

Revisiting Darwin's naturalization conundrum: explaining invasion success of non-native trees and shrubs in southern Africa

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Summary

1. Invasive species are detrimental ecologically and economically. Their negative impacts in Africa are extensive and call for a renewed commitment to better understand the correlates of invasion success.

2. Here, we explored several putative drivers of species invasion among woody non-native trees and shrubs in southern Africa, a region of high floristic diversity. We tested for differences in functional traits between plant categories using a combination of phylogenetic independent contrasts and a simulation-based phylogenetic ANOVA.

3. We found that non-native species generally have longer flowering duration compared with native species and are generally hermaphroditic, and their dispersal is mostly abiotically mediated. We also revealed that non-native trees and shrubs that have become invasive are less closely related to native trees and shrubs than their non-invasive non-native counterparts. Non-natives that are more closely related to the native species pool may be more likely to possess traits suited to the new environment in which they find themselves and thus have greater chance of establishment. However, successful invaders are less closely related to the native pool, indicating evidence for competitive release or support for the vacant niche theory.

4. *Synthesis.* Non-native trees and shrubs in southern Africa are characterized by a suite of traits, including long flowering times, a hermaphroditic sexual system and abiotic dispersal, which may represent important adaptations promoting establishment. We suggest that differences in the evolutionary distances separating the native species pool from invasive and non-invasive species might help resolve Darwin's naturalization conundrum.

Key-words: Darwin's naturalization hypothesis, dispersal, invasion ecology, phenology, pollination syndrome, sexual system

Introduction

Biological materials have been moved around the globe throughout human history. In southern Africa, non-native trees and shrubs have been introduced over the past three centuries to meet the growing demands for charcoal, timber production, ornaments, sand dune stabilization, etc. (Poynton 2009; Bennett 2010). However, many of these introduced species have naturalized and become invasive, posing severe economic and ecological challenges (Van Wilgen *et al.* 2001; Pimentel, Zuniga & Morrison 2005; Thuiller 2007; Hulme

2009). It is essential, therefore, to gain a better understanding of the factors that promote invasion success so that we can recognize future invaders before they become problematic and help develop pre-emptive management plans.

The search for common factors that predispose some introduced species to successfully naturalize and become invasive has been a major goal in invasion biology (Nentwig 2007; see also a recent review by Richardson & Pyšek 2012). This search has followed two general paths. First, species traits (Rejmánek 1995; Thuiller *et al.* 2006; Pyšek & Richardson 2007; Pyšek *et al.* 2014) or habitat characteristics (Levine, Adler & Yelenik 2004; Marvier, Kareiva & Neubert 2004; Alston & Richardson 2006) have been evaluated, and various biological traits have been suggested to enhance the competitiveness of non-native

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species over native species (Kolar & Lodge 2001; Pyšek & Richardson 2007; Violle *et al.* 2007; Ordonez & Olff 2013). However, the identification of predictive traits is challenging because it requires a great wealth of information on a species' biology that is often unavailable (Kolar & Lodge 2001). Further, traits that are strong predictors of invasion success for some taxa in one environment might not necessarily be good predictors for other clades or elsewhere (Kolar & Lodge 2001; Cadotte, Murray & Lovett-Doust 2006; Pyšek & Richardson 2007; Wolkovich *et al.* 2013). The recent rapid increase in, and availability of, molecular DNA data has motivated an alternative approach based on phylogenetic information.

Analysing species coexistence in the eastern United States, Darwin observed that introduced species are more likely to become naturalized and successful invaders in recipient environments where (phylogenetically) close relatives are absent. This hypothesis is often referred to as Darwin's naturalization hypothesis (DNH) (Daehler 2001; see also Rejmánek 1999). Phylogenetic approaches allow direct tests of DNH by comparing the phylogenetic distances separating native and invading species (Strauss, Webb & Salamin 2006). However, once again, empirical evidence has been mixed: whilst some studies have provided support for DNH (Rejmánek 1996; Ricciardi & Atkinson 2004; Strauss, Webb & Salamin 2006; Schaefer *et al.* 2011), others have not (Duncan & Williams 2002; Lambdon & Hulme 2006; Ricciardi & Mottiar 2006; Diez *et al.* 2009; Bezeng *et al.* 2013). One explanation for this discrepancy, which was also recognized by Darwin, is that closely related species may also share traits that pre-adapt them to a particular environment, and thus, non-native species more closely related to the native species pool would have an inherent advantage (Duncan & Williams 2002). These opposing predictions have been termed Darwin's naturalization conundrum (Diez *et al.* 2008).

In this study, we use a data set of putative key traits linked to invasion success in combination with a comprehensive phylogenetic tree of native and non-native trees and shrubs of southern Africa to evaluate the ecological and evolutionary determinants of invasion success in the region.

Materials and methods

STUDY AREA

We consider an area of southern Africa that includes Botswana, Mozambique, Namibia and Zimbabwe located south of the Zambezi River plus South Africa, Lesotho and Swaziland with a total land area of approximately 4 000 000 km². This region is a centre of high plant endemism, but many species are also highly threatened by various factors, including the introduction of alien plant species since the arrival of the first European settlers (Cowling *et al.* 2003; Henderson 2006).

SPECIES CHECKLIST AND PLANT BIOLOGICAL TRAITS

We compiled a matrix of native and non-native woody trees and shrubs for the region, encompassing 1400 taxa (1191 natives and 209

non-natives), representing 581 genera and 130 families (see Table S1 in supporting information). We follow O'Brien (1993) as a guide to defining woody taxa for our study as: perennial plants with an above-ground stem and secondary branches (with the exception of geoxyllic suffrutex *sensu* White 1976); however, we include species with a maximum height >0.5 m, and thus, the taxa we consider encompass more species than O'Brien's definition of trees (maximum height >2.5 m). We therefore refer to our included taxa collectively as woody trees and shrubs. In a very few instances, we included species that have been described as herbaceous within our sampling when they have sometimes also been considered as shrubs (e.g. *Tithonia* spp., *Hypericum perforatum*; Jama *et al.* 2000).

A checklist of non-native species was obtained from Henderson (2007), which forms the foundation for the Southern African Plant Invaders Atlas (SAPIA) data base, and supplemented with additional data from Coates Palgrave (2005). For native species, we used the species list from Maurin *et al.* (2014).

The categorization of non-native species as invasive and non-invasive is non-trivial, and published lists are frequently contradictory. Here, we follow the classification of Henderson (2007) (see Appendices 1–4 in Henderson 2007), which matches to the criteria for invasive species specified by Richardson *et al.* (2000a) and Pyšek *et al.* (2004). However, we combined Henderson (2007) naturalized and casual alien plants to form a single non-native non-invasive species category. We verified our classification in consultation with experts from the South African Biodiversity Institute and Center for Invasion Biology (CIB) at Stellenbosch University. Nonetheless, we acknowledge that there are a number of alternative data sources available (e.g. Van Wyk & Van Wyk 2013), and our classification may be subject to revision in the future. All species names were cross-checked for synonyms using *The Plant List* (www.plantlist.org) and the family names using the Angiosperm Phylogeny Group (APG III 2009) to match the classification followed by Maurin *et al.* (2014).

Although there is no consensus list of functional traits related to invasion success globally, numerous traits have been linked with species invasion locally and regionally (e.g. see Rejmánek 1995; Lake & Leishman 2004; Thuiller *et al.* 2006; Pyšek & Richardson 2007; Schaefer *et al.* 2011; Flores-Moreno *et al.* 2013; Wolkovich *et al.* 2013). Here, we focused on six traits that are commonly referred to in the invasion literature: maximum plant height, seed mass, sexual system, flowering time (first and last flowering months and duration of flowering period), primary dispersal mode and primary pollination syndrome. Data were collated from various sources as documented in Table S2. For sexual system, we combined species that were monoecious under the broad group 'hermaphrodite'. We additionally performed a sensitivity analysis by excluding monoecious species from the analysis. Finally, for both dispersal mode and pollination modes, we distinguished plants that use abiotic versus biotic dispersal agents.

PHYLOGENY RECONSTRUCTION

Phylogenetic tree reconstruction was conducted using a combined matrix of *matK* and *rbclLa* DNA sequences. Molecular DNA data were obtained from Maurin *et al.* (2014) for native species of southern Africa. DNA sequence data for non-natives were either obtained from Genbank/EBI (206 species) or sequenced directly from collected plant materials (26 species; Table S1). Phylogeny reconstruction was performed using BEAST following the steps outlined in Maurin *et al.* (2014), except that we used 21 calibration points (Table S3) rather than the 28 reported in Maurin *et al.* (2014), as runs failed to converge when the additional calibration points were included, even after

several weeks of processor time. The reconstructed phylogenetic tree represents relationships among 1400 native and non-native trees and shrubs species of southern Africa.

STATISTICAL ANALYSIS

All statistical analyses were performed in R (R Development Core Team 2013). First, we tested Darwin's naturalization hypothesis by comparing the phylogenetic nearest neighbour distance (PNND) between each non-native species (invasive and non-invasive) and its nearest native neighbour on the phylogenetic tree. If non-native species that are less related to native species are more successful invaders in southern Africa (as predicted by DNH), we would expect the average phylogenetic distance between invasives and natives (PNND_{invasive-native}) to be greater than the average phylogenetic distance between non-invasives and natives (PNND_{non-invasive-native}). Significance was assessed by comparing observed patterns to a null model in which non-native status was shuffled randomly 1000 times along the tips of the phylogeny.

Secondly, we tested for differences in plant functional traits between non-native and native categories using a combination of phylogenetic independent contrasts (PICs; Felsenstein 1985), a method that corrects for phylogenetic non-independence by taking differences (in trait values) between sister clades, and a simulation-based phylogenetic ANOVA (Garland *et al.* 1993).

We compared timing of first flowering month, last flowering month and duration of flowering period, using the phylogenetic ANOVA and post hoc comparisons of means using the function `phylANOVA` in the R package `Phytools` (Revell 2012). We evaluated sensitivity of our results to assumptions regarding the start of the growing season by exploring alternative start dates. Initially, we arbitrarily assumed a January start to the growing season, with months coded 1 (January) through 12 (December). Next, we shifted the start of the growing season to September (as most native species start flowering in September), with months coded 1 (September) through 12 (August).

We used the 'brunch' algorithm (Purvis & Rambaut 1995) as implemented in the R library `caper` (Orme *et al.* 2012), to explore the relationship between invasiveness and both maximum plant height and seed mass. The brunch algorithm conducts independent contrasts for models that include binary categorical variables (in this case invasiveness: invasive vs. non-invasive) where each clade can be unequivocally assigned to one state or the other. Nested contrasts deeper in the phylogeny are not included.

Finally, we calculated PICs (native–non-native) for each of our categorical variables: sexual system, pollination syndrome and dispersal mode, where each variable was scored as either 1 or 0. We then tested for a significant relationship between non-native status and each biological predictor in turn, using a *t*-test to evaluate whether the mean of the contrasts differed significantly from zero.

Results

The phylogeny of the regional pool is presented in Fig. 1. The phylogenetic distance between invasives and natives was significantly greater than that between non-invasives and natives [PNND_{invasive-native} = 250.26 Mya (millions of years) versus PNND_{non-invasive-native} = 241.75 Mya; Mann–Whitney *U*-test, *W* = 303 208, *P* < 0.001]. Further, comparing phylogenetic distances between non-native (invasive and non-invasive) and native plant categories using randomizations (shuffling taxa labels across the tips of the phylogeny), we

show that the mean observed PNND_{invasive-native} distance falls to the right of the null distribution, whereas the mean PNND_{non-invasive-native} falls to the left of this distribution (Fig. 2). Therefore, invasives tend to be less closely related to natives, whereas non-invasive species tend to be more closely related to natives, and this difference between invasives and non-invasives is highly significant.

In our analysis of flowering phenology, we found no evidence that first or last flowering month was related to invasion success, irrespective of when the start of the growing season was set (see Tables 1 and S4). However, non-natives (invasives and non-invasives combined) had significantly longer flowering times than native species (Holm–Bonferroni corrected *P* = 0.002 from phylogenetic ANOVA; Fig. 3; Table 1).

We found no significant difference in seed mass or maximum plant height between invasives and non-invasives (*P* > 0.05; Table 2). Data on pollination mode, dispersal and sexual system were not sufficiently complete to evaluate differences between non-native (invasives vs. non-invasives) species. However, in comparison with natives, non-natives were more often abiotically dispersed (*t* = 4.0; d.f. = 23; *P* = 0.005; Table 3) and hermaphroditic (*t* = 2.5; d.f. = 6; *P* = 0.04; Table 3). For sexual system, results were similar whether we treated monoecious species as hermaphrodites or excluded them from the analysis. Non-natives also tended to be abiotically pollinated, but so too did their native close relatives (*t* = 0.6; d.f. = 2; *P* > 0.05 for the comparison of non-natives versus native relatives; Table 3). Perhaps more notable than the ecological differences between natives and non-native species is, therefore, their ecological similarities; for example, out of the 62 possible phylogenetic contrasts with sufficient data, only four differed in primary pollination mode and seven differed in sexual system (Table 3).

Discussion

Identifying the factors that explain why some species become invasive whilst others do not remains a major challenge in invasion biology (Hayes & Barry 2008). Here, we explored the invasion success of non-native trees and shrubs in southern Africa, a centre of high woody plant diversity that is increasingly being impacted by anthropogenic modifications to the environment and climate. Various key biological traits have been linked to invasion success, including dispersal mode, pollination system, phenology, life-form and sexual system (e.g. Rejmánek 1995; Thuiller *et al.* 2006; Pyšek & Richardson 2007; Van Kleunen, Weber & Fischer 2010; Pyšek *et al.* 2014), but among the non-native trees and shrubs of southern Africa examined here, we found no strong differences in ecology or life history between invasive and non-invasive species. However, we show that invasive species are significantly less closely related to the native species pool than non-invasive species, with the latter tending to show closer phylogenetic affinities with the native tree and shrub community. We suggest that our results may help resolve Darwin's naturalization conundrum.

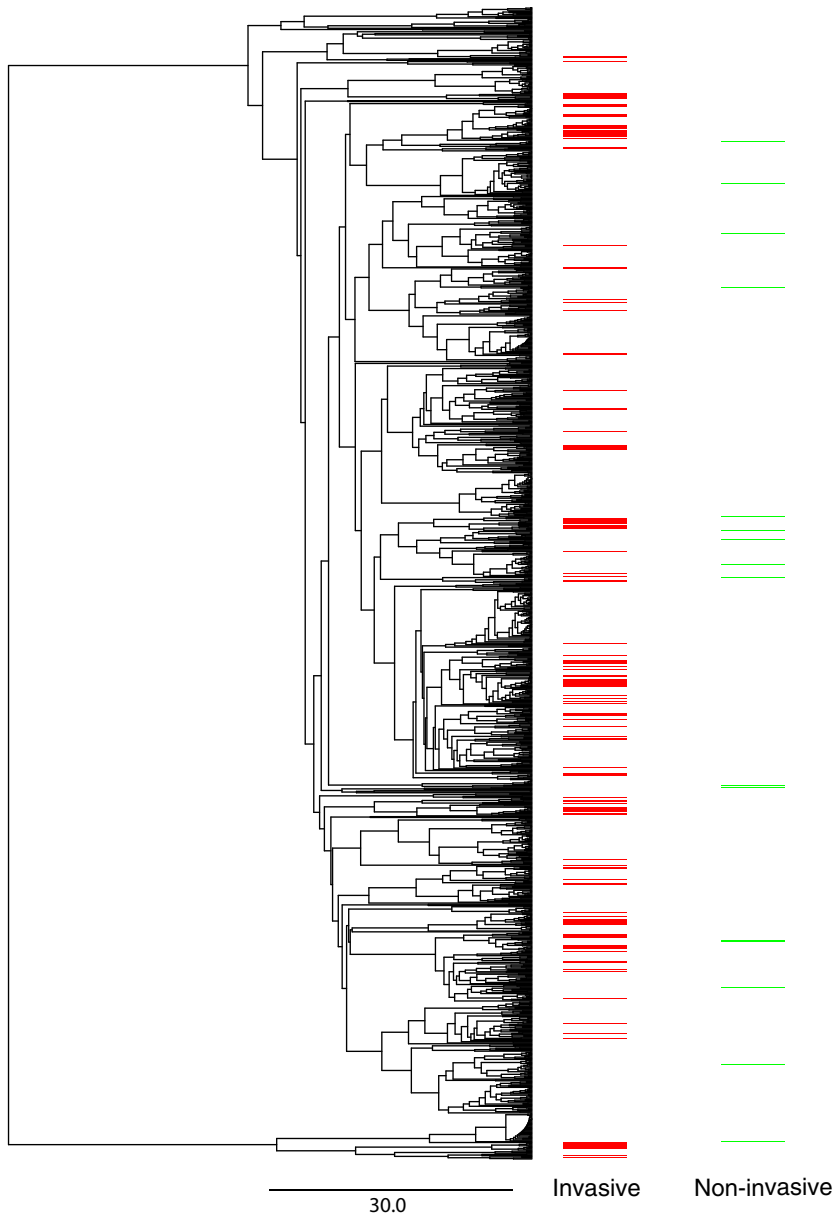


Fig. 1. Regional phylogeny of 1400 southern African native and non-native (invasive and non-invasive combined) trees and shrubs. Colour bars indicate the distribution of non-native species on the tree; red = invasive and green = non-invasive.

Darwin's naturalization conundrum reflects two apparently conflicting predictions regarding invasion success and phylogenetic distance between non-natives and the native species pool (Diez *et al.* 2008). First, non-natives distantly related to native species may be more successful invaders due to release from natural enemies (e.g. herbivores or pathogens) or because of weak competitive interactions with native species. Secondly, successful invaders might be expected to be more closely related to the native species pool because they share traits that pre-adapt them to the new environmental conditions in which they find themselves. Tests of Darwin's naturalization hypotheses have been mixed, and opposing predictions and mechanisms have been proposed (see Table 1 in Jones, Nuismer & Gomulkiewicz 2013). For example, there has been both documented evidence for increased susceptibility to attack by natural enemies (Hill & Kotanen 2009; Ness, Rollinson & Whitney 2011) and increased mutualisms (Richardson

et al. 2000b) among non-natives closely related to the native species pool. Further, in a cautionary note, Jones, Nuismer & Gomulkiewicz (2013) use a mathematical model to demonstrate that the influence of phylogenetic relatedness on invasion success is theoretically contingent upon the mode of interspecific interactions (through phenotypic similarities or phenotypic differences), which could additionally be scale dependent.

Previous work has highlighted the potential importance of spatial scale in resolving Darwin's naturalization conundrum (e.g. Procheş *et al.* 2008; Thuiller *et al.* 2010). For example, at broad scales, invasion success may be predicted by (pre) adaptation to the environment, whereas at finer spatial and taxonomic scales – the Darwin–Hutchinson zone identified by Vamosi *et al.* (2009) – invasion success may be determined more by biotic interactions. Thus, at large scales, invasives will tend to be more closely related to the native pool,

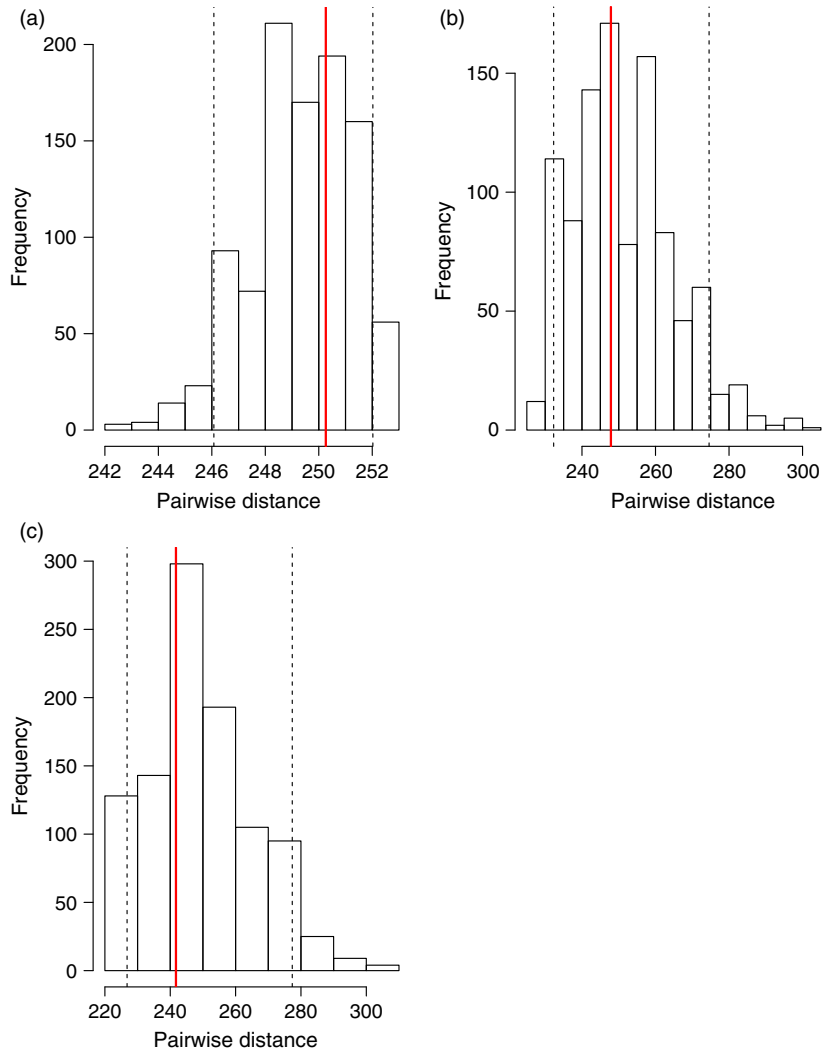


Fig. 2. Phylogenetic nearest neighbour distances separating (a) native from invasive species, (b) invasive from non-invasive species and (c) native from non-invasives. The difference between observed and the mean random values were assessed using 95% confidence interval (CI) from 1000 randomizations. Red lines indicate observed values, and black broken lines indicate 95% CI.

Table 1. Results of the phylogenetic analysis of variance of invasion success between natives vs. non-native and invasives vs. non-invasives with start of growing season set at January. Pt = Multiple corrected *P*-values from post hoc *t*-tests

Phenology	F Natives vs. non-natives	Pt Natives vs. non-natives	F Invasive vs. non-invasive	Pt Invasive vs. non-invasive
First flowering month	15.79	0.09	0.29	0.64
Last flowering month	0.64	0.74	0.08	0.80
Duration of flowering time	64.47	0.002	0.24	0.67

whereas at the finer scales at which species interact, invasives will tend to be less closely related to natives (Procheş *et al.* 2008; Thuiller *et al.* 2010). Here, we suggest a similar dichotomy might explain the observed differences between invasives and non-invasives in their relatedness to the native pool.

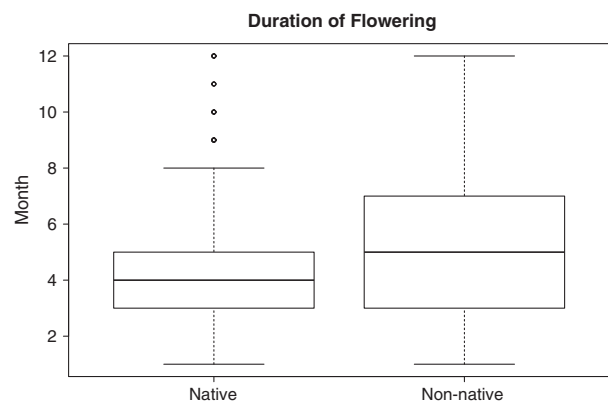


Fig. 3. Comparisons of phenological differences between non-native (invasive plus non-invasive) and native species. Boxes indicate the first and third quartiles, the horizontal bold line shows the median, the broken lines show the range of the data, and circles denote outliers.

Non-invasives represent non-native plants that have successfully established and have the ability to reproduce in their introduced ranges (i.e. naturalized *sensu* Richardson *et al.*

Table 2. Phylogenetic independent contrast on biological traits between natives vs. non-natives and invasives vs. non-invasives

Biological trait	Number of potential contrasts with data	T	d.f.	P-value
Maximum height (natives vs. non-natives)	103	0.47	102	0.49
Seed mass (invasives vs. non-invasives)	26	1.20	25	0.23
Maximum height (invasives vs. non-invasives)	22	3.07	21	0.10

T, *t* value from test statistics; d.f., degree of freedom; *P*-value, statistical significance.

Table 3. Phylogenetic independent contrast on biological traits between natives and non-natives (invasives plus non-invasives)

Biological trait	Number of potential contrasts with data	Number of contrasts differing in trait value	T	d.f.	P-value
Pollination (natives vs. non-natives)	62	4	0.6	2	>0.05
Dispersal (natives vs. non-natives)	74	24	4.0	23	0.005
Sexual system (natives vs. non-natives)	62	7	2.5	6	0.04

T, *t* value from test statistics; d.f., degree of freedom; *P*-value, statistical significance.

2000a), but have not spread aggressively so as to have detrimental effects on native plant communities. We suggest that these species might thus have traits that suit them to the environment, as reflected in their close phylogenetic affinities to the native species pool, allowing establishment, but may be biotically suppressed from becoming invasive. In contrast, invasive species represent a subset of naturalized species that have been able to spread aggressively from sites of introduction. We show that these species are less closely related to the native flora, perhaps indicating evidence of competitive release (Keane & Crawley 2002; Hill & Kotanen 2009) and/or support for the vacant niche theory (Elton 1958), whereby invasives are able to exploit resources unused by native species.

Our interpretations of phylogenetic patterns rest upon the assumption that key traits related to environmental adaptation and biotic interactions are conserved on the phylogeny, such that closely related species tend to share similar trait values (Wiens & Graham 2005; Wiens *et al.* 2010; Petitpierre *et al.* 2012; Davies *et al.* 2013). Although we suggest this is likely to be true on average, in some cases, close relatives might be

highly divergent, and thus, phylogeny should be used as a guide only. In addition, the relationship between phylogenetic distance and strength of competition remains a subject of debate (see e.g. Cahill *et al.* 2008; Mayfield & Levine 2010; Jones, Nuismer & Gomulkiewicz 2013), although our interpretation does not presume direct competition (or its absence in the case of invading species) between natives and non-natives.

Significant associations between key traits and invasion success have been reported elsewhere. For example, Pyšek *et al.* (2014) found that invasiveness of trees and shrubs across central Europe is favoured in tall woody plants that rely on biotic agents (i.e. animals or vertebrates) as their primary dispersal mode. In a separate study of the North American grassland ecosystem, invaders were shown to flower earlier (Willis *et al.* 2010) or later during the growing season in contrast to native species (Gerlach & Rice 2003; Pearson, Ortega & Sears 2012). However, we did not find any strong relationships between invasion success and biological traits. It is possible that our results in part reflect a lack of statistical power. Because our test of Darwin's naturalization hypothesis rests upon an assumption of tight evolutionary conservatism, we were careful to rigorously correct for phylogenetic non-independence in our analysis, which reduced degrees of freedom. In addition, we lacked sufficient data to compare pollination mode, dispersal, life-form and sexual system between non-native species (i.e. invasives and non-invasives). However, even where statistical power was reasonable, as for flowering phenology, we still do not detect a significant difference between invasives and non-invasives. Further, if the relationship between biotic traits and invasion success had been strong, we would still expect to detect it even with low sample size. It is possible, therefore, that we explored the wrong set of traits most relevant for invasion success in southern Africa. Alternatively, the traits conferring invasion success may be context specific (Hayes & Barry 2008; Moodley *et al.* 2014) and vary along the invasion continuum (Moodley *et al.* 2013; see also Pyšek *et al.* 2011). For example Pyšek *et al.* (2011) revealed a shift of pollination syndrome from introduction to invasion: at the introductory stage, insect-mediated pollination is dominant, but at the naturalization stage, wind-mediated and auto-pollination become dominant strategies, whereas at the invasion stage, non-native species co-opt pollinators of native species. The non-natives included in our analysis likely span all stages of invasion, thus providing mixed signals across this invasion continuum.

Although among non-native species we do not find a difference between invasives and non-invasives, non-natives (invasives and non-invasives combined) differed significantly from natives in duration of flowering time, primary dispersal mode and sexual system. Non-native species flower for longer, are more often hermaphroditic and dispersed using abiotic means in comparison with their native close relatives. Whilst we cannot control for the pool of potential dispersers in this analysis, we suggest that these traits might be linked to establishment success.

Differences in plant phenology between natives and non-natives have been demonstrated previously (e.g. Franks, Sim & Weis 2007; Matesanz, Gianoli & Valladares 2010; Willis

et al. 2010; Wolkovich & Cleland 2011; Anderson *et al.* 2012; Wolkovich *et al.* 2013; Pyšek *et al.* 2014). Two alternative models have been proposed to link phenology to invasion success: (i) the vacant niche (Elton 1958) and (ii) invader plasticity (Richards *et al.* 2006). According to the vacant niche theory, non-native species might successfully establish in new environments if there is little or no overlap in flowering times with native species. In the invader plasticity hypothesis, invading species shift phenologies to match the climatic regime in their new environments (Richards *et al.* 2006). However, species with longer flowering duration may simply stand a greater chance of successful pollination, and such a strategy might combine aspects of both the vacant niche and plasticity hypotheses.

Both dispersal syndrome and sexual system might also be linked to establishment success. Abiotic dispersal frees non-native species from relying upon animal dispersers that might not have equivalents in the non-native range, whereas hermaphroditism could facilitate establishment of non-native populations through auto-pollination where natural biotic pollinator agents are lacking (Baker 1955; Rambuda & Johnson 2004). Interestingly, these traits do not match to those associated with species invasion in temperate biomes (Gerlach & Rice 2003; Willis *et al.* 2010; Pyšek *et al.* 2014), emphasizing that the processes of establishment and invasion is likely highly context specific. However, it is important to note that the apparent success of hermaphroditic non-native species we observe could also be an artefact of biased introductions. For example, dioecious species might have been less favoured as potential crops or ornamentals during the introduction process, perhaps because they are either more difficult to grow or propagate artificially as single sex clones compared with hermaphroditic species.

Conclusion

We show that invasive trees and shrubs are less closely related to native trees than are non-invasive non-natives. We suggest that this pattern may help explain Darwin's naturalization conundrum. Non-natives that are more closely related to the native species pool might have greater chance of establishment because they are more likely to share traits that pre-adapt them to the new environment in which they find themselves. However, non-natives less closely related to the native community might be more likely to become invasive because they may gain from competitive release and/or vacant niches. We do not find any strong relationship between biotic traits and invasion success, which may reflect the context-dependent nature of species invasion. However, non-native species are more often abiotically dispersed, flower for longer and hermaphroditic, we suggest these traits may enhance establishment success, although further work is needed to explore the pool of potential colonizing species.

Acknowledgements

We thank Lesley Henderson of the South African Biodiversity Institute and Wilson J.R.U. of the Centre for Invasion Biology for consultation with the

non-native list and their categorizations. We also wish to acknowledge the International Development Research Centre IDRC, Canada, and the University of Johannesburg for funding. The first author acknowledges financial support from the Global Excellence and Stature Postgraduate Scholarship. Lastly, we would like to thank three anonymous referees for comments on an earlier draft of this manuscript.

Data accessibility

All data for this publication are deposited in Dryad repository (<http://dx.doi.org/10.5061/dryad.6t7t6>) (Bezeng *et al.* 2015).

Conflict of interest

None declared.

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Received 10 March 2015; accepted 13 April 2015

Handling Editor: Jason Fridley

Supporting Information

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

Table S1. Checklist of native and non-native woody trees and shrubs of southern Africa compiled from the literature and expert consultations with Genbank accession numbers.

Table S2. Trait database for the native and non-native (invasive and non-invasive combined) species in southern African region.

Table S3. Calibration points used for molecular clock dating. (MRCA = most recent common ancestor).

Table S4. Results of the phylogenetic analysis of variance of invasion success between natives vs. non-natives, and invasives vs. non-invasives with start of growing season set at September.