

## LETTER

# The effects of phylogenetic relatedness on invasion success and impact: deconstructing Darwin's naturalisation conundrum

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### Abstract

Darwin's naturalisation conundrum describes the paradox that the relatedness of exotic species to native residents could either promote or hinder their success through opposing mechanisms: niche pre-adaptation or competitive interactions. Previous studies focusing on single snapshots of invasion patterns have provided support to both sides of the conundrum. Here, by examining invasion dynamics of 480 plots over 40 years, we show that exotic species more closely related to native species were more likely to enter, establish and dominate the resident communities, and that native residents more closely related to these successful exotics were more likely to go locally extinct. Therefore, non-random displacement of natives during invasion could weaken or even reverse the negative effects of exotic–native phylogenetic distances on invasion success. The scenario that exotics more closely related to native residents are more successful, but tend to eliminate their closely related natives, may help to reconcile the 150-year-old conundrum.

### Keywords

Community phylogenetics, competition, Darwin's naturalisation hypothesis, invasion, niche.

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## INTRODUCTION

The invasion of ecosystems worldwide by non-native species has major ecological, social and economic consequences, and the ability to predict potential invaders and their ecological impacts has become a central challenge in invasion biology (Mack *et al.* 2000). Many studies have attempted to identify these potential invaders by examining their functional traits, especially those associated with resource use efficiency, reproductive potential and dispersal ability (Rejmánek & Richardson 1996; Simberloff 2009; Van Kleunen *et al.* 2010). However, predicting species invasion with these approaches has proven difficult, since traits that promote invasiveness may vary among taxa and habitats, and because some important functional traits are extremely difficult to identify and measure (Kolar & Lodge 2001; Moles *et al.* 2008).

With the increasing availability of phylogenetic information, an approach focusing on the phylogenetic relatedness between potential invaders and recipient communities, first proposed by Charles Darwin, has been gaining much attention (Proches *et al.* 2008; Thuiller *et al.* 2010). On the one hand, Darwin (1859) proposed that exotic species more distantly related to native communities tended to be more successful, as they would share fewer natural enemies and compete less intensively with the native species. This hypothesis now has been termed 'Darwin's naturalisation hypothesis' (Daehler 2001; Fig. 1a). On the other hand, Darwin also suggested that exotic species should be favoured in communities containing their

close relatives, because close relatives share similar traits and may favour similar environments, which was termed 'pre-adaptation hypothesis' (Ricciardi & Mottiar 2006; Fig. 1b). Altogether, these two opposing hypotheses, describing the potential contrasting influences of exotic–native phylogenetic similarity on species invasion, constitute Darwin's naturalisation conundrum (Diez *et al.* 2008; Thuiller *et al.* 2010).

Recent studies across numerous taxa and ecosystems have evaluated this conundrum (e.g. Duncan & Williams 2002; Strauss *et al.* 2006; Diez *et al.* 2009; Schaefer *et al.* 2011; Park & Potter 2013; Bezeng *et al.* 2015). However, the vast majority of studies to date have comprised large-scale observations at a single snapshot in time, and have supported the opposing hypotheses in roughly equal proportions (see Table S1 in Supporting Information for a summary). These studies, while offering important insights, may not yield generalised conclusions because they focused on different conceptual frameworks, spatial scales and invasion stages (Proches *et al.* 2008; Thuiller *et al.* 2010). There are three main limitations of previous observational studies. First, these single-observation investigations examine *a posteriori* pattern about invasion processes (Thuiller *et al.* 2010; Sol *et al.* 2014). These types of data often lack accurate information on the historical community composition dynamics during the invasion process, which ignore native species that have gone extinct locally or that have been displaced by the exotics. This point is especially germane since phylogenetically non-random extinction of native taxa can result in a misleading interpretation of the

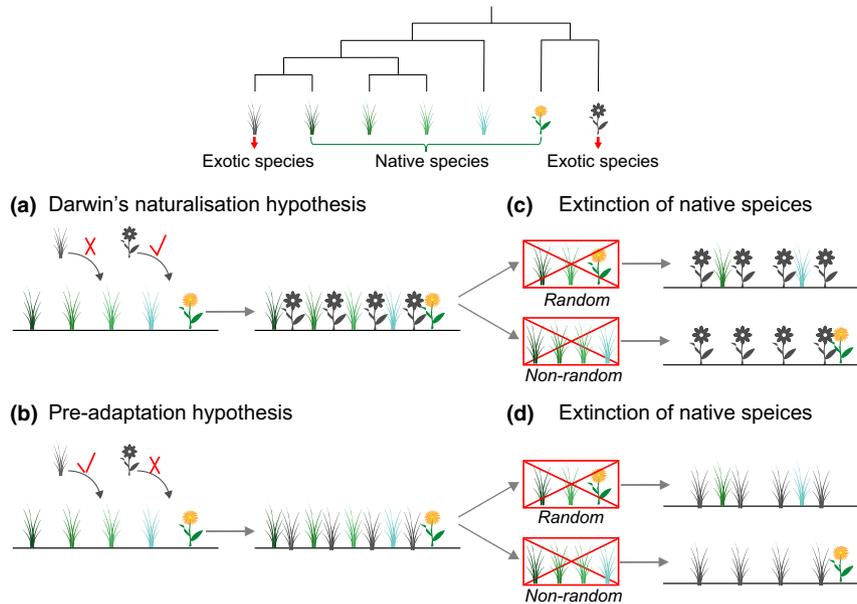
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**Figure 1** The potential effects of phylogenetic relatedness on exotic success and impact during invasion processes. (a) Darwin's naturalisation hypothesis (DNH) states that exotics closely related to natives are less likely to be successful, as they compete stronger with natives, but (b) pre-adaptation hypothesis (PAH) suggests that exotic species closely related to natives should be more successful, as they share the same ecological adaptations with natives. However, the non-random displacement of natives during invasion process can confound the phylogenetic patterns (c, d). For example, if exotic species closely related to natives are favoured (as suggested by PAH) but then compete stronger against their closely related natives, the long-term outcome can be the co-occurrence of exotics with their distantly related natives, as their closely related natives have been displaced, which is likely to be mistakenly interpreted as evidence for DNH without the temporal data (as shown in bottom panel of d).

phylogenetic patterns (Fig. 1c, d). For example, if exotics succeed better in communities with closely related natives and subsequently displace these natives as a result of competitive exclusion, the outcome observed in snapshot studies would be that exotics co-occur with their distantly related natives, which is likely to be interpreted incorrectly as support for Darwin's naturalisation hypothesis (as shown in the bottom panel of Fig. 1d). Second, it is questionable how observations at large spatial scales can help to resolve Darwin's naturalisation conundrum. As recent studies have suggested, Darwin's view of competition best applies to local scales where species share the same environment, and biotic interactions (e.g. competitive exclusion, facilitation, enemy release) take place (Jiang *et al.* 2010; Thuiller *et al.* 2010). However, most previous studies examined patterns at regional or continental scales (Table S1), much larger than the scales where species frequently interact and compete with each other. Third, a number of recent studies have recognised that the outcomes of tests of Darwin's conundrum are dependent on invasion stage (Diez *et al.* 2008; Schaefer *et al.* 2011). Invasions can be divided into a series of stages including introduction, establishment/naturalisation and subsequent outcome/spread/impact, and the ecological processes determining invasion success may differ among stages (Richardson *et al.* 2000; Kolar & Lodge 2001; Pyšek *et al.* 2004; Seastedt & Pyšek 2011; Li *et al.* 2015a). However, most recent studies have focused on only single invasion stage (i.e. naturalisation, spread, or impact; Table S1), and no study, to the best of our knowledge, has comprehensively examined phylogenetic patterns across multiple invasion stages over time. Therefore, long-

term, fine-scale studies, which include native community dynamics and multiple invasion stages, are critical to separate the mechanisms of the conundrum.

Another problem with Darwin's intuitive arguments and contemporary tests is that they have relied on a key assumption that the large niche overlap and strong competitive interactions between exotics and resident species hinder the success of exotics (Proches *et al.* 2008). However, the outcome of competitive interaction depends on not only the amount of niche overlap but also the relative competitive ability of the competitors (MacDougall *et al.* 2009). Compared with their closely related natives, exotic species, especially invasive ones, often have higher resource use efficiency and superior competitive ability (Vilà & Weiner 2004; Funk & Vitousek 2007; Van Kleunen *et al.* 2010). Therefore, if close relatives compete strongly, such competitive interactions may not necessarily limit the success of the exotics so long as they are superior competitors (MacDougall *et al.* 2009). Instead, successful exotics could suppress and potentially exclude their closely related natives with lower competitive ability. Thus, observational evidence that successful exotics tend to be distantly related to native residents could be driven either by the large niche overlap that suppresses the success of exotics in the presence of closely related species (Fig. 1a) or by the displacement of competitively inferior native species that are closely related to the exotics (MacDougall *et al.* 2009; Sol *et al.* 2014; as shown in bottom panel of Fig. 1d). Therefore, it is difficult to draw definitive conclusions on Darwin's conundrum based on any single-time investigations of natural communities.

Here, we present a phylogenetic analysis on the patterns of plant invasion using over 40 years of uninterrupted community data across 480 fine-scale permanent plots in the Buell-Small Succession Study (NJ, USA). By strictly classifying the invasion status of exotics in each plot, we tested Darwin's naturalisation conundrum across different invasion stages. Further, we also assessed the effects of exotic-native phylogenetic relatedness on the persistence probability of the native resident species during the invasion process, and provide the first evidence that the non-random displacement of native species could weaken or reverse the phylogenetic relatedness between successful exotics and native species.

## MATERIALS AND METHODS

### Study site and data collection

To examine the effect of phylogenetic relatedness on invasions at fine scales, we used data collected from a permanent-plot study of abandoned agricultural land in the Piedmont of New Jersey, USA (40°30' N, 74°34' W) – the Buell-Small Succession Study. To the best of our knowledge, these data represent the longest continuous study on plant invasion and post-agricultural succession. The study site comprises 10 agricultural fields abandoned in pairs from 1958 to 1966. Within each field, 48 permanently marked 0.5 × 2.0 m plots were arranged in a grid immediately after abandonment. In each year (alternate years since 1979), the permanent plots were sampled, and the percentage cover of all exotic and native species present in each plot was recorded (Pickett 1982; Li *et al.* 2015b). This landmark study has continued uninterrupted for more than 40 years (Meiners *et al.* 2004; Cadenasso *et al.* 2009), offering a unique opportunity to test Darwin's conundrum. Our analyses were restricted to years 1966–2009, as all fields cover this time series. This time period encompasses the full range of successional transitions: from short-lived to perennial herbaceous species, to shrub dominance, to the formation of a deciduous tree canopy. Because the 10 fields were sampled in alternate years (with half of the fields sampled each year), these data were condensed into 2-year intervals (e.g. data from year 2008 to 2009 were condensed together), to maintain even replication.

### Invasion stage

In this study, we defined exotic species as those which originated outside North America and were introduced intentionally or accidentally by humans (Gleason & Cronquist 1991). We strictly classified the status of exotics based on their specific performance in each plot, rather than defining them into *a priori* group. For this purpose, we classified three stages of invasion: introduction, establishment and dominance, according to the classification suggested by Seastedt & Pyšek (2011). Specifically, for each plot, exotic species were hierarchically classified by whether they were introduced (i.e. presented in the plot), established (persisted through time) or dominant (became abundant) in the plot or not. Here, we followed the work of Richardson *et al.* (2000) and Pyšek *et al.* (2004), and defined successfully established species as those introduced

exotics that appear to maintain self-sustaining populations for at least 10 years in the plots. Successfully dominant species are a subset of successfully established species that had higher abundance than any natives in the plot. For our analysis, we considered dominance as a later stage of invasion, rather than spread or impact, because dominance is well defined for our plot level analysis, and links directly to applied community management (Seastedt & Pyšek 2011).

### Phylogeny construction

We extracted the molecular phylogeny for all the native and exotic species that occurred in the Buell-Small Succession Study from a recent publication (Li *et al.* 2015b). Briefly, we obtained three commonly sequenced genes (*rbcL*, *matK* and *ITS*) from GenBank, and used one representative of early diverging seed plant – *Cycas revoluta* – to serve as an out-group. Of the 325 species, 259 had at least one gene represented in GenBank. For the remaining species, we used the sequences of congeners as a proxy. Six species of unknown origin, which could only be identified to genus level, were excluded from subsequent data analyses. Sequences were independently aligned using MUSCLE (Edgar 2004) and the best-fit model of nucleotide substitution for each region was selected by jModeltest (Posada 2008). The Bayesian phylogeny was reconstructed using BEAST version 1.7.5 (Drummond *et al.* 2012). The Bayesian MCMC chain was ran for 30 million generations, and convergence was checked using Tracer version 1.5 (<http://beast.bio.ed.ac.uk/Tracer>). The consensus tree with maximum clade credibility from the posterior distribution was used to quantify phylogenetic patterns by Tree Annotator 1.7.5 (Drummond *et al.* 2012). The reconstructed phylogenetic tree represents the relationships among all native and non-native species occurred in the Buell-Small Succession Study from 1966 to 2009 (Fig. S1).

### Phylogenetic patterns of invasion success

Exotic species recorded in each plot at each sampling time point during 1976–2009 were hierarchically classified into either successful or failed group for each of the three invasion stages. Three phylogenetic metrics were calculated to measure the phylogenetic distances of each exotic group to the native species in the plot: (1) the mean phylogenetic distance (MPD) to the all native species, (2) the abundance-weighted MPD (MPD<sub>ab</sub>) to the natives, weighted by the relative abundance of the natives and (3) the mean phylogenetic distance of each exotic species in the group to its nearest native relative (MNND) (Webb *et al.* 2002; Strauss *et al.* 2006). These metrics were calculated using the ICOMDIST function in Phylocom (Webb *et al.* 2008).

We used generalised linear mixed-effects models (GLMMs) with logit link and binomial error distribution to model the probability of invasion success (successful/failed) as a function of the phylogenetic distance of each exotic status group to natives in the plots. In these models, MPD, MPD<sub>ab</sub> or MNND was treated as a single continuous fixed factor independently, while the year of observation, the 10 fields and the 48 plots nested within each field were considered as random

effects. For establishment and dominance stages, only successfully introduced and established species were considered in the analysis to avoid the residual effects from previous stages. We fitted varying slope and varying intercept models to allow the slope parameters to vary by the year of observation, using the *lme4* package (Bates *et al.* 2014) in R version 3.10 (R Development Core Team 2014). The overall changes of exotics' invasion status were also modelled by mixed-effects sequential logistic regression, with the same fixed and random effects considered. Invasion status was coded by four levels in each plot for every year (failed introduced exotics, 0; successfully introduced but failed established exotics, 1; successfully established but failed dominant exotics, 2; successfully dominant exotics, 4), and the analysis was performed using the package *ordinal* (Christensen 2015) in R.

To determine the influence of historical changes in community compositions on phylogenetic patterns, we compared the results basing on historical and current community compositions. For current communities, we only considered the native and exotic species present in the plot in year 2009. For historical communities, analyses were replicated by averaging species compositions from 1989 to 2009 within each plot. We choose the 20-year time interval as a measure of the historical communities because the average time for an exotic species from introduction to establishment to dominance in a plot is about 20 years (Meiners *et al.* 2004). As other time intervals (e.g. 15, 25, and 30 years) yielded comparable results, only the results based on the 20-year time interval were reported. Again, the probabilities of invasion success were modelled by the same GLMMs and mixed-effects sequential logistic regressions, with plots nested within fields as random effects. Further, the square root-transformed cover of exotic species in each plot was also fitted as a function of their phylogenetic distances to the current and historical native residents, by GLMMs with the same random effects, assuming a Gaussian distribution of the response. Slope parameters of the fixed effects from the historical and current communities were compared to determine whether single-time investigations would produce biased results.

### Invasion impacts on native residents

To detect the impact of exotic invasion, all native species that had occurred in each plot during 1989–2009 were classified into two groups: persistent native species (the ones still persisted in 2009) and extinct native species (those disappeared by 2009). We calculated the MPD,  $MPD_{ab}$  and MNND of these two status groups to the successfully introduced, established and dominant exotics in each plot. The persistence probability of native species (persistent/extinct) was modelled by GLMMs, as a function of the phylogenetic distances from each native status group to the successful exotics in the three invasion stages, with plots nested within fields as random effects. We also modelled the persistence probability of native species for every possible 20-year time interval from 1966 to 2009 (e.g. 1966–1986, 1967–1987, etc.), by the same GLMMs with the time intervals added as a random effect.

## RESULTS

### Phylogenetic patterns of invasion success

When all the 10 560 records from the 480 plots from 1976 to 2009 were considered together, the GLMMs showed that the probabilities of successful introduction, establishment and dominance were negatively related to the phylogenetic distances to the native species present in the plots, which suggested that the successfully introduced, established and dominant exotic species were generally more closely related to the native residents than the failed ones (Table S2). This pattern was robust to different phylogenetic metrics (MPD,  $MPD_{ab}$  and MNND), and the inclusion and exclusion of different random effects (year, field and plot). Overall, the sequential logistic regression also suggested that the exotic species more closely related to the native residents were more likely to become more successful (Table S2).

When the historical community compositions during 1989–2009 were taken into account, we found a consistent pattern that the exotic species more closely related to native species were more likely to enter, establish and dominate the resident communities (except that introduction success was not associated with  $MPD_{ab}$ ; Fig. 2). When only the current community compositions were considered, however, patterns became more complicated. The exotic species more closely related to native species were still more likely to enter and establish (except introduction success that was not associated with  $MPD_{ab}$ ), whereas the successfully dominant species became more distantly related to the current native residents than the failed ones (Fig. 2). In addition, it was found that abundant exotics were closely related to the historical native residents, but distantly related to the current native residents in the plots (Fig. S2). Overall, the sequential logistic regression revealed that single-year observation of community compositions could underestimate the negative effects of exotic–native phylogenetic distances on invasion success (Fig. 2).

### Invasion impacts on native residents

We found that the persistence probability of the native species during 1989–2009 was significantly positively associated with MPD,  $MPD_{ab}$  and MNND to the successfully introduced, established and dominant exotic species in the plots (Fig. 3), which suggested that the persistent native species were more distantly related to the successful exotics than the extinct ones in the plots. Again, when all the possible 20-year time intervals from 1966 to 2009 were considered together, we found similar pattern, that is, the native species that were more closely related to the successful exotics were generally more likely to go extinct locally during the whole invasion process (Table S3).

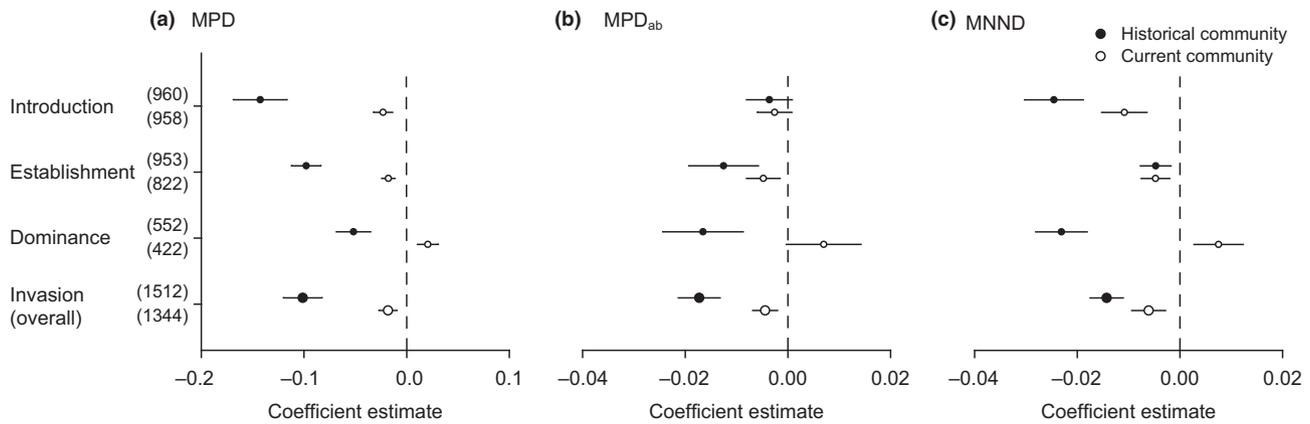
## DISCUSSION

Previous observational studies have shown that exotic species distantly related to the native species would occur in communities more frequently and successfully than closely related ones (e.g. Strauss *et al.* 2006; Schaefer *et al.* 2011; Bezeng

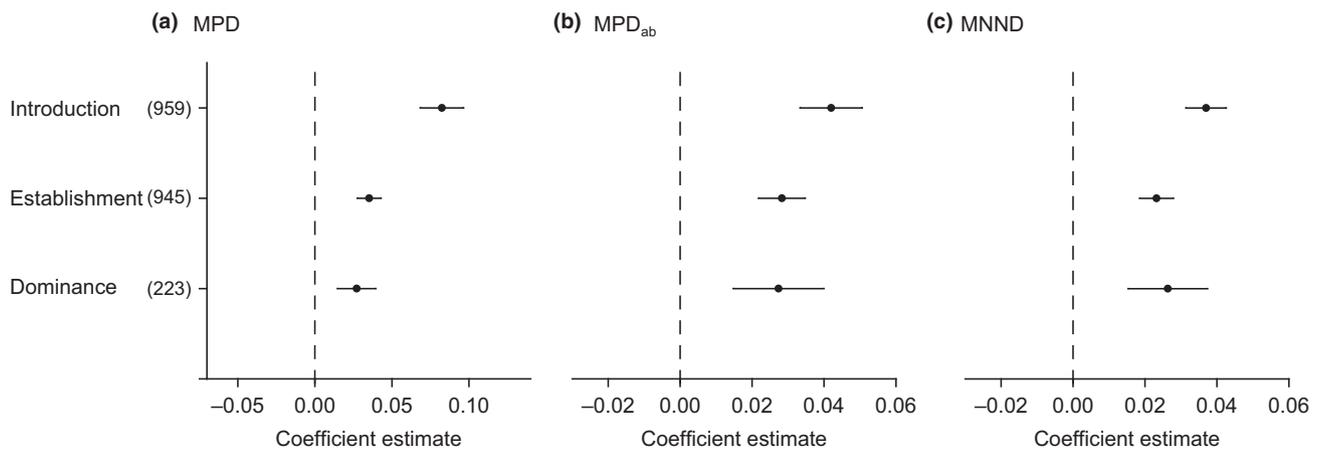
*et al.* 2015). Most studies have interpreted this pattern as evidence for Darwin's naturalisation hypothesis based on the assumption that strong competition from close native relatives could hinder the success of the invaders. In contrast, our long-term dynamic data showed that the exotics more closely related to the native species were more likely to enter, establish and dominate our survey plots (Fig. 2, Table S2), which supported the pre-adaptation hypothesis. Remarkably, we found that natives more closely related to the successful exotics were more likely to be displaced, and only the natives distantly related to the successful exotics could persist and co-occur with these exotics (Fig. 3, Table S3). This pattern

could be incorrectly interpreted as evidence for Darwin's naturalisation hypothesis using a single snapshot in time. Our study provided the first evidence that the non-random displacement of native species could result in a misleading interpretation of the phylogenetic patterns, which casts doubt on the ability of static snapshots of community compositions to resolve Darwin's conundrum.

Although the effects of phylogenetic relatedness on invasion success have been tested in numerous studies across taxa and ecosystems, the impacts of species invasion on exotic–native phylogenetic relatedness have rarely been considered (Bennett *et al.* 2014). A tacit assumption underlying previous



**Figure 2** The contrasting effects of phylogenetic distances of exotics to current and historical native residents on the probabilities of their introduction, establishment and dominance. The phylogenetic distances of each exotic status group to natives were calculated based on single year (current community, only considering species that were present in 2009) or temporal data (historical community, considering the cumulative performance of species from 1989 to 2009) respectively. Numbers correspond to sample sizes for each invasion stage. The effects of MPD, MPD<sub>ab</sub> and MNND on invasion success were modelled by generalised linear mixed-effects models and sequential logistic regression (see Materials and Methods for further details). Negative coefficient estimates (with 95% credible intervals plotted as bars) indicate that successful exotic species were generally more closely related to the native residents than the failed ones, while the positive values indicate the opposite.



**Figure 3** The effects of phylogenetic distances of native residents to successful exotics on their persistence probabilities during 1989–2009. We separately modelled the persistence probability of native species as a function of the phylogenetic distances (MPD, MPD<sub>ab</sub> and MNND) to the successfully introduced, established and dominant exotics in the plots, by generalised linear mixed-effects models (see Materials and Methods for further details). Numbers correspond to sample sizes for each invasion stage. Positive coefficient estimates (with 95% credible intervals plotted as bars) indicate that the persistent native species were more distantly related to the successful exotics than the extinct ones in the plots, while the negative values indicate the opposite.

investigations is that the native community is static, and the displacement of native species is rare. Such an assumption is likely invalid in natural communities, and it is necessary to incorporate native species displacement into Darwin's phylogenetic framework (Thuiller *et al.* 2010). A central tenet in Darwin's framework is that closely related species are more ecologically similar, and thus will compete more strongly with each other, which could repel the exotics (Darwin 1859). Our results present challenges to this framework, and suggest the strong competitive intensity among close relatives may not necessarily repel invaders, but instead may result in the loss of native species. In our study, the presence of closely related natives did not decrease the success probability of exotics (Fig. 2, Table S2), but the presence of closely related exotics significantly decreased the persistence probability of native species (Fig. 3, Table S3), which is consistent with the idea that competitive interaction suppress natives stronger than exotics. For example, *Rosa multiflora*, the most abundant exotic species in the study site, often colonises mid-successional fields along with a suite of closely (*Rubus* spp.) and more distantly related natives (e.g. *Parthenocissus quinquefolia* and *Toxicodendron radicans*). The invasive exotic became the dominant species in the system, relegating the native *Rubus* to low abundances or local extirpations, while other distantly related native species continued to increase and coexisted with *R. multiflora* in mid-successional communities (Meiners *et al.* 2015). These results highlight that, without information on temporal dynamic of native community compositions, the co-occurrence of exotics with their distantly related natives *per se* cannot be unambiguously considered as direct evidence for Darwin's naturalisation hypothesis.

The consistent phylogenetic patterns at three invasion stages provided strong support for pre-adaptation hypothesis, suggesting that environmental filtering determines the success of biological invasions (Ricciardi & Mottiar 2006). Environmental filtering has been generally supposed to outweigh the outcome of species interactions only at large spatial scales (Proches *et al.* 2008; Thuiller *et al.* 2010). However, our results were inconsistent with this traditional view and suggested that environmental filtering could also play important roles at fine scales. In fact, there is increasing evidence that close relatives often possess similar traits, occupy similar microhabitats and generate similar plant–soil feedbacks (Ackerly 2009; Burns & Strauss 2011; Reinhart *et al.* 2012; Anacker *et al.* 2014; Li *et al.* 2015a). Therefore, the microhabitats occupied by native residents are likely preferred for their closely related exotics, especially when competition between native and exotic species does not hinder the success of the exotics. In contrast, phylogenetically dissimilar exotics tend to be unable to survive in these microhabitats due to local microhabitat filtering. These results highlight the importance of local microhabitat filtering on community assembly at relatively small spatial scales, which have been largely neglected in previous studies.

Despite the reliable explanatory basis provided by our framework, several limitations of our study should be recognised. First, phylogenetic patterns of community assembly, such as Darwin's naturalisation conundrum, are often scale dependent (Proches *et al.* 2008; Thuiller *et al.* 2010). Results

obtained at fine scales including the results of this study are not necessarily applicable to large-scale patterns, such as those found in Strauss *et al.* (2006), Schaefer *et al.* (2011) and Bezeng *et al.* (2015). In fact, we found no significant phylogenetic patterns at the whole phylogeny scale (Fig. S1, Table S4). Second, this study focused on community composition dynamics over a long period of time, wherein the exotics have also encountered successional changes in native communities (Li *et al.* 2015b). That is, the phylogenetic patterns we found could be confounded by other extrinsic factors such as the changing environmental conditions over time (e.g. the development of shade), variation in the timing of exotic species colonisation and interactions among exotic species. Third, a restrictive definition of exotic species was used in this study. Yet, in a wider context, all newly arriving species (regardless of their origin) of a pre-existing community could be considered as invaders. Such a difference in definition of focal species may lead to distinct interpretations for a given observed phylogenetic pattern. Last but not at least, a critical assumption of the approach presented here is that phylogenetic relatedness captures ecological similarity among species, and that successfully dominant exotics have higher competitive ability than resident natives. There is growing evidence for the existence of phylogenetic niche conservatism (Ackerly 2009; Reinhart *et al.* 2012), and we believe it is plausible for us to consider the successful dominant species, which were more abundant than all native species, as better competitors than the natives in our study (Vilà & Weiner 2004; Funk & Vitousek 2007). However, studies that experimentally manipulate native phylogenetic community structure and the introduction of exotic species are needed to better understand the mechanisms driving invasion patterns.

Our study demonstrates that exotic species more closely related to native species often have greater chance to succeed, but natives that are closely related to these successful exotics also have greater chance to go locally extinct. By incorporating native species displacement into Darwin's phylogenetic framework, our study may help to reconcile the long-standing Darwin's conundrum. With the rapid development of phylogenetic technologies and data, the phylogenetic patterns of biological invasion could be systematically tested across different ecosystems at different scales, and hopefully will provide important guidelines for invasion risk assessment and management.

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## AUTHORSHIP

SPL, MWC, JTL and WSS developed and framed research questions. SJM collected the data used in this analysis. SPL, ZSH, HYS and SJM analysed the data. SPL and MWC wrote the first draft of the manuscript and all authors contributed to discussing the results and editing the manuscript.

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