Resistance of plant–plant networks to biodiversity loss and secondary extinctions following simulated environmental changes

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Summary

1. Plant interactions are fundamental processes for structuring plant communities and are an important mechanism governing the response of plant species and communities to environmental changes. Thus, understanding the role played by the interaction network in modulating the impact of environmental changes on plant community composition and diversity is crucial. Here, we aimed to develop a new analytical and conceptual framework to evaluate the responses of plant communities to environmental changes.

2. This framework uses functional traits as sensitivity measures for simulated environmental changes and assesses the consequences of microhabitat loss. We show here its application to an alpine plant community where we recorded functional traits [specific leaf area (SLA) and leaf dry matter content (LDMC)] of all plants associated with three foundation species or the surrounding open areas. We then simulated primary species loss based on different scenarios of environmental change and explored community persistence to the loss of foundation species.

3. Generally, plant community responses differed among environmental change scenarios. In a scenario of increasing drought alone (i.e. species with lower LDMC were lost first) or increasing drought with increasing temperature (i.e. species with lower LDMC and higher SLA were lost first), the plant community resisted because drought-tolerant foundation species tolerated those deteriorating conditions. However, in scenarios with increasing nitrogen input (i.e. species having lower SLA were lost earlier), foundation species accelerated species loss due to their early primary extinctions and the corresponding secondary extinctions of species associated to their microhabitat.

4. The resistance of a plant community depends on the driver of environmental change, meaning that the prediction of the fate of this system is depending on the knowledge of the main driver of environmental change. Our framework provides a mechanistic understanding of an ecosystem response to such environmental changes thanks to the integration of biology-informed criteria of species sensitivities to environmental factors into a network of interacting species.

Key-words: biodiversity loss, ecological networks, drought, facilitation, foundation species, nitrogen deposition, plant–plant interactions, trait-based extinction model

Introduction

There is evidence that global environmental changes are affecting the stability of ecosystems (Hautier *et al.* 2015) causing a world-wide decline in biodiversity (Cardinale *et al.* 2012) with unprecedented high extinction rates (Pimm *et al.* 2014). However, the consequences of environmental changes for biotic interactions are much less known (Bascompte & Jordano 2014; Michalet *et al.* 2014), despite the importance of species interactions for mediating species tolerance and community persistence under environmental changes (Ives & Cardinale 2004; Fortuna & Bascompte 2006; Memmott *et al.* 2007; Saavedra *et al.* 2013).

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Plant–plant interactions are fundamental processes for structuring plant communities (Klanderud 2005; Michalet *et al.* 2015). In alpine ecosystems, where harsh environmental conditions prevail (e.g. low temperature, poor soil), stress-tolerant foundation species (i.e. species that influence community structure and ecosystem processes, *sensu* Ellison *et al.* 2005) often promote species survival and growth, and community-level diversity, through creation of unique microhabitats (Cavieres *et al.* 2014). These effects have been attributed to facilitative effects of foundation species on their co-occurring plant species, for example through the ability of foundation species to ameliorate microenvironmental conditions (Schöb, Butterfield & Pugnaire 2012; Butterfield & Callaway 2013; McIntire & Fajardo 2014). Thus, understanding the role played by microhabitats created by foundation species in sustaining biodiversity with a changing climate is crucial (Ellison *et al.* 2005; Brooker 2006), especially in Mediterranean alpine ecosystems, where facilitation by foundation species is particularly relevant for plant community diversity (Schöb, Armas & Pugnaire 2013b; Michalet *et al.* 2014; Pistón *et al.* 2016). Consequently, plant–plant interactions matter, but our tests of their importance are generally pairwise. A holistic community-level approach that considers networks of interacting species would be useful and might improve our understanding of species and community responses to environmental changes. However, such a network approach has hardly been employed so far (but see Verdú & Valiente-Banuet 2008; Allesina & Levine 2011; Saiz & Alados 2011).

To investigate the resistance of a community to environmental perturbations, a common approach is to perform random extinctions or target extinctions that eliminate the most and the least connected species of an interaction network first (Solé & Montoya 2001; Dunne, Williams & Martinez 2002; Memmott, Waser & Price 2004; Verdú & Valiente-Banuet 2008). However, such an approach does not consider species sensitivity to specific environmental changes (Ives & Cardinale 2004; Curtsdotter *et al.* 2011). Functional traits can offer such a biology-informed, mechanistic link between prevailing environmental conditions and the likelihood of species survival (McGill *et al.* 2006; Garnier, Navas & Grigulis 2016). Indeed, by capturing essential aspects of species' ecophysiology, functional traits determine the sensitivity of plants to biotic and abiotic factors (Grime 2001; Westoby *et al.* 2002; Ackerly 2004; Schöb, Butterfield & Pugnaire 2012; Butterfield & Callaway 2013). Consequently, traits predispose plant species to extinction under certain kinds of environmental changes (Cardinale *et al.* 2012).

In this study, we present a new analytical and conceptual framework to simulate plant community persistence against environmental perturbations, showing its application to a Mediterranean alpine plant community dominated by three foundation species. We characterise the plant–plant interaction network and explore the consequences of foundation species loss for biodiversity using functional traits as a biological criterion of species'

sensitivity to environmental changes. We then estimate the loss of species that is caused by the primary loss of microhabitats created by foundation species (i.e. secondary extinctions *sensu* Brodie *et al.* 2014). We hypothesised that community persistence and the rate of species loss varied among environmental change scenarios, as would the role of foundation species in modulating the species loss.

Materials and methods

STUDY AREA

The study was performed in the Sierra Nevada Mountains (Spain, 2725 m a.s.l., 37·08134°N, −3·38127°E), where the importance of positive plant interactions for community structure and diversity is well documented (Schöb, Butterfield & Pugnaire 2012; Schöb *et al.* 2013a; Schöb, Armas & Pugnaire 2013b; Schöb *et al.* 2014; Pistón *et al.* 2016). The site was a relatively homogeneous 0·5 ha plot, with a patchy plant community dominated by three foundation species: the cushion-forming species *Arenaria tetraquetra* spp. *amabilis* (Bory) H. Lindb. Fil. (Caryophyllaceae) and *Plantago holosteum* Scop. (Plantaginaceae), and the tussock grass *Festuca indigesta* Boiss. (Poaceae). At the closest weather station in Pradollano (2500 m a.s.l.; 37·08333°N, −3·38333°E) mean growing season (May–September) temperature is 13·8 °C (average min 6·2 °C, average max 21·5 °C) and mean annual precipitation is 690 mm, with a dry summer period during July and August (http://es.climate-data.org). The habitat belongs to the oro-Mediterranean acidic grassland type characterised by low-productivity, siliceous gravel substrate with poorly developed soils and generally low soil organic matter and water content (Schöb, Butterfield & Pugnaire 2012). The examined foundation species are known to provide positive effects on some other plant species in the study area, mainly through provision of higher soil organic matter and soil water compared to bare ground (i.e. open) areas (Schöb, Butterfield & Pugnaire 2012; Schöb, Armas & Pugnaire 2013b; Schöb *et al.* 2017). This positive, facilitative effect was demonstrated by a better plant water status and higher reproductive output of subordinate species associated to foundation species (Schöb *et al.* 2014), indicating the dependency of subordinate species on microhabitats created by foundation species for their survival and reproduction.

Sampling was performed within the canopy area of 40 individuals of each of the three foundation species and in 10 open areas (hereafter, we refer to these samples as plots and to the each of the three foundation species and the open areas as different microhabitats respectively). We identified all individuals of plant species in each plot and subsequently refer to them as subordinate plant species either occurring within the canopy of foundation species or in the open microhabitat (see Appendix S1 in Supporting Information). As plant–plant interactions are local processes acting at fine spatial scale, sampling was performed at a centimetre scale, consistent with previous studies in the study area that inferred plant interactions from spatial patterns (Schöb, Butterfield & Pugnaire 2012; Schöb *et al.* 2013a, 2014; Schöb, Armas & Pugnaire 2013b; Pistón *et al.* 2016). Plot size was equal to the foundation species canopy size: 168 (8–406) cm^2 [mean (min − max)] for *Arenaria*; 149 (3–638) cm^2 for *Plantago;* 241 (<1–1018) cm^2 for *Festuca*. In the open we sampled circular plots (27·6 cm diameter or 598 cm^2) that were randomly placed in gaps between foundation species.

TRAIT-ENVIRONMENT RELATIONSHIPS

We used two functional traits with a known sensitivity to environmental conditions and related to resource use strategies: specific

leaf area (SLA) and leaf dry matter content (LDMC). SLA increases with soil nutrient availability (Ordoñez *et al.* 2009) and is related to photosynthesis and respiration (Garnier, Navas & Grigulis 2016). LDMC increases with drought (Ackerly 2004), where physically robust species have high LDMC with high carbon-construction costs (Westoby *et al.* 2002). Along this leaf economics spectrum (Díaz *et al.* 2016), species with high LDMC and low SLA have lower photosynthetic rates and slower return on investment, indicating a conservative growth strategy and high drought stress tolerance (due to reduced water loss). Vice versa, species with high SLA and low LDMC acquire resources faster, showing high competitive ability but lower stress tolerance (i.e. higher vulnerability to stress).

Thus, we assumed that under the scenario of (i) increasing drought alone (i.e. without temperature limitation), reducing water loss through high LDMC is a relevant strategy (Grime 2001; Ackerly 2004; Liancourt *et al.* 2015); (ii) combined increases of drought and temperature, LDMC may increase, whereas SLA decreases (Liancourt *et al.* 2015); (iii) increasing nutrients, a rapid resource-acquisitive strategy (i.e. high SLA) is beneficial and would confer a competitive advantage under the subsequent increase in competition (Wright *et al.* 2005; Liancourt *et al.* 2013; Garnier, Navas & Grigulis 2016). A scenario with temperature increase alone was not assessed because it is reasonable to assume that in such dry alpine ecosystem temperature increase alone, without changing water availability, would result in a more drought stress (i.e. scenario 1 and 2, IPCC 2014).

The trait measurement procedure followed a standard protocol (Pérez-Harguindeguy *et al.* 2013). For each individual subordinate plant and for five individuals of each foundation species the best-developed and most healthy leaf was collected ($n = 1340$). Leaves were fully rehydrated before determining the fresh mass and the leaf area, then they were dried at 80 °C for at least 72 h to determine dry mass. SLA was measured as the ratio between leaf area measured as one-sided surface area of an individual lamina (m^2) and leaf dry mass ($m^2 \ kg^{-1}$), and LDMC was measured as the ratio between leaf dry mass and water-saturated fresh mass ($g \ kg^{-1}$). The sampling took place at the peak of the growing season, between the end of July and the beginning of August 2011.

PLANT ASSOCIATION NETWORK

The network was built from the observed community matrix, i.e. the set of abundance data for n subordinate species growing within m microhabitats (i.e. the three foundation species and open areas), considering all plant species as nodes and co-occurrence between subordinate species and foundation species or open areas as pairwise links (Fig. 1). Then, the one preferred microhabitat for each subordinate species was identified with a community structure detection algorithm, which computed optimal partitioning of species into the four microhabitats. This algorithm maximises modularity with simulated annealing according to patterns of intra- and inter-module connections (Guimerà & Amaral 2005; Doulcier & Stouffer 2015).

SPECIES EXTINCTION MODEL

The species extinction procedure as a consequence of simulated environmental changes consisted of three main steps. First, for each iteration of primary extinction (see below), a species trait value was sampled from its trait distribution (i.e. a normal distribution with a mean equal to each species' observed trait mean over all microhabitats and the standard deviation equal to each species' observed standard deviation). With this procedure we accounted for intraspecific trait variation at the study site (i.e. species trait plasticity, Fig. S2).

Second, based on the above-mentioned relationships among leaf traits and environmental conditions, species were removed according to the following criteria. For increasing drought alone (hereafter scenario D), species were removed in order of increasing LDMC, with species having the lowest LDMC to be removed first. As increase in drought and temperature (hereafter scenario D & T) is based on both LDMC and SLA, to sort plant species within this bivariate trait space, a principal component analysis (PCA) was carried out, including species trait values as active variables. First, the correlation coefficients between the two variables were evaluated. Since we expected an inverse relationship between LDMC and SLA (Pérez-Harguindeguy *et al.* 2013), we selected
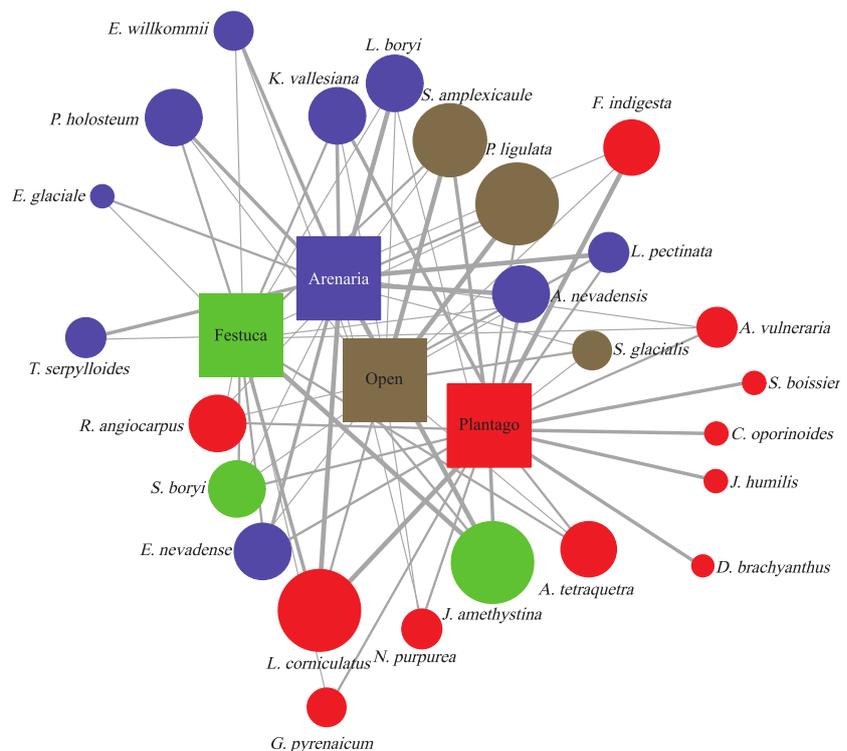

Fig. 1. Plant–plant network in the Sierra Nevada, Spain. Plant species are represented by nodes, whose dimensions are proportional to the species abundance. Links are proportional to the number of links (i.e. individuals) between species. Link length depends on node position according to the Kamada & Kawai force-directed algorithm (Csárdi & Nepusz 2006). Microhabitats are represented by rectangles, subordinate species by circles. Colours depict network modules (i.e. microhabitat preferences): blue for *Arenaria tetraquetra* spp. *amabilis,* green for *Festuca indigesta,* red for *Plantago holosteum* and brown for open microhabitat.

the main axis of the PCA that described the negative correlation between these two traits. Then, species were sorted according to their coordinates on the axis and removed in order of increasing values, with species having the lowest values along the selected axis (i.e. low LDMC and high SLA) to be removed first. For increasing nitrogen deposition (hereafter scenario N), species were removed in order of increasing SLA, with species having the lowest SLA to be removed first. Besides these three environmental change scenarios, we performed a random extinction model (hereafter scenario R) by randomly removing species from the network. For each scenario the corresponding trait space was divided into 25 equally spaced intervals, representing the primary extinction sequence. At each step (1, 2, 3, ..., 25), an increasing number of intervals of the trait range was removed from the viable trait space and plant species that did not fit this viable trait space were removed from the network. In other words, plant species that fell out of the range of surviving trait values were considered primary extinct. In the scenario R, an equal number of species was removed in each extinction sequence. Therefore, different to previous extinction models (Solé & Montoya 2001; Dunne, Williams & Martinez 2002; Memmott, Waser & Price 2004; Verdú & Valiente-Banuet 2008), such as scenario R, the biology-informed extinction sequences using functional traits could result in unequal numbers of species removed from the network during each primary extinction iteration, depending exclusively on the number of species assigned to each trait interval.

Third, besides primary extinctions, we considered also secondary extinctions (*sensu* Brodie *et al.* 2014). Since each foundation species provides specific and unique microenvironmental conditions (Ellison *et al.* 2005; Schöb, Butterfield & Pugnaire 2012; Schöb, Armas & Pugnaire 2013b; Schöb *et al.* 2013a; Butterfield & Callaway 2013; McIntire & Fajardo 2014), their loss can be compared to the loss of a microhabitat. Thus, we defined secondary extinctions as the loss of subordinate species due to microhabitat loss, i.e. the loss of those species that belonged to the module of a foundation species that got primary extinct.

Every primary extinction step was iterated 200 times (*n* replicates = 25 000). At the end of each iteration we computed: (i) the proportion of surviving species (i.e. relative species richness) within the network, calculated as the sum of species that survived divided by the total species richness; (ii) the proportion of secondary extinctions, calculated as the sum of secondary extinctions divided by the total number of extinctions (i.e. primary plus secondary); (iii) the persistence status of each plant species (i.e. survival, primary or secondary extinct).

STATISTICAL ANALYSIS

We used linear mixed effects models to test the response variables (i) proportion of surviving species and (ii) proportion of secondary extinctions as a function of the extinction scenarios (fixed effect), number of foundations species (fixed effect) and their interaction (fixed effect), with random effects being the iteration nested within each extinction step. To account for series autocorrelation, the steps along the sequences within each scenario were included in the first-order correlation model for the residual error component (Butler *et al.* 2007). The significance of the models was tested with Wald tests.

To confirm the relevance of the model, we assessed whether subordinate species differed in their probability of surviving or getting secondary extinct by fitting a multinomial logit model with the status of the species (survived, primary or secondary extinct) as response categories and the species as predictors (Venables & Ripley 2002). The primary extinction was considered as reference level. Then, to explore which biotic factors make species more likely to persist or to get secondary extinct, generalised linear models (GLM) were fitted with the module membership and the abundance of each subordinate species as predictors and the likelihood (i.e. the logit estimated by the multinomial logit model) of survival or to get secondary extinct as responses. The likelihood to get primary extinct was taken as reference level for these analyses. The significance of the models was tested with ANOVA tests and likelihood-ratio χ^2 estimation.

Analyses were performed in R 3.1.3. (R Core Team 2015) using *igraph* for network analysis (Csárdi & Nepusz 2006), *Rnetcarto* for network modularity (Doulcier & Stouffer 2015), *asreml* for mixed effects models (Butler *et al.* 2007), *pascal* for Wald tests and *nnet* for the multinomial logit model (Venables & Ripley 2002).

Results

PLANT ASSOCIATION NETWORK RESPONSE

The plant association network was composed of four modules corresponding to the four microhabitat types (Fig. 1). The *Plantago* module was the most species rich, with 11 associated subordinate species, followed by the *Arenaria* module composed of nine associated subordinate species, the *Festuca* module with two associated subordinate species and the *open* module with three associated subordinate species.

The three environmental change scenarios and the number of foundation species had significantly interactive effects on the proportion of surviving species (Table 1). In scenario D of increasing drought alone, in scenario D & T of increasing drought and temperature, and in scenario random, species diversity smoothly decreased in the first half of the sequence, with, on average, 50% of the species disappearing after removal of c. 40% of the trait space (Fig. 2). Then, in the second half of the sequence a further

Table 1. Fixed effects test and variance component estimates (standard error) for linear mixed-effects models

	Species survival	Secondary extinctions
Fixed effects		
Intercept	$F_{1,13\ 163} = 70.0$***	$F_{1,15\ 015} = 10.4$***
Scenario	$F_{3,13\ 163} = 838.6$***	$F_{3,15\ 015} = 3230.0$***
Foundation sp	$F_{3,13\ 163} = 12310.0$***	$F_{3,15\ 015} = 14080.0$***
Scenario × Foundation	$F_{9,13\ 163} = 345.4$***	$F_{9,15\ 015} = 136.2$***
Variance components		
Step/Iteration	9.0×10^{-3} (1.0×10^{-5})	5.3×10^{-7} (3.4×10^{-11})
Series autocorrelation		
ρAR1	0.5 (6.1×10^{-3})	0.4 (6.6×10^{-3})

The number of foundation species and its interaction with the five environmental change scenarios are predictors of species survival and secondary extinctions. ***$P < 0.001$.
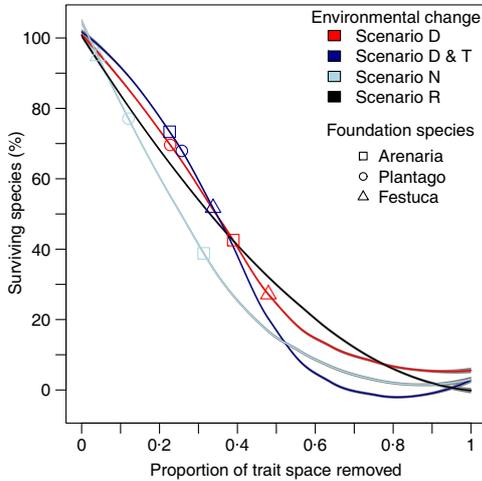
Fig. 2. Species diversity response (*y*-axis) to the three environmental change scenarios and the random model along the removal sequence (*x*-axis). Scenario D: increasing drought alone; Scenario D & T: increasing drought and temperature; Scenario N: increasing nitrogen deposition; Scenario R: random model. Squares (*Arenaria tetraquetra* ssp. *amabilis*), circles (*Plantago holosteum*) and triangles (*Festuca indigesta*) show where each foundation species goes extinct on average. Lines fitted with a local polynomial surface (mean ± 95% CI).
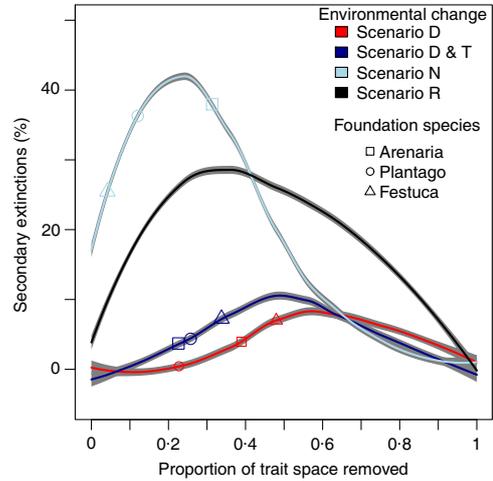

Fig. 3. Secondary extinctions (*y*-axis) in response to the three environmental change scenarios and the random model along the removal sequence (*x*-axis). Scenario D: increasing drought alone; Scenario D & T: increasing drought and temperature; Scenario N: increasing nitrogen deposition; Scenario R: random model. Squares (*Arenaria tetraquetra* ssp. *amabilis*), circles (*Plantago holosteum*) and triangles (*Festuca indigesta*) show where each foundation species goes extinct on average. Lines fitted with a local polynomial surface (mean ± 95% CI).

intensification of environmental changes caused less extinction. In scenario D, *Arenaria*, *Plantago* and *Festuca* disappeared after removal of 39, 23 and 48% of the trait space, respectively, whereas in scenario D & T they disappeared after 23, 26 and 34% respectively. These scenarios produced less secondary extinction events (4 and 5% on average respectively) and created hump-shaped responses of secondary extinctions, which made up to 10% of the species losses when 56 and 49% of the trait spaces were removed respectively (Fig. 3). Scenario N of increasing nitrogen deposition produced a constant steep decline in species diversity, with 50% of species disappearing when c. 25% of the trait space was removed (Fig. 2). After removal of 40% of the trait space, species diversity showed a slower nonlinear decrease. This scenario caused the highest secondary extinction rates (on average 20%), with a right-skewed hump-shaped pattern along the trait range removal sequence (Fig. 3). Here, *Arenaria*, *Plantago* and *Festuca* disappeared after removal of 31, 12 and 4% of the trait space respectively.

SUBORDINATE SPECIES PERSISTENCE

Subordinate plant species exhibited different likelihood of survival or secondary extinction within the network (Fig. 4, Table S1). Over all scenarios, module membership significantly explained the likelihood of subordinate species to survive or get secondary extinct ($G_3^2 = 23.17$, $P < 0.001$, $G_3^2 = 581.98$, $P < 0.001$ respectively; Table S2). Subordinate species associated to *Arenaria* and *Plantago* modules were significantly less likely to survive ($t = -2.58$, $P < 0.05$, $t = -2.87$, $P < 0.05$ respectively), and significantly more
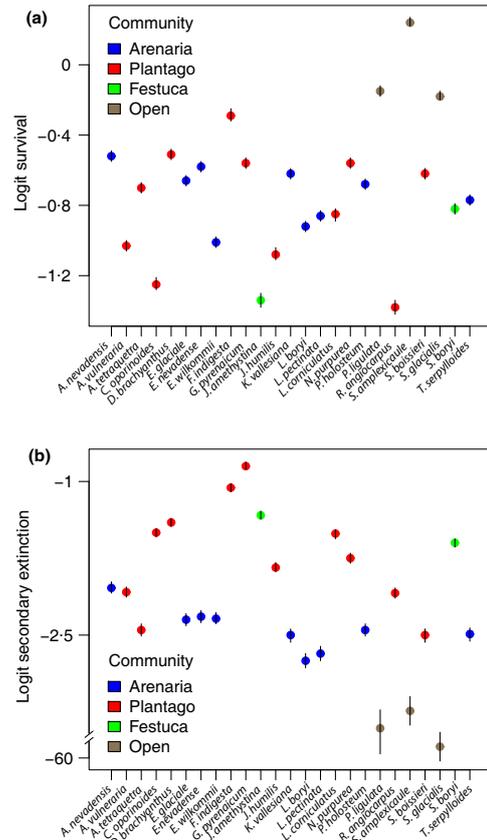

Fig. 4. Multinomial loglinear model of the differences among subordinate species (*x*-axis) in their probability (i.e. logit) of persistence within the network (*y*-axis), i.e. surviving (a) or getting secondary extinct (b). For the 95% confidence intervals (*y*-axis in (b) rescaled for clarity), see Table S1.

likely to get secondary extinct ($t = 12.89$, $P < 0.001$, $t = 15.21$, $P < 0.001$ respectively) compared to subordinate species associated with *Festuca* and the open microhabitat.

Discussion

Our assessment of the resistance of alpine plant communities to microhabitat loss using functional traits as a proxy for species' susceptibility showed that extinction rates were dependent on the type of environmental perturbation. Indeed, the order and timing of breakdown of the plant interaction network sustained by the foundation species differed substantially among the three environmental change drivers. The plant interaction network underlying the studied plant community was rather fragile to a simulated increase in nitrogen deposition. Conversely, the plant interaction network resisted against moderate drought alone or drought combined with temperature increases. Community persistence against these latter environmental perturbations can be explained by the fact that in these two scenarios foundation species remained longer in the network, thereby slowing down biodiversity loss compared to a random extinction simulation. These results might indicate the relevance of plant association networks in modulating the impact of different environmental changes on species diversity and community persistence. Thus, within the limits of our assumptions, predictions of the fate of species and communities depend on the knowledge of the main driver of environmental change at the location of interest and how this environmental perturbation affects the plant interaction network.

Climate warming has recently been proved to change the composition and the structure of alpine plant communities, leading to a decline and disappearance of cold-adapted plant species (Gottfried *et al.* 2012). Furthermore, Hautier *et al.* (2015) found a biodiversity decline in response to nitrogen enrichment in experimental grassland communities. Our simulation suggested that nitrogen deposition could alter plant network structure, resulting in potentially accelerated species loss. In other words, just a small shift in the corresponding functional trait space, i.e. a removal of species with lower SLA values, caused the loss of foundation species and therefore a disproportionate increase in secondary extinctions. This is consistent with a fragile ecosystem in which small environmental perturbation causes the primary extinction of a small but important fraction of species that have critical cascading effects (Fortuna & Bascompte 2006; Memmott *et al.* 2007; Rezende *et al.* 2007).

Species distribution models suggest that decreasing precipitation plays an important role in determining the potential impacts of climate change on vegetation, mainly due to habitat loss (Engler *et al.* 2011). We found that drought may not be the main driving factor for species loss in the dry alpine climate of the Sierra Nevada (Spain). We suggest that the general tolerance to drought of the species growing in this environment (Giménez-Benavides,

Escudero & Iriondo 2007), in particular that of foundation species, might actually allow this vegetation to better resist further increase in drought compared to other environmental perturbations.

Having shown that plant–plant interaction networks responded in different ways to different environmental perturbations, we next explored how the role of foundation species differed across the different scenarios. The emerging patterns of secondary extinctions with increasing drought alone or increasing drought combined with temperature probably resemble the pattern of extinctions following the order in species abundance, with rare species becoming extinct first (Memmott, Waser & Price 2004). Under these circumstances, it is expected that the loss of least connected (Solé & Montoya 2001; Dunne, Williams & Martinez 2002) or least abundant (Verdú & Valiente-Banuet 2008) species does not have important negative consequences on network structure. Conversely, in the scenarios N, where foundation species got lost early in the extinction sequence, species diversity declined rapidly also due to higher rates of secondary extinctions. This suggests that in our study system, increases in nitrogen availability might negatively affect survival of the foundation species. This might be due to increasing competitive pressure from colonising subordinate species (Schöb *et al.* 2013a, 2014), and finally competitive exclusion of the foundation species (McAuliffe 1984).

Taken together, in this dry alpine ecosystem dominated by drought-tolerant species, moderate increases in drought stress may not have important consequences for the plant community (Miranda *et al.* 2009). This effect might particularly be due to the high drought resistance of the foundation species present (Schöb, Butterfield & Pugnaire 2012; Schöb *et al.* 2013a) and the role these species play in the plant interaction network. On the other hand, changes that favour more competitive species might accelerate changes in the plant community (Michalet *et al.* 2014), also due to the extinction of the less competitive foundation species (McAuliffe 1984; Liancourt, Callaway & Michalet 2005; Maestre *et al.* 2009).

Conclusions

Our study is one of the few attempts to analyse the consequences of environmental changes on ecological networks and their species by taking into account the species' sensitivities to those environmental drivers (Tylianakis *et al.* 2008). Our simulation approach approximates species deletion according to global trait-environment relationships. Furthermore, we take into account that species are plastic and include the observed trait plasticity in our models. Thus, our trait-based extinction model in response to environmental change is biology-informed, and therefore likely to be more ecologically meaningful than previous extinction models based only on the level of species interconnectedness (i.e. species degree) or random species removal (e.g. Solé & Montoya 2001; Dunne, Williams & Martinez 2002;

Memmott, Waser & Price 2004; Verdú & Valiente-Banuet 2008). Nevertheless, our study has limitations in that it is mainly static: we did not account for birth and mortality changes within species, nor for range shifts of species into new potentially suitable habitats, nor the immigration of new species from lower altitudes. We did not consider potential changes in network structure nor the interaction rewiring, i.e. the establishment of new interactions. Furthermore, we ignored the potential effects of differences in microhabitat size. Nevertheless, our approach represents a conceptual advance for linking functional ecology with network theory into a unified framework that could improve predictions on community responses to environmental change. As such, we foster its use with all types of interactions (e.g. predator–prey), environmental changes (e.g. disturbance) and corresponding response traits (e.g. body mass).

Acknowledgements

Data accessibility

Network data available from the Dryad Digital Repository https://doi.org/10.5061/dryad.35q01 (Losapio & Schöb 2017). ʀ scripts uploaded as supporting information.

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Supporting Information

Details of electronic Supporting Information are provided below.

Appendix S1. Conceptual framework, trait distributions and model coefficients.
Fig. S1. Conceptual framework.
Fig. S2. Trait distributions.
Table S1. Multinomial loglinear model of the differences among subordinate species in their persistence within the network.
Table S2. Likelihood ratio chi-square and model coefficients for generalised linear models.
Data S1. R scripts.