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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

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

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

2   **Type of article:** Standard paper

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4   **Traits of neighbouring plants and space limitation determine intraspecific**

5   **trait variability in semi-arid shrublands.**

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24   Word count in the summary: 247

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

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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.

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Introduction

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

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

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 13ºC 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 *NR = ∑(total volume of neighbouring individuals)/volume of the subordinate individual* (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

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

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

NEIGHBOURING PLANT TRAITS

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

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

199   volume:

200   $NWM = \sum p_i \ x \ Trait_i$ (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).

207

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

9

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^2) 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, rainfall²,

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

262 The resulting value is compared to a χ^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, α =

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   AIC = C + 2k   (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 (rainfall²) 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. cocciferra*

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. cocciferra*

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. tenaccisima* (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

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

Discussion

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

RESPONSE OF INTRASPECIFIC TRAIT VARIABILITY TO RAINFALL

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

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

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

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

RESPONSE OF INTRASPECIFIC TRAIT VARIABILITY TO THE LOCAL NEIGHBOURHOOD

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

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

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

persistence against environmental changes and micro-evolutionary impact on species

coexistence and community assembly (Liancourt *et al.* 2012).

ii) Species-specific response: the response of ITV to environmental constraints was

strongly species-specific (see also Albert *et al*. 2010). Species differed both in their sensitivity

to rainfall and neighbours and in the way they adjusted their trait values (Fig. 4, Appendix

S2). However, strong correlations between SLA and individual plant height were also

observed (Fig. 4), highlighting that coordinations among traits determine their phenotypic

plasticity to changes in both abiotic and biotic factors. In a modelling study comparing 13

grass species from temperate grasslands, Maire *et al.* (2013) showed that the coordination

among multiple traits within species is related to plant functional strategies and to the carbon

economy within individual plants. They identified key trade-offs occurring at the intraspecific

level predicting responses to environmental changes with relatively high accuracy. Species

plastic strategies of Mediterranean systems are largely ignored, and comparative approaches

are needed to evaluate how physiological and allometric constraints within plant species

determine patterns of ITV across species.

iii) Trait-specific responses: the response of ITV to both abiotic and biotic factors

varied depending on the trait considered. Maximum plant height and SLA were generally

more variable than LA. Whole plant traits such as maximum plant height are highly sensitive

to the environment (Marks 2007), reflecting both species ontogeny and plant performance in a

given environment. Specific leaf area is a key trait by which plants adjust resource acquisition

to the local limiting resources (Maire *et al*. 2013). This trait is more variable than traits related

to leaf morphology such as LA, which are strongly constrained by plant allometry (see the

corner rule, Maire *et al.* 2013). Taking into account ITV might be particularly critical for

traits related to whole plant architecture and leaf economic spectrum when studying

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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

509

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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.

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Figures

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

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

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

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.

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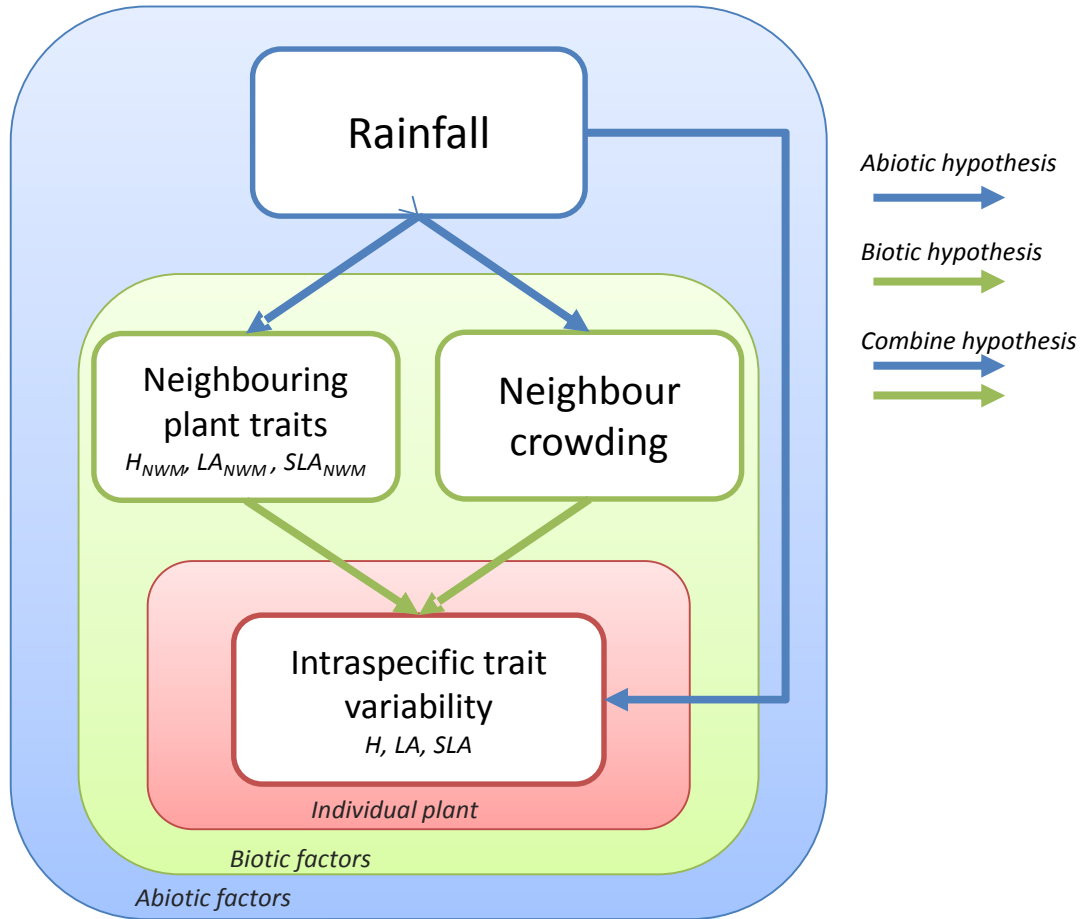
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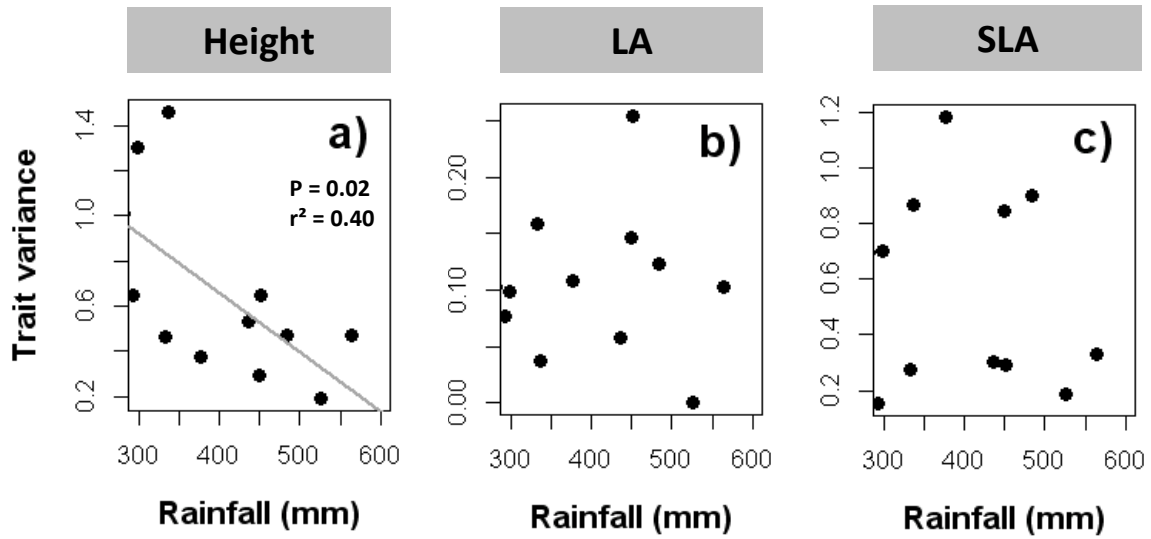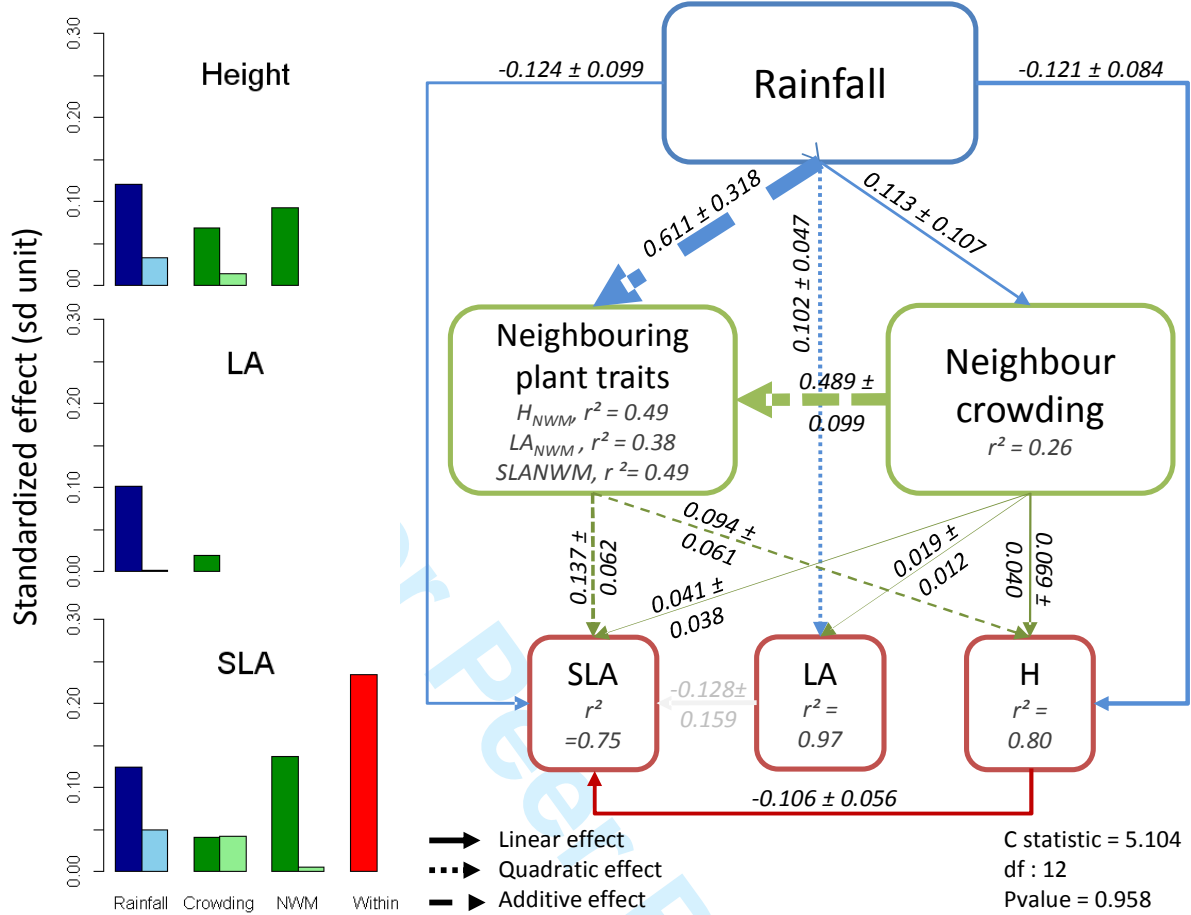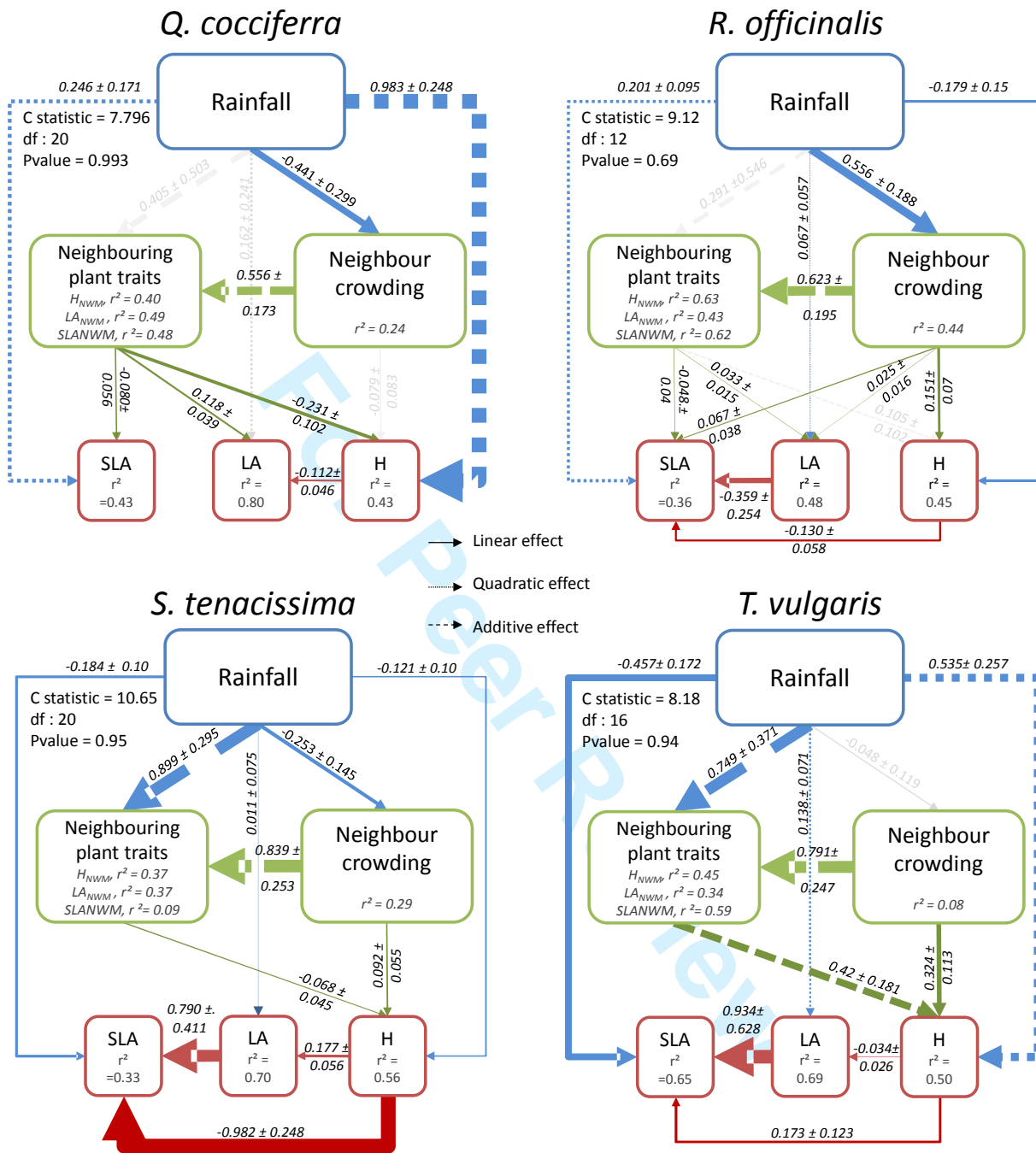
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Fig. 5.

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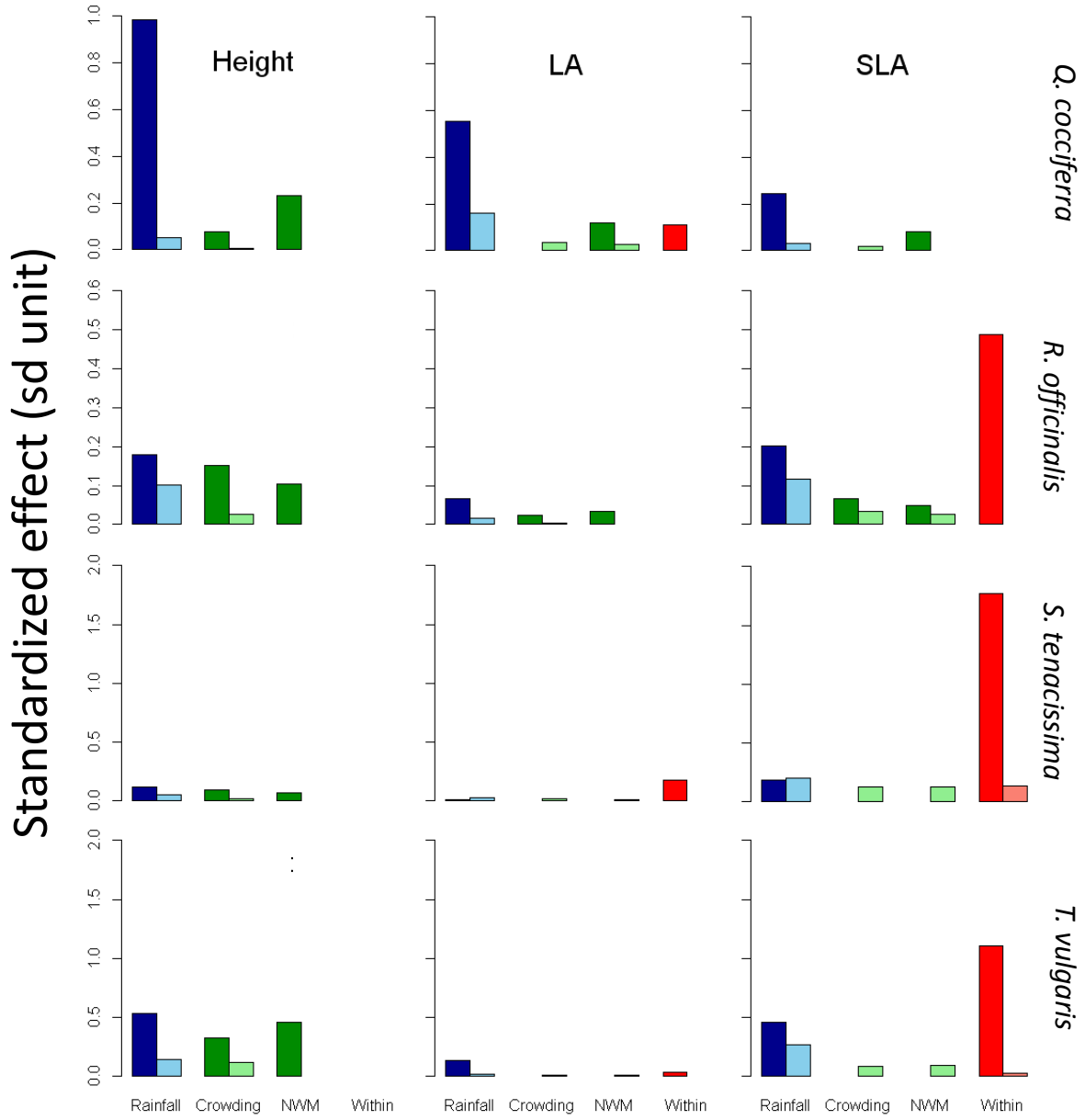
Appendices

Appendix S1 Parameter estimates (slope) from averaged models including all target species together for maximum plant height (a), Leaf Area (b) and Specific Leaf Area (c). When the standard error does not cross the zero line, the predictors under consideration are statistically significant. The significance of predictors is based on the best 5% of all potential models. The averaging model procedures were based on linear mixed effect models. The individual trait values were the response variables, and rainfall, rainfall², crowding and neighbouring plant traits (H_{NWM}, LA_{NWM} and SLA_{NWM}) were the predictors. Height was also introduced as a predictor of LA and SLA to grasp potential ontogenetic effects and to consider potential coordination among traits. Height and LA were introduced for SLA. Site was used as a random factor to control for the hierarchical design. Species was also used as a random effect for models including all target species together to avoid inter-specific differences. We also present the results of averaging model procedures including interactions between rainfall and crowding and rainfall and neighbouring plant traits (panels d, e and f).
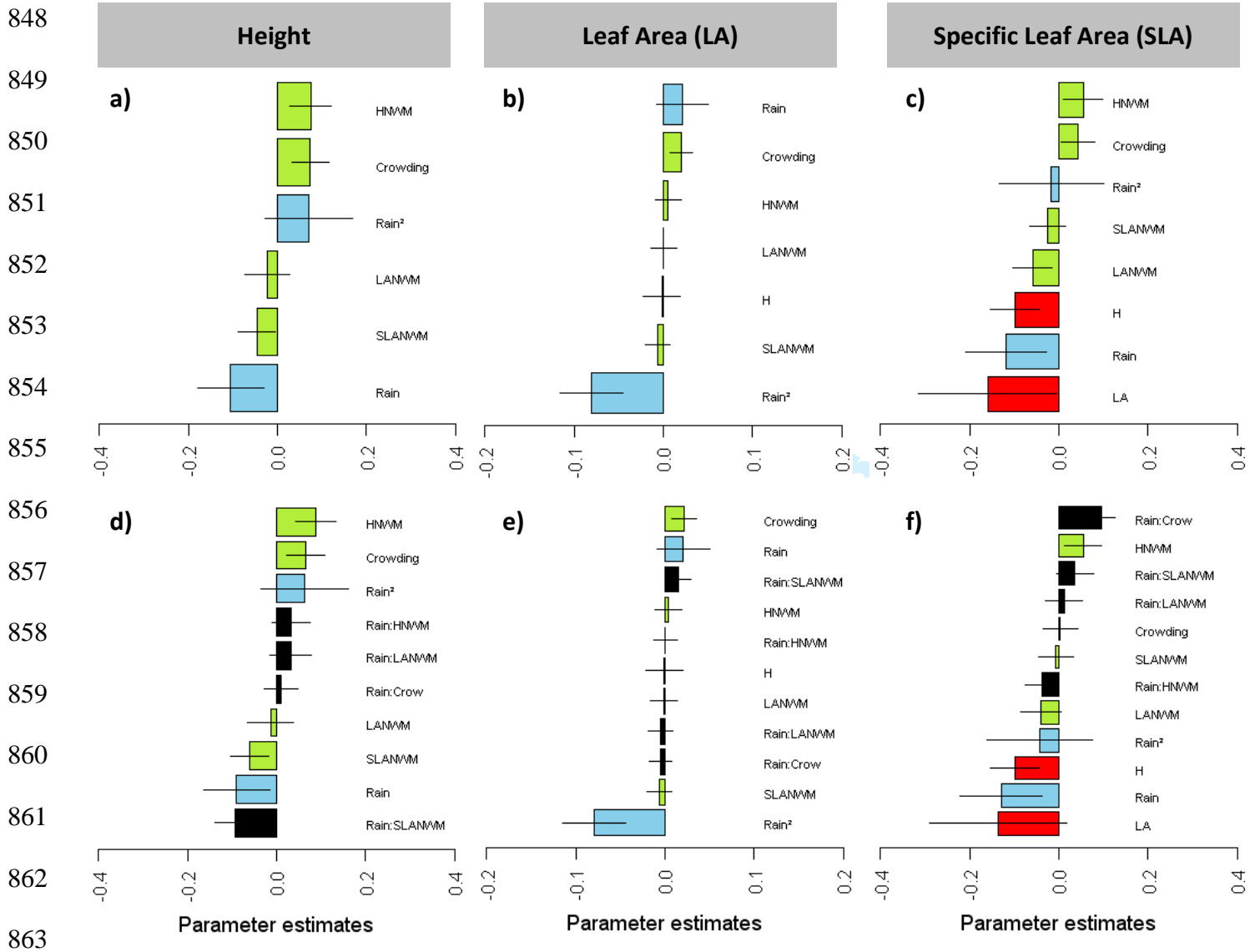
864   **Appendix S2** Parameter estimates (slope) from averaged models for each target species

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^2, 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.

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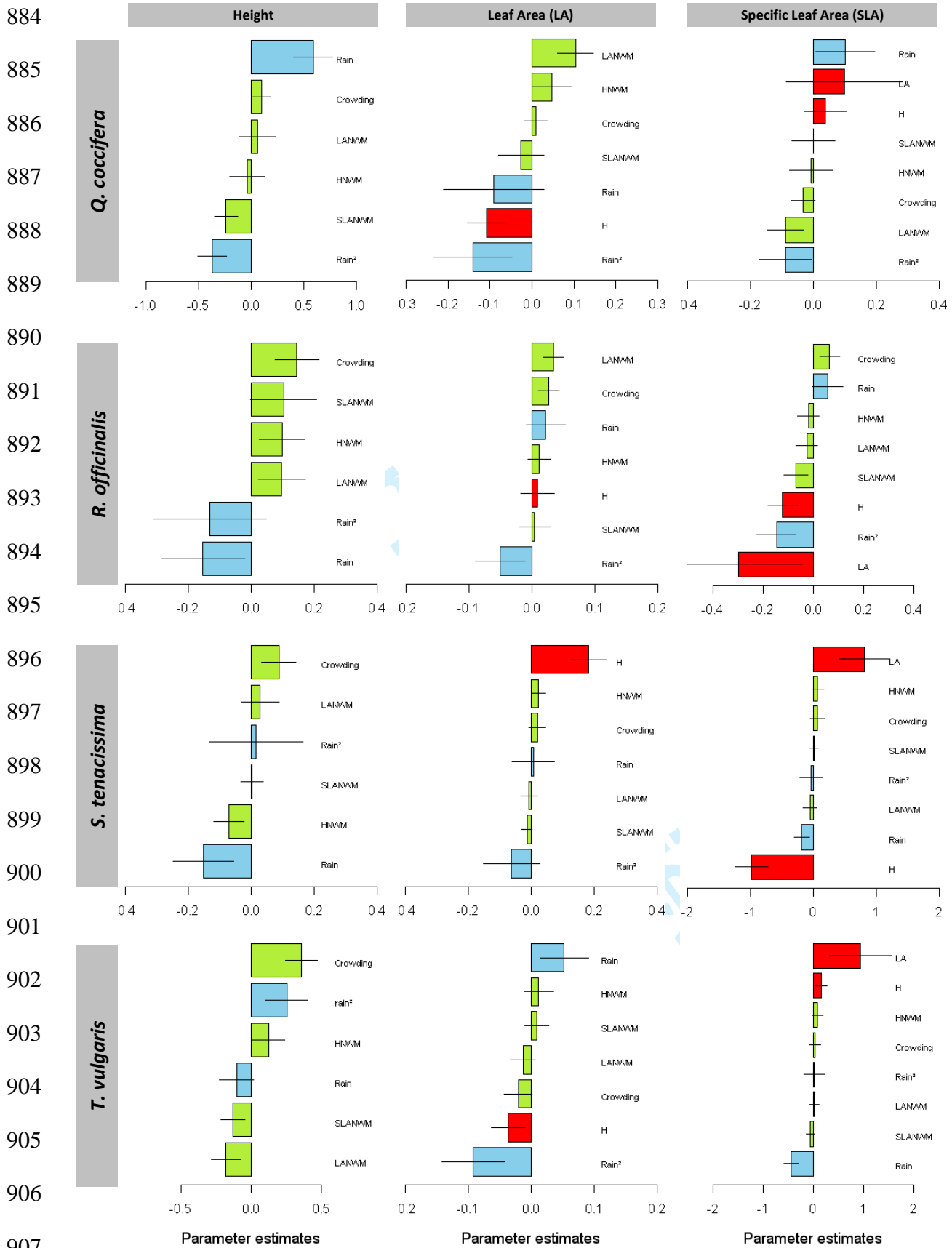
909 **Appendix S3** Model selection for all target species together (confirmatory multilevel path

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 χ^2 value.

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

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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 χ^2

967   value.

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

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

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

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