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# Invasive *Prosopis* associated with large, but idiosyncratic, ecosystem changes and loss of native biodiversity across India

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## Abstract

Non-native invasive species can have strong negative impacts on biodiversity and ecosystem processes across spatial scales. However, comprehensive understanding of the impacts of non-native plant invasions is biased by a disproportionate focus on individual components of complex impacts at small spatial scales. Thus, evaluating the impacts of invasive species across climate gradients and diverse biogeographic regions is exceptionally valuable. Our goal was to determine if different facets of community and ecosystem impacts of a global invader are consistent and correlated with each other across a wide range of ecosystem types. We quantified and integrated measurements of the characteristics of stands of woody perennials, understory soil properties, and understory vegetation related to the impact of the globally invasive tree, *Prosopis juliflora*, across a large rainfall gradient in India. We sampled seven sites in tropical deciduous forest, savanna, and shrub biomes invaded by *Prosopis* across India. Substantial decreases in native plant richness were consistently associated with *Prosopis* invasion, but *Prosopis* increased non-native plant richness and biomass, consistent with invasional meltdown. However, other than richness, most impacts on communities and ecosystem properties were highly variable among sites and path analysis revealed highly variable connections among stand structure, soil characteristics, and climate. Our regional scale patterns indicate that *Prosopis* has substantial but idiosyncratic impacts on native ecosystems and communities, and that different components of impact are poorly integrated. These results contribute to understanding of the highly variable impacts of even an exceptionally dominant invader, but experimentally identifying the mechnisms that underpin these impacts might be needed to extract generality from its conditional effects.

**Keywords** Invasion impacts · *Prosopis juliflora* · Non-native species · Plant invasion · Soil properties · Patch characteristics · Spatial site variation

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## Introduction

Non-native invasive species can have strong negative impacts on biodiversity and ecosystem processes (Winter et al. 2009; Vilà et al. 2011; Early et al. 2016; Seebens et al. 2018; McGeoch & Jetz 2019), but aboveground net primary productivity (ANPP) commonly increases with invasions (Liao et al. 2018; Callaway et al. 2025) and has been interpreted as positive impact of invasions (see Simberloff et al. 2012 for discussion). These impacts, however, are complex and appear to vary with climate, soils, and recipient communities and ecosystems (Vilá et al. 2011; Aerts et al. 2017; Bradley et al. 2019; Pearse et al. 2019). Understanding the causes of this variation is urgent because of the ongoing spread and establishment potential of introduced non-native species (Ricciardi & Cohen 2007; Liao et al. 2021).

Ecologists have rarely attempted to simultaneously examine and link multiple changes in communities and ecosystems in response to invasions of non-native species (see Hulme et al. 2013; Blackburn et al. 2014; Livingstone et al. 2020). Non-native species impacts can manifest in a complex suite of community changes that could manifest as reductions or increases in the number of species, the elimination of dominant or rare species, changes in the relative abundance of species, promotion of non-native species, or affecting particular phylogenetic or functional groups of other species (Livingstone et al. 2020). Moreover, these effects can vary substantially with different abiotic or biotic backgrounds and in different ranges of non-native species (Pyšek et al. 2012; Livingstone et al. 2020; Cadotte 2023). For example, *Chrysanthemoides monilifera* subsp. *rotundata* invasion in Australia reduced the richness of particular functional groups in fore dune shrublands but affected a different suite of functional groups in hind dunes (Mason & French 2008). Sitzia et al. (2012, 2018) provide an exceptional examination of the diverse impacts of *Robinia pseudoacacia* on plant communities, functional traits, and ecosystem characteristics, but without fully linking them to each other. In contrast, Vilà et al. (2006) integrated the impact of several invaders on biodiversity and soil properties across Mediterranean islands. Finally, Gundale et al. (2024) and Carboni et al. (2021) integrated variation in invasive species traits with their impacts on communities and ecosystems, but at small scales, thus warranting such integration at much larger scales.

Invasive trees provide good opportunities for exploring how the scale of investigation and variation in the traits of an invader, such as height, canopy dominance, and abundance influence diverse invasion impacts such as understory soil properties and vegetation. For example, Sitzia et al. (2018) reported that increasing proportions of *Robinia pseudoacacia*, an invasive tree in Europe, correlated with higher soil C/N ratios, available soil phosphorus and lower total phenolics, and structured understory herbaceous and shrub communities. Such linking of tree structural characteristics to understory vegetation and soil properties could help to unravel the context dependency of invasion impacts. Native and non-native tree canopies can substantially alter understory communities and ecosystems, and these effects can be species-specific (Zinke 1962; Hobbie et al. 2006; Callaway 2007; Yelenik et al. 2021; Liao et al. 2008; Kaur et al. 2012; Gibbons et al. 2017; Marler 2020).

Robust assessments of impact can be achieved by including the responses of native species to invaders, and especially the loss of native species at a particular location over time (Prior et al. 2017). Murugan et al. (2020) found an increase in plant diversity and a decrease in soil nitrogen in response to the removal of *Prosopis* on the southeastern coast of India. However, such experimental and temporal assessments are difficult to apply at large scales and the impacts of invasive species can persist long after their removal (Reynolds et al. 2017). Thus, large-scale assessments usually must be correlative, and should include comparisons of community and ecosystem properties under canopies (a) of non-native vs. native species (Ordonez et al. 2010; Leffler et al. 2014), (b) of invaded vs. non-invaded habitat at larger scales (Hejda et al. 2009), (c) in the native vs. invaded ranges of invasive species (Beckmann et al. 2009; Hierro et al. 2009; Kaur et al. 2012; Becerra et al. 2018), and (d) of the strength of impacts related to the abundance of invasive and native species (Dong et al. 2015; Ledger et al. 2015; Linders et al. 2019; Bradley et al. 2019).

To quantify and integrate the complex impacts of non-native plant invasion across multiple sites in the non-native range, we studied the non-native tree *Prosopis juliflora* (Swartz) DC (hereafter *Prosopis*) across seven sites where it is highly invasive, spanning about 1000 km in India across a strong climatic gradient. *Prosopis* is native to Central America, northern South America, and the Caribbean islands, and has invaded arid and semi-arid communities of Asia, Africa, the Middle East, Australia and the Hawai'ian islands (Pasiecznik et al. 2001; Kaur et al. 2012; Pasha & Reddy 2024). A large body of evidence indicates that *Prosopis*-invaded habitats are associated with lower native diversity than nearby non-invaded habitats (El-Keblawy & Al-Rawai 2007; Kaur et al. 2012, 2014; Ayanu et al. 2015; Mukherjee et al. 2017; Linders et al. 2019; Slate et al. 2020). Soils in sites invaded by *Prosopis* are associated with higher levels of nutrients than that in non-invaded areas (El-Keblawy & Al-Rawai 2007; Kaur et al. 2012; Shiferaw et al. 2021). Patch characteristics, including canopy cover, circumference, and density of *Prosopis juliflora* (hereafter *Prosopis*) may correspond with its impact on communities and ecosystems. These characteristics could be related to the

performance of *Prosopis*, as they may influence the allelochemical effects produced by *Prosopis* (Damasceno et al. 2017) or correlate with variation in the belowground allocation and development of *Prosopis* and thus resource acquistiton and competitive impacts. High resource supply can increase the intensity of competition (Brooker et al. 2005; Besaw et al. 2011; Hautier et al. 2018) and thus invasion impacts are likely to be stronger in mesic, fertile, and productive environments (Perpa et al. 2013; Davis et al. 2000; Dawson et al. 2012). However, as for many other invasive species (Hulme et al. 2013), we do not know how these and other impacts of *Prosopis* manifest across regions, climates, and recipient communities and ecosystems.

To overcome these constraints to understanding the complex impacts of tree invasions, we asked (i) whether the impact of *P. juliflora* on diversity and productivity of native and non-native understory species and soil properties is consistent along a broad biogeographic gradient? (ii) Whether impacts on communities and ecosystems are correlated with *Prosopis* stand characteristics? And (iii) whether different impacts of *Prosopis* were linked in predictable ways? (Fig. 1).

## Methods

### Study sites and sampling

We sampled seven sites in tropical deciduous forest, savanna, and shrub biomes invaded by *Prosopis* across India. The environmental parameters of these sites are shown in Table S1. The sampled sites varied from roughly 400 to 1100 mm·yr$^{-1}$ in annual precipitation, with generally dry springs and very wet summers. Mean annual temperatures range from 13 to 34 °C (Table S1). Based on the National Bureau of Soil Survey and Land Use Planning agencies, soil types and fertility vary substantially among the sites (see Table S2 and Table S3).

At each of the seven sites, we sampled two types of overstory vegetation, patches with nearly monodominant *Prosopis* overstories and patches with native overstory. We sampled 11 to 25 *Prosopis* trees in invaded patches and from 13 to 23 native trees or shrubs in non-invaded patches (Fig. S1, Table S4). Hereafter, we use the term "patch" to indicate a replicate within a site, which was either centred on a single tree, or on a group of four shrubs and use the term "plot" for the *Prosopis*-invaded or non-invaded areas where understory vegetation was sampled. Four shrubs were sampled in sites where native patches were much smaller with shrubby physiognomies, as four shrubs appeared to be roughly equivalent in area to native patches with tree physiognomies at other xeric sites. This was necessary to allow equal four 50 × 50 cm$^2$ plot sampling of impact as described below.

In total, we sampled 123 *Prosopis* patches and 121 native patches across all seven sites, with an average of 17.6 *Prosopis* patches (range 11–25) per site and 17.3 native patches (11–24) per site. The vegetation plots consisted of a total of 492 quadrats under canopies of *Prosopis* patches and 484 quadrats under canopies of native species in non-invaded patches (see Table S4).

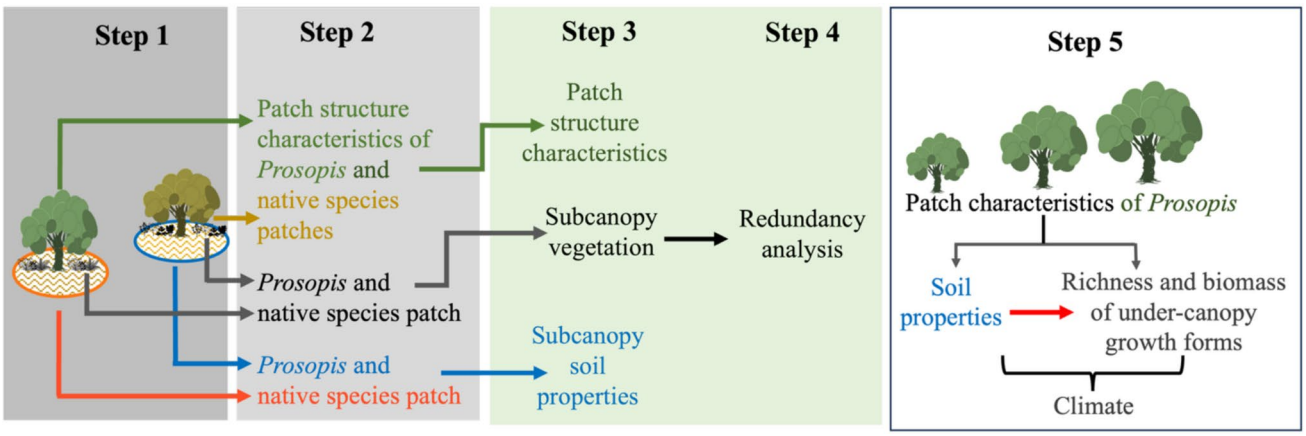


**Fig. 1** Schematic representation of potential relationships among patch structure characteristics, subcanopy soil properties and vegetation growth forms between *Prosopis* and native patches across multiple sites. **Step 1:** Collect data on patch structure characteristics, soil properties and biomass of each individual species under subcanopies of *Prosopis* or native species patches across seven sites (Andhra Pradesh; Delhi; Punjab; Rajasthan; Haryana; Dwarka, Gujarat; and Rann of Kutch, Gujarat). **Step 2:** Measure important soil variables that discriminate *Prosopis* and native species plots using PCA; NMDS and use rank abundance curves to study species distribution patterns under canopies of *Prosopis* and native species. **Step 3**: Compare differences in patch characteristics, soil properties and biodiversity estimations between *Prosopis* and native species patches. **Step 4**: Conduct redundancy analysis (RDA) using biomass of unique species to ordinate plant species in the *Prosopis* and native species plots. Rank importance of species from greatest to least impact using random forest classification. **Step 5:** Use partial least squares path model to integrate the direct and indirect effects of climate, patch type (invaded vs. native), and the richness and biomass of native species

Target patches were selected at all seven *Prosopis*-invaded sites and four non-invaded sites with the wandering quarter method (Catana 1963; Fig. S2A) and in three non-invaded sites (Haryana; Dwarka, Gujarat; and Rann of Kutch, Gujarat) characterized by shrub-like native vegetation with the line transect method (Fig. S2B). The comparison of invaded and non-invaded plots allowed assessment of the variation in the responses of native communities across a wide range of environments (Hejda et al. 2009). We randomly selected a central point at each site and projected four 20-m transects from this point, one in each of the cardinal directions, and thus, sampling occurred within roughly one hectare at each site. Starting from the central point, we sampled the nearest tree (patch) within a 90° angle, using the wandering quarter protocol, centered to form 45° on either side of the transect, facing away from the starting point (Fig. S2A). The nearest patch within this angle was identified, and the distance between the point and the first patch was recorded. With the last sampled patch as the next vertex, the next nearest patch in the direction of the transect was sampled. Details on the number of sites and patches are presented in Table S2. At the three sites where native vegetation was characterized at least in part by large shrubs, patches were identified using the line transect method in which points were randomly chosen on four 20-m transects, again radiating in the cardinal directions from a central point (Fig. S2B). At each random point, the four closest shrubs were used for measurements, and the four were combined to make one patch.

Various characteristics of the tree or shrub representing a patch were measured including height, a standard metric of tree size—circumference at breast height (CBH; Akpo et al. 2020), and diameter of the canopy for all patches at all sites. The distances between the adjacent patches was measured and its reciprocal value was used as a measure of density at each site (Avery & Burkhart 2002). Height was measured with a distance meter (Leica Disto D510; Hunter et al. 2013). For trees (patches) identified with the wandering quarter protocol, four $50 \times 50$ cm$^2$ quadrats were placed equidistant from the edge of the canopy and the trunk under canopies (Fig. S2). For patches (four adjacent shrubs) determined with the line transect protocol, one $50 \times 50$ cm$^2$ quadrats were placed under each of the four shrubs. In each plot, aboveground biomass was collected, oven-dried at 60 °C for 48 h, and separated into individual species. This gave us measurements of species richness, and aboveground biomass for the following six species groups based on growth form and origin: native and non-native herbs, native and non-native shrubs, and native and non-native saplings. The biomass of each species from the four quadrats under each patch was pooled, thus, each patch was used as one biological replicate for all analyses.

## Soil analysis

Soil samples were collected from 10–15 cm below the soil surface, thus not including the litter. Organic horizons were absent, and thus primarily mineral soils in the A horizon were sampled. Samples were collected in each of the four quadrats comprising each patch, and soils from the four quadrats under each patch were pooled and thus one patch was used as one biological replicate (Fig. 1; Table S4). Five g of air-dried soil was soaked with 25 mL double distilled water (DDW) and shaken for 1 h at room temperature, followed by filtration through Whatman # 1 filter paper. The soil suspension was used to measure pH (pH meter, Thermo Scientific Orion star A11) and electrical conductivity (EC, Conductivity meter, Metrex, Digital pH, Conductivity cum Temperature meter model 231- R) following Piper (1944). Soil organic carbon (SOC) was estimated after Walkley and Black (1934). Soil exchangeable phosphate ($PO_4^{3-}$) was measured by shaking 5 g air-dried soil with 25 mL 2.5% acetic acid for 1 h and filtered through Whatman # 42 filter paper. Soil $PO_4^{3-}$ levels were measured by using the ammonium molybdate method (Allen 1989). A second 5 g of air-dried soil was soaked with 25 mL DDW, shaken for 20 min and then filtered. The filtrate was used to determine total phenolic content with the Folin-Ciocalteu reagent (Swain and Hillis 1959). Soil nitrate ($NO_3^-$) concentrations were determined by soaking 50 g air dried soil with 15 mL water for five days. Five g aliquots were soaked and shaken with 10 mL 0.5 M potassium sulphate for 1 h and filtered through nitrate-free Whatman # 42 filter paper (Anderson & Ingram 1993). Soil $NO_3^-$ content was quantified as the absorbance of the chromophore at 410 nm, generated upon the reaction of $NO_3^-$ in the sample with salicylic acid under highly basic conditions (NaOH, pH > 12), against the known range of potassium nitrate standard (Anderson & Ingram 1993). Soil ammonium ($NH_4^+$) concentrations were measured by using indophenol method (Tzollas et al. 2010). Concentrations of $NO_3^-$, $NH_4^+$ and $PO_4^{3-}$ were expressed as mg/g soil. Soil respiration was measured by the closed static chamber—alkali trap method (Anderson 1982; Haney et al. 2008). The $CO_2$ released was reverse calculated as the amount of NaOH consumed over 24 h (see Inderjit et al. 2010). Soil respiration measurement was expressed as mg $CO_2$/g soil/h.

## Statistical analysis

Understory vegetation: For each site, paired species composition comparisons between *Prosopis* and native patches were carried out using distance-based ordinations. Non-Metric Dimensional Scaling (NMDS) was conducted using Bray–Curtis distances on normalized species biomass matrices in the R package "vegan" (Dixon 2003; Oksanen

et al. 2020). NMDS is appropriate for dealing with missing pairwise distances applied to a dissimilarity matrix, as in our study, since many species only occurred at one site and in either *Prosopis* or native patches. The dissimilarity matrices were prepared in R package "MASS" using function "metaMDS" (Venables and Ripley 2002) on a data frame for the aboveground biomass for each species occurring under *Prosopis* or native canopies, separately for each of the seven sites. Plots for NMDS were visualized using the R package "ggplot2" (Wickham 2009). Individual patches (*Prosopis* vs. native species) at each site were plotted as point objects. Patches that are more similar to one another appear closer together in ordination space. Inherent to non-dimensional scaling, the scale of the axes and the orientation of the plot are arbitrary. To test if *Prosopis* and native species patches had significantly different mean dissimilarities, we calculated intergroup differences using ANOSIM (Analysis of Similarity) and R-statistic as implemented in the R package vegan. R values close to 1 suggest similarity within a given site is high, while similarities between patches are minimal, whereas values approximating zero suggest minimal difference between within-site and between-site similarities. The stress value indicates the adequacy of reproduction in reduced dimensions, and a value > 0.3 is recommended (Goral and Schellenberg 2018).

To visualize species richness and evenness under canopies of *Prosopis* and native species, we conducted rank abundance analyses for each site (Whittaker 1965). We used the relative biomass of each species (relative to the total biomass at a site in either *Prosopis* or native patches). The $\log_{10}$ (relative biomass + 1) of each species was plotted on the *y*-axis with the abundance rank of the species arranged from high to low on the *x*-axis. Steeper slopes of rank abundance curves indicate lower levels of species evenness, and the relative dominance of fewer species (Wilson 1991; McCarthy et al. 2018). We calculated the linear slope of rank abundance curves for *Prosopis* vs. native species patches for each of the seven sites. An independent sample t-test was conducted between the slope values of rank abundance curves for communities under canopies of *Prosopis* and those under canopies of native species for each site. To visualize the differences in species distribution between *Prosopis* and native species patches, Redundancy analysis (RDA) was carried out separately for each of the seven sites. We identified species that were common to both *Prosopis* and native species patches and those which were exclusive to either one or another in each of the seven sites sampled.

Understory soils: Separate Principal Component Analyses (PCA) were performed for soil characteristics for each of the seven sites, based on pH, EC, SOC, $PO_4^{3-}$, $NH_4^+$, $NO_3^-$, total phenolics, and soil respiration. Data were inspected for normality with QQ plots and the Shapiro–Wilk's test. $\text{Log}_{10}$ transformations were carried out for pH, EC, $PO_4^{3-}$, $NH_4^+$, and $NO_3^-$. Using the package "FactoMineR" (Lê et al. 2008), before conducting PCA, the data frame was scaled to unit variance to avoid potential dominance of a given variable in lieu of using relatively larger measurement units. The package "factoextra" (Kassambara and Mundt 2020) was used to extract Eigenvalues and variances of principal components and to visualize the results for individuals and variables in a biplot. Eigenvalues were examined, and the dimensions were truncated to the first two principal components (Kaiser 1961). Information on eigenvalues and the proportion of variances retained by the principal components (PCs) were extracted using the R package "factoextra". The directions with the largest variances were projected as principal components and the variance retained by each principal component was measured by using the eigenvalue.

Patch structure, soil properties, and understories: To simplify and display variation and examine the consistency among sites, we selected prominent variables for patch characteristics, vegetation, and soils for mean comparisons. These included the canopy spread, density, and trunk circumference, native herbaceous richness and biomass, non-native herbaceous richness and biomass, and soil concentrations of phenolics, $NO_3^-$, and $NH_4^+$. We displayed means and variation using boxplots calculated in Sigmaplot 15.0. One-way ANOVAs were used to compare means at a site and two-way ANOVAs, with site and patch type as fixed factors (SigmaPlot 15.0).

Partial least squares (PLS) path model: We conducted a PLS path model to integrate the direct and indirect effects of climate, patch type (*Prosopis* vs. native patch), and the richness and biomass of native species. We began with an a priori model based on the following assumptions: (1) climate conditions can directly affect native performance, while it can also indirectly affect native performance through affecting patch characteristics, soil total phenolics and nutrient contents; (2) patch type had similar effects on native performance as climate conditions; (3) patch characteristics can also affect native performance directly and indirectly through affecting soil total phenolics and nutrient contents (Fig. S3). Only the most important indicators were considered for the PLS path model. For climate, we used mean annual precipitation and evapotranspiration as indicators. For patch characteristics, we used density, CBH, and canopy spread. For soil allelochemicals and nutrients, we used total phenolics and nitrogen ($NO_3^-$, and $NH_4^+$) because of their prominence in our ordinations and their potential roles in *Prosopis* invasion from the literature (Kaur et al. 2012; Damasceno et al. 2017), and for simplicity. All indicators were assigned as reflective indicators – i.e., latent variables considered to cause the observed indicators. We used the R package 'plspm' to construct the PLS path model with

default settings: (a) standardized data; (b) centroid weighting scheme; (c) tolerance criterion = 1e-6; (d) maximum iterations = 100 (Sanchez et al. 2024). Two adjustments were made to the final model of native species biomass: (1) evapotranspiration was multiplied by −1 to make the directions of the contributions of precipitation and evapotranspiration to climate background consistent; (2) density was removed from the analysis due to its small loading (< 0.7) on patch structure characteristics. For the final model of native species richness, in addition to the adjustments made above, we also removed precipitation from the model due to its small loading.

## Results

### Characteristics of *Prosopis* versus native patches

Across the seven sites, nearly monodominant *Prosopis* patches were 91% denser than native species patches and populated by trees or shrubs with larger canopies (5.4 ± 0.3 vs. 3.1 ± 0.3 m diameter) and stem circumferences (20.1 ± 1.6 vs. 19.5 ± 2.1 cm; Fig. 2). A much more striking aspect of our results, and more relevant to our purpose of understanding biogeographic variation in impact, these patch characteristics varied a great deal among sites. *Prosopis* density was higher than that of native species at three (Haryana, Dwarka, Gujrat and Rann of Kutch) of the seven sites, and the effect of site was much stronger ($F_{6,228} = 63.2$; $P < 0.001$; Fig. 2S2: Table S5) than the effect of provenance (*Prosopis* vs. natives; $F_{1,228} = 7.5$; $P < 0.001$). *Prosopis* patches had higher mean stem circumference at all seven sites (except Andhra Pradesh and Rajasthan) than native patches, but again, the

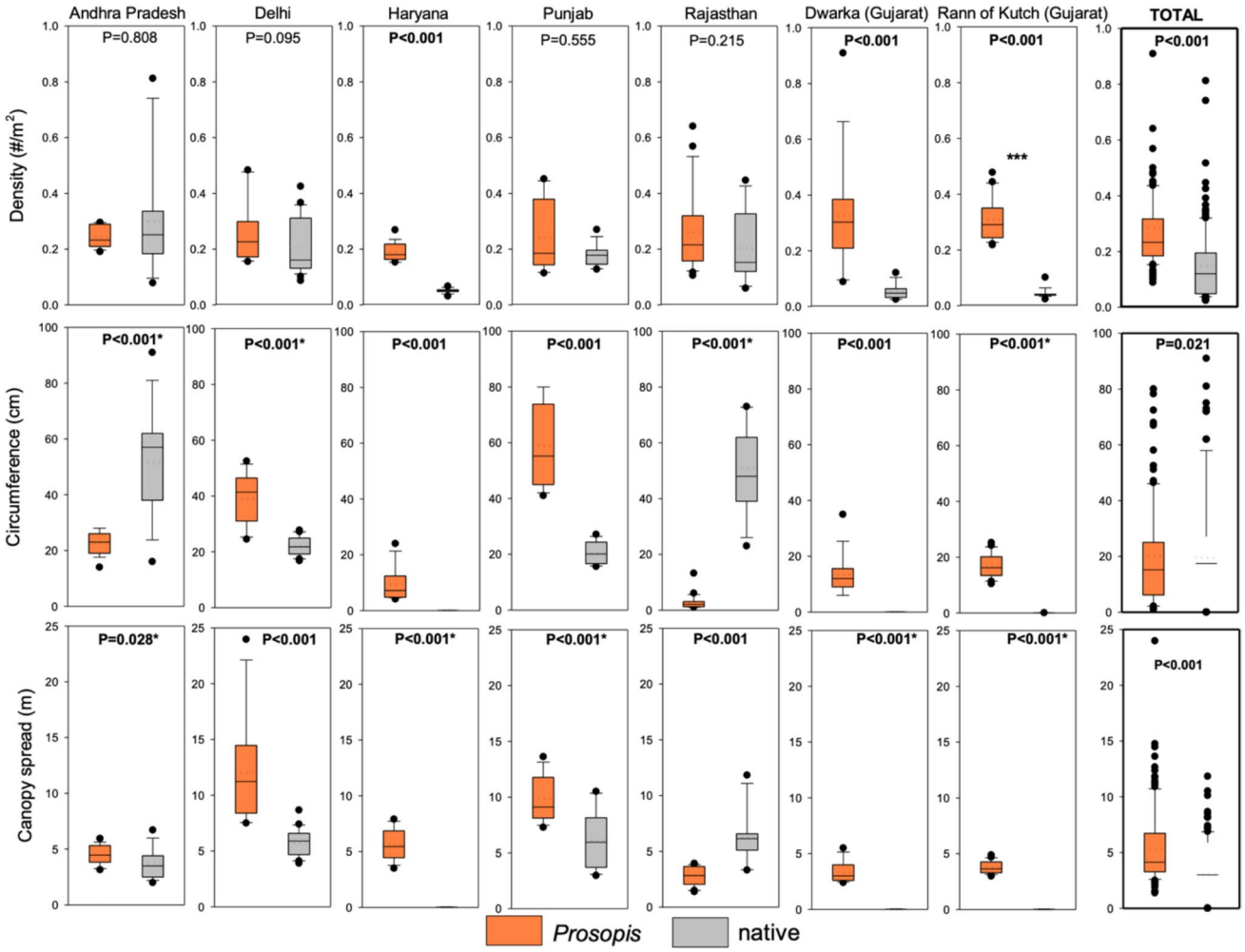


**Fig. 2** Box plots for the site characteristic of density, and the patch characteristics of tree circumferece at breast height and tree canopy diameter for *Prosopis* vs. native patches at each of the seven sites. Dashed lines show means

effect of site ($F_{6,228}$ = 110.6; P < 0.001) was much stronger than the effect of provenance ($F_{1,228}$ = 5.4; P = 0.021; Fig. 2). *Prosopis* patches had larger individual canopies than native patches at all sites except one, Rajasthan. The interaction between site and provenance was highly significant for all three patch tree structural characteristics (P < 0.001).

## Impact of *Prosopis* on understory vegetation

NMDS of understory plant communities, including herbaceous and woody species, showed striking differences between *Prosopis* and native patches at all sites but Rann of Kutch in the State of Gujarat (Fig. 3A). Only two samples under native patches at the Andhra Pradesh site showed an overlap with *Prosopis* samples. Larger differences were observed in ranked dissimilarities (ANOSIM) between *Prosopis* and native patches at five sites, but not at Andhra Pradesh (R = 0.706) or Rann of Kutch (R = 0.192; Fig. 3A).

Of the 62 most common native species under native canopies across all sites, 27 species (44%) did not occur under *Prosopis* at any site, suggesting landscape-scale exclusion of natives by the invader. Of the 34 most common native species under *Prosopis*, 17 (50%) did not occur under natives at any site (Table S6). Of the 18 non-native understory species in *Prosopis* patches, seven (39%) did not occur under native canopies at any site, suggesting large-scale promotion of other non-native species (Table S6). However, because of the broad geographic scope of the sampling, only two of these common species occurred at multiple sites (Table S6).

Rank abundance curves of total biomass illustrated the loss and near-loss of species under *Prosopis* at all sites but Rann of Kutch (Fig. 3B). Slope values for the sites other than Rann of Kutch were steeper for invaded than uninvaded patches, ranging from −0.377 to −0.842 under *Prosopis* vs. −0.276 to −0.440 under natives, showing greater dominance by just a few species, and indicating the exclusion of large numbers of native species. Slope values for rank-biomass curves were steeper for *Prosopis* patches (Fig. 3B). Shallower slopes for the native patches indicate higher evenness (Whittaker 1965). *Prosopis* juveniles were found at four sites (Punjab, Haryana, Delhi and Rann of Kutch) and only under the canopies of mature *Prosopis* trees.

For a more detailed focus on sites, we compared the richness and total biomass of all species combined, native species, and non-native species. Across all sites, total species richness under *Prosopis* was on average 37% lower than under natives (Fig. 4), and one of the more consistent outcomes of impact. Total species richness was lower under *Prosopis* than under native canopies at all sites but Delhi, where the effect of overstory provenance was not significant, and perhaps due to the fact that Delhi had lower vegetation biomass compared to the other sites (Fig. 4). However, the intensity of these impacts on richness was highly variable, ranging from a 19% reduction at Haryana to 73% at Rajasthan (Fig. 4). The apparent impact of *Prosopis* was greater when considering only native species, which were 49% lower under *Prosopis* than under native species across all sites combined (Fig. 4). Furthermore, *Prosopis* was associated with significantly lower native species richness at all seven sites, with decreases ranging from 33% at Dwarka (Gujarat) to 69% at Rajasthan. The richness of non-native species showed a pattern opposite to that of natives, with an increase from a mean of 1.1 non-native species per plot under native canopies to 2.1 species under *Prosopis*, across all sites combined (Fig. 4). This pattern was highly variable, with only three sites (Haryana, Punjab and Dwarka (Gujarat)) showing significant increases in non-native richness in *Prosopis* patches, but with no sites showing fewer non-natives in *Prosopis* patches (Fig. 4).

The relationship between overstory provenance and understory biomass was less consistent than that for species richness, though overall patterns were similar (Fig. 5). *Prosopis* patches were associated with a 46% decrease in total herbaceous biomass, relative to native patches, across all sites combined, but this impact was significant at only three sites. Across all sites combined, *Prosopis* was associated with a 75% decrease in native biomass, and this was significant at four sites. *Prosopis* was associated with a 137% increase in non-native biomass averaged across the six sites where non-native species were present (Fig. 5). This effect, however, was inconsistent across sites, with only two sites showing significant increases. Although not included in Fig. 5, and strikingly different than our results for herbaceous biomass, *Prosopis* had strong positive associations with some native shrub species, *Justicia adhatoda* (syn. *Adathoda vesica*) in Delhi, Punjab, and Haryana, and *Bergera koenigii* (syn. *Murraya koenigii*) in Punjab. These shrubs were not recorded in non-invaded plots at these sites (Fig. S4, S5, S6).

## Impact on soil properties

The PCA of soil variables, including total phenolics, $NO_3^-$, $NH_4^+$, $PO_4^{3-}$, soil respiration, EC, and pH were different between native species and *Prosopis* patches at all sites (Fig. 6). Because *Prosopis* harbors N-fixing symbionts (Benata et al. 2008) and its leaves contain high concentrations of an amino acid L-tryptophan and phenolic compounds (Nakano et al. 2003; Damasceno et al. 2017), we compared the means and variation of $NH_4^+$, $NO_3^-$ and total phenolics in understory soil at each of the seven sites. Across all sites, total phenolic concentrations in soils were 65.6 ± 1.5 µg/g under *Prosopis* patches vs. 46.9 ± 1.5 µg/g under native patches ($F_{1,228}$ = 176.9; P < 0.001; Fig. 7).

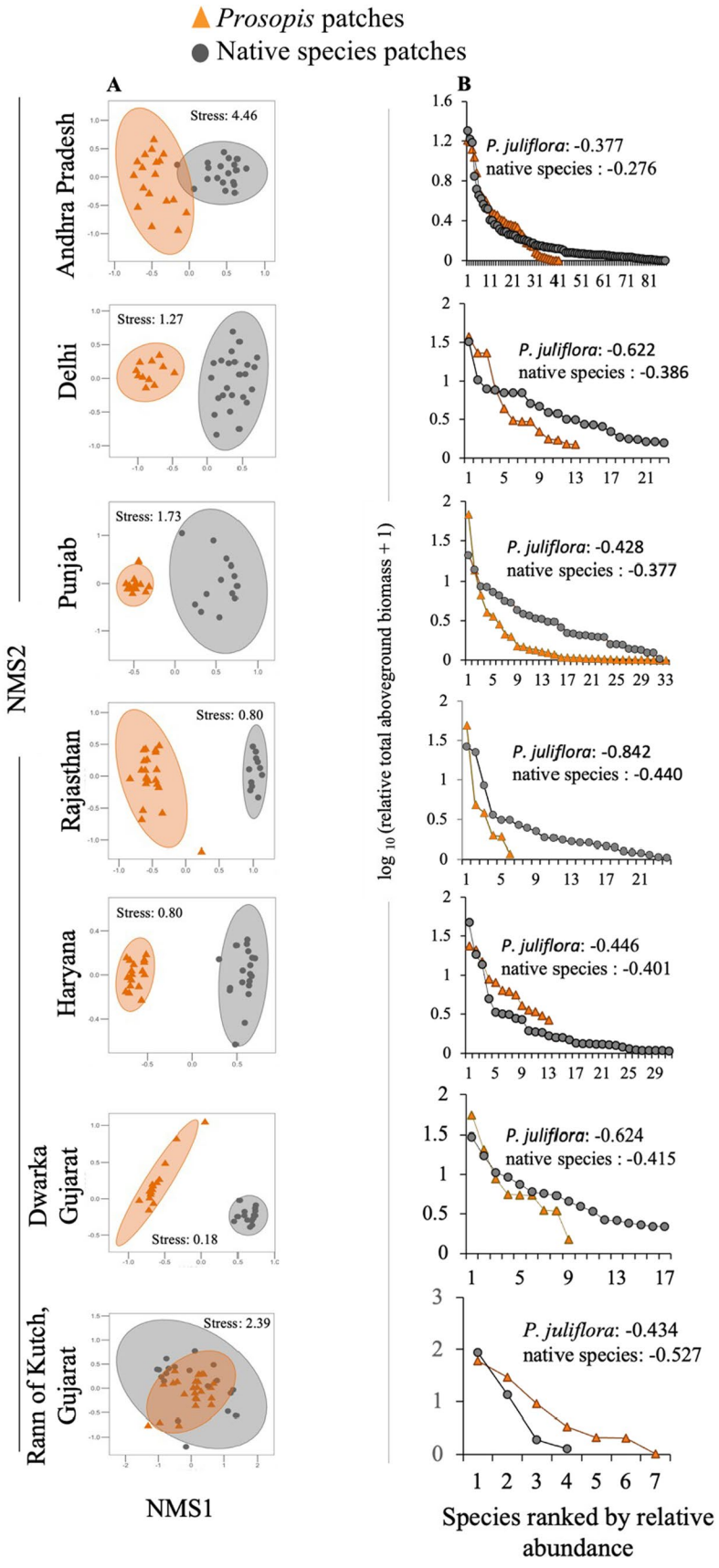


**Fig. 3** A, Ordination of vegetation under canopies of *Prosopis* or native patches in seven sites based on Non-Metric Dimensional Scaling (NMDS). Dissimilarity matrix was prepared from total biomass of each species occurring under respective canopy of each patch. Each point represents individual patch. B, Rank abundance curves depicting the comparative species distribution pattern under *Prosopis* or native species patch in each site. Slope values for rank abundance curves correspond to *Prosopis* or native patches in each plot

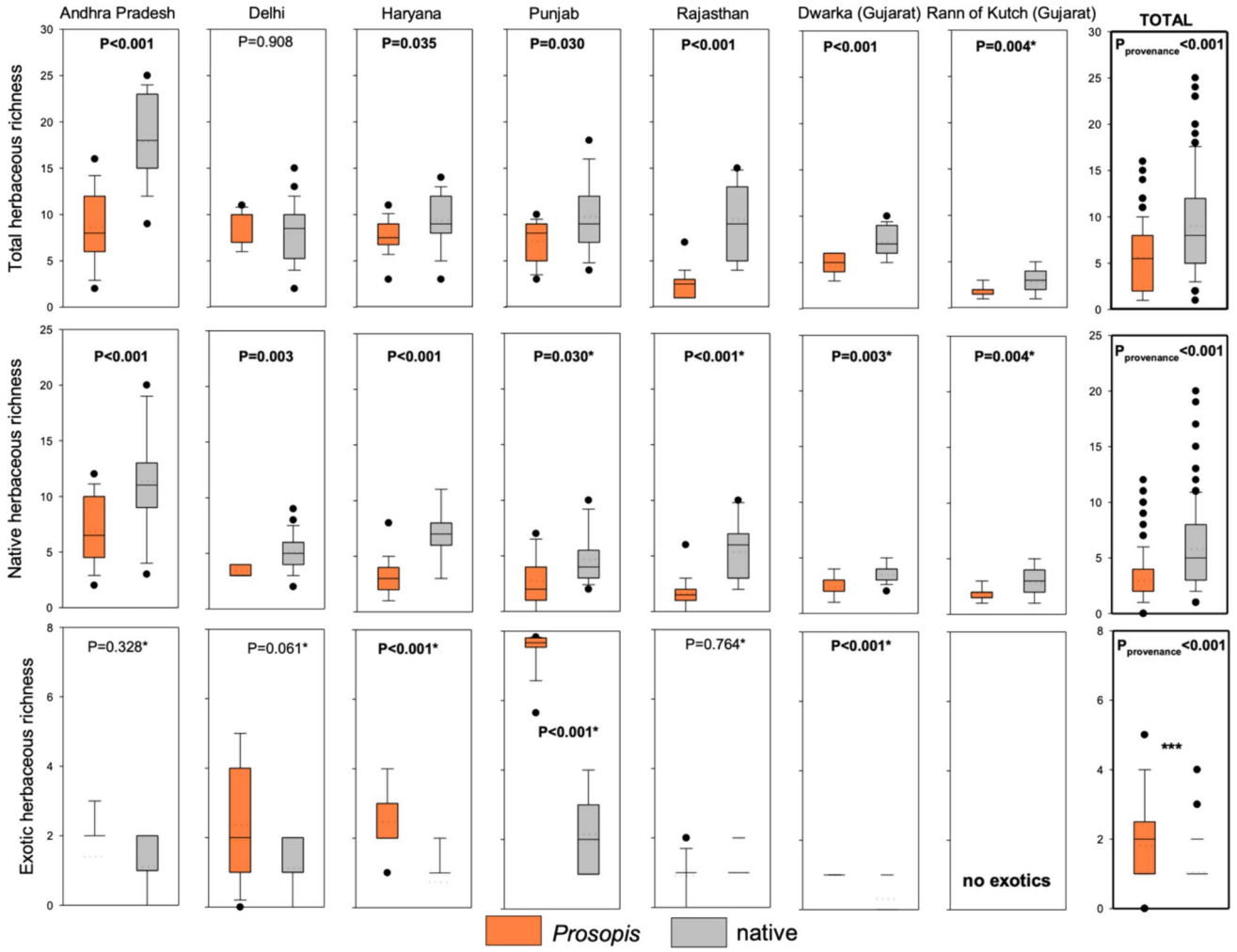


**Fig. 4** Box plots for the total richness of herbaceous species, native herbaceous species, and non-native (exotic) herbaceous species in the understories of *Prosopis* vs. native patches at each of the seven sites. Dashed lines show means

Again, variation among sites was high with concentrations under *Prosopis* ranging from 0 to over 80 µg/g, with four sites showing higher concentrations of total phenolics under *Prosopis* and two sites showing higher concentrations under native species patches. Soil at five of the seven sites had higher concentrations of $NH_4^+$ under *Prosopis*, but Rajasthan was the opposite, with higher $NH_4^+$ under natives. Soil $NH_4^+$ under *Prosopis* ranged from less than 1 mg/g soil at Rajasthan to almost 4 mg/g soil at Delhi, but across all sites soil $NH_4^+$ was 1.17±0.11 mg/g soil under *Prosopis* vs. 0.90±0.06 mg/g under natives ($F_{1,228}=84.6$; df=1,228; P<0.001; Fig. 7). However, the effect of site was much stronger than the effect of provenance ($F_{6,228}=271.4$; df=6,228; P<0.001). Soil $NO_3^-$ concentrations did not differ in soil under *Prosopis* vs. under natives across all sites combined, was higher under *Prosopis* at four sites, and higher under natives at two sites (Fig. 7).

## Integrating climate, patch characteristics, and *Prosopis* impacts

In the path analyses, native herbaceous species richness was directly and negatively associated with patch type (*Prosopis* vs. native) (Coefficient=−0.31, P<0.001; Fig. 8). There were also a weak indirect positive effect of patch type on native richness through increasing soil total phenolic concentration (Coefficient=0.16, P=0.027), and weak effects of patch type and traits on soil nitrogen concentration ($Coefficient_{type}=0.07$, P=0.029; $Coefficient_{trait}=0.75$, P<0.001; Fig. 8). In other words, the presence of *Prosopis* had a negative impact on native species richness, but this was not explained by the indirect effects of climate or the characteristics of *Prosopis* trees or soil nutrients. Native biomass was directly and negatively associated with *Prosopis* invasion (Coefficient=−0.36, P<0.001). There was also a weak indirect negative effect of patch type on native biomass through variation in the characteristics of *Prosopis* trees; larger

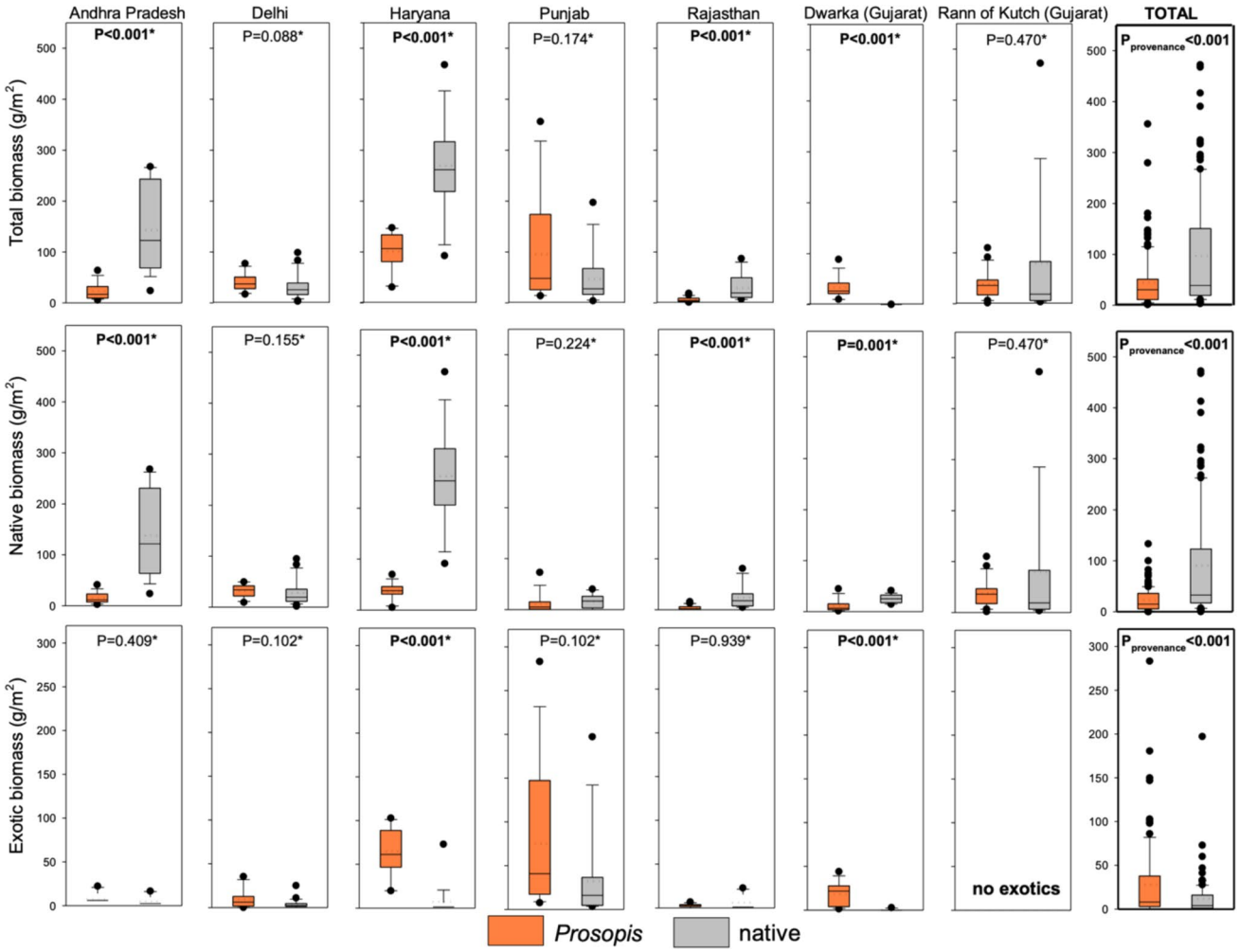


**Fig. 5** Box plots for the aboveground biomass of all herbaceous species, native herbaceous species, and non-native (exotic) herbaceous species in the understories of *Prosopis* vs. native patches at each of the seven sites. Dashed lines show means

trees had more negative impact on native biomass (Coefficient = −0.38, P = 0.074). Increased evapotranspiration rate and reduced precipitation were associated directly with lower native richness (Coefficient = 0.16, P = 0.435) and biomass (Coefficient = 0.24, P < 0.001), but also indirectly associated with reduced native performances by increasing patch density, height, and canopy spread. Soil phenolic concentration was positively associated with *Prosopis* invasion (Coefficient = 0.13 [P = 0.266] ~ 0.16 [P = 0.027]) and climate (Coefficient = 0.63 ~ 0.72, P < 0.001), both directly and indirectly through patch characteristics (Coefficient = 0.36 ~ 0.43, P < 0.001), which consequently increased native richness. Soil nitrogen concentration was positively associated with climate (Coefficient = 0.53 ~ 0.60, P < 0.001) but not *Prosopis* invasion, either directly or indirectly through patch characteristics (Coefficient = 0.75 ~ 0.79, P < 0.001), which consequently reduced both native richness and biomass.

## Discussion

Our results show that *Prosopis* was associated with differences in soil properties, species composition, and species dominance across seven sites, except for vegetation at Rann of Kutch, the salt desert site. Native species richness was consistently lower under canopies of *Prosopis*, relative to patches of native tree species in non-invaded habitats, across our biogeographic-scale gradient, including an apparent landscape-scale elimination of some species. However, when we attempted to integrate climate, patch characteristics, soil properties, and plant communities, the only detectable negative impact on native richness was simply the presence of *Prosopis*. The direct effect of climate was much weaker than the direct effect of *Prosopis* invasion. Indirect effects expressed through patch characteristics and soils were also negligible. This is not consistent with other studies finding that invaders suppress natives through ecosystem effects (Carboni et al. 2021), indicating that

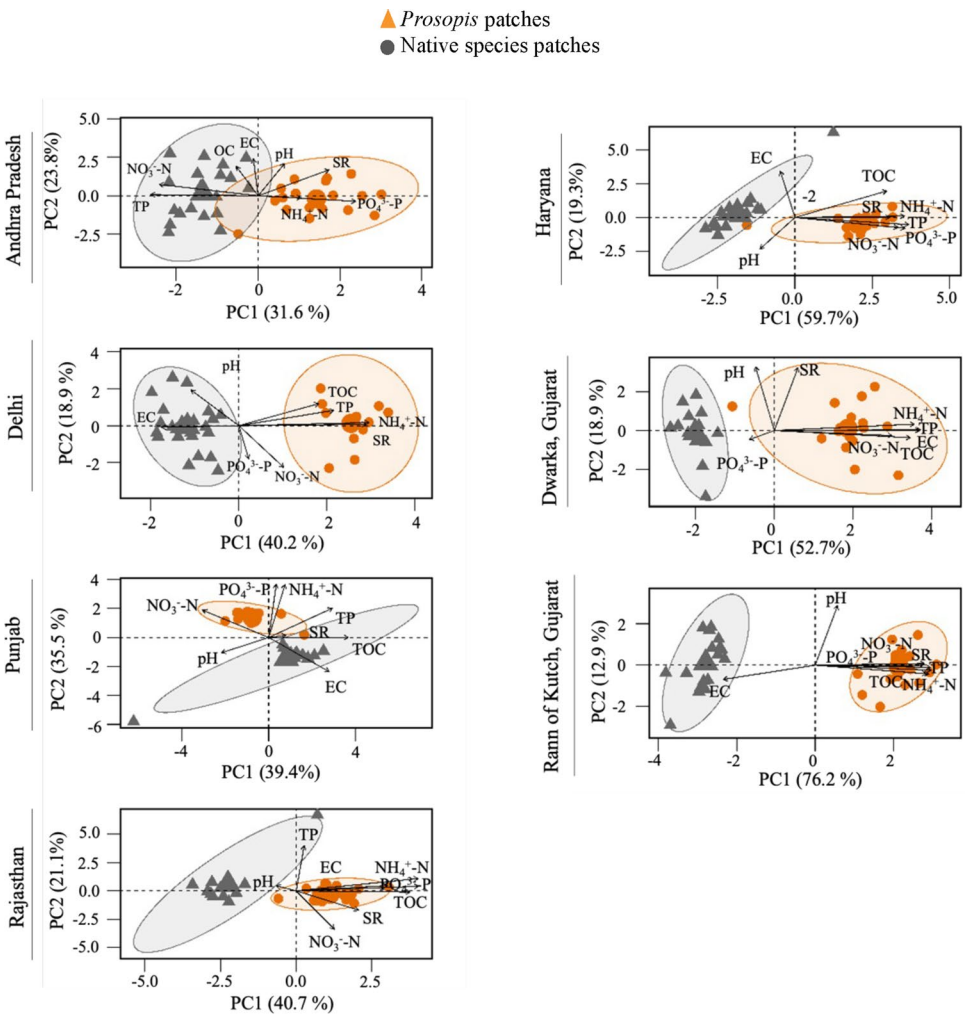


**Fig. 6** Principal component analysis (PCA) to show the contribution of soil variables toward the separation of soils associated to *Prosopis juliflora* or native species across eight regions. *Prosopis juliflora* or native species patches soils were discriminated on the basis of eight soil variables, pH, electrical conductivity (EC), soil organic carbon (SOC), $PO_4^{3-}$, $NH_4^+$, $NO_3^-$, total phenolics (TP) and soil respiration (SR). Percent contribution of different soil variables to the first two principal components PC1 and PC2 is given in the Table S7

either above ground competition was the driving factor or that we did not measure a key edaphic variable that was influenced by *Prosopis*. However, another way to look at it is that *Prosopis* suppressed native species diversity and biomass despite substantial variation in climate, patch characteristics, and soil properties.

Despite their weak associations among different facets of impact in our study, the variables we integrated have been important in other studies of invasions. Linking the impacts of invasion to patch characteristics of invaders is rare, but other studies have found that the density and cover of invaders in patches corresponded with their impact (Ortega & Pearson 2005; Gooden et al. 2009). In our study, the patch density and size of *Prosopis* did not correspond well with negative impacts of *Prosopis* patches on native species richness or biomass, but path analyses indicated that native biomass was negatively associated with patch traits (Fig. 8).

*Prosopis* produces a large number of chemicals (Damasceno et al. 2017), and some of these are thought to suppress native species, but soil phenolic concentrations did not explain much of the significant negative relationship of *Prosopis* with native richness or biomass. High levels of soil nutrients, especially nitrogen, are thought to give invaders an advantage (Besaw et al. 2011; Sardans et al. 2017), but the generally positive effect of *Prosopis* on $NH_4^+$ concentrations was not associated with native richness or biomass (Fig. 8). The bottom line is that *Prosopis* patches were consistently associated with much lower native richness and the absence of many native species, but we found no consistent explanatory patch or soil variables for this effect. This is important to consider in the context of reviews and meta-analyses that report strong concomitant decreases in native species richness, increases in soil nitrogen, and other ecosystem changes (Ehrenfeld 2003; Xu et al. 2022). These impacts are crucial but may not occur in an integrated or cause-and-effect way. Various measurements of invasion, including those of biodiversity and soil properties should be used together to formally classify invasions and their impacts (Catford et al. 2012; Blackburn et al. 2014; Barney et al. 2015). Many invasive species have strong negative impacts on the plant diversity and abundance of natives (e.g., Pyšek et al. 2012; Early et al. 2016; McGeoch and

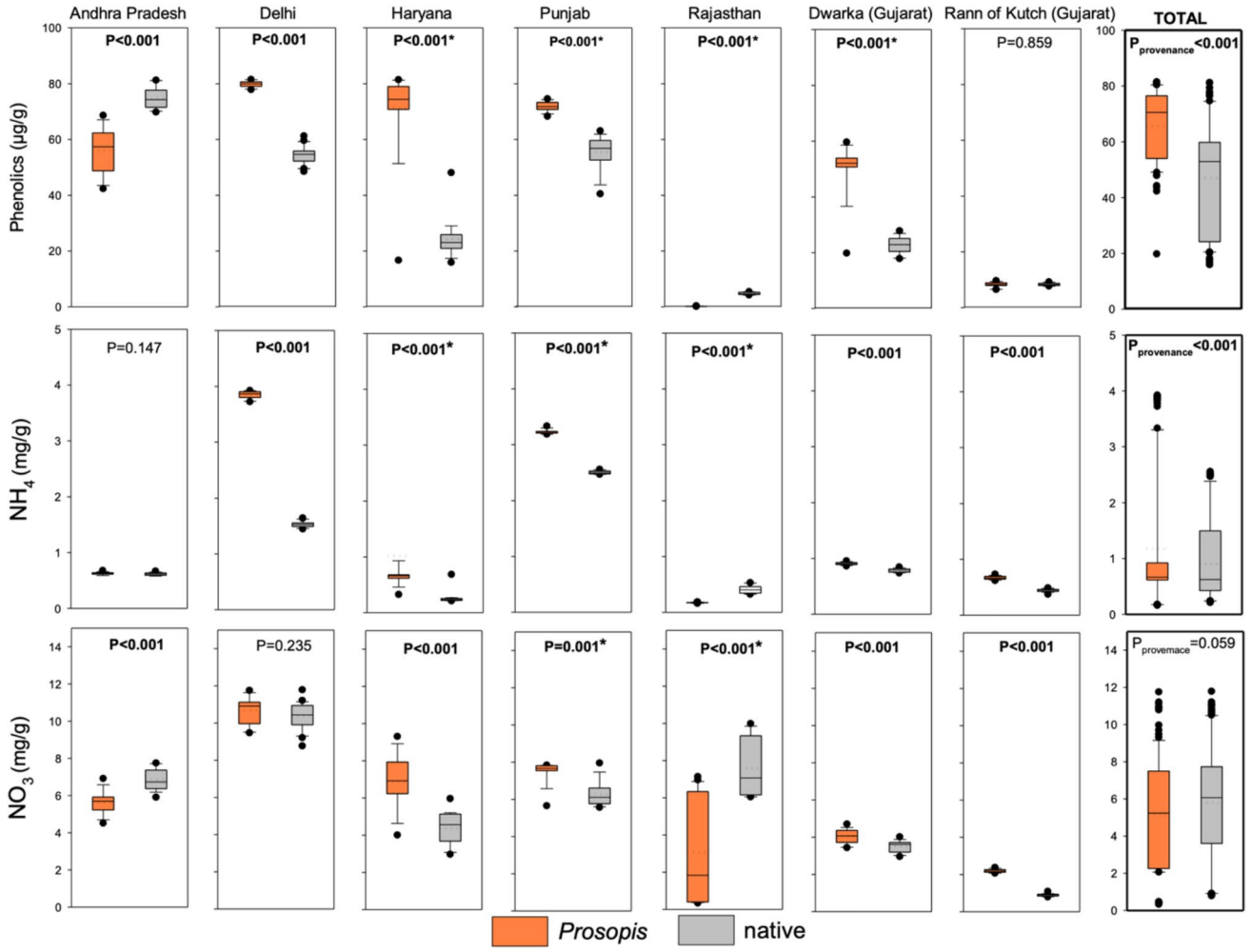


**Fig. 7** Box plots for soil total phenolic, $NH_4^+$ and $NO_3^-$ concentrations in the understories of *Prosopis* vs. native patches at each of the seven sites. Dashed lines show means

Jetz 2019; Livingstone et al. 2020), but such impacts could vary from local extinction to neutral effects to even facilitation (Hejda and Pyšek 2006; Meffin et al. 2010; Cavieres 2021; Livingstone et al. 2020; Farrer et al. 2021; Yin et al. 2022). Dong et al. (2015) quantified the impacts of *Solidago canadensis* on plant diversity at the regional scale in China but did not address the impacts of this invasion on ecosystem characteristics. Additionally, several studies have reported much stronger suppression of species by trees and shrubs in their non-native ranges than in their native ranges (Inderjit et al. 2011; Zheng et al. 2015; Becerra et al. 2018; Davis et al. 2019a, b), including *Prosopis* (El-Keblawy & Al-Rawai 2007; Kaur et al. 2012; Shackleton et al. 2014) indicating that the impact of these invaders on biodiversity is not due to an inherent property of the invader that is consistently expressed in both native and non-native ranges, but dependent on regional and biogeographical differences in community ecology between ranges – i.e., ecological-evolutionary processes (Davis et al. 2019a, b; Pearse et al. 2019).

Most studies that have quantified the impacts of invaders have measured changes in species richness (e.g., Hejda et al. 2009; Mollot et al. 2017; Bradley et al. 2019; Kaur et al. 2012; Linder et al. 2019), but such measures of α diversity are likely to underestimate invasion-driven compositional changes, for example when the communities have equal numbers of species gain and loss (Vellend et al. 2013; Dornelas et al. 2014; Supp & Ernest 2014; Blowes et al. 2019). In addition to the effects of invaders on biodiversity, they can alter species dominance, diversity, and structure in recipient plant communities (Pal et al. 2015; Gentili et al. 2019; Dyderski and Jagodziński 2021), as we demonstrate in our rank-abundance curves (Fig. 3B). For example, such changes may be a shift towards dominance by a few native or non-native species, indicated by the steeper declines in most of our rank-abundance curves (Fig. 3B). This is reflected in the responses of key species, for example the loss of the natives *Cynodon dactylon*, *Aristida redacta, Cymbopogon coloratus, Setaria verticillata, Dicanthium*

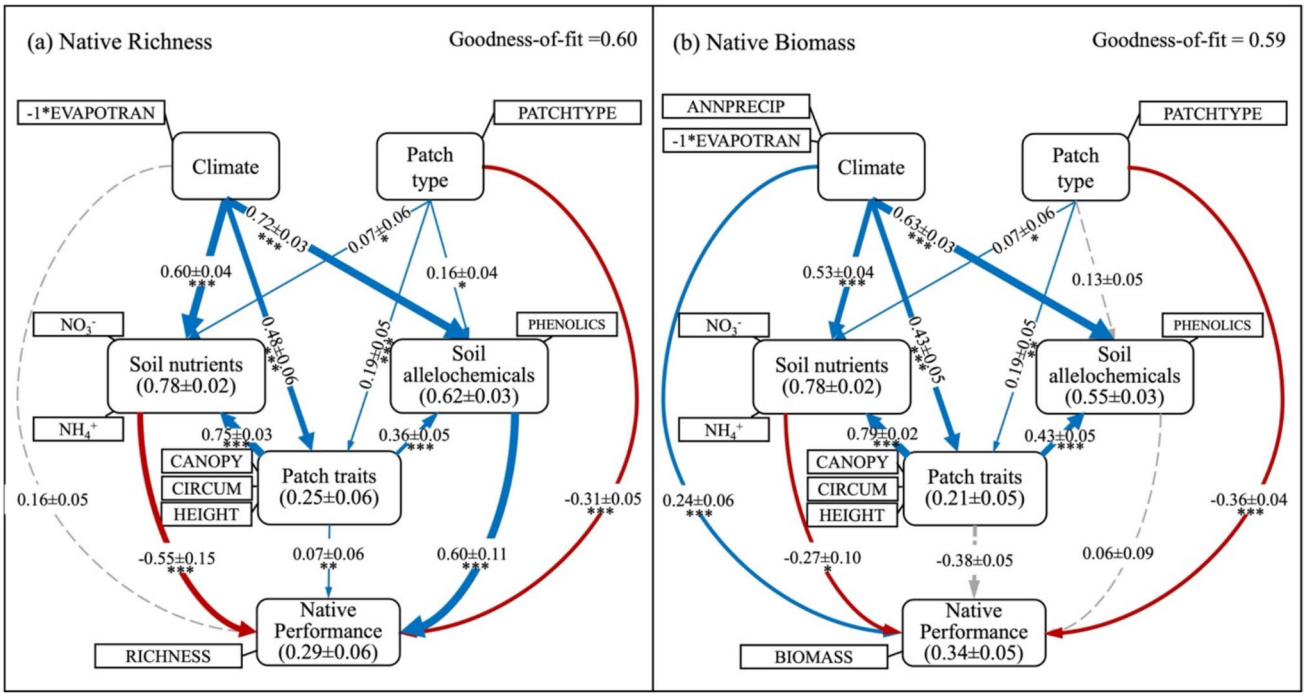


**Fig. 8** Partial least squares (PLS) path model (a variance-based SEM) to integrate the direct and indirect effects of climate, patch type (*Prosopis* vs. native patches), and the understory richness and biomass of native species. The number in brackets in each block shows the $R^2$ being explained by other blocks pointing to the focal block. Paths in red depict negative associations, while paths in blue depict positive associations. Path thickness indicates the magnitude of association, with thicker lines indicating more pronounced positive or negative associations. Significant paths are marked by asterisks (* $p<0.05$, ** $p<0.01$, *** $p<0.001$). EVAPOTRAN: mean annual evapotranspiration; ANNPRECIP: mean annual precipitation; HEIGHT: mean plant height; CIRCUM: mean circumference at breast; CANOPY: mean diameter of the canopy. Indicator weights (relative contributions) and path coefficients are given in Table S9 and Table S10

*annulatum, Tephrosia pumila, Fimbristylis dichotoma*, and *Alysicarpus longifolius.* In contrast, the non-natives *Chrysopogon zizanoides*, *Ageratum conyzoides*, *Ipomoea carnea*, and *Croton bonplandianus* were found only under *Prosopis* canopies (Table S6).

Woody invasive plants commonly alter soil properties (Vitousek and Walker 1989; Ehrenfeld 2003; Weidenhamer and Callaway 2010; Waring et al. 2015; Pergl et al. 2023). In general, trees can develop species-specific patterns in the chemistry of their under-canopy soil primarily mediated by leaf litter and throughfall (see Zinke 1962; Boettcher and Kalisz 1990; Callaway and Nadkarni 1991; Lovett and Rueth 1999). For example, Finzi et al. (1998) found that soil nitrogen concentrations and mineralization rates varied among six species in a temperate deciduous forest, indicating that different species might generate a mosaic of ecosystem processes (Mueller et al. 2012). Our *Prosopis* vs. native patches comparisons across biomes showed striking differences in cumulative soil properties at all seven sites. Still, the specific characteristics showed substantial site-specific responses, as seen in the PCA analyses (Fig. 6). For example, *Prosopis* was associated with higher soil phenolics at four sites, higher soil $NH_4^+$ at five sites, and higher soil $NO_3^-$ at four sites, and with lower values of these variables at other sites. In other words, the impacts of *Prosopis* on soils appeared to be highly modified by site conditions. In its native range, nutrient accumulation under *Prosopis glandulosa* was reported to be affected by water availability (Virginia 1986). Schade et al. (2003) reported that the effects of *Prosopis velutina* trees on soil nitrogen availability in the Sonoran Desert depended on landscape position, with trees in xeric conditions having stronger positive effects than canopies in mesic riparian areas. However, in our case, the impact of *Prosopis* on soil nitrogen was not associated with annual precipitation but, positively with evapotranspiration.

We only compared means for the biomass of herbaceous species under native and *Prosopis* canopies, but this was the large majority of ANPP in the understory at our sites. Total herbaceous biomass was not impacted by *Prosopis* as consistently as species richness, which was significantly lower under *Prosopis* patches at three sites but significantly higher at one site. However, the impact on total biomass was complicated by the different provenance of the understory species. The biomass of native species decreased at most sites and over all sites combined, whereas the biomass of non-native species increased. Interestingly, the native shrub *J. adhatoda* was found only in *Prosopis* patches in Punjab and Haryana. Another native shrub, observed only in Punjab, *B.*

*koenigii*, produced more biomass in *Prosopis* patches than in native patches (Fig. S4, S5, S6). The two sites, Punjab and Haryana, have similar annual precipitation amounts and timing, temperatures, and are in similar eco-regions, i.e., hot subhumid for Haryana and Punjab (Table S1).

The higher biomass of non-native species in the understory of *Prosopis* patches at two sites and across all sites combined shows its positive impact on non-native species. Regardless, the relationship of *Prosopis* with understory biomass was highly variable and the only significant correlations were positive relationships between non-native biomass and tree canopy size and trunk circumference and with soil phenolic concentrations (Fig. 8). We know of few studies of invasive trees on understory biomass. Dyderski and Jagodziński (2021) found that invading patches of *Prunus serotina* in forests in Poland correlated with increased biomass of understory shrubs. In contrast, invasive *Pinus contorta* in Argentina strongly suppresses native herbaceous productivity (Moyano et al. 2024). Ferraina et al. (2021) found that *Gleditsia triacanthos*, an invasive tree in Brazil encroaching into grasslands, suppressed aboveground productivity.

Both for species richness and for biomass, the contrasting effects of *Prosopis* on native vs. non-native understory species is consistent with "invasional meltdown", a process in which invasive species promote or facilitate other invasive species (Simberloff and von Holle 1999). Meltdown has been reported as a form of succession, when early non-native invaders promote later invaders (Flory and Bauer 2014; O'Loughlin and Green 2017; see reviews by Braga et al. 2018; Cavieres 2021; Kuebbing 2020) through their effects on trophic interactions (Green et al. 2011; Meza-Lopez and Siemann 2015). We know of no other reports of invasive trees disproportionately facilitating other non-native species, although positive effects of non-natives on each other are not uncommon (Kuebbing and Nuñez 2015; Cavieres 2021). However, in our case, *Prosopis* increased the richness and biomass of non-native species while decreasing that of natives. The mechanism for this is not clear, but correlations suggest that increasing soil nitrogen (non-native richness and $NO_3^-$, Pearson correlation coefficient, $r=0.86$, $P<0.001$), non-native biomass, $NO_3^-$, $r=0.96$, $P<0.001$), might contribute to the success of non-native species in the understory. Slate et al. (2020) found that non-native *Prosopis juliflora* in the United Arab Emirates was associated with much lower species richness in their understories, relative to open vegetation, than its native congener *P. cineraria*, but that the former was associated with higher densities of agricultural weeds. Other studies indicate that the allelopathic effects of litter from invasive shrubs and trees are more inhibitory to species from their non-native ranges than species from their native range (Inderjit et al. 2011; Kaur et al. 2012; Zheng et al. 2015; Becerra et al. 2018), raising questions about the role of eco-evolutionary history, or novelty, in *Prosopis* invasions.

There are several caveats to consider. First, despite the large spatial scale of our sampling, data were only collected once, and temporal dynamics can be important for the evaluation of impacts (e.g., Prior et al. 2017). Second, our results are correlative, and experimental approaches such as mentioned in the Introduction are needed to separate the effects of *Prosopis* from the effects of site. However, invaded and native plots at a site were close to each other, and had the same average temperature, precipitation, and biome type (Table S1). This suggests that *Prosopis* is responsible for the differences between *Prosopis* and native plots but further experimentation is needed. Darwin suggested that species invading areas with congeneric natives might meet with more resistance than habitats without congeners—the naturalization hypothesis (Darwin 1859), which was explored in global detail by Fan et al. (2023), but this does not seem to hold for *Prosopis juliflora*. Ideas about "eco-evolutionary experience" have expanded on this to encompass various novel traits, that might not be phylogenetically determined, in the biogeographical regions where they invade, that might provide advantages for invaders over naïve natives (Callaway and Aschehoug 2000; Callaway and Ridenour 2004; Saul et al. 2013; Saul and Jeschke 2015). Eco-evolutionary experience, or novelty, is the notion that long-term evolutionary relationships in native communities promote stability and diversity, and that breaking those relationships, as in exotic invasions, disrupts this stability (Saul et al. 2013). In a large-scale study of wetlands, Pearse et al. (2019) found that non-native plant species had greater per-capita effects on other species and that they were associated with a greater loss of species richness than natives, supporting the eco-evolutionary novelty of non-natives because of their "outsized impacts on communities". Trees appear to have similar eco-evolutionary effects in biogeographical studies. For example, many species in the Pinaceae, which is a northern hemisphere family, have been introduced to the southern hemisphere for agroforestry, and some have escaped and become invasive (Richardson et al. 1994). The effects of two of these species, *Pinus contorta* and *P. elliotii*, have been compared in native vs. non-native ranges and found to have stronger inhibitory effects in the non-native ranges (Brewer et al. 2018; Davis et al. 2019a, b). *Prosopis juliflora* does appear to have effects on native species that are different than its native congener *P. cineraria*, and this is consistent with the idea of eco-evolutionary novelty (Kaur et al. 2012; Slate et al. 2020).

## Conclusion

Our results are correlative (Fig. 8), but the SEM suggests potential causal relationships between climate, patch type (*Prosopis* vs. native patches), and the understory richness and biomass of native species. There have been many studies of the effects of plant invasions on community diversity (Hejda et al. 2009, 2021; Pyšek et al. 2012; Lenda et al. 2013) and on the physicochemical aspects of the soil (Vilà et al. 2011; Castro-Díez et al. 2014; Stefanowicz et al. 2016; Rodríguez-Caballero et al. 2017; Pergl et al. 2023) but they are usually studied in isolation (Hulme et al. 2013) or not fully integrated, and if integrated they are restricted in geographical scope (see Linders et al. 2019). Our sites covered a three-fold difference in rainfall, and we collected detailed patch characteristics, community structure, and soil properties and integrated these factors to identify potential drivers of the consistent loss of biodiversity. *Prosopis* restructured understory community composition, appeared to eliminate particular native species, increased the abundance of non-native species, and altered soil characteristics. However, these changes were not strongly correlated with each other. The strong relationships that emerged in path analyses were between increases in tree size in patches due to *Prosopis*, decreases in native biomass, increases in soil phenolics and nitrogen concentrations, and increases in the diversity and biomass of non-native species in the understory (Fig. 8), patterns consistent with disproportional competitive advantages of the invader against natives and promotion of other exotics, as in invasional meltdown.

**Supplementary Information** The online version contains supplementary material available at https://doi.org/10.1007/s11258-025-01569-z.

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**Author contributions** Inderjit conceived the research idea and funded the project; Inderjit designed the research; SM carried out the field work supported by Inderjit. SM carried out lab work and statistical analyses. SK conducted soil analyses. RMC and Inderjit developed conceptual framework and wrote the manuscript. HL conducted path analyses and contributed to conceptual integration. LK prepared Tables S1, S2 and S3, and edited the manuscript. JP carried out initial statistical analysis. MWC helped design the study in the field and edited the manuscript. All authors provided their inputs on the manuscript.

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**Data availability** Data files available on figshare.com. https://doi.org/10.6084/m9.figshare.30217237

## Declarations

**Competing interests** The authors declare no competing interests.

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