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Multidimensional ecological analyses demonstrate how interactions between functional traits shape fitness and life history strategies

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Abstract

1. Traditionally, trait-based studies have explored single-trait-fitness relationships. However, this approximation in the study of fitness components is often too simplistic, given that fitness is determined by the interplay of multiple traits, which could even lead to multiple functional strategies with comparable fitness (i.e. alternative designs).
2. Here we suggest that an analytical framework using boosted regression trees (BRT) can prove more informative to test hypotheses on trait combinations compared to standard linear models. We use two published datasets for comparisons: a botanical garden dataset with 557 plant species (Herben, 2012, *Journal of Ecology*, *100*, 1522) and an observational dataset with 83 plant species (Adler, 2014, *Proceedings of the National Academy of Sciences*, *111*, 740).
3. Using the observational dataset, we found that BRTs predict the role of traits on the relative importance of survival, growth and reproduction for population growth rate better than linear models do. Moreover, we split species cultivated in different habitats within the botanical garden and observed that seed and vegetative reproduction depended on trait combinations in most habitats. Our analyses suggest that, while not all traits impact fitness components to the same degree, it is crucial to consider traits that represent different ecological dimensions.
4. *Synthesis*. The analysis of trait combinations, and corresponding alternative designs via BRTs, represent a promising approach for understanding and managing functional changes in vegetation composition through measurement of suites of relatively easily measurable traits.

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*Roberto Salguero-Gómez and Carlos P. Carmona shared senior co-authorship.

KEYWORDS
alternative design, boosted regression tree (BRT), elasticity, fitness, functional trait, population growth rate, trade-off, vegetative reproduction

1 | INTRODUCTION

Trait-based approaches are extensively used in ecology to examine species interactions (Kunstler et al., 2016; Schöb, Macek, Pistón, Kikvidze, & Pugnaire, 2017) and species response to environmental change (Cornwell & Ackerly, 2009; Kimball et al., 2016). However, although the link between traits and fitness is essential for the definition of *functional* traits (Violle et al., 2007; Salguero-Gómez, Violle, Gimenez, & Childs, 2018), evidence linking traits and fitness proxies remains scarce (but see Adler et al., 2014; Martínez-Vilalta, Mencuccini, Vayreda, & Retana, 2010; Poorter et al., 2008; Shipley et al., 2016; Visser et al., 2016).

One possible reason for the limited evidence is that most studies examining trait-fitness relationships consider individual traits (Adler et al., 2014; Marks, 2007). These analytical strategies contrast with the fact that fitness is determined by the integrated phenotype (Laughlin & Messier, 2015). Approximations such as ordination axes that do not explicitly account for interactive effects between traits (de Bello, Lepš, & Sebastià, 2005), are also not a satisfactory solution since the effects of traits can also be non-additive. Either by additive or non-additive effects, it is likely that the interplay of multiple traits could lead to single or multiple performance peaks with comparable fitness, the latter called *alternative designs*. Alternative designs are recognised as an important mechanism behind the evolution and maintenance of trait diversity (Marks & Lechowicz, 2006) and are expected within and across biological communities (e.g. Pivovaroff et al., 2016; Valladares, Skillman, & Pearcy, 2002). Considering multiple traits from different ecological dimensions (Laughlin, 2014) can help us to uncover the relationship between traits and fitness components, and to examine the existence of single optima (i.e. a single performance peak) versus alternative designs. However, open questions still remain on how to explore alternative designs and whether they could improve the predictability of trait-fitness relationships within an environment.

Considering multiple dimensions of plant traits (e.g. in leaf traits, stem traits, seed traits, etc; Díaz et al., 2016; Wright et al., 2004) is essential for exploring the relationship between the environment, traits and fitness (Marks & Lechowicz, 2006) and to predict community assembly (Laughlin, 2014) or life history evolution (Salguero-Gómez et al., 2018). This task, however, is not a straightforward one. A current advantage that allows robust conclusions is the increased availability of trait data in databases (e.g. Cordlandwehr et al., 2013; Kazakou et al., 2014). Moreover, linear regression models have been the most common approach so far (Adler et al., 2014; but see Kleyer et al., 2012). Linear models, however, are limited when exploring the complex effects of multiple traits on fitness, arising from their lack of flexibility in dealing with incomplete datasets or nonlinear responses among predictors. Recently, alternative methods that address this complexity have been suggested (Carmona, Bello, Mason, & Lepš, 2016; Laughlin & Messier, 2015). Among these, regression trees are a useful tool to account for interactions among different traits (de Bello et al., 2005) although they tend to have low predictive performance (Schulz, Cayuela, Rey-Benayas, & Schröder, 2011). Boosted regression trees methods (BRT; Friedman, Hastie, & Tibshirani, 2000, Elith, Leathwick, & Hastie, 2008) solve this problem by combining a large number of regression trees added together in sequence. This confers several advantages such as automatically accounting for nonlinearities, including interactions according to the size of trees used (Elith et al., 2006), which traditional regression models do not. BRTs also fit all possible combinations of exploratory variables, allowing for the potential to generate hypotheses on trait combinations.

Here, we propose the use of BRTs to include interactions between traits when examining trait-fitness relationships. To show the possible advantages of this approach, we reanalysed two published datasets to answer two questions: (a) does considering interactions between traits by using BRTs result in a higher predictive ability as compared to linear models? and (b) can one use BRTs to identify distinct combinations of traits that result in similar fitness (i.e. alternative designs)? To that end, first, we compared the ability of BRTs with linear models to predict the full life cycle of a species reanalysing data from Adler et al. (2014). Second, we used a dataset with species cultivated in different habitats within a botanical garden (Herben, Nováková, Klimešová, & Hrouda, 2012) to test whether functional alternative designs play a key role in shaping fitness components within a given habitat. We chose these datasets because they are key references in this field of research, include a high number of species and, despite that they might not be ideal to characterise trait-fitness relationship, they can serve as a clear benchmark for comparing new approaches. Although we focus on plants because trait and fitness information is currently much more extensive in this kingdom (Hortal et al., 2015), we highlight how our proposed framework can span to other taxa.

2 | MATERIALS AND METHODS

Data were obtained from two published studies: Adler et al. (2014) and Herben et al. (2012), which collectively used information from the COMPADRE Plant Matrix Database (Salguero-Gómez et al., 2015), TRY (Kattge et al., 2011), LEDA (Kleyer et al., 2008), CLO-PLA3 (Klimešová, Danihelka, Chrtek, Bello, & Herben, 2017) and Herben, Suda, and Klimešová (2017).

2.1 | Comparing BRT versus linear models

Adler et al. (2014) used five traits describing the anatomy and physiology, and calculated elasticities of three vital rates (survival, growth and reproduction) of 222 plant species worldwide. They used elasticities, which express the effect that a relative change in a given vital rate would have on population growth rate (de Kroon, Plaisier, Groenendael, & Caswell, 1986). Elasticities are often used in ecology and conservation to interpret the demographic processes that are most important to the performance of a population (Caswell, 2001; de Kroon, Groenendael, & Ehrlén, 2000). The authors obtained the demographic information from matrix population models available in the COMPADRE Plant Matrix Database v. 3.0.0 (Salguero-Gómez et al., 2015). Elasticities were calculated per species by an arithmetic element-by-element average of the matrix population models available for each population per species, a standard procedure in comparative demography (Salguero-Gómez et al., 2016; Silvertown & Franco, 1993). Information on leaf lifespan, leaf N, specific leaf area (SLA), seed mass and wood density was obtained from the TRY database (Kattge et al., 2011; references for the original sources of TRY data used in Adler et al., 2014 are included in the Supporting Information). The overlap between TRY and COMPADRE spanned a global range of biomes (i.e. artic, desert, temperate forest, temperate grassland, tropical forest and tropical savannah) and growth forms (i.e. perennial herbs, palms, shrubs, succulents and trees). The trait data corresponded to mean values for each trait for each species, after duplicated sources information and outliers (>3 *SD* from mean) had been discarded.

Because not all traits were available for all species, we excluded species with information for fewer than two traits. Leaf lifespan and wood density were excluded altogether because information for them was lacking for a high proportion of species, and, unlike BRT models, linear models cannot handle missing observations. These criteria resulted in 80, 83 and 83 plant species for reproduction, survival and growth, respectively. To evaluate the ability of functional traits to explain variation across vital rate elasticities, we fitted a separate model for each of the three elasticities for a total of six models (three linear and three BRT models; see "Analysis" section below). Vital rate elasticities were logit-transformed prior to modelling, whereas traits were log-transformed. An extended summary including range and number of predictors per species is shown in Table S1 in Appendix S1.

2.2 | Traits as predictors of reproductive output

Herben et al. (2012) used data for 951 species from the collection of native plants of central European Flora, growing in the botanical garden of the Faculty of Science in Prague (http://www.bz-uk.cz; see also Herben et al., 2017). Since each species was grown under abiotic conditions that resembled their natural habitats, reproduction in the garden should resemble that of the plants in their natural settings. These habitats comprised (a) shaded and (b) open calcareous steppes, (c) meadow habitat, (d) oak forest habitat, (e) sandy habitat and (f) wet and humid habitat along a stream. Traits for these species were collected from the LEDA (Kleyer et al., 2008) and CLO-PLA3 databases (Klimešová et al., 2017). Selected aboveground traits were total leaf area, maximum mature height, SLA and seed mass, while vegetative bud banks traits were bud bank size and depth (i.e. all inactive buds that can give rise to new shoots located on the soil surface or belowground), and traits of clonal growth were clonal multiplication, lateral spread, life history, shoot lifespan and persistence of connections between ramets (Table S2).

As a proxy for demographic processes, the authors used spontaneous seed and vegetative reproduction, assessing the number of times the new offspring had to be thinned by local gardeners (data on seed and vegetative reproduction in Herben et al., 2017). To measure seed and vegetative reproduction, scores were assigned using the same ordinal scale across species that were growing in the garden for at least 10 years. Scores ranged from 1 to 5 with the lowest for species that did not reproduce in the garden and the highest for those that multiplied spontaneously and had to be thinned more than once per year (Table 1 in Herben et al., 2012). For an extended description of the methods see Methods S1. This approach to define fitness components can have limitations because (a) growth and multiplication records are not fully quantitative, and (b) it comes with lower control of environmental conditions than in a designed experiment. Nonetheless, it allows comparison across many species in different habitats rendering such dataset valuable for the present study. We fitted separate BRT models for each habitat to study the effect of trait interactions on different reproductive outputs: seed (*n* = 538 species) and vegetative (*n* = 556 species; Table S3).

2.3 | Analysis

We fitted BRT models to analyse the effect of the considered traits and their interactions on each fitness component (for the observational dataset) or reproductive output (botanical garden dataset). We fitted these models using the function *gbm.step* in the *dismo* package (Hijmans, Phillips, Leathwick, & Elith, 2017) in R v3.1.1. In order to calibrate the models, we first adjusted the model parameters, which included (a) the learning rate (*lr*, determining the contribution of each tree to the growing model. A slower learning rate, that is, small value of *lr*, increases the number of trees required and reduces the amount by which the individual initial trees contribute to the final model; Elith et al., 2008), (b) bag fraction, which controls the proportion of the data that is randomly chosen to train each new tree. This parameter introduces stochasticity and improves the predictive performance by reducing the variance of the final model. Therefore, final models will be slightly different each time they are run. The default is bag fraction 0.5, which means that at each iteration, 50% of the data are drawn at random, without replacement, from the full training set; Elith et al., 2008), and (c) step size, the number of trees to add at each cycle of the boosting algorithm, while we fixed (d) tree complexity at 15 (*tc* controls the maximum level of interactions that can be achieved, see below for further explanations). We selected the combination of these parameters that yielded the highest explained deviance based on a minimum of 1,000 trees, following Elith et al. (2008). Further step-by-step details on the BRT method can be found in Appendix S2.

Once learning rate, bag fraction and step size were selected, we quantified improvements in BRT model predictive ability as more complex interactions were added by running models with increasing tree complexity. For each model, we used values of *tc* ranging between 1 (where there is only one split in the tree, and no interactions between studied traits), to 15 (which means that the trees include several splitting rules allowing for highly complex interactions among traits). This procedure is described in depth in Tables S4 and S5 and Appendix S2. To provide confidence intervals of our model predictions, we simulated 100 trees for each model and *tc* value. We estimated the predictive capacity via R^2 of each of these models, as well as the relative influence of each predictor on each response variable. Afterwards, the 100 values of each combination of response variable and *tc* value were averaged in order to have an estimation of R^2 mean and variability, and the relative influence of variables (Carmona, Röder, Azcárate, & Peco, 2013). In order to select an optimum *tc* value, we fitted ANOVAs with R^2 as response variable and *tc* values as explanatory variable and performed a Tukey test. We selected the lowest *tc* value that did not show significant differences compared to the largest *tc* value, indicating that model performance had reached a plateau.

We used the observational dataset to compare the performance of BRT versus linear models for predicting each of the three vital rate elasticities. To do so, we performed models for survival, growth and reproduction separately. A great deal of environmental heterogeneity exists both in COMPADRE and TRY, and most trait and vital rate data for a given species come from multiple populations, making estimations of trait-fitness relationships unreliable for biological interpretations of within-environments species differentiations (considering that fitness landscapes change with environment; Laughlin & Messier, 2015, Salguero-Gómez et al., 2018). However, environmental heterogeneity is non-central to our first goal: to use these data to perform a methodological test, comparing the predictive abilities of both methods.

In the case of BRTs, for each of the three vital rate elasticities, we selected the model parameters using the procedure described above (Table S4 for details). Once the models were fitted, we estimated their predictions for all the species in the dataset. For linear models, we fitted a saturated model (considering the number of observations) for each vital rate elasticity. This model included the simple effects of the traits, their pairwise interactions and the quadratic terms of the traits as predictors. We used the *dredge* function (Barton, 2018) to evaluate all potential simpler models nested within the saturated one, and calculated the AIC of each model. From the AIC-ranked models, we selected the subset of models within five AIC points of the most parsimonious one and averaged their predicted values, giving more weight to the predictions of the most plausible models as per their AIC weights. This way, for each vital rate elasticity, we attained two predicted values for each species: one given by the BRT approach, and one by the linear model approach. Finally, we compared BRTs and linear models using Pearson correlation coefficients between the observed and predicted values. Models with a high correlation between observed and predicted values have higher predictive ability than models with a low correlation.

To explain the role of functional traits as determinants of reproductive outputs (botanical garden dataset), we fitted a BRT model for each combination of reproductive output and habitat. For each of these models we inspected R^2 mean values as well as the 95% CIs for each *tc* to examine whether the explanatory capacity of the models improves as the tree complexity was increased (see above). BRT models also report the relative influence of the different predictors, which is an indicator of their contribution in reducing overall model deviance. We calculated the relative influence of each predictor as the mean of the influences of the 100 simulations for the selected *tc* optimum value. We used *tc* optimum values and the function *gbm.interactions* to test whether interactions were detected and modelled, and for reporting the interaction magnitude of each pair of predictors.

This function forms predictions for each considered pair of predictors while setting the rest of the variables to their means (Elith et al., 2008). This function creates, for each possible pair of predictors, a temporary grid of variables representing combinations of values at fixed intervals along each of their ranges. Then, it uses a linear model to relate the predictions to the two marginal predictors, fitting them as factors. The residual variance in this linear model indicates the relative strength of each interaction (Elith et al., 2008). We represented these interactions plotting changes in reproductive outputs across the phenotypic space using partial dependence plots (function *gbm.perspective*) for each reproductive output and habitat combination.

In addition, for plants of each habitat in the botanical garden, we checked if phylogenetic relatedness influenced our results due to species' common ancestry. We accounted for phylogeny by using residuals from regression models where the response variables, the reproductive outputs, were regressed on the axes of a Principal Coordinates Analysis (PCoA) of a species pairwise cophenetic distance matrix (a method equivalent to the first step in phylogenetic eigenvector regression; Diniz-Filho, Sant'Ana, & Bini, 1998). The obtained phylogenetic residuals for that model were used as a new response variable in BRT models estimates, following the same modelling process explained above. While it would be preferable to directly include phylogeny into the BRT models, to our knowledge, this is not possible with this kind of regression models, and it represents an advancement that falls beyond the scope of this manuscript. For an extended description of the methods see Methods S2 in Appendix S1.

All statistical analyses were conducted in R v3.1.1 using the *dismo* (Hijmans et al., 2017) and *multcomp* packages (Hothorn, Bretz, & Westfall, 2017).

3 | RESULTS

3.1 | BRTs versus linear models

BRT models systematically predicted trait-fitness relationships better than linear models for the elasticities of population growth rate to reproduction, survival and to growth (Figure 1). The correlations between predicted versus observed values were 36.11%, 25.00% and 22.67% greater for BRT models than linear models for reproduction, survival and growth, respectively. The results of the selection of linear models are in Table S6 in Appendix S1.

3.2 | Traits as predictors of reproductive outputs

For each habitat within the botanical garden, we quantified the improvement in model predictive abilities as interactions between traits were added. A lower degree of complexity of interactions among traits was necessary to predict seed reproduction compared to vegetative reproduction. In three out of five habitats, BRT models predicted seed reproduction without interactions among trait predictors (model predictive ability stabilised at *tc* = 1), while vegetative reproduction was better predicted by models including trait interactions, with the exception of the sandy habitat (Table S7). Regardless of the habitat, the proportion of variance explained for seed reproduction (from ~0.1 to ~0.4) was lower than that explained for vegetative reproduction (ranging between ~0.2 and ~0.7; Figure 2). The highest proportion of variance explained corresponded to the meadow habitat (~0.4 and ~0.7 for seed and vegetative reproductions, respectively), while the shaded calcareous steppe showed the lowest (~0.1 and ~0.2). We only found a relatively strong phylogenetic signal for vegetative reproduction in the open calcareous steppe (Table 1). After accounting for phylogeny in the analysis of this habitat, the proportion of explained variance in vegetative reproduction increased from 30% to 40%.

Belowground bud banks and traits of clonal growth were important predictors regardless of the type of reproduction output. Seed reproduction decreased abruptly with high lateral spread (LS) and small seed mass values (relative influences of ~30% and 20% in the meadow, respectively). However, in the wet habitats seed reproduction decreased abruptly with high seed mass (relative influence ~20%; Figure 3 and Figure S1a). In the habitats where seed reproduction was better predicted by single traits, the most important traits varied depending on the habitat. In general, vegetative reproduction sharply increased with high LS for all habitats where trait interactions were important (relative influence ~40%) with the exception of the sandy habitat (LS with a relative influence ~0%), where the bud bank size was the most important predictor (Figure 4). In the case of the open calcareous steppe, and accounting for phylogenetic relationships, vegetative reproduction increased with large bud bank size and LS (both with relative influence ~30%) and decreased with SLA (relative influence ~10%; Figures S1b and S2). Persistence of connections between mother and daughter shoots, the number of offspring per parent shoot and life history were consistently among the less important traits influencing both seed and vegetative reproduction. The results of the magnitude of the pairwise interactions among predictors for seed and vegetative reproduction are in Tables S8 and S9.

Finally, we found functional alternative designs that yielded equivalent vegetative reproduction values only in the meadow

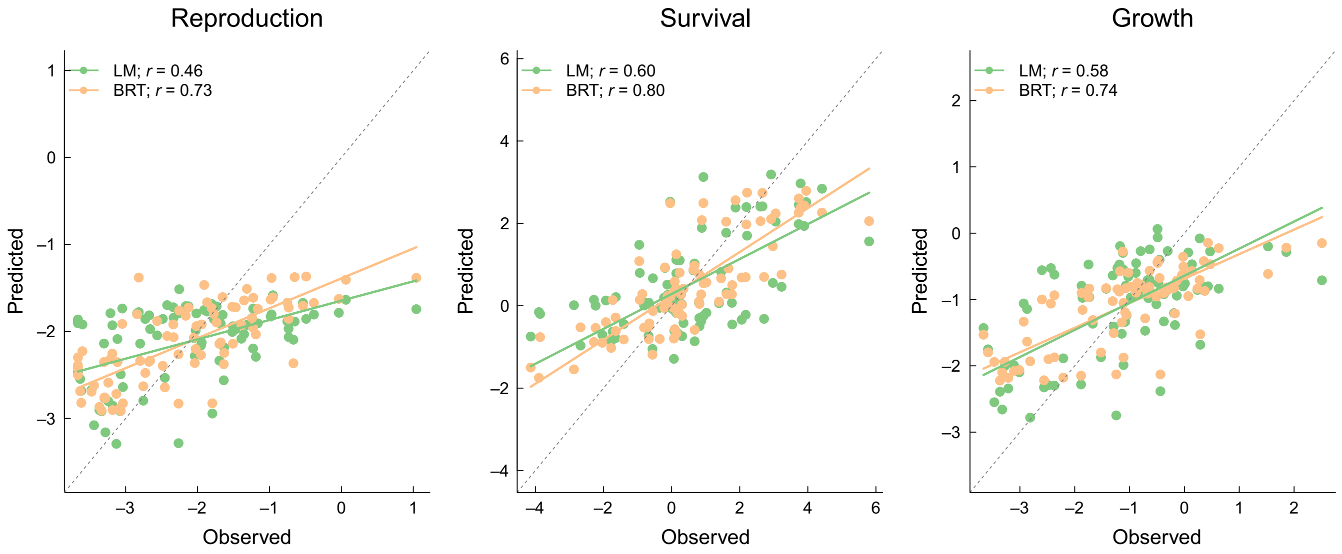

FIGURE 1 Boosted Regression Trees (BRT) models are better predictors of the relationship between traits and fitness than linear models alone. We obtained observed versus predicted values for both types of models using data from three vital rates elasticities (survival, growth, and reproduction) of plant species worldwide (observational dataset; Adler et al., 2014). For BRTs (orange lines), we calculated one model for each of the three vital rate elasticities using SLA, leaf N content and seed mass using tree complexity (*tc*) optimum and selected parameters (Table S3). For linear models (LM; green lines), we also performed a standard major axis regression for each of the three vital rate elasticities including the same traits, their pairwise interactions and the quadratic terms of the traits. We show Pearson correlation coefficient on the top-left

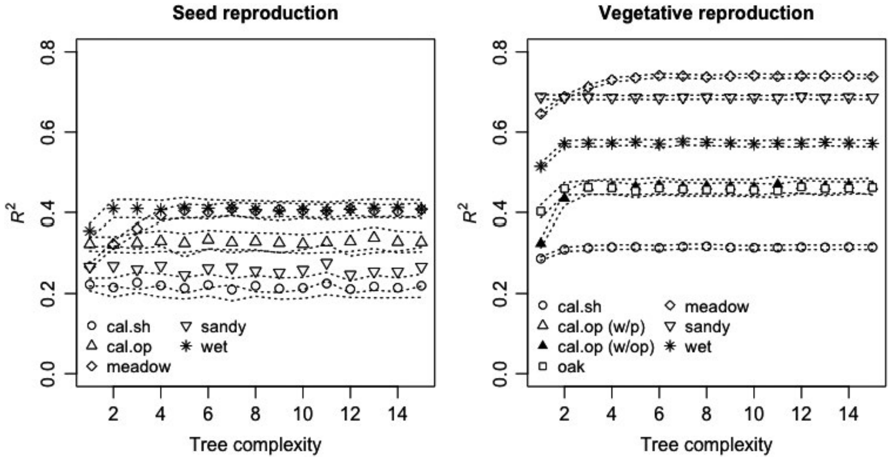

FIGURE 2 Vegetative reproduction is better explained by interactions among functional traits than by single trait models in almost all habitats. However, in three out of five habitats, single trait models explained seed reproduction better than trait interactions. Plots show the relationship between R^2 and tree complexity (*tc*) for each response variable and reproductive output obtained from Boosted Regression Trees (BRT). Dotted lines indicate ±95% CIs. Different symbols indicate different habitats within the botanical garden (Herben et al., 2012). Cal.op (w/p): open calcareous steppe (with phylogeny); Cal.op (w/op): open calcareous steppe (without phylogeny); Cal.sh: shaded calcareous steppe

TABLE 1 Summary statistics and estimate of phylogenetic signal (Pagel's λ) for each reproductive output and habitat within the botanical garden

	Shaded Cal. St.	Open Cal. St.	Meadow	Oak	Sandy	Wet
Seed rep.						
n	75	92	147	70	53	101
Mean	2.667	2.685	2.741	2.685	3.245	2.911
SD	1.287	1.128	1.194	1.128	1.017	1.167
λ	5.47E-05	6.61E-05	6.61E-05	NA	6.65E-05	0.253
p	1	1	1	NA	1	1
Veg. rep.						
n	76	92	147	69	53	101
Mean	2.500	2.087	2.639	2.232	2.132	2.752
SD	1.465	1.323	1.374	1.330	1.301	1.322
λ	4.75E-05	0.552	7.24E-05	0.269	5.58E-05	4.75E-05
p	1	0.014	1	1	1	1

Abbreviations: Shaded Cal. St.: shaded calcareous steppe; Open Cal. St.: open calcareous steppe.

habitats. The interaction plot between SLA and LS showed two distinct peaks, for high and low values of SLA, separated by a valley of low reproductive outputs in between (Figure 5 and Figure S3). To check if these alternative designs were significantly different, we extracted the predictions of the 100 performed models, fixing all variables to their means, except SLA (values ranging between 10 and 40 mm^2/mg) and LS, which was fixed at 0.2 cm (Figure 5). Then we plotted the mean prediction and its confidence intervals along the SLA gradient, revealing that there were indeed two different peaks separated by a valley and hence alternative designs (Figure S3).

4 | DISCUSSION

This study, by using BRT, demonstrates that trait interactions can matter for multiple trait effects on fitness. Models considering single traits are therefore likely to provide an incomplete evaluation of the trait-fitness relationship. In 83% of the cases in the botanical garden dataset the values of vegetative reproduction were better explained by models including interactions among traits. On the other hand, the values of seed reproduction were better explained by trait interactions for the meadow and wet habitats, but models without trait interactions sufficed to explain seed reproduction for the calcareous steppe and sandy habitats. Here we show the crucial importance of considering interactions among traits that depict different ecological dimensions (e.g. roots, branches, leaves, etc.; Laughlin, 2014) to reliably assess trait-by-environment effects on fitness, as well as to explore the existence of complex adaptive landscapes in community assembly and life history studies. We demonstrate that demographic processes can be determined by combinations of traits. Therefore, boosted regression trees appear as a better alternative than traditional linear regressions to predict

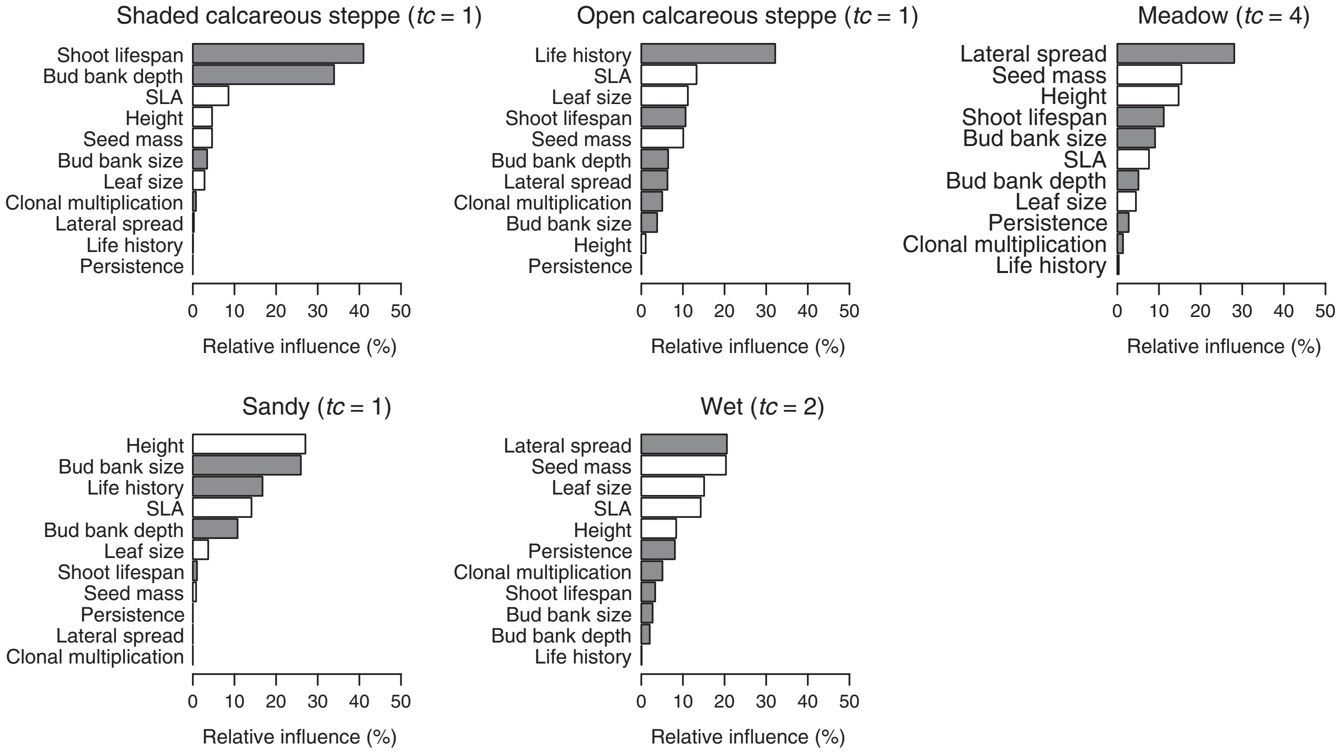

FIGURE 3 Seed reproduction depends on interactions between aboveground, bud banks and clonal traits. The ranked relative influence of multiple traits was calculated by the mean of 100 simulations for a tree complexity (*tc*) optimum value using Boosted Regression Trees (BRT; see Figure 2) and the botanical garden dataset. White colour indicates aboveground traits while grey colour indicates bud bank and clonal growth traits

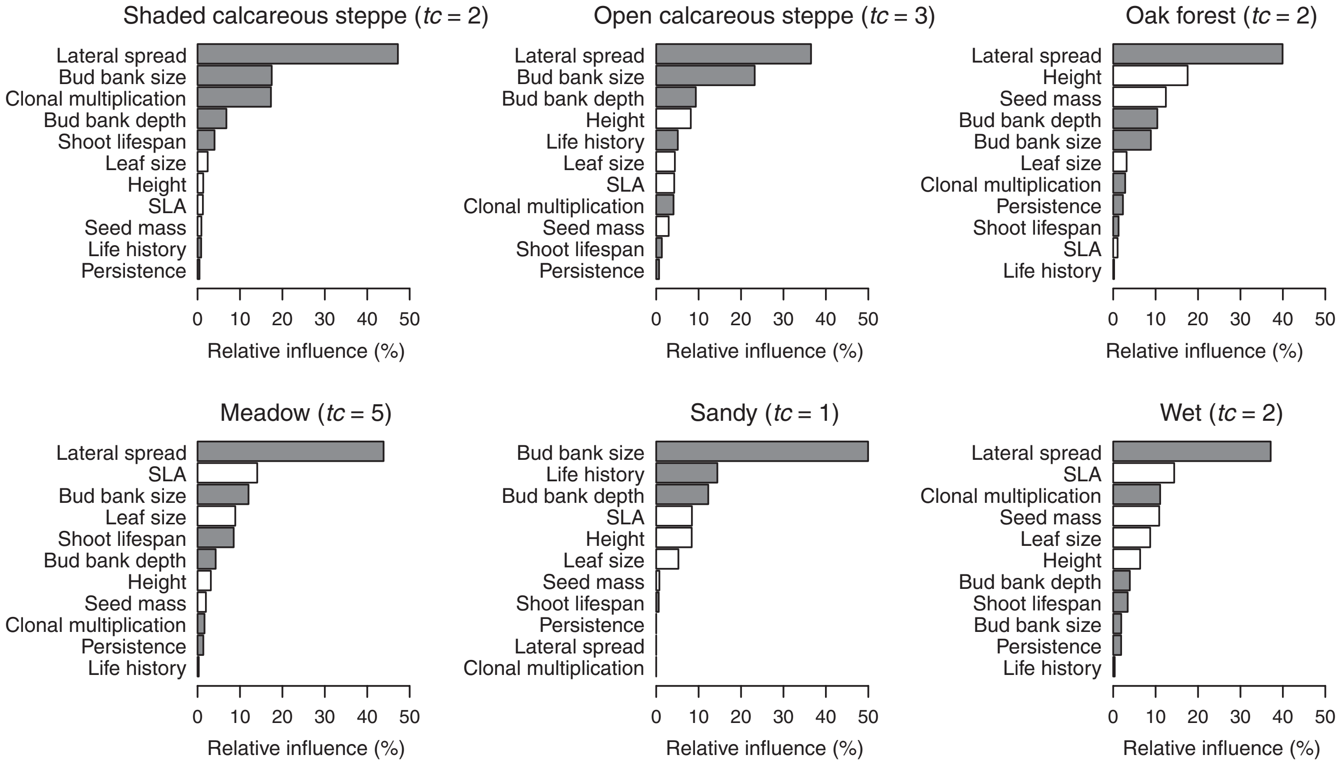

FIGURE 4 Vegetative reproduction depends on interactions between aboveground, bud banks and clonal traits. The ranked relative influence of multiple traits was calculated by the mean of 100 simulations for a tree complexity (*tc*) optimum value using Boosted Regression Trees (BRT; see Figure 2) and the botanical garden dataset. White colour indicates aboveground traits while grey colour indicates bud bank and clonal growth traits

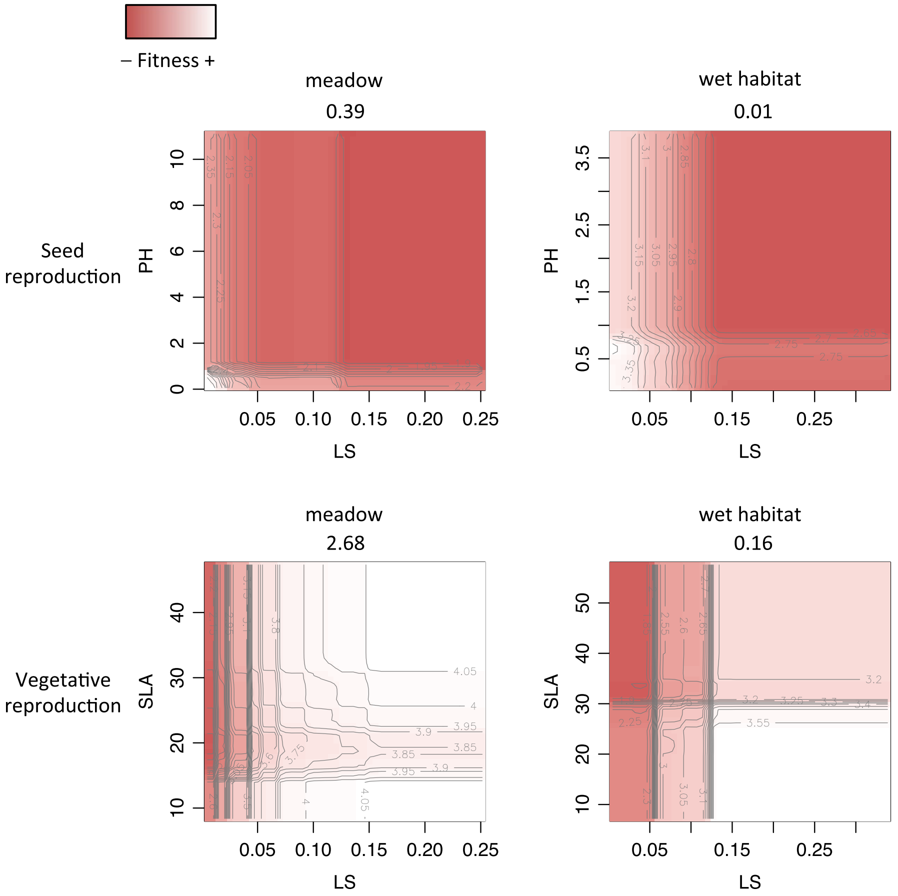

FIGURE 5 Fitness landscapes of the first and second ranked pairwise interactions (left and right panels, respectively) using the optimum values of model parameters (see Figure 2 and Table S4) and the botanical garden dataset. The strength of two-way interactions between determinants of seed and vegetative reproduction is shown above each plot. Brighter and darker tones represent high and low fitted values, respectively. LS: lateral spread; PH: maximum height; SLA: specific leaf area

species' fitness components and account for nonlinear relationships and trait interactions.

4.1 | The potential of boosted regression trees at pinpointing multiple trait interactions to predict fitness

BRT models are a powerful tool to analyse complex ecological datasets (Elith et al., 2008). We found that BRTs predict the role of traits on the relative importance of survival, growth and reproduction for population growth rate (de Kroon et al., 1986) better than linear models do. A growing body of literature quantifies this difference in performance between models for several ecological questions (e.g. Dortel et al., 2013; Elith et al., 2006; Leathwick, Elith, Francis, Hastie, & Taylor, 2006; Moisen et al., 2006; Naghibi & Pourghasemi, 2015). For any particular response variable, the resulting linear model is the single, most parsimonious model that describes the relationship between the response and predictors. However, the BRT model is an ensemble method that fits many models combining them to provide more robust estimates of the response variable (Elith et al., 2008). Here, trying to ensure a fair comparison between methods, we simulated a similar approach by combining the predictions of the most parsimonious set of linear models through model averaging techniques. Still, BRT clearly outperformed linear models in our dataset.

The benefits of using BRT models for this kind of analyses go beyond their superior predictive ability. Most importantly, linear models assume additivity between predictors. This means that they cannot properly account for the combined and interactive effect of traits, where, for instance, the positive effect of one trait on fitness depends on the effect of other traits. Beside this biologically superior property, BRT models can accommodate missing values (Friedman et al., 2000). In our analysis, in order to fit BRT and linear models to the same datasets, we had to remove species for which we were lacking some predictors (since linear models fully disregard observations when there are missing values for any of the predictors). This ultimately led us to completely discard some traits with a relatively high proportion of missing information. Considering the sparsity of information for some traits in the existing databases, the ability of BRTs to predict for observations with missing values appears as a major advantage for this kind of models. Another important advantage is that BRTs automatically fit interactions between predictors and nonlinear responses in a way that could not be achieved with a linear model (Elith et al., 2008).

Therefore, BRTs appear to be powerful for exploring trait-fitness relationships and generating new hypotheses with respect to trait interactions and fitness.

4.2 | The relevance of interaction complexity for the reproductive output

An emergent question from this research is why seed reproduction is best predicted by combinations of traits in some habitats (e.g. meadows and wet) but not in others (e.g. shaded and open calcareous steppes). This result could be due to the fact that not all traits are equally *functional* for all habitats (Violle et al., 2007). The influence of traits analysed here on seed reproduction might be indirect and mediated by trade-offs involving other traits that we did not include, such as traits related to the size, architecture and shape spectrum (Díaz et al., 2016; Lönnberg & Eriksson, 2013; Olson, Aguirre-Hernández, & Rosell, 2009; Thompson, Band, & Hodgson, 1993) or flowering phenology (Laughlin, 2014; Wright et al., 2010).

Moreover, trait-fitness relationships are likely complex resulting from the interaction of a large set of traits. BRT models improved the predictive power compared to modelling the effects of all traits as additive effects, as done in Herben et al. (2012). Analysing clonal traits alone (Herben et al., 2012) or leaf–height–seed (LHS) traits (Westoby, 1998), explained a modest portion of the observed variability of seed and vegetative reproduction (Klimešová, Tackenberg, & Herben, 2016). Moreover, our results show that, in the habitats where trait interactions were better predictors of both reproductive outputs than single traits, lateral clonal spread was the most important trait. Herben et al. (2012), combining the data of all habitats in a single analysis, found that the main predictors of seed reproduction were SLA and lateral spread, whereas for vegetative reproduction none of the aboveground traits were important. Despite the differences, our results agree with the notion that seed and vegetative reproduction result from a wide array of traits (Herben et al., 2012) and their relative importance can shift among habitats.

4.3 | The importance of considering traits from different ecological dimensions

A different architecture of aboveground, bud banks and clonal growth traits influenced seed and vegetative reproductions in each habitat. Bud banks and clonal growth traits have been rarely considered in community assembly studies (but see e.g., Klimeš, Klimešová, Hendriks, & Groenendael, 1997; Klimešová & Herben, 2015; Klimešová et al., 2017), even though they constitute an axis of specialisation independent of the LHS system (Klimešová et al., 2016; Vojtkó et al., 2017). We second Laughlin (2014)'s call to fully consider the multidimensionality of plant traits, measuring leaf, stem, root (absent in the most updated global map of trait correlations by Díaz et al., 2016) and flowering traits and their interactions. Belowground traits, particularly, seem of vital importance for moving forward, a step that is finally attainable through the recently released FRED database (Iversen et al., 2017). Our results support the idea of including traits from different organs and whole-plant properties to truly understand fitness differences.

Phylogenetic relatedness influenced the multi-trait driven-effects on vegetative reproduction only in the open calcareous steppe. In this case, the relative importance of lateral spread declined and almost equalled the importance of bud bank size, although both traits were still the most important when considering phylogenetic relatedness and when not. Similarly, Herben, Tackenberg, and Klimešová (2016), found that disturbance parameters (like the proportional change in cover of bare ground in one event), soil and climatic factors were related to clonal growth traits and bud banks, respectively, and these relationships did not change when species phylogeny was taken into account. Together with our results, this supports the existence of specific strategies involving aboveground, bud banks and clonal traits and that lateral spread and bud bank size and the vegetative reproduction in the open calcareous steppe could have evolved together.

4.4 | The importance of alternative designs depends on the environment

While traits interact in complex ways, resulting in different combinations of traits that can yield equivalent fitness values, we only found alternative designs in the meadow habitat. This is likely the result of different ecological strategies contributing to fitness (Salguero-Gómez et al., 2016), so that coordinated shifts in the values of traits compensate each other. In the meadow habitat, both high and low SLA values combined with high lateral spread resulted in high vegetative reproduction. As SLA is a proxy of individual growth rate (Pérez-Harguindeguy et al., 2013; Poorter & Garnier, 2007; Westoby, 1998; but see Shipley, 2006), this suggests that both slow and fast-growing clonal plants that are able to spread further away from the ramets are successful in the meadow habitat. Interestingly, our results show that SLA was among the most important traits for most of the habitats. This example also highlights the importance of trait interactions shaping plant reproduction and that caution is needed when discarding the role of a given trait to plant fitness based on single trait-fitness relationships (Májeková, Bello, Doležal, & Lepš, 2014; Poorter et al., 2008).

Besides meadows, we did not find strong evidence of alternative designs in the other habitats although trait interactions were important in the majority of cases. For example, we found a single optimum for vegetative reproduction in the wet habitat when lateral spread combined with values smaller than *c.* 30 mm^2/mg of SLA. There are several potential explanations for this. First, we may have not included in our analysis traits that cause species to have similar reproductive outputs in a habitat (Violle et al., 2007). Second, considering the relatively high values of tree complexity that were selected and the way we examined trait effects by visually inspecting single traits and pairwise interactions, we cannot discard that we have not been able to visualise all potential alternative strategies. This is because alternative strategies could also arise at higher dimensionalities. Alternatively, there may actually be no alternative strategies in these habitats when just a single strategy is systematically the winning one (Westoby, Falster, Moles, Vesk, & Wright, 2002).

Our study demonstrates that including complex trait interactions is necessary to adequately quantify the multiple dimensions of plant traits, including bud banks and clonal growth traits, which are the key determinants of both sexual and vegetative reproduction. Specifically, at least in the meadow habitat, traits interacted in complex ways to yield equivalent fitness values. Therefore, the existence of such alternative designs challenges our ability to detect the mechanisms responsible for species coexistence. Ultimately, future studies should measure multiple trait dimensions to understand the effects of whole phenotypes on fitness (Laughlin, 2018). An important next step is to collect functional traits of species at the same locations where demographic databases have already been collected (see the on-going work of StrateGo Network; Salguero-Gómez et al., 2018). These coordinated efforts ultimately will improve filling the current geographic and knowledge gaps. Furthermore, our approach using BRT models represents a promising approach for predicting and managing functional changes in vegetation composition.

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AUTHORS' CONTRIBUTIONS

F.d.B., L.G. and R.S.-G. obtained the data, N.P., F.d.B., C.P.C. and R.S.-G. designed the study, L.G. performed phylogenetic analyses, N.P. performed the rest of analysis with the support of C.P.C., N.P. wrote the first draft of the manuscript, and all authors contributed to revisions.

DATA ACCESSIBILITY

Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.45qc0rc (Pistón et al., 2019).

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SUPPORTING INFORMATION

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