Phylogenetic relatedness as a tool in restoration ecology: a meta-analysis

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Biotic interactions assembling plant communities can be positive (facilitation) or negative (competition) and operate simultaneously. Facilitative interactions and posterior competition are among the mechanisms triggering succession, thus representing a good scenario for ecological restoration. As distantly related species tend to have different phenotypes, and therefore different ecological requirements, they can coexist, maximizing facilitation and minimizing competition. We suggest including phylogenetic relatedness together with phenotypic information as a predictor for the net effects of the balance between facilitation and competition in nurse-based restoration experiments. We quantify, by means of a Bayesian meta-analysis of nurse-based restoration experiments performed worldwide, the importance of phylogenetic relatedness and life-form disparity in the survival, growth and density of facilitated plants. We find that the more similar the life forms of neighbouring plants are the greater the positive effect of phylogenetic distance is on survival and density. This result suggests that other characteristics beyond life form are also contained in the phylogeny, and the larger the phylogenetic distance, the less is the niche overlap, and therefore the less is the competition. As a general rule, we can maximize the success of the nurse-based practices by increasing life-form disparity and phylogenetic distances between the neighbour and the facilitated plant.

Keywords: Bayesian meta-analysis; competition; facilitation; plant coexistence

1. INTRODUCTION

The unprecedented level of native habitat perturbation and the concomitant loss of biodiversity demand that ecologists fill the gap between restoration science and practice [1,2]. This means that ecological restoration will be a key process for the conservation of biodiversity, which can benefit from the fast-growing body of knowledge acquired among disciplines such as community ecology or evolutionary ecology. In this regard, one of the big challenges is to determine the way plant communities are assembled through biotic interactions [3], or, in other words, to know how redundant different species are in communities [4] for restoration purposes.

Biotic interactions assembling plant communities can be positive or negative and they usually operate simultaneously [5]. For example, a nurse plant may buffer extreme air temperatures, enhancing the establishment of other plants (i.e. facilitation), but may also limit the growth of the facilitated plants by reducing the availability of nutrients (i.e. competition). Understanding the net effects of the combination of facilitation and competition is therefore crucial to determine the performance of the

species involved in the interaction. Furthermore, facilitative interactions, together with posterior competition, are among the proposed mechanisms triggering succession [6] and such succession may lead disturbed communities towards steady states very similar to the undisturbed community (see [7,8] for experimental evidence). Despite the good opportunity that plant facilitation represents for the ecological restoration of disturbed communities, it has not been used for restoration purposes until the 21st century [9]. Such a gap is consistent with the traditional lack of attention that positive interactions have suffered under the predominant view of competition as an omnipresent force shaping ecological interactions and communities [10]. In contrast to competition-focused afforestation techniques, in which seedlings are planted after eliminating the pre-existing vegetation, restoration based on facilitation, also known as nurse-based restoration, consists of planting the plants spatially associated with other plants, which provides them with a favourable microhabitat [11]. Nurse-based restoration experiments have been increasingly performed in different types of ecosystems worldwide, with varying success (see [12] for a recent review). Similarly to other restoration approaches, such as the framework species method [13], nurse-assisted planting may promote more rapid natural succession in disturbed habitats [14]. For example, nurse-based restoration accelerates the recovery of the structure of a

burnt Mediterranean community by increasing species diversity and evenness [7].

Species behaving as good nurses able to launch succession in semi-arid communities have morphological and functional characteristics different from the beneficiary plant species [14–16]. Interestingly, such characteristics are also valuable predictors of how good a species is as a nurse in restoration experiments [12]. This result is consistent with the limiting similarity concept, which predicts that species with similar traits will not coexist in the community because of great niche overlap [17] (but see [18] for alternative coexistence mechanisms). This concept has been suggested as a framework to develop trait-based community assembly restoration practices of invaded systems [19]. Similarly, we suggest that nurse-based restoration practices may benefit from the inclusion of phenotypic information by ensuring that the nurse and the facilitated plant species are phenotypically different. But phenotype is composed by a complex array of interacting traits that are not always measurable. Under this situation, phylogeny can inform us about the unmeasured dimensions of the phenotype given that most of the traits are evolutionarily conserved [20]. If all the relevant information were known about species traits then phylogeny would not provide additional information [21]. However, we seldom have all the relevant phenotypic information, or, even worse, we ignore what is the relevant trait for the success of the facilitated plant. When traits are evolutionarily conserved, the phenotype of one species is expected to resemble that of closely related species. Thus, by looking at the phylogenetic distance between two species, we can infer the phenotypic distance between them. Obviously, this inference will not work under evolutionary trait convergence or fast phenotypic divergence [22–25]. Under trait convergence, distantly related species will be phenotypically similar, but under fast trait divergence, phylogenetic distance may be a wrong predictor of the phenotypic distance with respect to interaction outcomes. In the latter case, phenotypic differences are so large that phylogenetic differences are irrelevant. The existence of all these different possibilities emphasizes the necessity to test the assumption of using phylogenetic information as a proxy for phenotypic and niche dimensions [24].

The facts that facilitative interactions in nature occur between distantly related species and competition occurs between closely related species support the rationale of using phylogenetic relatedness as a proxy for the net effects of the balance between facilitation and competition [26–29] (but see [30]). In addition, such phylogenetic signature, together with experimental evidence, indicates that facilitative and competitive interactions are, to some extent, species-specific, and hence it is relevant to select the correct pairs of nurse and facilitated plant species for restoration practices [31,32].

Our goal in this study is to unite the principles of ecology and evolutionary biology to show that a phylogenetic framework can be used successfully to significantly improve efforts to restore disturbed habitats. As far as we know, no study on ecological restoration has integrated phylogenetic information to better predict the success of the planned activities. We suggest that coexistence between distantly related species produced by phenotypic disparity is a general solution to ecological restoration problems everywhere. For phenotypic and phylogenetic variables to be widely useful in ecological restoration, especially in areas where species databases are not available, they should be extremely easy to collect. For easiness of measure, we selected the life-form disparity and the phylogenetic distance between the neighbour and the facilitated species. Life form may encapsulate a complex array of phenotypic characters and has been proved to be determinant in the outcome of the nurse-based restoration experiments [12,14]. Phylogenetic distances can be easily obtained with the help of a Web and iPhone application named TimeTree, which is a public knowledge-base of divergence times [33]. By using these two simple measures in a Bayesian meta-analysis of nurse-based restoration experiments performed across different ecosystems worldwide, we quantify the importance of phylogenetic relatedness and life-form disparity to predict the success of facilitated plants in terms of survival, growth and density. Given the species-specificity of facilitation and competition, we also quantify the relative importance of the identity of the nurse and the facilitated species to the outcome of the interaction.

2. MATERIAL AND METHODS

(a) *Database*

We used the database compiled by Gómez-Aparicio [12], consisting of published studies where interactions among plants were manipulated to restore degraded habitats worldwide from temperate and tropical humid and semi-arid ecosystems, as well as wetlands. The effect of neighbours on the facilitated (hereafter target) plant performance components such as emergence, survival, growth and density was estimated as a function of several predictors such as study duration, the life form of the neighbour and target species, and the ecosystem type. As we are interested in pairwise interactions between a neighbour and a target species, we excluded from the database those cases where several neighbour or several target species were mixed in the same experiment. The final database for survival analyses yielded a total of 31 studies containing 188 suitable cases with 52 neighbour and 75 target species. For growth (measured as biomass or height) analyses, we used 22 studies containing 85 suitable cases with 38 neighbour and 50 target species. For density (measured as the number of individuals or cover per a given area) analyses, 17 studies were used, finally yielding 56 suitable cases with 20 neighbour and 34 target species. Emergence could not be analysed because of the low sample size. The final database is available in the electronic supplementary material.

For each selected study we took (i) the identity of the neighbour species, (ii) the identity of the target species, and (iii) the effect size and its variance. Effect size indicates the magnitude of the neighbour effect on survival, growth or density of target plants in relation to the open ground. The effect size for survival (ln (OR)) was calculated as the natural log of the ratio of the odds of survival in the presence of neighbours (experimental group) to the odds of survival in their absence (control group). The effect sizes for growth and density data (ln(RR)) were calculated as the natural log of the ratio of the mean outcome in the experimental group to that of the control group. Effect sizes greater than zero indicate a positive effect of neighbours on target plants (facilitation), whereas values lower than zero indicate a negative effect of neighbours (competition). All effect sizes and the associated variances are shown in the electronic supplementary material.

We added to the database two new variables intended to capture phenotypic and phylogenetic disparity between the nurse and the facilitated plants. For simplicity, we selected the life-form disparity between the neighbour and the target species as a measure of phenotypic disparity. Life-form disparity was calculated as the absolute difference between the life forms of the neighbour and target species after coding life forms as $1 =$ herbs, $2 =$ shrubs and $3 =$ trees. Phylogenetic distance was calculated as the distance (in million years, Myr) connecting neighbour and target species in the phylogenetic tree through their most recent common ancestor. The phylogenetic distances were obtained from a phylogeny generated with the help of the program Phylomatic [34]. This program generates a phylogenetic tree by matching the family names of our study species with those contained in a backbone phylogeny, which is the megatree based on the work of the Angiosperm Phylogeny Group [35]. The nodes of the tree were dated with the help of the bladj algorithm implemented in Phylocom 3.41 software [34]. This algorithm dates the nodes based on the ages of Wikström et al.'s [36] database and distributes evenly the undated nodes between the dated nodes. To ensure that our phylogenetic distances were similar to those obtained with the TimeTree application, we correlated the phylogenetic distances obtained with Phylomatic and TimeTree applications and found a high degree of correlation ($r = 0.90$; $n = 75$, $p < 1 \times 10^{-15}$).

(b) Statistical analyses

We ran Bayesian meta-analyses by fitting generalized linear mixed models using Markov chain Monte Carlo (MCMM) techniques with the help of the MCMCglmm package for R [37]. The effect size of survival, growth or density was the dependent variable in the model and their variances were passed to the *mev* argument of MCMCglmm [38]. Life-form disparity and the logarithm of phylogenetic distance between neighbour and target species were included as predictors. Different sources of pseudoreplication can be accounted for in this analysis (i.e. study, species, author, country, etc.) and we focused on that coming from the use of the same species in different experiments. Thus, the identities of neighbour and target species were included as random, grouping factors.

We ran 13 000 MCMC iterations, with a burn-in period of 3000 iterations and convergence of the chain tested by means of an autocorrelation statistic. The default priors ($\nu = 0$, $V = 1$) were used except for growth analyses where a stronger prior ($\nu = 1$, $V = 0.002$) was required owing to numerical problems of singularity in the mixed model equations. To assess the sensitivity of the analyses to alternative prior specifications, we re-ran all the models with different priors, and results were consistent.

The overall effect size was estimated by running the models without predictors. The effect of predictors (life-form disparity and phylogenetic distance) was estimated by calculating the 95% credible interval of their posterior distribution and computing the probability that such effect is larger than zero (pMCMC). The proportion of remaining variance explained by each grouping factor (neighbour and target species identity) was estimated by calculating the 95% credible interval of its posterior distribution. It should be noted that this interval will never contain zero because variances are bounded to be positive [39]. Therefore, a wide credible interval with an extremely low bound suggests an insignificant effect of the grouping factor.

To quantify at what phylogenetic depth our results were occurring, we re-ran the analyses after sequentially removing cases with different phylogenetic distance between the neighbour and target species (from 0 to 300 Myr, each 50 Myr).

3. RESULTS

The study cases contained the whole range of life-form disparities and a wide range of phylogenetic distances between neighbours and their target plants (figure 1). Phylogenetic distance was significantly correlated with life-form disparity across the whole database ($F_{1,174} = 40.2$; $p < 0.001$) but only explained 18 per cent of the variance. This low percentage indicates that phylogeny may still contain additional information about the similitude of species traits others than life-form disparity. This fact allows us to test the role of both variables on the effects of neighbours on survival, growth and density of target plants.

Across all the studies, neighbours had an overall positive effect on survival (effect size $= 0.42$; [0.22, 0.61] 95% credible interval; pMCMC < 0.001). When including the species identities and predictors in the model (table 1), the positive effect on survival strongly increased with life-form disparity between the neighbour and the target plant. The significant negative interaction between life-form disparity and phylogenetic distance indicates that the lower the disparity between the life forms of the two species, the higher the effect of their phylogenetic distance on survival of the target species. The identity of the neighbour explained a percentage of remaining variance ranging from 32 to 57 per cent, whereas the identity of the target plant was irrelevant to explain the effects of neighbours on plant survival. All these results were robust to the removal of cases in which the phylogenetic distance between the neighbour and the target species was lower than 100 Myr.

The neighbour's overall effects on the growth of target plants across all studies was not significant (effect size $= 0.05$; [-0.09, 0.61] 95% credible interval; pMCMC $= 0.44$). Also, the model including predictors and species identities (table 2) indicated that neither life-form disparity nor phylogenetic distance was relevant to explain the effect of neighbours on the growth of target plants. The identity of the neighbour did not explain a significant portion of the remaining variance, but that of the target explained between 19 and 39 per cent. Results were consistently non-significant after removing cases at different phylogenetic distances.

Density of target plants was negatively affected by the presence of neighbours (effect size $= -0.36$; [-0.69, -0.02] 95% credible interval; pMCMC $= 0.04$). The model with predictors and species identities (table 3) shows that such a negative effect was alleviated with increasing life-form disparity and phylogenetic distance. The significant interaction term indicates that the beneficial effect of phylogenetic distance on density increases when life forms of the neighbour and target plant species are similar. The identity of both neighbours and target species did not explain a great proportion of remaining variance in the model, as suggested by the wide confidence interval having its lower limit close to zero. All these results were robust to the removal of cases in which the
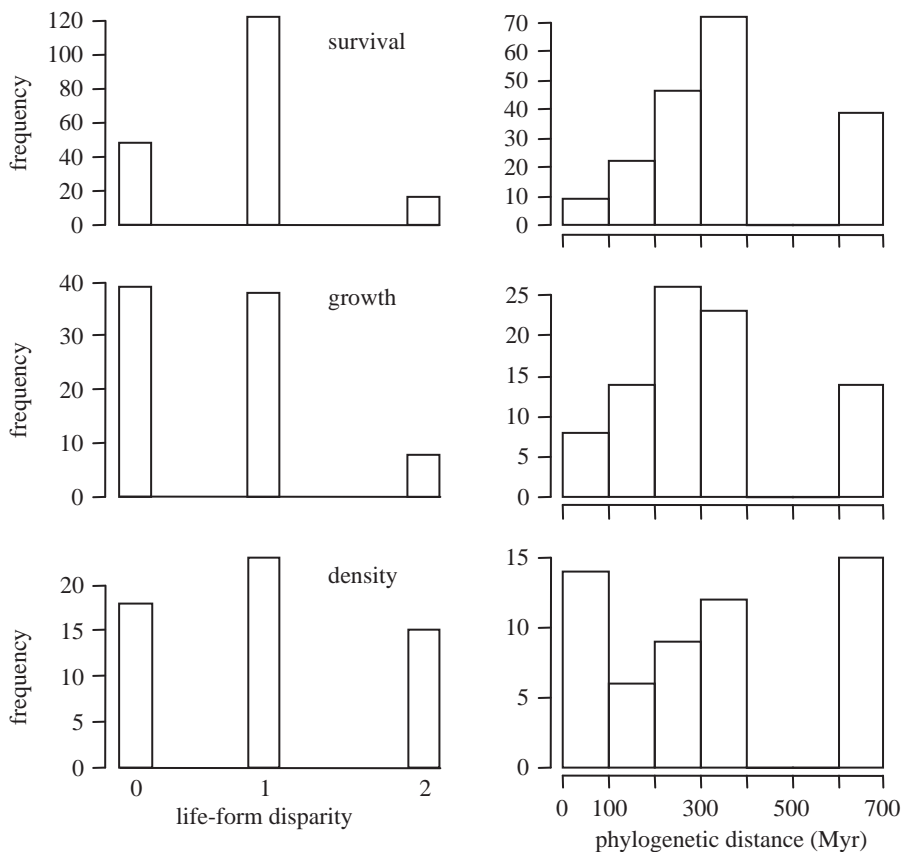
Figure 1. Frequency distribution of life-form disparity and phylogenetic distance values between the neighbour and target plant species in the final database. Life-form disparity is the difference between the life forms of the neighbour and target species when coded as 1 = herbs, 2 = shrubs and 3 = trees. Phylogenetic distance is the distance (Myr) connecting neighbour and target species in the phylogenetic tree through their most recent common ancestor.

Table 1. Effect of neighbours on survival of target plants as a function of the life-form disparity (LFdisp) and phylogenetic distance between the neighbour and the target species. Neighbour and target species identity were considered as random factors.

	posterior mean	lower 95% CI	upper 95% CI	pMCMC
fixed effects				
intercept	−0.359	−1.636	1.065	0.558
phylo distance	0.145	−0.093	0.394	0.252
LFdisp	2.785	0.683	5.268	0.020
phylo × LFdisp	−0.445	−0.876	−0.094	0.038
		proportion of remaining variance explained		
random effects				
neighbour		0.314	0.576	
target		1.8×10^{-15}	9.2×10^{-5}	

phylogenetic distance between the neighbour and the target species was lower than 260 Myr.

4. DISCUSSION

Traditional restoration practices were based on the elimination of assumed competitors by eliminating pre-existing neighbours, but now the increasing evidence that positive interactions between plants may facilitate species coexistence and trigger succession has recently led to nurse-based restoration practices [9,11]. Facilitation tends to occur between distantly related species, whereas competition tends to be high between closely related

species [27]. Coexistence of distantly related species and the competition–relatedness hypothesis formulated by Darwin are two sides of the same coin. However, while competition has been repeatedly invoked in ecology, coexistence mediated by positive interactions has not [10]. Here, we show how phylogenetic relatedness among species can be used as an informative tool in nurse-based restoration practices.

The effects of neighbours on target plants in restoration experiments worldwide were positive for survival, neutral for growth and negative for density. The positive effects of neighbour plants on survival of target plants increase when both species have different life forms. In such a

Table 2. Effect of neighbours on growth of target plants as a function of the life-form disparity (LFdisp) and phylogenetic distance between the neighbour and the target species. Neighbour and target species identity were considered as random factors.

	posterior mean	lower 95% CI	upper 95% CI	pMCMC
fixed effects				
intercept	−0.463	−1.500	0.345	0.326
phylo distance	0.077	−0.096	0.244	0.396
LFdisp	−0.072	−2.362	2.137	0.952
phylo × LFdisp	0.020	−0.366	0.421	0.924
		proportion of remaining variance explained		
random effects				
neighbour		1.1×10^{-4}	0.013	
target		0.191	0.390	

Table 3. Effect of neighbours on density of target plants as a function of the life-form disparity (LFdisp) and the phylogenetic distance between the neighbour and the target species. Neighbour and target species identity were considered as random factors.

	posterior mean	lower 95% CI	upper 95% CI	pMCMC
fixed effects				
intercept	−3.129	−5.846	−0.396	0.026
phylo distance	0.584	0.042	1.123	0.038
LFdisp	2.976	0.201	5.779	0.042
phylo × LFdisp	−0.507	−0.985	−0.011	0.048
		proportion of remaining variance explained		
random effects				
neighbour		0.061	0.545	
target		3.64×10^{-17}	3.65×10^{-10}	

case, the phylogenetic distance between both species is not very relevant for survival. This is consistent with the finding that congeneric *Opuntia* species may coexist when morphological disparity is high (erect versus decumbent platyopuntias [40]). However, when both species have the same life form, phylogenetic distances should be maximized to ensure that other phenotypic traits do differ. This is because other characteristics beyond life form are also contained in the phylogenetic information, and the larger the phylogenetic distance, the less the niche overlap, and therefore the less the competition. The negative effects of neighbours on the density of target plants can be mitigated with increasing life-form disparity and phylogenetic distance. If neighbour and target species belong to the same life form, we should again ensure that both species are phylogenetically distant to minimize the negative effects of neighbours on the density of target plants. Our analyses revealed that the minimum phylogenetic distance between both species to ensure survival should be around 100 Myr, but much longer (260 Myr) to minimize negative effects on density. Interestingly, this age falls within the range of mean phylogenetic distance between nurses and beneficiary plants found in natural communities (244–343 Myr; [28] and [29] for Mexican desert and Mediterranean shrub communities, respectively).

Our results clearly show that complementing phenotypic with phylogenetic information is useful to predict the success of nurse-based restoration practices. This approach has proved useful at the community and ecosystem levels. At the community level, morphological and phylogenetic distances between alien and native plants significantly explain the impact of invaders in the reproductive success of co-flowering native plants. On the one hand, the effect of aliens on visitation and reproductive success was most detrimental when alien and focal species had similar flower symmetry or colour, and on the other hand, the phylogenetic relatedness between alien neighbours and focals influenced the reproductive success effect size [41]. At the ecosystem level, phylogenetic and functional diversity complement each other as predictors of the effect of biodiversity on ecosystem functioning in grassland biodiversity–ecosystem functioning experiments [42]. We are confident that our results, although based on pairwise interactions, can be applied to restoration to communities with multiple species. In fact, Castillo *et al.* [43] have shown experimentally that phylogenetic relatedness can be successfully used as a predictor of plant performance in multi-specific assemblages.

It is well known that not all species of competitors have equivalent effects on a target species [44,45]. Species-specific differences in competitive effects have been found in many neighbourhood analyses [44,46–49]. Similarly, species-specificity in facilitative interactions also occurs, and the identity of both the nurse and the target plant is relevant to understand the outcome of the interaction [31,50,51]. Here, we have quantified for the first time the relative importance of the taxonomic

identities of the neighbour and the target plant species in the outcome of the interaction established in restoration experiments. These results show that the identity of the neighbour is strongly relevant for the survival, but not for the growth or density, of the target species. On the other side, the identity of the target plant is only relevant to explain the neighbour's effect on its growth rate. All these results are consistent with the species-specificity shown by both nurses and facilitated plant species in facilitation and competition networks [51]. Such species-specificity follows a non-random phylogenetic pattern, indicating that phylogenetic history has a pervasive influence not only on recruitment stages where facilitation predominates, but also on adult stages where competition starts to act. Given the concordance of results found in nature with those obtained in restoration experiments, we recommend the inclusion of phylogenetic information in restoration practices.

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