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 (i.e. 'biotic resistance', 'environmental filtering' and 'functional equivalence' hypotheses).

Location

Balearic islands (Western Mediterranean).

Methods

We quantified 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 (GLMMs), analyses of phylogenetic community structure and Generalised Linear Mixed Models using Markov chain Monte Carlo techniques (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 invader's identity. Invader's or island's identity did not explain native species' probabilities of becoming locally extinct. Rather, the likelihood of extinction was mainly explained by species' abundance, with scarcer species exhibiting a higher chance to become 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 in 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.

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), ecosystem alteration (e.g. Vilà *et al.*, 2011; Pyšek *et al.*, 2012) and economic impact (Pimentel *et al.*, 2000). Understanding how biological invasions affect the composition and structure of invaded communities is thus crucial to preserve natural ecosystems and to secure 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 on the previously suggested possibility that both establishment and impact of invaders are linked to the 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 becomes established. If established, however, the likelihood of extinction of those species with which the invader's niche overlaps to a greater extent 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 establish. 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 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 such 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 the invasion as both competitive and environmental adversities 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 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 attention has been drawn to investigate 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 to obtain reliable estimates of ecological distance in comparative studies encompassing a large amount of species. This limitation has led numerous researchers to embrace the use of phylogenetic distances as an indirect way to measure 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 investigating the impact of such invaders on local biodiversity patterns 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 tend to disappear more often (Gerhold *et al.*, 2011). Indeed, the relationships among phylogenetic structure, competition and ecological niche are complex, making observed patterns difficult to measure (Pausas & Verdú, 2010) and interpret (Cadotte 2014; Sol *et al.* 2014b). However, the central assumption that phylogenetic distance reflects ecological distance has been supported by experimental 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 section for more details). Thus, a phylogenetic community analysis can provide important insights into the community-level consequences of the invasion process, allowing addressing 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 the 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? Specifically, we first test whether native non-invaded communities are phylogenetically over-dispersed, 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 vs. invaded local assemblages to ask why some species become extinct from local assemblages while others do not. We do this by examining if i) species more closely related to the invader disappear more frequently from invaded plots, as predicted under the “biotic resistance” hypothesis; ii) there is a non-random extinction of clusters of closely-related species, which is expected under the “environmental filtering” hypothesis based on that species sharing specific ecological attributes form clustered phylogenetic patterns; and iii) 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 x 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 paired 109 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 sixteen 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 together all species found in the surveyed plots of both islands (401 species in total; see Appendix S1) by using the Phylomatic package as implemented in Phylocom 4.2 (Webb *et al.* 2011). The family, genus and species names from our surveys were matched to those from a megatree (R20120829.xlm) 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. By using “bladj” procedure in Phylocom (Webb *et al.* 2011) 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 from 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 vs. 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 "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 Models (GLMMs) were used to investigate the relative influence of invasive species' identity (*Carpobrotus*, *Ailanthus* and *Oxalis*), plot status (non-invaded vs. invaded) and region (Mallorca vs. Menorca) in phylogenetic species diversity (PDiv), MeanPDist, and MinPDist). We used the package "nlme" in R (Pinheiro *et al.*, 2011). We also analyzed 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" section).

Phylogenetic structure of native and invaded local assemblages

To assess the importance of both inter-specific competition and specific species' attributes in the assemblage of such local communities (see Fig. 1), the phylogenetic structure of all non-invaded and invaded assemblages was studied following the framework presented by Webb and colleagues (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 how invaded assemblages were 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 i) 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; ii) phylogenetic clustering should increase in invaded assemblages if the invasive species acts as a filter, hindering the persistence of species sharing some specific traits; iii) 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 the mean pairwise species phylogenetic distances (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 complimentary 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 native species’ chances 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 burnin 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 of 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 becoming more frequently 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 most rare 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 (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 to become 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 to the non-invaded plots (Table 1). Such a pattern was highly consistent in *Ailanthus*- and *Carpobrotus*-invaded plots, but did not occur in the case of *Oxalis*-invaded assemblages ($p > 0.19$ in both islands; Table 2; see also Figure 2). Between the two invaders that did cause declines in PDiv, the degree of phylogenetic loss was higher when local assemblages were invaded by *Carpobrotus* than when invaded by *Ailanthus* (Table 2). In addition to a lower PDiv, the invaded local assemblages also contained less species and those species present exhibited a lower abundance compared to the non-invaded assemblages (Table 1).

Native phylogenetic diversity and amount of phylogenetic diversity loss

More phylogenetically diverse local assemblages tended to lose higher amounts of phylogenetic diversity than less diverse assemblages ($t = 3.26$, $df = 107$, $p = 0.001$; Fig. 3). However, this loss was mainly driven by *Ailanthus* ($t = 5.39$, $df = 36$, $p < 0.001$). The invasion by *Carpobrotus* caused a severe phylogenetic loss independently of the diversity of the native community invaded ($t = 0.68$, $df = 36$, $p = 0.499$; Figure 3). Although *Oxalis* invasion 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 ($t = 2.74$, $df = 31$, $p\text{-value} = 0.010$).

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 regarding 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 $= 0.50 \pm 0.84$ and the mean number of overdispersed plots $= 0.50 \pm 0.84$. 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 $= 1.83 \pm 2.23$ and mean number of overdispersed plots $= 1.00 \pm 0.63$ from a sample of 15-23 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 ($t = -0.54$; $df = 5$; $p\text{-value} > 0.20$) and the number of overdispersed plots ($t = 1.46$; $df = 5$; $p\text{-value} > 0.60$)). Results regarding mean nearest taxon phylogenetic distance to the invasive species provided similar results (see Appendix S2).

Assessing which mechanisms determine native species' chances to persist in invaded assemblages

Despite the analysis of the phylogenetic structure provided 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 to non-invaded plots (Table 1). This was even true in Menorca for *Oxalis*-invaded plots -despite that local assemblages did not show 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 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 species’ chances to persist in an invaded local assemblage. In fact, abundance itself can also vary across species in a consistent way. Such 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 chances that a given species acts as a physical facilitator for the success of other species increase with phylogenetic distance (Verdú *et al.*, 2012), which is even a better predictor for

359 facilitation than life form, suggesting decreased interspecific competition via a decreased niche
360 overlap (Verdú *et al.*, 2012). Based on such empirical evidence, some authors have even
361 suggested that phylogenetic relatedness can best represent ecological similarity than single or
362 even small groups of ecological traits (Cadotte *et al.*, 2009). The possibility remains that some
363 key niche adaptations that are little conserved throughout the evolutionary history of the
364 lineages may have produced extinction patterns resembling those produced by functional
365 equivalences even when they are not (see Appendix S4). However, evidence suggests that both
366 life history (Davies *et al.*, 2013) and ecological interactions (Gómez *et al.*, 2010) exhibit
367 phylogenetic conservatism in plants.

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

379 Bearing the above limitations in mind, the central role of the “functional equivalence”
380 hypothesis in explaining the observed biodiversity loss in invaded plots is supported by four
381 lines of evidence. First, the abundance of each species largely determined its chances to become
382 extinct, with rare species becoming more frequently extinct from local assemblages and more
383 abundant species having higher chances to persist. In fact, invaded plots exhibited a decrease in
384 the mean abundance of native individuals compared to non-invaded plots, which can drive the
385 most rare species to extinction by stochastic effects. Although variation in species’ local
386 abundance has long been acknowledged to be an important factor determining extinction
387 dynamics (Kembel, 2009; Cadotte *et al.*, 2010), analyses of biological invasions have rarely
388 considered how differences in species’ abundance *per se* determine their chances to become
389 extinct. Interestingly, this result is in disagreement to Powell *et al.*’ (2013) results that most
390 common species are the most affected by invasion and further research should assess if this is a
391 consequence of differences in the scale of analysis (see Proches *et al.*, 2008), the species studied
392 or other environmental and/or regional differences. Second, phylogenetically diverse local
393 assemblages tended to lose higher 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 over-dispersion in invaded communities, which would be expected if inter-specific competition determined species' chances to become 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 over-dispersed phylogenetically than expected by chance. Rather, communities seem to have been mainly 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 tended to disappear more frequently and in a consistent way across invaded plots. This finding suggests that inter-specific 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 higher 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 in occasions 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, space availability for native species is largely reduced and proportionally more individuals from the native community are replaced by the invasive. We have shown that the amount of phylogenetic diversity loss is highest in *Carpobrotus* invasions and that the amount of such loss is, unlike for the other invasive species

studied, independent from the phylogenetic diversity of the native assemblage. Contrarily, *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 inter-specific 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 do 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 little structured communities 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 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 disturbances for centuries (Cowling *et al.*, 1996). Such disturbances may have altered competition regimes and favored simple ecological communities mainly governed by dispersal (Bartomeus *et al.*, 2012). Alternatively, the importance of random process might be more general, as suggested by stochastic niche theory (Tilman, 2004). The distinctness in life form and life history among the invader species studied here favors the possibility that results might be replicated in different biological scenarios. However, provided the idiosyncrasy of biological communities we claim that 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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609 **List of brief titles for the items in the Supplementary Material:**

610 Appendix S1: Phylogeny encompassing all species included in the study

611 Appendix S2: Analyses of phylogenetic structure of local communities

612 Appendix S3: Species significantly affected by the invasion

613 Appendix S4: Alternative mechanism of the “Environmental Filtering” hypothesis

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615

616 **Biosketch:**

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

622

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

626

627

628 **Tables**

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

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Dependent variable	Factor	Estimate	Std.Error	t-value	p-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

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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” section for further explanations on how these parameters were estimated.

Species and Island	Invasion status	Paired plots	PDiv $\pm$ SE	p-value	MNTD $\pm$ SE	p-value	MeanPDist $\pm$ SE	p-value
Oxalis 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	
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	
Ailanthus 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	
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	
Carpobrotus 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	
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	

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 modeled with a Binomial generalized linear mixed model in the Bayesian R-package “MCMCglmm” following Hadfield (2010), see methods section 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

Figures

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 after A) 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, species chances to become extinct are independent of traits that do not show phylogenetic signal (e.g. 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 from 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 from their phylogenetic relatedness to the invasive species (e.g. also irrespective to 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. Size of the forms refers to the abundance of each species and its form 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.

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.

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 *Oxalis* and *Ailanthus*-invaded local assemblages 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 = 0 are provided for reference.

696 Figure 2

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Supporting information

Appendix S1.

Figure S1: Complete phylogeny of all species found in invaded and non-invaded plots for the three invasive species *Ailanthus altissima*, *Carpobrotus* spp. and *Oxalis pes-caprae* in Mallorca and Menorca.

Appendix S2: Results of analyses testing for phylogenetic clustering and evenness in the structure of the local communities included in the study.

Table S2: Number of local assemblages with significantly even (i.e. overdispersed) or clustered phylogenetic structures measured for both the mean pairwise phylogenetic distance (MPDist) and the mean distance separating each species in the community from its closest relative (MNTDist). These have been estimated by comparing the standardized effect size of MPDist and MNTDist in communities by comparing null models generated by using “species.pool” and “richness” simulations in Picante (Kembel *et al.* 2013). By using “sample.pool” the community data matrix was randomized by drawing species from pool of species occurring in at least one community with equal probability while “richness” null models are drawn by randomizing the community data matrix abundances within samples while maintaining the species richness constant for each assemblage constant (Kembel *et al.* 2013). Results are shown for “species.pool” randomizations but they were similar when simulations were conducted using the “richness” method. Alternative analyses without accounting for the abundance of species provided similar results (not shown). Numbers correspond to number of plots that are significantly phylogenetically overdispersed ($p > 0.95$; i.e. even plots) and those that are significantly phylogenetically clustered ($p < 0.05$).

		<i>Oxalis</i>		<i>Ailanthus</i>		<i>Carpobrotus</i>		
		Mallorca	Menorca	Mallorca	Menorca	Mallorca	Menorca	
Non-invaded								mean $\pm$ SE
MeanPDist	Overdispersed	0	2	0	1	0	0	0.5 $\pm$ 0.34
	Clustered	0	0	2	1	0	0	0.5 $\pm$ 0.34
MNTD	Overdispersed	1	1	1	2	1	0	1 $\pm$ 0.26
	Clustered	2	2	6	0	0	1	1.83 $\pm$ 0.91
Invaded								mean $\pm$ SE
MeanPDist	Overdispersed	1	1	1	1	0	0	0.67 $\pm$ 0.21
	Clustered	0	0	0	0	0	0	0 $\pm$ 0
MNTD	Overdispersed	1	1	0	1	0	2	0.83 $\pm$ 0.31
	Clustered	0	0	3	0	0	1	0.67 $\pm$ 0.49

Appendix S3: Identifying which species are significantly affected by the invasion

We assessed if some species showed consistently high (or low) chances to become extinct when a nonnative species becomes abundant in their native range irrespective with their abundance. Replicated observations within each of the sampled species were included in species-level paired t-tests to identify which species tended to consistently disappear more than expected from invaded local assemblages, provided their abundance in non-invaded plots. We also assessed if some species were more abundant in invaded local assemblages than expected given their abundance. Phylogenetic relatedness was not included here because it was previously shown not to play a relevant role in the chances of native species to disappear in invaded plots. We replicated the analysis by comparing both data on presence and abundance of each species in invaded vs. non-invaded plots. Thus, a species-level analysis of abundance data on each species showed that some species tended to consistently and significantly decrease from Invaded plots. For some species, consistency across islands and the identity of the invasive species could not be evaluated simply because they were not present in these plots. This is because species composition varied importantly among islands and habitats invaded by the three different species. Results from an analysis based on presence rather than abundance provided similar results (all species below the significance level of 0.01 were significant using both approaches; not shown). However, we detected the presence of two species that became significantly more abundant in Invaded plots (see Table below). Altogether, such results show that although neutral processes have been shown to play a remarkable role at determining which species will become extinct from invaded assemblages, some species are indeed more (or less) affected than predicted by such neutral scenarios, suggesting that they might have some traits that make them more (or less) vulnerable to extinction by invasive species.

Table S3: List of those species consistently and significantly decreasing and increasing from invaded local assemblages.

Species abundance	Estimate	df	p-value
Species decreasing more than expected			
<i>Plantago_coronopus</i>	7.22	17	0.00004
<i>Helichrysum_stoechas</i>	4.40	9	0.00092
<i>Lotus_cytisoides</i>	4.52	24	0.00411
<i>Crucianella_maritima</i>	2.50	5	0.00675
<i>Pistacia_lentiscus</i>	3.17	29	0.00678
<i>Parapholis_incurva</i>	5.33	8	0.00920
<i>Sonchus_oleraceus</i>	1.85	25	0.02232
<i>Desmazeria_rigida</i>	2.22	17	0.02780
<i>Asteriscus_aquaticus</i>	9.17	5	0.03098
<i>Brachypodium_retussum</i>	8.67	5	0.03409
Species increasing more than expected			
<i>Avena_sp</i>	-3.62	12	0.00592
<i>Bromus_madritensis</i>	-4.19	15	0.02569

Appendix S4:

Figure S4: Alternative mechanism of the “Environmental Filtering” hypothesis commented in the Discussion of the results. In this scenario, species do not become extinct at random. Rather, as in the Functional equivalence scenario, species sharing a given attribute (e.g. the ability to live in habitats with low C/N soil ratios) tend to show higher chances to become extinct. However, the main difference with the present model is that here the presence / absence of the attribute does not show any phylogenetic pattern. Thus, the pattern seems to be distributed at random but species chances to become extinct are not random, rather extinction depends on whether they possess such particular trait or not. The star symbol represents the invasive species. Species vanished from the native assemblage are represented in grey. Size of the forms refers to the abundance of each species and its form represents the presence of a given trait (e.g. triangles correspond to species that do not tolerate low C/N ratios in the soil). For simplification, abundance and species traits are represented as categorical.

Establishment

Environmental filtering

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