



Random processes and phylogenetic loss caused by plant invasions

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ABSTRACT

Aim Although biological invasions represent a major cause of biodiversity loss, the actual mechanisms driving species extinctions remain insufficiently understood. Here we investigate the role of three processes as drivers of phylogenetic loss in invaded local plant communities, namely the 'biotic resistance', 'environmental filtering' and 'functional equivalence' hypotheses.

Location Balearic Islands (western Mediterranean).

Methods We quantified the phylogenetic diversity and structure of 109 pairs of invaded and non-invaded local plant communities from two Mediterranean islands. Each pair contained one control plot and one plot invaded either by the deciduous tree *Ailanthus altissima*, the succulent subshrubs *Carpobrotus* spp. or the pseudoannual geophyte *Oxalis pes-caprae*. We combined generalized linear models, analyses of phylogenetic community structure and generalized linear mixed models using a Markov chain Monte Carlo technique (MCMCglmm) to contrast the 'biotic resistance', 'environmental filtering' and 'functional equivalence' hypotheses.

Results While the phylogenetic structure of the non-invaded communities was not more clustered or overdispersed than expected by chance, minimum phylogenetic distance to the invasive species increased in invaded assemblages, in which the magnitude of phylogenetic diversity loss ranged from 6 to 37% depending on the invader's identity. Invader or island identity did not explain the probabilities of native species becoming locally extinct. Rather, the likelihood of extinction was mainly explained by species abundance, with scarcer species exhibiting a higher chance of becoming locally extinct. Species identity explained a small fraction of the variation in extinction risk (12%), independently of each species' evolutionary history.

Main conclusions The most relevant driver of local extinction is a stochastic process where less abundant species tend to disappear more frequently irrespective of their evolutionary history. This has strong implications for conservation because it suggests that in the study region the invaders are unlikely to drive regional and global extinctions except in cases where the native species is already rare.

Keywords

Biotic resistance, community assembly, ecological impact, environmental filtering, extinction mechanisms, invasive plants, island, niche, phylogenetic community structure.

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INTRODUCTION

Biological invasions are considered one of the main agents of human-induced global changes, representing a major cause of

biodiversity loss (Simberloff *et al.*, 2013) and ecosystem alteration (e.g. Vilà *et al.*, 2011; Pyšek *et al.*, 2012) and having a large economic impact (Pimentel *et al.*, 2000). Understanding how biological invasions affect the composition and structure of

invaded communities is thus crucial for preserving natural ecosystems and securing the invaluable ecosystem services they provide to human societies (Cardinale *et al.*, 2012; Powell *et al.*, 2013). Surprisingly, however, there is still an insufficient understanding of the mechanisms by which non-native organisms alter the structure of native communities.

Here we draw attention to the previously suggested possibility that both the establishment and impact of invaders are linked to features of the recipient community (Levine & D'Antonio, 1999). The most obvious bridge between both processes is biotic resistance (Elton, 1958). Under the biotic-resistance scenario, highly species-diverse recipient communities reduce the chances that a non-native species will become established. If established, however, the likelihood of extinction of those species having a niche which overlaps to a greater extent with that of the invader is predicted to be higher (Fargione *et al.*, 2003).

However, other less obvious scenarios potentially linking establishment and impact are also possible. For example, if competition in the invaded community is weak and environmental adversity is strong, then the invader will only succeed if it has the adaptations needed to survive and reproduce in the novel environment (Shea & Chesson, 2002; Sol, 2015), a possibility supported by growing evidence (Lambdon *et al.*, 2008; Bartomeus *et al.*, 2012). Under these circumstances we generally expect the likelihood of establishment to be low because numerous species may not have the appropriate adaptations to become established. Moreover, in case of establishment success the impact on native species should be low as well, because the non-native species is predicted to occupy a niche that is not monopolized by other species (Tilman, 2004). However, if the invader is able to alter the environment in some way, for example by modifying the structure of the vegetation or by changing soil properties (e.g. Liao *et al.*, 2008), then we could expect a non-random extinction pattern in which the most affected species will be those that are ecologically more distant from the invader (i.e. less tolerant to those particular environmental alterations).

Finally, if communities are primarily assembled by random processes, where all species are ecologically equivalent (*sensu* Hubbell, 2001), the invader will encounter less resistance to its invasion as both competitive and environmental challenges will be weak (Tilman, 2004; Sol, 2015). Under this scenario, a certain degree of local extinction is still expected due to demographic stochasticity if the presence of the non-native species reduces the size of the native community, which should increase the likelihood of extinction of the least abundant species (Adler *et al.*, 2007). In this case, no consistency is expected in the identity of species loss among communities when their abundance is taken into account. Such a random pattern of species loss contrasts with the predictability of both changes in the phylogenetic structure and the identity of species lost under the 'biotic resistance' and certain 'environmental filtering' scenarios. Discerning between random and non-random patterns is relevant, because the extinction of species with particular features might be expected to have a higher impact on biodiversity and ecosystem functioning than random losses (Cardinale *et al.*, 2012; Sol *et al.*, 2014a).

While much work has been done on investigating the undoubtedly relevant question of how the properties of the community affect establishment, the extent to which community properties determine the impact of invaders has largely been neglected. One obvious difficulty is in obtaining reliable estimates of ecological distance in comparative studies encompassing a large number of species. This limitation has led numerous researchers to embrace the use of phylogenetic distance as an indirect way of measuring ecological distance among species (Cavender-Bares *et al.*, 2009; Wiens *et al.*, 2010). Community-level processes such as biotic resistance, environmental filtering and random processes often leave phylogenetic traces in the assemblage of communities (Fig. 1). Thus traces can be used to discern which processes have driven the organization of biological communities (Davies, 2006). By comparing species assemblages in invaded and non-invaded communities exposed to similar environmental conditions, phylogenetic information allows the impact of such invaders on local biodiversity patterns to be investigated beyond classical studies on impacts on species richness or diversity (Vilà *et al.*, 2006). For example, the minimum phylogenetic distance of the invaders to native species in invaded and non-invaded plots can serve to assess whether species more closely related to the invasive one tend to disappear more often (Gerhold *et al.*, 2011). Indeed, the relationships among phylogenetic structure, competition and ecological niche are complex, making it difficult to measure (Pausas & Verdú, 2010) and interpret (Cadotte, 2014; Sol *et al.*, 2014b) observed patterns. However, the central assumption that phylogenetic distance reflects ecological distance has been supported by experimental work as well as by comparative analysis across a broad range of ecological systems (Cadotte *et al.*, 2009; Cavender-Bares *et al.*, 2009; Gómez *et al.*, 2010; Wiens *et al.*, 2010; Burns & Strauss, 2011; Verdu *et al.*, 2012; Davies *et al.*, 2013); see Discussion for more details). Thus, a phylogenetic community analysis can provide important insights into the community-level consequences of the invasion process, allowing us to address questions that otherwise would be impossible to study (Cavender-Bares *et al.*, 2009).

Here we adopt a phylogenetic community approach to investigate the impact of invasion by three non-native plants on native plant local assemblages. The studied communities were located in the Mediterranean Basin, a region with numerous endemic species and largely vulnerable to the introduction of non-native species (Sala, 2000; Hulme, 2004). We compared adjacent paired control and invaded plots across two Mediterranean islands. 'Invaded' plots had been successfully colonized by either the pseudoannual geophyte *Oxalis pes-caprae*, the deciduous tree *Ailanthus altissima* or the perennial succulent subshrub *Carpobrotus* spp. Previous work in the same study system showed patterns of significant loss of native plant species diversity in invaded plots (Vilà *et al.*, 2006). We extend this previous work by asking three questions related to the mechanisms determining this diversity loss. First, is there also a general loss of phylogenetic diversity in invaded communities compared with non-invaded communities? Second, if so, is such phylogenetic diversity loss related to the phylogenetic structure of the native communities?

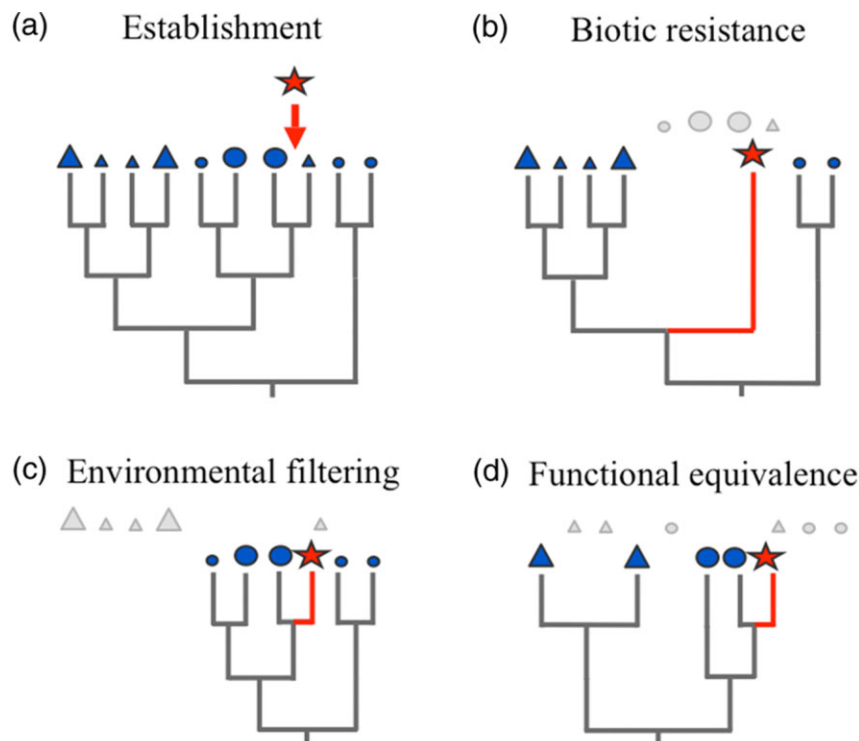


Figure 1 Diagram representing the patterns of phylogenetic impact that can be left as a trace of different ecological mechanisms leading to the local extinction of native species. (a) Establishment: after an invasive species becomes established. (b) Biotic resistance: species becoming extinct are those more closely related to the invasive. This is because their ecological niches tend to be more similar, and individuals of these species are expected to compete more intensively for certain limited resources. Under this scenario, a species' chances to become extinct are independent of traits that do not show a phylogenetic signal (e.g. a species' ability to live in habitats with low C/N ratios). (c) Environmental filtering: species becoming extinct are exclusively those sharing some specific ecological attributes irrespective of their phylogenetic relatedness to the invasive species (e.g. not able to persist in soils with low C/N ratios). (d) Functional equivalence: less abundant species tend to become extinct irrespective of their phylogenetic relatedness to the invasive species (e.g. also irrespective of their ability to tolerate soils with low C/N ratios). The star symbol represents the invasive species. Species vanished from the native assemblage are represented above the phylogenetic tree, with no corresponding tree branch. The size of the symbols refers to the abundance of each species and its type represents the presence of a given trait (e.g. triangles might correspond to species that do not tolerate low C/N ratios in the soil). For simplification, abundance and species traits are represented as categorical.

Specifically, we first test whether native non-invaded communities are phylogenetically overdispersed, clustered or random, which should respectively reflect that the community is organized by competition, filtering or random processes (Davies, 2006). Then, we compare such phylogenetic patterns with those of their paired invaded plots to test whether the invasion was associated with increases in either overdispersion or clustering. Finally, we further compare the phylogenetic patterns of non-invaded and invaded local assemblages to ask why some species become extinct from local assemblages while others do not. We do this by examining if: (1) species more closely related to the invader disappear more frequently from invaded plots, as predicted under the 'biotic resistance' hypothesis; (2) there is a non-random extinction of clusters of closely related species, which is expected under the 'environmental filtering' hypothesis in which species that share specific ecological attributes form clustered phylogenetic patterns; and (3) less abundant species tend to be less frequently observed in invaded plots, supporting the 'functional-equivalence' hypothesis.

METHODS

Vegetation sampling

Vegetation sampling was conducted in spring across the two Mediterranean islands, Mallorca (3640 km²) and Menorca (700 km²). Because our aim was to study the community-level consequences of invasive species in different contexts, we chose three different invasive species known to be widespread in the Mediterranean islands (Hulme, 2004). These species differed in life forms (a perennial succulent, *Carpobrotus* spp; a pseudoannual geophyte, *Oxalis pes-caprae*; and a tree, *Ailanthus altissima*; hereafter *Carpobrotus*, *Oxalis* and *Ailanthus*) and the habitat type they invade. For more details on these species life-history traits, their invasive history and their performance in the Mediterranean Basin see Vilà *et al.* (2006).

For each of the three invaders, a 2 m × 2 m paired-plot design was established between 15 and 23 times per species across each island. The minimum distance between sites within an island

was 1 km. Sampling sites were chosen after a careful survey to ensure the paired plots shared similar substrate and habitat characteristics (for further details see Vilà *et al.*, 2006). Moreover, plots where other non-native species were present were excluded to make sure that the detected effects were the consequence of the presence of the species under study. This resulted in a total of 109 paired plots. One of the plots was placed where the invader had been spontaneously established and the other was placed in a random direction where the presence of the invasive species was not detected. We refer to these plots as the 'invaded' and 'non-invaded' plots, respectively. The non-invaded plot was placed at an adequate distance to avoid spatial-scale sampling differences between different species while minimizing distance from the invaded plot (i.e. 2 m from the invaded plot in the case of *Carpobrotus* and *Oxalis* and 5 m in the case of *Ailanthus*). Each plot was divided into 16 0.25-m² subplots, within which all species presences were recorded. Abundances for each species within each plot ranged from 0 (absent from the plot) to 16 (present in all subplots).

Phylogenetic tree construction

We assembled a general phylogenetic tree by pooling all species found in the surveyed plots of both islands (401 species in total; see Appendix S1 in Supporting Information) by using the Phylomatic package as implemented in PHYLOCOM 4.2 (Webb *et al.*, 2008). The family, genus and species names from our surveys were matched with those from a megatree (R20120829.xml) available in the online third version of Phylomatic (Webb, 2012). This megatree is based on information available from the last version of the Angiosperm Phylogeny Group (2009), which includes branch lengths. Using the 'blad' procedure in PHYLOCOM (Webb *et al.*, 2008) branch lengths of our general phylogeny were scaled using known node ages from Wikström *et al.* (2001).

Based on this general phylogeny, we then subsequently pruned species absent from each level of analysis by using the 'drop.tip' function from the Ape package in R (Paradis *et al.*, 2004) to obtain a single phylogeny for each combination of island (Mallorca and Menorca), invasive species (*Carpobrotus*, *Ailanthus* and *Oxalis*) and plot invasive status (invaded or non-invaded plots). Therefore, we obtained 12 phylogenies that were used to compute measures of diversity at the island level for each species and invasion treatment. Finally, the phylogenetic trees of each local assemblage were obtained by pruning species absent from each of the studied plots. This yielded a total of 218 phylogenetic trees (i.e. 109 pairs of invaded and non-invaded plots) from which we conducted the analyses at the local species assemblage level.

Phylogenetic analyses

We first compared total phylogenetic diversity of invaded versus non-invaded local assemblages to assess if there was a global decrease of such phylogenetic diversity associated with invasion. Phylogenetic diversity was estimated by computing the sum of the total phylogenetic branch length of each plot's phylogenetic

tree (i.e. Faith's total phylogenetic diversity) (Faith, 1992) using the 'picante' package in R (Kembel *et al.*, 2013). This measure was taken for all surveyed plots. Following the same procedure we also computed the mean phylogenetic distance (MeanPDist) of all species within a community and the minimum phylogenetic distance (MinPDist), which is defined as the phylogenetic distance of the invasive species to its closest relative within the recipient plot, also known as mean nearest taxon distance. In order to be able to compare if invaded plots hold less closely related species to the invasive one than non-invaded plots, we artificially simulated the presence of the invasive species in the non-invaded plots and compared the distance to its closest species.

Generalized linear mixed models (GLMMs) were used to investigate the relative influence of the identity of the invasive species (*Carpobrotus*, *Ailanthus* or *Oxalis*), plot status (non-invaded versus invaded) and region (Mallorca versus Menorca) in phylogenetic species diversity (PDiv), MeanPDist, and MinPDist. We used the package 'nlme' in R (Pinheiro *et al.*, 2015). We also analysed if such factors affected the number of native species (i.e. species richness) and their mean abundance (i.e. native carrying capacity). We conducted paired *t*-tests to detail differences among invaded and non-invaded plots for each invasive species and island (see Results).

Phylogenetic structure of native and invaded local assemblages

To assess the importance of both interspecific competition and specific species attributes in the assemblage of such local communities (see Fig. 1), the phylogenetic structure of all 218 non-invaded and invaded assemblages was studied following the framework presented by Webb *et al.* (2002). We first investigated the occurrence of such patterns in non-invaded local assemblages because we hypothesized that different degrees of biotic resistance or environmental filtering in non-invaded communities would determine the phylogenetic structure of communities after the invasion. We assume that non-invaded assemblages have a phylogenetic structure that is representative of the invaded assemblages prior to invasion (Vilà *et al.*, 2006; Powell *et al.*, 2013). Subsequently, we compared patterns of phylogenetic structure variation in non-invaded assemblages with those from invaded assemblages to understand changes in such structures that, given the number of replicates included in the analyses, might be associated with the invasion process.

Our not necessarily mutually exclusive predictions are that: (1) phylogenetic overdispersion (i.e. phylogenetic evenness) will increase in invaded assemblages compared with non-invaded ones if inter-specific competition driven by the invasive species plays a relevant role in determining the phylogenetic structure of the assemblage; (2) phylogenetic clustering should increase in invaded assemblages if the invasive species acts as a filter, hindering the persistence of species sharing some specific traits; (3) more random processes should be involved if there is not an important degree of clustering

and/or overdispersion in non-invaded assemblages. In the latter case, we also expect a non-significant increase of the degree of phylogenetic overdispersion and/or clustering in invaded assemblages, consistent with – but not necessarily evidence for – the ‘functional equivalence’ hypothesis. Specifically, we measured the standardized effect size of MeanPDist and mean distance separating each species in each local assemblage from its closest relative (mean nearest taxon distance, MNTD) (Kembel *et al.*, 2013). Note that this is different from MinPDist in that MNTD represents the mean of all minimum phylogenetic distances for each of the species within the assemblage, not exclusively from the invasive species. We then compared the scores obtained for MeanPDist and MNTD with those obtained from a null distribution of species within the community. Such distributions were standardized by the standard deviation of phylogenetic distances in the null community following Kembel *et al.* (2013). Thus, *ses.MeanPD* and *ses.MNTD* are based on simulations conducted to test the possibility that both MNTD and MeanPDist between all pairs of species within a local assemblage are significantly different from the distances expected if assemblages were assembled at random. We conducted such analyses while accounting for the abundance of species (Cadotte *et al.*, 2010) and by randomizing communities at both the species and individual level (‘richness’ and ‘species.pool’) by using the ‘Picante’ R package (Kembel *et al.*, 2013). It has been shown that *ses.MeanPD* and *ses.MNTD* indices provide complementary phylogenetically relevant information; *ses.MeanPD* provides better insight for tree-wide patterns of phylogenetic clustering or overdispersion while *ses.MNTD* is more sensitive to phylogenetic patterns closer to the tree tips (Kembel *et al.*, 2013).

Assessing which factors determine the chances of native species to persist in local assemblages

To address why some native species persist in local assemblages while others do not, the presence/absence of each native species in each pair of plots was used as the response variable and modeled with a binomial generalized linear mixed model in the Bayesian R-package ‘MCMCglmm’ (Hadfield, 2014). Phylogenetic relatedness, island and the identity of the invasive species were included in the model as random effects, and non-informative priors were used to run the models, which were run for 1,100,000 iterations with a burn-in of 100,000 and a thinning interval of 20 (see Hadfield, 2014). This allowed us to test if species with a shared phylogenetic history tended to respond similarly to invasion by the three investigated species while accounting for the fact that such patterns may be more similar within the same island or when the same invasive species was present. Because the ‘functional equivalence’ hypothesis predicts that the less abundant species will be those the more frequently become extinct, we used the abundance of each native species in its paired non-invaded plot to assess if this was a significant predictor of its chances to become extinct from the invaded plot. In other words, we

assessed if the rarest species are more frequently lost from local assemblages due to random processes. This analysis was replicated for each invasive species and for each island studied (a total of six models encompassing 218 sampled plots).

Because no general evidence was found that closely related species responded similarly to the invasive species (a pattern that could arise from both biotic resistance and environmental filtering processes), we asked if species tend to show consistent chances of becoming extinct when their abundance in non-invaded plots was taken into account, irrespective of their shared evolutionary history. We used a MCMCglmm approach where the identity of the species was included as a random factor while its abundance (the only factor that was found to be significant in the previous model) was included as a fixed factor.

RESULTS

Phylogenetic diversity loss, species richness and native carrying capacity

Phylogenetic diversity (PDiv) generally decreased in the invaded plots compared with the non-invaded plots (Table 1). Such a pattern was highly consistent in plots invaded by *Ailanthus* and *Carpobrotus* but did not occur in the case of *Oxalis*-invaded assemblages ($P > 0.19$ in both islands; Table 2; see also Fig. 2). Between the two invaders that did cause declines in PDiv, the degree of phylogenetic loss was higher when local assemblages

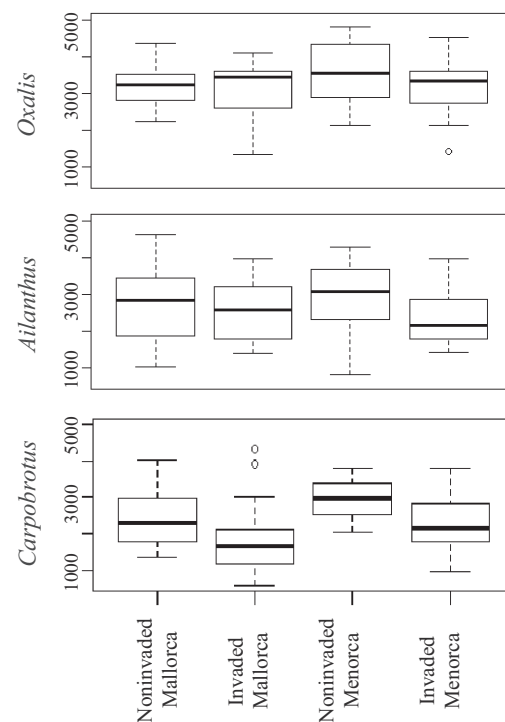


Figure 2 Total phylogenetic diversity in control and invaded plots by the invasive species *Oxalis pes-caprae*, *Ailanthus altissima* and *Carpobrotus* spp. in two Mediterranean islands.

Table 1 Generalized linear models indicating general patterns of the number of native species lost and their abundances (native carrying capacity), phylogenetic diversity, mean phylogenetic distance among species, and minimum phylogenetic distance from a native species to the invasive species in invaded communities. Island was included in the model coded as a random factor. The model takes *Oxalis* as a reference in comparisons among species.

Dependent variable	Factor	Estimate	SE	<i>t</i> -value	<i>P</i> -value
Number of species $R^2 = 0.32$	(Intercept)	21.37	1.12	18.9	<0.0001
	Treatment: invaded	-2.52	0.76	-3.3	0.0011
	Invasive: <i>Ailanthus</i>	-6.25	0.95	-6.6	<0.0001
	Invasive: <i>Carpobrotus</i>	-8.18	0.95	-8.6	<0.0001
Phylogenetic diversity (PDIV) $R^2 = 0.38$	(Intercept)	3523.96	130.36	22.8	<0.0001
	Treatment: invaded	-432.91	108.07	-3.7	0.0001
	Invasive: <i>Ailanthus</i>	-659.37	135.61	-4.3	<0.0001
	Invasive: <i>Carpobrotus</i>	-967.49	135.61	-6.4	<0.0001
Mean phylogenetic distance among species (MeanPDist) $R^2 = 0.29$	(Intercept)	506.05	11.49	44.0	<0.0001
	Treatment: invaded	5.29	2.81	1.9	0.0609
	Invasive: <i>Ailanthus</i>	11.72	3.50	3.3	0.0009
	Invasive: <i>Carpobrotus</i>	-1.84	3.50	-0.5	0.6003
Minimum phylogenetic distance from invasive species (MinPDist) $R^2 = 0.16$	(Intercept)	357.88	17.18	20.8	<0.0001
	Treatment: invaded	27.70	9.33	3.0	0.0033
	Invasive: <i>Ailanthus</i>	47.02	11.62	4.0	0.0001
	Invasive: <i>Carpobrotus</i>	44.48	11.62	3.8	0.0002
Native carrying capacity $R^2 = 0.38$	(Intercept)	112.19	9.13	12.3	<0.0001
	Treatment: invaded	-23.81	3.97	-6.0	0.0210
	Invasive: <i>Ailanthus</i>	-32.06	4.95	-6.5	<0.0001
	Invasive: <i>Carpobrotus</i>	-39.77	4.95	-8.0	<0.0001

Table 2 Mean \pm SE of phylogenetic diversity (PDIV), nearest taxon phylogenetic distance among the most closely related species in relation to the invasive (MNTD; note that this is simulated in the case of non-invaded plots), and mean distance between all pairs of species computed for each local assemblage (MeanPDist) in invaded (I) and non-invaded plots (NI). See Methods for further explanations on how these parameters were estimated.

Species and island	Invasion status	Paired plots	PDIV \pm SE	<i>P</i> -value	MNTD \pm SE	<i>P</i> -value	MeanPDist \pm SE	<i>P</i> -value
<i>Oxalis</i> Mallorca	Non-invaded	17	3258 \pm 142	>0.71	365 \pm 12.6	>0.71	520.9 \pm 3.9	>0.40
	Invaded		3172 \pm 175		371.5 \pm 13.2		516.9 \pm 4.6	
<i>Oxalis</i> Menorca	Non-invaded	16	3517 \pm 211	>0.19	361.9 \pm 11.8	0.02	496.4 \pm 3.1	>0.15
	Invaded		3213 \pm 218		390.7 \pm 10.3		501.1 \pm 3.6	
<i>Ailanthus</i> Mallorca	Non-invaded	23	2747 \pm 206	0.03	440.2 \pm 9.6	>0.94	528.4 \pm 3.4	>0.42
	Invaded		2318 \pm 175		441.3 \pm 12.0		531.0 \pm 2.7	
<i>Ailanthus</i> Menorca	Non-invaded	15	2961 \pm 264	0.01	368.8 \pm 28.3	>0.27	507.2 \pm 8.4	>0.33
	Invaded		2124 \pm 209		415.6 \pm 26.7		517.2 \pm 5.6	
<i>Carpobrotus</i> Mallorca	Non-invaded	23	2586 \pm 203	<0.0001	417.4 \pm 16.7	0.04	514.9 \pm 4.6	0.04
	Invaded		1539 \pm 202		456.9 \pm 12.2		526.8 \pm 5.5	
<i>Carpobrotus</i> Menorca	Non-invaded	15	2939 \pm 144	<0.001	352.9 \pm 18.1	0.01	486.3 \pm 5.5	>0.28
	Invaded		2004 \pm 216		418.5 \pm 18.6		495.2 \pm 6.5	

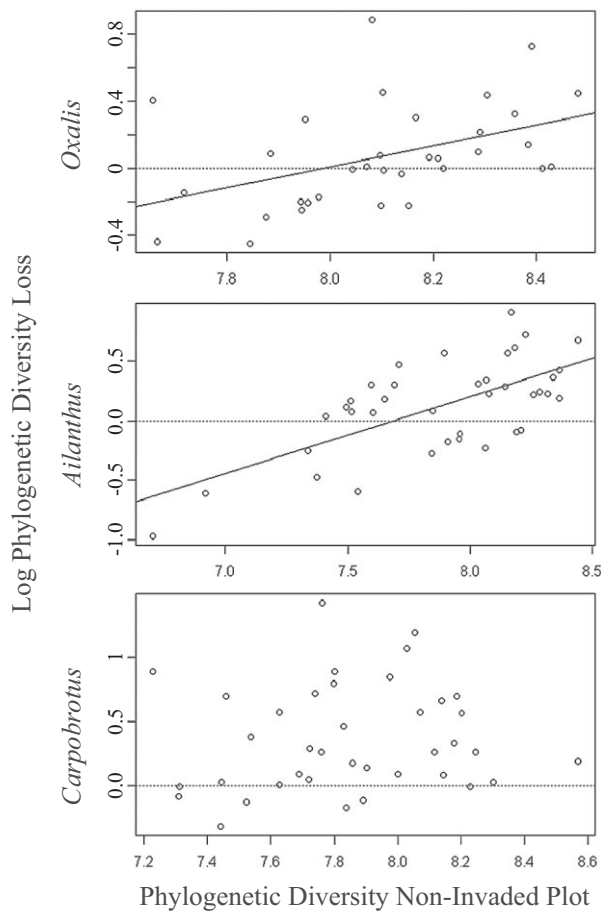


Figure 3 Relationship between the amount of phylogenetic diversity loss and phylogenetic diversity of each local assemblage for each invasive species. The relationship is significant for local assemblages invaded by *Oxalis* and *Ailanthus*, although the effect was more important for *Ailanthus*. However, the amount of phylogenetic loss was highest in *Carpobrotus*-invaded assemblages irrespective of the initial amount of phylogenetic diversity of the recipient community. Dotted lines representing values of phylogenetic loss equal to zero are provided for reference.

were invaded by *Carpobrotus* than when invaded by *Ailanthus* (Table 2). In addition to a lower PDiv, the invaded local assemblages also contained fewer species, and those species present exhibited a lower abundance compared with the non-invaded assemblages (Table 1).

Native phylogenetic diversity and amount of phylogenetic diversity loss

More phylogenetically diverse local assemblages tended to lose greater amounts of phylogenetic diversity than less diverse assemblages ($t = 3.26$, d.f. = 107, $P = 0.001$; Fig. 3). However, this loss was mainly driven by *Ailanthus* ($t = 5.39$, d.f. = 36, $P < 0.001$). Invasion by *Carpobrotus* caused a severe phylogenetic loss independently of the diversity of the native community invaded ($t = 0.68$, d.f. = 36, $P = 0.499$; Fig. 3). Although invasion

by *Oxalis* did not lead to a general decrease in phylogenetic diversity (see above) the amount of phylogenetic loss increased with phylogenetic diversity of the native species assemblages ($t = 2.74$, d.f. = 31, P -value = 0.010).

Phylogenetic structure of non-invaded and invaded communities

The phylogenetic structure of non-invaded local assemblages was not more clustered or overdispersed than expected by chance with regard to the mean phylogenetic distance among species within the community. From a sample that ranged from 15 to 23 non-invaded plots for each species and island, the mean number of clustered plots was 0.50 ± 0.84 and the mean number of overdispersed plots was 0.50 ± 0.84 . This is against the prediction that such assemblages were primarily structured through competition or environmental filtering. Rather, the phylogenetic structure was consistent with a more random process of assemblage. Similar results were found for invaded local assemblages (mean number of clustered plots 1.83 ± 2.23 and mean number of overdispersed plots 1.00 ± 0.63 from a sample of 15 to 23 invaded plots). Moreover, no significant differences were found in the phylogenetic structure of non-invaded compared with invaded local assemblages [paired t -tests comparing the number of clustered plots ($t = -0.54$; d.f. = 5; P -value > 0.20) and the number of overdispersed plots ($t = 1.46$; d.f. = 5; P -value > 0.60)]. Results regarding MNTD to the invasive species provided similar results (see Appendix S2).

Assessing which mechanisms determine the chances of native species persisting in invaded assemblages

Despite the analysis of the phylogenetic structure providing evidence that the plant communities were not primarily organized through competition, it is still possible that the introduction of an invader in a community creates new competitive pressures that could explain why particular native plants go extinct. In fact, we found that species phylogenetically more related to the invader tended to be less often present in the invaded communities, as indicated by a higher MinPDist in invaded plots compared with non-invaded plots (Table 1). This was even true in Menorca for *Oxalis*-invaded plots, despite the local assemblages not showing an overall decrease in phylogenetic diversity, but not for *Ailanthus* (Table 2).

The main predictor of local species extinction risk in invaded plots was the local abundance of the species. Indeed, for the three invaders in both islands, less abundant species in non-invaded plots had a higher probability of being absent in the invaded plots than more abundant species (MCMCglmm: $P < 0.00001$; Table 3). Furthermore, we did not find a significant effect of the island or the identity of the invasive species in driving the species to extinction (see Model 1 in Table 3). Likewise, closely related species were not found to show similar responses to invasion, as phylogenetic relationship among

Table 3 Generalised linear mixed models using Markov chain Monte Carlo techniques (MCMCglmm models) investigating the presence/absence of each native species in each pair of invaded–non-invaded plots. The response variable was modelled with a binomial generalized linear mixed model in the Bayesian R-package MCMCglmm following Hadfield (2010) (see Methods for model specifications). Phylogenetic relatedness, island and the identity of the invasive species were included in Model 1 as random factors to control for possible differential effects under different ecological scenarios. The abundance of each native species in its paired non-invaded plot was included as ‘Fixed factor’. In Model 2, the identity of each species was included to estimate its role irrespective from phylogenetic history (which was not significant in Model 1). Abundance of the species in the invaded plot was included in the analysis because it was shown to be the only significant factor in Model 1. The amount of variation explained refers to the proportion of variation in the data explained by each of the factors included in the model.

	Random factors	Variation explained	Fixed factors	P-value
Model 1	Phylogenetic relatedness	<0.01	Abundance of the species in non-invaded plot	<0.00001
	Island	<0.01		
	Identity of the invasive species	<0.01		
Model 2	Identity of the native species	0.118	Abundance of the species in non-invaded plot	<0.00001

species explained less than 1% of the variation in the presence/absence of native plants in invaded areas.

The above results are consistent with the ‘functional equivalence’ hypothesis. However, this does not necessarily imply that the identity of species does not play any role in determining a species’ chances of persisting in an invaded local assemblage. In fact, abundance itself can also vary across species in a consistent way. Such a possibility is indeed supported by the finding that some species were consistently lost in the invaded plots regardless of their abundance (see Model 2 in Table 3; Appendix S3).

DISCUSSION

Our phylogenetic analyses of replicated pairs of invaded and non-invaded local plant assemblages across two Mediterranean islands suggest that phylogenetic diversity generally declines in invaded assemblages. This reinforces the widely accepted view that plant invasions lead to important decreases in native biodiversity (Vilà *et al.*, 2011) not only estimated as taxonomic diversity but also in terms of evolutionary history. Unlike what is generally assumed, however, much (albeit not all) of the reported phylogenetic loss appears to be due to random processes rather than to ecological processes such as interspecific competition or environmental filtering.

In a phylogenetic-based analysis like ours, the main assumption is that phylogenetic distance is a good surrogate of ecological distance and that closely related species will have similar ecological roles within a given species assemblage. Although some authors have suggested that this assumption may not be general (e.g. Mayfield & Levine, 2010), the link between phylogenetic and ecological distance has recently received important empirical support (Burns & Strauss, 2011). The strongest support comes from experimental studies (Burns & Strauss, 2011; Allan *et al.*, 2013) but also from comparative

analyses like ours. For instance, the chance that a given species acts as a physical facilitator for the success of other species increases with phylogenetic distance (Verdú *et al.*, 2012), which is even a better predictor for facilitation than life form, suggesting decreased interspecific competition via a decreased niche overlap (Verdú *et al.*, 2012). Based on such empirical evidence, some authors have even suggested that phylogenetic relatedness can better represent ecological similarity than single or even small groups of ecological traits (Cadotte *et al.*, 2009). The possibility remains that some key niche adaptations that are little conserved throughout the evolutionary history of the lineages may have produced extinction patterns resembling those produced by functional equivalences, even when they are not (see Appendix S4). However, evidence suggests that both life history (Davies *et al.*, 2013) and ecological interactions (Gómez *et al.*, 2010) exhibit phylogenetic conservatism in plants.

Another limitation of our study is the use of a space-for-time approach (Thomaz *et al.*, 2012), which assumes that native species that are absent in the invaded local assemblages but are present in the surrounding non-invaded areas have become extinct in the former. We tackled this limitation by ensuring that the paired plots shared similar substrate and habitat characteristics (Thomaz *et al.*, 2012) and by replicating the sampling in two different islands (Vilà *et al.*, 2006). Moreover, the reasonably large number of replicates sampled for each island and each invasive species minimizes the likelihood of such type-I statistical error. Finally, the close proximity between our control and invaded plots (2–5 m) minimizes the chances that there are important environmental differences between both types of plots. However, the alternative that some species we considered extinct had never been present in the particular plot cannot completely be ruled out (Gerhold *et al.*, 2011).

Bearing the above limitations in mind, the central role of the ‘functional equivalence’ hypothesis in explaining the observed biodiversity loss in invaded plots is supported by four lines of evidence. First, the abundance of each species largely determined

its chances of becoming extinct, with rare species becoming more frequently extinct from local assemblages and more abundant species having higher chances of persisting. In fact, invaded plots exhibited a decrease in the mean abundance of native individuals compared with non-invaded plots, which can drive the rarest species to extinction by stochastic effects. Although variation in species local abundance has long been acknowledged to be an important factor determining extinction dynamics (Kembel, 2009; Cadotte *et al.*, 2010), analyses of biological invasions have rarely considered how differences in species abundance per se determine their chances of becoming extinct. Interestingly, this result is in disagreement with the results of Powell *et al.* (2013) that the commonest species are the most affected by invasion, and further research should assess if this is a consequence of differences in the scale of analysis (see Proches *et al.*, 2008), the species studied or other environmental and/or regional differences. Second, phylogenetically diverse local assemblages tended to lose greater amounts of phylogenetic diversity than less diverse assemblages, which is also to be expected if extinctions occur at random. The alternative possibility would be that higher species richness reflects stronger biotic resistance, and hence whenever an invader overcomes this resistance a cascade of extinctions through competition is generated. Consistent with a recent experimental approach (Bennett *et al.*, 2013), this was not supported by our results because there was no evidence of increased phylogenetic overdispersion in invaded communities, which would be expected if interspecific competition determined the chances of species becoming extinct (Darwin, 1859; Elton, 1958). Third, if the characteristics that affect tolerance to the invaders are shared by phylogenetically related species, then we should be able to detect a phylogenetic signal in the manner in which species respond to the invader. On the contrary, phylogenetic effects explained a negligible part of the variation in extinction risk, suggesting that the extinction patterns are not strongly influenced by shared evolutionary history. Finally, the view that species loss in invaded plots corresponds to stochastic processes is consistent with the results from our community-level analyses showing that native species assemblages were not more clustered or overdispersed phylogenetically than expected by chance. Rather, communities seem to have mainly been built from a random assemblage of species from the regional pool with independence of their phylogenetic relationship (Adler *et al.*, 2007; Bennett *et al.*, 2013; Narwani *et al.*, 2013). Under such conditions, we expect little biotic or environmental resistance toward invaders and, once established, no phylogenetic patterns in the species that are lost.

Importantly, however, although the main mechanism is generally 'neutral', the decline associated with the presence of the invader seems to be non-random for a few native species. Those few native species that were most closely related to the invasive ones tended to disappear more frequently and in a consistent way across invaded plots. This finding suggests that interspecific competition accounts for a small fraction of the extinction patterns observed in our sampled plots. Because in richer communities the invader is more likely to encounter close relatives, this could also explain in part why

phylogenetically diverse local assemblages tended to lose greater amounts of phylogenetic diversity. The analyses based on the phylogenetic component of local communities provided good evidence that the consequences of invasion in native communities were on occasion dependent on the identity of the invasive species. This can be due to intrinsic traits of the invasive species or to properties of the invaded communities. For instance, the creeping, mat-forming succulent nature of *Carpobrotus* facilitates its strong monopolization of space (Traveset & Richardson, 2006). Thus, the availability of space for native species is largely reduced and proportionally more individuals from the native community are replaced by the invasive one. We have shown that the amount of loss of phylogenetic diversity is highest in *Carpobrotus* invasions and that the amount of such loss is, unlike for the other invasive species studied, independent of the phylogenetic diversity of the native assemblage. In contrast, *Oxalis* does not exert a significant impact in the phylogenetic diversity of the recipient assemblage, presumably because its phenology differs importantly from that of most Mediterranean species (Vilà *et al.*, 2006), avoiding interspecific competition for resources with native species.

In general, the extinction of species with particular features or from phylogenetically isolated clades is expected to have a higher impact on biodiversity than a random loss (Cardinale *et al.*, 2012). This is because when these species are lost so too are certain ecosystem functions and a disproportionate fraction of phylogenetic history (Cardinale *et al.*, 2012; Sol *et al.*, 2014a). Moreover, if local extinctions are random with respect to species identity, the consequences for regional or global extinctions should be lower, as different species will disappear in different places. Indeed, our results fit well with the observation that a few native plants have gone globally extinct as a result of non-native species (Sax & Gaines, 2008). Our results also highlight that even in communities with little structure some particular species can be strongly affected by the presence of the invader. For example, by combining the study of phylogenetic diversity loss with specific measures of the increase in the minimum distance among species we have been able to identify that although *Oxalis* invasions do not significantly decrease native species diversity, the most closely related species do tend to disappear. This complexity of responses could partially explain why the impact of invaders is often difficult to detect in field studies (HilleRisLambers *et al.*, 2012).

The predominance of random processes in shaping plant community assemblages and the impact of the invader may reflect the specific features of Mediterranean Basin communities, which have been subjected to strong human-driven disturbance for centuries (Cowling *et al.*, 1996). Such disturbance may have altered competition regimes and favoured simple ecological communities mainly governed by dispersal (Bartomeus *et al.*, 2012). Alternatively, the importance of random processes might be more general, as suggested by stochastic niche theory (Tilman, 2004). The distinctiveness life forms and life histories of the invader species studied here favours the possibility that results might be replicated in different biological scenarios.

However, given the idiosyncrasy of biological communities, future research should evaluate whether our conclusions can be generalized to other biogeographic regions as well as consider if similar patterns emerge when studying the impacts of other non-native species, particularly those that are closely related to natives.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web-site.

Appendix S1 Phylogeny encompassing all species included in the study.

Appendix S2 Analyses of phylogenetic structure of local communities.

Appendix S3 Species significantly affected by the invasion.

Appendix S4 Alternative mechanism of the 'environmental filtering' hypothesis.

BIOSKETCH

Oriol Lapiedra is a post-doctoral fellow at the University of Rhode Island (URI) with broad interests in understanding how organisms deal with the consequences of both current and past environmental changes. Approaches to study lineage evolution, community assembly and behavioural changes include retrospective phylogenetic comparative methods, evolutionary models and field experiments.

Authors contributions: M.V. and A.T. conducted field work. O.L., D.S., A.T. and M.V. designed the study. O.L. and D.S. conducted the data analyses. O.L., D.S., A.T. and M.V. contributed to writing the paper.

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