1 **Survival rates indicate that correlations between community-weighted mean traits and**

2 **environments can be unreliable estimates of the adaptive value of traits**

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40   **Abstract**

41   Correlations between community-weighted mean (CWM) traits and environmental gradients are

42   often assumed to quantify the adaptive value of traits. We tested this assumption by comparing

43   these correlations with models of survival probability using 46 perennial species from long-term

44   permanent plots in pine forests of Arizona. Survival was modeled as a function of trait-by-

45   environment interactions, plant size, climatic variation, and neighborhood competition. The

46   effect of traits on survival depended on the environmental conditions, but the two statistical

47   approaches were inconsistent. For example, CWM specific leaf area (SLA) and soil fertility were

48   uncorrelated. However, survival was highest for species with low SLA in infertile soil, a result

49   which agreed with expectations derived from the physiological tradeoff underpinning leaf

50   economic theory. CWM trait-environment relationships were unreliable estimates of how traits

51   affected survival, and should only be used in predictive models when there is empirical support

52   for an evolutionary tradeoff that affects vital rates.

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63   **Introduction**

64   The search for phenotypic traits that explain species interactions and compositional

65   turnover along environmental gradients is a major research priority because quantifying the

66   adaptive value of traits will increase the generality of our understanding of species coexistence

67   and responses to global change (HilleRisLambers *et al.* 2012; Adler *et al.* 2013; Kraft *et al.*

68   2015b). Functional traits are heritable properties that influence organism fitness, but their effect

69   on fitness will depend on the environmental context because variation in traits is underpinned by

70   evolutionary tradeoffs (Grime 2001). There are two common approaches for quantifying the

71   fitness of a phenotype. The 'likelihood' approach assesses the correlation between community-

72   weighted mean (CWM) traits (average traits weighted by species abundances) and environmental

73   gradients (Ackerly 2003; Shipley *et al.* 2006). The 'vital rates' approach models fitness

74   components, such as survival, growth rate, and reproduction, directly as functions of trait-by-

75   environment interactions, because the effect of traits on fitness should depend on the

76   environment (Laughlin & Messier 2015).

77   The likelihood approach assumes that average trait values in a community are biased

78   toward the optimum trait value for that environment because they are the most frequent trait

79   value in the community. Several trait-based models (e.g., CATS, Traitspace, fourth corner and

80   RLQ analyses, Trait Driver Theory) rely on central tendencies of traits at the community level, in

81   some form or another, for understanding the importance of traits in community assembly

82   (Shipley *et al.* 2011; Laughlin *et al.* 2012; Dray *et al.* 2014; Enquist *et al.* 2015; Warton *et al.*

83   2015). If a sample of CWM traits is significantly correlated with an environmental gradient, then

84   the logical interpretation of this pattern is that the trait has adaptive value along that gradient

85   (Ackerly 2003). If a trait value is more common (*i.e.*, statistically *likely*) in one environment than

86   another, then species that possess this trait value should exhibit high fitness in that environment

87   (Fig. 1A).

88   Observed shifts in mean trait values along environmental gradients are interpreted as

89   reflections of physiological trade-offs that drive environmental filtering of regional species pools

90   (Cornwell & Ackerly 2009; Shipley *et al.* 2011; Enquist *et al.* 2015). Examples abound where

91   CWM traits vary predictably along gradients of temperature, precipitation, soil fertility, and

92   disturbance (Cornwell & Ackerly 2009; Sonnier *et al.* 2010; Fortunel *et al.* 2014; Jager *et al.*

93   2015; Ames *et al.* 2016). These relationships can be useful when the aim is to predict the

94   distribution of species and traits across broad spatial scales (Asner *et al.* 2017). However, CWM

95   trait-environment correlations can only be used to explain the value of the trait for fitness when

96   fitness components (*i.e.*, demographic rates) are driven by trait-by-environment interactions (Fig.

97   1B, and see Fig. S1). In other words, the effect of traits on fitness must depend on the

98   environmental context. There are few strong empirical tests of this assumption (Shipley *et al.*

99   2016). Muscarella and Uriarte (2016) found mixed evidence for the assumption that CWM traits

100   reflect optimum trait values, and highlighted the need to analyze demographic data to determine

101   whether CWM trait values in a community reflect the optimum trait value for a given

102   environment.

103   The likelihood approach is attractive because of its low data requirements and broad

104   applicability to many datasets, but it has four important weaknesses. First and foremost, trait-

105   environment correlations do not measure fitness components directly (Laughlin & Messier

106   2015). Second, CWM trait-environment relationships could be biased if they are driven by a

107   single dominant species or a large-statured species (Legendre *et al.* 1997; Grime 1998). Small-

108   statured species may be well-adapted to the conditions, but because their low abundances

109   contribute little to the CWM trait value, their fitness is discounted by such an analysis. Third,

110   species composition is dynamic (Adler *et al.* 2006). The dominant trait value in a community at a

111   snapshot in time could be the product of environmental conditions in the past or recent

112   disturbance (Blonder *et al.* 2017), and it could be influenced by dispersal limitation (Ozinga *et*

113   *al.* 2005). Fourth, the likelihood approach assumes that the fitness function is strictly unimodal,

114   *i.e.,* that there is only one optimum trait value for an environment (Muscarella & Uriarte 2016).

115   The complementary coexistence of functionally diverse species (Hooper 1998) and the

116   observation of rugged fitness landscapes (Poelwijk *et al.* 2007) raises doubts about a single

117   optimum trait value. Given these weaknesses, can we assume that CWM trait-environment

118   correlations are robust proxies for the adaptive value of traits?

119   Our objective was to conduct a rigorous test of the widespread assumption that CWM

120   trait-environment correlations reflect the adaptive value of functional traits. Fitness, as measured

121   by lifelong reproductive output, is difficult to quantify. Here we focus on survival, a critical vital

122   rate for perennial herbs (Adler *et al.* 2014). There are four possible outcomes when comparing

123   interpretations of statistical analyses using the likelihood and vital rates approaches (Table S1).

124   When the likelihood approach shows no CWM trait-environment correlations, and trait-by-

125   environment interactions do not significantly affect vital rates, then both approaches agree that

126   the trait has no adaptive value (option #1). When there is no CWM trait-environment correlation

127   but the trait-by-environment interactions affect vital rates, then the trait may have adaptive value

128   along the gradient, but the CWM traits are being driven by other factors that vary spatially or

129   temporally (option #2). In contrast, when there is a CWM trait-environment correlation but no

130   trait-by-environment interaction affecting vital rates, then the trait could be influencing a

131   different fitness component, such as growth or reproduction (Visser *et al.* 2016), or the CWM

132   trait may be generated by a single large or dominant species (option #3). Finally, when the

133   likelihood approach shows strong CWM trait-environment correlations and when trait-by-

134   environment interactions significantly affect vital rates (and agree in the direction of the

135   relationships), then both approaches provide evidence that the trait has adaptive value (option

136   #4).

137   The concordance between the likelihood and vital rates approaches has never been

138   directly tested, possibly because of the large data requirements that are needed to do so. We have

139   overcome this limitation by analyzing a long-term (10 yr) dataset from northern Arizona in

140   which we estimated CWM traits and the relationship between traits and survival across 46

141   perennial plant species in permanent plots along strong orthogonal gradients in soil properties.

142   Specifically, we tested the hypothesis that CWM trait-environment correlations are generated by

143   trait-by-environment interactions affecting survival. We found that the effect of traits on survival

144   depended on the environment, but that CWM trait-environment correlations are unreliable

145   estimates of how functional traits influence survival along environmental gradients.

146

147   **Methods**

148   *Study system and approach*

149   This study was conducted within a 700 km^2 landscape dominated by ponderosa pine

150   forest near Flagstaff, Arizona (35.19° N, 111.65° W) on the Coconino National Forest between

151   the elevations of 2000 to 2500 m. The mean annual precipitation of Flagstaff is 565 mm and the

152   mean annual temperature is 7.7 °C. For this analysis we used 89 permanent 1-m^2 chart quadrats

153   mapped between 2003 and 2012 that span a range of soil types developed from basalt, limestone,

154   and sandstone parent materials (Laughlin *et al.* 2011).

155   We tested our hypothesis in two steps: we fit CWM traits as functions of soil gradients,

156   and then modeled survival probability using generalized linear mixed models (GLMM) to

157   determine if survival was driven by trait-by-soil interactions (Fig. 1). Our primary interest was to

158   estimate the strength of the interactions between each of three traits and the two soil properties to

159   compare with the CWM trait-environment regression models. Our survival models accounted for

160   the many other factors known to influence individual plant survival: plant size, inter-annual

161   climatic variation, and local neighborhood competition (Lasky *et al.* 2014; Chu & Adler 2015;

162   Kunstler *et al.* 2016).

163

164   *Demographic data*

165   One of the few ways to determine demographic parameters for perennial plant species is

166   by the long-term mapping of individuals on permanent plots (Clements 1907). This technique

167   allows both the location and basal area of individuals to be tracked through time. We compiled

168   survivorship data for 13,822 individuals representing 46 herbaceous perennial species (10

169   graminoids and 36 forbs). Species were mapped as either points or polygons depending on

170   growth form. We tracked individuals through time based on their spatial location in the quadrats

171   (Lauenroth & Adler 2008).

172   For species mapped as points, survivors are classified as any genet identified in year $t + 1$

173   which is < 5 cm from a conspecific in year t. If in the current year, more than one individual is

174   within the neighborhood of a "parent" plant, then all individuals inherit that same identity

175   (Lauenroth & Adler 2008). Second, a recruit is defined as a genet in year $t + 1$ which is > 5 cm

176   from any conspecific in year t. For species mapped as polygons, the tracking rules are based on

177   areas of overlapping polygons, as opposed to distances between points. At time $t,$ a 5 cm buffer

178   is added to all polygons of a given species. At time $t + 1$, if an individual does not overlap with

179   any polygon from the previous year, it is labeled a recruit. Otherwise, it acquires the identity of

180   the individual with which it shares the greatest overlap (Lauenroth & Adler 2008). This allows

181   for individual plants to fragment and coalesce over time. These assumptions and tracking rules

182   are appropriate for the ponderosa pine-bunchgrass ecosystem since most herbaceous species in

183   our quadrats have the potential for clonal growth. A distance of 5 cm was chosen to account for

184   both mapper error and the potential for vegetative growth (Lauenroth & Adler 2008). Analyses

185   of plant demography and coexistence have been shown to be insensitive to this buffer distance

186   (Chu & Adler 2015). Complete details and assumptions of the algorithms are detailed in

187   Lauenroth and Adler (2008).

188   Forbs and graminoids were mapped differently, so we used the following procedure to

189   convert points and polygons into the same 'currency' of abundance, *i.e.*, foliar cover.

190   Measurements of basal cover and foliar cover were made on most of these species in an

191   independent dataset in the same region (Moore *et al.* 2006). We developed lifeform-level (i.e.

192   graminoids, forbs, and ground-rosette forbs) and species-level regression models to predict foliar

193   cover from basal cover (see Table S2 and Figure S2 for details). These predictions of foliar cover

194   produced the correct average ratio of 2:1 graminoid-to-forb cover (Moore *et al.* 2006).

195   We used a radius of 15 cm to define the local neighborhood surrounding each focal plant

196   because the strength of plant-plant interactions was found to decrease rapidly beyond a radius of

197   10 cm in western USA rangelands (Chu & Adler 2015). We used a slightly larger radius than this

198   in order to include more potential competitors, and to limit edge effects we excluded all

199   individuals within 5 cm of the quadrat border.

200

201   *Environmental conditions*

202   We analysed a variety of soil properties to select two uncorrelated soil properties that

203   reflect independent edaphic gradients (see Supplementary Information for detailed methods). We

204   selected sand content and soil C:N ratio because they were orthogonal variables that reflect

205   different aspects of the soil environment (Figure S3). Soil with high sand content were higher in

206   pH and tended to be warmer and drier than soil with low sand content. C:N ratio was orthogonal

207   to sand content, and soil with low C:N ratios have greater available nitrogen.

208   We computed average annual temperatures and total annual water-years using data

209   obtained from the National Climatic Data Center (www.ncdc.noaa.gov) for the Flagstaff,

210   Arizona region. Gaps in the data were supplemented with local weather stations. Water-years

211   were defined as the total precipitation that fell from October of previous year through September

212   of current year. We compared models to pre-select whether to use the current or previous year's

213   precipitation and temperature. Based on AIC, we chose the current year's temperature and the

214   previous year's water-year (hereafter, precipitation) because they were superior predictors of

215   plant survival (Table S3).

216

217   *Functional traits*

218   We used three functional traits thought to influence plant performance along gradients of

219   soil properties and climatic conditions: specific leaf area (SLA), specific root length (SRL), and

220   flowering phenology (see Supplementary Information for detailed methods). These traits loaded

221   on distinct axes of variation and so reflect different dimensions of plant function in this flora

222   (Laughlin *et al.* 2010). SLA reflects a trade-off between performance and persistence where

223   leaves with high SLA have short lifespans and high rates of gas exchange (Poorter *et al.* 2009).

224   Species with high SLA are thought to exhibit superior performance in soils that are rich in water

225   and mineral nutrients (Jager *et al.* 2015; Maire *et al.* 2015). SRL reflects the foraging potential of

226   the root per unit carbon investment. Species with high SRL are thought to be superior foragers

227   when soil nutrients, especially phosphorus, are limited because they are better able to proliferate

228   into nutrient-rich patches of soil (Laliberté *et al.* 2015). Flowering date reflects phenological

229   differences that may reflect tolerance of water limitation, where early flowering 'cool-season'

230   species tolerate cooler conditions and wetter soils, and late-flowering 'warm-season' species

231   tolerate warmer conditions and drier soils.

232

233   *Data analysis*

234   First, we computed quadrat-level CWM trait values, which represent the average value of

235   a given trait within a quadrat weighted by the relative abundance of each species. CWM traits

236   were calculated for each trait in each of the k quadrats as $CWM_k = \sum_{i=1}^{S} t_i p_{ik}$, where t_i is the

237   mean trait of species i, p_{ik} is the relative foliar cover of species i in plot k, and S is the number of

238   species in the plot. We computed CWM traits for each quadrat in each year, but these average

239   trait values did not change appreciably throughout the study period so we used the average

240   CWM for each quadrat across all years. We first fit multiple regression models that tested for

241   interaction effects between soil sand content and C:N ratio, but no interactions among soil

242   properties were detected ($P > 0.05$). We also tested for nonlinear relationships by including a

243   quadratic predictor variable, but there was no evidence of nonlinear relationships ($P > 0.05$).

244   Therefore, we illustrate the simple linear relationships in bivariate scatterplots.

245   Second, survival was modeled using a logit link function within a GLMM of the general

246   form:

$$247 \quad logit(survival) = \alpha + \gamma_{sp} + size\beta_{sp} + \delta_{quad} + \tau_{yr} + size\beta_1 + trait\beta_2 + CNratio\beta_3$$

$$248 \qquad\qquad + sand\beta_4 + precip\beta_5 + temp\beta_6 + intraCover\beta_7 + interCover\beta_8$$

$$249 \qquad\qquad + trait \times CNratio\ \beta_9 + trait \times sand\ \beta_{10} + trait \times precip\ \beta_{11}$$

$$250 \qquad\qquad + trait \times temp\ \beta_{12} + trait \times intraCover\ \beta_{13} + trait \times interCover\ \beta_{14}$$

251 To maintain model tractability, each model tested the effects of a single trait and its interactions;

252 we did not test for higher-ordered multi-trait interactions. This model included three random

253 effects, eight main effects (not including the global intercept α), and six interactions. We

254 modeled species as a random intercept (γ_{sp}) to account for species-level differences in survival

255 that were unrelated to the traits. These random species effects were allowed to exhibit random

256 slopes (β_{sp}) with respect to plant size because the effect of size on survival can differ among

257 species (Fig. S4). We modeled quadrats as random intercepts (δ_{quad}) to account for spatial

258 autocorrelation (Fig. S5) and we modeled years as random intercepts (τ_{yr}) to account for annual

259 variation in survival unrelated to inter-annual climate (Fig. S6).

260   Two conditions had to be satisfied in order for us to consider a trait-by-environment

261 interaction to be 'strong'. First, the interaction terms in the GLMM had to be statistically

262 significant ($\alpha = 0.05$). Second, the slope of the relationship between the trait and logit survival

263 must switch signs over the length of the environmental gradient (Fig. 1C). This was computed as

264 the first partial derivative of the fitted model (see Supplementary Information). We consider

265 statistically significant interactions as 'weak' if the slope of the trait – logit survival relationship

266 does not switch signs along the environmental gradient, or as 'strong' if the slope does switch

267 signs. This is important because 'strong' interactions indicate that there is a change in the rank

268 order of fitness across the gradient, which is required for there to be a predictable change in

269 CWM trait values across the gradient (Fig. 1).

270   We simultaneously accounted for other factors known to affect survival. We used foliar

271   plant cover of the individual to account for plant size. The previous year's precipitation and the

272   current year's temperature and their interactions with the trait of the focal plant were used to

273   account for climatic effects (Table S3). We partitioned the effects of local neighborhood

274   competition into four different effects. First, the cover of conspecifics accounts for the main

275   effect of intraspecific competition on focal plant survival. Second, the interaction between

276   conspecific cover and the trait of the focal plant accounts for how the trait mediates the effect of

277   intraspecific competition on the survival of the focal plant. Third, the cover of heterospecifics

278   accounts for the main effect of interspecific competition on focal plant survival, and fourth, we

279   account for the interaction between heterospecific cover and the trait of the focal plant (Kunstler

280   *et al.* 2016).

281   We used the 'glmer' function in the 'lme4' package in R to fit these models (Bates *et al.*

282   2015). We computed the marginal R^2 (hereafter, R^2_m, the proportion of variance explained by the

283   fixed effects) and the conditional R^2 (hereafter, R^2_c, the proportion of variance explained by both

284   fixed and random effects) using the 'piecewiseSEM' package in R (Lefcheck 2015).

285

286   **Results**

287   *Comparison of likelihood and vital-rates approaches*

288   CWM specific leaf area (SLA) was not related to either sand content ($R^2 < 0.01$, Fig. 2A)

289   or soil C:N ratio ($R^2 = 0.01$, Fig. 2D). In the survival analysis, the interaction between SLA and

290   sand content was not significant ($P = 0.11$, Table 1, Fig. 2B,C), so the vital rates approach agreed

291   with the likelihood approach with respect to SLA and sand content (outcome #1 in Table S1).

292   However, there was a significant interaction between SLA and soil C:N ratio (Fig. 2E, Table 1).

293   In high C:N ratio soil, survival was highest for species with low SLA and lowest for species with

294   high SLA. The slope of the relationship between SLA and logit survival switched from positive

295   to negative along the soil C:N ratio gradient (Fig. 2F); therefore, the vital rates and likelihood

296   approaches were inconsistent with respect to the effect of SLA on survival along a soil C:N ratio

297   gradient (outcome #2 in Table S1).

298   CWM specific root length (SRL) was positively related to sand content ($R^2 = 0.33$, Fig.

299   3A) and negatively related to soil C:N ratio ($R^2 = 0.11$, Fig. 3D). In the survival analysis, there

300   was a significant interaction between SRL and soil sand content, such that survival was highest

301   for species with low SRL in soil with low sand content (Fig. 3B, Table 1). However, the slope of

302   the relationship between SRL and logit survival did not switch from negative to positive across

303   the sand content gradient, indicating a relatively weak interaction (Fig. 3C); therefore, the

304   interpretations of the likelihood and vital rates results were in disagreement (outcome #3 in Table

305   S1). The interaction between SRL and soil C:N ratio was not significant (Fig. 3E, Table 1), also

306   conflicting with the results of the likelihood approach (outcome #3 in Table S1).

307   CWM flowering date was positively related to sand content ($R^2 = 0.21$, Fig. 4A) and

308   negatively related to soil C:N ratio ($R^2 = 0.10$, Fig. 4D). The survival analysis showed a

309   significant interaction between flowering date and sand content, such that survival was higher for

310   species with later flowering dates in sandy soil and lower for species with early flowering dates

311   in sandy soil (Fig. 4B, Table 1). The slope of the relationship between flowering date and logit

312   survival switched from negative to positive along the sand content gradient (Fig. 4C). Therefore,

313   with respect to flowering date and sand content, the likelihood and vital rates approaches were in

314   agreement (outcome #4 in Table S1). However, the interaction between flowering date and soil

315   C:N ratio was not significant (Figs. 4E, 4F, Table 1), conflicting with the results of the likelihood

316   approach (outcome #3 in Table S1).

317

318   *Other factors affecting survival*

319   No trait exhibited significant main effects on survival (Table 1, Fig. 5A,D,G). In other

320   words, the effects of traits on survival always depended on the abiotic and biotic context. SLA of

321   the focal plant interacted with intraspecific cover, such that species with low SLA had higher

322   survival where neighborhood competition with conspecifics was low and species with high SLA

323   exhibited higher survival where cover of conspecifics was high (Fig. 5B). SLA weakly interacted

324   with temperature and precipitation, such that species with low SLA had the highest survival in

325   cold and dry years (Fig. 5C,D). SRL did not interact with intraspecific cover (Fig. 5F). SRL

326   weakly interacted with temperature and precipitation such that low SRL was associated with

327   higher survival at low temperatures (Fig. 5G) and high precipitation in the previous year (Fig.

328   5H). Flowering date interacted weakly with intraspecific cover (Fig. 5J), but interacted strongly

329   with inter-annual climate. Survival was highest for species with late flowering dates in hot years

330   with dry previous years, whereas survival was highest for species with early flowering dates in

331   cool years with wet previous years (Fig. 5K,L).

332   Among all the trait-independent main effects, focal plant size was the most important

333   predictor of survival (Table 1). Large plants exhibited significantly higher survival probabilities

334   (Fig. S7A) and this size-dependence differed among species (Fig. S4). Intraspecific and

335   interspecific cover of the local neighborhood surrounding the focal plants were each negatively

336   related to survival, but intraspecific cover exhibited the stronger effect (Fig. S7B,C). Neither

337   precipitation in the previous year nor temperature of the current year were significantly related to

338   survival (Fig. S7D,E). Sand content was negatively related to survival and soil C:N content was

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339   positively related to survival (Fig. S7F,G).

340   The fixed effects in the survival models explained approximately 16% of total variation

341   in survival ($R^2_m = 0.16$), leaving approximately 26% of the variation accounted for by the

342   random effects ($R^2_c = 0.42$). Random species effects (standard deviation [SD] for the random

343   intercept = 0.97) accounted for more variation than random quadrat effects (SD for the random

344   intercept = 0.12) or random year effects (SD for the random intercept = 0.36) (Figs. S4, S5, S6).

345

346   **Discussion**

347   By synthesizing data on long-term demographic rates and functional traits across a strong

348   gradient in soil properties, we conducted a rigorous test of the assumption that CWM trait-

349   environment correlations are accurate reflections of the adaptive value of traits. After accounting

350   for focal plant size, climatic effects, and local neighborhood competitive interactions (Chu &

351   Adler 2015; Kraft *et al.* 2015a), we have shown that the effects of traits on survival depends on

352   the environmental conditions. However, we observed inconsistencies between the likelihood and

353   vital rates approaches (Laughlin & Messier 2015), contradicting the hypothesis that CWM trait-

354   environment correlations are generated by trait-by-environment interactions affecting survival. If

355   the likelihood and vital rates approaches were consistent, then we should have only observed

356   outcomes #1 and #4 as listed in Table S1, but we observed all four possible outcomes. We

357   conclude that CWM trait-environment correlations are unreliable estimates of how traits mediate

358   survival probabilities across environmental gradients. CWM traits are often used to estimate

359   optimum trait values, but processes such as environmental change, disturbance, and dispersal

360   limitation can shift CWM traits from an optimum value. Linking vital rates to trait-by-

361   environment interactions will advance our understanding of trait-based habitat filtering and will

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362   improve our ability to accurately predict how species and communities respond to environmental

363   gradients.

364   No trait exhibited independent main effects on survival because the adaptive value of

365   traits depended on the environmental context. For example, variation in SLA is underpinned by a

366   physiological trade-off between metabolic rate and leaf longevity (Poorter *et al.* 2009). The vital

367   rates analysis supported the prediction from leaf economics theory that conservative phenotypes

368   would have high survival in resource-poor environments (Maire *et al.* 2015): species with low

369   SLA had higher survival in high C:N ratio soil and species with high SLA had higher survival in

370   low C:N ratio soil (Fig. 2F). However, the likelihood approach failed to detect the positive effect

371   of low SLA on survival in high C:N ratio soil because there was no correlation between CWM

372   SLA and soil C:N ratio. This suggests that other unmeasured factors, such as grazing or other

373   disturbances (Strahan *et al.* 2015) or dispersal limitation (Ozinga *et al.* 2005), have shifted the

374   CWM trait values in each plot away from any optimal value (Table S1). In other words, a CWM

375   trait-environment correlation is the result of multiple processes, and we urge caution when

376   interpreting these correlations as evidence for the adaptive value of a trait in the absence of a

377   known physiological trade-off that can explain the correlation.

378   The predictive power of the survival models was limited (marginal $R^2 < 0.20$), suggesting

379   that other drivers of survival were missing from the models. The empirical interaction effects

380   were rarely as strong as theoretical expectations (Fig. 1), and many significant interaction terms

381   were not considered to be 'strong' because the slope of the trait and logit survival relationship

382   did not switch signs along the length of the environmental gradient. The predictive power of

383   these models could be low because survival is influenced by complex trait combinations

384   expressed at the level of the whole phenotype. For example, low SRL may confer higher survival

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385   in low sand content soil, but high SRL leads to low survival probabilities across the entire sand

386   content gradient (Fig. 3); however, species with high SRL might exhibit higher probabilities of

387   survival in sandy soil if they also exhibit later flowering times (Fig. 4). Explicit tests of the

388   effects of multiple trait combinations via higher-ordered trait-by-trait-by-environment

389   interactions is an important next step toward understanding the effects of whole-organism

390   phenotypes on fitness; however, expanding models to higher-ordered interactions will

391   exponentially increase the number of model parameters and will require sufficient data for

392   accurate estimation.

393   Discrepancies between the likelihood and vital rates may occur if a trait is influencing

394   another fitness component other than survival. There was surprisingly no detectable interaction

395   between SRL and soil C:N ratio despite the CWM trait-environment correlation between these

396   two variables. Similarly, there was no detectable flowering date-by-soil C:N ratio interaction

397   despite the CWM trait-environment correlation between these two variables. These discrepancies

398   could possibly be explained if SRL and flowering date were influencing growth rates or

399   reproduction (Table S1). For example, SRL is positively related to relative growth rate (Comas

400   & Eissenstat 2004; Kramer-Walter *et al.* 2016), and phenological differences among species

401   could affect reproductive success in changing climates (Galen & Stanton 1991; Cleland *et al.*

402   2007).

403   Temporal dynamics in these communities were driven by two main factors: local

404   competitive interactions and inter-annual climatic variability. Intraspecific competitive effects on

405   focal plant survival was much stronger than interspecific competitive effects on survival because

406   survival probability approached zero in the presence of high abundances of the same species

407   (Fig. S7B). The traits of the focal plant moderated the effects of competition on survival. For

408   example, herbaceous plant species with high SLA had higher survival when competition with

409   conspecifics was high, whereas species with low SLA had higher survival in the absence of

410   competition. This suggests that productive phenotypes are winners when competition with

411   conspecifics is most fierce.

412   Inter-annual variation in temperature and precipitation also influenced plant survival, but

413   phenological differences moderated these survival responses. Specifically, species with later

414   flowering dates, which tend to be affiliated with a warm-season strategy or the C_4 photosynthetic

415   pathway (Laughlin *et al.* 2010), had higher survival than species with early flowering dates

416   following drought years. Late flowering species had higher survival in hot years and early

417   flowering species had higher survival in cool years, suggesting that quantitative traits can be

418   used to forecast how species and communities will respond to inter-annual climatic variation and

419   changing climate (Anderegg *et al.* 2016). Inter-annual climatic variation has been shown to have

420   a stabilizing effect on species coexistence (Adler *et al.* 2006), and phenotypic traits provide a

421   generalizable predictor of how species respond to yearly climatic variation.

422   It could be argued that CWM trait-environment relationships are better metrics of

423   adaptation than demographic rates because they are the integrated sum of many vital rates over a

424   longer period of time. Moreover, CWM traits implicitly include the effects of species

425   interactions and other unmeasured processes. In contrast, survival probability and other fitness

426   components may be sensitive to factors such as disturbance that vary stochastically over time and

427   space. For this and other practical reasons, the likelihood approach will likely remain a useful

428   tool for generating predictions about species and community distributions in an era of global

429   change. CWM traits also have clearer effects on ecosystem processes. However, if we assume

430   that a CWM trait-environment relationship reflects the adaptive value of a trait in the absence of

431 a known physiological trade-off, this could lead to incorrect predictions of responses for other

432 species in different ecosystems. In other words, correlative patterns will most successfully be

433 used to make general predictions if the correlation is underpinned by an evolutionary tradeoff

434 driven by a physiological mechanism that influences vital rates.

435 Community-weighted mean traits are easy to compute but difficult to interpret. We hope

436 that our results motivate others to undertake the challenging task of quantifying how the effect of

437 traits on individual and population-level fitness depends on the environmental context. A

438 phenotype may be dominant because of higher survival, growth, and/or reproduction (Adler *et al.*

439 2014), so if a trait affects survival differently than it affects growth rates or reproduction (Visser

440 *et al.* 2016), then effects on lifelong fitness are obscured. Future work that estimates the effects

441 of multiple trait combinations on total fitness, by integrating all vital rates to estimate

442 population-level growth rates (λ) using Integral Projection Models, may provide much-needed

443 insight into how phenotypes affect fitness across environmental gradients.

444

445 **Acknowledgements**

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631 **Table 1.** GLMM standardized coefficients and their significance, and model fit statistics for each

632 of the three trait-based models. Significant terms are in bold.

| Term	Specific leaf area		Specific root length		Flowering date	
	Coefficient	*P*-value	Coefficient	*P*-value	Coefficient	*P*-value
Intercept	-0.472	0.0640	**-0.600**	**0.0206**	**-0.513**	**0.0404**
Trait	-0.202	0.2015	-0.213	0.1092	0.066	0.6857
Precipitation (previous year)	-0.014	0.9430	-0.006	0.9734	-0.001	0.9956
Temperature (current year)	0.013	0.9459	0.007	0.9713	-0.011	0.9540
Sand content	**-0.195**	**<0.0001**	**-0.220**	**<0.0001**	**-0.184**	**<0.0001**
Soil C:N ratio	**0.097**	**0.0351**	**0.123**	**0.0101**	**0.131**	**0.0067**
Local intraspecific cover	**-0.502**	**<0.0001**	**-0.469**	**<0.0001**	**-0.458**	**<0.0001**
Local interspecific cover	**-0.107**	**<0.0001**	**-0.104**	**<0.0001**	**-0.100**	**<0.0001**
Focal plant size	**0.777**	**<0.0001**	**0.813**	**<0.0001**	**0.816**	**<0.0001**
Trait × Precipitation	**0.040**	**0.0031**	**-0.095**	**<0.0001**	**-0.087**	**<0.0001**
Trait × Temperature	**0.048**	**0.0009**	**0.056**	**<0.0001**	**0.114**	**<0.0001**
Trait × Sand content	-0.029	0.1381	**0.086**	**<0.0001**	**0.085**	**<0.0001**
Trait × Soil C:N ratio	**-0.079**	**<0.0001**	-0.036	0.0586	0.015	0.3698
Trait × Intraspecific cover	**0.146**	**<0.0001**	-0.037	0.0516	**0.068**	**0.0001**
Trait × Interspecific cover	**-0.033**	**0.0208**	**-0.068**	**0.0001**	-0.025	0.0974
Model fit statistics						
$R^2_{marginal}$	0.166		0.164		0.161	
$R^2_{conditional}$	0.428		0.422		0.423	

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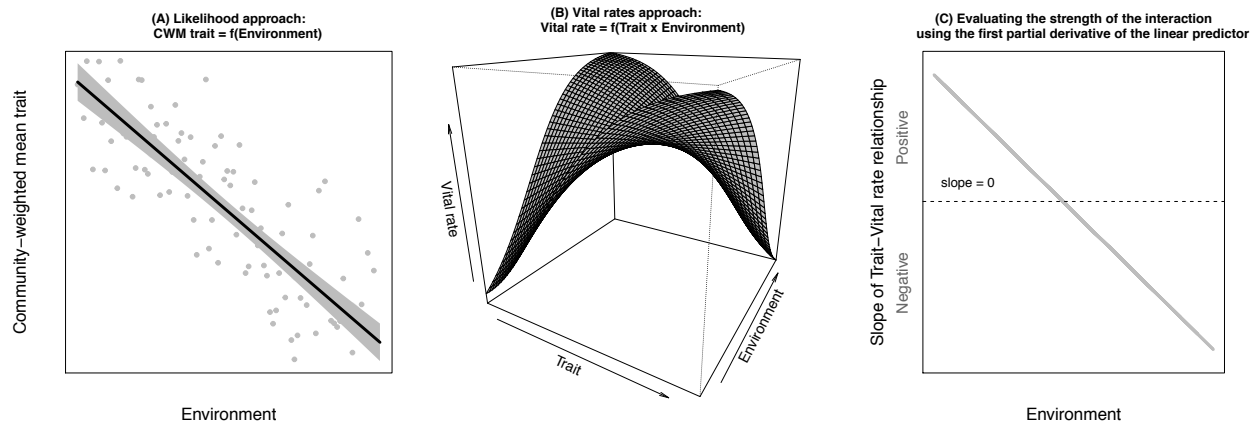
Figure 1. (A) The 'likelihood' approach assesses the correlation between community-weighted

mean (CWM) traits and environmental gradients. (B) The 'vital rates' approach models fitness

components, *i.e.*, vital rates such as survival and growth rate, directly as functions of species-

level trait-by-environment interactions. If the likelihood approach is an accurate assessment of

the adaptive value of traits, then fitness components must be functions of trait-by-environment

interactions. For example, (A) if a CWM trait is negatively correlated with an environmental

gradient, then (B) high values of that trait will only confer high fitness at the low end of the

environmental gradient, leading to an observed interaction between the trait and environment

that affects fitness. The presence of a saddle in panel B at intermediate trait values denotes a

switch in sign of the slope of the trait-vital rate relationship; see the discussion in Supplementary

Information and Fig. S1 for details. (C) The strength of the linear interaction can be assessed by

viewing how the sign of the slope of the trait-vital rate relationship, i.e. the first partial derivative

($\partial / \partial T$) of the model, changes along the environmental gradient. In this theoretical example, the

slope switches from positive to negative along the environmental gradient; note how it is

consistent with the sign of the slope in panel A.

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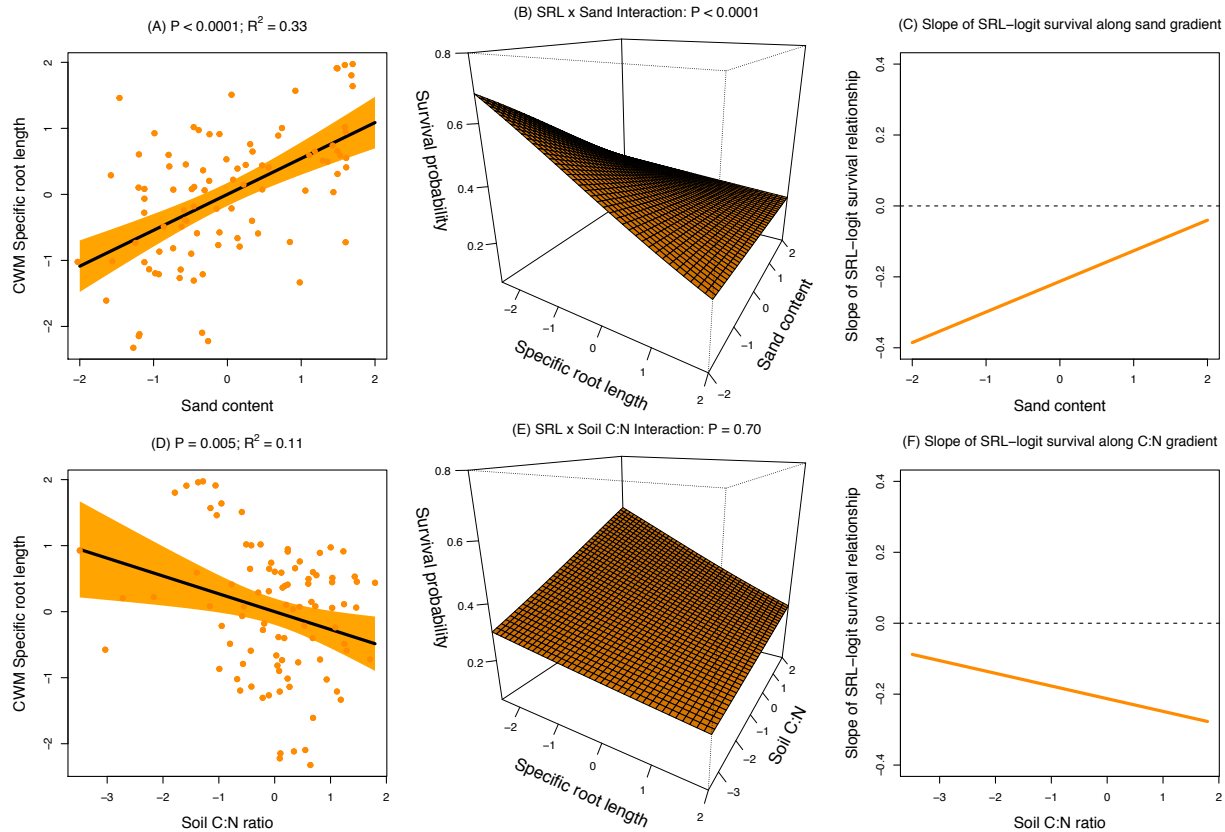
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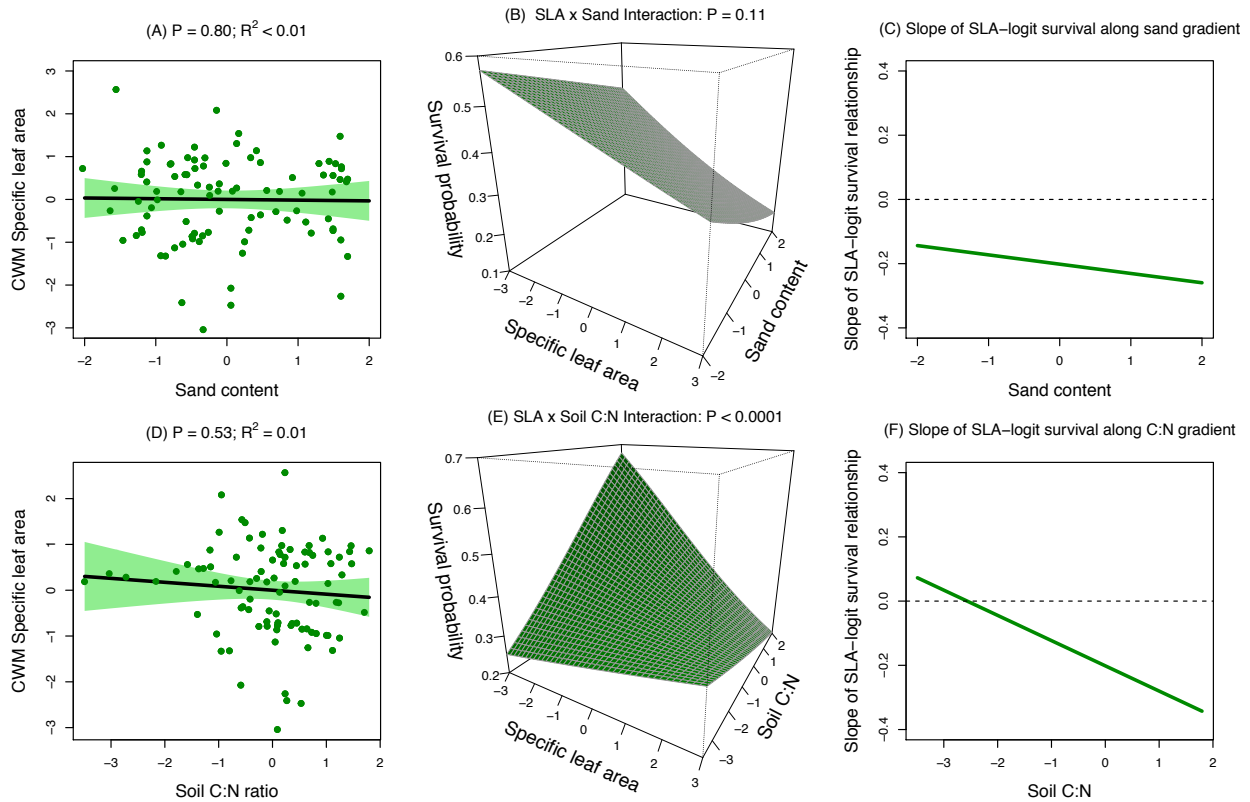
Figure 2. Comparison of likelihood and vital rates approaches for examining the adaptive value

of specific leaf area (SLA) along two soil property gradients. The first column illustrates the

results of the likelihood approach, where community-weighted mean (CWM) SLA was regressed

on each soil property across the 89 quadrats (A, D). The second column illustrates the results of

the vital rates approach, where the GLMM fitted predictions of survival probability (curved

surfaces) illustrate the interactions between the trait and each soil property (B, E). The third

column illustrates how the slope of the trait-logit survival relationship changes along each soil

property gradient, and the dotted line indicates a slope of zero (C, F). All variables have been

scaled to unit variance.

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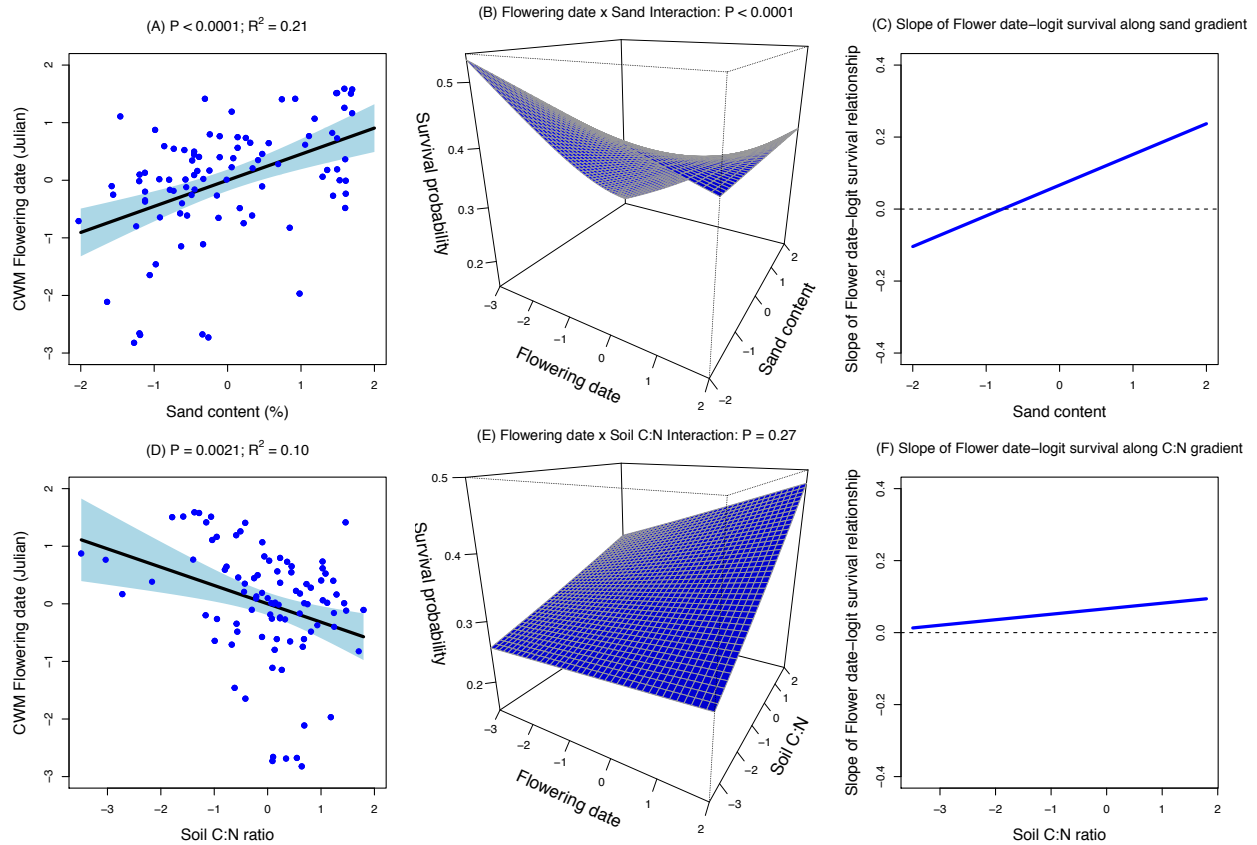
Figure 3. Comparison of likelihood and vital rates approaches for examining the adaptive value of specific root length (SRL) along two soil property gradients. The first column illustrates the results of the likelihood approach, where community-weighted mean (CWM) SRL was regressed on each soil property across the 89 quadrats (A, D). The second column illustrates the results of the vital rates approach, where the GLMM fitted predictions of survival probability (curved surfaces) illustrate the interactions between the trait and each soil property (B, E). The third column illustrates how the slope of the trait-logit survival relationship changes along each soil property gradient, and the dotted line indicates a slope of zero (C, F). All variables have been scaled to unit variance.

Figure 4. Comparison of likelihood and vital rates approaches for examining the adaptive value of flowering date along two soil property gradients. The first column illustrates the results of the likelihood approach, where community-weighted mean (CWM) flowering date was regressed on each soil property across the 89 quadrats (A, D). The second column illustrates the results of the vital rates approach, where the GLMM fitted predictions of survival probability (curved surfaces) illustrate the interaction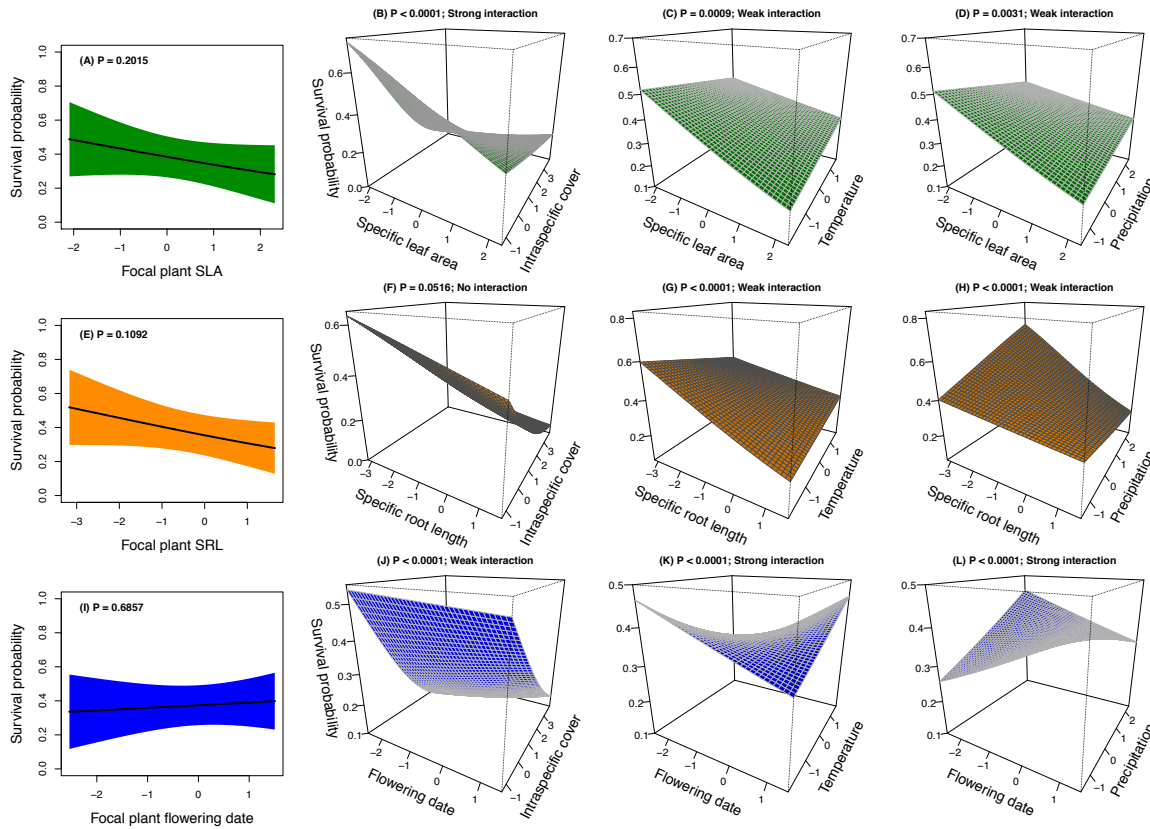s between the trait and each soil property (B, E). The third column illustrates how the slope of the trait-logit survival relationship changes along each soil property gradient, and the dotted line indicates a slope of zero (C, F). All variables have been scaled to unit variance.

Figure 5. Main effects of the focal plant trait (first column on left) and trait-by-environment interaction effects (three columns on right) estimated in the GLMMs. For the non-significant main effects, lines represent model fitted predictions and shading represents 95% confidence intervals. For the interaction effects, curved surfaces represent the GLMM predictions as functions of the interactions between each trait and environmental variable. The *P*-values indicate the significance of the interaction terms; 'weak' interactions did not exhibit trait – logit survival relationships that switched signs along the length of the environmental gradient, whereas 'strong' interactions exhibited trait – logit survival relationships that switched signs. All variables have been scaled to unit variance.