraints are both substantial sources of trait variations at the individual level, and can blur processes underlying changes in ITV. Considering and disentangling combined sources with an individual perspective would help to refine our predictions for community assembly and functional ecology.

Key-words: abiotic environment, community assembly, determinants of plant community diversity and structure, functional diversity, plant interactions, semi-arid Mediterranean shrublands, trait-based approach

Introduction

Intraspecific trait variability (ITV hereafter) arises from both heritable genetic variation and phenotypic plasticity (e.g.

Schlichting & Levin 1986) and represents the range of trait values exhibited by a species grown in various environments (Violle *et al.* 2007). ITV represents a significant contribution to the overall functional trait variability (e.g. Cianciaruso *et al.* 2009; Hulshof & Swenson 2010; Auger & Shipley 2013; Le Bagousse-Pinguet *et al.* 2014a) and can be similar to or greater than interspecific trait variability in some cases

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(Valladares *et al.* 2000; Albert *et al.* 2010; Messier, McGill & Lechowicz 2010). Accounting for ITV can improve predictions about species interactions (Kraft *et al.* 2014), community assembly and dynamics (Fridley, Grime & Bilton 2007; Jung *et al.* 2010; Bolnick *et al.* 2011; Le Bagousse-Pinguet *et al.* 2014a), and ecosystem processes (Fridley & Grime 2010).

Disentangling the relative effects of abiotic and biotic factors on ITV constitutes an important step prior to further investigation on how ITV is linked to community assembly. Abiotic factors have been shown to impact ITV (e.g. Fajardo & Piper 2011), and species with different ecological strategies will exhibit contrasting ITV responses to these factors (Grime & Mackey 2002; Maire *et al.* 2013). At the interspecific level, neighbouring plants can affect the growth and survival of other species by occupying the surrounding area and limiting the available space (i.e. crowding, e.g. Harley & Bertness 1996). Neighbouring plants can also affect the growth and the survival of other species by either decreasing (competition: Grime 1973; Tilman 1982) or increasing the local available resources (facilitation: Callaway 2007). Few studies to date have attempted to quantify the effects of neighbouring plants on ITV (Fridley, Grime & Bilton 2007), and none have assessed how local neighbourhood and abiotic factors combined, impact on ITV. Violle *et al.* (2012) strongly encouraged 'to investigate the spatial structure of trait distribution to estimate the importance of these fine-scales processes (biotic interactions), especially in plants' (see also Fajardo & Piper 2011).

The effect of neighbouring plants on the local abiotic environment can be evaluated by assessing their functional 'effect traits' (e.g. Suding *et al.* 2008). Competitors with different trait attributes can have contrasting effects on their neighbourhood (Gross *et al.* 2009; Schöb, Butterfield & Pugnaire 2012; Le Bagousse-Pinguet *et al.* 2013). In temperate systems, tall species can significantly decrease light availability, negatively impacting both the survival and the growth of smaller species (Grime 2006; Violle *et al.* 2009). Effect traits can also mediate the ability of nurse plant species to facilitate other subordinate species (Schöb, Butterfield & Pugnaire 2012; Le Bagousse-Pinguet *et al.* 2013). For instance, nurse plants with high leaf area (LA) can increase soil moisture, which facilitates water stress-intolerant species (Gross *et al.* 2008). If ITV also responds to biotic factors (Violle *et al.* 2012), significant relationships between neighbouring plant traits and the ITV of focal species should occur.

We aimed to disentangle the direct and indirect effects of rainfall, crowding and neighbouring plant traits on ITV. The range of ITV of four dominant plant species was quantified along a regional rainfall gradient in semi-arid Mediterranean shrublands from Spain. These environments constitute appropriate ecosystems to test the response of ITV to biotic processes for the following reasons. Large phenotype variability has been reported along rainfall gradients such as that studied here (Rubio de Casas *et al.* 2009), suggesting that ITV is an important factor determining plant persistence and community

assembly in semi-arid Mediterranean shrublands (Gross *et al.* 2013). These shrublands are organized in crowded patches of vegetation, in which coexisting species can exhibit contrasting functional trait values (Gross *et al.* 2013). Finally, water stress and the occurrence of biotic interactions within vegetation patches are important factors affecting plant growth and survival in semi-arid Mediterranean communities (Novoplanski & Goldberg 2001; Pugnaire, Armas & Maestre 2011; Gross *et al.* 2013).

We focused on three functional traits related to the competitive ability and/or tolerance to water stress, that is plant height, LA and specific leaf area (SLA) (e.g. Westoby *et al.* 2002; Wright *et al.* 2004). These traits respond to both rainfall and biotic interactions and are key determinants of community structure and ecosystem functioning in semi-arid Mediterranean communities (Gross *et al.* 2013; Valencia *et al.* 2015). We tested three hypotheses (Fig. 1): (i) ITV will respond to rainfall only (abiotic hypothesis), (ii) ITV will respond to neighbouring plants only (biotic hypothesis), and (iii) ITV will respond to both rainfall and neighbouring plants (combined hypothesis). Several scenarios can occur within the biotic and combined hypotheses. ITV may respond either to independent, but direct effects of rainfall and neighbouring plants, or to the indirect effect of rainfall mediated by neighbouring plants. Also, ITV may respond to crowding and neighbouring plant traits separately or may respond to their combined effects. For instance, Gross *et al.* (2008) found that effect traits can be as important as the standing crop biomass in explaining the impact of neighbouring plants on biotic interactions. We hypothesized that (i) rainfall will have a

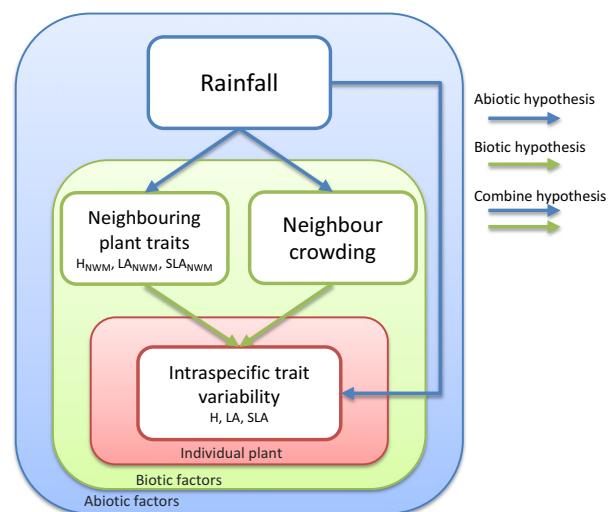


Fig. 1. Graphical representation of the three hypotheses between rainfall (blue box), neighbouring plants (green box: crowding and neighbouring plant traits) and the intraspecific trait variability of subordinate individuals (red box) for height (H), leaf area (LA) and specific leaf area (SLA) used in this study. Blue arrows represent the abiotic hypothesis, and green arrows represent the biotic hypothesis. The combined hypothesis includes both pathways. Neighbour weighted mean index for height, LA and SLA is denoted as H_{NWM} , LA_{NWM} and SLA_{NWM} , respectively.

stronger impact on ITV than neighbouring plants in the shrublands studied, (ii) increasing water stress will decrease the individual trait values for height and SLA and the range of ITV (variance), as water stress will select for more similar functional trait values (Grime 2006), and (iii) the effect traits of neighbouring plants will impact the trait values of individual plants (Fajardo & Piper 2011; Violle *et al.* 2012). If neighbouring plant traits impact ITV, they may alleviate the direct, positive effect of increased rainfall on trait values (e.g. due to competition).

Materials and methods

STUDY AREA

Twelve shrublands were studied along a rainfall gradient from central to south-eastern Spain (see Gross *et al.* 2013 for details). The climate is Mediterranean semi-arid, with annual rainfall and temperature values ranging from 283 to 564 mm and from 13 to 18 °C, respectively. The selection of study sites aimed to capture the significant range of rainfall variability that is observed in semi-arid shrublands and to reduce between-site variability associated with vegetation, slope, aspect and soil type. All the sites shared the same soil type (Lithic Calciorthid; Soil Survey Staff 1994) and were located on south-facing slopes. Vegetation at all sites was a shrubland dominated by species such as *Rosmarinus officinalis* L. and *Quercus coccifera* L., representative of vegetation occurring along the studied rainfall gradient (Quero *et al.* 2013).

TARGET SPECIES

Four dominant species widespread in semi-arid shrublands, and steppes of the Mediterranean Basin (Maestre *et al.* 2009) were measured to test the response of ITV to abiotic and biotic constraints: the large sprouting shrub and encroacher *Q. coccifera* (9% of the total cover along the studied rainfall gradient), the non-sprouting shrubs *R. officinalis* (44% of the total cover) and *Thymus vulgaris* L. (6% of the total cover) and the perennial grass *Stipa tenacissima* L. (9% of the total cover). These species play a major role in the maintenance of ecosystem functioning of the studied shrublands (Maestre *et al.* 2009; Quero *et al.* 2013; Valencia *et al.* 2015).

Target individuals measured in the field were either (i) isolated on bare soil areas, (ii) dominant within the vegetation patch (i.e. the tallest individuals) or (iii) subordinate within the vegetation patch (i.e. the smallest individuals). Only subordinate individuals within vegetation patches were used in our analyses because (i) only a few individuals were isolated on bare soil areas to test for the abiotic effect (7% of the total data set) and (ii) we assumed that plant neighbours have an impact mainly on smaller individuals. We estimated a volume for all target subordinate and neighbouring individuals (i.e. all individuals in direct contact with the given target subordinate plant) along the rainfall gradient. The volume was estimated using a visual index, ranging from one to five (five being the highest volume). A volume of five was first attributed to the largest individual occurring in a given site. Then, volumes were attributed to target subordinate individuals and neighbouring individuals, relative to the volume of the largest individual. A neighbour volume ratio (NR) was calculated between the volume of target subordinate individuals and the total volume of neighbouring individuals in contact. We used a volume ratio because it has been previously shown that neighbouring plant

size can affect the performance of subordinate species (Grime 1973). We calculated NR as:

$$NR = \frac{\sum \text{Total volume of neighbouring individuals}}{\text{Volume of the subordinate individual}} \quad (1)$$

When $NR > 1$, the volume of neighbouring plants was higher than the volume of the subordinate individual, and the target individual was considered as a subordinate individual. When $NR < 1$, the volume of neighbours was lower than that of the target individual, and the target individual was considered as a dominant individual. To test the impact of neighbouring plants on the ITV of subordinate individuals only, all data with target individuals being either dominant ($NR < 1$) or isolated were excluded from further analyses.

TRAIT MEASUREMENTS

Three functional traits related to leaf morphology and plant size were selected: maximum plant height (i.e. the maximal height where green LA was present), LA and SLA. Size-related traits such as height (H) are related to plant water use efficiency and competitive ability (e.g. Westoby *et al.* 2002). Height has also been suggested to be an important functional trait of shrubs such as *Q. coccifera* and affects the functional outcomes of shrub encroachment in drylands (Maestre *et al.* 2009; Eldridge *et al.* 2011). Traits such as LA are related to light interception and water stress tolerance (Westoby *et al.* 2002). Specific leaf area is related to the leaf economic spectrum, reflects the relative growth rate of plants and is associated with plant strategies to acquire, use and/or conserve resources such as light, nutrients and water (Wright *et al.* 2004).

Trait measurements were conducted during a short period within the growing season of 2011 (from 20th to 25th of March) to avoid late spring or summer drought and any phenological bias. All traits were measured following standard protocols (Pérez-Harguindeguy *et al.* 2013). At each site, we randomly selected 10 individuals of each of the four target species to maximize ITV in our sampling selection (Carmona *et al.* 2015).

NEIGHBOURING PLANT TRAITS

To test the impact of neighbouring plant traits on the ITV of the four target species, we first recorded the taxonomic identity of all neighbouring individuals touching the target subordinate individual. The volume of all individuals for a given neighbouring species, i , was compared to that of all neighbouring individuals in contact with the subordinate individual, p_i . Then, we calculated the mean trait values (mean trait values for height, LA and SLA) for each of the neighbouring species using trait values measured in a given site. A neighbour weighted mean index (NWM) was calculated for height (mean neighbour height: H_{NWM}), LA (mean neighbour LA: LA_{NWM}) and SLA (mean neighbour SLA: SLA_{NWM}) using the mean trait values of the neighbouring species and the volume of each neighbouring individual in direct contact with a focal subordinate individual. Thus, NWMs quantify the 'effect traits' of all neighbouring individuals in direct contact with each of the target subordinate individuals. This index is similar to the community weighted mean index of Lavorel *et al.* (2008) and allows the calculation of the mean trait values of neighbours accounting for their respective volume:

$$NWM = \sum p_i \times \text{Trait}_i, \quad (2)$$

where p_i is the volume of all individuals of a neighbouring species i relative to the volume of the whole neighbouring species in contact

with a subordinate individual, and Trait_{*i*} is the mean trait value of the species *i*. Our approach offers a practical way to link biotic interactions to ITV. However, we also acknowledge that it cannot differentiate between the type of interactions involved (i.e. competition or facilitation), nor explicitly evaluate the mechanisms underlying them (i.e. which resources are mediating local interactions; e.g. Violle *et al.* 2009).

STATISTICAL ANALYSES

The response of ITV to rainfall, crowding and neighbouring plant traits was assessed using two statistical approaches. First, we used a variance partitioning method (De Bello *et al.* 2011) to assess changes in intraspecific trait variance along the rainfall gradient evaluated. Secondly, we used confirmatory multilevel path analyses (Shipley 2009) to assess the direct and indirect effects of rainfall, crowding and neighbouring plant traits on ITV.

Intraspecific trait variance along the rainfall gradient

The intraspecific trait variance was quantified for each of the 12 sampled sites. The method of variance partitioning used (De Bello *et al.* 2011) is equivalent to the decomposition of the quadratic entropy diversity (Rao 2010). For a given trait, the method corresponds to the traditional variance partitioning of sum of squares in ANOVA, with species identity as the explanatory variable. Here, the diversity within species corresponds to the within samples effect. The intraspecific trait variance is calculated; first, as the variance of trait values within each of the four target species (intraspecific trait variance). Then, a weighted average of all intraspecific trait variances is computed for each study site, and this being the weight determined by the number of individuals per species (see De Bello *et al.* 2011 for details).

Changes in intraspecific trait variance were assessed along the rainfall gradient using linear regression models. Intraspecific trait variances for height, LA and SLA were used as the response variables, and rainfall was used as the predictor. A quadratic term (rainfall²) was also included in the models, as trait variances can follow nonlinear responses along the studied rainfall gradient (Gross *et al.* 2013).

Effects of rainfall, crowding and neighbouring plant traits on ITV

Prior to the confirmatory multilevel path analyses, preliminary linear mixed effect models were performed for all target species together (Appendix S1, Supporting information) and separately (Appendix S2). These analyses aimed to (i) determine whether nonlinear effects of rainfall should be included in further analyses, (ii) select the neighbouring plant traits impacting on the trait values of the subordinate individuals and (iii) assess which traits of subordinate individuals are impacted by crowding. Crowding was estimated using the total volume of neighbouring individuals in contact with the target individual, because the size of neighbouring plants (and not the number) is required to fully assess crowding effects (Stoll & Weiner 2000). The linear mixed effect models were performed for each trait separately using the function *lmer* in the R package *lme4* (Bates *et al.* 2015). A model averaging procedure was applied to estimate the effects of predictors, based on the best 5% of all potential models, using the function *dredge* in the R package *MuMIn* (Barton 2013). The individual trait values were used as the response variables, and rainfall, rainfall², crowding and neighbour-

ing plant traits (H_{NWM} , LA_{NWM} and SLA_{NWM}) as predictors. Plant height was also introduced as a predictor of LA and SLA to consider potential coordinated changes among traits (Maire *et al.* 2013). Plant height is related to plant species performance and ontogeny, which are two important factors potentially impacting the expression of other traits (Maire *et al.* 2013). LA was introduced as a predictor of SLA because these two traits are partly mathematically related (Vile *et al.* 2005). Site was used as a random factor to control for the hierarchical nature of our survey. Species was also used as a random factor in the models including all target species together to remove any potential effects of interspecific trait differences on ITV.

Confirmatory multilevel path analyses (Shipley 2009, 2013) were conducted to test the causal relationships between rainfall, crowding, neighbouring plant traits (H_{NWM} , LA_{NWM} and SLA_{NWM}) and the trait values (height, LA and SLA) of subordinate individuals. The confirmatory multilevel path analysis is based on directed acyclic causal graphs (i.e. box-and-arrow causal diagrams without feedback loops; Fig. 1). The graphs are used to specify the direct and indirect causal relationships between the examined variables implied by each competing hypothesis. The validity of each path model is tested by deriving the set of independence claims from each graph. Using multilevel/mixed effect models, the probabilities p_i of each of the k independence claims are obtained, which are then combined into a C statistic:

$$C = -2 \sum_{i=1}^k \ln(p_i) \quad (3)$$

The resulting value is compared to a chi-square distribution with $2k$ degrees of freedom (Shipley 2009). If the value of the C statistic is lower than the specified significance level (here, $\alpha = 0.05$), the path model (and the corresponding hypothesis) is rejected, as the data have departed significantly from expectations under the tested causal model (see Appendices S3 and S4). We used the AIC statistic for d-step tests (Shipley 2013) when several models (and corresponding hypotheses) were selected. We used the following formula:

$$\text{AIC} = C + 2k \quad (4)$$

where C is the C statistic and k is the total number of free parameters.

To test the independence claims, we used linear mixed models, using the function *lmer* in the R package *lme4* (Bates *et al.* 2015) within the R language and software environment for statistical computing version 2.15.1. Model assumptions were tested by inspecting the residuals as per Pinheiro & Bates (2000). Individual path coefficients leading to endogenous variables (i.e. the variables in the graphs with arrows leading to them) were fitted using REML and tested for significance using conditional t -tests (Pinheiro & Bates 2000). Direct and indirect effects were computed using standardized path coefficients following Grace & Bollen (2005).

A confirmatory multilevel path analysis was first performed for the subordinate individuals of the four target species together (Appendix S3); this allowed us to detect potential general trends in the individual response of trait values to rainfall and neighbouring plants. The approach was repeated by treating each target species separately (i.e. one model per trait and target species, Appendix S4), assuming that the four target species with contrasting functional attributes may potentially respond differently to rainfall and neighbouring plant traits.

Rainfall was considered in the confirmatory multilevel path analyses as the exogenous variable (variable X1 in Appendix S3 and S4).

Crowding (X2), neighbouring plant traits (H_{NWM} : X3, LA_{NWM} : X4 and SLA_{NWM} : X5) and the trait values of subordinate individuals (height: X6, LA: X7 and SLA, X8) were considered as endogenous variables. Following the results of preliminary model selections, we also introduced a quadratic term (rainfall^2) in the models to take the nonlinear effect of rainfall into account (Appendices S1 and S2). Site was included as a random factor to account for the hierarchical nature of our survey. Species was introduced as a random factor when considering all target species together to avoid the response of trait values due to interspecific differences.

All trait values were log-transformed and all variables were standardized using z -scores prior statistical analyses (Appendix S5). All statistical analyses were performed using R (R Core Team 2012 version 2.15.1).

Results

The intraspecific trait variance of plant height linearly decreased with increasing rainfall (Fig. 2a: $r^2 = 0.40$, $P = 0.02$). No relationship was observed between rainfall and the ITV of LA (Fig. 2b: $r^2 < 0.01$, $P = 0.25$) and SLA (Fig. 2c: $r^2 = 0.03$, $P = 0.32$). The confirmatory path analyses supported both the biotic and the combined hypotheses for all models (Appendices S3 and S4). Nonetheless, the combined hypothesis was always the best supported model when considering all target species together (Fig. 3) or separately (Fig. 4). The abiotic hypothesis was never supported by our data (Appendices S3 and S4).

Overall, plant height decreased linearly with increasing rainfall (Fig. 3). However, contrasting responses were observed among target species. *Rosmarinus officinalis* and *S. tenacissima* showed a decrease in height with increasing rainfall, while *Q. coccifera* and *T. vulgaris* had the opposite response (Fig. 4). Crowding had an overall direct, positive effect on height (Fig. 3); this pattern was found for all target species except *Q. coccifera* (Fig. 4). Finally, the effect of neighbouring plant traits on height varied, depending on the target species under consideration (Figs 3 and 4). Mean neighbour height increased the height of subordinate individuals (Appendix S1), particularly for *R. officinalis* and *T. vulgaris* (Appendix S2). In contrast, mean neighbour height decreased the height of *S. tenacissima* (Appendix S2). Mean neighbour LA had opposing effects on the height of subordinate individuals, being positive for *R. officinalis* and negative for *T. vulgaris*. An overall negative effect of mean neighbour SLA on height (Appendix S1) occurred for *Q. coccifera* and *T. vulgaris* (Appendix S2).

Leaf area was most impacted by rainfall (Figs 3 and 5). The effects of rainfall were mostly nonlinear (Fig. 3, Appendix S1), except for *S. tenacissima* (Fig. 4, Appendix S2). Crowding had a very weak positive effect on LA (Fig. 4), which was only observed for *R. officinalis* (Fig. 4). Our model including all target species together did not detect effects of neighbouring plant traits on LA (Fig. 3). Nonetheless, positive relationships between mean neighbour LA and the LA of subordinate individuals were observed for *Q. coccifera* and *R. officinalis* (Fig. 4, Appendix S2). Finally, within-species co-variations were observed between LA and plant height (Fig. 4, Appendix S2). Leaf area decreased with increasing height for *Q. coccifera* and *T. vulgaris*, but increased in *S. tenacissima* (Appendix S2).

Specific leaf area primarily responded to observed within-species variations of LA and plant height (Fig. 3). Specific leaf area of *R. officinalis* and *S. tenacissima* decreased with increasing individual plant height, while SLA of *T. vulgaris* increased with height (Fig. 4). Specific leaf area decreased with increasing rainfall (Fig. 3). This negative relationship was nonlinear in *Q. coccifera* and *R. officinalis* (Fig. 4). Crowding had a weak positive effect on SLA (Fig. 3), which was only observed in *R. officinalis* (Fig. 4). Significant relationships between neighbouring plant traits and SLA were observed (Fig. 3), but only in *Q. coccifera* and *R. officinalis* (Fig. 4). Specific leaf area decreased with increasing mean neighbour LA and mean neighbour SLA in *Q. coccifera* and *R. officinalis*, respectively (Appendix S2).

Rainfall had strong direct effects on all traits (Fig. 3). However, direct effects of crowding and neighbouring plant traits were as strong as those of rainfall, particularly for plant height and SLA. Indirect effects were generally weaker than direct effects, except in the case of crowding (Fig. 3). The effects of crowding on SLA were considerably mediated by neighbouring plant traits. The relative importance of rainfall and neighbours strongly differed across species (Fig. 5). *Q. coccifera* was mostly affected by rainfall for all traits, although neighbouring plant traits had a substantial effect. The effects of crowding and neighbouring plant traits were as strong as those of rainfall on the ITV of *R. officinalis* and *T. vulgaris*, particularly for height. Finally, it is important to note that SLA strongly correlated with within-species variations in plant height and LA, suggesting that within-species trait coordination is an important contributor to ITV (Fig. 3: Within). Within-species co-variations between SLA with both

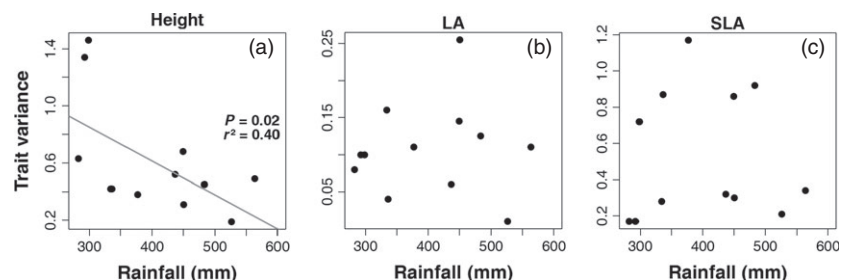


Fig. 2. Relationships between rainfall and intraspecific trait variance for (a) plant height, (b) leaf area (LA) and (c) specific leaf area (SLA). Grey lines are presented when significant.

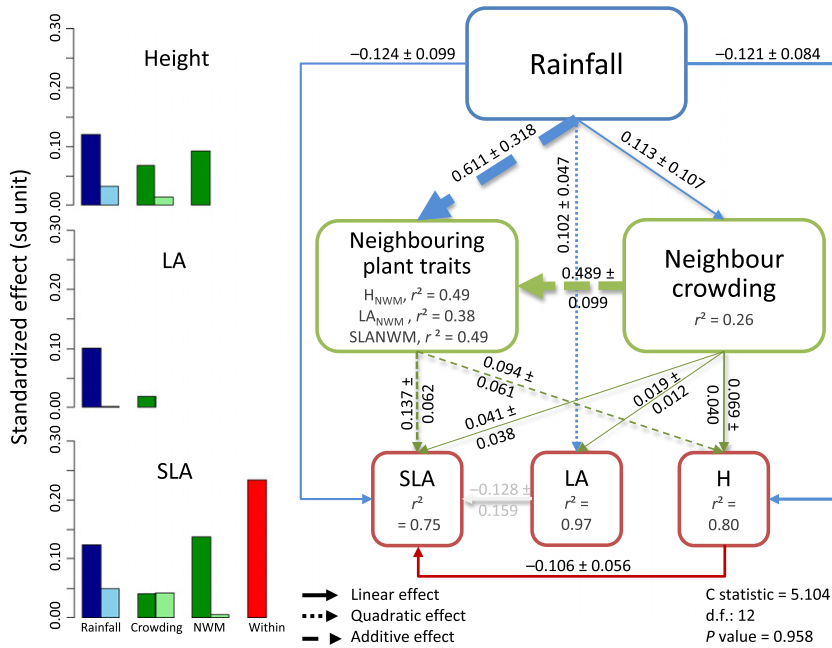


Fig. 3. Selected path model for all species together (combined hypothesis, see Appendix S3). Direct and indirect relationships between rainfall, crowding, neighbouring plant traits (H_{NWM} , LA_{NWM} and SLA_{NWM}) and the trait values of subordinate individuals [plant height, leaf area (LA) and specific leaf area (SLA)] are represented. Right panels: the selected models were consistent with the data. Path coefficients are shown for each pair of connected variables. Blue arrows represent the effect of rainfall, green arrows represent the impact of neighbouring plants (crowding and neighbouring plant traits), and red arrows indicate trait co-variation within individual plants. Arrow width is proportional to the standardized path coefficients. Grey arrows represent non-significant relationships. Left panels: absolute effect sizes of the direct (dark colours) and indirect (light colours) effects for each model parameter.

plant height and LA were observed for all target species except *Q. coccifera* (Fig. 5).

Discussion

Our study is one of the first to specifically disentangle the relative contribution of abiotic factors and local neighbourhoods to ITV. Our findings highlight the overwhelming importance of local plant neighbourhoods in determining ITV along a regional rainfall gradient, even when considering a set of dominant species characterized by contrasting ecological strategies. The biotic and the combined hypotheses were selected in all cases (the abiotic hypothesis was always rejected) highlighting that ITV is fundamentally related to biotic interactions (Kraft *et al.* 2014). An important implication of our findings is that ITV can be particularly important to adjust the phenotype of sessile organisms to the local environment (Schwinning & Weiner 1998; Violle *et al.* 2012). Therefore, examining the effects of biotic interactions on ITV advances our understanding of how plant species cope with the combination of local biotic interactions and regional environmental gradients, and thus help us in understanding the mechanisms driving community assembly.

RESPONSE OF INTRASPECIFIC TRAIT VARIABILITY TO RAINFALL

The variance of ITV within communities for plant height increased with water stress (Fig. 2); moreover, strong differences were observed in subordinate individual height between species along the rainfall gradient (Fig. 4). These results contrast with our hypothesis that increasing water stress will decrease the individual trait values for height and SLA and the range of ITV for all species similarly (environmental fil-

tering hypothesis: Grime 2006). The increased variance of ITV for plant height with water stress may be explained by the increase in soil heterogeneity (Bradshaw & Hardwick 1989) and bare soil with water stress (Appendix S6). All target species (except *Q. coccifera*) increased in size with increasing water stress. Many ecological processes may explain this unexpected result. Among those processes, our result may be explained by the release from competitive interactions with increasing water stress, as also observed along a broad soil moisture gradient in subalpine grasslands (Le Bagousse-Pinguet *et al.* 2014b). For instance, *S. tenacissima* is a typical species from dry Mediterranean regions that is well adapted to dry conditions, and its northern distribution is limited by the competition with tall shrubs and trees (Armas, Kikvidze & Pugnaire 2009). Alternatively, it may indicate the occurrence of facilitative interactions often described in water-limited ecosystems (e.g. Pugnaire, Armas & Maestre 2011).

Rainfall did not affect the intraspecific trait variance of LA (Fig. 2), but modified the LA of all subordinate individuals (Fig. 3). This result indicates that all species tended to respond in a similar manner to rainfall. Nonlinear relationships occurred along the rainfall gradient for most of the species under consideration, although LA generally decreases in a regular manner with soil water availability (Abrams, Kubiske & Mostoller 1994). The observed nonlinear response of LA may reflect strong adaptation of the studied species to water stress, as they would only change LA under very dry conditions (Schulze, Beck & Müller-Hohenstein 2005). Specific leaf area increased with water stress, reflecting a tendency to increase growth rates in response to short-term vegetative seasons in the dry part of the rainfall gradient studied (Niinemets 2001; Poorter *et al.* 2009). Gross *et al.* (2013) also found on the same study sites an overall increase in SLA at the community level at the extreme dry end of the gradient

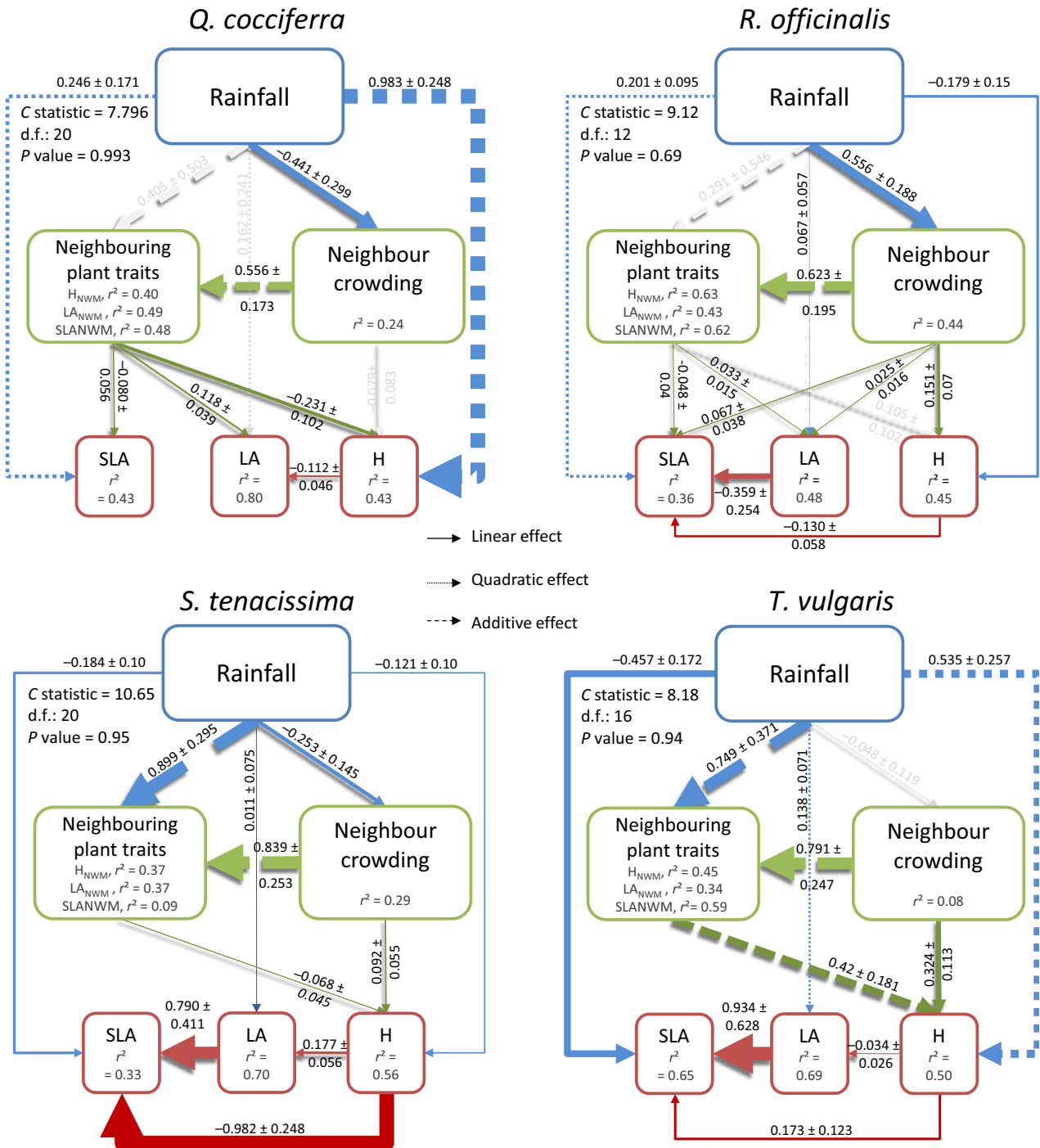


Fig. 4. Selected path models for each target species separately. Direct and indirect relationships between rainfall, crowding, neighbouring plant traits (H_{NWM} , LA_{NWM} and $SLANWM$) and the trait values of subordinate individuals are represented. Blue arrows represent the effect of rainfall, green arrows represent the effect of neighbouring plants (crowding and neighbouring plant trait), and red arrows indicate trait co-variation within individual plants. Path coefficients are shown for each pair of connected variables. Arrow width is proportional to the standardized path coefficients. Grey arrows represent non-significant relationships.

due to increased abundance of summer deciduous species. Our results indicate that these patterns could also be due to an increase in SLA at the intraspecific level. However, our findings contrast with those from Rubio De Casas *et al.* (2007), who found low variations in the SLA of *Q. coccifera* in populations under different environmental conditions.

These authors argued that counter-directional tuning to the sun and shade conditions within canopies of evergreen organisms may buffer the influence of the environment on the mean leaf phenotypic response. Our results may differ from those of Rubio De Casas *et al.* (2007) because of the increased length of the abiotic gradient under consideration.

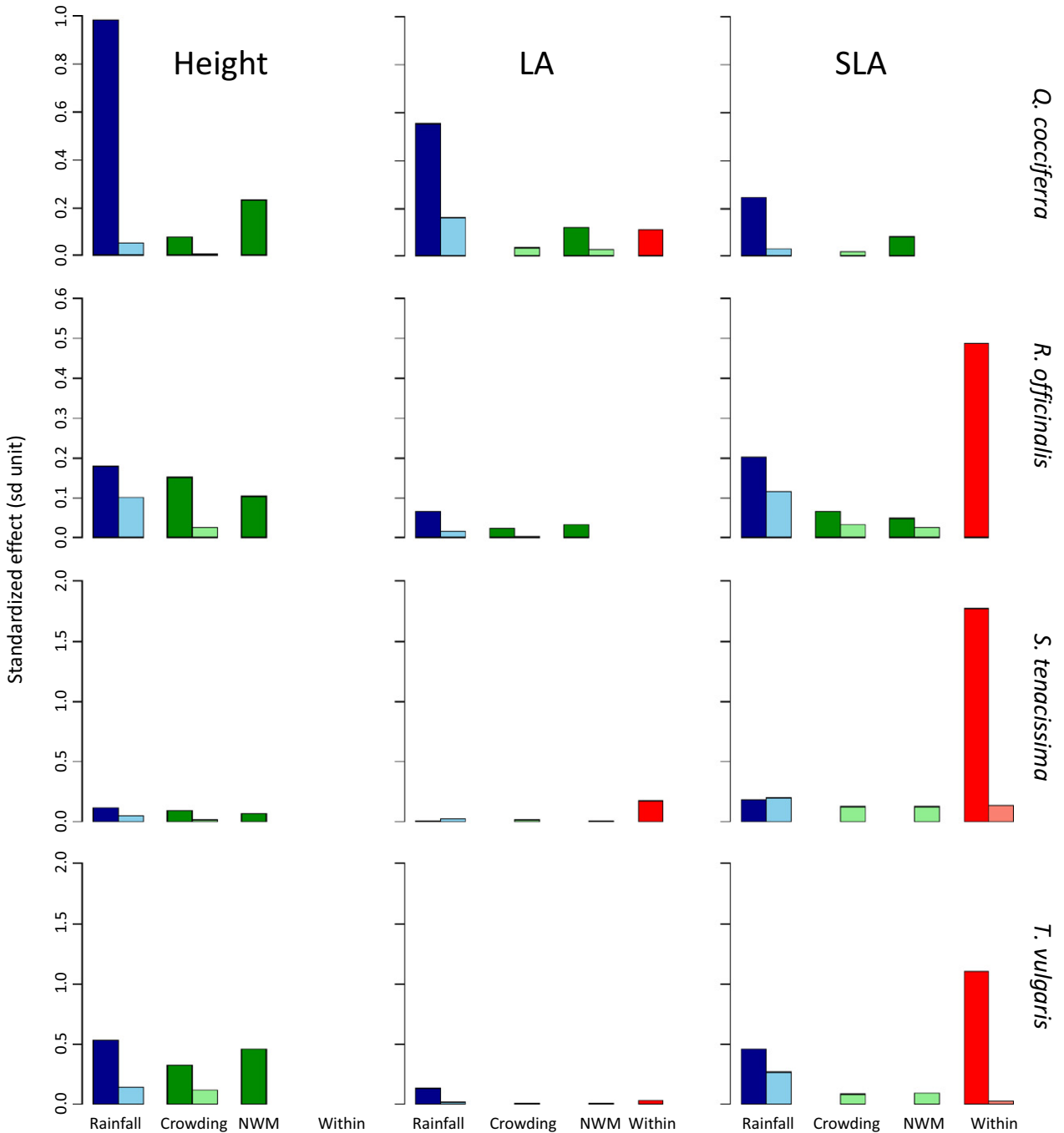


Fig. 5. Absolute effect sizes of the direct (dark colours) and indirect (light colours) effects of rainfall (blue), crowding and neighbouring plant traits (green) on the trait values of subordinate individuals (height, LA and SLA) (red) for the four studied target species separately (*Quercus coccifera*, *Rosmarinus officinalis*, *Stipa tenacissima* and *Thymus vulgaris*). Model selections among the three hypotheses (abiotic-only, biotic-only and combined hypotheses) for each species and each functional trait are presented in Appendix S4.

A relatively large rainfall gradient may push individuals to a breaking point and thus adapt to very dry conditions in order to survive.

RESPONSE OF INTRASPECIFIC TRAIT VARIABILITY TO THE LOCAL NEIGHBOURHOOD

Our data supported both the biotic and combined hypotheses and suggested that the effects of crowding and neighbouring

plant traits were as strong as the effect of rainfall. Rainfall, crowding and neighbouring plant traits had mostly direct effects, in accordance with recent findings from grasslands (Mason *et al.* 2011). However, weak indirect effects occurred, highlighting that the effect of rainfall on ITV can also be mediated by crowding and neighbouring plant traits (Figs 3 and 4). We acknowledge that our study did not consider interactive effects between rainfall and the local neighbourhood, and it may have potentially underestimated the strength of

indirect effects of rainfall mediated by the local neighbourhood (see Appendix S1 for interactions among factors). Furthermore, our approach was restricted to subordinate individuals, that is individuals which are the most likely to be impacted by their plant neighbours. Considering dominant individuals would have certainly affected our results and may have increased the effect of rainfall relative to local neighbourhood on ITV.

Neighbouring plant traits were as strong predictors as crowding in explaining changes in ITV. Increasing neighbour density has been shown to increase the strength of competitive interactions among plants when space becomes limiting (Grime 1973; Harley & Bertness 1996). Mean neighbour height and crowding tended to increase the height of individuals, therefore selecting for tall subordinate individuals only (Grime 2006; Schamp, Chau & Aarssen 2008; Gross *et al.* 2013). However, the strong impact of neighbouring plant traits on ITV also suggests that the functional identity of neighbours is independent from crowding. Neighbouring plant traits have been shown to determine both the magnitude and the direction of neighbour effects on local limiting resources, that is whether neighbours impact on local limiting resources positively (facilitation: Gross *et al.* 2009) or negatively (competition: e.g. Schamp, Chau & Aarssen 2008; Violle *et al.* 2009). Further studies are needed to improve our understanding on how ITV responds to the local biotic environments. Our approach does not elucidate the mechanistic links between effect traits and ITV because (i) it did not explicitly measure limiting resources in the studied system and its relationship with neighbouring traits, and (ii) the response of ITV to the local neighbourhood was strongly species-dependent.

IMPLICATIONS FOR FUNCTIONAL AND COMMUNITY ECOLOGY

Our study provides a hierarchical framework based on simple effect traits to quantify the effect of plant neighbours on ITV and to disentangle their effects from those of the abiotic environment. Our study identified knowledge gaps that should be considered for improving the use of trait-based approaches in functional and community ecology:

1 Plasticity vs. local adaptation: Changes in ITV may arise from either a plastic adjustment of plant phenotypes to neighbours (Schwinning & Weiner 1998) or from local adaptation (Sultan 2004). Plant populations have been suggested to adapt to local competitive and facilitative environments (Liancourt *et al.* 2012). Future research may aim to develop an individual trait-based approach to increase our mechanistic understanding of population persistence against environmental changes and micro-evolutionary impact on species coexistence and community assembly (Liancourt *et al.* 2012).

2 Species-specific response: The response of ITV to environmental constraints was strongly species-specific (see also Albert *et al.* 2010). Species differed both in their sensitivity to rainfall and neighbours and in the way they adjusted their trait values (Fig. 4, Appendix S2). However, strong correlations

between SLA and individual plant height were also observed (Fig. 4), highlighting that coordinations among traits determine their phenotypic plasticity to changes in both abiotic and biotic factors. In a modelling study comparing 13 grass species from temperate grasslands, Maire *et al.* (2013) showed that the coordination among multiple traits within species is related to plant functional strategies and to the carbon economy within individual plants. They identified key trade-offs occurring at the intraspecific level predicting responses to environmental changes with relatively high accuracy. Species plastic strategies of Mediterranean systems are largely ignored, and comparative approaches are needed to evaluate how physiological and allometric constraints within plant species determine patterns of ITV across species.

3 Trait-specific responses: The response of ITV to both abiotic and biotic factors varied depending on the trait considered. Plant height and SLA were generally more variable than LA. Whole-plant traits such as plant height are highly sensitive to the environment (Marks 2007), reflecting both species ontogeny and plant performance in a given environment. Specific leaf area is a key trait by which plants adjust resource acquisition to the local limiting resources (Maire *et al.* 2013). This trait is more variable than traits related to leaf morphology such as LA, which are strongly constrained by plant allometry (see the corner rule, Maire *et al.* 2013). Taking into account, ITV might be particularly critical for traits related to whole-plant architecture and leaf economic spectrum when studying community assembly processes. However, mean trait values might be sufficient to capture between species traits variations for leaf morphological traits.

4 Effect traits and limiting resources: All neighbouring plant traits selected in our study impacted ITV, suggesting that neighbour effects are multifactorial and do not necessarily have the same effects on individual target plants. For instance, mean neighbour height is hypothesized to relate to asymmetric light competition and competition for space (Grime 2006; Schamp, Chau & Aarssen 2008; Violle *et al.* 2009). In drylands, it can also be related to the presence of tall nurse plants and facilitation (Gross *et al.* 2013). Also, increasing mean neighbour SLA may indicate the presence of fast-growing shrub species (summer deciduous species) in the neighbourhood of a focal individual, and competition for soil resources (Gross *et al.* 2013). Increasing community level SLAs have been recently shown to negatively impact soil fertility and C : N pools in drylands (Valencia *et al.* 2015), leading to strong competition between fast- and slow-growing species (Gross *et al.* 2013). Finally, high mean neighbour LA may indicate the occurrence of large leaves and tall tussock species such as *S. tenacissima*, which have important impacts on neighbours by modifying microclimate conditions (Maestre, Bautista & Cortina 2003). Using plant removal experiments to investigate the relationship between neighbouring plant traits and local limiting resources can be of particular interest to provide a mechanistic understanding of the outcome of biotic interactions along abiotic stress gradients in water-limited ecosystems, an important unsolved debate (Soliveres, Smit & Maestre 2015).

Conclusions

In this study, we assessed the relative impacts of rainfall and the local neighbourhood on ITV in semi-arid Mediterranean communities. The effects of crowding and neighbouring plant traits on ITV were as strong as those of rainfall in a water-limited environment and were mostly direct and independent. More generally, sources of individual trait variation due to both abiotic and biotic constraints may call for adopting an individual, rather than a species trait-based community ecology to better predict how individuals assemble in communities.

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Data accessibility

All data associated with this manuscript are available in Appendix S5.

References

Abrams, M.D., Kubiske, M.E. & Mostoller, S.A. (1994) Relating wet and dry year ecophysiology to leaf structure in contrasting temperate tree species. *Ecology*, **75**, 123–133.

Albert, C.H., Thuiller, W., Yoccoz, N.G., Douzet, R., Aubert, S. & Lavorel, S. (2010) A multi trait approach reveals the structure and the relative importance of intra- versus interspecific variability in plant traits. *Functional Ecology*, **24**, 1192–1201.

Armas, C., Kikvidze, Z. & Pugnaire, F.I. (2009) Abiotic conditions, neighbour interactions, and the distribution of *Stipa tenacissima* in a semiarid mountain range. *Journal of Arid Environment*, **73**, 1084–1089.

Auger, S. & Shipley, B. (2013) Inter-specific and intraspecific trait variation along a short environmental gradient in an old-growth temperate forest. *Journal of Vegetation Science*, **24**, 419–428.

Barton, K. (2013) *MuMIn: Multi-Model Inference*. R package version 1.9.5. (CRAN r-Project, online). Available at <http://cran.r-project.org/web/packages/MuMIn/MuMIn.pdf>.

Bates, D., Maechler, M., Bolker, B.M. & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, available at <http://arxiv.org/abs/1406.5823>.

Bolnick, D.I., Amarasekare, P., Araujo, M.S., Bürger, R., Levine, J.M., Novak, M. et al. (2011) Why intraspecific trait variation matters in community ecology. *Trends in Ecology and Evolution*, **26**, 183–192.

Bradshaw, A.D. & Hardwick, K. (1989) Evolution and stress-genotypic and phenotypic components. *Biological Journal of the Linnean Society*, **37**, 137–155.

Callaway, R.M. (2007) *Positive Interactions and Interdependence in Plant Communities*. Springer, Dordrecht, The Netherlands.

Carmona, C.P., Rota, C., Azcarate, F.M. & Peco, B. (2015) More or less: sampling strategies of plant functional traits across local environmental gradients. *Functional Ecology*, **29**, 579–588.

Cienciaruso, M.V., Batalha, M.A., Gaston, K.J. & Petcey, O.L. (2009) Including intraspecific variability in functional diversity. *Ecology*, **90**, 81–89.

De Bello, F., Lavorel, S., Albert, C.H., Thuiller, W., Grigulis, K., Dolezal, J., Janecek, S. & Leps, J. (2011) Quantifying the relevance of intraspecific trait variability for functional diversity. *Methods in Ecology and Evolution*, **2**, 163–174.

Eldridge, D.J., Bowker, M.A., Maestre, F.T., Roger, E., Reynolds, J.F. & Whitford, W.G. (2011) Impacts of shrub encroachment on ecosystem structure and functioning: towards a global synthesis. *Ecology Letters*, **14**, 709–722.

Fajardo, A. & Piper, F.I. (2011) Intraspecific trait variation and covariation in a widespread tree species (*Nothofagus pumilio*) in Southern Chile. *New Phytologist*, **189**, 259–271.

Fridley, J.D. & Grime, J.P. (2010) Community and ecosystem effects of intraspecific genetic diversity in grassland microcosms of varying species diversity. *Ecology*, **91**, 2272–2283.

Fridley, J.D., Grime, J.P. & Bilton, M. (2007) Genetic identity of interspecific neighbours mediates plant responses to competition and environmental variation in a species-rich grassland. *Journal of Ecology*, **95**, 908–915.

Grace, J.B. & Bollen, K.A. (2005) Interpreting the results from multiple regression and structural equation models. *Bulletin of the Ecological Society of America*, **86**, 283–295.

Grime, J.P. (1973) Competitive exclusion in herbaceous vegetation. *Nature*, **242**, 344–347.

Grime, J.P. (2006) Trait convergence and trait divergence in herbaceous plant communities: mechanisms and consequences. *Journal of Vegetation Science*, **17**, 255–260.

Grime, J.P. & Mackey, J.M.L. (2002) The role of plasticity in resource capture by plants. *Evolutionary Ecology*, **16**, 299–307.

Gross, N., Robson, T.M., Lavorel, S., Albert, C.H., Le Bagousse-Pinguet, Y. & Guillemin, R. (2008) Plant response traits mediate the effects of subalpine grasslands on soil moisture. *New Phytologist*, **180**, 652–662.

Gross, N., Kunstler, G., Liancourt, P., De Bello, F., Suding, K.N. & Lavorel, S. (2009) Linking individual response to biotic interactions with community structure: a trait-based framework. *Functional Ecology*, **23**, 1167–1178.

Gross, N., Börger, L., Soriano-Morales, S.I., Le Bagousse-Pinguet, Y., Quero, J.-L., Garcia-Gomez, M., Valencia-Gomez, E. & Maestre, F.T. (2013) Uncovering multiscale effects of aridity and biotic interactions on the functional structure of Mediterranean shrublands. *Journal of Ecology*, **101**, 637–649.

Harley, C.D.G. & Bertness, M.D. (1996) Structural interdependence: an ecological consequence of morphological responses to crowding in marsh plants. *Functional Ecology*, **10**, 654–661.

Hulshof, C.M. & Swenson, N.G. (2010) Variation in leaf functional trait values within and across individuals and species: an example from a Costa Rican dry forest. *Functional Ecology*, **24**, 217–223.

Jung, V., Violle, C., Mondy, C., Hoffmann, L. & Muller, S. (2010) Intraspecific variability and trait-based community assembly. *Journal of Ecology*, **98**, 1134–1140.

Kraft, N.J.B., Crutsinger, G.M., Forrester, E.J. & Emery, N.C. (2014) Functional trait differences and the outcome of community assembly: an experimental test with vernal pool annual plants. *Oikos*, **123**, 1391–1399.

Lavorel, S., Grigulis, K., McIntyre, S., Williams, N.S.G., Gardén, D., Dorough, J. et al. (2008) Assessing functional diversity in the field – methodology matters!. *Functional Ecology*, **22**, 134–147.

Le Bagousse-Pinguet, Y., Forey, E., Touzard, B. & Michalet, R. (2013) Disentangling the effects of water and nutrients for studying the outcome of plant interactions in sand dune systems. *Journal of Vegetation Science*, **24**, 375–383.

Le Bagousse-Pinguet, Y., de Bello, F., Vandewalle, M., Leps, J. & Sykes, M.T. (2014a) Species richness of limestone grasslands increases with trait overlap: evidence from within- and between-species functional diversity partitioning. *Journal of Ecology*, **102**, 466–474.

Le Bagousse-Pinguet, Y., Maalouf, J.-P., Touzard, B. & Michalet, R. (2014b) Importance, but not intensity of plant interactions relates to species diversity under the interplay of stress and disturbance. *Oikos*, **123**, 777–785.

Liancourt, P., Choler, P., Gross, N., Thibert-Plante, X. & Tielbörger, K. (2012) How facilitation may interfere with ecological speciation. *International Journal of Ecology*, **2012**, 725487.

Maestre, F.T., Bautista, S. & Cortina, J. (2003) Positive, negative, and net effects in grass-shrub interactions in Mediterranean semi-arid grasslands. *Ecology*, **84**, 3186–3197.

Maestre, F.T., Bowker, M.A., Puche, M.D., Belén Hinojosa, M., Martínez, I., García-Palacios, P. et al. (2009) Shrub encroachment can reverse desertification in semi-arid Mediterranean grasslands. *Ecology letters*, **12**, 930–941.

- Maire, V., Gross, N., Hill, D., Martin, R., Wirth, C., Wright, I.J. *et al.* (2013) Disentangling coordination among functional traits using an individual-centred model: impact on plant performance at intra- and interspecific levels. *PLoS One*, **8**, e77372.
- Marks, C.O. (2007) The causes of variation in tree seedling traits: the roles of environmental selection versus chance. *Evolution*, **61**, 455–469.
- Mason, N.W.H., de Bello, F., Doležal, J. & Lepš, J. (2011) Niche overlap reveals the effects of competition, disturbance and contrasting assembly processes in experimental grassland communities. *Journal of Ecology*, **99**, 788–796.
- Messier, J., McGill, B.J. & Lechowicz, M.J. (2010) How do traits vary across ecological scales? A case for trait-based ecology. *Ecology Letters*, **13**, 838–848.
- Niinemets, U. (2001) Global-scale climatic controls of leaf dry mass per area, density, and thickness in trees and shrubs. *Ecology*, **82**, 453–469.
- Novoplanski, A. & Goldberg, D.E. (2001) Effects of water pulsing on individual plant performance and competitive hierarchies in plants. *Journal of Vegetation Science*, **12**, 199–208.
- Pérez-Harguindeguy, N., Díaz, S., Gamier, E., Lavorel, S., Poorter, H., Jaureguiberry, P. *et al.* (2013) New handbook for standardised measurement of plant functional traits worldwide. *Australian Journal of Botany*, **61**, 167–234.
- Pinheiro, J.C. & Bates, D.M. (2000) *Mixed Effect Models in S and S-PLUS*. Springer, New York, USA.
- Poorter, H., Niinemets, Ü., Poorter, L., Wright, I.J. & Villar, R. (2009) Causes and consequences of variation in leaf mass per area (LMA): a meta-analysis. *New Phytologist*, **182**, 565–588.
- Pugnaire, F.I., Armas, C. & Maestre, F.T. (2011) Positive plant interactions in the Iberian Southeast: mechanisms, environmental gradients, and ecosystem function. *Journal of Arid Environments*, **75**, 1310–1320.
- Quero, J.L., Maestre, F.T., Ochoa, V., Garcia-Gomez, M. & Delgado-Baquerizo, M. (2013) On the importance of shrub encroachment by sprouter, climate, species richness and anthropic factors for ecosystem multifunctionality in semi-arid Mediterranean ecosystems. *Ecosystems*, **16**, 1248–1261.
- R Development Core Team (2012) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria. Available at <http://www.R-project.org/>.
- Rao, C.R. (2010) Quadratic entropy and analysis of diversity. *Sankhya: The Indian Journal of Statistics*, **72**, 70–80.
- Rubio De Casas, R., Vargas, P., Pérez-Corona, E., Manrique, E., Quintana, J.R., Garcia-Verdugo, C. *et al.* (2007) Field patterns of leaf plasticity in adults of the long-lived evergreen *Quercus coccifera*. *Annals of Botany*, **100**, 325.
- Rubio de Casas, R., Vargas, P., Pérez-Corona, E., Cano, E., Manrique, E., Garcia-Verdugo, C. *et al.* (2009) Variation in sclerophylly among Iberian populations of *Quercus coccifera* L. is associated with genetic differentiation across contrasting environments. *Plant Biology*, **11**, 464–472.
- Schamp, B.S., Chau, J. & Aarssen, L.W. (2008) Dispersion of traits related to competitive ability in an old-field plant community. *Journal of Ecology*, **96**, 204–212.
- Schlichting, C.D. & Levin, D.A. (1986) Phenotypic plasticity: an evolving plant character. *Biological Journal of the Linnean Society*, **29**, 37–47.
- Schöb, C., Butterfield, B.J. & Pugnaire, F.I. (2012) Foundation species influence trait-based community assembly. *New Phytologist*, **196**, 824–834.
- Schulze, E.D., Beck, E. & Müller-Hohenstein, K. (2005) *Plant Ecology*. Springer, Heidelberg, Germany.
- Schwinning, S. & Weiner, J. (1998) Mechanisms determining the degree of size-asymmetry in competition among plants. *Oecologia*, **113**, 447–455.
- Shipley, B. (2009) Confirmatory path analysis in a generalized multilevel context. *Ecology*, **90**, 363–368.
- Shipley, B. (2013) The AIC model selection method applied to path analytic models compared using d-separation test. *Ecology*, **94**, 560–564.
- Soil Survey Staff (1994) *Keys to Soil Taxonomy*, 6th edn. USDA Soil Conservation Service, pp. 524. Pocahontas Press, Blacksburg, VA, USA
- Soliveres, S., Smit, C. & Maestre, F.T. (2015) Moving forward on facilitation research: response to changing environments and effects on the diversity, functioning and evolution of plant communities. *Biological Reviews*, **90**, 297–313.
- Stoll, P. & Weiner, J. (2000) A neighbourhood view of interactions among individual plants. *The Geometry of Ecological Interactions: Simplifying Spatial Complexity* (eds U. Dieckmann, R. Law & J.A.J. Metz), pp. 11–27. Cambridge University Press, Cambridge.
- Suding, K.N., Lavorel, S., Chapin, F., Cornelissen, J., Díaz, S., Garnier, E. *et al.* (2008) Scaling environmental change through the community-level: a trait-based response-and-effect framework for plants. *Global Change Biology*, **14**, 1125–1140.
- Sultan, S.E. (2004) Promising directions in plant phenotypic plasticity. *Perspectives in Plant Ecology, Evolution and Systematics*, **6**, 227–233.
- Tilman, D. (1982) *Resource Competition and Community Structure*. Princeton University Press, Princeton, NJ.
- Valencia, E., Maestre, F.T., Le Bagousse-Pinguet, Y., Quéro, J.L., Tamme, R., Börger, L. *et al.* (2015) Functional diversity enhances the resistance of ecosystem multifunctionality to aridity in Mediterranean drylands. *New Phytologist*, **206**, 660–671.
- Valladares, F., Wright, S.J., Lasso, E., Kitajima, K. & Pearcy, R.W. (2000) Plastic phenotypic response to light of 16 congeneric shrubs from a Panamanian rainforest. *Ecology*, **81**, 1925–1936.
- Vile, D., Garnier, E., Shipley, B., Laurent, G., Navas, M.-L., Roumet, C. *et al.* (2005) Specific leaf area and dry matter content estimate thickness in laminar leaves. *Annals of Botany*, **96**, 1129–1136.
- Violle, C., Navas, M.L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I. *et al.* (2007) Let the concept of trait be functional! *Oikos*, **116**, 882–892.
- Violle, C., Garnier, E., Lecoqeur, J., Roumet, C., Pouteur, C., Blanchard, A. *et al.* (2009) Competition, traits and resource depletion in plant communities. *Oecologia*, **160**, 747–755.
- Violle, C., Enquist, B.J., McGill, B.J., Jiang, L., Albert, C.H., Hulshof, C. *et al.* (2012) The return of variance: intraspecific variability in community ecology. *Trends in Ecology and Evolution*, **27**, 244–252.
- Westoby, M., Falster, D.S., Moles, A.T., Vesk, P.A. & Wright, I.J. (2002) Plant ecological strategies: some leading dimensions of variation between species. *Annual Review of Ecology and Systematics*, **33**, 125–159.
- Wright, I.J., Reich, P.B., Westoby, M., Ackerly, D.D., Baruch, Z., Bongers, F. *et al.* (2004) The worldwide leaf economics spectrum. *Nature*, **428**, 821–827.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Results of the linear mixed effect models including all target species together.

Appendix S2. Results of the linear mixed effect models for each target species separately.

Appendix S3. Results of the confirmatory multilevel path analysis including all target species together.

Appendix S4. Model selection and results of the confirmatory multilevel path analyses for each target species separately.

Appendix S5. Trait data for subordinate individuals and neighbours.

Appendix S6. Relationship between bare soil area and rainfall along the studied gradient.