



Swansea University  
Prifysgol Abertawe



## Cronfa - Swansea University Open Access Repository

---

This is an author produced version of a paper published in :

*Journal of Ecology*

Cronfa URL for this paper:

<http://cronfa.swan.ac.uk/Record/cronfa26956>

---

### Paper:

Le Bagousse-Pinguet, Y., Borger, L., Quero, J., García-Gómez, M., Soriano, S., Maestre, F. & Gross, N. (2015). Traits of neighbouring plants and space limitation determine intraspecific trait variability in semi-arid shrublands. *Journal of Ecology*, 103(6), 1647-1657.

<http://dx.doi.org/10.1111/1365-2745.12480>

---

This article is brought to you by Swansea University. Any person downloading material is agreeing to abide by the terms of the repository licence. Authors are personally responsible for adhering to publisher restrictions or conditions. When uploading content they are required to comply with their publisher agreement and the SHERPA RoMEO database to judge whether or not it is copyright safe to add this version of the paper to this repository.

<http://www.swansea.ac.uk/iss/researchsupport/cronfa-support/>

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

Journal:	<i>Journal of Ecology</i>
Manuscript ID:	JEcol-2015-0045.R1
Manuscript Type:	Standard Paper
Date Submitted by the Author:	18-Aug-2015
Complete List of Authors:	<p>Le Bagousse-Pinguet, Yoann; University of South Bohemia, Department of Botany          Börger, Luca; Swansea University, Department of Biosciences          Quero, José-Luis; Universidad Rey Juan Carlos, Departamento de Biología y Geología          Garcia-Gomez, Miguel; Universidad Rey Juan Carlos, Departamento de Biología y Geología          Soriano, Sara; Inra, CEBC          Maestre, Fernando; Universidad Rey Juan Carlos, Departamento de Biología y Geología          Gross, Nicolas; Inra, CEBC</p>
Key-words:	abiotic environment, community assembly, determinants of plant community diversity and structure, functional diversity, plant-plant interactions, trait-based approach, semi-arid Mediterranean shrublands

1 **Running Head:** Trait variability and community assembly

2 **Type of article:** Standard paper

3

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

6 Yoann Le Bagousse-Pinguet<sup>1\*</sup>, Luca Börger<sup>2, 3,4</sup>, José-Luis Quero<sup>5</sup>, Miguel García-Gómez<sup>6, 7</sup>,  
7 Sara Soriano<sup>2, 3</sup>, Fernando T. Maestre<sup>6</sup> and Nicolas Gross<sup>2, 3</sup>

8 <sup>1</sup>*Department of Botany, Faculty of Science; University of South Bohemia, Branisovska 31,*  
9 *CZ-370 05 Ceske Budejovice, Czech Republic*

10 <sup>2</sup>*INRA, USC1339 (CEBC-CNRS), F-79360, Beauvoir sur Niort, France.*

11 <sup>3</sup>*CEBC-CNRS (UPR 1934), F-79360, Beauvoir sur Niort, France.*

12 <sup>4</sup>*Department of Biosciences, College of Science, Swansea University, Singleton Park,*  
13 *Swansea, SA2 8PP, UK.*

14 <sup>5</sup>*Departamento de Ingenieria Forestal, Escuela Tecnica Superior de Ingenieria Agronomica y*  
15 *de Montes, Universidad de Cordoba, Edificio Leonardo da Vinci. Campus de Rabanales, Ctra*  
16 *N-IV km 396. C.P, 14071 Cordoba, Spain*

17 <sup>6</sup>*Área de Biodiversidad y Conservación, Departamento de Biología y Geología, Física y*  
18 *Química Inorgánica, Escuela Superior de Ciencias Experimentales y Tecnología,*  
19 *Universidad Rey Juan Carlos, C/ Tulipán s/n, 28933 Móstoles, Spain.*

20 <sup>7</sup>*Departamento de Ingeniería y Morfología del Terreno, Escuela Técnica Superior de*  
21 *Ingenieros de Caminos, Canales y Puertos, Universidad Politécnica de Madrid, Calle*  
22 *Profesor Aranguren s/n, 28040 Madrid, Spain.*

23 \*Correspondence author. Email: [y.b-pinguet@orange.fr](mailto:y.b-pinguet@orange.fr)

24 Word count in the summary: 247

25 Word count in the main text: 5576, References: 70, Figure: 5, Appendices: 6

## 26 **Summary**

- 27 1. Understanding how intraspecific trait variability (ITV) responds to both abiotic and biotic  
28 constraints is crucial to predict how individuals are assembled in plant communities, and  
29 how they will be impacted by ongoing global environmental change.
- 30 2. Three key functional traits [maximum plant height, leaf area (LA) and specific leaf area  
31 (SLA)] were assessed to quantify the range of ITV of four dominant plant species along a  
32 rainfall gradient in semi-arid Mediterranean shrublands. Variance partitioning and  
33 confirmatory multilevel path analyses were used to assess the direct and indirect effects of  
34 rainfall, **space limitation (crowding)**, and neighbouring plant traits on ITV.
- 35 3. The direct effect of the local neighbourhood on the trait values of **subordinate individuals**  
36 was as strong as the effect of rainfall. The indirect effect of rainfall however, mediated by  
37 the effect of the local neighbourhood on the trait values of **subordinate individuals**, was  
38 weak. Rainfall decreased the height and SLA of subordinate individuals, but increased  
39 their LA. Neighbouring plant traits were just as strong predictors as crowding in  
40 explaining changes in ITV.

41 *Synthesis* Our study provides a framework to disentangle the direct effects of abiotic factors  
42 and their indirect effects on ITV mediated by the local neighbourhood. Our results  
43 highlight that abiotic and biotic constraints are both substantial sources of trait variations  
44 at the individual level, and can blur processes underlying changes in ITV. Considering  
45 and disentangling combined sources with an individual perspective would help to refine  
46 our predictions for community assembly and functional ecology.

47 **Key-words:** abiotic environment, community assembly, functional diversity, plant  
48 interactions, trait-based approach, semi-arid Mediterranean shrublands.

49

50

## 51 **Introduction**

52 **Intraspecific trait variability (ITV hereafter)** arises from both heritable genetic variation and  
53 **phenotypic plasticity (e.g. Schlichting & Levin 1986)**, and represents the range of trait values  
54 **exhibited by a species grown in various environments (Violle *et al.* 2007)**. ITV represents a  
55 **significant contribution to the overall functional trait variability (e.g. Cianciaruso *et al.* 2009;**  
56 **Hulshof & Swenson 2010; Auger & Shipley 2013; Le Bagousse-Pinguet *et al.* 2014a)**, and  
57 **can be similar to or greater than interspecific trait variability in some cases (Valladares *et al.***  
58 **2000; Albert *et al.* 2010; Messier *et al.* 2010)**. Accounting for ITV can improve predictions  
59 **about species interactions (Kraft *et al.* 2014)**, community assembly and dynamics (Fridley *et*  
60 *al.* 2007; Jung *et al.* 2010; Bolnick *et al.* 2011; Le Bagousse-Pinguet *et al.* 2014a), and  
61 **ecosystem processes (Fridley & Grime 2010)**.

62 Disentangling the relative effects of abiotic and biotic factors on ITV constitutes an  
63 important step prior to further investigation on how ITV is linked to community assembly.  
64 Abiotic factors have been shown to impact ITV (e.g. Fajardo & Piper 2011), and species with  
65 different ecological strategies will exhibit contrasting ITV responses to these factors (Grime  
66 & Mackey 2002; Maire *et al.* 2013). **At the interspecific level, neighbouring plants can affect**  
67 **the growth and survival of other species by occupying the surrounding area and limiting the**  
68 **available space (i.e. crowding, e.g. Harley & Bertness 1996)**. Neighbouring plants can also  
69 **affect the growth and the survival of other species by either decreasing (competition: Grime**  
70 **1973; Tilman 1982) or increasing the local available resources (facilitation: Callaway 2007)**.  
71 Few studies to date have attempted to quantify the effects of neighbouring plants on ITV  
72 (Fridley *et al.* 2007), **and none have assessed how local neighbourhood and abiotic factors**  
73 **combined, impact on ITV**. Violle *et al.* (2012) strongly encouraged “*to investigate the spatial*  
74 *structure of trait distribution to estimate the importance of these fine-scales processes (biotic*  
75 *interactions), especially in plants.*” (see also Fajardo & Piper 2011).

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

87           We aimed to disentangle the direct and indirect effects of rainfall, **crowding** and  
88 neighbouring plant traits on ITV. The range of ITV of four dominant plant species was  
89 quantified along a regional rainfall gradient in semi-arid Mediterranean shrublands from  
90 Spain. These environments constitute appropriate ecosystems to test the response of ITV to  
91 biotic processes for the following reasons. Large phenotype variability has been reported  
92 along rainfall gradients such as that studied here (Rubio de Casas *et al.* 2009), suggesting that  
93 ITV is an important factor determining plant persistence and community assembly in semi-  
94 arid Mediterranean shrublands (Gross *et al.* 2013). **These shrublands are organized in**  
95 **crowded patches of vegetation, in which co-existing species can exhibit contrasting functional**  
96 **trait values (Gross *et al.* 2013). Finally, water stress and the occurrence of biotic interactions**  
97 **within vegetation patches are important factors affecting plant growth and survival in semi-**  
98 **arid Mediterranean communities (Novoplansky & Goldberg 2001; Pugnaire *et al.* 2011; Gross**  
99 ***et al.* 2013).**

100 We focused on three functional traits related to the competitive ability and/or tolerance  
101 to water stress, i.e. maximum plant height, leaf area and specific leaf area (e.g. Westoby *et al.*  
102 2002; Wright *et al.* 2004). These traits respond to both rainfall and biotic interactions, and are  
103 key determinants of community structure and ecosystem functioning in semi-arid  
104 Mediterranean communities (Gross *et al.* 2013, Valencia *et al.* 2015). We tested three  
105 hypotheses (Fig. 1): (i) ITV will respond to rainfall only (abiotic hypothesis); (ii) ITV will  
106 respond to neighbouring plants only (biotic hypothesis), and (iii) ITV will respond to both  
107 rainfall and neighbouring plants (combined hypothesis). Several scenarios can occur within  
108 the biotic and combined hypotheses. ITV may either respond to independent, but direct  
109 effects of rainfall and neighbouring plants, or to the indirect effect of rainfall mediated by  
110 neighbouring plants. Also, ITV may respond to crowding and neighbouring plant traits  
111 separately, or may respond to their combined effects. For instance, Gross *et al.* (2008) found  
112 that effect traits can be as important as the standing crop biomass in explaining the impact of  
113 neighbouring plants on biotic interactions. We hypothesized that: (i) rainfall will have a  
114 stronger impact on ITV than neighbouring plants in the shrublands studied; (ii) increasing  
115 water stress will decrease the individual trait values for height and specific leaf area and the  
116 range of ITV (variance), as water stress will select for more similar functional trait values  
117 (Grime 2006); and (iii) the effect traits of neighbouring plants will impact the trait values of  
118 individual plants (Fajardo & Piper 2011; Violle *et al.* 2012). If neighbouring plant traits  
119 impact ITV, they may alleviate the direct, positive effect of increased rainfall on trait values  
120 (e.g. due to competition).

121

## 122 **Material and Methods**

123 STUDY AREA

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

134

#### 135 TARGET SPECIES

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

144 Target individuals measured in the field were either, (i) isolated on bare soil areas; (ii)  
145 dominant within the vegetation patch (i.e. the tallest individuals); or (iii) subordinate within  
146 the vegetation patch (i.e. the smallest individuals). Only subordinate individuals within  
147 vegetation patches were used in our analyses because 1) only a few individuals were isolated  
148 on bare soil areas to test for the abiotic effect (7% of the total dataset) and 2) we assumed that



149 plant neighbours have an impact mainly on smaller individuals. We estimated a volume for all  
150 target subordinate and neighbouring individuals (i.e. all individuals in direct contact with the  
151 given target subordinate plant) along the rainfall gradient. The volume was estimated using a  
152 visual index, ranging from one to five (five being the highest volume). A volume of five was  
153 first attributed to the largest individual occurring in a given site. Then, volumes were  
154 attributed to target subordinate individuals and neighbouring individuals, relative to the  
155 volume of the largest individual. A Neighbour volume Ratio (NR) was calculated between the  
156 volume of target subordinate individuals and the total volume of neighbouring individuals in  
157 contact. We used a volume ratio because it has been previously shown that neighbouring plant  
158 size can affect the performance of subordinate species (Grime 1973). We calculated NR as:

$$159 \quad NR = \sum(\text{total volume of neighbouring individuals}) / \text{volume of the subordinate individual} \quad (2)$$

160 When  $NR > 1$ , the volume of neighbouring plants was higher than the volume of the  
161 subordinate individual, and the target individual was considered as a subordinate individual.

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

166

## 167 TRAIT MEASUREMENTS

168 Three functional traits related to leaf morphology and plant size were selected: maximum  
169 plant height, leaf area (LA) and specific leaf area (SLA). Size-related traits such as height (H)  
170 are related to plant water use efficiency and competitive ability (e.g. Westoby *et al.* 2002).  
171 Height has also been suggested to be an important functional trait of shrubs such as *Q.*  
172 *coccifera*, and affects the functional outcomes of shrub encroachment in drylands (Maestre *et*  
173 *al.* 2009; Eldridge *et al.* 2011). Traits such as leaf area (LA) are related to light interception

174 and water stress tolerance (Westoby *et al.* 2002). Specific leaf area (SLA) is related to the leaf  
175 economic spectrum, reflects the relative growth rate of plants, and is associated with plant  
176 strategies to acquire, use and/or conserve resources such as light, nutrients and water (Wright  
177 *et al.* 2004).

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

184

#### 185 NEIGHBOURING PLANT TRAITS

186 To test the impact of neighbouring plant traits on the ITV of the four target species, we first  
187 recorded the taxonomic identity of all neighbouring individuals touching the target  
188 subordinate individual. The volume of all individuals for a given neighbouring species,  $i$ , was  
189 compared to that of all neighbouring individuals in contact with the subordinate individual,  $p_i$ .  
190 Then, we calculated the mean trait values (mean trait values for height, LA and SLA) for each  
191 of the neighbouring species using trait values measured in a given site. A Neighbour  
192 Weighted-Mean index (NWM) was calculated for height (neighbour-mean height:  $H_{NWM}$ ), LA  
193 (neighbour-mean LA:  $LA_{NWM}$ ) and SLA (neighbour-mean SLA:  $SLA_{NWM}$ ) using the mean  
194 trait values of the neighbouring species and the volume of each neighbouring individual in  
195 direct contact with a focal subordinate individual. Thus, NWMs quantify the “effect traits” of  
196 all neighbouring individuals in direct contact with each of the target subordinate individuals.  
197 This index is similar to the Community Weighted Mean index of Lavorel *et al.* (2008), and

198 allows the calculation of the mean trait values of neighbours accounting for their respective  
199 volume:

$$200 \quad NWM = \sum p_i \times Trait_i \quad (1)$$

201 where  $p_i$  is the volume of all individuals of a neighbouring species  $i$  relative to the volume of  
202 the whole neighbouring species in contact with a **subordinate** individual, and  $Trait_i$  is the  
203 mean trait value of the species  $i$ . Our approach offers a practical way to link biotic interactions  
204 to ITV. However, we also acknowledge that it cannot differentiate between the type of  
205 interactions involved (i.e. competition or facilitation), nor explicitly evaluate the mechanisms  
206 underlying them (i.e. which resources are mediating local interactions; e.g. Violle *et al.* 2009).

## 208 STATISTICAL ANALYSES

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

214 *Intraspecific trait variance along the rainfall gradient* - The intraspecific trait variance was  
215 quantified for each of the 12 sampled sites. The method of variance partitioning used (de  
216 Bello *et al.* 2011) is equivalent to the decomposition of the quadratic entropy diversity (Rao  
217 2010). **For a given trait, the method corresponds to the traditional variance partitioning of sum  
218 of squares in ANOVA, with species identity as the explanatory variable.** Here, the diversity  
219 within species corresponds to the within samples effect. The intraspecific trait variance is  
220 calculated; first, as the variance of trait values within each of the four target species  
221 (intraspecific trait variance). Then, a weighted average of all intraspecific trait variances is

222 computed for each study site, this being the weight determined by the number of individuals  
223 per species (see de Bello *et al.* 2011 for details).

224 Changes in intraspecific trait variance were assessed along the rainfall gradient using  
225 linear regression models. Intraspecific trait variances for height, LA and SLA were used as  
226 the response variables, and rainfall was used as the predictor. A quadratic term (rainfall<sup>2</sup>) was  
227 also included in the models, as trait variances can follow non-linear responses along the  
228 studied rainfall gradient (Gross *et al.* 2013).

229 *Effects of rainfall, crowding and neighbouring plant traits on ITV* – Prior to the confirmatory  
230 multilevel path analyses, preliminary linear mixed effect models were performed for all target  
231 species together (Appendix S1) and separately (Appendix S2). These analyses aimed to: 1)  
232 determine if non-linear effects of rainfall should be included in further analyses; 2) select the  
233 neighbouring plant traits impacting on the trait values of the subordinate individuals; 3) assess  
234 which traits of subordinate individuals are impacted by crowding. Crowding was estimated  
235 using the total volume of neighbouring individuals in contact with the target individual,  
236 because the size of neighbouring plants (and not the number) is required to fully assess  
237 crowding effects (Stoll & Weiner 2000). The linear mixed effect models were performed for  
238 each trait separately using the function *lmer* in the R package *lme4* (Bates *et al.* 2015). A  
239 model averaging procedure was applied to estimate the effects of predictors, based on the best  
240 5% of all potential models, using the function *dredge* in the R package *MuMIn* (Barton 2013).  
241 The individual trait values were used as the response variables, and rainfall, rainfall<sup>2</sup>,  
242 crowding and neighbouring plant traits ( $H_{NWM}$ ,  $LA_{NWM}$  and  $SLA_{NWM}$ ) as predictors.  
243 Maximum plant height was also introduced as a predictor of LA and SLA to consider  
244 potential coordinated changes among traits (Maire *et al.* 2013). Maximum plant height is  
245 related to plant species performance and ontogeny, which are two important factors  
246 potentially impacting the expression of other traits (Maire *et al.* 2013). LA was introduced as

247 a predictor of SLA because these two traits are partly mathematically related (Vile *et al.*  
248 2005). Site was used as a random factor to control for the hierarchical nature of our survey.  
249 Species was also used as a random factor in the models including all target species together to  
250 remove any potential effects of interspecific trait differences on ITV.

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

$$261 \quad C = -2 \sum_{i=1}^k \ln(p_i) \quad (1)$$

262 The resulting value is compared to a  $\chi^2$  distribution with  $2k$  degrees of freedom (Shipley  
263 2009). If the value of the  $C$ -statistic is lower than the specified significance level (here,  $\alpha =$   
264  $0.05$ ) the path model (and the corresponding hypothesis) is rejected, as the data have departed  
265 significantly from expectations under the tested causal model (see appendices S3 and S4). We  
266 used the AIC statistic for d-step tests (Shipley 2013) when several models (and corresponding  
267 hypotheses) were selected. We used the following formula:

$$268 \quad AIC = C + 2k \quad (2)$$

269 where  $C$  is the  $C$  statistic and  $K$  is the total number of free parameters.

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

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

285 Rainfall was considered in the confirmatory multilevel path analyses as the exogenous  
286 variable (variable X1 in Appendix S3 and S4). Crowding (X2), neighbouring plant traits  
287 ( $H_{NWM}$ : X3,  $LA_{NWM}$ : X4 and  $SLA_{NWM}$ , X5) and the trait values of subordinate individuals  
288 (height: X6, LA: X7 and SLA, X8) were considered as endogenous variables. Following the  
289 results of preliminary model selections, we also introduced a quadratic term (rainfall<sup>2</sup>) in the  
290 models to take the non linear effect of rainfall into account (Appendices S1 and S2). Site was  
291 included as a random factor to account for the hierarchical nature of our survey. Species was  
292 introduced as a random factor when considering all target species together to avoid the  
293 response of trait values due to interspecific differences.

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

297

## 298 **Results**

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

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

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

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

337 Rainfall had strong direct effects on all traits (Fig. 3). However, direct effects of  
338 crowding and neighbouring plant traits were as strong as those of rainfall, particularly for  
339 maximum plant height and SLA. Indirect effects were generally weaker than direct effects,  
340 except in the case of crowding (Fig. 3). The effects of crowding on SLA were considerably  
341 mediated by neighbouring plant traits. The relative importance of rainfall and neighbours  
342 strongly differed across species (Fig. 5). *Q. coccifera* was mostly affected by rainfall for all  
343 traits, although neighbouring plant traits had a substantial effect. The effects of crowding and



344 neighbouring plant traits were as strong as those of rainfall on the ITV of *R. officinalis* and *T.*  
345 *vulgaris*, particularly for height. Finally, it is important to note that SLA strongly correlated  
346 with within-species variations in plant height and LA, suggesting that within-species trait  
347 coordination is an important contributor to ITV (Fig. 3: Within). Within-species co-variations  
348 between SLA with both plant height and leaf area were observed for all target species except  
349 *Q. coccifera* (Fig. 5).

350

## 351 **Discussion**

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

365

## 366 **RESPONSE OF INTRASPECIFIC TRAIT VARIABILITY TO RAINFALL**

367 The variance of ITV within communities for maximum plant height increased with water  
368 stress (Fig. 2); moreover, strong differences were observed in subordinate individual height

369 between species along the rainfall gradient (Fig. 4). These results contrast with our hypothesis  
370 that increasing water stress will decrease the individual trait values for height and specific leaf  
371 area and the range of ITV for all species similarly (environmental filtering hypothesis: Grime  
372 2006). The increased variance of ITV for plant height with water stress may be explained by  
373 the increase in soil heterogeneity (Bradshaw & Hardwick 1989) and bare soil with water  
374 stress (Appendix S6). All target species (except *Q. coccifera*) increased in size with  
375 increasing water stress. This unexpected result may be explained by the release of competitive  
376 interactions with increasing water stress, as also observed along a broad soil moisture gradient  
377 in subalpine grasslands (Le Bagousse-Pinguet *et al.* 2014b). For instance, *S. tenacissima* is a  
378 typical species from dry Mediterranean regions that is well adapted to dry conditions, and its  
379 northern distribution is limited by the competition with tall shrubs and trees (Armas *et al.*  
380 2009). Alternatively, it may indicate the occurrence of facilitative interactions often described  
381 in water-limited ecosystems (e.g. Pugnaire *et al.* 2011).

382         Rainfall did not affect the intraspecific trait variance of LA (Fig. 2), but modified the  
383 LA of all subordinate individuals (Fig. 3). This result indicates that all species tended to  
384 respond in a similar manner to rainfall. Non linear relationships occurred along the rainfall  
385 gradient for most of the species under consideration, although LA generally decreases in a  
386 regular manner with soil water availability (Abrams *et al.* 1994). The observed non-linear  
387 response of LA may reflect strong adaptation of the studied species to water stress, as they  
388 would only change leaf area under very dry conditions (Schulze *et al.* 2005). Specific leaf  
389 area increased with water stress, reflecting a tendency to increase growth rates in response to  
390 short-term vegetative seasons in the dry part of the rainfall gradient studied (Niinemets 2001;  
391 Poorter *et al.* 2009). Gross *et al.* (2013) also found on the same study sites an overall increase  
392 in SLA at the community level at the extreme dry end of the gradient due to increased  
393 abundance of summer deciduous species. Our results indicate that these patterns could also be

394 due to an increase in SLA at the intraspecific level. However, our findings contrast with those  
395 from Rubio de Casas *et al.* (2007), who found low variations in the SLA of *Q. coccifera* in  
396 populations under different environmental conditions. These authors argued that counter-  
397 directional tuning to the sun and shade conditions within canopies of evergreen organisms  
398 may buffer the influence of the environment on the mean leaf phenotypic response. Our  
399 results may differ from those of Rubio de Casas *et al.* (2007) because of the increased length  
400 of the abiotic gradient under consideration. A relatively large rainfall gradient may push  
401 individuals to a breaking point and thus adapt to very dry conditions in order to survive.

402

#### 403 RESPONSE OF INTRASPECIFIC TRAIT VARIABILITY TO THE LOCAL 404 NEIGHBOURHOOD

405 Our data supported both the Biotic and Combined hypotheses, and suggested that the effects  
406 of crowding and neighbouring plant traits were as strong as the effect of rainfall. Rainfall,  
407 crowding and neighbouring plant traits had mostly direct effects, in accordance with recent  
408 findings from grasslands (Mason *et al.* 2011). However, weak indirect effects occurred,  
409 highlighting that the effect of rainfall on ITV can also be mediated by crowding and  
410 neighbouring plant traits (Figs. 3 & 4). We acknowledge that our study did not consider  
411 interactive effects between rainfall and the local neighbourhood, and it may have potentially  
412 underestimated the strength of indirect effects of rainfall mediated by the local neighbourhood  
413 (see Appendix S1 for interactions among factors). Furthermore, our approach was restricted to  
414 subordinate individuals, i.e. individuals which are the most likely to be impacted by their  
415 plant neighbours. Considering dominant individuals would have certainly affected our results,  
416 and may have increased the effect of rainfall relative to local neighbourhood on ITV.

417 Neighbouring plant traits were as strong predictors as crowding in explaining changes  
418 in ITV. Increasing neighbour density has been shown to increase the strength of competitive

419 interactions among plants when space becomes limiting (Grime 1973; Harley & Bertness  
420 1996). Mean-neighbour height and crowding tended to increase the height of individuals,  
421 therefore selecting for tall subordinate individuals only (Grime 2006; Schamp *et al.* 2008;  
422 Gross *et al.* 2013). However, the strong impact of neighbouring plant traits on ITV also  
423 suggests that the functional identity of neighbours is independent from crowding.  
424 Neighbouring plant traits have been shown to determine both the magnitude and the direction  
425 of neighbour effects on local limiting resources, i.e. whether neighbours impact on local  
426 limiting resources positively (facilitation: Gross *et al.* 2009) or negatively (competition: e.g.  
427 Schamp *et al.* 2008; Violle *et al.* 2009). Further studies are needed to improve our  
428 understanding on how ITV responds to the local biotic environments. Our approach does not  
429 elucidate the mechanistic links between effect traits and ITV because (i) it did not explicitly  
430 measure limiting resources in the studied system and its relationship with neighbouring traits;  
431 (ii) the response of ITV to the local neighbourhood was strongly species-dependent.

432

### 433 **IMPLICATIONS FOR FUNCTIONAL AND COMMUNITY ECOLOGY**

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

438 *i) Plasticity vs. local adaptation:* changes in ITV may arise from either a plastic  
439 adjustment of plant phenotypes to neighbours (Schwinning & Weiner 1998) or from local  
440 adaptation (Sultan 2004). Plant populations have been suggested to adapt to local competitive  
441 and facilitative environments (Liancourt *et al.* 2012). Future research may aim to develop an  
442 individual trait-based approach to increase our mechanistic understanding of population

443 persistence against environmental changes and micro-evolutionary impact on species  
444 coexistence and community assembly (Liancourt *et al.* 2012).

445 *ii) Species-specific response:* the response of ITV to environmental constraints was  
446 strongly species-specific (see also Albert *et al.* 2010). Species differed both in their sensitivity  
447 to rainfall and neighbours and in the way they adjusted their trait values (Fig. 4, Appendix  
448 S2). However, strong correlations between SLA and individual plant height were also  
449 observed (Fig. 4), highlighting that coordinations among traits determine their phenotypic  
450 plasticity to changes in both abiotic and biotic factors. In a modelling study comparing 13  
451 grass species from temperate grasslands, Maire *et al.* (2013) showed that the coordination  
452 among multiple traits within species is related to plant functional strategies and to the carbon  
453 economy within individual plants. They identified key trade-offs occurring at the intraspecific  
454 level predicting responses to environmental changes with relatively high accuracy. Species  
455 plastic strategies of Mediterranean systems are largely ignored, and comparative approaches  
456 are needed to evaluate how physiological and allometric constraints within plant species  
457 determine patterns of ITV across species.

458 *iii) Trait-specific responses:* the response of ITV to both abiotic and biotic factors  
459 varied depending on the trait considered. Maximum plant height and SLA were generally  
460 more variable than LA. Whole plant traits such as maximum plant height are highly sensitive  
461 to the environment (Marks 2007), reflecting both species ontogeny and plant performance in a  
462 given environment. Specific leaf area is a key trait by which plants adjust resource acquisition  
463 to the local limiting resources (Maire *et al.* 2013). This trait is more variable than traits related  
464 to leaf morphology such as LA, which are strongly constrained by plant allometry (see the  
465 corner rule, Maire *et al.* 2013). Taking into account ITV might be particularly critical for  
466 traits related to whole plant architecture and leaf economic spectrum when studying

467 community assembly processes. However, mean trait values might be sufficient to capture  
468 between species traits variations for leaf morphological traits.

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

487

## 488 CONCLUSIONS

489 In this study, we assessed the relative impacts of rainfall and the local neighbourhood on ITV  
490 in semi-arid Mediterranean communities. The effects of crowding and neighbouring plant  
491 traits on ITV were as strong as those of rainfall in a water-limited environment, and were

492 mostly direct and independent. More generally, sources of individual trait variation due to  
493 both abiotic and biotic constraints may call for adopting an individual, rather than a species  
494 trait-based community ecology to better predict how individuals assemble in communities.

495

## 496 **Acknowledgements**

497 Y.L.B.P is supported by the project Postdoc USB (reg.no. CZ.1.07/2.3.00/30.0006) realized  
498 through EU Education for Competitiveness Operational Programme. This project is funded by  
499 the European Social Fund and the Czech State Budget. This research was funded by the  
500 European Research Council under the European Community's Seventh Framework  
501 Programme (FP7/2007-2013)/ERC Grant agreement n° 242658 (BIOCOM) awarded to  
502 F.T.M. F.T.M. acknowledges support from the Spanish Ministerio de Educación (“Salvador  
503 de Madariaga program”, PR2010-0230) and from a Humboldt Research Award from the  
504 Alexander von Humboldt Stiftung during the writing of the manuscript. J.L.Q. acknowledges  
505 support from the BIOCOM project. We are very grateful to the Editor and one anonymous  
506 reviewer for valuable comments on earlier versions of the manuscript, to Dr. A. Hartigan for  
507 editing the text and improving the English, and to the Spanish “Guardia Civil” for their  
508 technical assistance during the field work.

509

## 510 **References**

- 511 Abrams, M.D., Kubiske, M.E. & Mostoller, S.A. (1994) Relating wet and dry year  
512 ecophysiology to leaf structure in contrasting temperate tree species. *Ecology*, **75**, 123-  
513 133.
- 514 Albert, C.H., Thuiller, W., Yoccoz, N.G., Douzet, R., Aubert, S. & Lavorel, S. (2010) A multi  
515 trait approach reveals the structure and the relative importance of intra- versus  
516 interspecific variability in plant traits. *Functional Ecology*, **24**, 1192–1201.

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

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

523 Barton, K (2013) *MuMIn: Multi-model inference*. R package version 1.9.0 ed.

524 Bates, D., Maechler, M., Bolker, B.M. & Walker, S. (2015). Fitting Linear Mixed-Effects  
525 Models using lme4. *Journal of Statistical Software*, <http://arxiv.org/abs/1406.5823>.

526 Bolnick, D.I, Amarasekare, P., Araujo, M.S., Bürger, R., Levine, J.M., Novak, M. *et al.*  
527 (2011) Why intraspecific trait variation matters in community ecology. *Trends in*  
528 *Ecology and Evolution*, **26**, 183-192.

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

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

533 Carmona, C.P., Rota, C., Azcarate, F.M. & Peco, B. (2015) More or less: sampling strategies  
534 of plant functional traits across local environmental gradients. *Functional Ecology*, **29**,  
535 579-588.

536 Cianciaruso, M.V., Batalha, M.A., Gaston, K.J. & Petchey, O.L. (2009) Including  
537 intraspecific variability in functional diversity. *Ecology*, **90**, 81-89.

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



541 Eldridge, D.J., Bowker, M.A., Maestre, F.T., Roger, E., Reynolds, J.F. & Whitford, W.G.  
542 (2011) Impacts of shrub encroachment on ecosystem structure and functioning: towards  
543 a global synthesis. *Ecology Letters*, **14**, 709–722.

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

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

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

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

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

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

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

558 Gross, N., Robson, T.M., Lavorel, S., Albert, C.H., Le Bagousse-Pinguet, Y. & Guillemin, R.  
559 (2008) Plant response traits mediate the effects of subalpine grasslands on soil moisture.  
560 *New Phytologist*, **180**, 652–662.

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

564 Gross, N., Börger, L., Soriano-Morales, S.I., Le Bagousse-Pinguet, Y., Quero, J-L., Garcia-  
565 Gomez, M., Valencia-Gomez, E. & Maestre, F.T. (2013) Uncovering multiscale effects

566 of aridity and biotic interactions on the functional structure of Mediterranean  
567 shrublands. *Journal of Ecology*, **101**, 637-649.

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

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

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

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

579 Lavorel, S., Grigulis, K., McIntyre, S., Williams, N.S.G., Garden, D., Dorrough, J. *et al.*  
580 (2008) Assessing functional diversity in the field—methodology matters! *Functional*  
581 *Ecology*, **22**, 134–147.

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

585 Le Bagousse-Pinguet, Y., de Bello, F., Vandewalle, M., Leps, J. & Sykes, M.T. (2014a)  
586 Species richness of limestone grasslands increases with trait overlap: evidence from  
587 within- and between-species functional diversity partitioning. *Journal of Ecology*, **102**,  
588 466-474.

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

592 Liancourt, P., Choler, P., Gross, N., Thibert-Plante X. & Tielbörger K. (2012) How  
593 facilitation may interfere with ecological speciation. *International Journal of Ecology*,  
594 doi:10.1155/2012/725487

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

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

600 Maire V., Gross N., Hill D., Martin R., Wirth C., Wright I.J. *et al.* (2013) Disentangling  
601 coordination among functional traits using an individual-centred model: Impact on plant  
602 performance at intra- and interspecific levels. *Plos One*, **8**, e77372.

603 Marks, C.O. (2007). The causes of variation in tree seedling traits: the roles of environmental  
604 selection versus chance. *Evolution*, **61**, 455–469.

605 Mason, N.W.H., de Bello, F., Doležal, J., Lepš, J. (2011) Niche overlap reveals the effects of  
606 competition, disturbance and contrasting assembly processes in experimental grassland  
607 communities. *Journal of Ecology*, **99**, 788-796.

608 Messier, J., McGill, B.J. & Lechowicz, M.J. (2010) How do traits vary across ecological  
609 scales? A case for trait-based ecology. *Ecology Letters*, **13**, 838–848.

610 Niinemets, U. (2001) Global-scale climatic controls of leaf dry mass per area, density, and  
611 thickness in trees and shrubs. *Ecology*, **82**, 453-469.

612 Novoplanski, A. & Goldberg, D.E. (2001) Effects of water pulsing on individual plant  
613 performance and competitive hierarchies in plants. *Journal of Vegetation Science*, **12**,  
614 199-208.

615 Pérez-Harguindeguy, N., Díaz, S., Garnier, E., Lavorel, S., Poorter, H., Jaureguiberry, P. *et al.*  
616 (2013) New handbook for standardised measurement of plant functional traits  
617 worldwide. *Australian Journal of Botany*, **61**, 167-234.

618 Pinheiro, J.C. & Bates, D.M. (2000) *Mixed effect models in S and S-PLUS*. Springer, New-  
619 York, USA.

620 Poorter, H., Niinemets, Ü., Poorter, L., Wright, I.J. & Villar, R. (2009) Causes and  
621 consequences of variation in leaf mass per area (LMA): a meta-analysis. *New*  
622 *Phytologist*, **182**, 565–588.

623 Pugnaire, F.I., Armas, C. & Maestre, F.T. (2011) Positive plant interactions in the Iberian  
624 Southeast: mechanisms, environmental gradients, and ecosystem function. *Journal of*  
625 *Arid Environments*, **75**, 1310-1320.

626 Quero, J.L., Maestre, F.T., Ochoa, V., Garcia-Gomez, M. & Delgado-Baquerizo, M. (2013)  
627 On the importance of shrub encroachment by sprouter, climate, species richness and  
628 anthropic factors for ecosystem multifunctionality in semi-arid mediterranean  
629 ecosystems. *Ecosystems*, **16**, 1248-1261.

630 R Development Core Team (2012) R: A language and environment for statistical computing.  
631 R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL  
632 <http://www.R-project.org/>.

633 Rao, C.R (2010) Quadratic entropy and analysis of diversity. *Sankhya: The Indian Journal of*  
634 *Statistics*, **72**, 70–80.

- 635 Rubio De Casas, R., Vargas, P., Perez-Corona, E., Manrique, E., Quintana, J.R., Garcia-  
636 Verdugo, C. *et al.* (2007) Field patterns of leaf plasticity in adults of the long-lived  
637 evergreen *Quercus coccifera*. *Annals of Botany*, **100**, 325.
- 638 Rubio de Casas, R., Vargas, P., Pérez-Corona, E., Cano, E., Manrique, E., García-Verdugo,  
639 C. *et al.* (2009) Variation in sclerophylly among Iberian populations of *Quercus*  
640 *coccifera* L. is associated with genetic differentiation across contrasting environments.  
641 *Plant Biology*, **11**, 464–472.
- 642 Schamp, B.S., Chau, J. & Aarssen, L.W. (2008) Dispersion of traits related to competitive  
643 ability in an old-field plant community. *Journal of Ecology*, **96**, 204–212.
- 644 Schöb, C., Butterfield, B.J. & Pugnaire, F.I. (2012) Foundation species influence trait-based  
645 community assembly. *New Phytologist*, **196**, 824–834.
- 646 Schlichting, C.D. & Levin, D.A. (1986) Phenotypic plasticity: an evolving plant character.  
647 *Biological Journal of the Linnean Society*, **29**, 37–47
- 648 Schulze, E.D., Beck, E. & Müller-Hohenstein, K. (2005) *Plant Ecology*, Springer,  
649 Heidelberg.
- 650 Schwinning, S. & Weiner, J. (1998) Mechanisms determining the degree of size-asymmetry  
651 in competition among plants. *Oecologia*, **113**, 447–455.
- 652 Shipley, B. (2009) Confirmatory path analysis in a generalized multilevel context. *Ecology*,  
653 **90**, 363–368.
- 654 Shipley, B. (2013) The AIC model selection method applied to path analytic models  
655 compared using d-separation test. *Ecology*, **94**, 560–564.
- 656 Soil Survey Staff (1994) *Keys to Soil Taxonomy*. 6th edn. USDA Soil Conservation Service,  
657 pp.524. Pocahontas Press, Blacksburg, U.S.A.

658 Soliveres, S., Smit, C. & Maestre, F.T. (2015) Moving forward on facilitation research:  
659 response to changing environments and effects on the diversity, functioning and  
660 evolution of plant communities. *Biological Reviews*, **90**, 297–313.

661 Stoll, P. & Weiner, J. (2000) A neighbourhood view of interactions among individual plants.  
662 *The Geometry of Ecological Interactions: Simplifying Spatial Complexity* (eds U.  
663 Dieckmann, R. Law & J.A.J. Metz), pp 11-27. Cambridge University Press, Cambridge.

664 Suding, K.N., Lavorel, S., Chapin, F., Cornelissen, J., Díaz, S., Garnier, E. *et al.* (2008)  
665 Scaling environmental change through the community-level: a trait-based response-and-  
666 effect framework for plants. *Global Change Biology*, **14**, 1125-1140.

667 Sultan, S.E. (2004) Promising directions in plant phenotypic plasticity. *Perspectives in Plant*  
668 *Ecology, Evolution and Systematics*, **6**, 227-23.

669 Tilman, D. (1982) *Resource competition and community structure*. Princeton University  
670 Press, Princeton, New Jersey.

671 Valladares, F., Wright, S.J., Lasso, E., Kitajima, K. & Pearcy, R.W. (2000) Plastic phenotypic  
672 response to light of 16 congeneric shrubs from a Panamanian rainforest. *Ecology*, **81**,  
673 1925–1936.

674 Valencia, E., Maestre, F.T., Le Bagousse-Pinguet, Y., Quéro J.L., Tamme, R., Börger L. *et al.*  
675 (2015) Functional diversity enhances the resistance of ecosystem multifunctionality to  
676 aridity in Mediterranean drylands. *New Phytologist*, in press.

677 Vile, D., Garnier, E., Shipley, B., Laurent, G., Navas, M-L., Roumet, C. *et al.* (2005) Specific  
678 leaf area and dry matter content estimate thickness in laminar leaves. *Annals of Botany*,  
679 **96**, 1129-1136.

680 Violle, C., Navas, M.L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I. *et al.* (2007) Let the  
681 concept of trait be functional! *Oikos*, **116**, 882–892.

- 682 Violle, C., Garnier, E., Leconte, J., Roumet, C., Pédure, C., Blanchard, A. *et al.* (2009)  
683 Competition, traits and resource depletion in plant communities. *Oecologia*, **160**, 747-  
684 755.
- 685 Violle, C., Enquist, B.J., McGill, B.J., Jiang, L., Albert, C.H., Hulshof, C. *et al.* (2012) The  
686 return of variance: intraspecific variability in community ecology. *Trends in Ecology*  
687 *and Evolution*, **27**, 244-252.
- 688 Westoby, M., Falster, D.S., Moles, A.T., Vesk, P.A. & Wright, I.J. (2002) Plant ecological  
689 strategies: some leading dimensions of variation between species. *Annual Review of*  
690 *Ecology and Systematics*, **33**, 125–159.
- 691 Wright, I.J., Reich, P.B., Westoby, M., Ackerly, D.D., Baruch, Z., Bongers, F. *et al.* (2004)  
692 The worldwide leaf economics spectrum. *Nature*, **428**, 821–827.

## 694 **Supporting Information**

695 Additional supporting information may be found in the online version of this article:

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

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

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

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

702 **Appendix S5** Trait data for subordinate individuals and neighbours.

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

704

705

706

707 **Figures**

708 **Fig. 1.** Graphical representation of the three hypotheses between rainfall (blue box),  
709 neighbouring plants (green box: crowding and neighbouring plant traits), and the intraspecific  
710 trait variability of subordinate individuals (red box) for height [H], leaf area [LA] and specific  
711 leaf area [SLA]) used in this study. Blue arrows represent the abiotic hypothesis, and green  
712 arrows represent the biotic hypothesis. The combined hypothesis includes both pathways.  
713 Neighbour Weighted-Mean index for height, LA and SLA are denoted as  $H_{NWM}$ ,  $LA_{NWM}$  and  
714  $SLA_{NWM}$ , respectively.

715  
716 **Fig. 2.** Relationships between rainfall and intraspecific trait variance for a) maximum plant  
717 height, b) leaf area (LA) and c) specific leaf are (SLA). Grey lines are presented when  
718 significant.

719  
720 **Fig. 3.** Selected path model for all species together (combined hypothesis, see appendix S3).  
721 Direct and indirect relationships between rainfall, crowding, neighbouring plant traits ( $H_{NWM}$ ,  
722  $LA_{NWM}$ ,  $SLA_{NWM}$ ) and the trait values of subordinate individuals [maximum plant height, leaf  
723 area (LA) and specific leaf area (SLA)] are represented. Right panels: the selected models  
724 were consistent with the data. Path coefficients are shown for each pair of connected  
725 variables. Blue arrows represent the effect of rainfall, green arrows represent the impact of  
726 neighbouring plants (crowding and neighbouring plant traits), and red arrows indicate trait co-  
727 variation within individual plants. Arrow width is proportional to the standardized path  
728 coefficients. Grey arrows represent non-significant relationships. Left panels: absolute effect  
729 sizes of the direct (dark colours) and indirect (light colours) effects for each model parameter.

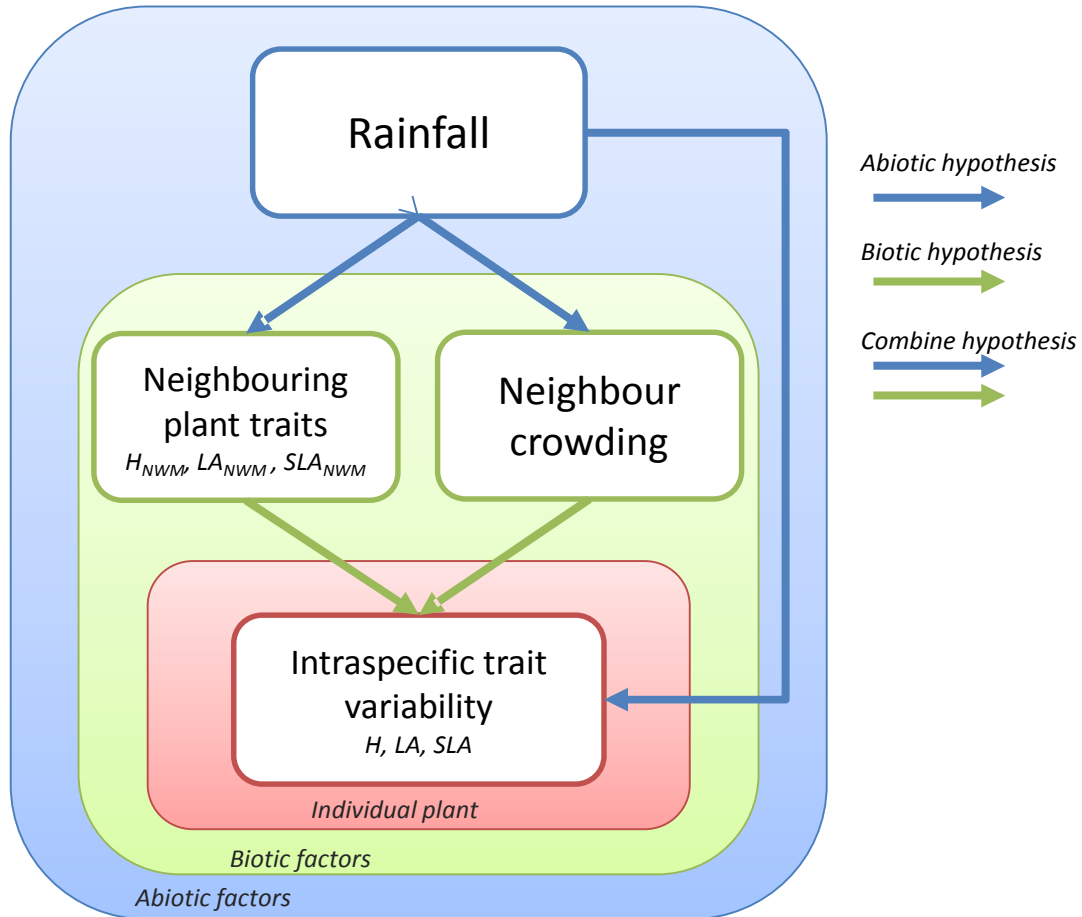
730



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

738  
739 **Fig. 5.** Absolute effect sizes of the direct (dark colours) and indirect (light colours) effects of  
740 rainfall (blue), crowding and neighbouring plant traits (green) on the trait values of  
741 subordinate individuals (height, LA, SLA) (red) for the four studied target species separately  
742 (*Q. coccifera*, *R. officinalis*, *S. tenacissima* and *T. vulgaris*). Model selections among the three  
743 hypotheses (abiotic-only, biotic-only and combined hypotheses) for each species and each  
744 functional trait are presented in Appendix S4.

745  
746  
747  
748  
749  
750  
751  
752  
753  
754  
755



757

758

759

760

761

762

763

764

765

766

767

768

769 **Fig. 2.**

770

771

772

773

774

775

776

777

778

779

780

781

782

783

784

785

786

787

788

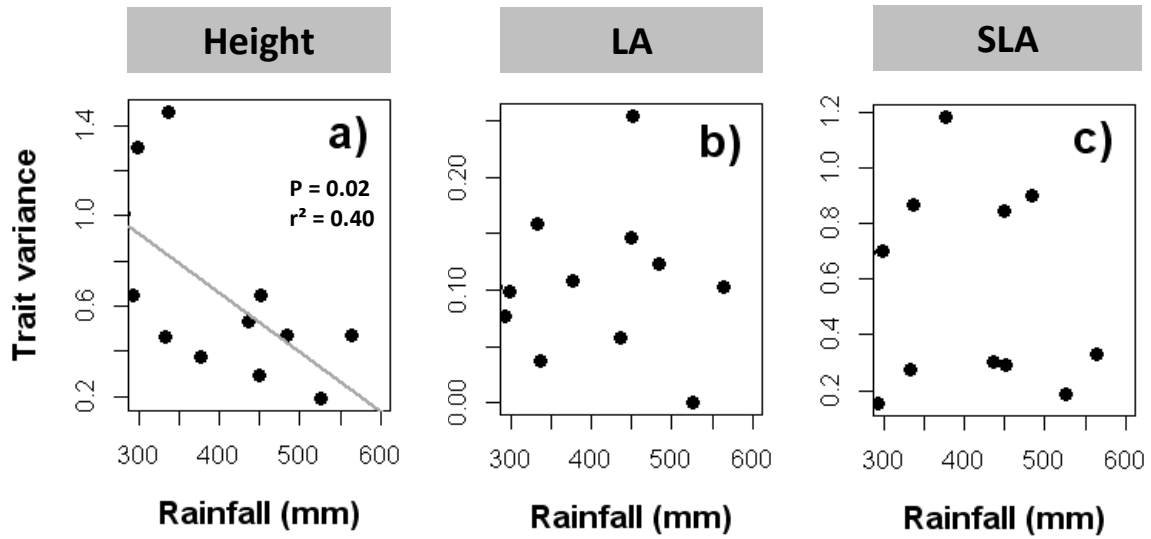
789

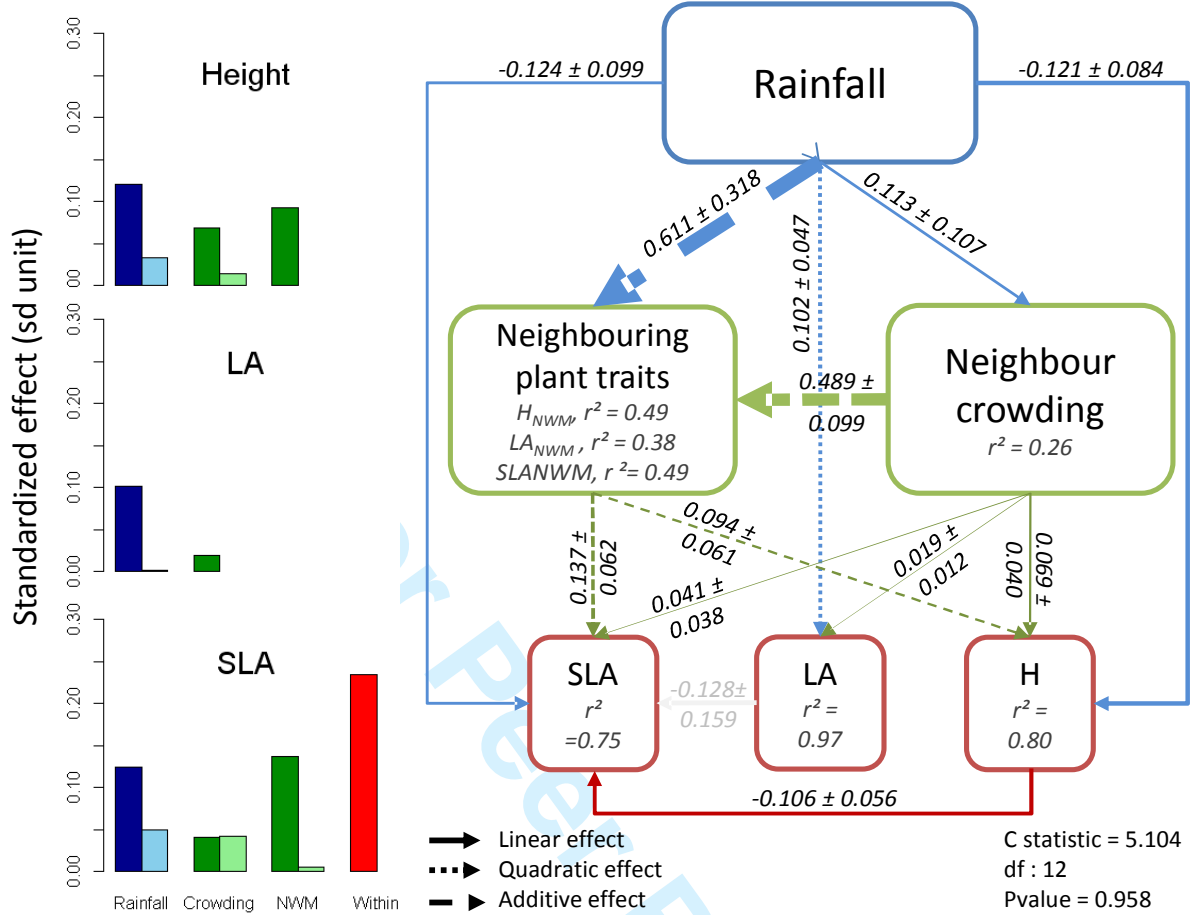
790

791

792

793





795

796

797

798

799

800

801

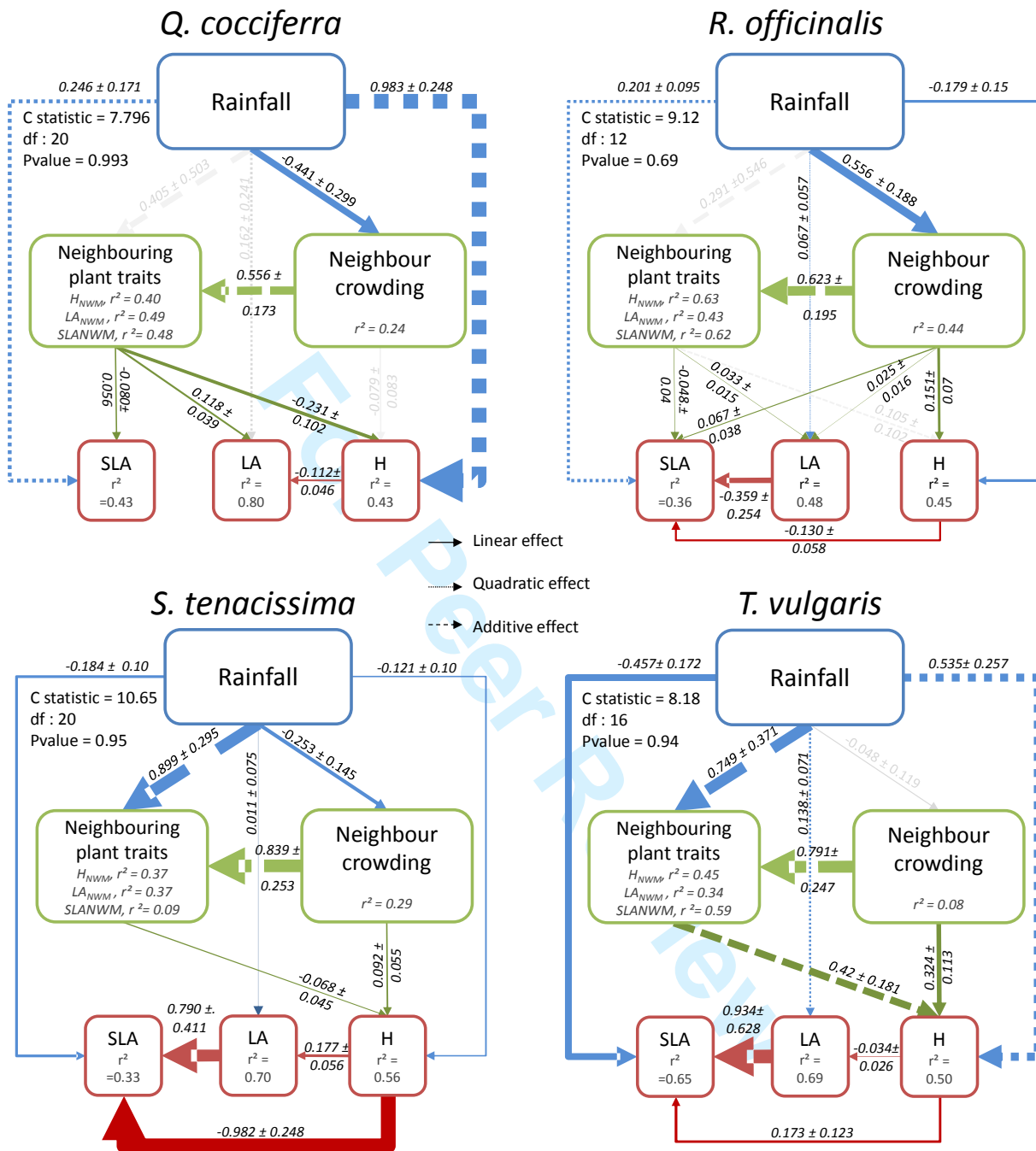
802

803

804

805

806



808

809

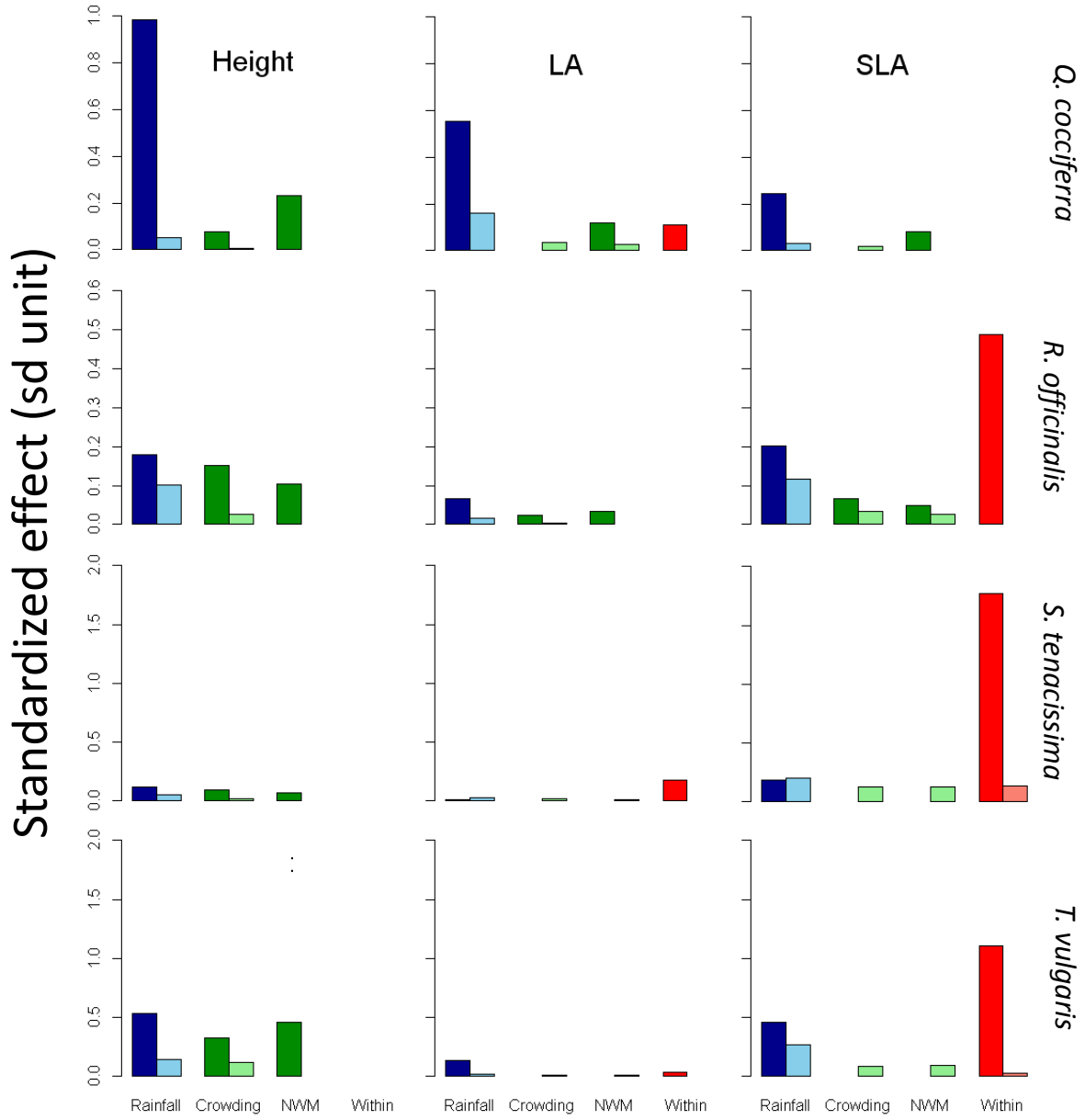
810

811

812

813

815



816

817

818

819

820

821

822

823 **Appendices**

824 **Appendix S1** Parameter estimates (slope) from averaged models including all target species  
825 together for maximum plant height (a), Leaf Area (b) and Specific Leaf Area (c). When the  
826 standard error does not cross the zero line, the predictors under consideration are statistically  
827 significant. The significance of predictors is based on the best 5% of all potential models. The  
828 averaging model procedures were based on linear mixed effect models. The individual trait  
829 values were the response variables, and rainfall, rainfall<sup>2</sup>, crowding and neighbouring plant  
830 traits ( $H_{NWM}$ ,  $LA_{NWM}$  and  $SLA_{NWM}$ ) were the predictors. Height was also introduced as a  
831 predictor of LA and SLA to grasp potential ontogenetic effects and to consider potential  
832 coordination among traits. Height and LA were introduced for SLA. Site was used as a  
833 random factor to control for the hierarchical design. Species was also used as a random effect  
834 for models including all target species together to avoid inter-specific differences. We also  
835 present the results of averaging model procedures including interactions between rainfall and  
836 crowding and rainfall and neighbouring plant traits (panels d, e and f).

837

838

839

840

841

842

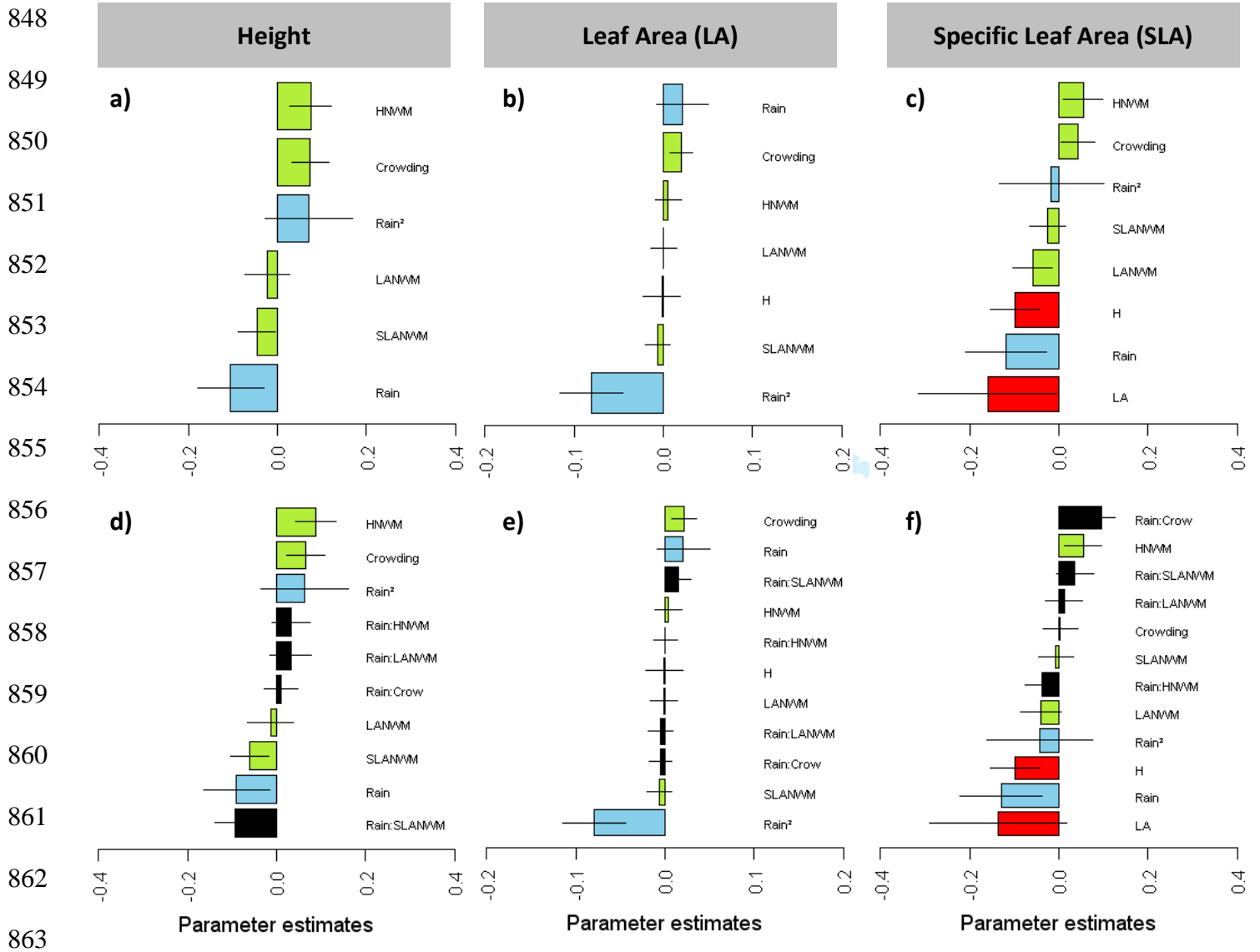
843

844

845

846

847





864 **Appendix S2** Parameter estimates (slope) from averaged models for each target species  
865 separately and each trait (height, Leaf Area and Specific Leaf Area). When the standard error  
866 does not cross the zero line, the predictors under consideration are statistically significant.  
867 The significance of predictors is based on the best 5% of all potential models. The averaging  
868 model procedures were based on linear mixed effect models. The individual trait values were  
869 the response variables, and rainfall, rainfall<sup>2</sup>, crowding and neighbouring plant traits ( $H_{NWM}$ ,  
870  $LA_{NWM}$  and  $SLA_{NWM}$ ) were the predictors. Height was also introduced as a predictor of LA  
871 and SLA to grasp potential ontogenetic effects and to consider potential coordination among  
872 traits. Height and LA were introduced for SLA. Site was used as a random factor to control  
873 for the hierarchical design.

874

875

876

877

878

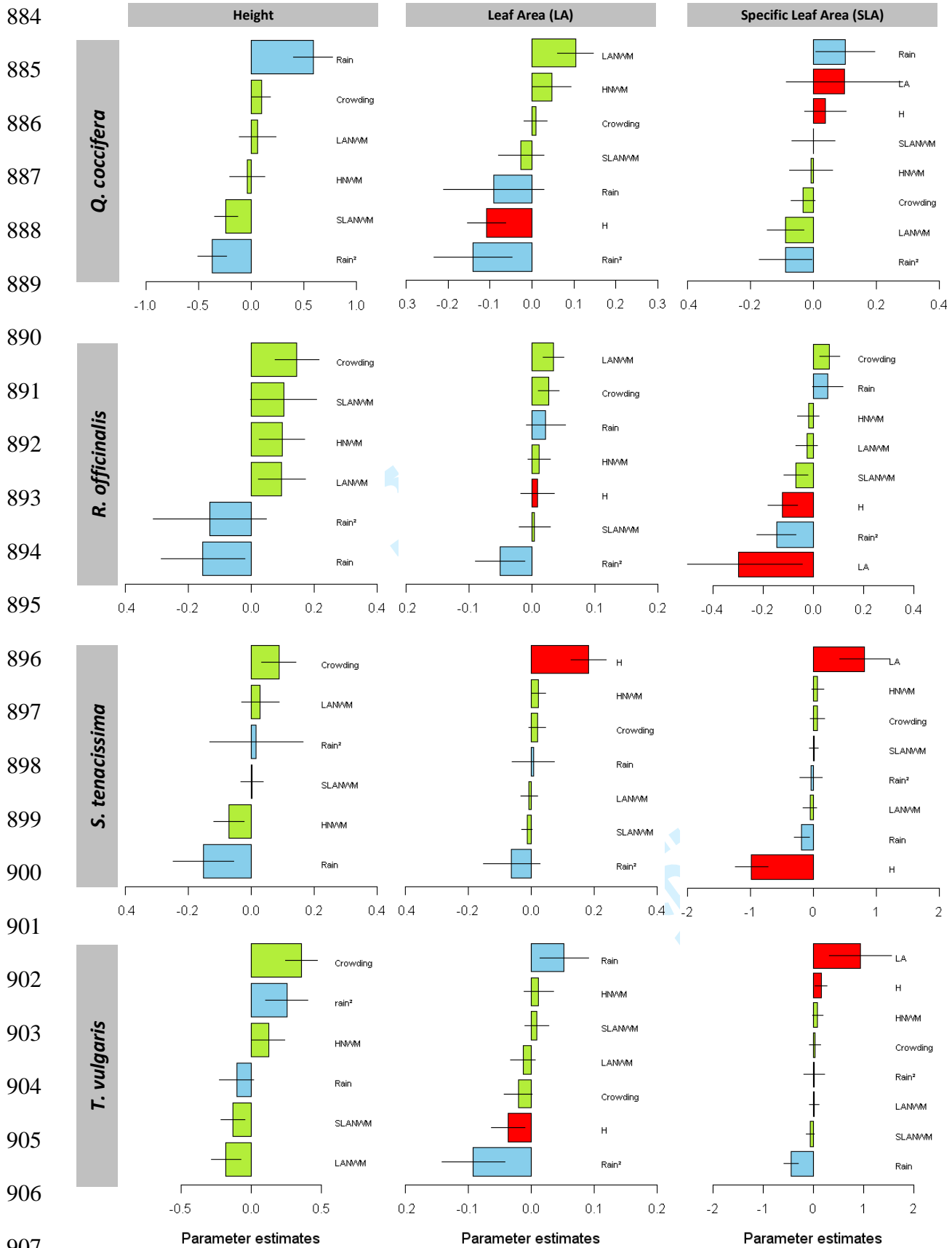
879

880

881

882

883



909 **Appendix S3** Model selection for all target species together (confirmatory multilevel path  
910 analysis). Key to variables:  $X_1$  = Rainfall,  $X_2$  = Crowding,  $X_3$  = HNWM,  $X_4$  = LANWM,  $X_5$   
911 = SLANWM,  $X_6$  = height of subordinate individuals,  $X_7$  = LA of subordinate individuals,  $X_8$   
912 = SLA of subordinate individuals, (spe/site) = inclusion of species and sites as random  
913 factors.  $\{X_k\}$  means that variables  $X_i$  and  $X_j$  are independent conditional on variable  $X_k$  (thus  
914 variation in  $X_i$  does not imply variation in  $X_j$  if  $X_k$  is held constant). \* The p-value is obtained  
915 by comparing the value of the C statistic for each hypothesis to a chi-square distribution with  
916 the same degrees of freedom – note that a model is rejected if the C statistic is significantly  
917 different from the  $\chi^2$  value.

918  
919  
920  
921  
922  
923  
924  
925  
926  
927  
928  
929  
930  
931  
932  
933

934  
935  
936  
937  
938  
939  
940  
941  
942  
943  
944  
945  
946  
947  
948  
949  
950  
951  
952  
953  
954  
955  
956  
957  
958

All species together						
Hypotheses	D-step claim of independence	Formula	Ho	P value	C statistic	P value of C* (DF)
<b>Abiotic</b>	(X2; X3)   {X1}	$X3 \sim X2 + X1$ (spe/site)	$X2 = 0$	<0.001	101.995	<0.001 (38)
	(X2; X4)   {X1}	$X4 \sim X2 + X1$ (spe/site)	$X2 = 0$	0.003		
	(X2; X5)   {X1}	$X5 \sim X2 + X1$ (spe/site)	$X2 = 0$	0.979		
	(X3; X4)   {X1}	$X4 \sim X3 + X1$ (spe/site)	$X3 = 0$	<0.001		
	(X3; X5)   {X1}	$X5 \sim X3 + X1$ (spe/site)	$X3 = 0$	<0.001		
	(X4; X5)   {X1}	$X5 \sim X4 + X1$ (spe/site)	$X4 = 0$	<0.001		
	(X2; X6)   {X1}	$X6 \sim X2 + X1$ (spe/site)	$X2 = 0$	0.030		
	(X2; X7)   {X1}	$X7 \sim X2 + X1$ (spe/site)	$X2 = 0$	0.110		
	(X2; X8)   {X1, X6, X7}	$X8 \sim X2 + X1 + X6 + X7$ (spe/site)	$X2 = 0$	0.155		
	(X3; X6)   {X1}	$X6 \sim X3 + X1$ (spe/site)	$X3 = 0$	0.034		
	(X3; X7)   {X1}	$X7 \sim X3 + X1$ (spe/site)	$X3 = 0$	0.566		
	(X3; X8)   {X1, X6, X7}	$X8 \sim X3 + X1 + X6 + X7$ (spe/site)	$X3 = 0$	0.218		
	(X4; X6)   {X1}	$X6 \sim X4 + X1$ (spe/site)	$X4 = 0$	0.579		
	(X4; X7)   {X1}	$X7 \sim X4 + X1$ (spe/site)	$X4 = 0$	0.811		
	(X4; X8)   {X1, X6, X7}	$X8 \sim X4 + X1 + X6 + X7$ (spe/site)	$X4 = 0$	0.425		
	(X5; X6)   {X1}	$X6 \sim X5 + X1$ (spe/site)	$X5 = 0$	0.169		
	(X5; X7)   {X1}	$X7 \sim X5 + X1$ (spe/site)	$X5 = 0$	0.709		
	(X5; X8)   {X1, X6, X7}	$X8 \sim X5 + X1 + X6 + X7$ (spe/site)	$X5 = 0$	0.508		
(X6; X7)   {X1}	$X7 \sim X6 + X1$ (spe/site)	$X6 = 0$	0.929			
<b>Biotic</b>	(X1; X2)   {∅}	$X2 \sim X1$ (spe/site)	$X1 = 0$	0.280	27.274	0.395 (26) AIC = 81.274
	(X1; X3)   {X2}	$X3 \sim X1 + X2$ (spe/site)	$X1 = 0$	0.487		
	(X1; X4)   {X2, X3}	$X4 \sim X1 + X2 + X3$ (spe/site)	$X1 = 0$	0.775		
	(X1; X5)   {X2, X3, X4}	$X5 \sim X1 + X2 + X3 + X4$ (spe/site)	$X1 = 0$	0.069		
	(X1; X6)   {X2, X3, X5}	$X6 \sim X1 + X2 + X3 + X5$ (spe/site)	$X1 = 0$	0.140		
	(X1; X7)   {X2}	$X7 \sim X1 + X2$ (spe/site)	$X1 = 0$	0.071		
	(X1; X8)   {X2, X3, X4, X6, X7}	$X8 \sim X1 + X2 + X3 + X4 + X6 + X7$ (spe/site)	$X1 = 0$	0.407		
	(X3; X7)   {X2}	$X7 \sim X3 + X2$ (spe/site)	$X3 = 0$	0.653		
	(X4; X6)   {X2, X3, X5}	$X6 \sim X4 + X2 + X3 + X5$ (spe/site)	$X4 = 0$	0.405		
	(X4; X7)   {X2}	$X7 \sim X4 + X2$ (spe/site)	$X4 = 0$	0.931		
	(X5; X7)   {X2}	$X7 \sim X5 + X2$ (spe/site)	$X5 = 0$	0.453		
	(X5; X8)   {X2, X3, X4, X6, X7}	$X8 \sim X5 + X2 + X3 + X4 + X6 + X7$ (spe/site)	$X5 = 0$	0.424		
(X6; X7)   {X2}	$X7 \sim X6 + X2$ (spe/site)	$X6 = 0$	0.857			
<b>Combined</b>	(X3; X7)   {X1, X2}	$X7 \sim X3 + X1 + X2$ (spe/site)	$X3 = 0$	0.965	5.104	0.958 (12) AIC = 79.104
	(X4; X6)   {X1, X2, X3, X5}	$X6 \sim X4 + X1 + X2 + X3 + X5$ (spe/site)	$X4 = 0$	0.368		
	(X4; X7)   {X1, X2}	$X7 \sim X4 + X1 + X2$ (spe/site)	$X4 = 0$	0.958		
	(X5; X7)   {X1, X2}	$X7 \sim X5 + X1 + X2$ (spe/site)	$X5 = 0$	0.740		
	(X5; X8)   {X1, X2, X3, X4, X6, X7}	$X8 \sim X5 + X1 + X2 + X3 + X4 + X6 + X7$ (spe/site)	$X5 = 0$	0.360		
	(X6; X7)   {X1, X2}	$X7 \sim X6 + X1 + X2$ (spe/site)	$X6 = 0$	0.901		

959 **Appendix S4** Model selection for each target species separately (confirmatory multilevel path  
960 analyses). Key to variables:  $X_1$  = Rainfall,  $X_2$  = Crowding,  $X_3$  = HNWM,  $X_4$  = LANWM,  $X_5$   
961 = SLANWM,  $X_6$  = height of subordinate individuals,  $X_7$  = LA of subordinate individuals,  $X_8$   
962 = SLA of subordinate individuals, (site) = inclusion of sites as a random factor.  $\{X_k\}$  means  
963 that variables  $X_i$  and  $X_j$  are independent conditional on variable  $X_k$  (thus variation in  $X_i$  does  
964 not imply variation in  $X_j$  if  $X_k$  is held constant). \* The p-value is obtained by comparing the  
965 value of the C statistic for each hypothesis to a chi-square distribution with the same degrees  
966 of freedom – note that a model is rejected if the C statistic is significantly different from the  $\chi^2$   
967 value.

968

969

970

971

972

<i>Q. coccifera</i>						
Hypotheses	D-step claim of independence	Formula	Ho	P value	C statistic	P value of C* (DF)
<b>Abiotic</b>	{X2; X3}   {X1}	$X3 \sim X2 + X1$ (site)	$X2 = 0$	0.024	104.149	<0.001 (40)
	{X2; X4}   {X1}	$X4 \sim X2 + X1$ (site)	$X2 = 0$	0.031		
	{X2; X5}   {X1}	$X5 \sim X2 + X1$ (site)	$X2 = 0$	0.450		
	{X3; X4}   {X1}	$X4 \sim X3 + X1$ (site)	$X3 = 0$	0.001		
	{X3; X5}   {X1}	$X5 \sim X3 + X1$ (site)	$X3 = 0$	<0.001		
	{X4; X5}   {X1}	$X5 \sim X4 + X1$ (site)	$X4 = 0$	<0.001		
	{X2; X6}   {X1}	$X6 \sim X2 + X1$ (site)	$X2 = 0$	0.143		
	{X2; X7}   {X1, X6}	$X7 \sim X2 + X1 + X6$ (site)	$X2 = 0$	0.274		
	{X2; X8}   {X1}	$X8 \sim X2 + X1$ (site)	$X2 = 0$	0.634		
	{X3; X6}   {X1}	$X6 \sim X3 + X1$ (site)	$X3 = 0$	0.382		
	{X3; X7}   {X1, X6}	$X7 \sim X3 + X1 + X6$ (site)	$X3 = 0$	0.077		
	{X3; X8}   {X1}	$X8 \sim X3 + X1$ (site)	$X3 = 0$	0.603		
	{X4; X6}   {X1}	$X6 \sim X4 + X1$ (site)	$X4 = 0$	0.084		
	{X4; X7}   {X1, X6}	$X7 \sim X4 + X1 + X6$ (site)	$X4 = 0$	0.008		
	{X4; X8}   {X1}	$X8 \sim X4 + X1$ (site)	$X4 = 0$	0.291		
	{X5; X6}   {X1}	$X6 \sim X5 + X1$ (site)	$X5 = 0$	0.019		
	{X5; X7}   {X1, X6}	$X7 \sim X5 + X1 + X6$ (site)	$X5 = 0$	0.083		
	{X5; X8}   {X1}	$X8 \sim X5 + X1$ (site)	$X5 = 0$	0.756		
	{X6; X8}   {X1}	$X8 \sim X6 + X1$ (site)	$X6 = 0$	1.000		
	{X7; X8}   {X1}	$X8 \sim X7 + X1$ (site)	$X7 = 0$	0.522		
<b>Biotic</b>	{X1; X2}   {∅}	$X2 \sim X1$ (site)	$X1 = 0$	0.099	37.540	0.310 (34) AIC =71.540
	{X1; X3}   {X2}	$X3 \sim X1 + X2$ (site)	$X1 = 0$	0.624		
	{X1; X4}   {X2, X3}	$X4 \sim X1 + X2 + X3$ (site)	$X1 = 0$	0.203		
	{X1; X5}   {X2, X3, X4}	$X5 \sim X1 + X2 + X3 + X4$ (site)	$X1 = 0$	0.189		
	{X1; X6}   {X2, X5}	$X6 \sim X1 + X2 + X5$ (site)	$X1 = 0$	0.005		
	{X1; X7}   {X4, X6}	$X7 \sim X1 + X4 + X6$ (site)	$X1 = 0$	0.362		
	{X1; X8}   {X4}	$X8 \sim X1 + X4$ (site)	$X1 = 0$	0.300		
	{X2; X7}   {X4, X6}	$X7 \sim X2 + X4 + X6$ (site)	$X2 = 0$	0.822		
	{X2; X8}   {X4}	$X8 \sim X2 + X4$ (site)	$X2 = 0$	0.525		
	{X3; X6}   {X2, X5}	$X6 \sim X3 + X2 + X5$ (site)	$X3 = 0$	0.704		
	{X3; X7}   {X4, X6}	$X7 \sim X3 + X4 + X6$ (site)	$X3 = 0$	0.360		
	{X3; X8}   {X4}	$X8 \sim X3 + X4$ (site)	$X3 = 0$	0.796		
	{X4; X6}   {X2, X5}	$X6 \sim X4 + X2 + X5$ (site)	$X4 = 0$	0.465		
	{X5; X7}   {X4, X6}	$X7 \sim X5 + X4 + X6$ (site)	$X5 = 0$	0.719		
	{X5; X8}   {X4}	$X8 \sim X5 + X4$ (site)	$X5 = 0$	0.597		
	{X6; X8}   {X4}	$X8 \sim X6 + X4$ (site)	$X6 = 0$	0.566		
{X7; X8}   {X4}	$X8 \sim X7 + X4$ (site)	$X7 = 0$	0.557			
<b>Combined</b>	{X2; X7}   {X1, X4, X6}	$X7 \sim X2 + X1 + X4 + X6$ (site)	$X2 = 0$	0.737	7.796	0.993 (20) AIC =63.796
	{X2; X8}   {X1, X4}	$X8 \sim X2 + X1 + X4$ (site)	$X2 = 0$	0.788		
	{X3; X6}   {X1, X2, X5}	$X6 \sim X3 + X1 + X2 + X5$ (site)	$X3 = 0$	0.360		
	{X3; X7}   {X1, X4, X6}	$X7 \sim X3 + X1 + X4 + X6$ (site)	$X3 = 0$	0.405		
	{X3; X8}   {X1, X4}	$X8 \sim X3 + X1 + X4$ (site)	$X3 = 0$	0.987		
	{X4; X6}   {X1, X2, X5}	$X6 \sim X4 + X1 + X2 + X5$ (site)	$X4 = 0$	0.715		
	{X5; X7}   {X1, X4, X6}	$X7 \sim X5 + X1 + X4 + X6$ (site)	$X5 = 0$	0.766		
	{X5; X8}   {X1, X4}	$X8 \sim X5 + X1 + X4$ (site)	$X5 = 0$	1.000		
	{X6; X8}   {X1, X4}	$X8 \sim X6 + X1 + X4$ (site)	$X6 = 0$	0.836		
{X7; X8}   {X1, X4}	$X8 \sim X7 + X1 + X4$ (site)	$X7 = 0$	0.530			

<i>R. officinalis</i>						
Hypotheses	D-step claim of independence	Formula	Ho	P value	C statistic	P value of C* (DF)
<b>Abiotic</b>	(X2; X3)   {X1}	$X3 \sim X2 + X1$ (site)	$X2 = 0$	<0.001	105.361	<0.001 (38)
	(X2; X4)   {X1}	$X4 \sim X2 + X1$ (site)	$X2 = 0$	0.364		
	(X2; X5)   {X1}	$X5 \sim X2 + X1$ (site)	$X2 = 0$	0.883		
	(X3; X4)   {X1}	$X4 \sim X3 + X1$ (site)	$X3 = 0$	<0.001		
	(X3; X5)   {X1}	$X5 \sim X3 + X1$ (site)	$X3 = 0$	<0.001		
	(X4; X5)   {X1}	$X5 \sim X4 + X1$ (site)	$X4 = 0$	<0.001		
	(X2; X6)   {X1}	$X6 \sim X2 + X1$ (site)	$X2 = 0$	0.014		
	(X2; X7)   {X1}	$X7 \sim X2 + X1$ (site)	$X2 = 0$	0.060		
	(X2; X8)   {X1, X6, X7}	$X8 \sim X2 + X1 + X6 + X7$ (site)	$X2 = 0$	0.065		
	(X3; X6)   {X1}	$X6 \sim X3 + X1$ (site)	$X3 = 0$	0.035		
	(X3; X7)   {X1}	$X7 \sim X3 + X1$ (site)	$X3 = 0$	0.187		
	(X3; X8)   {X1, X6, X7}	$X8 \sim X3 + X1 + X6 + X7$ (site)	$X3 = 0$	0.667		
	(X4; X6)   {X1}	$X6 \sim X4 + X1$ (site)	$X4 = 0$	0.095		
	(X4; X7)   {X1}	$X7 \sim X4 + X1$ (site)	$X4 = 0$	0.041		
	(X4; X8)   {X1, X6, X7}	$X8 \sim X4 + X1 + X6 + X7$ (site)	$X4 = 0$	0.857		
	(X5; X6)   {X1}	$X6 \sim X5 + X1$ (site)	$X5 = 0$	0.937		
	(X5; X7)   {X1}	$X7 \sim X5 + X1$ (site)	$X5 = 0$	0.563		
	(X5; X8)   {X1, X6, X7}	$X8 \sim X5 + X1 + X6 + X7$ (site)	$X5 = 0$	0.196		
(X6; X7)   {X1}	$X7 \sim X6 + X1$ (site)	$X6 = 0$	0.500			
<b>Biotic</b>	(X1; X2)   {∅}	$X2 \sim X1$ (site)	$X1 = 0$	0.007	33.817	0.140 (26) AIC = 75.817
	(X1; X3)   {X2}	$X3 \sim X1 + X2$ (site)	$X1 = 0$	0.959		
	(X1; X4)   {X2, X3}	$X4 \sim X1 + X2 + X3$ (site)	$X1 = 0$	0.876		
	(X1; X5)   {X2, X3, X4}	$X5 \sim X1 + X2 + X3 + X4$ (site)	$X1 = 0$	0.142		
	(X1; X6)   {X2, X3, X4}	$X6 \sim X1 + X2 + X3 + X4$ (site)	$X1 = 0$	0.189		
	(X1; X7)   {X2, X4}	$X7 \sim X1 + X2 + X4$ (site)	$X1 = 0$	0.347		
	(X1; X8)   {X2, X5, X6, X7}	$X8 \sim X1 + X2 + X5 + X6 + X7$ (site)	$X1 = 0$	0.041		
	(X3; X7)   {X2, X4}	$X7 \sim X3 + X2 + X4$ (site)	$X3 = 0$	0.881		
	(X3; X8)   {X2, X5, X6, X7}	$X8 \sim X3 + X2 + X5 + X6 + X7$ (site)	$X3 = 0$	0.572		
	(X4; X8)   {X2, X5, X6, X7}	$X8 \sim X4 + X2 + X5 + X6 + X7$ (site)	$X4 = 0$	0.451		
	(X5; X6)   {X2, X3, X4}	$X6 \sim X5 + X2 + X3 + X4$ (site)	$X5 = 0$	0.145		
	(X5; X7)   {X2, X4}	$X7 \sim X5 + X2 + X4$ (site)	$X5 = 0$	0.707		
(X6; X7)   {X2, X4}	$X7 \sim X6 + X2 + X4$ (site)	$X6 = 0$	0.867			
<b>Combined</b>	(X3; X7)   {X1, X2, X4}	$X7 \sim X3 + X1 + X2 + X4$ (site)	$X3 = 0$	0.751	9.126	0.692 (12) AIC = 71.126
	(X3; X8)   {X1, X2, X5, X6, X7}	$X8 \sim X3 + X1 + X2 + X5 + X6 + X7$ (site)	$X3 = 0$	0.251		
	(X4; X8)   {X1, X2, X5, X6, X7}	$X8 \sim X4 + X1 + X2 + X5 + X6 + X7$ (site)	$X4 = 0$	0.473		
	(X5; X6)   {X1, X2, X3, X4}	$X6 \sim X5 + X1 + X2 + X3 + X4$ (site)	$X5 = 0$	0.195		
	(X5; X7)   {X1, X2, X4}	$X7 \sim X5 + X1 + X2 + X4$ (site)	$X5 = 0$	0.618		
	(X6; X7)   {X1, X2, X4}	$X7 \sim X6 + X1 + X2 + X4$ (site)	$X6 = 0$	0.971		

<i>S. tenacissima</i>						
Hypotheses	D-step claim of independence	Formula	Ho	P value	C statistic	P value of C* (DF)
<b>Abiotic</b>	(X2; X3)   {X1}	$X3 \sim X2 + X1$ (site)	$X2 = 0$	0.062	56.412	0.016 (36)
	(X2; X4)   {X1}	$X4 \sim X2 + X1$ (site)	$X2 = 0$	0.019		
	(X2; X5)   {X1}	$X5 \sim X2 + X1$ (site)	$X2 = 0$	0.125		
	(X3; X4)   {X1}	$X4 \sim X3 + X1$ (site)	$X3 = 0$	<0.001		
	(X3; X5)   {X1}	$X5 \sim X3 + X1$ (site)	$X3 = 0$	0.402		
	(X4; X5)   {X1}	$X5 \sim X4 + X1$ (site)	$X4 = 0$	0.021		
	(X2; X6)   {X1}	$X6 \sim X2 + X1$ (site)	$X2 = 0$	0.187		
	(X2; X7)   {X1, X6}	$X7 \sim X2 + X1 + X6$ (site)	$X2 = 0$	0.442		
	(X2; X8)   {X1, X6, X7}	$X8 \sim X2 + X1 + X6 + X7$ (site)	$X2 = 0$	0.567		
	(X3; X6)   {X1}	$X6 \sim X3 + X1$ (site)	$X3 = 0$	0.277		
	(X3; X7)   {X1, X6}	$X7 \sim X3 + X1 + X6$ (site)	$X3 = 0$	0.318		
	(X3; X8)   {X1, X6, X7}	$X8 \sim X3 + X1 + X6 + X7$ (site)	$X3 = 0$	0.537		
	(X4; X6)   {X1}	$X6 \sim X4 + X1$ (site)	$X4 = 0$	0.818		
	(X4; X7)   {X1, X6}	$X7 \sim X4 + X1 + X6$ (site)	$X4 = 0$	0.951		
	(X4; X8)   {X1, X6, X7}	$X8 \sim X4 + X1 + X6 + X7$ (site)	$X4 = 0$	0.934		
	(X5; X6)   {X1}	$X6 \sim X5 + X1$ (site)	$X5 = 0$	0.823		
(X5; X7)   {X1, X6}	$X7 \sim X5 + X1 + X6$ (site)	$X5 = 0$	0.419			
(X5; X8)   {X1, X6, X7}	$X8 \sim X5 + X1 + X6 + X7$ (site)	$X5 = 0$	0.815			
<b>Biotic</b>	(X1; X2)   {∅}	$X2 \sim X1$ (site)	$X1 = 0$	0.072	37.603	0.308 (34) AIC = 73.603
	(X1; X3)   {X2}	$X3 \sim X1 + X2$ (site)	$X1 = 0$	0.056		
	(X1; X4)   {X2, X3}	$X4 \sim X1 + X2 + X3$ (site)	$X1 = 0$	0.077		
	(X1; X5)   {X2, X3, X4}	$X5 \sim X1 + X2 + X3 + X4$ (site)	$X1 = 0$	0.328		
	(X1; X6)   {X2, X3}	$X6 \sim X1 + X2 + X3$ (site)	$X1 = 0$	0.213		
	(X1; X7)   {X6}	$X7 \sim X1 + X6$ (site)	$X1 = 0$	0.859		
	(X1; X8)   {X6, X7}	$X8 \sim X1 + X6 + X7$ (site)	$X1 = 0$	0.106		
	(X2; X7)   {X6}	$X7 \sim X2 + X6$ (site)	$X2 = 0$	0.451		
	(X2; X8)   {X6, X7}	$X8 \sim X2 + X6 + X7$ (site)	$X2 = 0$	0.509		
	(X3; X7)   {X6}	$X7 \sim X3 + X6$ (site)	$X3 = 0$	0.313		
	(X3; X8)   {X6, X7}	$X8 \sim X3 + X6 + X7$ (site)	$X3 = 0$	0.648		
	(X4; X6)   {X2, X3}	$X6 \sim X4 + X2 + X3$ (site)	$X4 = 0$	0.500		
	(X4; X7)   {X6}	$X7 \sim X4 + X6$ (site)	$X4 = 0$	0.931		
	(X4; X8)   {X6, X7}	$X8 \sim X4 + X6 + X7$ (site)	$X4 = 0$	0.578		
	(X5; X6)   {X2, X3}	$X6 \sim X5 + X2 + X3$ (site)	$X5 = 0$	0.834		
	(X5; X7)   {X6}	$X7 \sim X5 + X6$ (site)	$X5 = 0$	0.416		
(X5; X8)   {X6, X7}	$X8 \sim X5 + X6 + X7$ (site)	$X5 = 0$	0.796			
<b>Combined</b>	(X2; X7)   {X1, X6}	$X7 \sim X2 + X1 + X6$ (site)	$X2 = 0$	0.442	10.65	0.955 (20) AIC = 60.65
	(X2; X8)   {X1, X6, X7}	$X8 \sim X2 + X1 + X6 + X7$ (site)	$X2 = 0$	0.567		
	(X3; X7)   {X1, X6}	$X7 \sim X3 + X1 + X6$ (site)	$X3 = 0$	0.318		
	(X3; X8)   {X1, X6, X7}	$X8 \sim X3 + X1 + X6 + X7$ (site)	$X3 = 0$	0.537		
	(X4; X6)   {X1, X2, X3}	$X6 \sim X4 + X1 + X2 + X3$ (site)	$X4 = 0$	0.442		
	(X4; X7)   {X1, X6}	$X7 \sim X4 + X1 + X6$ (site)	$X4 = 0$	0.951		
	(X4; X8)   {X1, X6, X7}	$X8 \sim X4 + X1 + X6 + X7$ (site)	$X4 = 0$	0.934		
	(X5; X6)   {X1, X2, X3}	$X6 \sim X5 + X1 + X2 + X3$ (site)	$X5 = 0$	0.847		
	(X5; X7)   {X1, X6}	$X7 \sim X5 + X1 + X6$ (site)	$X5 = 0$	0.419		
(X5; X8)   {X1, X6, X7}	$X8 \sim X5 + X1 + X6 + X7$ (site)	$X5 = 0$	0.815			



<i>T. vulgaris</i>						
Hypotheses	D-step claim of independence	Formula	Ho	P value	C statistic	P value of C* (DF)
<b>Abiotic</b>	(X2; X3)   {X1}	$X3 \sim X2 + X1$ (site)	$X2 = 0$	0.003	66.23	0.002 (36)
	(X2; X4)   {X1}	$X4 \sim X2 + X1$ (site)	$X2 = 0$	0.035		
	(X2; X5)   {X1}	$X5 \sim X2 + X1$ (site)	$X2 = 0$	0.612		
	(X3; X4)   {X1}	$X4 \sim X3 + X1$ (site)	$X3 = 0$	0.012		
	(X3; X5)   {X1}	$X5 \sim X3 + X1$ (site)	$X3 = 0$	0.187		
	(X4; X5)   {X1}	$X5 \sim X4 + X1$ (site)	$X4 = 0$	0.444		
	(X2; X6)   {X1}	$X6 \sim X2 + X1$ (site)	$X2 = 0$	0.001		
	(X2; X7)   {X1, X6}	$X7 \sim X2 + X1 + X6$ (site)	$X2 = 0$	0.497		
	(X2; X8)   {X1, X6, X7}	$X8 \sim X2 + X1 + X6 + X7$ (site)	$X2 = 0$	0.926		
	(X3; X6)   {X1}	$X6 \sim X3 + X1$ (site)	$X3 = 0$	0.029		
	(X3; X7)   {X1, X6}	$X7 \sim X3 + X1 + X6$ (site)	$X3 = 0$	0.620		
	(X3; X8)   {X1, X6, X7}	$X8 \sim X3 + X1 + X6 + X7$ (site)	$X3 = 0$	0.601		
	(X4; X6)   {X1}	$X6 \sim X4 + X1$ (site)	$X4 = 0$	0.976		
	(X4; X7)   {X1, X6}	$X7 \sim X4 + X1 + X6$ (site)	$X4 = 0$	0.544		
	(X4; X8)   {X1, X6, X7}	$X8 \sim X4 + X1 + X6 + X7$ (site)	$X4 = 0$	0.746		
	(X5; X6)   {X1}	$X6 \sim X5 + X1$ (site)	$X5 = 0$	0.137		
	(X5; X7)   {X1, X6}	$X7 \sim X5 + X1 + X6$ (site)	$X5 = 0$	0.503		
(X5; X8)   {X1, X6, X7}	$X8 \sim X5 + X1 + X6 + X7$ (site)	$X5 = 0$	0.477			
<b>Biotic</b>	(X1; X2)   {∅}	$X2 \sim X1$ (site)	$X1 = 0$	0.636	30.695	0.431 (30) AIC = 68.695
	(X1; X3)   {X2}	$X3 \sim X1 + X2$ (site)	$X1 = 0$	0.595		
	(X1; X4)   {X2, X3}	$X4 \sim X1 + X2 + X3$ (site)	$X1 = 0$	0.474		
	(X1; X5)   {X2, X3, X4}	$X5 \sim X1 + X2 + X3 + X4$ (site)	$X1 = 0$	0.062		
	(X1; X6)   {X2, X3, X4, X5}	$X6 \sim X1 + X2 + X3 + X4 + X5$ (site)	$X1 = 0$	0.074		
	(X1; X7)   {X6}	$X7 \sim X1 + X6$ (site)	$X1 = 0$	0.114		
	(X1; X8)   {X6, X7}	$X8 \sim X1 + X6 + X7$ (site)	$X1 = 0$	0.036		
	(X2; X7)   {X6}	$X7 \sim X2 + X6$ (site)	$X2 = 0$	0.566		
	(X2; X8)   {X6, X7}	$X8 \sim X2 + X6 + X7$ (site)	$X2 = 0$	0.978		
	(X3; X7)   {X6}	$X7 \sim X3 + X6$ (site)	$X3 = 0$	0.485		
	(X3; X8)   {X6, X7}	$X8 \sim X3 + X6 + X7$ (site)	$X3 = 0$	0.720		
	(X4; X7)   {X6}	$X7 \sim X4 + X6$ (site)	$X4 = 0$	0.487		
	(X4; X8)   {X6, X7}	$X8 \sim X4 + X6 + X7$ (site)	$X4 = 0$	0.750		
	(X5; X7)   {X6}	$X7 \sim X5 + X6$ (site)	$X5 = 0$	0.945		
(X5; X8)   {X6, X7}	$X8 \sim X5 + X6 + X7$ (site)	$X5 = 0$	0.959			
<b>Combined</b>	(X2; X7)   {X1, X6}	$X7 \sim X2 + X1 + X6$ (site)	$X2 = 0$	0.497	8.185	0.943 (16) AIC = 66.185
	(X2; X8)   {X1, X6, X7}	$X8 \sim X2 + X1 + X6 + X7$ (site)	$X2 = 0$	0.926		
	(X3; X7)   {X1, X6}	$X7 \sim X3 + X1 + X6$ (site)	$X3 = 0$	0.620		
	(X3; X8)   {X1, X6, X7}	$X8 \sim X3 + X1 + X6 + X7$ (site)	$X3 = 0$	0.601		
	(X4; X7)   {X1, X6}	$X7 \sim X4 + X1 + X6$ (site)	$X4 = 0$	0.544		
	(X4; X8)   {X1, X6, X7}	$X8 \sim X4 + X1 + X6 + X7$ (site)	$X4 = 0$	0.746		
	(X5; X7)   {X1, X6}	$X7 \sim X5 + X1 + X6$ (site)	$X5 = 0$	0.503		
(X5; X8)   {X1, X6, X7}	$X8 \sim X5 + X1 + X6 + X7$ (site)	$X5 = 0$	0.477			

**Appendix S5** Trait values of each subordinate individual of the four dominant species along the rainfall gradient [maximum plant height (H), Leaf Area (LA) and Specific Leaf Area (SLA)]. Data of neighbouring plants (NWMH, NWMLA, NWMSLA and crowding) are also presented. Trait data are log-transformed and all variables are z-scored.

rainfall	Species	H	LA	SLA	NWMh	NWMLa	NWMSla	Crowding
-0.888	Qcoccifera	-0.057	0.269	-0.389	0.544	1.469	-0.619	2.022
-0.888	Qcoccifera	-0.032	0.415	-0.667	0.149	1.285	0.885	2.925
-0.888	Qcoccifera	0.156	0.258	-0.600	-0.184	0.871	0.220	1.119
-0.888	Qcoccifera	-0.219	0.811	-0.419	0.331	1.479	-0.566	1.119
-0.888	Qcoccifera	0.018	0.519	-0.358	0.061	1.001	1.093	1.721
-0.888	Qcoccifera	1.331	0.196	0.023	-0.042	0.658	0.940	2.323
0.203	Qcoccifera	1.282	0.339	-0.419	0.761	0.864	-1.023	-0.385
0.203	Qcoccifera	0.470	0.308	-0.207	0.271	-0.929	0.972	-0.987
0.203	Qcoccifera	1.360	0.316	-0.679	0.846	1.559	-1.302	0.819
0.203	Qcoccifera	0.134	0.418	-0.325	0.463	1.377	0.568	0.217
0.203	Qcoccifera	0.134	-0.146	0.181	0.271	-0.929	0.972	-0.987
0.349	Qcoccifera	1.252	0.463	0.010	0.061	-0.418	-0.439	1.420
0.349	Qcoccifera	0.757	0.322	-0.051	-0.273	-0.199	-0.531	0.217
0.349	Qcoccifera	1.302	0.679	0.151	0.421	1.029	-0.811	4.128
0.349	Qcoccifera	1.611	0.628	0.205	0.283	1.362	-1.188	0.367
0.349	Qcoccifera	1.350	0.514	-0.060	0.281	0.796	-0.339	-0.084
0.349	Qcoccifera	1.831	0.299	0.071	0.281	0.796	-0.339	-0.084
0.349	Qcoccifera	1.831	0.775	0.419	0.530	0.926	-0.838	-0.385
0.698	Qcoccifera	1.416	0.348	-0.034	-1.500	-0.074	1.180	-0.385
0.698	Qcoccifera	1.282	0.243	-0.079	-0.446	-0.488	1.404	1.270
0.698	Qcoccifera	0.322	0.468	0.250	-0.408	-0.947	0.839	0.217
0.698	Qcoccifera	1.210	0.392	-0.351	0.715	0.018	1.184	2.624
0.698	Qcoccifera	1.504	0.254	-0.178	-0.934	-1.170	1.912	-0.385
0.698	Qcoccifera	0.757	0.737	0.087	1.180	0.266	0.646	1.119
0.698	Qcoccifera	2.097	0.139	-0.033	-1.202	-0.174	0.856	0.217
0.698	Qcoccifera	1.210	0.162	-0.624	-1.101	-0.977	1.336	-0.385
0.698	Qcoccifera	1.680	0.331	-0.591	1.275	0.427	-0.460	1.119
1.157	Qcoccifera	1.262	-0.155	-0.266	-0.155	0.972	-0.831	-0.385
1.157	Qcoccifera	1.469	-0.293	-0.268	0.784	1.037	-0.526	1.721
1.157	Qcoccifera	1.379	-0.132	-0.159	0.220	1.059	-0.611	0.518
1.157	Qcoccifera	0.813	0.005	-0.237	-0.062	0.680	-0.593	0.518
1.157	Qcoccifera	1.032	-0.030	-0.097	-0.238	0.661	0.412	0.819
1.157	Qcoccifera	0.827	-0.018	0.030	-0.118	0.892	0.242	1.420
1.157	Qcoccifera	1.761	-0.118	-0.463	-0.046	0.999	-0.771	1.420
1.157	Qcoccifera	2.080	-0.096	0.060	0.169	1.065	-1.420	-0.385
1.157	Qcoccifera	1.146	-0.068	-0.196	0.005	1.115	-0.052	0.518
1.157	Qcoccifera	1.252	-0.080	0.036	-0.202	-0.078	-0.054	0.518
1.553	Qcoccifera	1.379	0.139	0.005	0.504	-0.585	-0.101	0.819
1.553	Qcoccifera	1.252	0.287	-0.541	-0.895	-0.767	1.156	0.518
1.553	Qcoccifera	1.961	-0.015	-0.195	0.836	0.563	-0.302	1.721
1.553	Qcoccifera	1.157	0.255	-0.482	-0.456	0.038	0.355	0.217
1.553	Qcoccifera	1.087	0.107	-0.262	0.159	0.752	-0.226	0.518
1.553	Qcoccifera	0.241	0.107	-0.262	0.054	-0.596	1.386	0.217
1.553	Qcoccifera	-0.434	0.187	-0.094	-1.395	-0.068	0.807	-0.385
1.553	Qcoccifera	1.262	-0.162	0.049	-0.647	-0.521	0.631	0.217

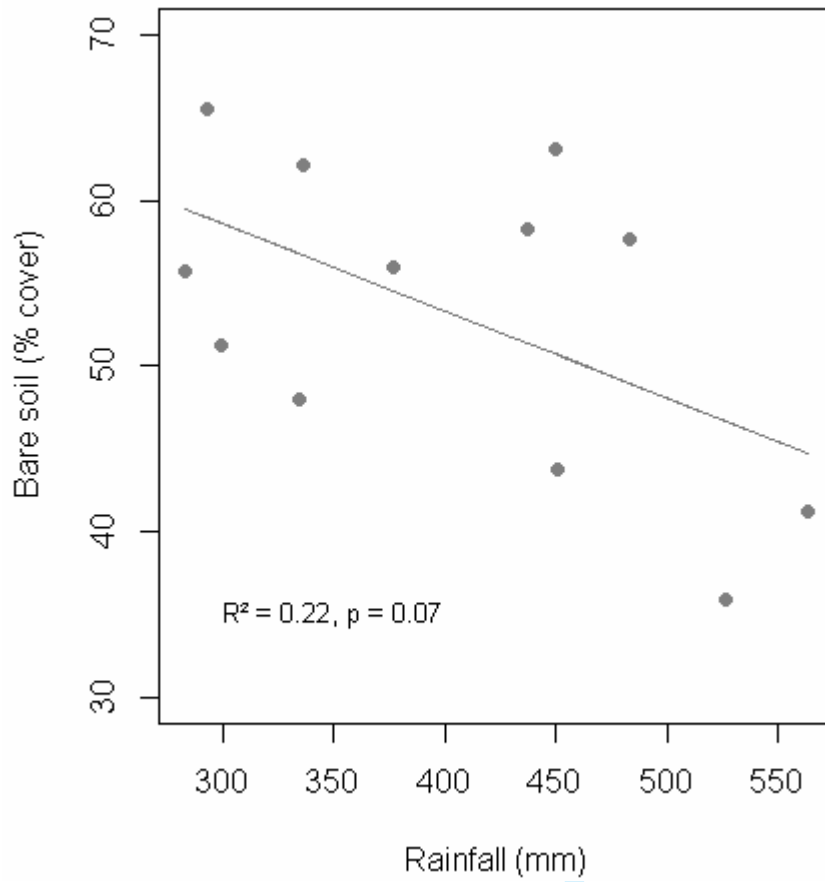
-1.331	Rofficinalis	-0.032	-0.426	-0.305	-2.583	-1.122	0.556	-0.385
-1.331	Rofficinalis	0.488	-0.385	-0.890	-1.127	1.213	0.359	-0.987
-1.331	Rofficinalis	0.088	-0.585	-0.289	-4.952	-0.982	1.215	-0.987
-1.331	Rofficinalis	-0.611	-0.423	-0.258	0.574	1.766	-1.455	-0.686
-1.331	Rofficinalis	-0.163	-0.454	-0.178	-1.318	-1.426	1.341	0.518
-1.331	Rofficinalis	0.134	-0.253	-0.641	0.005	1.378	-0.316	0.217
-1.331	Rofficinalis	-0.307	-0.355	-0.854	-2.009	-1.036	1.068	-0.686
-1.331	Rofficinalis	-0.502	-0.269	-0.496	-2.468	-0.718	1.159	-0.686
-1.266	Rofficinalis	0.522	-0.774	0.156	-0.139	1.316	-0.094	-0.385
-1.266	Rofficinalis	0.088	-0.590	-0.223	-1.213	-1.817	0.951	-0.385
-1.266	Rofficinalis	0.111	-0.590	-0.216	-0.139	1.316	-0.094	-0.385
-1.266	Rofficinalis	0.668	-0.606	0.327	-0.358	1.041	0.373	0.518
-1.266	Rofficinalis	-0.163	-1.262	-0.152	-1.107	-1.847	0.427	-1.287
-1.266	Rofficinalis	-1.099	-0.605	0.165	0.198	1.476	0.163	-0.686
-1.266	Rofficinalis	0.920	-0.480	-0.246	0.172	1.476	-0.242	-0.084
-1.266	Rofficinalis	0.199	-0.463	0.058	0.947	1.972	-1.687	-0.385
-1.266	Rofficinalis	-0.136	-0.574	-1.060	0.504	1.731	-0.491	0.217
-1.266	Rofficinalis	0.452	-0.399	0.041	-0.057	1.373	-0.314	0.217
-0.888	Rofficinalis	0.605	-0.381	-0.484	1.713	0.869	-1.008	0.217
-0.888	Rofficinalis	0.452	-0.317	0.080	0.717	-0.478	-0.033	0.217
-0.888	Rofficinalis	1.262	-0.375	-0.800	-0.382	0.947	1.228	0.819
-0.888	Rofficinalis	-0.163	-0.326	-0.103	-3.047	-2.556	0.495	-0.686
-0.888	Rofficinalis	0.302	-0.348	-0.221	-1.395	-1.155	0.426	-0.385
-0.888	Rofficinalis	0.813	-0.275	-0.567	-0.042	1.319	0.686	1.119
-0.888	Rofficinalis	-0.248	-0.581	-0.294	-2.653	-0.130	0.715	-0.987
-0.888	Rofficinalis	0.539	-0.287	-0.111	-0.255	1.484	0.043	-0.084
-0.888	Rofficinalis	-0.163	-0.529	-0.531	-2.076	-0.068	0.824	-1.287
-0.888	Rofficinalis	0.813	-0.336	-0.435	0.257	1.681	-0.276	-0.084
-0.865	Rofficinalis	0.505	-0.411	-0.550	-1.380	-1.243	0.909	-0.385
-0.865	Rofficinalis	0.156	-0.563	-0.038	-1.133	-0.862	3.040	-0.385
-0.865	Rofficinalis	0.088	-0.417	0.281	-1.953	-1.058	1.302	-0.686
-0.865	Rofficinalis	-0.770	-0.567	0.085	-1.584	-1.012	1.196	-0.987
-0.865	Rofficinalis	0.042	-0.269	-0.179	-1.472	-1.001	1.714	-0.987
-0.434	Rofficinalis	-0.191	-0.410	0.229	0.615	1.812	-0.793	-0.385
-0.434	Rofficinalis	0.652	-0.350	-0.106	1.433	1.002	-0.423	-0.385
-0.434	Rofficinalis	-0.248	-0.531	0.055	0.615	1.812	-0.793	-0.385
-0.434	Rofficinalis	0.742	-0.516	-0.010	0.894	1.401	-0.358	0.819
-0.434	Rofficinalis	0.505	-0.452	0.093	0.523	1.765	-0.602	-0.686
-0.434	Rofficinalis	0.785	-0.530	0.005	-0.253	1.386	0.045	0.217
0.203	Rofficinalis	0.452	-0.350	0.058	2.036	0.313	-0.928	-0.385
0.203	Rofficinalis	-0.219	-0.337	0.021	0.947	1.972	-1.687	-0.686
0.203	Rofficinalis	0.088	-0.435	0.333	0.947	1.972	-1.687	-0.987
0.203	Rofficinalis	0.621	-0.381	-0.319	0.947	1.972	-1.687	-0.686
0.203	Rofficinalis	0.042	-0.171	-0.197	2.036	0.313	-0.928	-0.385
0.349	Rofficinalis	0.088	-0.298	-0.077	-0.441	0.169	-0.131	-0.385
0.349	Rofficinalis	-1.458	-0.449	0.440	-0.530	0.341	0.296	-0.987
0.349	Rofficinalis	-1.458	-0.284	0.088	-0.292	1.101	0.050	-0.385
0.349	Rofficinalis	-0.649	-0.304	0.220	1.350	1.369	-0.778	1.420
0.349	Rofficinalis	0.572	-0.273	0.577	0.289	1.458	-0.735	0.819
0.349	Rofficinalis	-1.528	-0.223	0.093	0.409	0.674	-0.570	0.518
0.349	Rofficinalis	0.018	-0.361	0.069	1.255	0.281	-0.465	0.819
0.349	Rofficinalis	-1.760	-0.352	0.702	-0.558	0.249	-0.113	0.217
0.349	Rofficinalis	-0.277	-0.241	0.528	0.383	1.583	-0.560	0.819
0.698	Rofficinalis	0.470	-0.426	-0.427	-1.696	-0.364	1.544	0.518

0.698	Rofficinalis	0.434	-0.131	-0.474	-1.240	-0.186	1.351	-0.385
0.698	Rofficinalis	0.241	-0.632	-0.802	0.382	-0.050	0.927	0.969
0.698	Rofficinalis	-0.109	-0.332	0.030	-1.544	-0.376	1.817	-0.385
0.698	Rofficinalis	0.488	-0.233	-0.783	1.346	0.474	0.103	0.518
0.698	Rofficinalis	0.933	-0.328	-0.071	1.519	0.238	0.113	0.217
0.698	Rofficinalis	-0.007	-0.346	-0.382	-1.162	0.238	1.086	-0.234
0.698	Rofficinalis	0.854	-0.412	0.176	1.226	0.346	0.509	3.376
0.698	Rofficinalis	0.488	-0.386	-0.488	-2.041	-0.825	1.812	-0.987
1.157	Rofficinalis	-0.109	-0.379	-0.307	-0.262	1.260	0.123	-0.987
1.157	Rofficinalis	0.178	-0.601	0.083	1.054	0.173	-0.611	1.420
1.157	Rofficinalis	0.302	-0.585	-0.069	0.997	1.037	-0.171	-0.385
1.157	Rofficinalis	0.881	-0.423	0.059	0.410	-0.005	0.275	2.323
1.157	Rofficinalis	0.470	-0.537	-0.328	0.929	1.534	-1.434	-0.686
1.157	Rofficinalis	0.111	-0.563	0.042	-0.369	1.248	-0.662	-0.084
1.157	Rofficinalis	-0.468	-0.447	0.139	-0.448	1.366	-2.334	-0.385
1.157	Rofficinalis	0.799	-0.573	-0.322	-0.280	1.027	-1.713	-0.084
1.157	Rofficinalis	0.322	-0.537	-0.135	0.553	0.884	-0.325	-0.084
1.157	Rofficinalis	1.043	-0.404	-0.395	0.108	1.479	0.039	-0.686
1.553	Rofficinalis	-1.267	-0.421	0.028	-1.215	-0.370	-0.063	2.925
1.553	Rofficinalis	-0.191	-0.408	-0.129	-2.112	-0.144	0.652	1.119
1.553	Rofficinalis	-1.458	-0.415	-0.040	-0.527	-0.138	-0.548	1.420
1.553	Rofficinalis	-0.728	-0.382	-0.083	0.460	-0.140	0.539	2.323
1.553	Rofficinalis	-0.369	-0.393	-0.321	-1.572	-0.394	0.316	1.119
1.553	Rofficinalis	-0.109	-0.533	0.259	-1.172	-0.638	-0.674	-0.385
1.553	Rofficinalis	0.241	-0.417	0.080	-0.367	0.122	0.212	4.128
1.553	Rofficinalis	-0.434	-0.441	-0.348	-0.738	0.312	-0.754	2.022
1.553	Rofficinalis	0.360	-0.388	0.175	-1.238	0.118	-0.175	2.624
1.553	Rofficinalis	-0.434	-0.161	-0.211	-1.320	-0.042	0.018	3.225
-1.331	Stenacissima	0.522	1.455	-1.083	-0.020	-0.888	-0.156	0.518
-1.331	Stenacissima	0.178	1.006	-0.659	0.004	-1.050	-0.328	-0.686
-1.331	Stenacissima	0.728	1.026	-2.980	-1.236	-0.845	0.255	-0.686
-1.331	Stenacissima	0.134	0.923	-2.014	-0.032	-1.062	-0.207	-0.385
-1.331	Stenacissima	0.698	1.176	-0.694	-0.179	-0.859	-0.183	0.217
-1.331	Stenacissima	0.302	1.027	-1.202	-1.363	-0.699	0.556	-0.385
-1.331	Stenacissima	-0.007	0.946	-0.561	-0.060	-0.801	-0.550	-0.385
-1.331	Stenacissima	0.220	0.944	-1.020	-0.918	-1.331	0.741	-0.084
-1.331	Stenacissima	-0.136	0.846	-0.876	-1.000	-1.120	0.609	-1.287
-1.331	Stenacissima	0.088	0.869	-0.775	0.311	-1.053	-0.867	-0.836
-1.266	Stenacissima	0.683	1.349	-0.564	-0.181	-0.795	0.720	0.819
-1.266	Stenacissima	0.813	1.313	-0.585	-1.240	-1.356	0.352	-0.385
-1.266	Stenacissima	0.416	1.382	-0.420	-1.258	-1.492	0.722	-0.686
-1.266	Stenacissima	0.199	1.334	-0.908	-0.624	-1.477	0.549	0.217
-1.266	Stenacissima	0.894	1.560	-0.985	0.061	-1.156	0.256	0.819
-1.266	Stenacissima	0.868	1.347	-1.035	-0.292	-1.295	0.126	-0.385
-1.266	Stenacissima	0.983	1.520	-1.060	-0.076	-1.251	0.298	0.819
-0.888	Stenacissima	0.322	1.759	-0.864	0.139	-1.189	-0.544	-0.686
-0.888	Stenacissima	0.894	1.749	-0.755	0.076	-1.223	0.124	-0.686
-0.888	Stenacissima	0.522	1.485	-0.358	-2.175	-2.158	0.864	-0.987
-0.888	Stenacissima	0.757	1.784	-0.588	-1.260	-2.061	0.849	-0.385
-0.888	Stenacissima	0.813	1.625	-0.309	-0.131	-0.696	1.512	1.420
-0.888	Stenacissima	0.605	1.814	-0.726	0.611	0.836	-4.287	-1.287
-0.888	Stenacissima	0.398	1.769	-0.468	-0.220	0.379	0.565	0.217
-0.888	Stenacissima	0.894	1.791	-1.322	-0.103	-1.218	0.164	-0.686
-0.888	Stenacissima	0.933	1.668	-0.844	0.165	-0.651	-0.446	0.518

-0.888	Stenacissima	0.668	1.749	-0.494	0.371	1.730	-0.445	0.217
-0.865	Stenacissima	0.813	1.112	-0.983	-0.110	-0.936	0.664	-0.084
-0.865	Stenacissima	0.728	1.103	-0.715	-0.168	-0.060	0.511	-0.385
-0.865	Stenacissima	0.652	1.061	-1.075	-0.055	-0.825	0.505	0.518
-0.865	Stenacissima	0.178	1.049	-0.376	-0.034	-0.822	0.753	0.518
-0.865	Stenacissima	0.621	0.984	-1.092	-0.025	0.282	1.232	-0.234
-0.865	Stenacissima	0.018	1.054	0.264	0.128	-0.864	-0.600	-0.084
-0.865	Stenacissima	0.111	0.953	-0.434	0.170	-1.131	0.222	0.668
-0.865	Stenacissima	0.728	1.312	-1.149	0.204	-0.820	0.538	0.217
-0.865	Stenacissima	0.199	1.102	-1.312	-0.438	-1.260	0.508	0.518
-0.865	Stenacissima	-0.338	1.431	0.943	0.466	-0.989	-0.298	-0.385
-0.434	Stenacissima	0.652	1.432	-1.143	0.410	-0.970	-0.177	0.518
-0.434	Stenacissima	0.728	1.469	-0.179	0.396	-1.016	-0.274	-0.385
-0.434	Stenacissima	0.241	1.485	-0.498	0.505	-0.894	-0.216	-0.686
-0.434	Stenacissima	0.199	1.361	-1.064	0.277	-0.845	-0.392	1.119
-0.434	Stenacissima	0.522	1.462	-1.345	0.712	-0.877	-0.876	-1.287
-0.434	Stenacissima	0.683	1.360	-0.419	0.042	-1.123	0.102	-0.084
-0.434	Stenacissima	0.178	1.161	0.309	0.712	-0.877	-0.876	-0.987
-0.434	Stenacissima	0.134	1.241	-0.545	0.073	-1.024	1.039	0.217
0.203	Stenacissima	0.470	1.231	-1.382	0.712	-0.877	-0.876	-1.287
0.203	Stenacissima	0.683	1.327	-1.278	0.712	-0.877	-0.876	-0.987
0.203	Stenacissima	0.398	1.265	-2.354	0.712	-0.877	-0.876	-1.287
0.203	Stenacissima	0.470	1.241	0.059	0.712	-0.877	-0.876	-0.987
0.203	Stenacissima	0.178	1.217	-0.958	4.063	0.642	3.739	-0.385
0.203	Stenacissima	0.379	1.232	-3.421	0.712	-0.877	-0.876	-0.385
0.203	Stenacissima	0.668	1.356	-1.489	0.712	-0.877	-0.876	-1.287
0.203	Stenacissima	0.398	1.370	-1.242	0.712	-0.877	-0.876	-0.987
0.349	Stenacissima	-0.307	1.046	-0.783	-0.757	-0.588	0.180	-0.686
0.349	Stenacissima	-0.369	1.161	-0.700	-0.590	-0.094	-0.287	-0.686
0.349	Stenacissima	0.065	1.147	-0.645	0.872	1.687	-1.394	-0.084
0.349	Stenacissima	-0.136	1.161	0.349	-0.126	-0.489	-0.484	-0.686
0.349	Stenacissima	0.042	1.337	-0.318	0.738	1.584	-1.318	0.217
0.349	Stenacissima	-0.770	0.980	0.111	0.833	1.486	-1.257	-0.084
0.349	Stenacissima	-0.502	1.144	1.344	0.712	-0.877	-0.876	-0.686
0.349	Stenacissima	0.302	1.352	-1.571	0.454	1.042	-1.068	0.518
0.698	Stenacissima	0.621	1.621	-1.214	-0.670	-0.960	1.055	-0.084
0.698	Stenacissima	0.470	1.088	-1.385	-0.476	-0.346	0.134	-0.385
0.698	Stenacissima	0.452	1.431	-0.974	-0.972	-0.581	-0.129	0.217
0.698	Stenacissima	0.434	1.393	-1.351	-0.252	-0.364	0.081	-0.686
0.698	Stenacissima	0.220	1.234	-0.479	1.944	0.464	-1.131	1.511
0.698	Stenacissima	0.605	1.252	-0.872	0.118	-0.443	-0.125	-0.385
1.157	Stenacissima	0.042	1.347	-0.899	0.673	-0.124	-0.372	-0.987
1.157	Stenacissima	0.111	1.325	-0.827	1.207	0.013	1.821	-0.987
1.157	Stenacissima	-0.248	0.978	-0.814	0.832	-0.339	0.062	-1.287
1.157	Stenacissima	-0.136	1.330	-0.523	0.832	-0.339	0.062	-0.987
1.157	Stenacissima	0.322	1.071	-0.795	0.062	0.027	-0.448	-1.287
1.157	Stenacissima	-0.083	1.206	-0.484	-0.600	-0.513	-0.126	-1.287
1.157	Stenacissima	0.134	1.276	-0.912	-0.794	-0.138	0.737	-0.686
1.157	Stenacissima	0.134	1.364	-0.937	-0.402	-1.159	0.618	-0.987
1.157	Stenacissima	0.241	1.106	-1.046	0.197	-0.097	-1.114	-0.385
1.157	Stenacissima	0.282	1.337	-0.992	-0.647	-0.129	-0.070	-0.686
-1.437	Tvulgaris	-0.688	-1.366	1.900	-0.274	-0.948	1.223	-1.287
-1.437	Tvulgaris	-1.392	-1.398	2.474	1.262	0.118	3.290	-0.686
-1.437	Tvulgaris	-0.688	-1.470	2.384	-0.274	-0.948	1.223	-0.686

-1.437	Tvulgaris	-0.949	-1.487	1.731	0.992	-0.211	2.163	0.969
-1.437	Tvulgaris	-0.611	-1.394	2.331	-0.274	-0.948	1.223	-0.686
-1.437	Tvulgaris	-0.770	-1.474	1.977	1.087	0.118	3.430	0.367
-1.437	Tvulgaris	-0.856	-1.394	2.331	1.031	-0.103	2.138	0.217
-1.266	Tvulgaris	-0.856	-1.751	1.599	-1.107	-1.847	0.427	-1.287
-1.266	Tvulgaris	-1.392	-1.740	2.553	0.069	0.712	-0.332	-0.084
-1.266	Tvulgaris	-1.846	-1.623	1.867	-1.206	-0.973	1.038	-0.987
-1.266	Tvulgaris	-0.812	-1.884	2.325	0.217	1.122	-0.254	1.119
-1.266	Tvulgaris	-1.267	-1.826	1.865	0.142	-1.109	-0.215	0.518
-1.266	Tvulgaris	-1.047	-1.568	2.306	0.361	0.544	-0.639	0.518
-1.266	Tvulgaris	-1.939	-1.496	2.674	-1.250	-1.900	-0.844	-1.588
-1.266	Tvulgaris	-0.502	-1.531	2.196	0.066	-0.520	0.080	0.518
-0.888	Tvulgaris	-1.939	-1.186	1.303	-1.050	-1.046	3.026	-1.287
-0.888	Tvulgaris	-1.528	-1.329	0.607	-0.078	-1.120	0.129	-0.084
-0.888	Tvulgaris	-1.760	-1.153	0.613	-0.623	-0.066	1.765	-0.686
-0.888	Tvulgaris	-1.392	-1.336	1.321	-0.258	1.187	-0.406	-0.686
-0.888	Tvulgaris	-1.528	-1.234	0.720	0.476	-0.377	-0.698	-0.385
-0.888	Tvulgaris	-0.949	-1.317	1.203	1.133	0.633	1.192	1.119
-0.888	Tvulgaris	-1.601	-1.156	2.408	0.712	-0.877	-0.876	-0.686
-0.888	Tvulgaris	-0.997	-1.284	1.267	0.872	1.687	-1.394	-0.084
-0.434	Tvulgaris	-3.508	-1.149	1.699	-0.600	-0.513	-0.126	-1.287
-0.434	Tvulgaris	-1.939	-1.249	1.459	0.793	1.207	-1.125	-0.084
-0.434	Tvulgaris	-2.518	-1.149	1.838	0.712	-0.877	-0.876	-0.686
-0.434	Tvulgaris	-1.939	-1.263	1.762	1.783	0.567	-0.700	-0.385
-0.434	Tvulgaris	-2.668	-1.226	1.586	2.088	0.710	-1.422	-1.588
-0.434	Tvulgaris	-2.143	-1.082	1.736	0.947	1.972	-1.687	-1.287
0.338	Tvulgaris	-0.949	-1.345	0.681	0.712	-0.877	-0.876	-0.385
0.338	Tvulgaris	-0.538	-1.470	1.844	0.712	-0.877	-0.876	-0.385
0.338	Tvulgaris	-2.518	-1.213	2.364	0.712	-0.877	-0.876	-0.385
0.338	Tvulgaris	-0.949	-1.334	1.278	0.712	-0.877	-0.876	-0.385
0.338	Tvulgaris	-1.209	-1.262	1.754	0.712	-0.877	-0.876	-0.385
0.698	Tvulgaris	-0.434	-1.216	1.201	1.454	-0.013	-0.164	0.819
0.698	Tvulgaris	-0.538	-1.330	1.278	0.712	-0.877	-0.876	-0.385
0.698	Tvulgaris	-1.528	-1.173	1.796	1.746	0.203	0.143	-0.084
0.698	Tvulgaris	-1.458	-1.445	0.582	0.712	-0.877	-0.876	-0.686
0.698	Tvulgaris	-1.267	-1.398	1.205	1.174	-0.010	0.297	1.420
1.157	Tvulgaris	-2.037	-1.040	1.195	1.262	0.030	-0.769	0.217
1.157	Tvulgaris	-0.856	-1.262	1.351	1.123	0.287	-0.554	0.819
1.157	Tvulgaris	-1.528	-1.467	1.274	0.219	0.721	-2.241	-0.987
1.157	Tvulgaris	-3.027	-1.212	1.803	0.166	1.618	0.283	-0.385
1.157	Tvulgaris	-0.649	-1.145	1.616	0.304	0.721	-1.151	0.217
1.157	Tvulgaris	-0.997	-1.314	1.607	0.157	0.195	-0.962	0.819
1.157	Tvulgaris	-1.846	-1.318	1.878	-0.264	-0.573	-0.263	-0.385
1.157	Tvulgaris	-0.949	-1.405	1.928	1.044	0.366	-0.471	-0.686
1.157	Tvulgaris	-1.678	-1.346	0.637	0.179	0.821	-0.577	-0.084
1.157	Tvulgaris	-1.601	-1.261	1.484	2.036	0.313	-0.928	-1.588
1.553	Tvulgaris	-2.143	-1.345	-0.396	0.476	-0.377	-0.698	-0.385
1.553	Tvulgaris	-2.518	-1.470	-0.764	-0.883	0.416	-0.069	-1.588
1.553	Tvulgaris	-1.760	-1.535	-0.057	-0.654	0.112	-0.341	-0.385
1.553	Tvulgaris	-0.949	-1.213	2.184	-0.654	0.112	-0.341	-0.385
1.553	Tvulgaris	-0.538	-1.334	0.859	0.712	-0.877	-0.876	-0.987
1.553	Tvulgaris	-2.037	-1.330	0.299	-0.883	0.416	-0.069	-1.588

**Appendix S6** Relationship between the cover of bare soil area (%) and rainfall (mm) along the studied gradient. The cover of bare soil area was estimated as the average of four linear 30 m transects within each of the twelve study sites.



view