Received: 25 May 2024 | Accepted: 5 June 2024

DOI: 10.1002/ecs2.4966

ARTICLE

ECOSPHERE
AN ESA OPEN ACCESS JOURNAL

Phylogenetic relatedness of plant species co-occurring with an invasive alien plant species varies with elevation

Afshana[1] | **Jesús N. Pinto-Ledezma**[2] | **Zafar A. Reshi**[1]

[1]Department of Botany, University of Kashmir, Srinagar, Jammu and Kashmir, India

[2]Department of Ecology, Evolution and Behavior, University of Minnesota, Saint Paul, Minnesota, USA

Correspondence
Zafar A. Reshi
Email: zreshi@gmail.com

Funding information
National Science Foundation, Grant/Award Number: DEB-2017843; University Grants Commission (UGC), New Delhi, India, Grant/Award Number: 2-5/2016 (NS/PE)

Handling Editor: John Humphreys

Abstract

Darwin's naturalization conundrum posits that the alien species either succeed in the introduced region because they are phylogenetically related to the native species and thus tend to have niches similar to those of native species, or they are phylogenetically dissimilar to native species and thus occupy unfilled niches. This conundrum has received a lot of attention, but the findings regarding these two hypotheses have been contradictory. To reconcile the two seemingly contradictory hypotheses, we assessed the phylogenetic relationship of a highly widespread and invasive species, *Anthemis cotula* L. (focal species), separately with the native species and all its co-occurring species (including native and non-native species) along an elevation gradient. Our results show that the abundance of *A. cotula* declined continuously with an increase in elevation and with an increase in the number of both all co-occurring and native species only. The phylogenetic distance between the focal species and the native species based on weighted mean pairwise distance (MPD_{aw}) declined with elevation as well as native species richness. Our study also revealed that soil nutrients strongly influence the abundance of *A. cotula*; however, their effect on the phylogenetic distance between the focal and other species is negligible. These findings suggest a strong role of microecological factors and spatial heterogeneity in the abundance distributions of invasive species and community assembly. Thus, it could be concluded that the phylogenetic relationship of *A. cotula* with co-occurring all or only native species varies with elevation and species richness, adding another layer of complexity to the resolution of Darwin's naturalization conundrum.

KEYWORDS
Darwin's naturalization conundrum, focal species, Himalaya, phylogenetic metrics

Jesús N. Pinto-Ledezma and Zafar A. Reshi contributed equally to the work reported here.

This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.
© 2024 The Author(s). *Ecosphere* published by Wiley Periodicals LLC on behalf of The Ecological Society of America.

INTRODUCTION

Invasive alien species are an outcome of a multistage process that begins with the intentional or unintentional transport and introduction of propagules of species by human beings into non-native regions well beyond their natural dispersal limits (Blackburn et al., 2011; Elton, 2020). Humans have been transporting species around the globe for centuries, and it has been accelerating in recent years due to an increase in trade and travel across countries and continents (Seebens et al., 2017). Today non-native species occur in Earth's all continents and seas (Turbelin et al., 2017), in every biome, habitat, community, and ecosystem (Elton, 2020). Although the alien species are mostly benign (Hettinger, 2021), the few highly invasive species significantly impact community structure and functioning (Hejda et al., 2009; Linders et al., 2019) alter species interactions (David et al., 2017) or displace populations of native species (Pyšek et al., 2020). These impacts cause huge economic (annual cost estimated at US $423 billion in 2019; IPBES, 2023) and ecological costs, with enormous consequences for human well-being and livelihoods (IPBES, 2023; Paini et al., 2016; Walsh et al., 2016).

Several hypotheses have been put forth to explain the success of non-native species in their introduced range (reviewed by Enders et al., 2020). Darwin also proposed two competing hypotheses (Darwin, 1859), namely Darwin's naturalization hypothesis (DNH; Rejmánek, 1996) and the preadaptation hypothesis (PAH; Ricciardi & Mottiar, 2006). DNH suggests that alien species that are more distantly related to native species in the introduced range are more likely to succeed because they are able to exploit the underutilized niches, thereby minimizing competition and have fewer common natural enemies (Cadotte et al., 2018). Conversely, the PAH proposes that alien species that are closely related to native species in the introduced range are more likely to succeed because they share similar traits and adaptations that allow them to tolerate that environment and overcome environmental filtering (Cadotte et al., 2018; Mack, 2003). The apparent contradiction between the two hypotheses is known as Darwin's naturalization conundrum (DNC) (Cadotte et al., 2018; Daehler, 2001). Many studies have addressed this conundrum (Cadotte et al., 2018; Li et al., 2014; Pinto-Ledezma et al., 2020), but the results have been contradictory (Thuiller et al., 2010), with some studies supporting DNH (Daehler, 2001; Schaefer et al., 2011; Strauss et al., 2006) and others supporting the PAH (Duncan & Williams, 2002). These contrasting results have been attributed to different factors, including the spatial (Park, Willis, et al., 2020) and temporal (Campbell & Mandrak, 2017; Pinto-Ledezma et al., 2020) scales at which these studies have been conducted, invasion stage of taxa examined (Ma et al., 2016; Omer et al., 2022), phylogenetic scale used (Trotta et al., 2021), and changes in species interactions (Li et al., 2022). Evidence suggests that DNH is operative at small spatial scales, whereas PAH is operative at larger spatial scales (Park, Feng, et al., 2020). Recently, Wang et al. (2023) provided evidence for reconciling DNC based on the changes in species interactions mediated by arbuscular mycorrhizal fungi along a stress gradient.

Elevation is also an important influence on the relative importance of biotic interactions and environmental filtering in determining community composition and invasion success (Duarte et al., 2021; Luo et al., 2023; McFadden et al., 2019). Studies have indicated that competition is more intense and frequent in low-elevation environments (Li et al., 2014) due to the relatively favorable environmental conditions that promote high species richness and overlap in resource use. In contrast, high-elevation environments characterized by harsher environmental conditions may limit the number of species that can survive and compete (Graham et al., 2012). In addition to the phylogenetic underpinning of successful invasions, abiotic factors that vary in relation to elevation also influence community assembly and species invasiveness (Li et al., 2015; Williams et al., 2018). For example, a decrease in the number of non-native species with elevation is attributed to the harshness of the climate at higher elevations (Pauchard et al., 2009), particularly caused by unfavorable temperature and precipitation conditions (Alexander et al., 2016; Haider et al., 2018; Seipel et al., 2011). At smaller scales, physical and chemical soil properties (e.g., temperature, moisture, nitrogen, pH) are the local factors that constrain species invasions (Buri et al., 2017; Gantchoff et al., 2018; Lembrechts et al., 2019; Soti et al., 2020; Stohlgren et al., 1999).

Given the role of biotic, abiotic, and anthropogenic factors in successful invasions across elevation gradients, we hypothesized that the phylogenetic relationship of a successful invader with co-occurring native and non-native species should vary with elevation. Accordingly, we theorized that phylogenetically distantly-related invaders should co-occur with species at low elevations to escape stronger competition (phylogenetic overdispersion—support for DNH), but the invader should be in the company of closely related species at high elevations due to stronger environmental filtering (phylogenetic clustering—support for PAH). Hence, we studied the phylogenetic structure of plant assemblages at different elevations in Kashmir Himalaya that were invaded by *Anthemis cotula* L., a highly invasive ruderal species (Box 1). Specifically, we asked the following question: Do the abundance and phylogenetic relatedness between the focal

BOX 1 *Anthemis cotula* L. as focal species

Anthemis cotula L. is a monocarpic annual plant species that belongs to the family Asteraceae and is commonly known as "mayweed or stinking chamomile," "dog fennel." The synonyms of *A. cotula* are *Anthemis foetida* Lam., *Chamaemelum cotula* (L.) All., *Maruta cotula* (L.) DC., *Maruta foetida* Gray, and *Matricaria cotula* (L.) Baill. (POWO, 2023). The species is native to Eurasia, especially in regions with a Mediterranean-type climate (Erneberg, 1999; Kay, 1971), and northern parts of Africa (POWO, 2023). It is believed that this species was introduced outside its native range via trade as a contaminant of crop seeds/propagules (CABI, 2021). *A. cotula*, due to its ruderal life history strategy (r-selected), colonizes disturbed habitats and grows as a common weed in arable land, farmyards, roadsides, moist meadows, and overgrazed pastures. A syndrome of traits, such as synchronous germination of its achenes with favorable climatic conditions (Reshi et al., 2012), protracted recruitment and demographic trade-off with pre-winter and post-winter cohorts (Reshi et al., 2012), over-compensatory growth upon herbivory (Shah et al., 2012), allelopathic potential (Allaie et al., 2006; Rashid & Reshi, 2012), widespread mycorrhizal association (Shah & Reshi, 2007), and high reproductive output (Kay, 1971; Rashid et al., 2007), contribute to its invasiveness in Kashmir Himalaya. This rapidly spreading species is considered a threat to the native biodiversity (Adhikari et al., 2020), and this threat of alien species is likely to exacerbate due to an increase in anthropogenic activities and global climate change (Downey & Richardson, 2016; Richardson & Pyšek, 2012).

invasive species, *A. cotula*, and the co-occurring native and alien plant species change with elevation? Given that the number of competitors in local communities can influence the presence and abundance of invasive species—enemy release hypothesis (ERH; Keane & Crawley, 2002)—we also asked: How does the number of species in local communities impacts the abundance and phylogenetic relationship of *A. cotula* in relation to elevation? Moreover, if the number of species that co-occur with *A. cotula* constrains its presence and abundance, a decrease in the focal species' abundance with an increase in the number of co-occurring species of local communities should occur. We further hypothesized that the phylogenetic relatedness of *A. cotula* with co-occurring species would decrease with increasing elevation and species richness. Testing our hypotheses is likely to shed light on the relative role of environmental and biotic factors in explaining the successful invasion of alien species.

METHODS

Study area

The study area for the present investigation was the Kashmir Himalaya, which includes the main Kashmir Valley and also the side valleys of Tilel, Guraiz, Keran, and Karnah (Dar & Khuroo, 2013). The region is not only part of the biogeographic province of the Northwest Himalaya in India (Rodgers & Panwar, 1988) but also the Himalayan biodiversity hotspot (Dar & Khuroo, 2020). It lies between geographical coordinates of 33°20′ to 34°54′ N latitude and 73°55′ to 75°35′ E longitude with an area of 15,948 km^2, of which nearly 64% is mountainous (Khuroo et al., 2007). Topographically, the region mainly comprises a deep elliptical bowl-shaped valley, which in the south and southwest is bound by the Pir Panjal range of Lesser Himalaya and in the north and northeast by the Zanskar range of the Greater Himalaya. The Valley of Kashmir is surrounded by high mountain ranges, with the altitude of the main valley ranging from 1500 to 1800 m above mean sea level (amsl), whereas the average height of its surrounding mountain ranges varies from 3000 to 4000 m amsl, the highest peak being Kolahoi (5420 m amsl). A characteristic and prominent geological feature of the region are the "Karawas," which are plateau-like tablelands formed during the Pleistocene Ice age and are composed of clay, sand, and silt of lacustrine origin (de Terra, 1934). The valley is traversed by the river Jehlum and its tributaries, which feed many world-famous freshwater lakes, such as Wular, Dal, and Anchar lakes. The climate of the region, marked by well-defined seasonality, resembles that of mountainous and continental areas of the temperate latitudes. The temperature ranges from an average daily maximum of 31°C and a minimum of 15°C during summer to an average daily maximum of 4°C and a minimum of −4°C during winter. It receives annual precipitation of about 1050 mm, mostly in the form of snow during the winter months. Due to the vast variety of edapho-climatic and physiographic heterogeneity, the region harbors diverse habitats, including forests, grasslands, subalpine and alpine meadows, lakes, springs, swamps, marshes, rivers, cultivated fields, orchards, montane scree slopes

and terraces, and permanent glaciers, which support equally diverse floristic elements (Gupta, 1982).

Like other parts of the world, Kashmir Himalaya is also beset with the menace of alien plant invasions. A total of 571 vascular alien plant species, belonging to 352 genera and 104 families, have been reported from the Kashmir Himalaya (Khuroo et al., 2007). This study reported that the number of alien plant species was higher in families such as Poaceae (60 species), Asteraceae (54 species), and Brassicaceae (30 species). However, families such as Amaranthaceae (83%) and Chenopodiaceae (71%) showed a higher percentage of aliens relative to the total number of plant species belonging to these families in the region. Most of the alien plant species in Kashmir Himalaya (38%) were native to Europe, followed by Asia (27%) and Africa (15%).

Field sampling

Field surveys were conducted across the Kashmir Himalaya in 2018, and *A. cotula* was found growing over an altitudinal range of 1587 to 3700 m amsl (Figure 1). Based on the population characteristics, particularly the size, 17 sampling sites were selected (each possessing >50% *A. cotula* cover) to cover more or less the entire spatial and altitudinal expanse of the species in the Kashmir Himalaya. The sampling sites supporting the populations of *A. cotula* were separated at least 15 km from each other. Though *A. cotula* was found to grow beyond 2700 m amsl, such populations were not considered for phytosociological studies because these populations were comprised of a few scattered individuals of *A. cotula*, and the number of species was very low, which could have reduced the reliability of metric calculations. The geographic coordinates, elevation, and soil characteristics of the 17 sampling sites are given in Appendix S1: Table S1.

A total of 10 quadrats (100 × 100 cm^2) were laid randomly at each sampling site during the peak growing season. In each quadrat, all the plant species co-occurring with *A. cotula* were noted, and their abundance was also recorded, and the abundance values were averaged to obtain mean abundance values per site. The samples of plant species collected during the field survey were processed using routine herbarium techniques and identified using relevant literature and herbarium records available in the Kashmir University Herbarium (KASH). The help of experts for correct identification was also sought wherever required. The synonyms and plant name authorships were ascertained from The Plant List (2013)

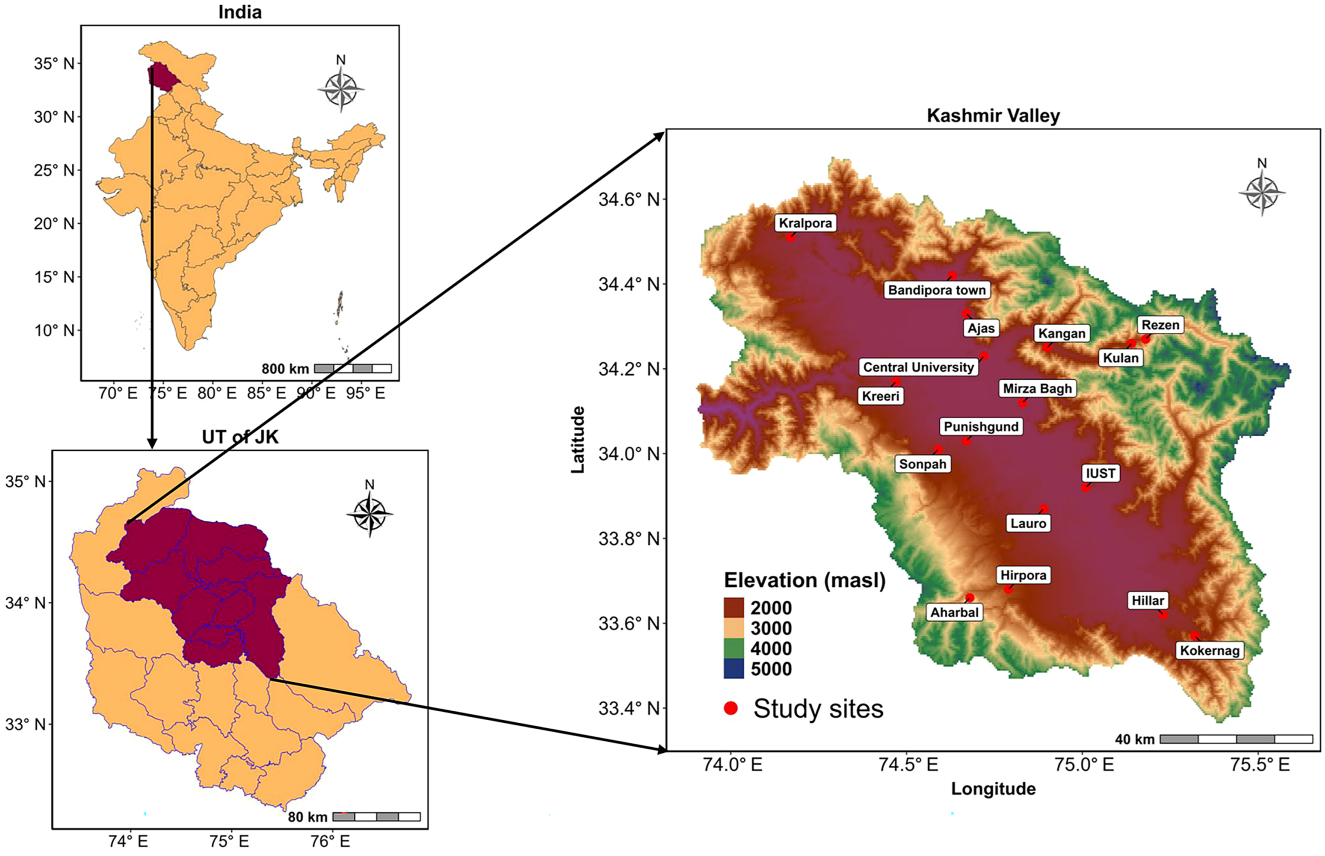


FIGURE 1 Location map of the study area and study sites.

using the function TPL() of the Taxonstand package (Cayuela et al., 2012) in R ("R Core Team," 2023). Moreover, various sources such as internet web pages, websites (www.efloras.org; https://powo.science.kew.org), and Khuroo et al. (2007) were used to assign the nativity to each plant species. The plant species were categorized into monocots and dicots and were further classified into annuals, biennials, and perennials based on their life span.

Phylogenetic tree

A phylogenetic tree (Figure 2) was constructed using the R package V.PhyloMaker (Jin & Qian, 2019). V.PhyloMaker uses the "GBOTB_extended.tree" as a backbone to insert missing species to their respective genera and families. This extended tree is an updated version of the Spermatophyta mega-phylogeny GBOTB (Smith & Brown, 2018) and includes 74,533 species and all families of extant vascular plants. The branch lengths of the imputed species were set using the BLADJ approach as implemented in V.PhyloMaker (Jin & Qian, 2019).

Soil analysis

A composite soil sample, representing a mixture of subsamples, was collected from each sampling site.

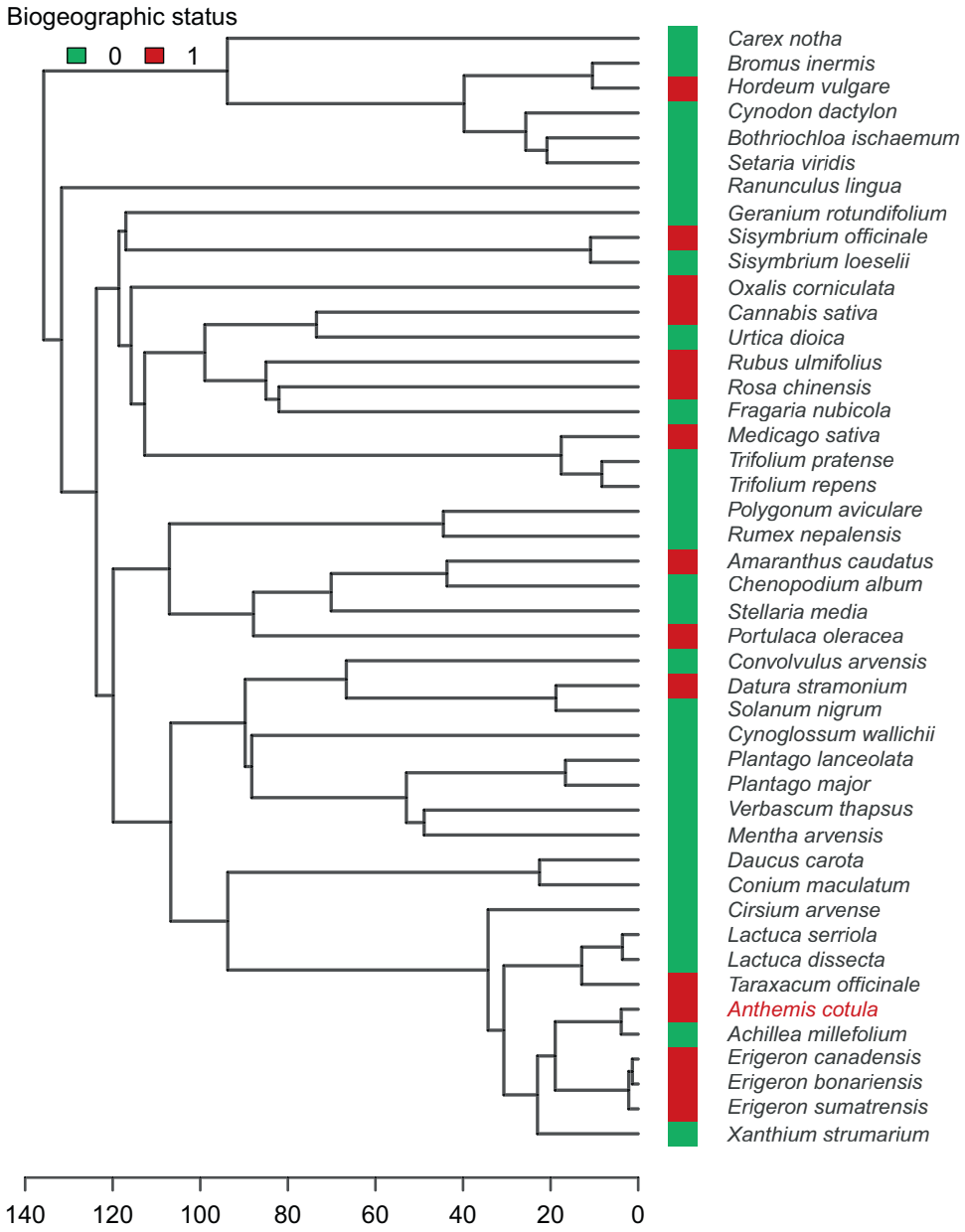


FIGURE 2 Phylogenetic tree used in this study. Green and red colors indicate the biogeographic status (native = 0 and introduced = 1). The focal species (*Anthemis cotula*) is highlighted in red.

Soil samples were collected by inserting a soil corer (2.25 cm diameter) vertically, and not tilted sideways, into the soil up to a depth of 15 cm. Five such soil samples from each site were thoroughly mixed and collected in plastic bags. In the laboratory, soil samples were gently crushed manually, air-dried, and sieved through a 2-mm sieve to eliminate debris. The soil samples were then immediately processed for analysis.

The soil pH was measured for soil and distilled water suspension in the ratio of 5:1 using a portable pH meter (SYSTRONICS Model: MKVI). Organic carbon was determined using Walkley and Black (1934) rapid titration method. Olsen's method (Olsen et al., 1954) was used for measuring phosphorus concentration. The flame photometry procedure outlined by Jackson (1973) was used to estimate total potassium (K), and sulfur was estimated using the calcium chloride method (Chesnin & Yien, 1951). Calcium (Ca) was estimated in ammonium acetate extracts of soil by titration with EDTA (Cheng & Bray, 1951). Soil characteristics are given in Appendix S1: Table S1.

Calculation of diversity metrics

To investigate the phylogenetic structure of *A. cotula*, we used the focal-species approach (Pinto-Ledezma et al., 2020; see also Miller et al., 2017). The focal-species approach allows for the quantification of the phylogenetic structure of a set of species that co-occur with a focal species in a particular community or sampling site. Put simply, the focal species' phylogenetic distance to all other community members is calculated and then averaged to obtain a single measure, for example, MPD_{focal}, mean phylogenetic-pairwise distance (MPD) of the focal species (see Pinto-Ledezma et al., 2020, for further details). We performed metric calculations that account for abundance (abundance-weighted MPD or MPD_{aw}) of co-occurring species with *A. cotula* in each of the 17 sampling sites (Figure 1). MPD_{aw} was estimated by setting the diagonal element of the weight matrix to zero (sensu Miller et al., 2013). This MPD version maximizes the distances between heterospecific individuals among co-occurring species, and it is particularly useful for assessing changes in the phylogenetic structure of local communities across environmental gradients (Miller et al., 2013, 2017).

Given that several non-native species were also found co-occurring with our focal species (Table 1), metric calculations were performed using all species (natives and non-natives) and using only native species. Overall, we estimated 34 metric values (17 sampling sites × 1 metric × 2 datasets) for *A. cotula*.

TABLE 1 Taxonomic conspectus of taxa growing in association with *Anthemis cotula*.

Group	Species	Genera	Families
Dicots	39	33	20
Monocots	6	6	2
Natives	30	27	19
Non-natives	15	13	10

Data analyses

Our analyses focused on assessing the probability of changes in abundance and phylogenetic relatedness of our focal species across elevation and local species richness. To do so, we modeled the association between the abundance and phylogenetic structure (MPD_{aw}) of our focal species against elevation and species richness using Bayesian linear models (BLMs). We assessed the effect of elevation or local species richness by testing the hypothesis that the high-density intervals (HDIs) or 95% credible intervals (CIs) of the BLM coefficients (slopes) do not overlap zero. To test the hypothesis for each model, we computed the evidence ratio (ER), which represents the posterior probability of a hypothesis against an alternative hypothesis—hypothesis = $\beta \neq 0$, in other words, β is $>0|<0$—where the values of ER greater than one indicate evidence supporting the hypothesis.

In addition, given that additional environmental variables like soil properties may (or may not) influence the patterns of species co-occurrence, we additionally built models in which the abundance and the phylogenetic structure of *A. cotula* were influenced by the soil characteristics of the sampling sites. BLMs were implemented in the probabilistic programming language Stan (Carpenter et al., 2017) through the R package "brms" (Bürkner, 2017). All analyses were run using 4 NUTS (No U-Turn Sampler) sampling chains for 5000 generations and discarding 20% as burn-ins. Note that all BLMs were run twice, one using the all-species dataset (natives and non-natives) and the other using the only-natives dataset. Finally, to gain more insights regarding the elevational patterns of species richness for native, non-native, and all the species (native + non-native), polynomial regressions were implemented. The best-fit function of polynomial regression was selected on the basis of Akaike information criterion (AIC) value.

RESULTS

General description of the data

In all, 44 plant species were recorded in association with *A. cotula* belonging to 39 genera and 22 families

(Table 1). Most of the species were dicots (39 species) and monocots were represented by only 6 species. Of the associated species, 30 were native to the region and 15, including *A. cotula*, were non-native.

The number of species varied across sites with a minimum of 12 species recorded at the elevation of 1592 m amsl and a maximum of 22 species recorded at an elevation of 2201 m amsl (Appendix S1: Figure S1). The native and non-native species belonging to dicots and monocots across sites are shown in Appendix S1: Figure S2. The number of species associated with *A. cotula* at the quadrat scale ranged from 6 to 9 across sites (Appendix S1: Figure S3).

A perusal of the data reveals that dicots were predominant across the elevations and the non-native species were almost entirely represented by dicots and only one non-native monocot was recorded during the present study in any of the sites.

Patterns of abundance and phylogenetic structure of *A. cotula*

The abundance of *A. cotula* varied considerably and showed a continued decline with increasing elevation and the number of species that co-occurred at each sampling site (Figure 3A,B; Appendix S1: Figure S4C,E). The pattern of continuous decline in abundance was consistent across datasets, that is, using all species (natives and non-natives) dataset and the only native species dataset.

The patterns of phylogenetic structure also varied; however, we observed shifts in the strength and direction of the associations between the degree of relatedness of *A. cotula* (measured as MPD_{aw}) and the covariables (elevation and richness). Specifically, we observed a shift from slightly positive associations between MPD_{aw} and the covariables using the all-species dataset (Appendix S1: Figure S4F) to negative associations using the native-only dataset (Figure 3C,D). This pattern of increasing phylogenetic clustering with increasing elevation and richness (in the native-only dataset) is consistent with the PAH.

Effects of elevation and local species richness on patterns of abundance and phylogenetic structure of *A. cotula*

We found strong evidence that both elevation and local species richness negatively influence the abundance of

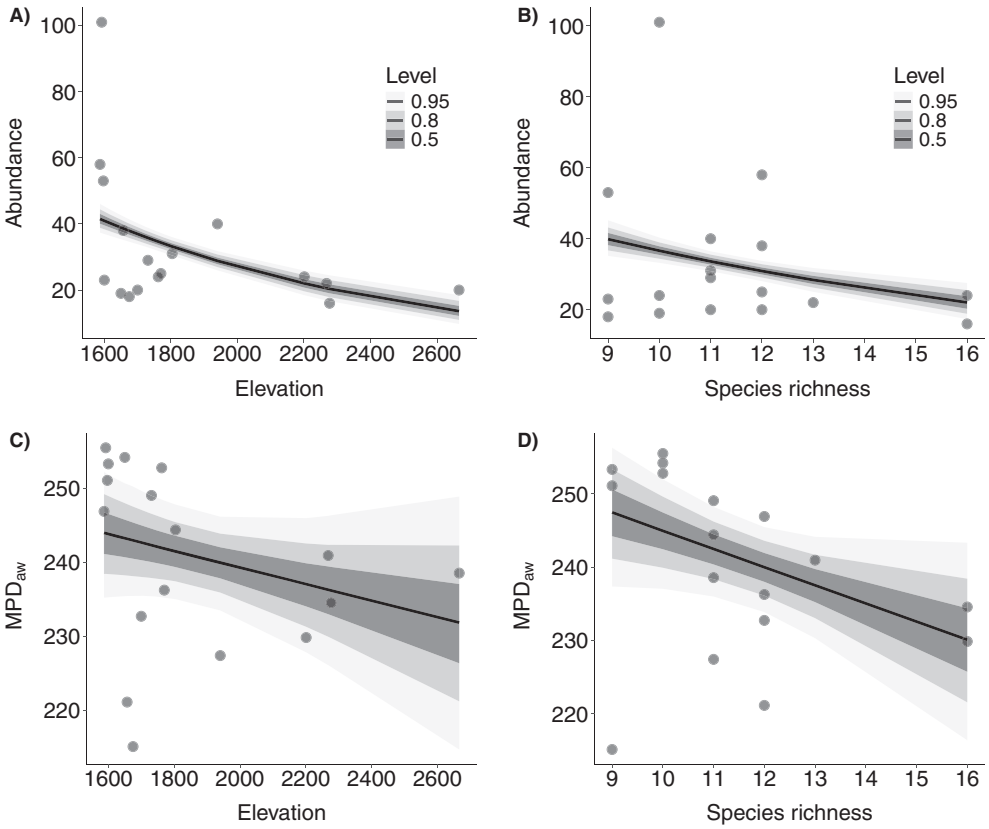


FIGURE 3 Marginal effects plots of changes in (A, C) abundance and phylogenetic structure of *Anthemis cotula* across elevation and (B, D) local native species richness. Continuous black lines represent the expected posterior predictions' slopes (with 50%, 80%, and 95% credible intervals in gray). MPD_{aw}, abundance-weighted mean pairwise distance.

A. cotula, and that the effect is consistent across datasets (Figure 4A,B). Indeed, our Bayesian models revealed strong evidence (all species, ER = Inf; natives only, ER = Inf) for the effect of both covariables on *A. cotula* abundance patterns (Table 2). For the phylogenetic structure under the all-species dataset, we found weak evidence for the effect of elevation (all species, ER = 2.101) and for the effect of local species richness (all species, ER = 1.551) (Table 2; see also Appendix S1: Figure S4D,F). Under the natives-only dataset, we found small evidence for the effect of elevation on MPD_{aw} (ER = 7.112; Figure 4A). Local species richness exerted a strong effect on the patterns of MPD_{aw} (ER = 21.456) (Figure 4B; Table 2).

We were also interested in exploring the effect of soil covariables on the patterns of abundance and phylogenetic structure (Appendix S1: Figure S5A,B). We found strong evidence that SOC, S, K, and N influence the abundance of *A. cotula* (ER[65.666, Inf]; Appendix S1: Table S2). For the phylogenetic structure, it seems that soil covariables do not strongly influence the patterns of MPD_{aw} for both datasets (Appendix S1: Figure S5B). Indeed, we found weak evidence for all the soil properties on MPD_{aw} (Appendix S1: Table S2, Figure S5).

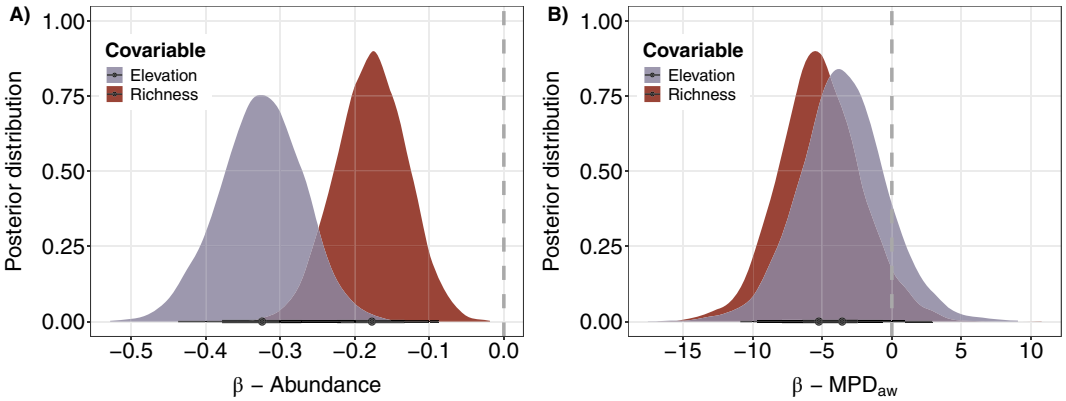


FIGURE 4 Posterior distribution of the marginal effects (slope coefficients [β]) of elevation and local species richness on (A) *Anthemis cotula* abundance and (B) phylogenetic structure. Each point (shown with black bars) represents the median β with its associated 95% high-density credible interval (HDI). MPD_{aw}, abundance-weighted mean pairwise distance.

TABLE 2 Comparative hypothesis testing for the biotic (species richness) and abiotic (elevation) covariables influencing the abundance and the phylogenetic structure of our focal species.

Dataset	Variable	Covariable	Estimate	CI lower −2.50%	CI upper −97.50%	Evidence ratio	Posterior distribution
All species	**Abundance**	**Elevation**	**−0.327***	**−0.415**	**−0.240**	***Inf***	**1**
All species	**Abundance**	**Richness**	**−0.242***	**−0.317**	**−0.168**	***Inf***	**1**
All species	MPD_{aw}	Elevation	1.421	−3.779	6.849	2.101	0.677
All species	MPD_{aw}	Richness	−0.791	−6.047	4.632	1.551	0.608
Native only	**Abundance**	**Elevation**	**−0.326***	**−0.421**	**−0.237**	***Inf***	**1**
Native only	**Abundance**	**Richness**	**−0.178***	**−0.257**	**−0.103**	***Inf***	**1**
Native only	MPD_{aw}	Elevation	−3.535	−8.640	1.672	7.112	0.877
Native only	**MPD_{aw}**	**Richness**	**−5.169***	**−9.859**	**−0.210**	**21.456**	**0.955**

Note: Rows in boldface indicate that the influence of the covariable is different from zero, that is, strong evidence. An asterisk (*) indicates that the parameter estimations are different from zero at alpha 0.05. See *Methods* for details of the evidence ratio (ER) calculation and interpretation.
Abbreviation: MPD_{aw}, abundance-weighted mean pairwise distance.

DISCUSSION

Elevation controls the phylogenetic structure of *A. cotula*

Our results revealed that the phylogenetic distance between our focal species and native species decreased with increasing elevation (Figure 3C), indicating that at lower elevations phylogenetically distantly-related native species are associated with *A. cotula* (support for DNH), and with increase in elevation, the focal species was more closely related to native species (support for PAH). This pattern could arise due to environmental filtering or competitive exclusion, where species with similar ecological requirements or competitive abilities are favored under harsher environmental conditions found at higher elevations (Shooner et al., 2018).

Our results also showed that the phylogenetic distance between the focal species and all species (native and non-native together) increased with elevation (Appendix S1: Figure S4F). This pattern could be driven by the non-native species that are adapted to specific environmental conditions at higher elevations, leading to an increase in phylogenetic diversity and distance. Positive species interactions (e.g., facilitation) could also impact the phylogenetic patterns of species co-occurrence. That is, the degree to which phylogenetically distant species co-occur increases with elevation (Bryant et al., 2008; Callaway et al., 2002) because of facilitation. For example, in a recent study in China (Banerjee et al., 2023), the role of facilitation by invasive aliens in the establishment of other alien species was invoked, and a phylogenetic basis for the invasional meltdown hypothesis (IMH) was provided (Banerjee et al., 2023), which relates to the positive interactions among invaders in promoting secondary invasions (Green et al., 2011). Also, it may be due to the competition for limiting resources at higher elevations, which results in the exclusion of close relatives with overlapping niches, thereby increasing the phylogenetic distances among species (Graham et al., 2014). *A. cotula* being a species that thrives in ruderal habitats, it is also quite likely that disturbance creates conditions suitable for other distantly-related co-occurring non-native species. Furthermore, *A. cotula* tracks roads and trails, which also serve as conduits for the spread of other alien species, thereby increasing the phylogenetic distance between the species assemblages, outweighing the effect of reduced competition.

Another noteworthy aspect of the present study is the observation that the abundance-based metric of phylogenetic distance (MPD_{aw}) is more informative as it detected more nuanced variation in the phylogenetic distance—particularly between the focal species and its co-occurring native species where it declined both with elevation and native species richness (Figure 3; Appendix S1: Figure S4). Other studies have also reported that abundance-weighted measures explain the phylogenetic relationship, given their least consideration of the phylogenetic contribution of consistently rare species (Miller et al., 2017). Because the abundance-weighted mean phylogenetic distance among individuals (MPD_{aw}) provides better insights into the phylogenetic relationships than incidence-based phylogenetic metrics, abundance-weighted metrics are particularly useful for studying the phylogenetic relationship of invasive species given that invasiveness is related to the spatial spread and abundance of an introduced species.

High local species richness constrains the spread of *A. cotula*

Our results also revealed a decline in phylogenetic distance between the focal species and the increasing richness of native species (Figure 3D). This pattern can be attributed to several underlying ecological mechanisms, such as niche partitioning or facilitative interactions, where species with similar ecological requirements partition resources more effectively or provide mutualistic benefits to one another (Jones et al., 2013; Stachowicz, 2001). As native species richness increases, the focal species may become more closely associated with phylogenetically related native species, leading to a decline in phylogenetic distance (Figure 3D). On the contrary, increase in phylogenetic distance with increasing species richness of both native and non-native species (Appendix S1: Figure S4) could be because of different evolutionary histories and ecological traits of introduced species compared with native species, leading to an increase in phylogenetic distance between the focal species and the entire species pool. Thus, it is quite evident that DNH and the PAH are most relevant when phylogenetic distance between the focal invasive species and its co-occurring native species is compared.

In sync with our hypotheses, the results further revealed that the abundance of *A. cotula* declined with increase in both elevation (Figure 3A; Appendix S1: Figure S4C) and species richness (Figure 3B; Appendix S1: Figure S4D). This decline could be due to both abiotic (e.g., climatic and soil conditions, anthropogenic disturbances) and biotic (e.g., propagule pressure, mutualists) factors. Among the climatic factors, low temperature or frost, in particular, at higher elevations prevents the establishment and persistence of a plant species due to high mortality rates (Bruelheide & Heinemeyer, 2002;

Taschler & Neuner, 2004; Woodward, 1997); in addition, variation in the intensity and spectral composition of solar radiation with altitude (Körner, 2003) inhibits plant growth (Angert, 2006) and reproduction (Woodward, 1990). A very short growing period to complete their life cycle (Beerling, 1993; Griffith & Watson, 2006) and a decrease in the number of propagules of alien species with elevation (Alexander et al., 2011) could also be responsible for the lower abundance of invasive species at higher elevations.

Decreased abundance of *A. cotula* with increasing species richness could be due to the competition offered by the co-occurring species and more complete filling of vacant niches. As evolutionary history also influences the elevational richness of seed plants (Sun et al., 2020), we also explored the pattern of species richness in relation to elevation (Appendix S1: Figure S6). The mid-elevation hump-shaped pattern of species richness in relation to elevation was observed for both native and all species (native and non-native species taken together). However, non-native species slightly declined with elevation and did not show a mid-elevational peak (Appendix S1: Figure S6C). Hump-shaped distribution with high richness at intermediate elevations has been widely reported globally (McCain & Grytnes, 2010; Peters et al., 2016; Rahbek, 1995, 2005), as well as in different parts of the Himalaya (Bhattarai & Vetaas, 2003, 2006; Carpenter, 2005; Grytnes & Vetaas, 2002; Liang et al., 2020; Manish et al., 2017; Sun et al., 2020). However, mid-elevational peak in species richness did not result in significant variation in phylogenetic distance between the focal species and its co-occurring species in these elevations.

In regard to the much highlighted role of scarce soil nutrients and low temperatures at higher elevations in selecting phylogenetically similar species—that is, selection of species equipped with preadapted traits necessary for their successful establishment in these challenging environments—our study showed a slightly positive influence of soil calcium on MPD_{aw} when considering all species (ER = 13; see also Appendix S1: Figure S5). Given the complex interactions between biotic and abiotic factors that determine the availability of soil nutrients, the actual mechanisms as to how soil nutrients influence the phylogenetic structure at the ecological scale are difficult to distinguish. Further research is needed to fully understand how and to what extent soil nutrients influence the successful invasion of introduced species. While the soil characteristics are considered local drivers of the fine-scale richness patterns of non-native species in mountain ecosystems (Buri et al., 2017; Gantchoff et al., 2018; Lembrechts et al., 2019), the relationship between species richness, species abundance, and phylogenetic diversity, as well as soil nutrients along elevation gradients, is challenging to tease apart.

CONCLUSIONS

Our findings support both DNH at lower elevations and the PAH at higher elevations. We highlighted the utility of abundance-based phylogenetic metrics, which provide nuanced insights into species interactions and community structure. Furthermore, the complex interplay between biotic and abiotic factors in relation to abundance, particularly of alien species and species richness, underscores the need for further research to unravel the mechanisms driving the phylogenetic relationships between the invasive alien species and their co-occurring species.

AUTHOR CONTRIBUTIONS

Afshana and Jesús N. Pinto-Ledezma did sampling and generated the data. Jesús N. Pinto-Ledezma and Zafar A. Reshi analyzed the data. Zafar A. Reshi, Jesús N. Pinto-Ledezma, and Afshana wrote and revised the manuscript. All authors have read and agreed with the final version of the manuscript.

ACKNOWLEDGMENTS

We thank Head, Department of Botany, University of Kashmir for providing laboratory facilities. Award of fellowship by the UGC-CSIR, India, to Afshana and the support to the corresponding author under the CPEPA by the University Grants Commission (UGC), New Delhi is also gratefully acknowledged. Jesús N. Pinto-Ledezma was supported by the US National Science Foundation (DEB-2017843).

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Afshana et al., 2024) are available from Figshare: 10.6084/m9.figshare.26308243.v1.

ORCID

Jesús N. Pinto-Ledezma https://orcid.org/0000-0001-6668-9670

REFERENCES

Adhikari, S., I. C. Burke, and S. D. Eigenbrode. 2020. "Mayweed Chamomile (*Anthemis cotula* L.) Biology and Management—A Review of an Emerging Global Invader." *Weed Research* 60: 313–322.

Afshana, J. N. Pinto-Ledezma, and Z. A. Reshi. 2024. "Data_species_abundance. Figshare. Dataset." https://doi.org/10.6084/m9.figshare.26308243.v1.

Alexander, J. M., J. M. Diez, S. P. Hart, and J. M. Levine. 2016. "When Climate Reshuffles Competitors: A Call for Experimental Macroecology." *Trends in Ecology & Evolution* 31: 831–841.

Alexander, J. M., C. Kueffer, C. C. Daehler, P. J. Edwards, A. Pauchard, T. Seipel, J. Arévalo, et al. 2011. "Assembly of Nonnative Floras along Elevational Gradients Explained by Directional Ecological Filtering." *Proceedings of the National Academy of Sciences of the United States of America* 108: 656–661.

Allaie, R. R., Z. Reshi, and B. A. Wafai. 2006. "Demographic Plasticity in Relation to Growth and Resource Allocation Pattern in *Anthemis cotula* – An Alien Invasive Species in Kashmir Himalaya, India." *Applied Ecology and Environmental Research* 4: 63–74.

Angert, A. L. 2006. "Growth and Leaf Physiology of Monkeyflowers with Different Altitude Ranges." *Oecologia* 148: 183–194.

Banerjee, A. K., F. Tan, H. Feng, X. Liang, J. Wang, M. Yin, H. Peng, Y. Lin, N. Zhang, and Y. Huang. 2023. "Invasive Alien Plants Are Phylogenetically Distinct from Other Alien Species across Spatial and Taxonomic Scales in China." *Frontiers in Plant Science* 14: 1075344.

Beerling, D. J. 1993. "The Impact of Temperature on the Northern Distribution Limits of the Introduced Species *Fallopia japonica* and *Impatiens glandulifera* in North-West Europe." *Journal of Biogeography* 20: 45–53.

Bhattarai, K. R., and O. R. Vetaas. 2003. "Variation in Plant Species Richness of Different Life Forms along a Subtropical Elevation Gradient in the Himalayas, East Nepal." *Global Ecology and Biogeography* 12: 327–340.

Bhattarai, K. R., and O. R. Vetaas. 2006. "Can Rapoport's Rule Explain Tree Species Richness along the Himalayan Elevation Gradient, Nepal?" *Diversity and Distributions* 12: 373–78.

Blackburn, T. M., P. Pyšek, S. Bacher, J. T. Carlton, R. P. Duncan, V. Jarošík, J. R. U. Wilson, and D. M. Richardson. 2011. "A Proposed Unified Framework for Biological Invasions." *Trends in Ecology & Evolution* 26: 333–39.

Bruelheide, H., and A. Heinemeyer. 2002. "Climatic Factors Controlling the Eastern and Altitudinal Distribution Boundary of *Digitalis purpurea* L. in Germany." *Flora* 197: 475–490.

Bryant, J. A., C. Lamanna, H. Morlon, A. J. Kerkhoff, B. J. Enquist, and J. L. Green. 2008. "Microbes on Mountainsides: Contrasting Elevational Patterns of Bacterial and Plant Diversity." *Proceedings of the National Academy of Sciences of the United States of America* 105: 11505–11.

Buri, A., C. Cianfrani, E. Pinto-Figueroa, E. Yashiro, J. E. Spangenberg, T. Adatte, E. Verrecchia, A. Guisan, and J. N. Pradervand. 2017. "Soil Factors Improve Predictions of Plant Species Distribution in a Mountain Environment." *Progress in Physical Geography* 41: 703–722. https://doi.org/10.1177/0309133317738162.

Bürkner, P.-C. 2017. "brms: An R Package for Bayesian Multilevel Models Using Stan." *Journal of Statistical Software* 80: 1–28.

CABI. 2021. Anthemis (chamomile). *CABI Compendium*. https://doi.org/10.1079/cabicompendium.5670

Cadotte, M. W., S. E. Campbell, S.-P. Li, D. S. Sodhi, and N. E. Mandrak. 2018. "Preadaptation and Naturalization of Nonnative Species: Darwin's Two Fundamental Insights into Species Invasion." *Annual Review of Plant Biology* 69(1): 661–684.

Callaway, R. M., R. W. Brooker, P. Choler, Z. Kikvidze, C. J. Lortie, R. Michalet, L. Paolini, et al. 2002. "Positive Interactions among Alpine Plants Increase with Stress." *Nature* 417: 844–48.

Campbell, S. E., and N. E. Mandrak. 2017. "Dissecting Spatiotemporal Patterns of Functional Diversity through the Lens of Darwin's Naturalization Conundrum." *Ecology and Evolution* 7: 3861–69.

Carpenter, B., A. Gelman, M. D. Hoffman, D. Lee, B. Goodrich, M. Betancourt, M. A. Brubaker, J. Guo, P. Li, and A. Riddell. 2017. "Stan: A Probabilistic Programming Language." *Journal of Statistical Software* 76: 1–32.

Carpenter, C. 2005. "The Environmental Control of Plant Species Density on a Himalayan Elevation Gradient." *Journal of Biogeography* 32: 999–1018.

Cayuela, L., Í. Granzow-de la Cerda, F. S. Albuquerque, and D. J. Golicher. 2012. "Taxonstand: An r Package for Species Names Standardisation in Vegetation Databases." *Methods in Ecology and Evolution* 3: 1078–83.

Cheng, K. L., and R. H. Bray. 1951. "Determination of Calcium and Magnesium in Soil and Plant Material." *Soil Science* 72: 449–458.

Chesnin, L., and C. H. Yien. 1951. "Turbidimetric Determination of Available Sulfates." *Soil Science Society of America Journal* 15: 149–151.

Daehler, C. C. 2001. "Darwin's Naturalization Hypothesis Revisited." *The American Naturalist* 158: 324–330. https://doi.org/10.1086/321316.

Dar, G. H., and A. A. Khuroo. 2013. "Floristic Diversity in the Kashmir Himalaya: Progress, Problems and Prospects." *Sains Malaysiana* 42(10): 1377–86.

Dar, G. H., and A. A. Khuroo, eds. 2020. *Biodiversity of the Himalaya: Jammu and Kashmir State*. Singapore: Springer.

Darwin, C. R. 1859. *On the Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life*, Ist ed. London: John Murray.

David, P., E. Thebault, O. Anneville, P. F. Duyck, E. Chapuis, and N. Loeuille. 2017. "Impacts of Invasive Species on Food Webs: A Review of Empirical Data." *Advances in Ecological Research* 56: 1–60.

de Terra, H. 1934. "Physiographic Results of a Recent Survey in Little Tibet." *Review* 24: 12–41.

Downey, P. O., and D. M. Richardson. 2016. "Alien Plant Invasions and Native Plant Extinctions: A Six-Threshold Framework." *AoB Plants* 8.

Duarte, M., M. Verdú, L. A. Cavieres, and R. O. Bustamante. 2021. "Plant–Plant Facilitation Increases with Reduced Phylogenetic Relatedness along an Elevation Gradient." *Oikos* 130: 248–259.

Duncan, R., P., and P. A. Williams. 2002. "Darwin's Naturalization Hypothesis Challenged." *Nature* 417: 608–9.

Elton, C. S. 2020. *The Ecology of Invasions by Animals and Plants*. New York: Springer.

Enders, M., F. Havemann, F. Ruland, M. Bernard-Verdier, J. A. Catford, L. Gómez-Aparicio, S. Haider, et al. 2020. "A Conceptual Map of Invasion Biology: Integrating Hypotheses into a Consensus Network." *Global Ecology and Biogeography* 29: 978–991.

Erneberg, M. 1999. "Effects of Herbivory and Competition on an Introduced Plant in Decline." *Oecologia* 118: 203–9.

Gantchoff, M. G., C. M. Wilton, and J. L. Belant. 2018. "Factors Influencing Exotic Species Richness in Argentina's National Parks." *PeerJ* 2018: e5514.

Graham, C. H., A. C. Carnaval, C. D. Cadena, K. R. Zamudio, T. E. Roberts, J. L. Parra, C. M. Mccain, et al. 2014. "The Origin and Maintenance of Montane Diversity: Integrating Evolutionary and Ecological Processes." *Ecography* 37(8): 711–19.

Graham, C. H., J. L. Parra, B. A. Tinoco, F. G. Stiles, and J. A. McGuire. 2012. "Untangling the Influence of Ecological and Evolutionary Factors on Trait Variation across Hummingbird Assemblages." *Ecology* 93: S99–S111.

Green, P. T., D. J. O'Dowd, K. L. Abbott, M. Jeffery, K. Retallick, and R. Mac Nally. 2011. "Invasional Meltdown: Invader–Invader Mutualism Facilitates a Secondary Invasion." *Ecology* 92: 1758–68.

Griffith, T. M., and M. A. Watson. 2006. "Is Evolution Necessary for Range Expansion? Manipulating Reproductive Timing of a Weedy Annual Transplanted beyond Its Range." *The American Naturalist* 167: 153–164. https://doi.org/10.1086/498945.

Grytnes, J. A., and O. R. Vetaas. 2002. "Species Richness and Altitude: A Comparison between Null Models and Interpolated Plant Species Richness along the Himalayan Altitudinal Gradient, Nepal." *American Naturalist* 159: 294–304.

Gupta, R. K. 1982. "Mediterranean Influence in the Flora of Western Himalaya." In *The Vegetational Wealth of the Himalayas*, edited by G. S. Paliwal, 1975–93. New Delhi: Puja Publishers.

Haider, S., C. Kueffer, H. Bruelheide, T. Seipel, J. M. Alexander, L. J. Rew, J. R. Arévalo, et al. 2018. "Mountain Roads and Non-Native Species Modify Elevational Patterns of Plant Diversity." *Global Ecology and Biogeography* 27: 667–678.

Hejda, M., P. Pyšek, and V. Jarošík. 2009. "Impact of Invasive Plants on the Species Richness, Diversity and Composition of Invaded Communities." *Journal of Ecology* 97: 393–403.

Hettinger, N. 2021. "Understanding and Defending the Preference for Native Species." *International Library of Environmental, Agricultural and Food Ethics* 33: 399–424.

IPBES. 2023. In *Summary for Policymakers of the Thematic Assessment Report on Invasive Alien Species and Their Control of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services*, edited by H. E. Roy, A. Pauchard, P. Stoett, T. Renard Truong, S. Bacher, B. S. Galil, P. E. Hulme, T. Ikeda, K. V. Sankaran, M. A. McGeoch, L. A. Meyerson, M. A. Nuñez, A. Ordonez, S. J. Rahlao, E. Schwindt, H. Seebens, A. W. Sheppard, and V. Vandvik. Bonn: IPBES Secretariat. https://doi.org/10.5281/zenodo.7430692.

Jackson, M. L. 1973. *Soil Chemical Analysis*. New Delhi: Prentice Hall of India Pvt. Ltd. 498p.

Jin, Y., and H. Qian. 2019. "V.PhyloMaker: An R Package that Can Generate Very Large Phylogenies for Vascular Plants." *Ecography* 42: 1353–59.

Jones, E. I., S. L. Nuismer, and R. Gomulkiewicz. 2013. "Revisiting Darwin's Conundrum Reveals a Twist on the Relationship between Phylogenetic Distance and Invasibility." *Proceedings of the National Academy of Sciences of the United States of America* 110(51): 20627–32.

Kay, Q. O. N. 1971. "Biological Flora of the British Isles No. 122. *Anthemis cotula* L." *Journal of Ecology* 59: 623–636.

Keane, R. M., and M. J. Crawley. 2002. "Exotic Plant Invasions and the Enemy Release Hypothesis." *Trends in Ecology & Evolution* 17: 164–170.

Khuroo, A. A., I. Rashid, Z. Reshi, G. H. Dar, and B. A. Wafai. 2007. "The Alien Flora of Kashmir Himalaya." *Biological Invasions* 9: 269–292.

Körner, C. 2003. *Alpine Plant Life: Functional Plant Ecology of High Mountain Ecosystems*. Berlin, Heidelberg: Springer.

Lembrechts, J. J., I. Nijs, and J. Lenoir. 2019. "Incorporating Microclimate into Species Distribution Models." *Ecography* 42: 1267–79.

Li, L., X. Xu, H. Qian, X. Huang, P. Liu, J. B. Landis, Q. Fu, et al. 2022. "Elevational Patterns of Phylogenetic Structure of Angiosperms in a Biodiversity Hotspot in Eastern Himalaya." *Diversity and Distributions* 28: 2534–48.

Li, S. P., T. Guo, M. W. Cadotte, Y. J. Chen, J. L. Kuang, Z. S. Hua, Y. Zeng, et al. 2015. "Contrasting Effects of Phylogenetic Relatedness on Plant Invader Success in Experimental Grassland Communities." *Journal of Applied Ecology* 52: 89–99.

Li, X. H., X. X. Zhu, Y. Niu, and H. Sun. 2014. "Phylogenetic Clustering and Overdispersion for Alpine Plants along Elevational Gradient in the Hengduan Mountains Region, Southwest China." *Journal of Systematics and Evolution* 52: 280–88.

Liang, J., Z. Ding, G. Lie, Z. Zhou, P. B. Singh, Z. Zhang, and H. Hu. 2020. "Species Richness Patterns of Vascular Plants and Their Drivers along an Elevational Gradient in the Central Himalayas." *Global Ecology and Conservation* 24: e01279.

Linders, T. E. W., U. Schaffner, R. Eschen, A. Abebe, S. K. Choge, L. Nigatu, P. R. Mbaabu, H. Shiferaw, and E. Allan. 2019. "Direct and Indirect Effects of Invasive Species: Biodiversity Loss Is a Major Mechanism by Which an Invasive Tree Affects Ecosystem Functioning." *Journal of Ecology* 107: 2660–72.

Luo, Y., M. Zhou, S. Jin, Q. Wang, and D. Yan. 2023. "Changes in Phylogenetic Structure and Species Composition of Woody Plant Communities across an Elevational Gradient in the Southern Taihang Mountains, China." *Global Ecology and Conservation* 42: e02412.

Ma, C., S. peng Li, Z. Pu, J. Tan, M. Liu, J. Zhou, H. Li, and L. Jiang. 2016. "Different Effects of Invader–Native Phylogenetic Relatedness on Invasion Success and Impact: A Meta-Analysis of Darwin's Naturalization Hypothesis." *Proceedings of the Royal Society B: Biological Sciences* 283: 20160663.

Mack, R. N. 2003. "Phylogenetic Constraint, Absent Life Forms, and Preadapted Alien Plants: A Prescription for Biological Invasions." *International Journal of Plant Sciences* 164: 185–196.

Manish, K., M. K. Pandit, Y. Telwala, D. C. Nautiyal, L. P. Koh, and S. Tiwari. 2017. "Elevational Plant Species Richness Patterns and Their Drivers across Non-Endemics, Endemics and Growth Forms in the Eastern Himalaya." *Journal of Plant Research* 130: 829–844.

McCain, C. M., and J. Grytnes. 2010. "Elevational Gradients in Species Richness." In *Encyclopedia of Life Sciences (ELS)*. Chichester: John Wiley & Sons, Ltd.

McFadden, I. R., B. Sandel, C. Tsirogiannis, N. Morueta-Holme, J. C. Svenning, B. J. Enquist, and N. J. B. Kraft. 2019. "Temperature Shapes Opposing Latitudinal Gradients of Plant Taxonomic and Phylogenetic β Diversity." *Ecology Letters* 22: 1126–35.

Miller, E. T., D. R. Farine, and C. H. Trisos. 2017. "Phylogenetic Community Structure Metrics and Null Models: A Review with New Methods and Software." *Ecography* 40: 461–477.

Miller, E. T., A. E. Zanne, and R. E. Ricklefs. 2013. "Niche Conservatism Constraints Australian Honeyeater Assemblages in Stressful Environments." *Ecology Letters* 16: 1186–94.

Olsen, S. R., C. V. Cole, F. S. Watanabe, and L. A. Dean. 1954. *Estimation of Available Phosphorus in Soils by Extraction with Sodium Bicarbonate*. Washington DC: US Department of Agriculture. Circular 939. 19 p.

Omer, A., T. Fristoe, Q. Yang, M. Razanajatovo, P. Weigelt, H. Kreft, W. Dawson, et al. 2022. "The Role of Phylogenetic Relatedness on Alien Plant Success Depends on the Stage of Invasion." *Nature Plants* 8: 906–914.

Paini, D. R., A. W. Sheppard, D. C. Cook, P. J. De Barro, S. P. Worner, and M. B. Thomas. 2016. "Global Threat to Agriculture from Invasive Species." *Proceedings of the National Academy of Sciences of the United States of America* 113: 7575–79.

Park, D. S., X. Feng, B. S. Maitner, K. C. Ernst, and B. J. Enquist. 2020. "Darwin's Naturalization Conundrum Can Be Explained by Spatial Scale." *Proceedings of the National Academy of Sciences of the United States of America* 117: 10904–10.

Park, D. S., C. G. Willis, Z. Xi, J. T. Kartesz, C. C. Davis, and S. Worthington. 2020. "Machine Learning Predicts Large Scale Declines in Native Plant Phylogenetic Diversity." *New Phytologist* 227: 1544–56.

Pauchard, A., C. Kueffer, H. Dietz, C. C. Daehler, J. Alexander, P. J. Edwards, J. R. Arévalo, et al. 2009. "Ain't No Mountain High Enough: Plant Invasions Reaching New Elevations." *Frontiers in Ecology and the Environment* 7: 479–486.

Peters, M. K., A. Hemp, T. Appelhans, C. Behler, A. Classen, F. Detsch, A. Ensslin, et al. 2016. "Predictors of Elevational Biodiversity Gradients Change from Single Taxa to the Multi-Taxa Community Level." *Nature Communications* 7: 13736.

Pinto-Ledezma, J. N., F. Villalobos, P. B. Reich, J. A. Catford, D. J. Larkin, and J. Cavender-Bares. 2020. "Testing Darwin's Naturalization Conundrum Based on Taxonomic, Phylogenetic, and Functional Dimensions of Vascular Plants." *Ecological Monographs* 90: e01420.

POWO. 2023. *Plants of the World Online*. Kew: Facilitated by the Royal Botanic Gardens. http://www.plantsoftheworldonline.org

Pyšek, P., P. E. Hulme, D. Simberloff, S. Bacher, T. M. Blackburn, J. T. Carlton, W. Dawson, et al. 2020. "Scientists' Warning on Invasive Alien Species." *Biological Reviews of the Cambridge Philosophical Society* 95: 1511–34.

R Core Team. 2023. *R: A Language and Environment for Statistical Computing*. Vienna: R Foundation for Statistical Computing.

Rahbek, C. 1995. "The Elevational Gradient of Species Richness: A Uniform Pattern?" *Ecography* 18: 200–205.

Rahbek, C. 2005. "The Role of Spatial Scale and the Perception of Large-Scale Species-Richness Patterns." *Ecology Letters* 8: 224–239.

Rashid, I., Z. Reshi, R. R. Allaie, and B. A. Wafai. 2007. "Germination Ecology of Invasive Alien *Anthemis cotula* Helps It Synchronise Its Successful Recruitment with Favourable Habitat Conditions." *Annals of Applied Biology* 150: 361–69.

Rashid, I., and Z. A. Reshi. 2012. "Allelopathic Interaction of an Alien Invasive Specie *Anthemis cotula* on Its Neighbours *Conyza canadensis* and *Galinsoga parviflora*." *Allelopathy Journal* 29: 77–92.

Rejmánek, M. 1996. "A Theory of Seed Plant Invasiveness: The First Sketch." *Biological Conservation* 78: 171–181.

Reshi, Z. A., M. A. Shah, I. Rashid, and N. Rasool. 2012. "*Anthemis cotula* L.: A Highly Invasive Species in the Kashmir Himalaya, India." In *Invasive Alien Plants: An Ecological Appraisal for the Indian Subcontinent*, edited by J. R. Bhatt, J. S. Singh, R. S. Tripathi, S. P. Singh, and R. K. Kohli, 108–125. Wallingford: CABI.

Ricciardi, A., and M. Mottiar. 2006. "Does Darwin's Naturalization Hypothesis Explain Fish Invasions?" *Biological Invasions* 8: 1403–7.

Richardson, D. M., and P. Pyšek. 2012. "Naturalization of Introduced Plants: Ecological Drivers of Biogeographical Patterns." *New Phytologist* 196: 383–396.

Rodgers, W. A., and S. H. Panwar. 1988. *Biogeographical Classification of India*. Dehradun: New Forest.

Schaefer, H., O. J. Hardy, L. Silva, T. G. Barraclough, and V. Savolainen. 2011. "Testing Darwin's Naturalization Hypothesis in the Azores." *Ecology Letters* 14: 389–396.

Seebens, H., T. M. Blackburn, E. E. Dyer, P. Genovesi, P. E. Hulme, J. M. Jeschke, S. Pagad, et al. 2017. "No Saturation in the Accumulation of Alien Species Worldwide." *Nature Communications* 8: 1–9.

Seipel, T., C. Kueffer, L. J. Rew, C. C. Daehler, A. Pauchard, B. J. Naylor, J. M. Alexander, et al. 2011. "Processes at Multiple Scales Affect Richness and Similarity of Non-Native Plant Species in Mountains Around the World." *Global Ecology and Biogeography* 21(2): 236–246.

Shah, M. A., and Z. Reshi. 2007. "Invasion by Alien *Anthemis cotula* L. in a Biodiversity Hotspot: Release from Native Foes or Relief from Alien Friends?" *Current Science* 92: 21–22.

Shah, M. A., Z. A. Reshi, and I. Rashid. 2012. "Synergistic Effect of Herbivory and Mycorrhizal Interactions on Plant Invasiveness." *African Journal of Microbiology Research* 6: 4107–12.

Shooner, S., T. J. Davies, P. Saikia, J. Deka, S. Bharali, O. P. Tripathi, L. Singha, M. Latif Khan, and S. Dayanandan. 2018. "Phylogenetic Diversity Patterns in Himalayan Forests Reveal Evidence for Environmental Filtering of Distinct Lineages." *Ecosphere* 9(5): e02157.

Smith, S. A., and J. W. Brown. 2018. "Constructing a Broadly Inclusive Seed Plant Phylogeny." *American Journal of Botany* 105: 302–314.

Soti, P. G., M. Purcell, and K. Jayachandran. 2020. "Soil Biotic and Abiotic Conditions Negate Invasive Species Performance in Native Habitat." *Ecological Processes* 9: 1–9.

Stachowicz, J. J. 2001. "Mutualism, Facilitation, and the Structure of Ecological Communities: Positive Interactions Play a Critical, but Underappreciated, Role in Ecological Communities by Reducing Physical or Biotic Stresses in

Existing Habitats and by Creating New Habitats on Which Many Species Depend." *BioScience* 51(3): 235–246.

Stohlgren, T. J., D. Binkley, G. W. Chong, M. A. Kalkhan, L. D. Schell, K. A. Bull, Y. Otsuki, G. Newman, M. Bashkin, and Y. Son. 1999. "Exotic Plant Species Invade hot Spots of Native Plant Diversity." *Ecological Monographs* 69: 25–46.

Strauss, S. Y., C. O. Webb, and N. Salamin. 2006. "Exotic Taxa less Related to Native Species Are More Invasive." *Proceedings of the National Academy of Sciences of the United States of America* 103(15): 5841–45.

Sun, L., J. Luo, L. Qian, T. Deng, and H. Sun. 2020. "The Relationship between Elevation and Seed-Plant Species Richness in the Mt. Namjagbarwa Region (Eastern Himalayas) and Its Underlying Determinants." *Global Ecology and Conservation* 23: e01053.

Taschler, D., and G. Neuner. 2004. "Summer Frost Resistance and Freezing Patterns Measured In Situ in Leaves of Major Alpine Plant Growth Forms in Relation to Their Upper Distribution Boundary." *Plant, Cell & Environment* 27: 737–746.

Thuiller, W., L. Gallien, I. Boulangeat, F. de Bello, T. Münkemüller, C. Roquet, and S. Lavergne. 2010. "Resolving Darwin's Naturalization Conundrum: A Quest for Evidence." *Diversity and Distributions* 16(3): 461–475.

Trotta, L. B., Z. A. Siders, E. B. Sessa, and B. Baiser. 2021. "The Role of Phylogenetic Scale in Darwin's Naturalization Conundrum in the Critically Imperilled Pine Rockland Ecosystem." *Diversity and Distributions* 27: 618–631.

Turbelin, A. J., B. D. Malamud, and R. A. Francis. 2017. "Mapping the Global State of Invasive Alien Species: Patterns of Invasion and Policy Responses." *Global Ecology and Biogeography* 26: 78–92.

Walkley, A. J., and I. A. Black. 1934. "Estimation of Soil Organic Carbon by the Chromic Acid Titration Method." *Soil Science* 37: 29–38.

Walsh, J. R., S. R. Carpenter, and M. J. Van Der Zanden. 2016. "Invasive Species Triggers a Massive Loss of Ecosystem Services through a Trophic Cascade." *Proceedings of the National Academy of Sciences of the United States of America* 113: 4081–85.

Wang, J., S. P. Li, Y. Ge, X. Y. Wang, S. Gao, T. Chen, and F. H. Yu. 2023. "Darwin's Naturalization Conundrum Reconciled by Changes of Species Interactions." *Ecology* 104: e3850.

Williams, E. W., R. S. Barak, M. Kramer, A. L. Hipp, and D. J. Larkin. 2018. "In Tallgrass Prairie Restorations, Relatedness Influences Neighborhood-Scale Plant Invasion while Resource Availability Influences Site-Scale Invasion." *Basic and Applied Ecology* 33: 37–48.

Woodward, F. I. 1990. "The Impact of Low Temperatures in Controlling the Geographical Distribution of Plants." *Philosophical Transactions of the Royal Society of London. B, Biological Sciences* 326: 585–593.

Woodward, F. I. 1997. "Life at the Edge: A 14-Year Study of a *Verbena officinalis* Population's Interactions with Climate." *Journal of Ecology* 85: 899–906.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Afshana, Jesús N. Pinto-Ledezma, and Zafar A. Reshi. 2024. "Phylogenetic Relatedness of Plant Species Co-Occurring with an Invasive Alien Plant Species Varies with Elevation." *Ecosphere* 15(9): e4966. https://doi.org/10.1002/ecs2.4966