

# Phylogenetically diverse native systems are more resistant to invasive plant species on Robben Island, South Africa<sup>1</sup>

Kowiyou Yessoufou, Bezeng S. Bezeng, Orou G. Gaoue, Thato Bengu, and Michelle van der Bank

**Abstract:** Alien invasive species are problematic both economically and ecologically, particularly on islands. As such, understanding how they interact with their environment is necessary to inform invasive species management. Here, we ask the following questions: What are the main functional traits that correlate with invasion success of alien plants on Robben Island? How does phylogenetic structure shape biotic interactions on the island? Using multiple approaches to explore these questions, we found that alien invasive species flower later during the year and for longer period, although flowering phenology was sensitive to alternative starting date. Additionally, we observed that alien invasive species are mostly abiotically pollinated and are generally hermaphroditic whilst their native counterparts rely on biotic pollinators, flower earlier, and are generally dioecious, suggesting that alien invasive and native species use different ecological niches. Furthermore, we found a facilitative interaction between an alien invasive legume and other invasive plants as predicted by the invasional meltdown hypothesis, but this does not influence the phylogenetic structure of plant communities. Finally, phylogenetically diverse set of native species are less receptive to alien invasive species. Collectively, our findings reveal how biotic interactions and phylogenetic relatedness structure alien invasive – native co-existence.

**Key words:** *Acacia cyclops*, biological invasions, evolutionary history, functional traits, invasional meltdown, niche partition.

**Résumé :** Les espèces envahissantes sont problématiques tant sur le plan économique qu'écologique, particulièrement sur des îles. En tant que tel, il est nécessaire de comprendre comment elles interagissent avec leur environnement pour guider leur gestion. Dans ce travail, les auteurs posent les questions suivantes : Quels sont les principaux caractères fonctionnels qui sont corrélés avec le potentiel envahissant des espèces exotiques sur Robben Island? Comment la structure phylogénétique façonne-t-elle les interactions biotiques sur l'île? À l'aide d'approches multiples, les auteurs trouvent que les espèces exotiques fleurissent plus tard et pendant une plus longue période, bien que la phénologie de la floraison était sensible à une date alternative de début de floraison. De plus, les auteurs observent que les espèces envahissantes sont principalement sujettes à une pollinisation abiotique et sont généralement hermaphrodites, tandis que les espèces indigènes bénéficient de pollinisateurs biotiques, fleurissent plus tôt et sont généralement dioïques, ce qui suggère que les espèces exotiques et indigènes occupent des niches écologiques différentes. Aussi, une interaction facultative entre une légumineuse envahissante et d'autres plantes envahissantes, tel que prédit sur la base de l'hypothèse de l'effondrement des espèces indigènes, a été observée, mais celle-ci n'influence pas la structure phylogénétique des communautés végétales. Finalement, des communautés de plantes indigènes qui sont diversifiées sur le plan phylogénétique sont moins sujettes à l'envahissement par des espèces exotiques. Ensemble, ces résultats révèlent comment les interactions

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biotiques et la parenté phylogénétique influencent la coexistence entre espèces exotiques et indigènes. [Traduit par la Rédaction]

*Mots-clés* : *Acacia cyclops*, invasions biologiques, histoire évolutive, caractères fonctionnels, effondrement des espèces indigènes.

## Introduction

The stability and productivity of ecosystems, as well as their ability to provide a diverse set of ecological services, correlate with their phylogenetic structure (Cadotte et al. 2008, 2009; Faith et al. 2010; Cadotte 2013). This structure could, however, be altered by invasion of alien species (Lessard et al. 2009), given that all ecosystems, irrespective of their geographic locations, are vulnerable to the invasion by alien species (Vilà et al. 2015).

However, because there is a scale dependency in how communities are structured (Swenson et al. 2006), the impacts of biological invasions on community structure would only be well understood if they are considered within an appropriate spatial scale (Procheş et al. 2008; Thuiller et al. 2010). At large spatial scales — where various ecological conditions are found — the ability of alien species to adapt to these conditions would more likely shape the pattern of invasion, whereas at smaller scales, (that is, within the “Darwin-Hutchinson zone”; Vamosi et al. 2009), species interactions become stronger and more determinant in driving invasion success (Procheş et al. 2008; Thuiller et al. 2010). Therefore, analyzing biological invasion at a small spatial scale, such as on Robben Island (South Africa) for example, which represents only 5 km<sup>2</sup> in size, becomes ideal for a better understanding of not only native – alien invasive species interactions, but also how these interactions are influenced by the phylogenetic structure of communities.

Studies attempting to understand such interactions have analyzed several functional traits that mediate species invasion (e.g., Bezeng et al. 2015). However, the identification of a universal functional trait that correlates with invasion success is still a major challenge due to (i) the unavailability of functional trait data for several species and (ii) the dynamic nature of species invasion process (i.e., changing over taxonomic groups and spatial scales; Kolar and Lodge 2001; Pyšek and Richardson 2007). In addition, although functional traits (Pyšek and Richardson 2007; Hayes and Barry 2008; Van Kleunen et al. 2010a, 2010b; Ordonez and Olff 2013; Pyšek et al. 2014; Bezeng et al. 2015) and ecological characteristics of recipient habitats (Levine et al. 2004; Marvier et al. 2004; Alston and Richardson 2006) correlate with invasion success of alien species, the universality of these variables has also been questioned (e.g., Hayes and Barry 2008).

Specifically in southern Africa, Bezeng et al. (2015) investigated six functional traits that could explain the invasion success of alien woody plants. They showed that, on the mainland southern Africa, invasiveness correlates with dispersal syndrome, sexual system, and

flowering phenology. Although functional traits mediate species interactions, these interactions were not explicitly investigated neither in an early study of biological invasion on Robben Island (Bezeng et al. 2013) nor in the most recent study of biological invasion on the mainland southern Africa (Bezeng et al. 2015). Additionally, because Bezeng et al. (2015) conducted their study on a very broad scale (southern Africa), it remains unclear whether the functional traits (and thus biotic interactions) they identified at the scale of mainland southern Africa are also important at a small scale particularly on Robben Island. Islands, in general, are more vulnerable to invasion than mainland (D’Antonio and Dudley 1995; Pyšek et al. 2012) due to their small size (Lonsdale 1999; Gimeno et al. 2006), the existence of unsaturated communities (Moulton and Pimm 1986), and their poor native species richness (MacArthur and Wilson 1967; but see Patiño et al. 2015). Also, the susceptibility of islands to alien invasive species is linked to their phylogenetically clustered communities (e.g., see Gerhold et al. 2011); that is, island communities are more phylogenetically homogeneous than expected by chance, and this reduces their resistance to alien invasive species.

In addition, the broad-scale approach used in Bezeng et al. (2015) may mask important biotic interactions that are rather well known to be stronger at local scale (Procheş et al. 2008; Thuiller et al. 2010). In particular, by calculating the mean nearest taxon distance (MNTD) and the mean phylogenetic distance (MPD) between each native and invasive species, Bezeng et al. (2013, 2015) used phylogenetic distance to distinguish between native and alien species (Darwin Naturalization Hypothesis). Here, we explored how this phylogenetic distance could be influenced by biotic interactions, particularly the facilitative interactions between alien species as predicted in invasional meltdown hypothesis (Simberloff and Von Holle 1999). The invasional meltdown hypothesis predicts that some alien species could interact with other alien species to facilitate the establishment and invasiveness of the latter (Simberloff and Von Holle 1999; Van Riper and Larson 2009). We suggest that the assessment of the influence of alien invasive species on phylogenetic structure rather than on species richness of native species may shed new light on the contribution of biotic interactions (using phylogenetic structure as a proxy for such interactions) to invasion success of alien species (Lessard et al. 2009; Gerhold et al. 2011).

Indeed, in their simplistic approach, Webb et al. (2002) suggested that a community that is phylogenetically clustered is most likely structured through ecological

filtering, whereas overdispersed communities are likely driven by competitive interactions (but see [Mayfield and Levine 2010](#)). Most studies have provided evidence that alien species have a negative impact on the number of native species in a given community. However, these studies remain silent on the importance of biotic interactions in increasing or decreasing the biotic resistance of a community in the face of alien invasion ([Lessard et al. 2009](#)). As such, investigating the change of phylogenetic structure of plant communities in response to alien invasion would more likely reveal how biotic interactions could explain the invasibility of a given community.

In the present study, we explored the following questions: (i) What functional traits correlate with successful invasion of alien species on Robben Island? (ii) Does the invasional meltdown hypothesis explain invasion success of alien species on Robben Island? (iii) How are native plant communities restructured in the face of invasion of alien species?

## Materials and methods

### Study site

Robben Island is located in the Western Cape Province of South Africa and was declared a World Heritage Site in 1999 ([South African History Online 2014](#)). The island is found 7.5 km away from its closest mainland site (west of Bloubergstrand), and stands some 30 m above sea level ([South African History Online 2014](#)). It is 4 km long and 2 km wide, with a total area of 5.07 km<sup>2</sup> ([Underhill et al. 2001](#)). The island harbours ~12% of the world's African Penguin populations *Spheniscus demersus* L. and ~4% of the world population of Bank Cormorants *Phalacrocorax neglectus* Wahlberg ([Underhill et al. 2001](#)), making it an ecologically important site. Nonetheless, human activities, for over four centuries, have severely degraded the natural vegetation of the island and promoted the introduction of alien species ([Chapman et al. 2000](#); [Le Maitre et al. 2000](#)).

### Data collection

In a recent study on Robben Island, we randomly selected 147 plots of 50 m × 50 m to study the phylogenetic basis of biological invasion (see details in [Bezeng et al. 2013](#)). After excluding 20 plots that fell into gardens, buildings, or bird nesting sites, we collected data on plant species composition (native + alien invasive species) of the remaining 127 plots. We define alien invasive plants as naturalized plants that produce reproductive offspring, often in very large numbers, at considerable distances from parent plants and thus have the potential to spread over a considerable area ([Richardson et al. 2000](#)).

We also compiled a checklist of all plant species occurring on the island based on the report of the Council for

Scientific and Industrial Research ([CSIR 2010](#)). Information on this report was further improved following multiple site visits that we conducted between December 2010 and April–September 2011 to survey plant community composition. In total, a checklist of 202 plant species was compiled, and these species were categorized as native or invasive (Table S1<sup>2</sup>) following [CSIR \(2010\)](#), [Bezeng et al. \(2013\)](#), and [Bezeng et al. \(2015\)](#). This checklist comprises 68 more plant species than that reported in [Bezeng et al. \(2013\)](#). For all species included in the checklist, we collated data on six functional traits. These traits include maximum plant height, main dispersal and pollination modes, sexual system, flowering phenology (i.e., first, last, and duration of flowering month), and life forms. These traits were specifically targeted on the premise that they have previously been linked to plant invasiveness in South Africa and elsewhere ([Rejmánek 1995](#); [Lake and Leishman 2004](#); [Thuiller et al. 2006](#); [Pyšek and Richardson 2007](#); [Schaefer et al. 2011](#); [Pearson et al. 2012](#); [Wolkovich et al. 2013](#); [Bezeng et al. 2015](#)). These traits were retrieved from well documented databases of South Africa's native and alien flora ([www.plantzafrica.com](#); [www.agis.agric.za](#); Table S1<sup>2</sup>) and from the most recent study on southern Africa's native and alien flora (see [Bezeng et al. 2015](#)). In addition, we recorded the presence or absence of the only alien invasive legume species (*Acacia cyclops* G. Don) in the 127 plots and assessed whether and how the presence of this legume influences the invasion success of alien invasive plants on Robben Island (following [Van Riper and Larson 2009](#)).

### DNA matrix and phylogeny reconstruction

We constructed our DNA matrix using the two DNA barcoding loci *rbcLa* and *matK*. Of the 202 species included in our checklist, we had DNA sequences available for 199 species (the following species, for which we did not have DNA sequences, were dropped from the analysis: *Cissampelos capensis*, *Corymbia gummifera*, and *Lycopersicon esculentum*). All phylogenetic analyses (presented below) were therefore based on the 199 species. These sequences include the 134 already-aligned sequences used in our previous study ([Bezeng et al. 2013](#)) and available on GenBank/EBI. In the present study, an additional set of 65 sequences were downloaded from GenBank/EBI and manually aligned following the existing matrix of 134 sequences of [Bezeng et al. \(2013\)](#). Information on taxonomy, voucher numbers in the herbarium of the University of Johannesburg, and GenBank/EBI accession numbers of all 199 plants are presented in Table S2<sup>2</sup>.

We used this DNA matrix to assemble the phylogeny of the Robben Island's flora including native and alien invasive species. We first performed a maximum likelihood (ML) analysis on the combined dataset (*rbcLa* +

<sup>2</sup>Supplementary data are available with the article through the journal Web site at <http://nrcresearchpress.com/doi/suppl/10.1139/gen-2018-0039>.

*matK*) using RAxML-HPC2 v.7.2.6 (Stamatakis et al. 2008) on the CIPRES cluster (Miller et al. 2009). We enforced a topological constraint following the APG III backbone from Phylomatic v.3 (Webb and Donoghue 2005). The phylogeny was rooted using representatives of Acrogymnospermae *Cupressus* L., *Pinus* L., and *Araucaria* Juss. (Cantino et al. 2007; Soltis et al. 2011). We then dated the phylogeny using a Bayesian Markov Chain Monte Carlo (MCMC) approach as implemented in BEAST v.1.4.8 (Drummond and Rambaut 2007). For the purpose of tree dating, we generated a RAxML starting tree that was adjusted so that branch lengths satisfied all fossil prior constraints using PATHd8 v.1.0 (Britton et al. 2007). Next, we selected GTR + I +  $\Gamma$  as the best model of sequence evolution for each partition based on the Akaike information criterion evaluated using MODELTEST (Nylander 2004). A speciation model following a Yule prior, which includes a parameter for describing the net rate of speciation and rate heterogeneity among lineages, was modelled using an uncorrelated relaxed clock lognormal model for rate variation among branches. We then conducted simultaneous searches of topology and divergence times. For this purpose, we applied a normal prior distribution and used 11 calibration points (Bell et al. 2010) but also included the root node of the Eudicots, which was set at 124 Mya (see Table S3<sup>2</sup>) and used the same credibility interval as in Bezeng et al. (2015). Monte Carlo Markov Chains were run for 100 million generations with trees sampled every 1000 generations. Log files, including prior and likelihood values, as well as the effective sample size (ESS), were examined using TRACER (Drummond and Rambaut 2007). Our ESS values were >200, suggesting adequate sampling. We combined the resulting tree files in LogCombiner v.1.7.5 (Drummond and Rambaut 2007), and discarded the first 20% trees as burn-in. The maximum clade consensus tree, with means and 95% highest posterior density (HPD) intervals, was generated with TreeAnnotator v.1.7.5 (Drummond and Rambaut 2007). The resulting phylogenetic tree represents the evolutionary relationships among 199 species comprising 86 native and 113 alien invasive species.

#### Statistical analysis

All statistical analyses were performed in R (R Core Team 2013). Prior to the analysis, following Bezeng et al. (2015), we categorized the main dispersal and pollination modes into biotic versus abiotic modes. Within sexual system, we distinguished between dioecy and hermaphroditism. We then tested whether alien invasive and native species differ in their functional traits using a combination of phylogenetic independent contrasts (PICs; Felsenstein 1985) and a simulation-based phylogenetic ANOVA (Garland et al. 1993).

Specifically, we firstly compared the timing of first flowering month, last flowering month, and duration of flowering period between invasive and native species, using the phylogenetic ANOVA and post-hoc compar-

isons of means using the function *phylANOVA* in the R package *Phytools* (Revell 2012). Our timing period follows the year calendar such that a species that flowers in January was coded 1, February 2... and December 12. However, our coding of start and end months of flowering might have been biased due to the fact that most native species in this region start flowering in September. To overcome this caveat, we shifted the start of the flowering month to September, with months coded as 1 (i.e., September) through 12 (i.e., August; see also Bezeng et al. 2015 for similar approach in the same geographic region).

Secondly, we used the *brunch* algorithm (Purvis and Rambaut 1995) implemented in the R library *caper* (Orme et al. 2012) to explore the relationship between species invasive status and maximum plant height. The *brunch* algorithm conducts independent contrasts for models that include binary categorical variables (in this case invasive vs. native) where each clade can be unequivocally assigned to one state or the other. Nested contrasts deeper in the phylogeny are not included. We calculated phylogenetic independent contrasts “PICs” (native vs. invasive) for each of the 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 invasive status and each functional trait in turn, using a t-test to evaluate whether the mean of the contrasts differed significantly from zero.

Next, we investigated the differences in life forms, comparing the number of species in each category (invasive vs. native) within each life form to the null expectation that the abundance of each species is independent of their invasion status (invasive or not). The associations between species categories (invasive vs. native) and life forms were assessed using Pearson’s  $\chi^2$  test. Furthermore, we measured species richness (native and invasive) in each plot (Table S4<sup>2</sup>) and explored the relationships between the presence of the only alien invasive legume species (*A. cyclops*), species diversity, and phylogenetic structure of native communities using one-way ANOVA.

Finally, we tested how alien invasive plants influence the phylogenetic structure of native plant communities. The ideal situation to test this is to compare the current structure of native communities to the original structure of these communities when alien species were not yet introduced to the island. To get around the difficulty inherent to the non-availability of community phylogenetic structure of the original flora of the island, we assessed how the phylogenetic structure of the set of native species that co-exist in the same communities (plots) with alien invasive species changes when the number of alien invasive species increases. We expect these changes, if any, to mirror the influence of invasive species on the phylogenetic structure of native communities.

To this end, we subdivided each community (here plot) into two sub-communities based on species invasion status (native vs. invasive), i.e., native and invasive sub-communities. The Faith's phylogenetic diversity (PD), the net relatedness index (NRI), and the net taxon index (NTI) were used as metrics of phylogenetic structure for each sub-community (Webb et al. 2002). We further calculated the mean phylogenetic distance (MPD) and mean nearest taxon distance (MNTD) for each sub-community and used non-metric multi-dimensional scaling (NMDS) to assess the multi-variate structure of these sub-communities based on MPD and MNTD (Webb et al. 2002).

Phylogenetic structures are measured as NRI and NTI and interpreted as follows: A significantly positive NRI or NTI indicates an underdispersed or clustered community that contains more phylogenetically closely related species than expected by chance. A significantly negative NRI or NTI means that the community is overdispersed; that is, it contains more distantly related species than expected by chance. If NRI or NTI are statistically not different from zero, this means that the community has a phylogenetically random structure (Webb et al. 2002).

NRI and NTI can also be used as a predictor of dominant interactions within a community: Positive NRI or NTI is indicative ecological filtering whereas negative values are indicative of competitive interactions. For the calculation of NRI and NTI, the null model "pool.taxa.labels" (phylogeny pool) in the R library Picante (Kembel et al. 2010) was used. This corresponds to a shuffle of phylogeny tip labels (across all taxa included in phylogenetic tree). The species pool for the null model is all species recorded on Robben Island and present on the phylogenetic tree.

On these various variables calculated (NRI, NTI, and PD) for native and invasive plants, we run the following two tests. The first test is the Pearson correlation between the phylogenetic structures of native and invasive sub-communities. If there is a significant correlation, this implies that there are interactions between both sub-communities, and an absence of correlation implies no influence. The second test was a simple linear regression between the phylogenetic structure of native ( $NRI_{\text{native}}$ ) and the number of invasive species in the same community. A positive relationship means that overdispersed native communities tend to have lower number of invasive species and vice versa (see Fig. 5C).

## Results

The phylogeny assembled for the island's flora is presented in Fig. 1 with red dots indicating the phylogenetic distribution of alien invasive species (see also Fig. S1<sup>2</sup> with full species names). Using this phylogeny to correct for species non-independence, we showed that invasiveness correlates with pollination syndrome, sexual system, and flowering phenology but not with dispersal

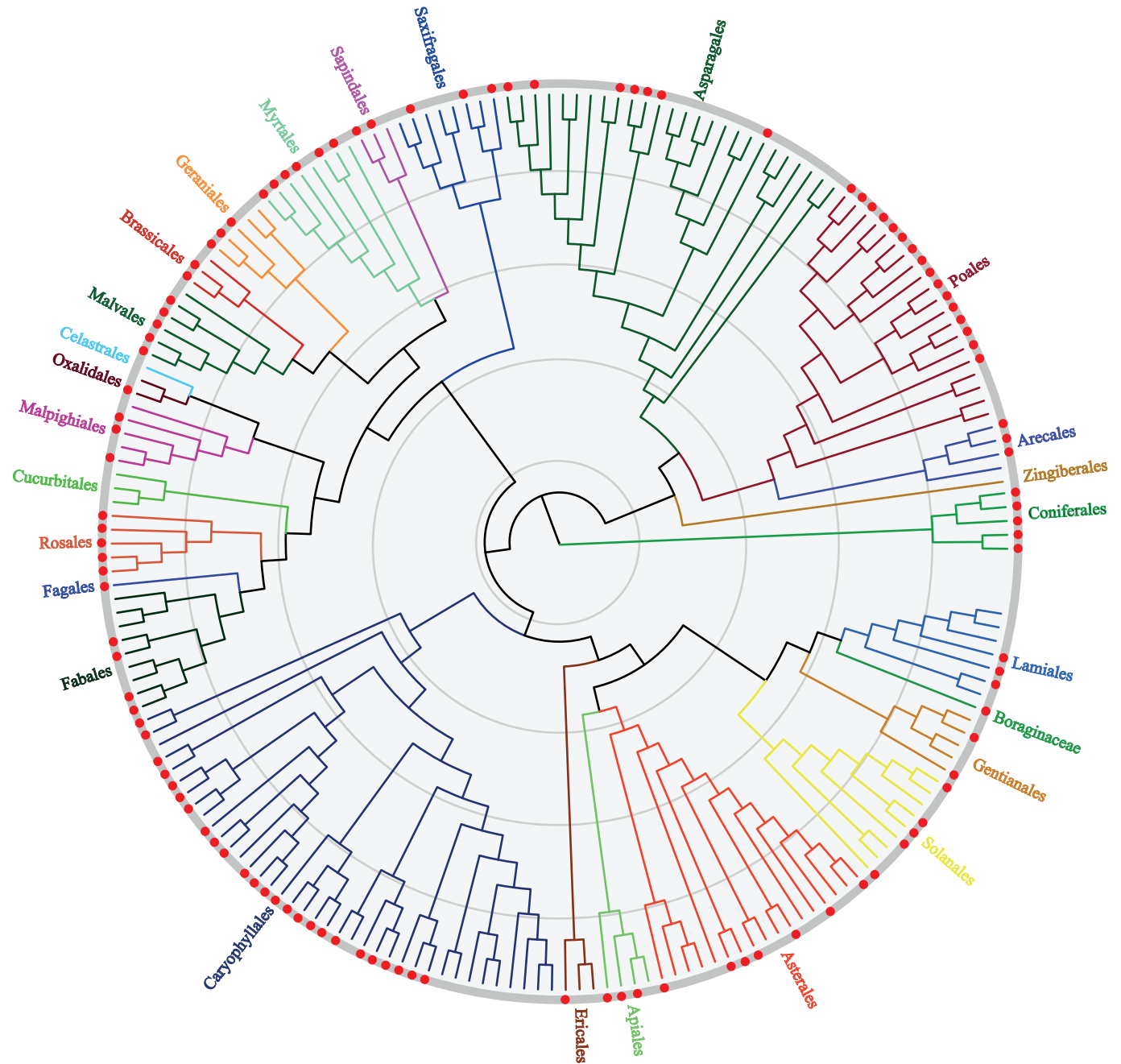
modes and maximum plant height (Table 1). Specifically, alien invasive species are more often abiotically pollinated ( $P = 0.004$ ; Fig. 2A) and hermaphroditic ( $P = 0.03$ ; Fig. 2B) compared to native species, which are generally biotically pollinated and dioecious (Table 1). In addition, alien invasive species flowered later in the year ( $P = 0.001$ ; Fig. 3A) and for longer period ( $P = 0.009$ ; Fig. 3B) as opposed to native species which flowered early in the year and for shorter period (Table 2). This pattern still holds even after Holm-Bonferroni correction (Table 2). However, when the start and end flowering dates were shifted to accommodate the start of flowering period of most native species in this region (September), we still found no evidence that first flowering month was related to invasion success. Interestingly, we observed that our coding of last flowering time was sensitive to the initial approach used. Notwithstanding, the duration of flowering period remains a significant variable distinguishing alien invasive from native species irrespective of when species start or end their flowering (Table 2).

Invasive species were also more likely to be climbers, grasses, herbs, and trees than expected by chance whilst native species were more bulbs, shrubs, and succulent than expected ( $\chi^2 = 22.28$ ,  $df = 6$ ,  $P = 0.0011$ ).

Next, we found that, as the diversity of invasive species in a community increases, the diversity of native species decreases, but this negative impact is less pronounced in the presence of the invasive legume *A. cyclops* (Fig. 4A). The total diversity (native + invasive species richness) was higher in plots with legume than in plots without legume (One-way ANOVA,  $P = 0.011$ , Table S1<sup>2</sup>; Fig. 4B). There was, however, no effect of legume presence on the diversity of native species ( $P = 0.954$ , Table S2<sup>2</sup>; Fig. 4C). Nonetheless, the diversity of invasive species increased significantly in the presence of legume ( $P = 0.001$ , Table S3<sup>2</sup>; Fig. 4D), indicating that the presence of legume benefits only the establishment of alien invasive plants, although there was no evidence of legume influence on the phylogenetic structure of native (NRI,  $P = 0.731$ ; NTI,  $P = 0.358$ ) and invasive sub-communities (NRI,  $P = 0.218$ ; NTI,  $P = 0.108$ ; Table S6<sup>2</sup>).

Finally, we explored the relationships between invasive species and phylogenetic structure of communities. The overwhelming majority of native sub-communities were phylogenetically clustered whereas almost half of invasive sub-communities was clustered and the other half was overdispersed (Table S7<sup>2</sup>; Fig. S2<sup>2</sup>), suggesting perhaps that native and invasive species that co-exist in the same community exhibit different phylogenetic structures. NMDS separates both sub-communities based on phylogenetic distances, thus supporting the differences in phylogenetic structure of native versus invasive sub-communities (Figs. 5A, 5B). However, the structure of one sub-community did not influence the other (Pearson's correlation  $r_{\text{NRI}} = 0.01$ ,  $P = 0.83$  and  $r_{\text{NTI}} = -0.01$ ,  $P = 0.27$ ; Fig. S1<sup>2</sup>). Nonetheless, there was a significant

**Fig. 1.** The most comprehensive phylogeny of Robben Island’s flora. Red dots indicate the phylogenetic distribution of alien invasive plants on the phylogeny. Species names are not included for clarity but see Fig. S1<sup>2</sup> with full species names. Species orders are instead indicated at the tips of the phylogeny.

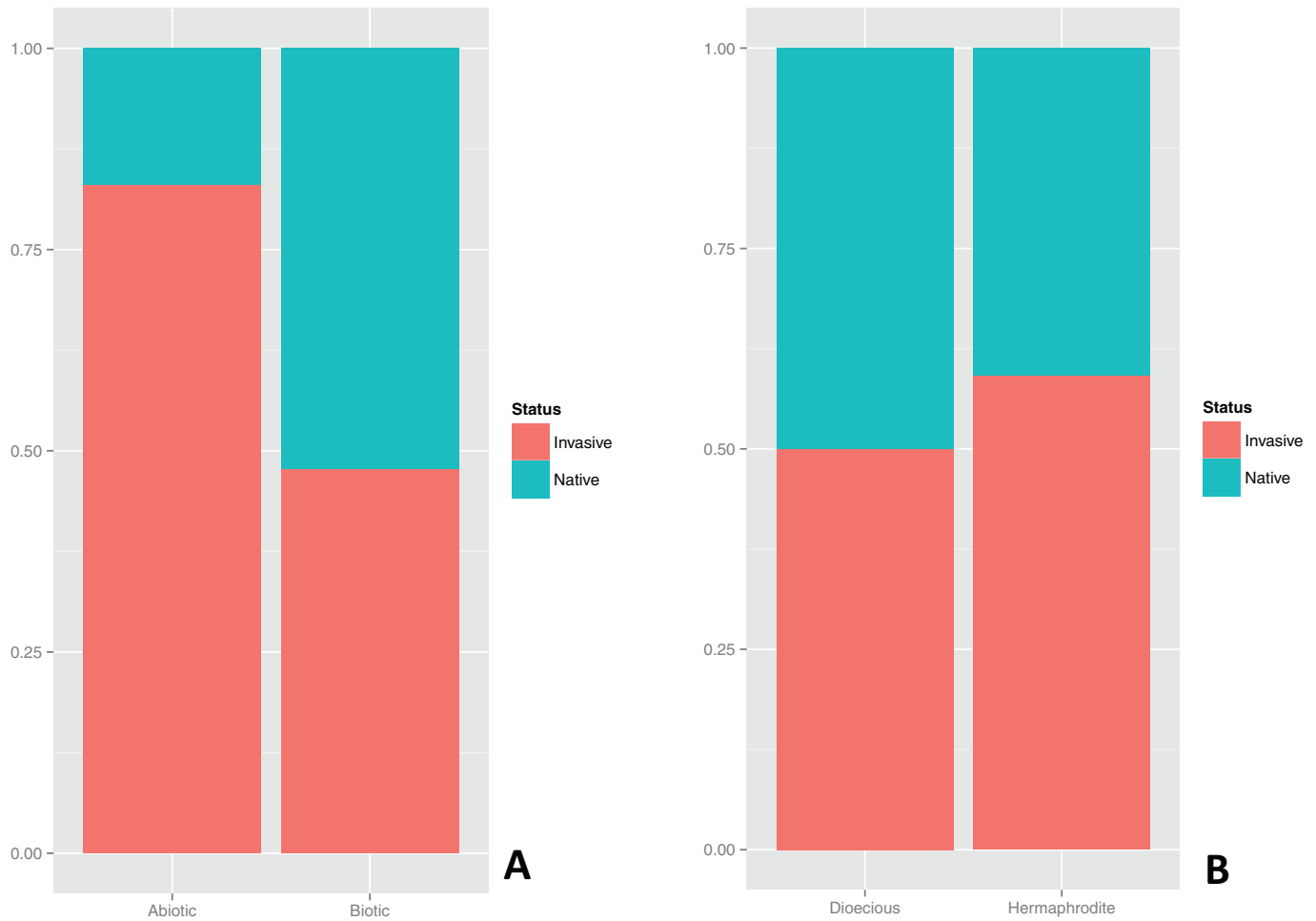


**Table 1.** Phylogenetic independent contrast (PIC) on biological trait between native and invasive species.

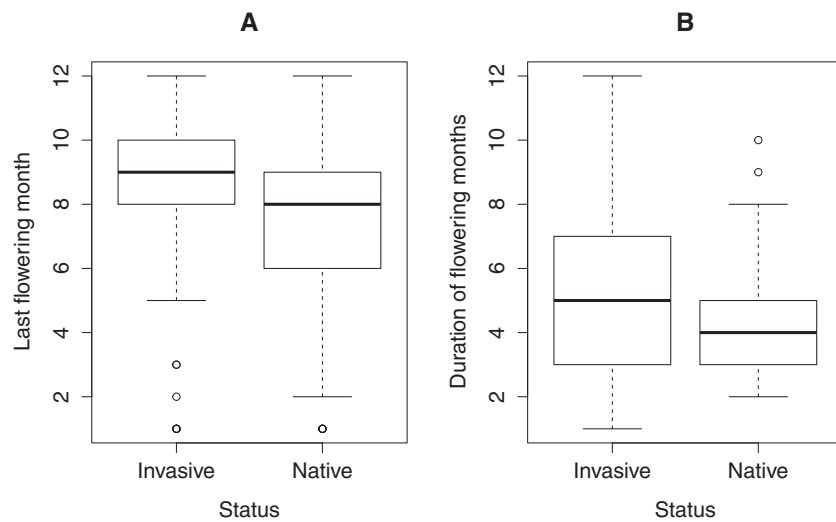
Biological trait	No. of valid contrasts	No. of contrasts with a trait difference (applicable for binary traits)	t	df	P
Pollination (biotic vs. abiotic)	63	26	2.7	24	0.004
Dispersal (biotic vs. abiotic)	58	3	0.5	2	0.76
Maximum height (numerical)	45	NA	0.17	44	0.68
Sexual system (dioecious vs. hermaphroditic)	39	7	2.6	7	0.03

**Note:** PICs are signed, and significant differences from a null expectation of a mean of zero were tested. The direction of the patterns follows an alphabetical order (invasive → native). t, t-value from test statistics; df, degree of freedom; P, p-value for statistical significance.

**Fig. 2.** Stacked plots indicating the differences in (A) pollination mode and (B) sexual system between invasive and native species. See [Table 1](#) for statistical significance.



**Fig. 3.** Phenological differences between native and alien invasive species. (A) Differences in last flowering time and (B) differences in duration of flowering time; flowering time is measured as the first month where flowering occurs. See [Table 2](#) for statistical significance.

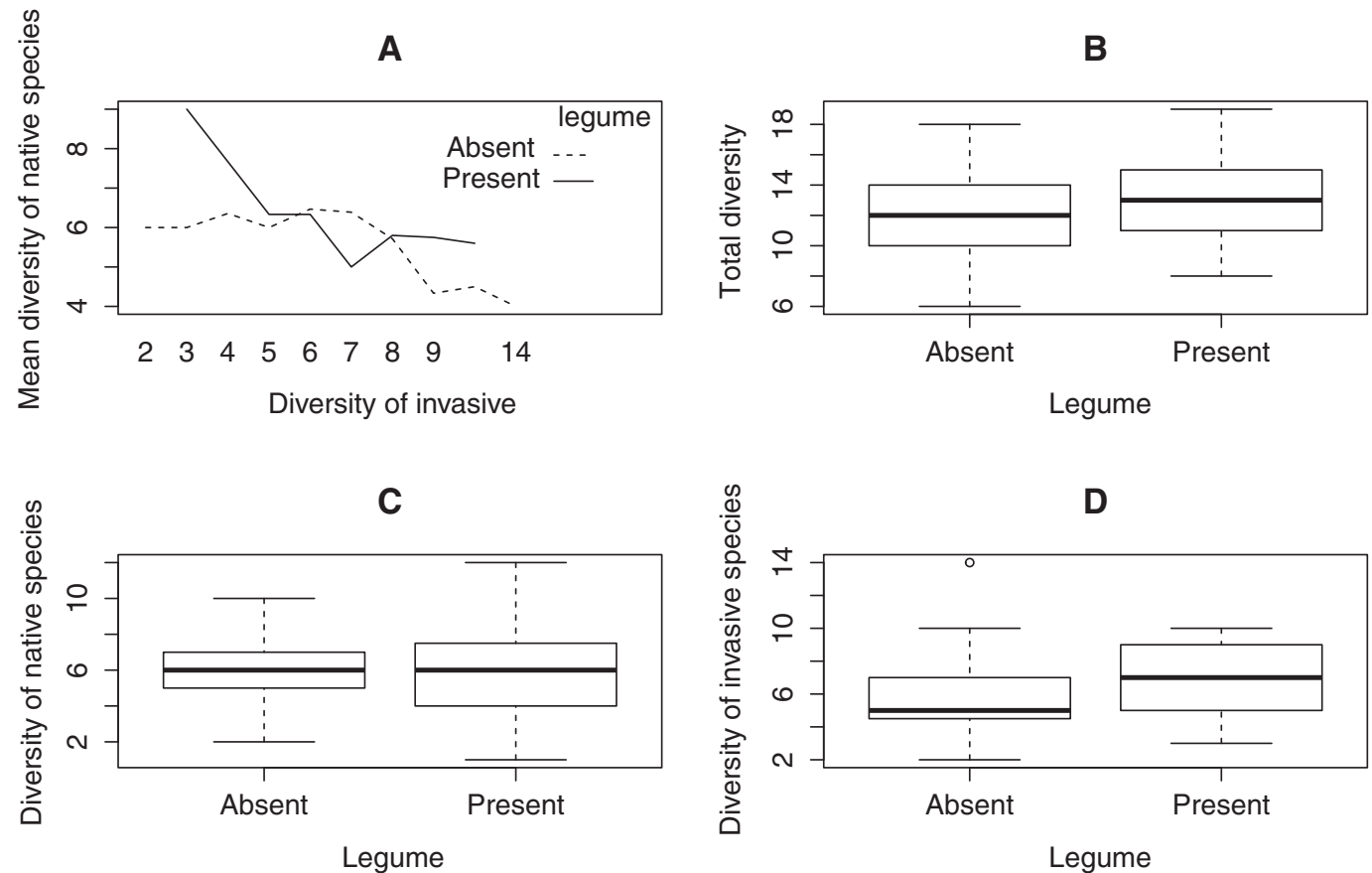


**Table 2.** Results of the phylogenetic analysis of variance of invasion success.

Flowering phenology	Flowering month starts in January (i.e., 1) and ends in December (i.e., 12)			Flowering month starts in September (i.e., 1) and ends in August (i.e., 12)		
	F	$P_f$	$P_t$ (invasive vs. native)	F	$P_f$	$P_t$ (invasive vs. native)
First flowering month	3.68	0.18	0.18	3.66	0.18	1.914
Last flowering month	26.59	0.001**	0.001**	5.10	0.37	0.129
Duration of flowering time	15.44	0.009**	0.009**	15.19	0.009**	0.009**

**Note:** F, F from observed data;  $P_f$ , p-values for F resulting from 1000 simulations;  $P_t$ , multiple corrected P values from posthoc t-tests. The direction of the patterns follows an alphabetical order (invasive → native).

**Fig. 4.** (A) Trends in relationships between native and invasive species diversity and (B–D) effects of invasive legume on various diversities. (B) Legume effects on total diversity, (C) native diversity, and (D) invasive diversity. Species diversity is measured as species richness, and total diversity = invasive + native species diversity. Significance of relationships is reported in the text.



positive correlation between the NRI-based phylogenetic structure of native sub-communities and the number of invasive species ( $P = 0.01$ ; Fig. 5C), indicating that phylogenetically diverse native communities are less prone to invasion of alien species. This pattern was even more strongly supported when comparing phylogenetic diversity of native and invasive sub-communities ( $P = 0.005$ , Fig. 5D).

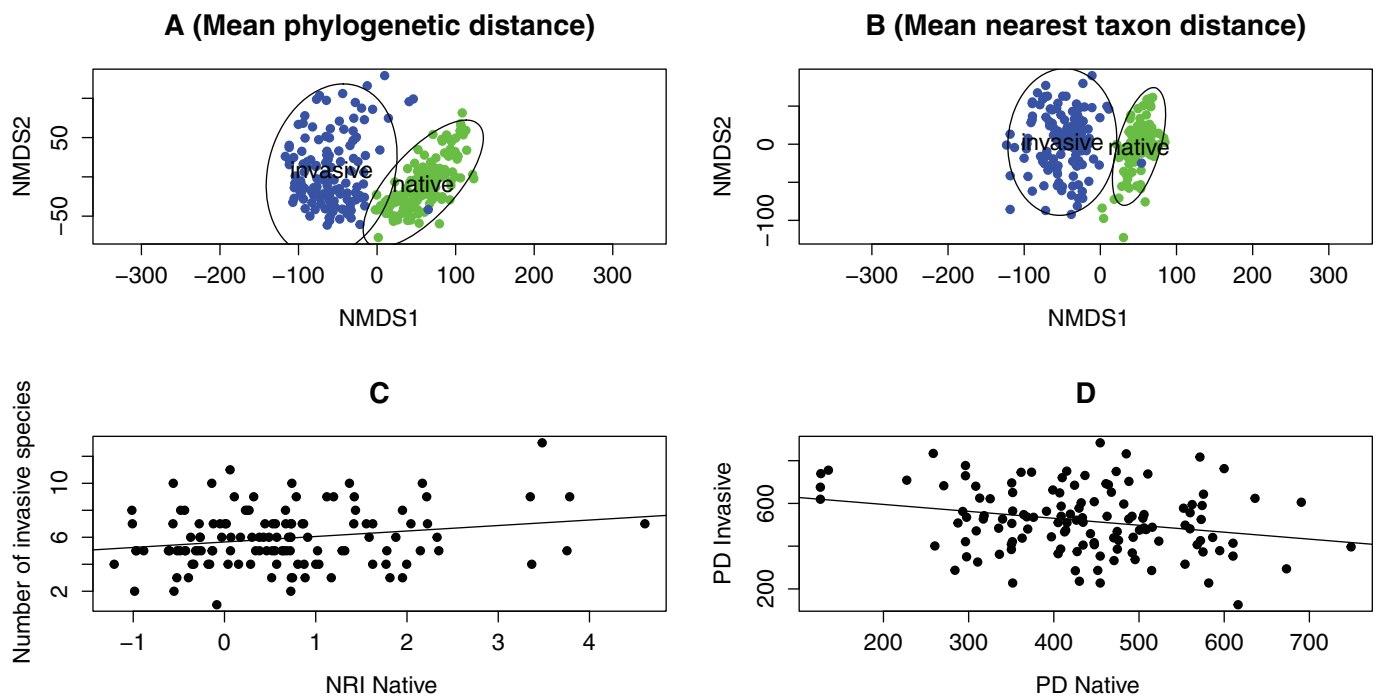
**Discussion**

We found that plant height and dispersal modes do not correlate with invasion success on Robben Island. However, plant height has been reported to correlate

with invasion success elsewhere (Pyšek et al. 2014), and obviously the dispersal ability is a key factor promoting the spread of species. Our finding that plant height and dispersal mode do not distinguish invasive from native species perhaps highlights the context specificity of biological invasion (Hayes and Barry 2008). Both invasive and native plants rely on biotic agents for dispersal, although we would expect alien invasive plants to use predominantly abiotic dispersers, since they might not find adequate resident biotic agents for dispersal on the island, their new environment. However, it is still possible that alien plant species were dispersed, following their



**Fig. 5.** (A, B) Non-metric multi-dimensional scaling (NMDS) analysis and (C, D) relationships between native and invasive species. NRI, net related index; PD, phylogenetic diversity. Positive and significant value of NRI means the community is richer in more closely related species than expected by chance (phylogenetically clustering); Negative and significant NRI means the community is richer in less closely related species than expected by chance (phylogenetic overdispersion). High PD means tendency towards overdispersion.



introduction to the island, predominantly by abiotic factors (winds, etc.), and later went through “invasional meltdown” (Simberloff and Von Holle 1999; i.e., their dispersal could be further promoted by other alien biotic dispersers). To elucidate this, further studies on the dispersal ecology of plants on the island are required.

Pending this investigation, our analysis showed that invasive plants differed from the native ones in many other ways. For example, they are more often hermaphroditic as opposed to native plants that are generally dioecious. Hermaphroditism might provide an advantage towards invasion success by facilitating auto-pollination where natural biotic pollinator agents are lacking (Baker 1955; Rambuda and Johnson 2004; Bezeng et al. 2015). Successful invasion is a result of complex biological processes along the introduction–naturalization–invasion continuum (Richardson and Pyšek 2012; Yessoufou et al. 2016). Pollination syndrome plays an important role at each step of the continuum. Pyšek et al. (2011) found that pollination of alien plants is insect-mediated at the introduction stage, wind-mediated at naturalization stage, and indistinguishable from native plants at invasion stage. If this pattern is generalizable, we would expect, as we found for dispersal mode, that alien invasive and native plants would share similar pollination syndrome. The fact that we found a different pattern is again a support for context specificity of biological invasions (Moodley et al. 2014).

Furthermore, we found that alien invasive plants on the island also differ from native in their flowering phenology. Such differences have also been reported in other studies (Wolkovich et al. 2013; Franks et al. 2007; Matesanz et al. 2010; Willis et al. 2010; Wolkovich and Cleland 2011; Anderson et al. 2012; Pearson et al. 2012; Pyšek et al. 2014; Bezeng et al. 2015), and the underlying explanation relies on two scenarios termed the vacant niche (Elton 1958) and invasion plasticity scenarios (Richards et al. 2006). If there is little or no overlap in flowering times between alien invasive and native species, the mismatch in flowering period may have been used by alien species to be pollinated and dispersed quickly before native species start flowering (vacant niche scenario). As predicted by the invasion plasticity scenario, alien plants could also shift their phenology in response to ecological constraints imposed by their new environments (Richards et al. 2006). On Robben Island, alien invasive species flower for longer periods as opposed to natives, a pattern that is consistent with the vacant niche scenario.

Additionally, we found that the duration of flowering time for invasive species is longer than that of native. This longer flowering time may further provide an advantage for alien plants to pollinate and disperse. What’s more, there are more alien invasive plants than expected in the forms of climbers, grasses, herbs, and trees whilst native species are disproportionately bulbs, shrubs, and

succulents. This niche partitioning (here in term of differences in life-forms) between alien invasive and native species might be indicative of weak competitive interactions between native plants and successful invaders.

However, there was evidence for a positive effect of our model legume (*A. cyclops*) on invasive species (see also Van Riper and Larson 2009) as we found that the diversity of invasive species increases significantly in the presence of *A. cyclops*. This positive effect could indicate a facilitative interaction of the alien invasive *A. cyclops* with other invasive species via soil enrichment in atmospheric nitrogen, a scenario that matches the fluctuating resource availability hypothesis (Davis et al. 2000), which predicts a mechanistic relationship between invasiveness and resource availability. *Acacia cyclops* could also have a facilitative effect on invasive species through its architecture that can provide shade, which in turn would reduce evapotranspiration and increase soil moisture, all of which can facilitate the establishment and spread of other alien species. Also, *A. cyclops* could increase the depth of soils and the soil organic matter content through increases in leaf and woody debris inputs into the soil. Overall, we suggest that *A. cyclops* may be acting as a nurse plant for other alien species (see also Van Riper and Larson 2009 for similar effect of a legume on alien species in Badlands National Park), matching the invasional meltdown prediction (Simberloff and Von Holle 1999).

Nonetheless, the positive effect of *A. cyclops* on other invasive species did not affect the phylogenetic structure of both native and invasive sub-communities. In contrast, we found a strong relationship between the richness of invasive species and the phylogenetic structure of native sub-communities. In particular, phylogenetically overdispersed native sub-communities tend to accommodate a lower number of alien invasive species whilst a higher diversity of invasive species was found in phylogenetically homogenized native sub-communities (see also Gerhold et al. 2011). These results suggest perhaps a stronger ability of competitive exclusion of phylogenetically diverse native systems, and indicate that, on Robben Island, native communities dictate not just the taxonomic identity of alien species as previously reported elsewhere (e.g., see Gerhold et al. 2011) but also impose a phylogenetic structure to the set of invasive species to co-exist with.

In this study, we focused on the invasion stage and compare biological traits of invasive versus native plants. We showed that alien and native plants do not differ in height and dispersal mode, but they do differ significantly in pollination syndrome, sexual system, flowering phenology, and life forms. These differences suggest a niche partitioning between both species categories. We also found that the presence of *A. cyclops* facilitates only the diversity of alien invasive species, but this does have no impact on phylogenetic structure of communities.

However, there was a strong relationship between invasive species and phylogenetic structure of natives such that the diversity of invasive species is low where native species form a phylogenetically overdispersed system. Collectively, our findings provide evidence for facilitative interactions between an alien invasive legume and other alien species (Simberloff and Von Holle 1999; Van Riper and Larson 2009) and indicate that this facilitation is stronger in phylogenetically less diverse native communities. Our study therefore sheds new light on the invasion pattern on Robben Island and suggests that limiting the introduction of alien legume and maintaining a phylogenetically diverse native system (in term of species richness and life-forms) would help control the spread of alien species.

#### Disclosure statement

The authors declare that they have no conflict of interest.

#### Notes on contributor

K.Y. conceived and designed the project; K.Y., B.S.B., T.B., and M.V.D.B. collected data; K.Y. and B.S.B. analysed the data; K.Y., T.B., O.G.G., and B.S.B. wrote the manuscript.

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