

RESEARCH ARTICLE

The impact of species phylogenetic relatedness on invasion varies distinctly along resource versus non-resource environmental gradients

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Handling Editor: Martin Nuñez**Abstract**

1. Understanding why some, but not other, plant communities are vulnerable to alien invasive species is essential for predicting and managing biological invasions. Darwin proposed two seemingly contradictory hypotheses on how native-invader relatedness influences invasion success, emphasizing, respectively, the importance of environmental filtering and competition between natives and invaders. Despite much recent empirical research on this topic, reconciling these two hypotheses, known as Darwin's naturalization conundrum, remains a challenge.
2. Using plot-level data from natural forests along elevational transects covering strong environmental gradients, we examined whether the invasion of the globally invasive species crofton weed (*Ageratina adenophora*) can be explained by environmental filtering and/or competition from closely related species linked to environmental gradients.
3. Abundant precipitation, warm temperatures, open canopies and postfire environments facilitated *A. adenophora* invasion, whereas resident taxonomic richness suppressed its invasion. Importantly, we found that invader-resident relatedness had a strong negative effect on invader cover under resource scarcity conditions (e.g. low water availability), but not under non-resource environmental stress gradients (e.g. low temperature).
4. *Synthesis and applications.* Our results suggest that the impact of species phylogenetic relatedness on invasion success varies distinctly along resource versus non-resource environmental gradients. These results help to reconcile Darwin's naturalization conundrum, thereby improving the ability to predict the success of

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alien plant invasions in a changing world. Our study stresses the need to consider adjusting forest species composition to strengthen their resistance to invasion, while taking into account resource and non-resource environmental gradients, particularly after wildfires.

KEYWORDS

biotic resistance, environmental gradients, phylogenetic limiting similarity, plant invasion, stress gradient hypothesis, wildfire

1 | INTRODUCTION

Invasive species widely spread beyond their native range under increasing globalization and climate change. Their range expansions bring along severe ecological and economic consequences for the invaded regions (Diagne et al., 2021; Ma et al., 2016; Novoa et al., 2021; Roy et al., 2023). Effective control and mitigation strategies for most invasive species remain limited, as do generalizations regarding how biotic and abiotic variables influence invasion success (Gallien & Carboni, 2017; Park et al., 2020). When arriving in a new habitat, nonnative species need to overcome environmental filtering in order to become established, namely, to encounter suitable abiotic environmental conditions (e.g. temperature, precipitation) that allow the species to survive, as well as to cope with adverse interactions from species in the recipient community (Blackburn et al., 2011). Understanding how these factors act in concert to regulate invasion success is essential for making accurate decisions when managing biological invasions in a changing environment (Fuentes-Lillo et al., 2021; Richardson & Pyšek, 2012).

Nonnative species distributions typically change along environmental gradients involving, for example, changes in temperature (Alexander et al., 2011) and water availability (Wang, Li, et al., 2022). Therefore, abiotic environmental filtering is often thought to be a major mechanism regulating the success of plant invasions. These gradients affect invasion success not only by directly altering the physiological status of the invading species but also indirectly via altering the strength of species interactions (Cadotte & Tucker, 2017; Kraft et al., 2015). For instance, the significance of competitive interactions in modulating nonnative species survival and persistence can shift along environmental gradients, where the importance of competition is often expected to diminish as natural environmental stress increases (Bertness & Callaway, 1994). However, the variation in the role of competition along the environmental gradients may also differ depending on whether gradients are resource-based (e.g. water, light and nutrients) (Davis et al., 2000; Funk & Vitousek, 2007) or non-resource-based (e.g. temperature, salinity) (Maestre et al., 2009). Non-resource stresses, such as cold temperature, may amplify the role of environmental filtering and the importance of mutualistic interactions among species, thereby reducing competition (Bertness & Callaway, 1994; Callaway, 2007). In contrast, in some environments, low water and nutrient availability could strengthen competition because of the scarcity of the limiting

resources that species share (Cortina & Maestre, 2005). Specifically, limited water availability can act as a significant selective pressure, intensifying competition between plant individuals under conditions of soil water scarcity (Soliveres & Maestre, 2014), which may in turn influence invasion success (Cavaleri & Sack, 2010). Furthermore, disturbances, such as wildfire, may reduce resident competition and increase available resources, resulting in changed community susceptibility to invasion (Davis et al., 2000). However, evidence for a shift in the relative significance of biotic resistance to exotic invasion, as well as the role of competitive interactions along different environmental gradients, remains scarce (Adams et al., 2022).

A host of hypotheses have been put forward to predict invasion resistance through competition with the recipient community (Enders et al., 2020). The diversity-invasibility hypothesis, as one of the most widely known hypotheses, posits that highly diverse communities lead to invasion resistance through increased competitive interactions (Elton, 1958; MacArthur et al., 1972). The rationale behind this idea is that higher numbers of species or functional groups would increase the chances of native species to occupy available niches and thus leave fewer open niches to be colonized by non-natives (Levine, 2000; Levine et al., 2004). In contrast, the 'rich get richer' hypothesis suggests that hot spots of diversity are more likely to be invaded and to contain a greater number of invader individuals (El-barougy et al., 2020; Levine, 2000; Levine et al., 2004; Stohlgren et al., 2003). These discrepancies in invader-resident relationships have been linked to scale and methodological differences between observational and experimental approaches (Tomasetto et al., 2019).

Compared to species richness, phylogenetic relatedness between species may be a better proxy for their niche dispersion and overlap, as more closely related species tend to share more similar traits, and thus, niches (El-barougy et al., 2020; Feng et al., 2019; Violle et al., 2011). In fact, Darwin proposed two of the earliest hypotheses on biological invasions, emphasizing the importance of the invader-native evolutionary relationships for determining invasion success (Darwin, 1859; Park et al., 2020). He posed, under what is now known as Darwin's naturalization hypothesis, that invaders more closely related to resident species should face stronger competition from resident communities due to stronger niche overlap (Daehler, 2001), thereby emphasizing the role of competition. He also proposed what is known as the preadaptation hypothesis, which states that successful invaders should be closely related to resident species because they inherit similar adaptations to local environmental conditions,

thereby emphasizing the role of environmental filtering (Cadotte et al., 2018; Ricotta et al., 2009). These seemingly contrasting hypotheses, now termed as Darwin's naturalization conundrum, have been tested by various studies with mixed results (Bennett, 2019; Bezeng et al., 2015; Ma et al., 2016; Ng et al., 2018; Park & Potter, 2013). Recent reviews have suggested that the two opposing hypotheses are not mutually exclusive but rather that successful alien species tend to be more closely related to natives at the larger spatial scale and more distantly related to natives at the local spatial scale (Byers & Noonburg, 2003; Ma et al., 2016). In other words, at large scales environmental filtering selects for invaders that are adapted to the conditions of the new area, but at small spatial scales, the role of competition for limiting resources becomes more important. Even so, results from studies that accounted for scale differences have not been consistent (e.g. Dethier & Hacker, 2005; El-barougy et al., 2020), pointing to the need to consider environmental variables when analysing the role of competitive invasive-native interactions, in particular resource and non-resource gradients.

Montane regions with steep environmental gradients provide invaluable natural laboratories to study the effects of biotic interactions with invasive species along various environmental gradients (Irl et al., 2021; Lembrechts et al., 2018). The Tibetan Plateau and its surrounding mountain ranges have a complex topography and large environmental gradients, and harbour one of the world's richest temperate floras (Ding et al., 2020). Increasing anthropogenic activities and the fast development of the transportation industry over the last 40 years have put the area at risk of biotic expansion (Rashid et al., 2021). The notorious alien invasive plant crofton weed *Ageratina adenophora* (Spreng.) R.M. King & H. Rob., which is native

to Mexico, has invaded more than 30 countries and regions worldwide. The invasion of *A. adenophora* has resulted in native plant displacement, thereby threatening diversity and ecosystem functions, but also causing serious economic losses to the forestry and animal husbandry sectors (Xu et al., 2014). Current evidence suggests that its competitive interactions with natives contribute significantly to its invasion success (Chen et al., 2021); however, it is unclear whether and how this role changes along different environmental gradients. In this study, we chose high mountain regions on the southeastern Tibetan Plateau as a model system since they represent the geographic frontier of *A. adenophora* invasion, and are characterized by steep elevational gradients with complex climates, disturbances (e.g. wildfire) and various invasion intensities. This model system facilitated disentangling the effects of various abiotic drivers (i.e. temperature, light, precipitation and disturbance) and covarying biotic resistance on plant invasion along environmental gradients.

In this contribution, we aim to test how invasion resistance to the globally invasive *A. adenophora* would vary with environmental conditions in the montane regions. As we expect that resource and non-resource environmental gradients may have different effects on interspecific competition, we further hypothesize that the pattern of biotic resistance shifts would be distinct along a gradient of resource availability such as precipitation versus non-resource environmental conditions such as temperature (Figure 1). To test these hypotheses, we examined the relationship between invader abundance and invader-resident evolutionary relatedness from high mountains with steep continuous environmental gradients. We also assessed whether the frequent wildfires on the southeastern Tibetan Plateau would affect the role of invader-resident relatedness for *A. adenophora* invasions.

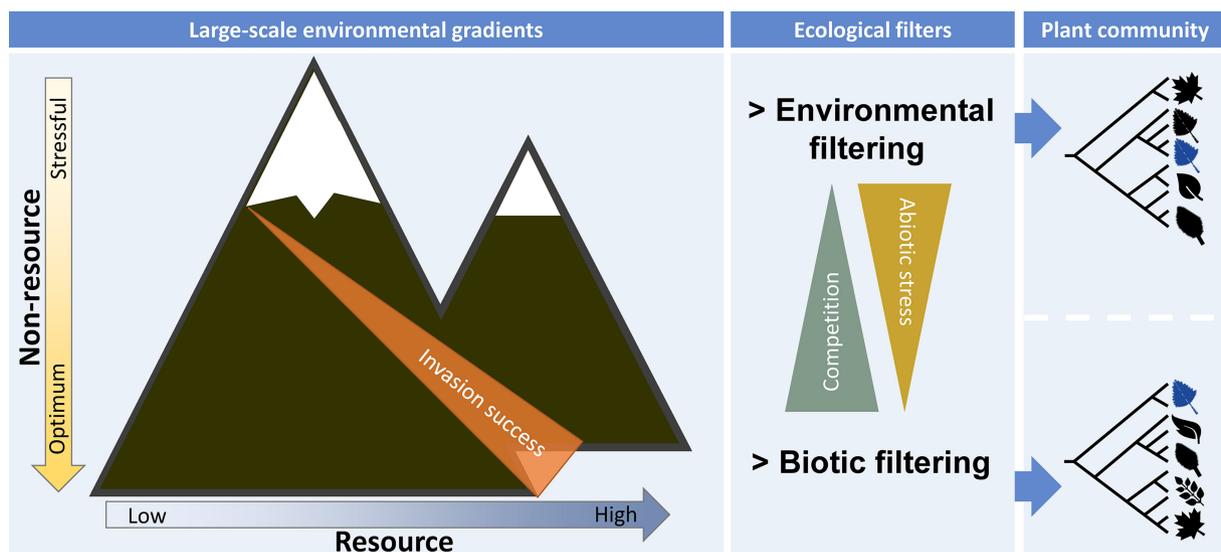


FIGURE 1 Conceptual representation of our hypotheses. Invasion success is conditioned by the effects of various distinct non-resource (e.g. temperature) and resource gradients (e.g. precipitation). We hypothesize that these will distinctly impact how ecological filters (i.e. environmental abiotic and through biotic interactions) modulate the strength of competitive interactions and, ultimately, biotic resistance to *Ageratina adenophora*. Under stronger environmental abiotic filters, we expect to find patterns consistent with the preadaptation hypothesis (i.e. natives and invaders are closely related). In contrast, under strong competitive environments (i.e. resource scarcity), we expect to find patterns in line with Darwin's naturalization hypothesis (i.e. native and invaders are distantly related). Invasive species' leaves are represented in blue, natives in black.

2 | MATERIALS AND METHODS

2.1 | Study site and target species

The study site was located in the southeastern portion of the Tibetan Plateau, adjacent to the Yunnan-Guizhou Plateau and Sichuan Basin (Figure 2). We chose the Anning River Valley in the Hengduan Mountains region of southwestern Sichuan, China, as the study region. This mountain system forms a ridged landscape with deep river gorges and tall dividing mountains that run roughly north to south and is thought to be among the most biologically diverse temperate regions (Boufford, 2014). The study region spans approximately 320 km from north to south (100°15'–103°35' E, 26°03'–29°32' N) and ranges from 1015–2441 m a.s.l. The region is characterized by a monsoon climate that connects the South Asian

and East Asian summer monsoons. The summer monsoon season lasts from May to September and contributes more than 80% of the annual total precipitation (Dong et al., 2019). High temperatures in spring and summer lead to increased evapotranspiration, resulting in reduced humidity levels. This decrease in moisture often causes droughts during both seasons (Li, Adu, et al., 2022), which in turn leads to increased risks of wildfires in mountainous areas during the spring. The Anning River, as a tributary of the Yalong River, is close to multiple highways in the deep and wide valley and forms one of the most prominent south–north invasion channels to the Tibetan Plateau for *A. adenophora*. This species first invaded the southern part of the Hengduan Mountains in Yunnan Province in the 1940s from Myanmar. Since then, it has spread rapidly from south to north along the valleys, and its average rate of expansion since 1990 is estimated to be 13.2 km year⁻¹ (Wang & Wang, 2006). Due to its high

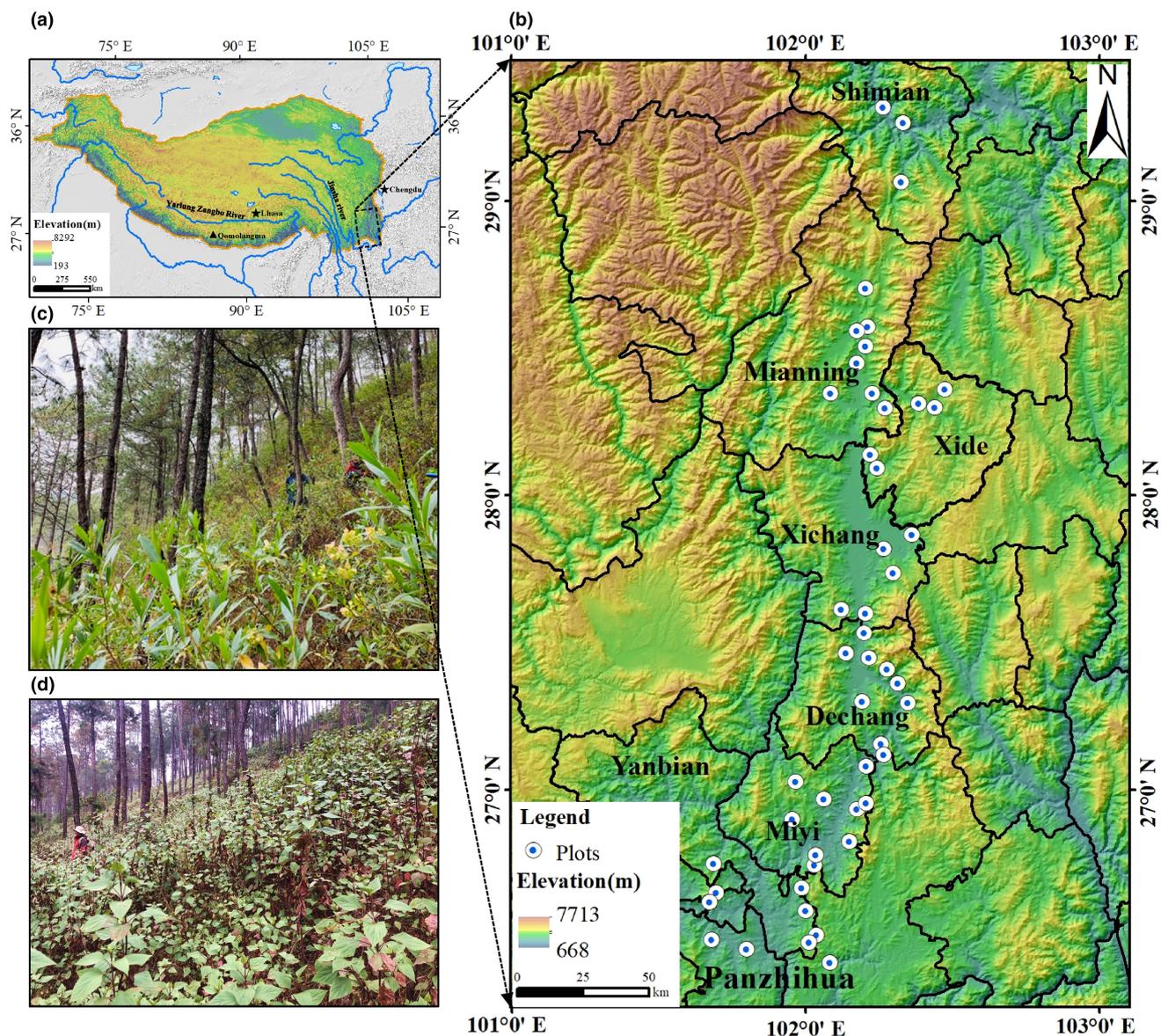


FIGURE 2 Location (a) and topographic map (b) of the study sites on the southeastern Tibetan Plateau, China, and the community before (c) and after (d) invasion by *Ageratina adenophora*.

seed production and ability to disperse via wind, water, soil movement and by clinging to animals and people, *A. adenophora* can grow in forest gaps, grasslands and ditch margins and on barren slopes, where it can rapidly form monocultural communities.

2.2 | Data collection

A total of 49 plots were preselected in the Anning River Valley region to encompass as many environmental conditions as possible using a geographical information system (GIS) in the laboratory and then located in the field with a portable GPS. No permission is needed to access the field sites. In 2019 and 2020, we established 20-m × 20-m plots in the study area that covered various invasion densities of *A. adenophora* (Figure 2). Five 5-m × 5-m quadrats were arranged using the five-point sampling method, with one 1-m × 1-m herb quadrat randomly located in each shrub sample. In each plot, all trees (including gymnosperms) with a diameter at breast height (DBH) ≥ 1 cm were measured and identified to species. For all the shrubs and herbs (including ferns) rooted in the quadrats, the height, cover and abundance (number of individuals) of each species, along with the slope aspect and gradient of the plots, were measured and recorded. We imaged the canopy using a lightweight visual camera (Sony Alpha 6000, Sony, Japan) to measure canopy closure by leaf area index (LAI) using the WinsCanopy software following Gough et al. (2020).

Mean annual temperature and mean annual precipitation at a 30-s (ca. 1 km) spatial resolution were obtained from the WorldClim database (www.worldclim.org). The relative radiation index was calculated to represent the intensity of sunshine on a forest stand based on aspect, slope gradient and latitude degrees following Paudel and Vetaas (2014). The study sites are located in the main region where forest fires occur in southwestern China. To evaluate the effect of wildfire on invader cover, we classified the plots into four severity degrees according to the heights of the fire scars (flame height) on the tree bark, and also considered the burnt ground area (fire duration) and the time since the last fire event or fire frequency following Clark and Miller (2001) and Wright et al. (2015): (I) not burned by fire (no fire traces); (II) light fire with scar heights < 1 m (burnt area < 1 ha and time of the last fire > 5 years); (III) moderate fire with scar heights of 1–2 m (burnt area < 5 ha and time of the last fire 2–4 years); (IV) severe fire with fire heights > 2 m (burnt area > 5 ha and time of the last fire < 2 years or annually, see online resource Table S1). Moreover, invader cover could also be expected to relate to distance from the site of first arrival in the region. However, this distance was not included in the model due to the strong collinearity between the south-to-north direction of *Ageratina adenophora* spread in the study area and variations in latitude and precipitation.

2.3 | Phylogenetic analyses

We used the phylogenetic structure of the resident community and invader-resident phylogenetic relatedness to assess the potential

competition within the resident community and between the invader and resident individuals. To this end, a phylogenetic tree was established using the R package U.PhyloMaker based on the megatree backbone phylogeny (<https://github.com/megatrees/>, Jin & Qian, 2022). The phylogenetic position of the species absent from the megaphylogeny (4 out of 130 in total) was inferred using congeneric representatives that were available (Park et al., 2020). We then quantified the community phylogenetic structure using the mean pairwise phylogenetic distance (α MPD) and the mean nearest-taxon distance (α MNTD) of the resident community for the shrub and the herb layer (Webb et al., 2002). To examine the effect of the phylogenetic relatedness between the invader and the recipient species, we calculated the mean observed phylogenetic similarity between the invader and all other individuals within the community (β MPD, phylogenetic distance × -1, with the largest value indicating the closest phylogenetic relatedness) (Li, Jia, et al., 2022; Metz et al., 2010). To correct for variation in species richness among neighbourhoods, the standard effect sizes (SES) of the mean pairwise phylogenetic distance, the mean nearest-taxon distance of the community and the mean phylogenetic similarity between the invader and the community (i.e. SES. α MPD, SES. α MNTD and SES. β MPD, respectively) were calculated as $SES = \frac{X_{obs} - \text{mean}(X_{null})}{sd(X_{null})}$, where X_{obs} is the observed value of α MPD, α MNTD and β MPD, and X_{null} are the 1000 values calculated based on null models of assemblages of species randomly drawn from the regional species pool (i.e. all the species found in the 49 plots). We did not calculate the MPD of the tree layer and excluded the fern species (< 4 in the 49 plots) from the herb layer. This is because including gymnosperm trees (mainly composed of *Pinus yunnanensis*) and fern species often results in a large effect on the average relatedness values in these communities. Further, after excluding the gymnosperms that dominate the canopy in the study region, focusing on just the remaining sparse canopy plants with < 10% cover may induce statistical bias.

2.4 | Statistical analyses

We examined the effects of environmental and biotic factors on *A. adenophora* invasion using generalized linear models (GLMs). The cover of *A. adenophora* (response variable) was used to represent invader abundance. As there were 18 variables in total (Table S2), we performed a Pearson correlation test (bivariate correlation > 0.7 for pre-judgement) and a principal component analysis (PCA) extracting 10 components that together explained more than 90% of the variance within the datasets. The abiotic factors included mean annual temperature, mean annual precipitation, relative radiation index and wildfire severity. The biotic factors included canopy closure; species richness of the tree, shrub and herb layers; standardized mean pairwise phylogenetic distance of the herb and shrub community; and standardized mean phylogenetic similarity between the invader and the herb community. To better understand changes in the effects of phylogenetic relatedness on invader abundance over environmental gradients, we further

tested the interaction between significant phylogenetic relatedness and each environmental variable.

Each continuous independent variable was standardized by subtracting from the mean of the variable and dividing by one standard deviation. The optimal model was chosen stepwise backwards using Akaike's information criterion (AIC, following the procedure described in Crawley, 2012), and the significance levels of the factors were derived by likelihood ratio tests. The mean effect sizes were calculated as Fisher's z-transformations of correlation coefficients between relatedness and invader cover. All analyses were conducted using the R 4.0.3 (R Core Team, 2020), with PCA run using the 'psych' package, GLMs run using the 'lme4' package (Bates et al., 2015) and visualization of the effect plots (including interaction terms) using the 'sjPlot' (Lüdtke, 2021) and 'ggplot2' (Wickham, 2016) packages for R.

To further examine the direct and indirect pathways via which phylogenetic invader-resident relatedness affects invasion along resource and non-resource environmental gradients, we performed piecewise structural equation modelling (SEM). Prior to SEM, we used PCA to reduce all abiotic components to two dimensions representing resource and non-resource environmental variables (mainly water versus temperature, Table S3). The existing structural equation modelling (SEM) approach lacks the capability to analyse

interaction relationships and direct as well as indirect pathways simultaneously. Consequently, we have devised piecewise SEMs that are founded on distinct ranges of environmental gradients, aiming to elucidate the aforementioned interaction relationships. More precisely, we partitioned the data into three segments along each principal component (PC) axis, then six SEMs were constructed to represent three stress levels of both PCs. We fit the SEMs using a generalized linear model with a binomial error distribution for binomial probability cover data and a linear model for continuous environmental variables. The SEMs were constructed using the package piecewiseSEM (Lefcheck, 2016) in R, and the model adequacy was evaluated using the likelihood ratio test and AIC (Table S4).

3 | RESULTS

3.1 | Abiotic effects on invasion

The GLMs showed that the invasion of *A. adenophora* significantly decreased with mean lower annual temperature (likelihood ratio test, $p < 0.01$, Figures 3a and 4), which is associated with higher elevation and latitude (Figure S1). The invasion of *A. adenophora* was

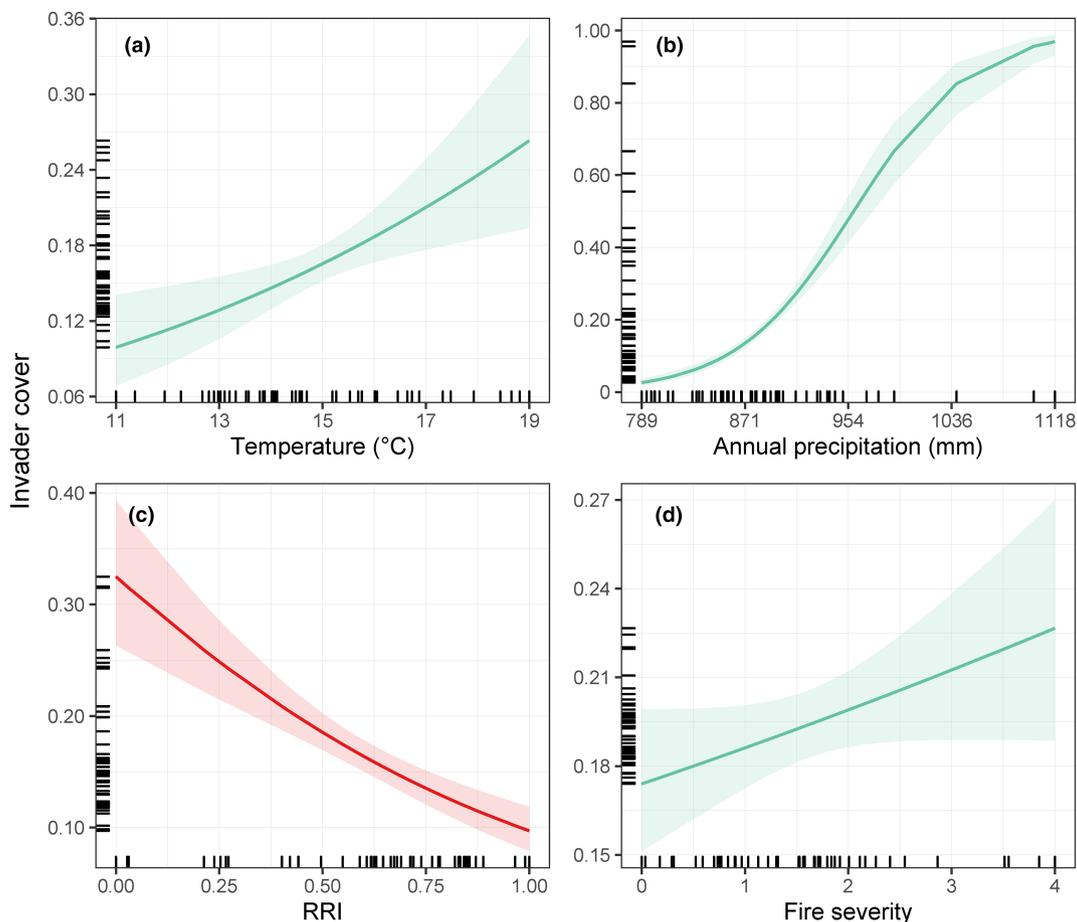


FIGURE 3 Effect plots of the abiotic factors on the patterns of invasion success. The expected invader cover in response to plot-level temperature (a), annual precipitation (b), relative radiation index (RRI) (c) and fire severity (d) are shown. The shaded areas represent the 95% confidence intervals.

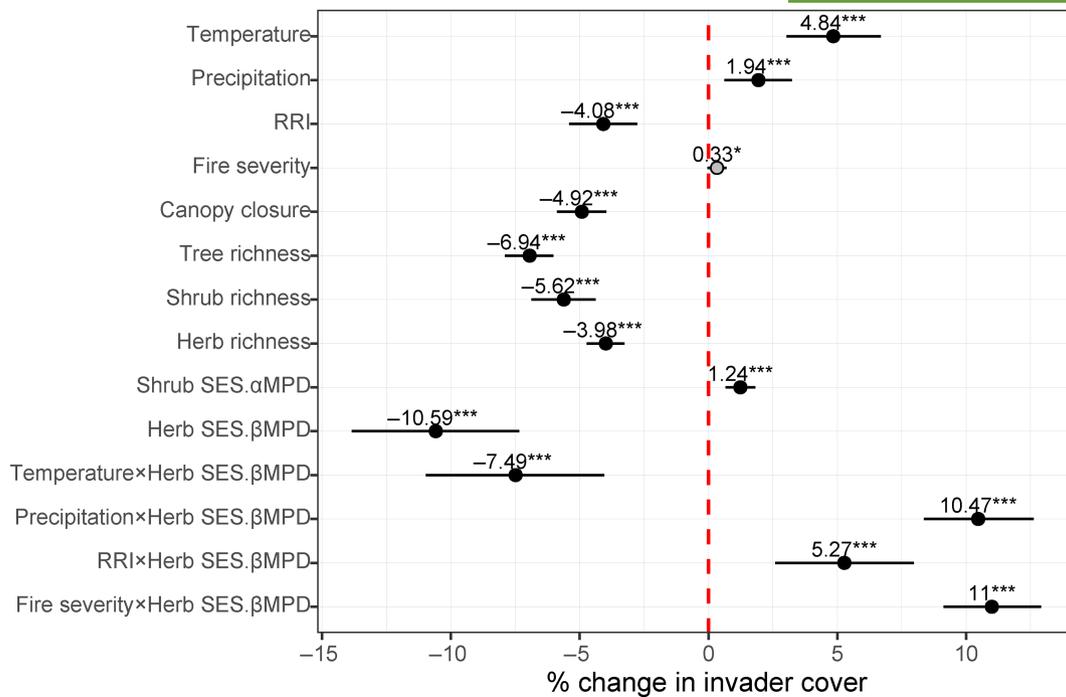


FIGURE 4 The effects of abiotic and biotic factors on invader success and interactions between environmental factors and standardized invader–native phylogenetic relatedness (SES.βMPD) of herbs. The mean effect sizes (\pm bias-corrected 95% bootstrap confidence intervals) of the relationships between the factors and invader cover are shown. The mean effect sizes were calculated as Fisher's z-transformations of correlation coefficients between relatedness and invasion success/impact. Black circles with *** indicate significant effects ($p < 0.05$), and grey circles with * signify marginally significant effects ($0.05 < p < 0.1$).

positively related to annual precipitation ($p < 0.01$, Figures 3b and 4) and negatively related to the relative radiation index ($p < 0.01$, Figure 3c), indicating that wet and shady conditions may contribute to invasion success. Furthermore, the severity of wildfire was marginally ($p = 0.052$) associated with *A. adenophora* invasion, with severe burns tending to favour intense postfire invasion (Figures 3d and 4).

3.2 | Biotic effects on invasion

In contrast to the relative radiation index, canopy closure showed a negative impact on the cover of *A. adenophora* ($p < 0.001$, Figures 4 and 5a), indicating that mature forests with closed canopy are more resistant to being invaded. The model also showed that the invader cover significantly decreased with the species richness of the tree layer ($p < 0.001$) and that of the shrub and herb layers ($p < 0.05$, Figures 4 and 5b–d).

There was a significant positive association between invasion and the standardized mean pairwise phylogenetic distance of the resident shrubs but a significant negative association between invasion and the standardized mean phylogenetic similarity between the invader and native species in the herb layer ($p < 0.001$, Figures 4 and 5e,f). All other phylogenetic variables calculated did not yield significant effects in our models. These results indicate that invasion resistance decreased with the degree of phylogenetic aggregation of resident shrubs but increased with the invader's phylogenetic relatedness to resident herbs.

3.3 | Changes in the phylogenetic effects of herbs on invader cover over environmental gradients

The relationship between invader cover and the standardized mean phylogenetic similarity between the invader and herbs in the community significantly (SES.βMPD; $p < 0.05$) changed along the environmental gradients of temperature, precipitation, relative radiation index and fire severity (Figures 4 and 6). The interactions between temperature and the herb SES.βMPD had a significantly negative effect on *A. adenophora* invasion ($p = 0.012$), with a steeper slope of negative phylogenetic effects in plots with higher temperature than in plots with lower temperatures (Figure 6a). There was a positive interaction between precipitation and the βMPD of herbs ($p = 0.001$, Figure 3), where the negative effects of SES.βMPD occurred mainly under conditions with relatively low (mean – 1 SD) or average amounts of precipitation, but the relationship between SES.βMPD and invasion was mild under conditions with higher amounts (mean + 1 SD) of precipitation (Figure 6b). The interaction between the relative radiation index and herb SES.βMPD on invasion was also significantly positive ($p < 0.001$, Figure 3), whereas the slope of the relationship between invader cover and SES.βMPD flattened with increasing relative radiation index (Figure 6c). Furthermore, in the plots without wildfire, the herb SES.βMPD had a significantly negative effect on *A. adenophora* invasion, while in plots after severe burns, the effect of the herb βMPD was significantly positive (Figure 6d).

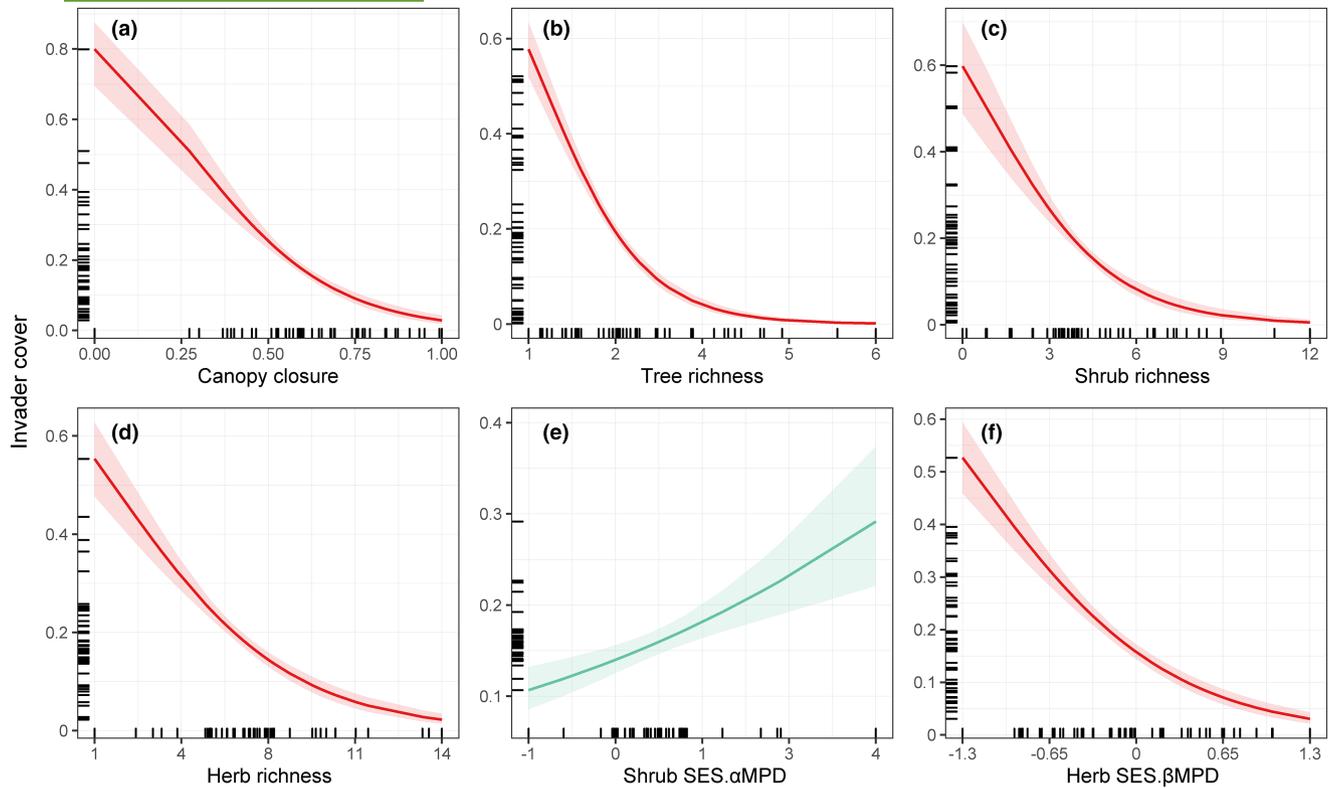


FIGURE 5 Effect plots of biotic factors on the patterns of invader cover. The expected invader cover in response to canopy closure (a), tree richness (b), shrub richness (c), herb richness (d), the standardized mean pairwise phylogenetic distance for shrubs (SES.αMPD) (e) and the standardized phylogenetic relatedness between the invader and resident herbs (SES.βMPD) (f) are shown. The shaded areas represent the 95% confidence intervals.

3.4 | Direct and indirect effects of resource and non-resource environmental variables on invasion

As with the GLM results, results of SEMs (Figure 7 and Table S4) showed that temperature and precipitation had a consistent positive direct effect on invasion in various scenarios (standard estimate 0.006–0.437). The SEMs revealed negative effects of standardized phylogenetic relatedness between the invader and the community on invasion under a variety of conditions (Figure 7b–g) but the negative effects increased along the non-resource environmental gradient from stressful to optimum (standard estimate 0.05 to –0.12, Figure 7a) and decreased along the resource gradient from stressful to abundant (standard estimate –0.151 to –0.05, Figure 7h). Furthermore, the SEMs also detected an increasing negative effect of temperature on standardized phylogenetic relatedness between the invader and the community as the temperature increased (Figure 7b–d, standard estimate 0.471 to –0.343), indicating distant invader-resident phylogenetic relatedness under warmer conditions but close invader-resident relatedness under colder stressful conditions. Moreover, the effect of temperature on standardized phylogenetic relatedness between the invader and the community changed along the precipitation gradient, shifting from a negative to a positive effect as precipitation increased (Figure 7e–g, standard estimate –0.371 to 0.736),

indicating a decrease in invader-resident phylogenetic relatedness with warmer temperatures under drought conditions but an increase under wetter conditions.

4 | DISCUSSION

Consistent with our hypothesis, we found the invader cover of *A. adenophora* varied with environmental gradients in the montane regions. Specifically, mean annual temperature and precipitation had clear positive effects on *A. adenophora* cover (Figures 3 and 4), indicating greater invader cover in warmer and wetter plots. Given that warmer temperatures were associated with lower elevations and latitudes, the positive effects of temperature pointed to a declining trend of *A. adenophora* invasion with increasing elevation and latitude. This trend is consistent with previous work showing that the abundance and richness of nonnative generalist species tend to decrease with elevation (Pauchard et al., 2009) and that these patterns are modulated by decreasing precipitation and temperature along the elevation gradient (Alexander et al., 2011; Daehler, 2005; Irl et al., 2021; Seipel et al., 2016; Tecco et al., 2015). However, a number of studies have found that alien plants follow an unimodal pattern along altitudinal gradients, with more species and higher abundances at mid-altitude locations (Arévalo et al., 2005; Jakobs et al., 2010; Tecco et al., 2015). For instance, Tecco et al. (2015)

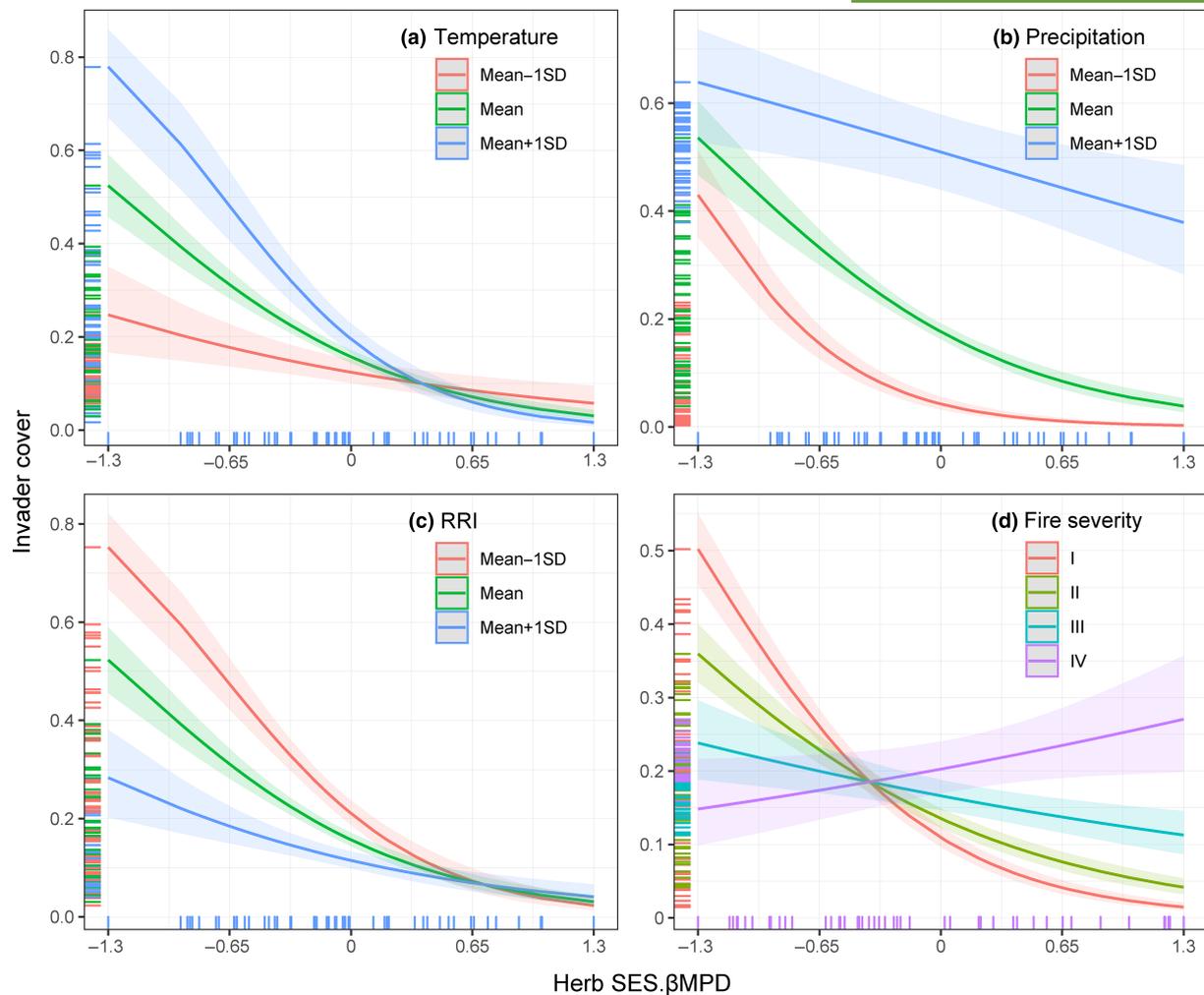


FIGURE 6 Changes in the relationship between invader cover and standardized phylogenetic relatedness (SES.βMPD) between the invader and resident herbs among different abiotic environmental gradients (plot-level mean, mean + 1 SD and mean – 1 SD of the annual temperature (a), precipitation (b), relative radiation index (c) and different fire severity levels (d)). The shaded areas represent the 95% confidence intervals.

found that the intersection between opposite soil temperature and moisture gradients at mid-elevation may actually result in more suitable temperatures and humid conditions in the dry season for the invasions of woody species in central Argentina. While the preference of *A. adenophora* for warmer temperatures may come across as good news for the prevention of this species in cold plateau regions, future climate warming (Guan et al., 2015; Mandel & Lipovetsky, 2021) is likely to facilitate the upward influx of *A. adenophora* onto the Tibetan Plateau.

Results showed a strong negative correlation between the relative radiation index and the invasion of *A. adenophora*, which points to a preference of the species for shady slopes. This pattern has also been described before for *A. adenophora* stating that the species behaves as an aggressive competitor, particularly under shaded conditions (Heystek et al., 2011). However, we also found a negative relationship between invader cover and canopy closure, consistent with previous findings that *A. adenophora* establishment and proliferation in forest interiors are facilitated by snow damage-induced

canopy gaps (Song et al., 2017). These apparently opposite responses of *A. adenophora* to light availability could be attributed to covarying soil moisture, nutrition and variations in light preferences among life stages. Experiments on germination and seedling life stages have documented that *A. adenophora* seeds do not germinate in dense shade (Auld & Martin, 1975; Song et al., 2017) and that seedling performance decreases at low irradiance levels. Further research is required to disentangle the effects of these variables on modulating this species' light preferences at different life stages. Furthermore, though not statistically significant, we found a marginally positive effect of wildfire on invader cover, which suggests severe wildfires aiding the invasion of *A. adenophora*. This finding is in line with the well-established hypothesis in invasion science posing that disturbance events alter local resource availability by decreasing canopy closure, killing native competitors or directly increasing resource supplies, thus promoting the success of invaders (Davis et al., 2000; Stevens & Latimer, 2015; Theoharides & Dukes, 2007). Ensuring that wildfires do not become too severe should, therefore, become a

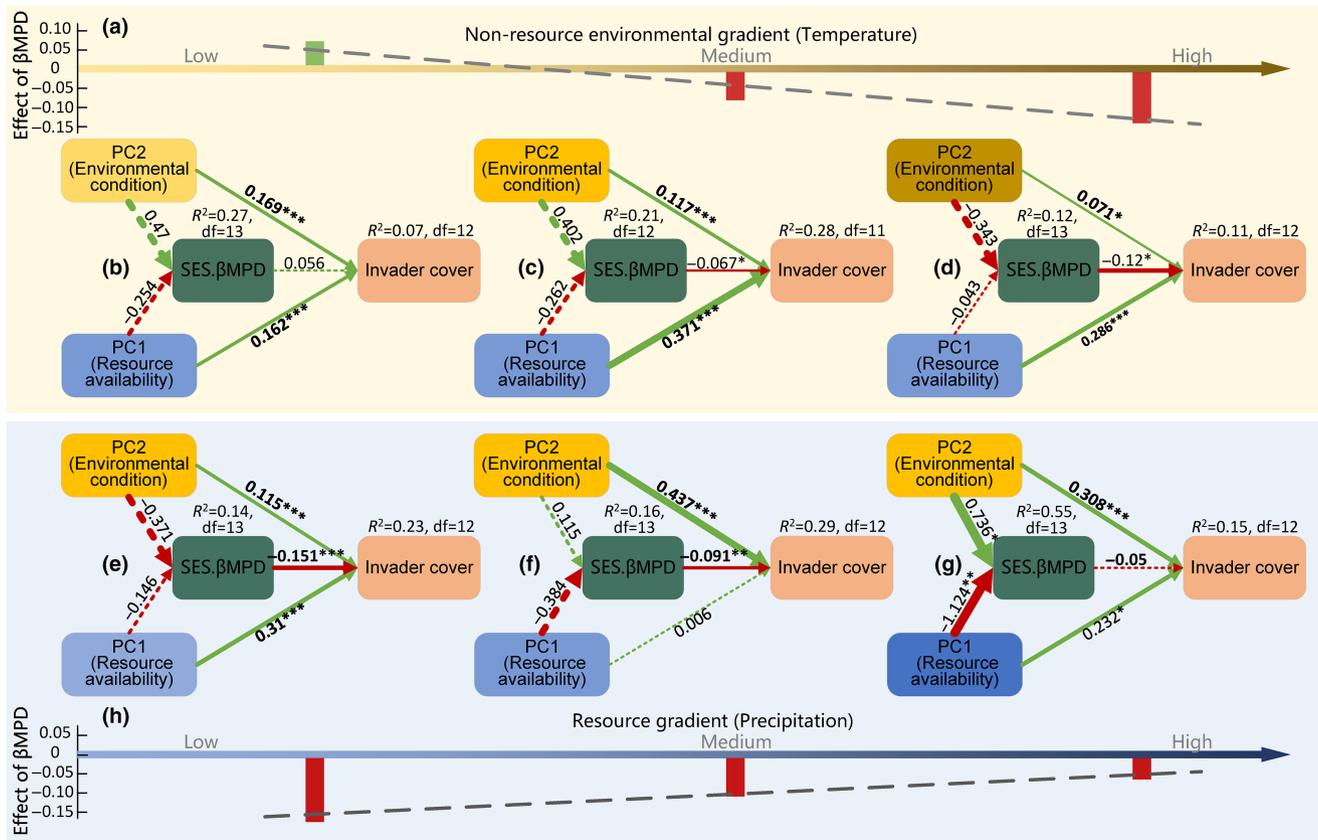


FIGURE 7 The results of structural equation modelling for the direct effects of PC1 (resource availability gradient, Precipitation) and PC2 (non-resource environmental gradient, Temperature) on invader cover, as well as their indirect effects via β MPD, under various scenarios of low (b), medium (c) and high (d) temperature and low (e), medium (f) and high (g) resource availability. The bars on the two-dimensional coordinates at the top (a) and bottom (h) represent the effects of β MPD on invader cover under a variety of non-resource environmental (b–d) and resource (e–g) conditions, respectively. Green and red arrows indicate positive and negative pathways and solid and broken lines indicate significant ($*p < 0.05$, $**p < 0.01$, $***p < 0.001$) and nonsignificant ($p \geq 0.05$) pathways, respectively. Numbers along the arrows, as well as the width of the arrows, are proportional to standardized path coefficients.

priority in managing plant invasions, although they are natural components of our study forests and many other ecosystems.

We found support for biotic resistance resulting from high diversity, aggregated community phylogenetic distances for the shrub layer and invader-resident community relatedness for the herb layer. In line with the idea that rich native communities would be more resistant to plant invasions, we found that *A. adenophora* invasion decreased as native tree, shrub and herb species richness increased (Davies et al., 2005; Tortorelli et al., 2020). This supports previous results for *A. adenophora* in the region (Chen et al., 2021) and a previous meta-analysis indicating that, as posed by the diversity-invasibility hypothesis (Levine & D'Antonio, 1999), rich communities have less resources available for the establishment and successful persistence of this species (Levine et al., 2004). The positive relationship between invader cover and community phylogenetic aggregation of the community's shrub layer suggested communities that are structured through environmental filtering and less through interspecific competition are more susceptible to invasion. Furthermore, when analysing phylogenetic relatedness between the invader and the native community as a proxy for competition intensity, our results supported the preadaptation

hypothesis for the herb layer. Namely, invader cover decreased as the herb communities became more phylogenetically dissimilar to *A. adenophora*. As in a previous study, the scientists did not find the same trend for the shrub layer in the community (Chen et al., 2021), which means the effect of direct competition is stronger within a given layer (e.g. the herb layer) with a greater number of close relatives (from the same family of Asteraceae) or similar functional type (e.g. herbaceous plants) in a community. Overall our results support the idea that competition for limited resources, resulting either from high species diversity or relatedness, is a predictor of invasion resistance. Therefore, when managing invasive species in forested alpine environments, we suggest a strong emphasis on ensuring a rich cover of shrub and herb species.

When considering the influence of environmental variables as modulators of invasion resistance, we found that the correlation between *A. adenophora* cover and phylogenetic relatedness between the invader and herbs in the community changed with different environmental gradients (Figures 6 and 7). The negative relationship tended to be intensified in plots with higher temperatures, less precipitation, less open canopy and no wildfires, which means that competition is more

important in warmer, low-moisture, low-light and high-biomass sites. In particular, high-intensity wildfires will leave space open for invasive species colonization, thus reducing the importance of competitive effects by the resident community. Traditional ecological theory also predicts weaker competition in less productive communities (Gallien & Carboni, 2017), supporting our findings that invader-native competition increases with the productivity gradient. However, our results are not entirely consistent with the idea that as stress increases, competitive interactions become less predominant (Callaway & Walker, 1997). Specifically, we found that less precipitation and shadier conditions tended to have more negative associations between invader cover and invader-native relatedness, while conditions with low-temperature conditions tended to have fewer negative associations. This can be explained as a result of resource environmental stress translating into strong competition for water and light, while less stressful non-resource environmental conditions (i.e. warmer temperature) could promote growth and increase competition for resources such as water and light (in shady areas). In contrast in alpine or subalpine ecosystems, low temperatures tend to promote environmental filtering, thereby minimizing the negative interaction of competition (Adams et al., 2022) and resulting in a weaker phylogenetic limiting similarity. This differentiation between resource- and non-resource-related factors may provide a possible explanation for the contrasting results in testing the prediction that the competition decreases under increasing environmental stress. Specifically, research conducted under drought stress conditions found no evidence of reduced competition (Callaway, 2007; Maestre & Cortina, 2004; Tielbörger & Kadmon, 2000), while studies in alpine and other environments broadly demonstrated reduced competition (Bertness & Ewanchuk, 2002; Callaway, 1998). Overall, our study stresses the need to consider 'resource' or 'non-resource' gradients when attempting to disentangle how biotic processes drive plant invasion success along environmental gradients, in order to better understand the contrasting biological processes on a given environmental gradient.

Our study provides novel insight into the mechanisms governing the invasion success of the worldwide invasive species *A. adenophora* along different environmental gradients. Nevertheless, some limitations of our study should be noted. First, our research focused on one single plant as a model invasive species, and it remains to be seen how well our findings can be applied to other species. Future studies should aim to consider multiple invasive species simultaneously to gain a more general understanding of mechanisms regulating biological invasions. Second, our model did not explicitly consider the time of the invader's arrival due to the correlation between the direction of *A. adenophora* expansion and the precipitation gradient in our study area. Assessing the effect of invader arrival time should be considered in future studies to improve invasion prediction. Furthermore, the resource gradient is often not completely independent of the non-resource gradient in shaping nonnative species invasion. While we were able to statistically separate the effects of the two gradients in our study, experiments that manipulate both gradient types in a single study are needed in the future to provide a more rigorous evaluation of our findings.

5 | CONCLUSIONS

Our findings suggest distinct ecological mechanisms by which phylogenetic invader-resident relatedness influenced invasion depending on the different types of environmental gradients. We found that the impact of invader-resident relatedness on *A. adenophora* invasion decreased along the stress gradients of non-resource environmental factors (e.g. low temperature, indicative of environmental filtering), but increased along the stress gradients of resource factors (e.g. low water availability, indicative of strong competitive interactions). These results provide a possible solution to Darwin's naturalization conundrum.

Our results also suggest that adjusting the species composition of forests in order to strengthen their resistance to invasion (as proposed by Hess et al., 2019) should be considered as a possible strategy for ecological management, and that this will need to account for resource and non-resource environmental gradients. In addition to the widely recognized increase in propagule pressure along roads (Arévalo et al., 2005; Iseli et al., 2023; Lembrechts et al., 2016), our findings indicate that intensifying anthropogenic activities such as anthropogenic wildfires and engineering disturbances could increase exotic plant invasion by altering resource availability and the resistance of native communities. These findings emphasize the need to promote comprehensive preventive strategies aimed at bolstering the resistance and resilience of indigenous communities against invasive species. This includes mitigating the adverse effects of human activities (e.g. anthropogenic forest fires, infrastructure, tourism) on natural ecosystems. Additionally, efforts should be made to enhance the invasion resistance of restored post-disturbed communities across various environmental gradients.

AUTHOR CONTRIBUTIONS

Guoyan Wang and Pei-Hao Peng designed the study, Tingbin Zhang and Xiaojuan Bie preselected the field plots, Guoyan Wang, Songlin Shi, Xiaojuan Zhang and Jing-Ji Li performed the plot investigation, Guoyan Wang and Xu Chen performed phylogenetic analyses and modelling work. Guoyan Wang wrote the first draft of the manuscript, Guoyan Wang, Lin Jiang and Florencia Yannelli contributed substantially to revisions.

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CONFLICT OF INTEREST STATEMENT

The authors have no conflict of interest to declare.

DATA AVAILABILITY STATEMENT

Data and code are available in Dryad Digital Repository at <https://doi.org/10.5061/dryad.4j0zpc8fg> (Wang, Zhang, et al., 2022).

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SUPPORTING INFORMATION

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

Figure S1: The correlation between abiotic and biotic variables.

Table S1: Wildfire information for the sample plots.

Table S2: Ten principal components explained >94% of the variance extracting from 20 abiotic and biotic components using principal component analysis (PCA).

Table S3: Two principal components explained >80% of the variance extracting from 5 abiotic components using principal component analysis (PCA).

Table S4: Parameter estimates from structural equation models (SEMs).

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