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The phylogenetic structure of plant facilitation networks changes with competition

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Summary

1. Ecological communities are assembled as complex networks of both positive (i.e. facilitation) and negative (i.e. competition) interactions. In networks established among plant species, many facilitative interactions occurring between a benefactor – a nurse – and a beneficiary – a facilitated seedling - turn into competition over time as the facilitated seedling grows and outcompetes the nurse. The facilitative associations that disappear over time are mainly restricted to closely related taxa, because close relatives tend to share niche requirements and compete more strongly for the same resources. In consequence, the phylogenetic structure of a network might change as positive associations become negative.

2. This study is aimed to characterize how the overall (i.e. nestedness and connectance) and the phylogenetic structure of facilitation networks in semi-arid communities change when facilitation turns into competition and some of the early species associations established by facilitation disappear.

3. We show that the initial facilitation networks retain the overall, but not the phylogenetic, structure. Phylogenetic analyses show that as seedlings, facilitated species tend to associate with the same subset of nurses while, on the contrary, nurses are indifferent to the identity of their facilitated seedlings. But when competition becomes important, closely related nurse species appear associated with only a subset of facilitated species in the community.

4. *Synthesis.* Temporal rearrangements in the phylogenetic structure of the facilitation networks provide evidence that plant–plant species interactions lead to highly species-specific networks in which the phylogenetic history has a pervasive influence not only on recruitment but also on adult community composition. The use of phylogenetic methods combined with complex network approaches opens the possibility to understand the complexity of ecological interactions occurring in nature as for example those occurring when biological invasions take place or those producing coextinction cascades following species removal from ecosystems.

Key-words: competition, complex networks, facilitation, phylogenetic signal, plant–plant interactions

Introduction

Complex network tools are the only way to represent and analyse the mega-diverse patterns of interactions that commonly occur in nature, such as gene regulation, protein interactions, metabolic networks, food webs, etc.(Albert & Barabási 2002; Newman 2003). In ecology, the recent use of complex network theory has provided valuable information on the generalities arising from different mutualistic interactions like pollination, seed dispersal, plant protection by ants and interactions between cleaners and clients in reef animals (Bascompte & Jordano 2007). One of the main characteristics of mutualistic networks is the high level of nestedness, i.e. the species that specialists interact with form subsets of the species that generalists interact with (Bascompte *et al.* 2003; Vázquez & Aizen 2004).

Plant facilitation is another important ecological interaction that occurs among many different taxa and across many ecosystems worldwide (Bruno & Bertness 2001). Complex

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network theory has recently been expanded to the study of multi-species plant communities in which more than 90% of the species recruit successfully only beneath the canopies of perennial plants and are therefore maintained via facilitation (Verdú & Valiente-Banuet 2008). A facilitative network among plant species is constituted by benefactor (nurse) species interacting with beneficiary (facilitated) species. The new approach has shown that plant communities governed by facilitation are assembled in networks that have the same nested structure as mutualistic networks, where a few generalist nurses facilitate the seedlings of a large number of species while the rest of nurses facilitate only a subset of them (Verdú & Valiente-Banuet 2008).

It is also known that some of these facilitative interactions occur during the early stages of establishment, but may turn into competition at later stages of the plant ontogeny or in response to temporal fluctuations in the environment (McAuliffe 1988; Miriti 2006; Soliveres *et al.* 2010). Consequently, the spatial associations between nurses and facilitated species may disappear with time when the facilitated seedlings grow and compete with the nurse. The facilitative interactions that disappear with time are not a random sample of all the possible interactions, but are typically restricted to closely related taxa (Valiente-Banuet & Verdú 2008). This is because closely related species tend to share similar niche requirements and therefore compete more strongly for the same resources. Thus, living in association with a close relative is the main constraint on the assemblage of plant facilitation networks, a constraint that drives their temporal dynamics (Valiente-Banuet & Verdú 2008; Verdú & Valiente-Banuet 2008). Ultimately, the phylogenetic diversity of plant communities (*sensu* Webb 2000; Cavender-Bares *et al.* 2004) will be related to the delayed influences of sequential facilitation and competition.

The phylogenetic signal (i.e. the tendency of closely related species to interact with the same set of species) seems ubiquitous among the ecological interactions such as those between plants and pollinators (Rezende *et al.* 2007), hosts and parasites (Ives & Godfray 2006), predators and prey (Bersier & Kehrli 2008; Rezende *et al.* 2009), plants and pathogens (Gilbert & Webb 2007; Vacher, Piou & Desprez-Loustau 2008) or plants and herbivores (Novotny *et al.* 2002; Weiblen *et al.* 2006). Thus, understanding the temporal dynamics of the phylogenetic structure of the ecological interactions is important to disentangle the ecological processes underlying the assembly of communities. Temporal changes in the identity of the species and their interactions could alter the overall structure of the network and particularly its phylogenetic structure. The few studies addressing temporal changes in mutualistic networks have shown that, although the identity, composition and interactions among species changed with time, the overall structure of the network remained stable, maintaining high levels of nestedness year after year (Olesen *et al.* 2008; Petanidou *et al.* 2008). However, no study has asked whether temporal changes in the identity of the interactions alter the phylogenetic structure of the network. The aim of this study is to characterize how the overall (i.e. nestedness and connectance) and the phylogenetic structure of facilitation networks in semi-arid communities change when facilitation turns into competition and some of the early species associations established by facilitation disappear. We predict that the temporal shifts from facilitation to competition occurring between closely related taxa (Valiente-Banuet & Verdú 2007) will concomitantly lead to changes in the phylogenetic structure of plant facilitation networks. Such changes are not trivial because phylogenetically structured networks are more prone to the loss of phylogenetic diversity following an extinction event (Rezende *et al.* 2007). Here, we show that the phylogenetic structure of plant facilitation networks changes with competition, and we briefly discuss the potential applications of this methodological approach to the conservation of biodiversity.

Materials and methods

STUDY SITES AND SAMPLING PROCEDURES

The study was replicated in seven arid and semi-arid Mexican plant communities strongly shaped by facilitation (Valiente-Banuet & Verdú 2007; Verdú & Valiente-Banuet 2008). The nursing effect in these areas (Tehuacan Valley and Baja California) was described by Valiente-Banuet & Ezcurra (1991), who experimentally found that seedling survival increased under the nurse shade where temperatures and evaporative demands are lower than on the open ground. Higher soil fertility beneath nurse canopies was of secondary importance. We also have experimental evidence of the temporal change from facilitation, mediated by distantly related nurses, to competition, mediated by closely related species (Castillo, Verdú & Valiente-Banuet 2010).

Three of these communities (Tetechera1, Cardonal and Tetechera2) are located in the tropical Tehuacán-Cuicatlán Valley, and the remaining four communities (Parena1, Parena2, Vizcaíno1 and Vizcaíno2) are located outside the tropics in the Sonoran Desert of Baja California, along a latitudinal gradient ranging from 24° to 28°50′ N. The three tropical desert communities are dominated by columnar cacti and shrubs (*Neobuxbaumia tetetzo, Mimosa luisana* and *Acacia coulteri* in Tetechera1; *Cephalocereus columna-trajani, Euphorbia antisyphillitica* and *Hechtia podantha* in Cardonal, and *Neobuxbaumia mezcalaensis, Pseudosmodingium multifolium, Acacia subangulata* and *Lippia graveolens* in Tetechera2). Tetechera1 and Cardonal are located near Zapotitlán de las Salinas (18°20′ N, 97° 28′ W) whereas Tetechera2 is located near San Juan Raya (latitude 18°19″ N, 97°38′ W). The two southernmost non-tropical communities (Parena1 and Parena2) are located in Punta Arena de la Ventana (24°01′ N, 109°52′ W). The Parena1 community is dominated by the columnar cactus *Pachycereus pringlei* and the trees *Prosopis articulata* and *Olneya tesota,* whereas Parena2 is dominated by the trees *Bursera microphylla*, *Cyrtocarpa edulis* and *Fouquieria diguetti*. The two northernmost non-tropical communities (Vizcaíno1 and Vizcaíno2) are located in the Vizcaíno region (27°33′–28°45′ N, 113°12′–113°58′ W). Vizcaíno1 is a creosote bush scrubland dominated by *Larrea tridentata*, *Ambrosia dumosa* and *Stenocereus gummosus*, whereas Vizcaíno2 is a sarcocaulescent shrubland dominated by the trees *Fouquieria columnaris* and *Pachycormus discolor*, the cactus *Pachycereus pringlei* and the shrubs *Ambrosia bryantii* and *Ambrosia chenopodiifolia*.

We used previous data on the spatial association between nurses and seedlings of beneficiary species in these same plant communities to build facilitation networks as explained below (Verdú & Valiente-

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Banuet 2008). It should be noted that self-facilitation (i.e. seedlings recruiting under conspecific adults) seldom occurs in this type of ecosystems and therefore facilitation cannot be confounded with limited seed dispersal (Castillo, Verdú & Valiente-Banuet 2010). Directed dispersal of fleshy-fruited species by animals towards nurses can also be confounded with facilitation (Pausas *et al.* 2006) but this is not the case in our study communities where facilitation occurs in both fleshy and non-fleshy fruited species. Actually most of the species inhabiting the seven communities studied recruit under nurses (96.0 ± 3.5%; Valiente-Banuet & Verdú 2007; Verdú & Valiente-Banuet 2008), whereas only 46.7 ± 6.4% of these species are dispersed by animals (birds and bats). Furthermore, experimental evidence exists that even in animal-dispersed species, seeds are dispersed on the open ground but germination and establishment in this microhabitat rarely occur, suggesting that facilitation is the result of the amelioration of the physical environment produced by nurse plants, rather than directing seed dispersal (Valiente-Banuet & Ezcurra 1991; Castillo & Valiente-Banuet 2010). These networks represent the early stage of facilitation interactions and will be termed 'seedling networks' hereafter. Later in time, the networks can be rearranged because many of these species associations disappear as facilitated seedlings grow and compete with the nurses. These networks will be termed 'adult networks' hereafter and reflect both persisting facilitation interactions and potential competitive interactions among species. Data to construct both seedling and adult networks were collected as described in Valiente-Banuet & Verdú (2007, 2008). For seedling networks we sampled four 100×10 m^2 transects in each community to estimate the total cover of perennial plants and open space. In each transect we counted the number of seedlings (small, non-reproductive plants) of each species growing beneath canopies of adults (reproductive plants) and in open spaces. To determine whether a species was facilitated we used a Chi-squared test contrasting if the percentage of individuals recruiting under canopies was greater than expected by the overall canopy cover in the community. Thus, we considered that facilitation occurred when more individuals than expected by chance were recruiting under nurse canopies. In addition, we recorded the nurse species with which each seedling was associated at the early stages (i.e. association between nurses and facilitated seedlings). For adult networks, we repeated the sampling procedure to record whether nurses and adults of facilitated species remained spatially associated. Two adults were considered to be associated when the trunk of one species was growing underneath the canopy of the other species. This allowed us to determine the nurse species associated with each facilitated species late in time (i.e. association between nurses and facilitated adults).

NETWORK STRUCTURE

We studied the temporal changes in both the overall and the phylogenetic structure of the seedling and adult facilitation networks following the outline depicted in Appendix S1in Supporting Information. Based on previous studies, we predicted that the overall structure of the network would not change with time (Olesen *et al.* 2008; Petanidou *et al.* 2008), but the phylogenetic structure would drastically change as a consequence of competition acting on closely related species (Valiente-Banuet & Verdú 2008). We explain below the parameters used to characterize the overall and the phylogenetic structure of facilitation networks.

OVERALL STRUCTURE OF THE NETWORKS

Facilitation networks can be described by quantitative matrices built with the number of individuals of each facilitated species occurring beneath each nurse species. When qualitative 0/1 matrices were needed for the calculation of some parameters (e.g. nestedness and connectance), adjacency matrices of nurse and facilitated species were filled with 1′s whenever a facilitated species was present under a nurse species, and 0′s otherwise. For each community we constructed a seedling and an adult network. We calculated nestedness (N seedlings and N adults in Appendix S1) and connectance (C seedlings and C adults in Appendix S1) to describe the overall structural parameters of the corresponding networks. Connectance was calculated as the fraction of directly interacting pairs of nurses and facilitated species relative to all potential species pairs. Nestedness was calculated as the NODF (nestedness based on overlap and decreasing fills) metric as implemented in the software ANINHADO (Guimarães & Guimarães 2006; Almeida-Neto *et al.* 2008). Statistical significance of nestedness was calculated by fitting 1000 replicates of the CE null model, which assigns each species a probability of interaction based on its connectivity. To compare nestedness values across networks with different sizes and connectances, we used relative nestedness, which is defined as $N^* = (N - N_R)/N_R$, where N is the observed nestedness in the matrix and N_R is the average nestedness of the 1000 random replicates generated from the CE null model (Bascompte *et al.* 2003).

PHYLOGENETIC STRUCTURE OF THE NETWORKS

To study the phylogenetic structure of the facilitation network it is necessary to obtain (i) a measure of the strength of the association between nurses and facilitated species and (ii) the phylogenetic trees of both nurses and facilitated species. Two measures of the strength of the association were used. The first one is the number of species interacting with each species (i.e. species degree in Appendix S1) while the second one takes into account the identity of the interacting species (i.e. species interaction in Appendix S1). Phylogenetic trees of nurse and facilitated species for each community were assembled with the help of the program Phylomatic as implemented in Phylocom 3.41 (Webb, Ackerly & Kembel 2008). This program matched the family names of our study species with those contained in a backbone phylogeny, a megatree built by the Angiosperm Phylogeny Group (Stevens 2005). Because the megatree is calibrated with age estimates from Wikström, Savolainen & Chase (2001), the program returns a calibrated tree of the study species with the undated nodes evenly distributed between dated nodes (Webb, Ackerly & Kembel 2008).

With the tree and the measures of strength association we calculated the phylogenetic signal in (i) the number of species interacting with each species (i.e. species degree) and (ii) the identity of those species (i.e. species interactions). In the first case, a significant phylogenetic signal would indicate that closely related species tend to interact with the same number of species (e.g. each Fabaceae nurse facilitates three species) whereas in the second case, a significant signal would show that closely related species tend to interact with the same set of species (e.g. each Fabaceae nurse facilitates *Mammillaria colina*, *Agave salmiana* and *Ipomoea arborescens*).

The phylogenetic signal in the species degree was calculated following the generalized least-squares (GLS) approach as implemented in the Matlab program PHYSIG.M (Blomberg, Garland & Ives 2003). This procedure calculates the K statistic, which is the ratio between the observed signal and that expected under a Brownian evolution model. The null model represents the lack of phylogenetic signal ($K = 0$). Significant signals may take values of either $K < 1$, indicating that close relatives resemble each other less than expected under Brownian motion evolution, or $K > 1$, indicating that close relatives

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are more similar than expected under Brownian motion. Statistical significance was calculated from a null model constructed with 1000 random permutations of the data across the tips of the tree. This analysis is designed for one guild and we therefore ran separate analyses for nurses (K_{nurse} in Appendix S1) and facilitated (K_{fac} in Appendix S1) species in each community. A significant signal through the nurse phylogeny indicates that closely related nurse species tend to facilitate a similar number of species; likewise, a significant signal through the facilitated species phylogeny indicates that closely related facilitated species tend recruit under a similar number of nurse species.

To account for the identity of the species interacting with each species, we calculated the phylogenetic signal of the facilitation interactions following the estimated generalized least-squares (EGLS) procedure of Ives & Godfray (2006). This procedure is similar to the Blomberg, Garland & Ives (2003) method described above to calculate phylogenetic signal but considering the matrix of interactions as the target trait. The method calculates the strength of the phylogenetic signal in the facilitative interactions acting through both the facilitated (d_{fac} in Appendix S1) and the nurse (d_{nurse} in Appendix S1) species phylogenies (see Fig. 1 for a graphical theoretical explanation and Fig. 2 for a practical example in one of the studied communities). We used the facilitation rate of nurse species k on facilitated species i (A_{ik}) as a measure of the strength of association between nurses and facilitated species following equation 4 in Ives & Godfray (2006):

$$A_{ik} = -\log\left(1 - \frac{F_{ik}}{H_i}\right)$$

where Hi is the number of individuals of the facilitated species i and F_{ik} is the number of individuals of species i recruited under the nurse species k. Note that there is a typo in the original article, indicating H_i/F_{ik} instead of the correct expression F_{ik}/H_i (A.G. Ives, personal communication).

The measure of strength of association (A_{ik}) makes sense in the context of facilitation because A_{ik} depends, as stated by Ives & Godfray (2006), on both the selectivity and abundance of host species, which are two crucial variables explaining the number of interactions occurring in facilitation networks (Verdú & Valiente-Banuet 2008).

The procedure estimates an EGLS model to fit A_{ik} in terms of the observed association strength and the separate effects of the nurse and facilitated species phylogenies. The model is based on the Ornstein–Uhlenbeck model of evolution with stabilizing selection and detects the presence of phylogenetic signal through the parameter d. This parameter determines the strength of phylogenetic signal, with $d = 0$ indicating the lack of phylogenetic correlation and $d = 1$ corresponding to the Brownian motion assumption. The goodness of fit of the different models was estimated by comparing the mean squared error calculated for (i) the full model (MSE_d), (ii) a 'star' phylogeny (MSE_{star}) and (iii) a Brownian evolution model (MSE_b). The model minimizing the mean squared error was considered the best fit. We

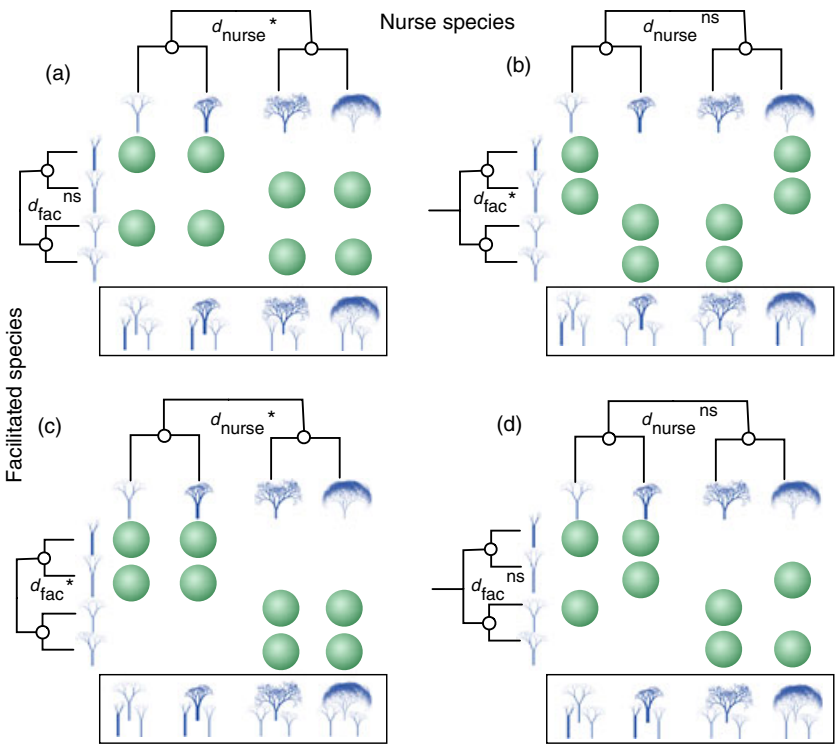

Fig. 1. Schematic representation of four communities (figures inside the rectangle) showing different phylogenetic structures in the plant facilitation networks. For each community, the pairwise interactions between nurse (in columns) and facilitated (in rows) species are indicated with circles along with their respective phylogenies. The phylogenetic signals (d values) in these interactions are marked with an asterisk when statistically significant and with 'ns' otherwise. A significant signal in the interaction matrix through the phylogeny of nurses (d_{nurse}*) occurs when a given species is facilitated by closely related nurse species. Similarly, signal through the facilitated plant phylogeny (d_{fac}*) occurs when specific nurses tend to facilitate closely related (facilitated) plants. The phylogenetic signal in the facilitation network may occur through the nurse phylogeny (community a), through the facilitated plant phylogeny (community b), through both nurse and facilitated plant phylogenies (community c), or may be absent (d).

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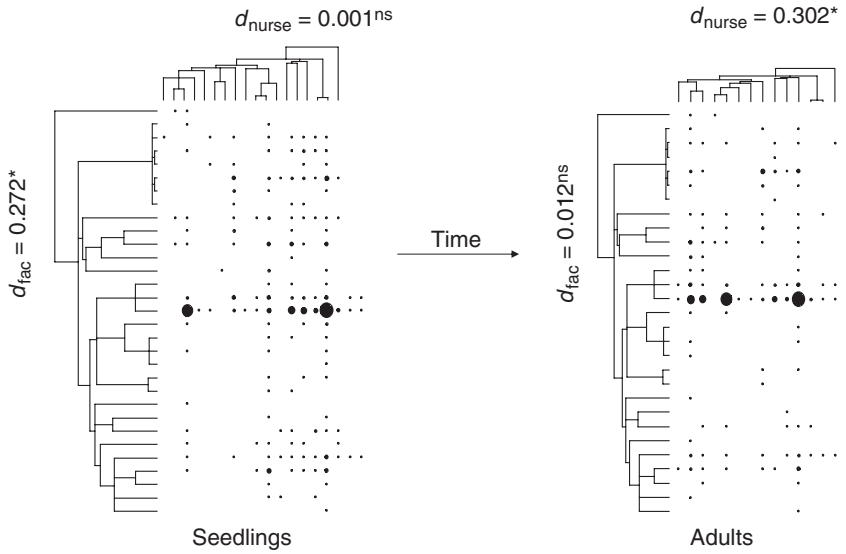

Fig. 2. Interactions occurring in the Parena2 community between nurses (columns) and facilitated plants (rows) in seedling (left) and adult (right) networks and the strength of the phylogenetic signal through different guilds (d_{nurse} and d_{fac}). The size of the circles is proportional to the number of facilitated individuals found beneath each nurse species. Significant phylogenetic signal is indicated with an asterisk (ns, otherwise) meaning that closely related species within a group tend to interact with the same species of the other group.

estimated d values for both nurse (d_{nurse}) and facilitated (d_{fac}) sets of species. Statistical significance was estimated by calculating bootstrap 95% confidence intervals (see Appendix S1 in Ives & Godfray (2006) for a discussion on the use of bootstrapping for calculating confidence intervals with this method).

Results

OVERALL STRUCTURE OF THE NETWORKS

When facilitated seedlings grow and start competing with nurses, some of the initial spatial associations disappear. These lost interactions averaged 43% of the early associations established by facilitation and ranged from 28% to 67% depending on the plant community (Table 1). Many nurse and facilitated species lost all their interactions as the latter turned into adults and therefore they were no longer connected to any other species in the adult network. The average percentage of unconnected facilitated species in the adult network was 33% (range 6–52%) and that of unconnected nurses was 24% (7–48%) across plant communities. The percentage of unconnected nurses was similar (Tetechera1, Cardonal), greater (Tetechera2, Parena1, Vizcaíno1) or lower (Parena2, Vizcaino2) than that of unconnected facilitated species.

Despite these temporal changes, the overall structure of the networks remained stable because nestedness did not significantly change with time from seedling ($n = 27.02 \pm 3.11$) to adult ($n = 30.7 \pm 4.53$) networks (Table 1; Paired t-test; $t = 0.065$, d.f $= 6$; $P = 0.95$ for relative nestedness). Similarly, network connectance did not significantly change with time from seedling ($C = 24.9 \pm 7.1$) to adult networks ($C = 27.5 \pm 3.24$) (Table 1; paired $t = -1.53$, d.f $= 6$, $P = 0.18$).

Table 1. Overall structure of the facilitation networks early in time (i.e. nurses and seedlings of facilitated plants) and late in time (i.e. nurses and adult facilitated plants). Fac, number of facilitated species; Nurse, number of nurse species; I, number of interactions; C, connectance; N, nestedness; $C = 100\ I/(F \times N)$ The temporal balance describes the percentage of facilitated (%F lost), nurses (%N lost) and interactions (%I lost) disappearing with time when comparing the seedling to the adult matrix

	Seedlings					Adults					Temporal balance		
Community	Fac	Nurse	I	C	N	Fac	Nurse	I	C	N	%F lost	%N lost	%I lost
Tetechera1	52	21	171	16	24.5**	27	11	73	25	28.9**	48	48	57
Cardonal	50	31	268	17	24.0**	30	20	136	23	27.6**	40	35	49
Tetechera2	65	27	374	21	24.5**	31	25	219	28	33.1**	52	7	41
Parena1	40	16	189	30	30.8**	31	14	133	31	31.4**	23	13	30
Parena2	31	18	143	26	25.4**	29	14	98	26	26.5**	6	22	31
Vizcaino1	30	19	172	30	30.3**	27	15	123	30	39.5**	10	21	28
Vizcaino2	35	13	158	35	29.9**	17	10	52	31	27.7*	51	23	67

*$P \leq 0.05$; **$P \leq 0.001$.

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PHYLOGENETIC STRUCTURE OF THE NETWORKS

The absence of phylogenetic signal in the degree of facilitated species (K_{fac}) in the seedling network indicates that seedlings of closely related species do not tend to recruit under a similar number of nurse species (Table 2). Similarly, the non-significant phylogenetic signals in the degree of nurse species (K_{nurse}) indicate that closely related nurses vary in the number of facilitated species they support. The same conclusions are reached in the adult networks (Table 2).

In contrast, phylogenetic signals appear in most of the networks when the identity of the interacting species is incorporated (Table 3). Accordingly, mean squared error estimations incorporating the phylogenetic signal (MSE_d) were always lower than MSE calculated under the assumptions of a star phylogeny (MSE_{star}) or Brownian motion evolution along the untransformed phylogeny (MSE_b). The magnitude of the significant signals was always less than 1, indicating lower values than expected under Brownian motion. Indeed, the fact that MSE_d was close to MSE_{star} indicates that the increase in model fit when integrating a phylogentic signal is not big. Interestingly, although weak, in all but one of the seedling networks, facilitation rates showed significant phylogenetic signals through the phylogeny of facilitated species. In contrast, the phylogeny of the nurses did not leave any signal in any of the seven communities.

As seedlings matured, the phylogenetic signals on the networks dramatically changed. In most of these adult networks, a phylogenetic signal through the phylogeny of the nurses emerged, and the early phylogenetic signal of the facilitated species disappeared in 3 communities, remained in three and appeared in one (Table 2 and Appendix S2 in Supporting Information).

Table 2. Phylogenetic signal in the number of species (degree) interacting with a facilitated plant (K_{fac}) or nurse species (K_{nurse}) in seedling networks (i.e. when facilitated plants are seedlings) and adult networks (i.e. when facilitated plants are adults). All values were non-significant

	DEGREE			
	Seedlings		Adults	
	K_{fac} (*P*-value)	K_{nurse} (*P*-value)	K_{fac} (*P*-value)	K_{nurse} (*P*-value)
Tetechera1	0.097 (0.906)	0.177 (0.849)	0.066 (0.920)	0.327 (0.841)
Cardonal	0.113 (0.769)	0.284 (0.651)	0.106 (0.786)	0.335 (0.735)
Tetechera2	0.110 (0.653)	0.118 (0.562)	0.140 (0.280)	0.241 (0.09)
Parena1	0.155 (0.725)	0.204 (0.579)	0.164 (0.727)	0.439 (0.164)
Parena2	0.243 (0.209)	0.345 (0.609)	0.247 (0.287)	0.749 (0.216)
Vizcaino1	0.111 (0.724)	0.282 (0.285)	0.073 (0.887)	0.324 (0.814)
Vizcaino2	0.074 (0.690)	0.131 (0.597)	0.144 (0.316)	0.161 (0.476)

Table 3. Phylogenetic signal in nurse-facilitated plant associations produced early in seedling networks (i.e. when facilitated plants are seedlings) and adult networks (i.e. when facilitated plants are adults). d_{fac} and d_{nurse} measure the strength of signal from the facilitated and nurse species phylogenies, respectively. Mean squared errors (MSE) are given for the cases when d_{fac} and d_{nurse} have estimated values (MSE_d), when $d_{fac} = 0$ and $d_{nurse} = 0$ (MSE_{star}), and when $d_{fac} = 1$ and $d_{nurse} = 1$ (MSE_b). Approximate bootstrap 95% confidence intervals are shown in parentheses. Significant phylogenetic signals are highlighted in bold

	Seedlings					Adults				
	d_{fac}	d_{nurse}	MSE_d	MSE_{star}	MSE_b	d_{fac}	d_{nurse}	MSE_d	MSE_{star}	MSE_b
Tetechera1	**0.428** (0.256, 0.585)	0 (0, 0.020)	0.095	0.125	0.422	0.039 (0, 0.371)	0 (0, 0.292)	0.208	0.230	0.691
Cardonal	**0.244** (0.0781, 0.4482)	0 (0, 0.0392)	0.053	0.060	0.164	**0.337** (0.099, 0.567)	0.0001 (0, 0.158)	0.098	0.115	0.307
Tetechera2	**0.012** (0.004, 0.023)	0 (0, 0.001)	0.077	0.079	0.357	0.002 (0, 0.041)	**0.207** (0.067, 0.368)	0.037	0.042	0.133
Parena1	**0.014** (0.002, 0.025)	0 (0, 0.001)	0.094	0.100	0.400	**0.482** (0.254, 0.682)	**0.148** (0.024, 0.375)	0.063	0.089	0.111
Parena2	**0.272** (0.088, 0.483)	0.001 (0, 0.103)	0.071	0.078	0.156	0.012 (0, 0.162)	**0.302** (0.050, 0.639)	0.192	0.212	0.369
Vizcaino1	**0.132** (0.009, 0.331)	0 (0, 0.036)	0.090	0.098	0.520	**0.235** (0.096, 0.526)	0 (0, 0.010)	0.127	0.159	0.379
Vizcaino2	0 (0, 0.018)	0.01 (0, 0.151)	0.160	0.166	0.756	**0.485** (0.202, 0.798)	**0.256** (0.042, 0.581)	0.175	0.232	0.233

Discussion

The main finding of this paper is that facilitation networks show an overall structure that is stable in space and time, but dramatically different if we account for the phylogenetic influences of nurse and facilitated species. Nurses facilitating seedlings of other species are assembled in a network of interactions characterized by a high level of nestedness. This pattern was generalized among all the communities studied and reveals a markedly non-random pattern of facilitative interactions in these communities. As the facilitated seedlings mature, many interactions with nurses disappear but the overall characteristics of the networks (nestedness and connectance) remain stable.

There is no significant phylogenetic signal if we consider the number of the facilitative interactions established by nurses (i.e. closely related nurse species do vary in the number of species facilitated) or facilitated species (i.e. closely related facilitated species do not recruit under a similar number of nurse species). Consequently, we cannot use the taxonomic affiliation to predict how many species a nurse can facilitate or how many nurse species a facilitated species can recruit under. However, strong predictions can be made when looking simultaneously at the phylogenetic identity of both interactors, supporting the idea that facilitative interactions are highly species-specific (Callaway 2007; Verdú & Valiente-Banuet 2008).

Most of the phylogenetic signals found in the facilitation interactions in our study communities at the seedling stage occur through the phylogenies of facilitated species but not through the nurse phylogenies. This means that when considering the overall interaction pattern, we do not detect a distinct influence of the higher taxa of the nurse community, i.e. a given facilitated species can be recorded growing beneath a random phylogenetic range of nurse taxa. However, a given nurse species tends to be associated with phylogenetically related facilitated species. In other words, closely related nurses do not facilitate the same set of species but closely related facilitated species tend to recruit under the same set of nurse species (see top-right panel of Fig. 1). The phylogeny of the nurses does not show a distinct signal on the interaction with their facilitated seedlings, in accordance with an absence of effect of the seedlings on the nurses. In contrast, the phylogeny of facilitated seedlings shows a signal in the interaction with their nurses suggesting that seedlings strongly depend on the regeneration niche provided by the nurses. The fact that closely related species have similar regeneration patterns is supported by the strong evolutionary conservatism of the regeneration niche shown in woody plants (Valiente-Banuet & Verdú 2007). The high specificity of the facilitative interactions at early stages is supported by both theoretical network models (Verdú & Valiente-Banuet 2008) and experimental studies showing that the performance of facilitated seedlings is dependent on the identity of the nurse (Carrillo-García, Bashan & Bethlenfalvay 2000; Puerta-Piñero, Gómez & Zamora 2006; Castillo, Verdú & Valiente-Banuet 2010)

As facilitated seedlings grow up, their physical environment requirements may change and therefore the sign of the interaction may also change with time. Many of the positive interactions turn into competition causing early species associations to disappear. A clear indication that competition is causing the change between seedling and adult networks is that temporal shifts from facilitation to competition occur between closely related taxa (see Valiente-Banuet & Verdú (2008) for a detailed analysis based on the competition – relatedness hypothesis). According to this pattern we have found that a new characteristic emerging in most of the adult networks is the appearance of a significant phylogenetic signal on the interaction pattern through the nurse phylogeny. In other words, closely related nurse species tend to be associated with the same subset of facilitated species in the community. It is clear that at this adult stage, nurses are no longer indifferent to the phylogenetic identity of their associated species because competition or mutualism may alter the outcome of the interaction (Valiente-Banuet & Verdú 2008). The nurse phylogeny significantly explains the structure of the adult networks since closely related nurses are expected to behave similarly in terms of competition and mutualism with their facilitated species. However, the net balance of the positive and negative interactions seems to be more complicated because all the possible combinations of phylogenetic signals are found in the seven study communities: no signal, signal through the phylogeny of the nurses, signal through the facilitated species phylogeny, and signals through the phylogeny of both guilds at the same time. Such differences suggest that, in addition to climatic factors, the geographical variation in the species composition itself would also drive community dynamics through its effects on facilitation of recruitment. For instance, the different composition of nurses in each community results in different facilitative associations for the same species (e.g. *Agave peacockii*, *Bouteloua gracilis*, *Justicia mexicana*) indicating that the outcome of these facilitation processes vary among the local populations and communities analysed and suggesting a potential geographic framework (Thompson 2005) of community patterns driven by plant–plant interactions.

Our results provide evidence that plant–plant species interactions lead to highly species-specific networks in which the phylogenetic history has a pervasive influence not only on recruitment but also on adult community composition. These results have deep implications for the conservation of biodiversity. As Ives & Godfray (2006) stated, we can use estimates of phylogenetic signals to predict the fate of novel interactions, as for example those produced when biological invasions take place. Detecting significant phylogenetic structure of the facilitation networks also allows predicting the amount of phylogenetic diversity lost following coextinction cascades (Rezende *et al.* 2007). The use of phylogenetic methods combined with complex network approaches opens the possibility to understand the complexity of ecological interactions occurring in nature.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Parameters used to test for the overall and the phylogenetic structure of seedling and adult facilitation networks.

Appendix S2. Interactions occurring between nurses and facilitated plants in seedling and adult networks and the strength of the phylogenetic signal through different guilds.

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Temporal changes in the overall structure

Nestedness (N seedlings) → Nestedness (N adults)

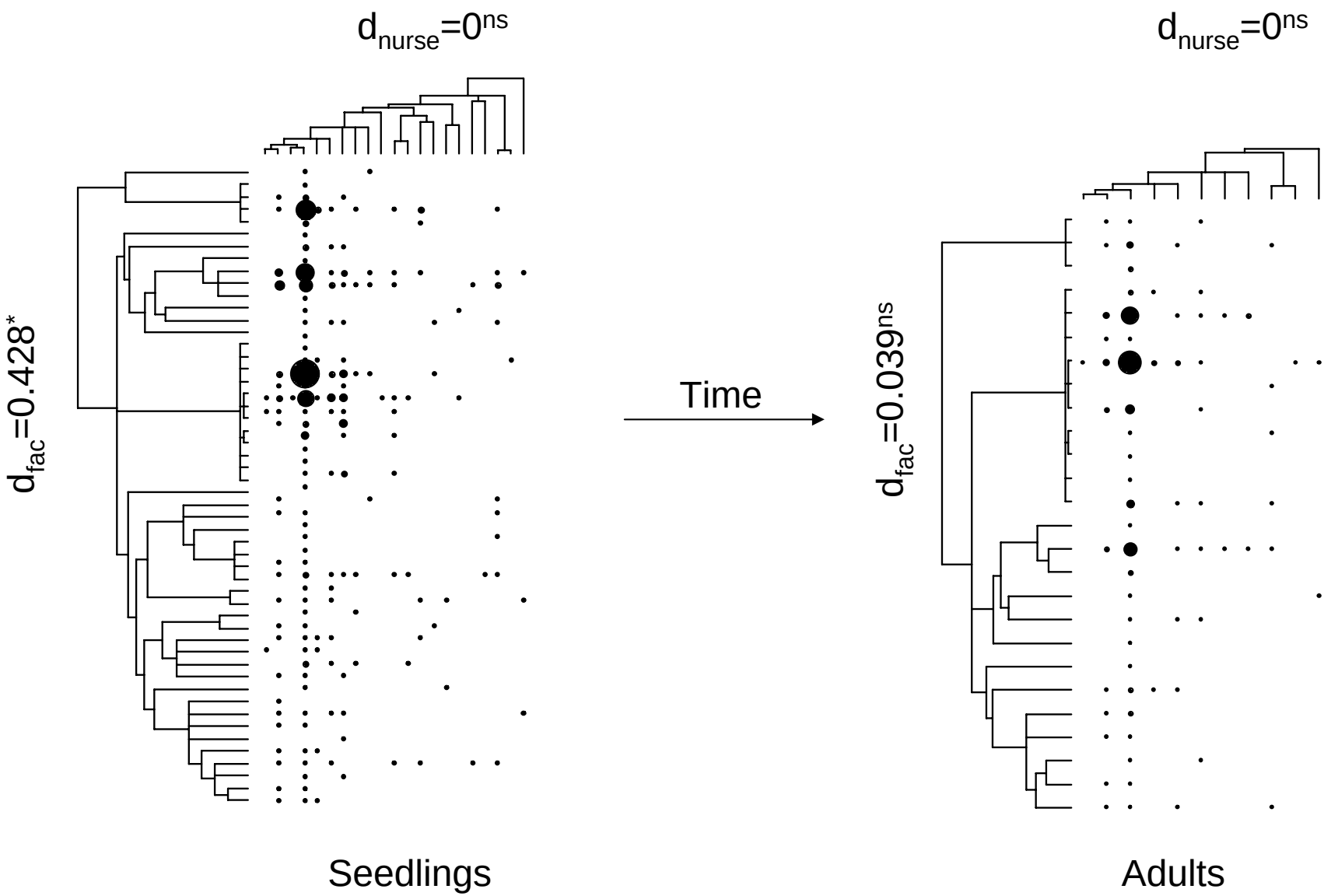
Connectance (C seedlings) → Connectance (C adults)

Temporal changes in the phylogenetic structure

Phylogenetic signal in species degree { Facilitated species (K_{fac} seedlings); Nurse species (K_{nurse} seedlings) } → Phylogenetic signal in species degree { Facilitated species (K_{fac} adults); Nurse species (K_{nurse} adults) }

Phylogenetic signal in species interactions { Facilitated species (d_{fac} seedlings); Nurse species (d_{nurse} seedlings) } → Phylogenetic signal in species interactions { Facilitated species (d_{fac} adults); Nurse species (d_{nurse} adults) }

Tetechera 1


$d_{nurse}=0^{ns}$
$d_{fac}=0.428^{*}$
Time
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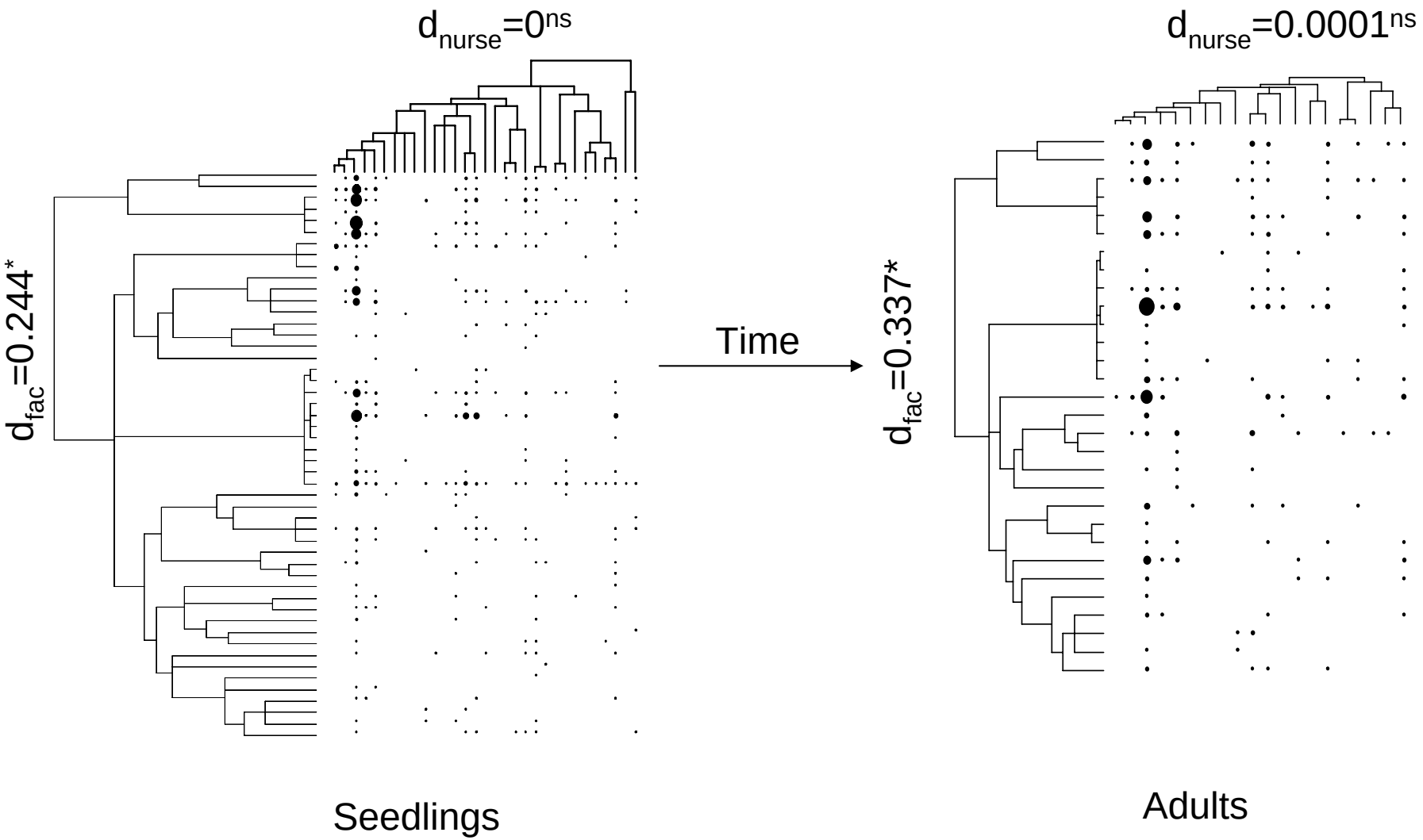
$d_{fac}=0.039^{ns}$
Seedlings
Adults

Cardonal


$d_{nurse}=0^{ns}$
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Time
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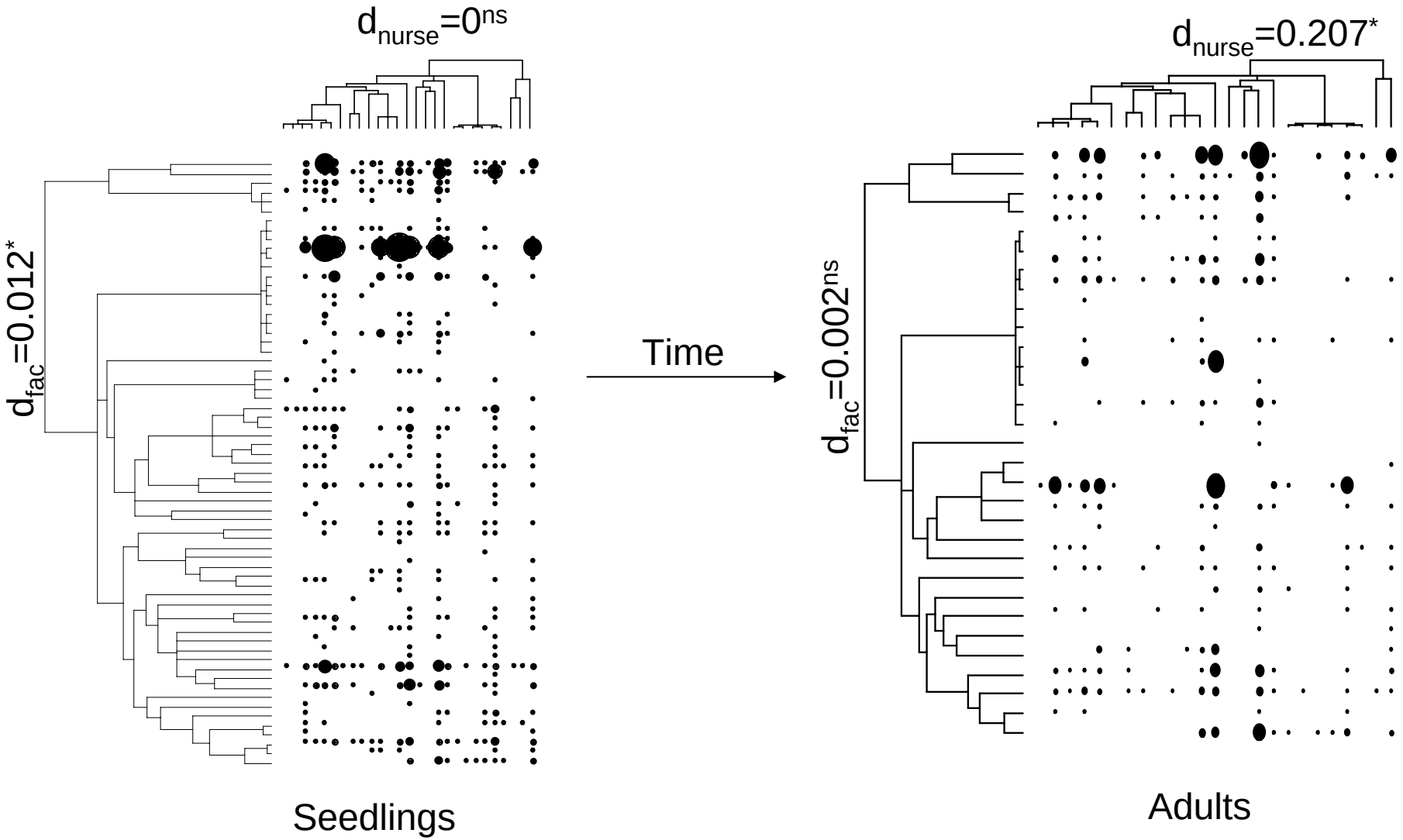
$d_{fac}=0.337^{*}$
Seedlings
Adults

Tetechera 2


$d_{nurse}=0^{ns}$
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Time
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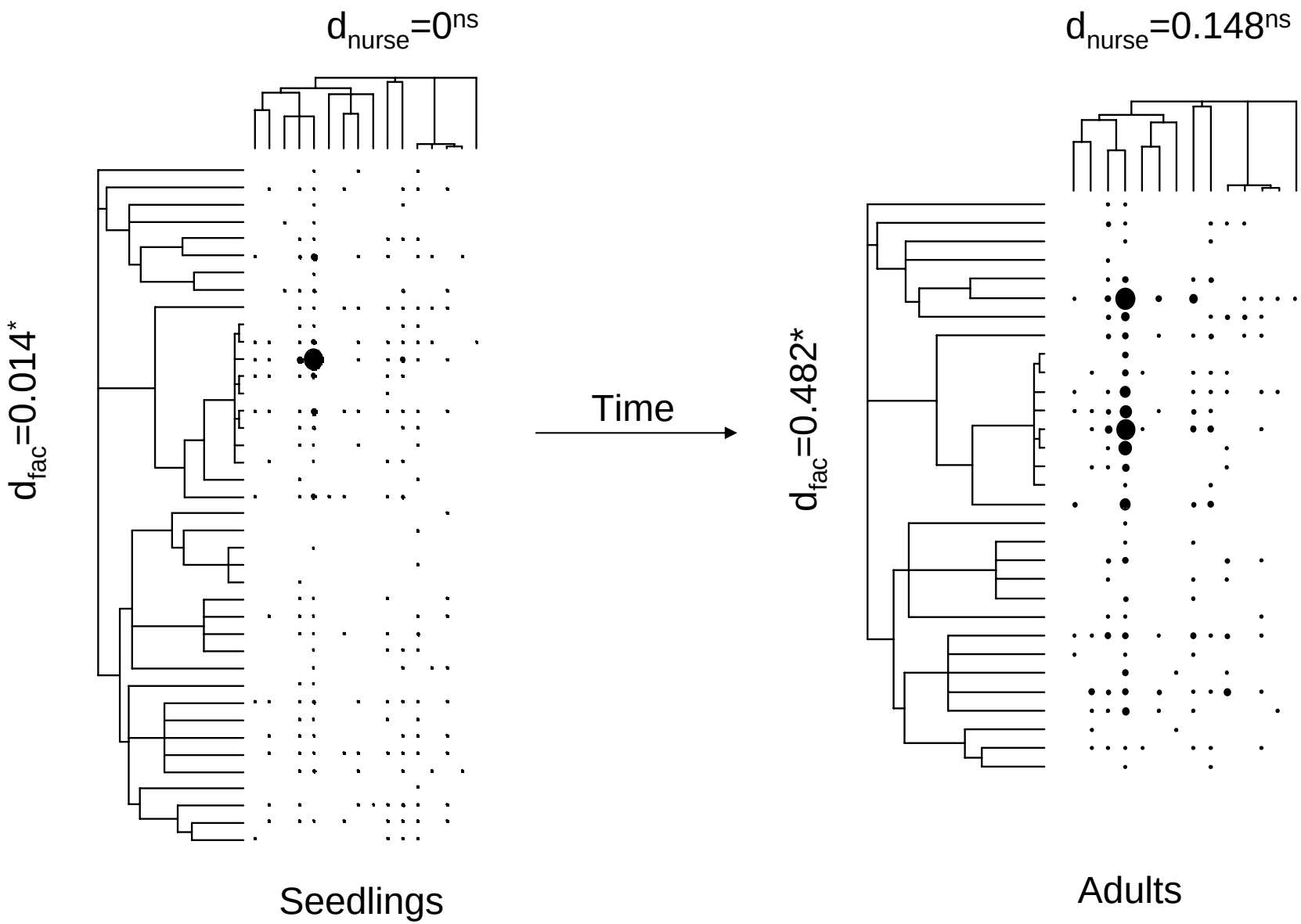
$d_{fac}=0.002^{ns}$
Seedlings
Adults

Parena1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$d_{fac}=0.014^{*}$
Time
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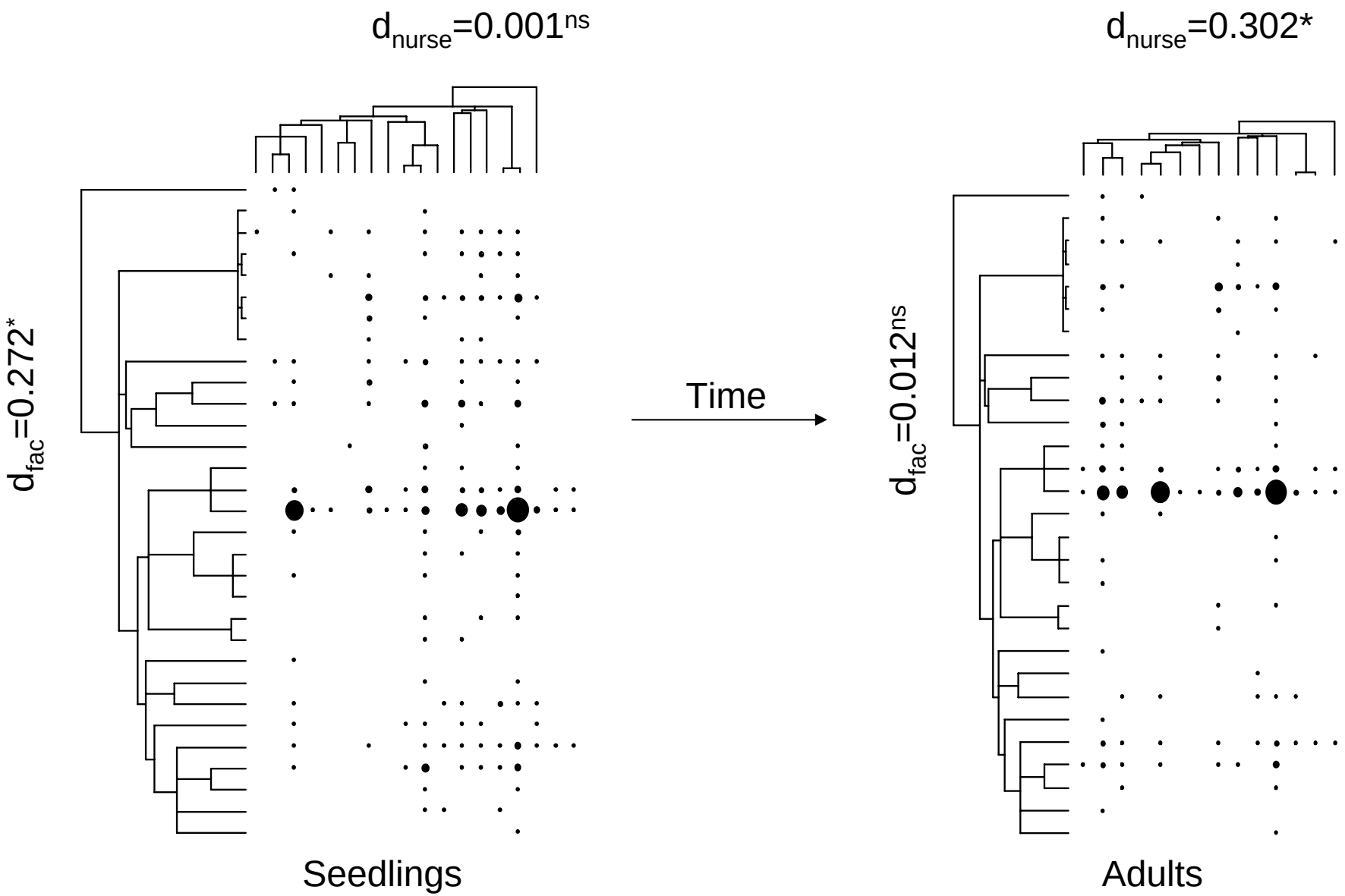
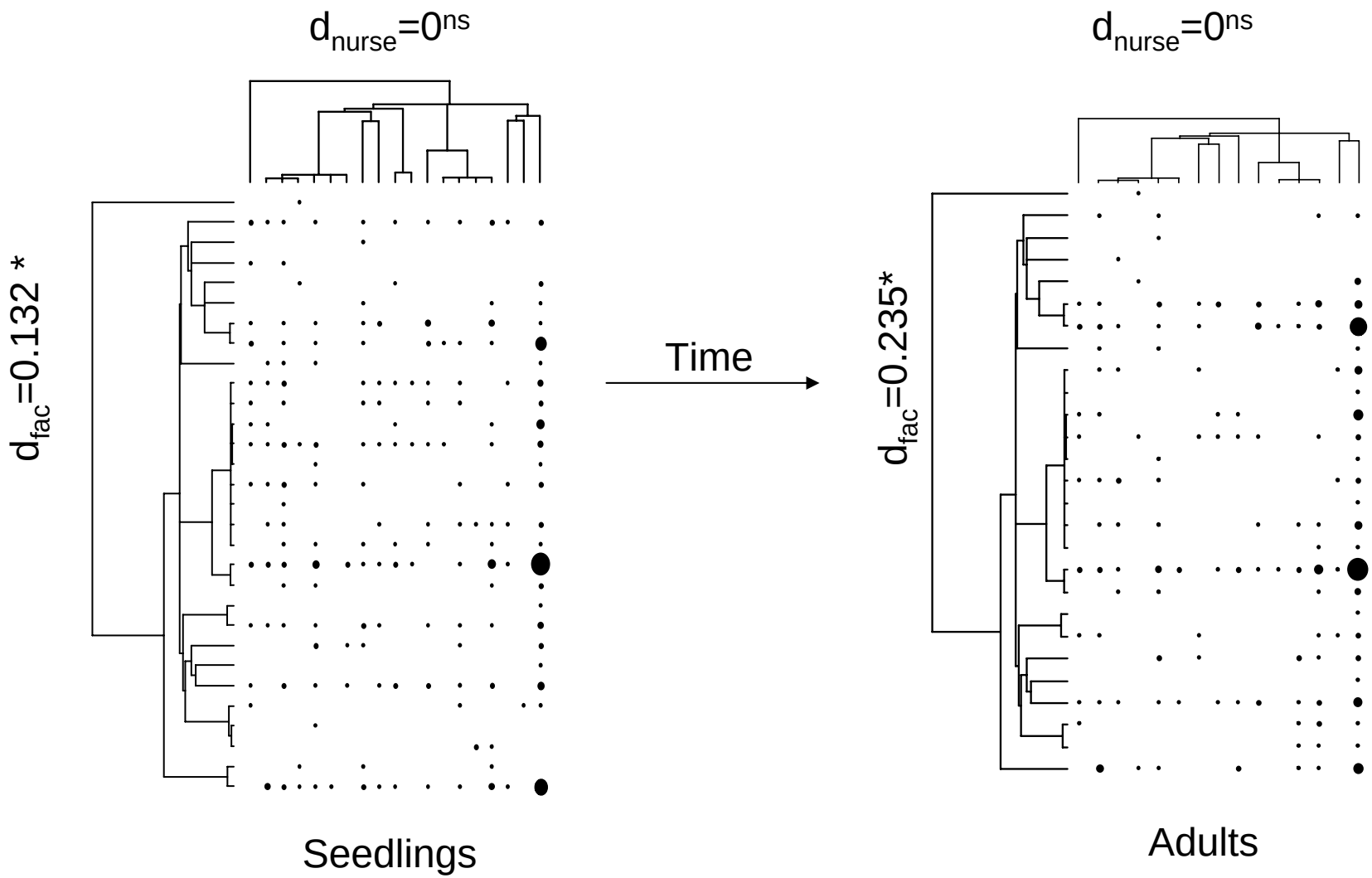
$d_{fac}=0.482^{*}$
Seedlings
Adults

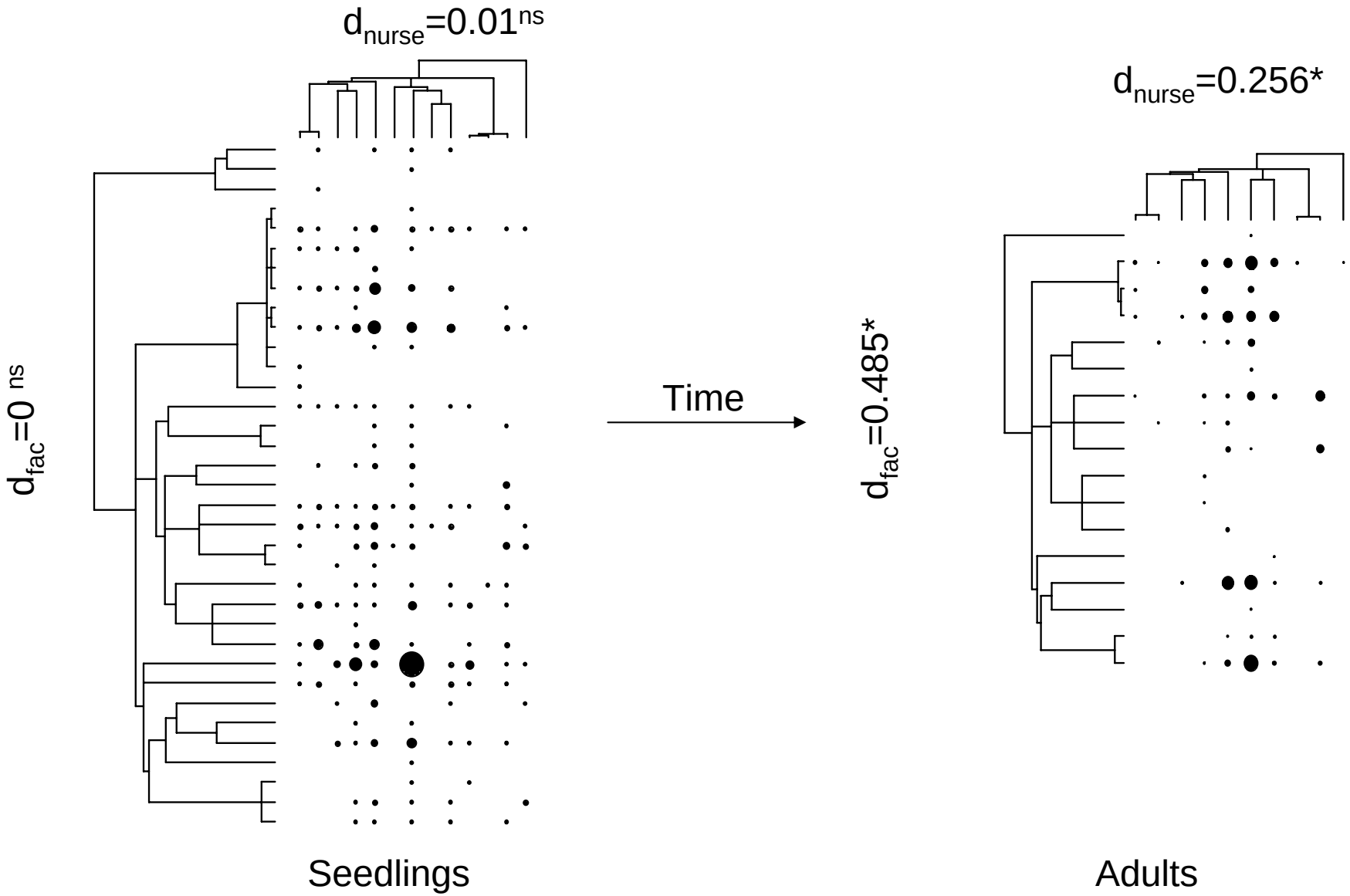
Parena2


$d_{nurse}=0.001^{ns}$
$d_{fac}=0.272^{*}$
Time
Seedlings
$d_{nurse}=0.302^{*}$
$d_{fac}=0.012^{ns}$
Adults

Vizcaíno 1


$d_{nurse}=0^{ns}$
$d_{fac}=0.132$ *
Time
Seedlings
$d_{nurse}=0^{ns}$
$d_{fac}=0.235$*
Adults

Vizcaíno 2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$d_{fac}=0^{ns}$
Time
$d_{nurse}=0.256^{*}$
$d_{fac}=0.485^{*}$
Seedlings
Adults