Role of species richness and human impacts in resisting invasive species in tropical forests

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Abstract

1. The biotic resistance hypothesis suggests that biodiversity-rich areas should be resistant to biological invasions. Globally, conservationists use this hypothesis to protect diverse ecosystems. However, supporting data are often contradictory, possibly due to several confounding factors. Complexity in inferences increases in the tropics, which are sparsely studied.

2. We hypothesize that human impacts, forest type and climate would modulate the relationship between native and invasive plant richness. To understand these interacting and varying effects of native richness and human disturbance on plant invasions, we sampled 354 grids of 25 km² with equal representation of protected areas (PAs) and multi-use areas (MAs) to record abundance of native and non-native plants from 34 PAs across five forest types in tropical India. We used linear mixed effect models to investigate the occurrence and abundance of invasive plants with respect to varying native richness, human impacts, forest types and climate.

3. Human use of forests increased the richness and abundance of invasive plants across all forest types. After accounting for human use, native species richness of tropical wet forests had a negative relationship with invasive plants richness and abundance, while the relationship reversed with increasing aridity and temperature. Human infrastructure facilitated invasions within PAs.

4. Synthesis. The biotic resistance hypothesis explained a lower number of invasions within protected tropical wet forests but not within dry forests. Human-free protected areas had lower richness and abundance of invasive plants across all systems, especially in wet tropical forests. Our results support the contextual importance of the biotic resistance hypothesis, while stressing the importance of protected areas, insulated from human impacts, to preserve the integrity of vulnerable natural systems.

KEYWORDS
biotic resistance, India, invasive plants, multi-use areas, protected areas, tiger reserves
1 | INTRODUCTION

With the growth of human population and associated transformation of natural systems into agro-industrial urban systems, humans have restructured global biota. This trend is likely increasing as the Anthropocene progresses. Two indices that exemplify the magnitude of these global changes are the loss in native biodiversity (IPBES, 2019a; IPCC, 2014) and prevalence of invasive species (IPBES, 2019b). Introduction and spread of invasive species even in the least modified parts of the earth, such as the Antarctic (Hughes et al., 2020), deep oceans (Levin & Le Bris, 2015), tropical rainforests (Wells et al., 2014) and African deserts (Schachtschneider & February, 2013), have questioned the resistance of these ecosystems to human-induced changes. In invasion ecology, ecological integrity is often measured as the capacity of an ecosystem to retain its native assemblage and resist change (inertia) despite being surrounded by invasive species, and its ability to regain its native assemblage (resilience) and functioning despite being invaded by invasive species (Chambers et al., 2019; Cushman & McGarigal, 2019). The former is popularly known as ‘biotic resistance’ and the latter as ‘biotic resilience’, more recently, it has been placed under the umbrella concept of ecological resilience that refers to the system’s capacity to self-maintain from changing into alternate states (Chambers et al., 2017; Hirota et al., 2011; Levine et al., 2016).

Scientists and conservationists worldwide have advocated conserving biodiverse areas by declaring them as protected, so as to retain their ecological resilience (Ghosh-Harirah et al., 2019; Pimm et al., 2014). However, a large number of invasive species are globally sprawling in protected areas (PAs, Mungi et al., 2020; Shackleton et al., 2020). This questions the premise of protecting biodiverse areas for retaining ecological resistance and resilience to biological invasions. The theory of biotic resistance suggests that species-rich native communities are less invasive (Elton, 1958; Fridley et al., 2007), since available niches are filled, and hence, the community offers a higher competition to invading species (Jannone et al., 2016; Shea & Chesson, 2002; Von Holle, 2013). However, evidence in support of the biotic resistance hypothesis is rare and data are often contradictory (Levine et al., 2004). It is hence important to understand if PAs serve as a relevant conservation strategy in controlling invasive species, particularly in the advent of global change. Simultaneously, we need to know if certain systems are more vulnerable to invasions compared to others, so as to prioritize the allocation of limited resources in effective control of invasive species.

Most studies on the biotic resistance hypothesis are restricted to temperate regions that have relatively simpler species assemblages (Smith & Côté, 2019; Tomasetto et al., 2019). Hyperdiverse tropics offer model systems, by sheer virtue of their diversity, to better explore the role of native species richness in biotic resistance. The lack of studies in tropical systems limits our understanding on the subject (Barlow et al., 2018). Tropics hold a disproportionately large amount of global biodiversity, which is at risk due to increasing demographic, socio-economic, climate change and environmental pressures (Edelman et al., 2014). Tropics are also experiencing a high spread and impacts from invasive species, which adds to the above-mentioned threats (Barlow et al., 2018).

Contradictions in the theory of biotic resistance, also known as the invasion paradox (Brooks et al., 2013; Fridley et al., 2007), arise due to differences in ecological assumptions and statistical designs in experimental and observational studies (Clark & Johnston, 2009; Peng et al., 2019; Smith & Côté, 2019). Observational studies often contradict the biotic resistance hypothesis, since they show a positive correlation between native and invasive species richness (e.g. Peng et al., 2019; Smith & Côté, 2019). This observed increase in invasive species with native species is likely due to the lack of control for environmental and biotic covariates, as well as spatial heterogeneity (i.e. intersystem variations) in these studies (Denslow & DeWalt, 2008; Fridley et al., 2007; Nunez-Mir et al., 2017; Perelman et al., 2007). Recent studies (e.g. Beaury et al., 2020) that account for these effects have found biotic resistance to be ubiquitous. Thus, to decipher the relationship between native and invasive species, it is pertinent to account for environmental settings (Melbourne et al., 2007; Smith & Côté, 2019; Tomasetto et al., 2019). In addition to the influence of environmental covariates and spatial heterogeneity, we believe that human activities would have a profound and varied influence on the vulnerability of ecosystems to biological invasions (Pyšek et al., 2010). A study that enhances our understanding of different tropical systems’ resistance and resilience to plant invasions, while accounting for environmental, biotic, and human impact covariates, would assist policy and management for effective conservation in a changing world.

We use data on plant communities (species richness and abundance) from five tropical forest types sampled from within PAs (least human impact) and pair them with data from the multi-use areas (MAs, high human impact) but having the same vegetation type. Within these areas, we explore how invasive plant richness and abundance correlate with climate, anthropogenic disturbance, forest type, protection regime and native plant richness. We hypothesize that after accounting for environmental covariates, the negative relationship in native and invasive plant richness (i.e. biotic resistance) should vary with forest type and human impacts. Our findings from across varied tropical forest systems show the importance of PAs in conserving native biodiversity from invasive species. Our study provides an enhanced understanding of the biotic resistance hypothesis in the tropics.

2 | MATERIALS AND METHODS

Tropical India is broadly divided into five forest types: dry thorn forest (i.e. savannas), dry deciduous forest, moist deciduous forest, semi-evergreen forest and evergreen forest (Champion & Seth, 1968). Across these forest types, least modified and maximum protected forests are found in the core region of the tiger reserves (Ghosh-Harirah et al., 2019). Hence, we selected these forest types to address our study hypotheses. Tiger reserves and many PAs in India are made up of a legally designated human-free core area and
a buffer (MA) surrounding this core (Jhala et al. 2021). In the buffer of a tiger reserve, local communities use the forests for their livelihoods that include agriculture, livestock grazing, collection of fuel wood and minor forest produce, but no timber-logging, polluting industries or mining are permitted (Narain et al., 2005). We sampled the core (PAs) and buffer (MAs) of 32 tiger reserves, one wildlife sanctuary and one national park (Figure S1) to encompass all of the above forest types to address our hypotheses. The wildlife sanctuary and national park sampled by us had large inviolate areas, with least human modifications surrounded by buffer forests (Ranjitsinh & Jhala, 2010). By sampling PAs and MAs at each site in all forest types, we addressed the effects of human impacts and variations due to forest types.

At each site, we systematically distributed sampling plots on randomly placed 2 km long transects laid in each administrative unit of the forest (beat ~16 km²). On every transect, concentric plots of 30 and 10 m diameter were sampled at every 400 m interval to record all tree species and signs of human impacts in the 30 m plot, and all shrub species in the 10 m plot (Jhala et al., 2017; Figure 1). Irrespective of being native or non-native, all trees were individually counted in 30 m plots and shrubs were quantified as percent cover in the 10 m plot using a modification of the Daubenmire’s scale (Daubenmire, 1968). We enumerated all angiosperms and gymnosperms, but did not record bryophytes, pteridophytes, epiphytes and members of family Poaceae. In the 30 m diameter plot, canopy density was visually estimated as percent cover. Simultaneously, human impacts were quantified as the (a) number of trees with lopped branches, (b) number of trees felled, (c) evidence of grass and bamboo cutting, (d) number of people seen from the plot, (e) number of livestock seen from the plot and (f) livestock–human foot trails within the plot. Sampling was conducted between November 2017 and January 2018, as maximum plant species were recorded during these post-monsoon months in India. Whenever required, regional floras and photographic guides were used to confirm taxonomy (e.g. Daniel et al., 2005; Krishen, 2013; Page, 2017; Sharma, 1993). We made herbaria and/or took digital photographs for species that could not be identified in the field and subsequently consulted plant taxonomists for their identification. At every plot, the geographic coordinates, date, data and photographs were recorded using a customized android app (viz. MSTripES). Sampling details were

![Location of vegetation survey grids (n = 354) in protected areas (PAs) and multi-use areas (MAs), across different forest types of India. For every PA, an equal number of grids (5 × 5 km) were sampled in PA and MA by sampling 22–55 plots per grid. Comparative native richness increased from dry thorn to evergreen forests, canopy was denser inside the PAs across all forest types, and highest number of invasive plants was recorded in moist deciduous forests](image)
separately published in the form of a field guide (Jhala et al., 2017) in regional languages.

A spatial grid of 5 × 5 km was subsequently developed in the GIS domain and all data from the sampled plots were spatially attached to these grids in ArcGIS 10.6.1. This spatial scale (25 km²) was considered appropriate to understand ecological interactions as well as for managerial interventions for invasive plants in the region (Mungi et al., 2020). The information on human impacts, canopy, species occurrence and abundance was computed at this grid scale. In each grid, the number of plots ranged between 26 and 55 and was found to be adequate based on species accumulation curves, as observed in the five forest types (Figure S2). All native plant species were considered for estimating native plant richness, whereas all non-native plant species were considered for estimating invasive plant richness (Khuroo et al., 2012; Pergl et al., 2018).

For an in-depth understanding of the relationship between richness of native plants and abundance of invasive plants, we selected 10 non-native species that were considered as high-concern invasive plants in India (Mathur et al., 2015; Mungi et al., 2019). These invasive plants were *Ageratina adenophora*, *Ageratum conyzoides*, *Chromolaena odorata*, *Hyptis suaveolens*, *Lantana camara*, *Mikania micrantha*, *Parthenium hysterophorus*, *Prosopis juliflora*, *Senna tora* and *Xanthium strumarium*. These invasive plants encompassed a range of species that either occurred across all forest types (e.g. *L. camara* and *P. hysterophorus*) or were restricted to only a few (e.g. *M. micrantha* and *X. strumarium*) and varied in abundances between sites.

2.1 | Environmental covariates

Each grid was assigned to a forest type using a high-resolution forest type data (FSI, 2009). Within the PA grids, we used only those grids that had no signs of human impacts, tree felling and livestock grazing. Some number of grids was selected from multi-used areas paired with each PAs. Thus, addressing the variability caused by human use and habitat heterogeneity. Our sample consisted of 354 grids of 25 km² (44 in dry thorn forest, 106 in dry deciduous forest, 106 in moist deciduous forest, 48 in semi-evergreen forest and 50 in evergreen forest) resulting in a coverage of 8,850 km² of forests (Figure 1).

Although we control for several human impacts through ground sampling, we could not control for proximity to forest fires, roads, human settlements and forest loss; variables that may result in higher propagules making grids more conducive for invasive plants (Mungi et al., 2018, 2020). However, we account for the effects of these variables on invasive species richness and abundance in our analysis by including proximity of sampled grids to burnt forest patches, linear infrastructure, human settlements and cleared forest patches as covariates. We hypothesized that more invasive species occur near these disturbance drivers. We use fire occurrence data from Fire Information for Resource Management System (Giglio et al., 2003; Schroeder et al., 2014) and estimate the mean Euclidean distance of each grid from fire occurrence. We also estimated the mean Euclidean distance of each grid from roads (Survey of India, 2011), railways (Survey of India, 2011) and urban settlements (Esch et al., 2017). Furthermore, we use forest loss information from the Global Forest Watch for the period 2001–2017 (Hansen et al., 2013), and calculated the mean Euclidean distance of each grid from lost forest patches. We use a square root transformation of these distances for our analysis so as to incorporate the biological threshold beyond which their impacts would be minimal. Apart from forest type and anthropogenic modifications, climate is also likely to influence richness and abundance of native as well as invasive plants (e.g. Adhikari et al., 2015; Joshi et al., 2020; Mungi et al., 2020). To account for the effect of climate, we used average annual precipitation and temperature of the warmest quarter from WorldClim (Fick & Hijmans, 2017). The data sources, scale and hypothesized effect of covariates on invasive species richness and abundance are explained in Table 1. Data used for analysis are available online (Mungi et al., 2021).

2.2 | Statistical analysis

We did not consider zero-inflated distribution since none of the sampled grids had zero native or invasive species. Furthermore, we assessed correlation within the environmental covariates using Pearson’s correlation coefficient and found no substantial correlation amongst the variables (Table S1). All covariates were Z-transformed so as to convert them to comparable scales. Thereafter, we used these datasets to explore linear cumulative relationships of (a) invasive plant richness and (b) invasive plant abundance with native plant richness, climatic variables and human impacts.

2.2.1 | Predictors of Invasive plant richness

Invasive plant richness was modelled using linear mixed effect models as a response to annual rainfall (R), temperature of warmest quarter (T), distance from human infrastructure (road, railways and urban settlements) (HD), distance from fire (FD) and distance from cleared forest patches (FLD) as fixed effects; while response to native richness (NR), canopy (C) and interaction between native richness and canopy was modelled as random effects conditional on forest type and protection regime (ForestPA). We first determined the best model for fixed effects and subsequently using the variables selected therein, added the random effects. The full model structure was:

\[
\text{Invasive plant richness} = \frac{(R + T + FD + FLD) + (NR + C + NR \times C) \times \text{ForestPA}}{\text{Response}} + \frac{\text{Fixed effect}}{\text{Random effect}}
\]

We fitted general LMM using the lme4 package in R (ver. 1.1.4; Bates et al., 2018). Model statistics were estimated using the nlme package.
While model fit was assessed by using the MuMIn package (Bartoń, 2018). We used Akaike information criterion (AIC; Akaike, 1973) to compare candidate models with different combinations of covariates for modelling invasive plant richness. Model with the least AIC was considered as the best model (Johnson & Omland, 2004). When models differed by < 5 AIC, we used model average estimates weighted by AIC weights to incorporate model uncertainty in parameter estimates. Coefficients of the best LMM explained the differential effect of covariates on invasive species richness in different forest types, which were interpreted for their ecological relevance.

2.2.2 Predictors of Invasive plant abundance

Invasive plants can colonize and increase in abundance only within a specified climatic niche (Mungi et al., 2020; Panda et al., 2018). Climatic variables and human impacts mask the influence of native plant richness on invasive species since models often extend beyond the climatic niche of the species and rarely control for human impacts. To control for the effect of human impacts and climatic niche, we selected only those grids that were within the core of PAs and the forest type within which the invasive species occurred for this analysis. For 10 high-concern invasive plants, we model the response

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**TABLE 1** Effects of different environmental covariates on the richness and densities of invasive plants in India, along with their relevance, resolution, and data source

| Covariates                                      | Relevance                                                                 | Data source & resolution               |
|-------------------------------------------------|---------------------------------------------------------------------------|----------------------------------------|
| **Fixed effects**                               |                                                                           |                                        |
| Rainfall                                        | Annual rainfall determines productivity and floral diversity across the tropics and the distribution of invasive plants in it (Goncalves et al., 2014; Mungi et al., 2020) | 1 km (Fick & Hijmans, 2017)            |
| Temperature                                     | Higher summer temperature and low rainfall determines the xeric floral diversity and invasions in it (Kannan et al., 2013; Panda et al., 2018) | 1 km (Fick & Hijmans, 2017)            |
| Distance from human infrastructure (roads, railways and settlement) | Areas near human use have higher propagule pressure of invasive plants as humans are primary agents for introducing these species, as well as areas near roads and railways have higher probability of spreading invasive species (Dar et al., 2015; Sharma & Raghubanshi, 2009) | 30 m (Esch et al., 2017; Survey of India, 2011) |
| Distance from fire                              | In wet forests, extensive fire causes loss of native plants and provides a window for establishment of invasive species, which act as a source of propagules (Hiremath & Sundaram, 2005; Mungi et al., 2018) | 100 m (Schroeder et al., 2014)         |
| Distance from cleared forest patches            | Cleared forest provides unutilized resources that can facilitate establishment of invasive species that subsequently act as a source of propagules (Mungi et al., 2020). Used as an index of propagule proximity | 30 m (Hansen et al., 2013)             |
| Native plant richness                          | Higher native richness can deter the establishment of non-native species viz. the biotic resistance hypothesis (Beaury et al., 2020) | Ground sampled                         |
| Canopy density                                  | Dense canopy reduces light availability to the understory, thereby reducing the growth of many understory plants (including invasive plants, Sharma & Raghubanshi, 2009) | Ground sampled                         |
| **Random effects**                              |                                                                           |                                        |
| Forest type                                     | Species assemblage and ecophysiology varies across different forest types, which can change the relationship of species with its environment (Beaury et al., 2020; Mungi et al., 2018) | 30 m (FSI, 2009)                       |
| Protected area                                  | By sampling within and outside protected areas, we control for several human impacts (Ratnam et al., 2019) | www.mstripes.in                         |
of their abundance to native plant richness, climatic variables and proximity to potential propague sources, using multivariate linear regression. Model with the least AIC was considered as the best model. We used the ‘lm’ command in R for these linear models.

2.3 Exploring niche space of high concern invasive plants

To understand how abundance of invasive plants respond to climatic variables and human impacts (source of propagules), we used data on abundance of 10 high concern invasive plants from within grids of PAs. We limit our analysis to PA grids, since in these grids, a multitude of human impacts were controlled (e.g. wood cutting, livestock grazing, extractive uses of forest produce etc.), so we could model the impact of proximity to roads, human habitation and forest loss (potential source of propagules) without confounding effects of other predictors.

We use canonical correspondence analysis (CCA) executed in package vegan in R (Oksanen et al., 2007) with abundance of invasive plants within 5 × 5 km grids and mean values of covariates of annual rainfall, maximum temperature of warmest month and proximity to source of propagules (proximity to human impacts, fire and cleared forest patches). We hypothesized that each invasive plant would differentially ordinate on the canonical components obtained from these climatic and propague proximity covariates. Subsequently, we mapped the sampled PA grids on covariates that had the maximum loadings of significant CCA components to better understand their ecological correlates.

3 RESULTS

Native species richness was high in semi-evergreen and evergreen forests, followed by moist and dry deciduous forest, while dry thorn forest had the least native species richness. Invasive species richness was highest in moist and dry deciduous forest, followed by dry thorn and semi-evergreen forest, whereas the least invasive species richness was observed in evergreen forest. Exploratory analysis revealed a positive trend in the native and invasive plant richness in dry thorn forest, dry and moist deciduous forest, while a negative trend was observed in semi-evergreen and evergreen forests (Figure 2). These correlations were significant only within PAs (Figure 2).

3.1 Predictors of the invasive plant richness

Invasive plant richness was best explained by fixed effects of climatic variables consisting of temperature of the warmest month and annual rainfall, and disturbance variables comprising of distance from burnt forest patches, distance from cleared forest patches and distance from human infrastructure (Table S2). After incorporating random effects (Table S3), invasive plant richness across different forest types was found to differ in their response to native plant richness, canopy cover and the interaction between these variables (Table 2). Fixed effects explained 5% variation in the data, while random effects conditional on forest types and protection explained 87% variation. Amongst random effects, canopy density was negatively related to invasive richness in semi-evergreen, moist deciduous and evergreen forests. Native plant richness was negatively related to invasive richness in PAs of semi-evergreen forests and all (protected and multi-use) areas of evergreen forests (Figure 3). The interaction between canopy cover and native plant richness was significant in most forest types, being positive in dry forests and negative in wet forests (Table 2; Figure 3).

3.2 Predictors of the invasive plant abundance

Best models explaining the abundance of invasive plants had significant effects of climatic, forest and human impact variables (Table 3). Human impacts (proximity to human transmitted propagules) significantly increased abundance of invasive plants; this effect was not observed or was insignificant for L. camara, P. hysterophorus and P. juliflora. Native plant richness alone or in interaction with canopy density reduced abundance of invasive plants in wet forests (M. micrantha, C. odorata, A. adenophora and A. conyzoides). Native plant richness had no significant relationship with invasive plant density of dry forests (P. juliflora, X. strumarium, H. suaveolens and S. tora). The R-squared value for all these models varied from 0.19 to 0.53 (Table 3).

The primary ordination axis of CCA explained 79% of the variation in abundance of invasive plants (Tables S1.1 and S1.2). This axis had the highest loadings for annual rainfall (~0.85) and temperature of the warmest quarter (0.94, Table S1.3). The 10 invasive plants segregate along their niche space defined by annual rainfall and temperature of the warmest month across tropical India (Figure 4).

4 DISCUSSION

Native species richness followed a moisture gradient being maximum in the wet forests (both semi-evergreen and evergreen) and least in the dry thorn forest. Whereas invasive richness had a parabolic relationship with moisture, being highest in moist deciduous forests and least in the wet evergreen and dry thorn forests. Native and invasive richness were positively correlated for dry forests (dry thorn, dry deciduous and moist deciduous) irrespective of their protection status. While in PAs of wet forests (semi-evergreen and evergreen) invasive plant richness was negatively correlated with native plant richness, MAs did not show any trends (Figure 2).

Across all forest types (moisture and temperature gradients) we found that PAs consistently had lower invasive plants compared to MAs (Figure 2). However, we had disparate results regarding the biotic resistance hypothesis. Patterns observed from wet forests were in consonance with the hypothesis, where invasive species
richness declined with increasing native plant richness, while in dry forests, invasive species richness increased along with native species richness.

Tiger reserves in wet forests (Kalakkad-Mundanthurai, Periyar, Anamalai, Parambikulam, Bhadra, Kali and Simlipal; Figure S1) resisted invasive plants by their species-rich communities and retained their ecological integrity. However, this relationship of biotic resistance was not significant for multi-use wet forests. This suggests that human use neutralizes the benevolent effect of native plant richness in resisting invasive plants. These results lend support to the creation of PAs in wet forest systems, where management activities restore native richness and reduce human use as a measure to arrest invasive species. Wet forest in the proximity of human disturbances (roads, railways, human settlements, burnt forest patches and cleared forest patches) had higher invasive species richness, possibly because these disturbed sites were sources of propagules. Forests around these disturbances were found to be densely invaded by *M. micrantha* and *C. odorata*, which were the major invasive species in wet forests. Developmental activities like linear infrastructure and clear felling (Nayak et al., 2020) in wet forests will likely result in fragmentation and subsequently reduce their biotic resistance and should therefore be curtailed within and in the proximity of PAs. Mitigation measures to maintain habitat connectivity for wildlife in the form of engineering solutions (Clevenger & Huijser, 2011) often utilized to justify such developmental activities in PAs cannot mitigate the detrimental effects of fragmentation on biotic resistance.

While protected tropical wet forests ubiquitously displayed biotic resistance, drier forests had a contrasting positive relationship with native richness. These forests (moist and dry deciduous forests and dry thorn forests) had lower native plant richness and canopy compared to wet forests (Figure 1). Dry forests have also been historically exploited for timber extraction (even in PAs), are currently grazed by livestock, and fragmented by agriculture, monoculture plantations and linear infrastructure (Nayak et al., 2020). Additionally, these remaining forests are historically modified in their composition by forestry practices (Joshi et al., 2018) that promoted fast-growing woody species were for either timber production or greening of the landscape (e.g. *P. juliflora*, *Leucaena leucocephala*; Ratnam et al., 2011). Promoting monotonous woody plants depletes the regeneration of herbaceous vegetation under it and can facilitate the growth of invasive plants by altering edaphic characteristics (Parr et al., 2014). Therefore, in these drier forests, the manifestation of biotic resistance could have been curtailed by compounding effects of contemporary and historical human use.

Dry thorn forests were found to have naturally sparse trees (low canopy cover) and limited number of species. Native richness and
TABLE 2  Coefficients of covariates used to assess the determinants of invasive plant richness in different tropical forest types using linear mixed regression for every protected and multi-use forest type. Increasing wetness of the forest is represented by darker green shades. Values in bold are significant (p value < 0.1)

| Forest          | I     | NR     | C       | NR°C    | R       | T       | FD      | FLD     | HD      |
|-----------------|-------|--------|---------|---------|---------|---------|---------|---------|---------|
| Dry thorn MA    | 12.13 | 1.01 (±4.13) | 0.08 (±1.21) | 0.24 (±0.63) | 0.11 (±0.23) | -0.42 (±0.22) | -0.42 (±0.16) | -0.39 (±0.21) | -1.43 (±0.15) |
| Dry thorn PA    | 16.36 | 5 (±4.38)  | 0.85 (±1.02)  | 0.71 (±0.59)  | 0.11 (±0.23)  | -0.42 (±0.22) | -0.42 (±0.16) | -0.39 (±0.21) | -1.43 (±0.15) |
| Dry deciduous MA| 16.12 | 2.86 (±1.01) | 0.21 (±0.94)  | 0.36 (±0.31)  | 0.11 (±0.23)  | -0.42 (±0.22) | -0.42 (±0.16) | -0.39 (±0.21) | -1.43 (±0.15) |
| Dry deciduous PA| 16.95 | 6.92 (±2.23) | 0.45 (±0.59)  | 1.17 (±0.51)  | 0.11 (±0.23)  | -0.42 (±0.22) | -0.42 (±0.16) | -0.39 (±0.21) | -1.43 (±0.15) |
| Moist deciduous MA | 21.56 | 1.64 (±0.47) | -2.24 (±0.88) | 0.11 (±0.19)  | 0.11 (±0.23)  | -0.42 (±0.22) | -0.42 (±0.16) | -0.39 (±0.21) | -1.43 (±0.15) |
| Moist deciduous PA | 21.14 | 2 (±0.52)  | -3.75 (±0.67) | 0.46 (±0.1)   | 0.11 (±0.23)  | -0.42 (±0.22) | -0.42 (±0.16) | -0.39 (±0.21) | -1.43 (±0.15) |
| Semi evergreen MA | 12.25 | 0.46 (±0.69) | -0.56 (±2.16) | 0.21 (±0.22)  | 0.11 (±0.23)  | -0.42 (±0.22) | -0.42 (±0.16) | -0.39 (±0.21) | -1.43 (±0.15) |
| Semi evergreen PA | 12.04 | -1.87 (±0.97) | -0.56 (±2.22) | -0.31 (±0.27) | 0.11 (±0.23)  | -0.42 (±0.22) | -0.42 (±0.16) | -0.39 (±0.21) | -1.43 (±0.15) |
| Evergreen MA    | 13.09 | -1.1 (±1.01) | -0.68 (±2.09) | -0.19 (±0.2)  | 0.11 (±0.23)  | -0.42 (±0.22) | -0.42 (±0.16) | -0.39 (±0.21) | -1.43 (±0.15) |
| Evergreen PA    | 7.72  | -2.02 (±1.06) | 0.67 (±2.1)   | -0.24 (±0.19) | 0.11 (±0.23)  | -0.42 (±0.22) | -0.42 (±0.16) | -0.39 (±0.21) | -1.43 (±0.15) |

Abbreviations: C, average canopy density; FD, distance from fire; FLD, distance from lost forest; Forest, forest type and protection regime, for example, evergreen protected area (PA), evergreen multi-used area (MA); HD, distance from human infrastructure; I, intercept; NR, richness of native plants; R, annual rainfall; T, mean temperature of warmest quarter.
invasive richness were both likely limited by nutrients and moisture in these forests (Guttal & Jayaprakash, 2007). The woodlands in the dry thorn forests, which are a product of the historical plantation activities, were found to have higher invasive richness as well as higher abundance of invasive plants like *P. juliflora*, *X. strumarium* and *S. tora*. However, despite the above results, areas protected from contemporary human use (Ranthambhore, Sariska, Kuno, Nauradehi; Figure S1) were found to have less richness and abundance of invasive plants.

Moist and dry deciduous forests though categorized as woodland are functionally a spatial mosaic of broadleaf forests and savannas (Kumar et al., 2020; Ratnam et al., 2016, 2019). These forests are spread across central and peninsular India and are heavily fragmented by anthropogenic land uses (Roy et al., 2013) and degraded by high density livestock grazing (Dave & Jhala, 2011). Large tracts of these forests are now restricted to PAs, which are dominated by tree cover (Nayak et al., 2020). Particularly dry deciduous forests that were substantially modified by plantations of timber species (e.g. *Tectona grandis*, *Acacia* sp.) during the colonial rule had positive correlation of native and invasive plant richness. Many PAs in these forest types (Pench, Satpuda, Nagarhole) still retain these plantations and therefore also exhibit high invasive plant richness (Figure S1). Invasive plants like *L. camara*, *S. tora* and *H. suaveolens* were found in high densities across these forests. Invasive richness was higher in areas with open canopy (e.g. Rajaji and Dudhwa), and as canopy density increased, the invasive richness declined (e.g. Corbett and Valmiki; Figure S1). Dominant invasive species in these forests (*L. camara*, *A. adenophora* and *A. conyzoides*) were found at high density either in open canopy areas or around human disturbances.

We attribute the contrasting pattern of biotic resistance in wet and dry forests to the super abundance of propagules made available in and around dry forests by current and historical human impacts. Dry forests have been traditionally used more by people than the contemporary wet forests. The management activities in dry forests involved plantation of non-native species that had high invasiveness (e.g. *P. juliflora*; Mungi & Qureshi, 2018), or were brought in the proximity through imported seeds for agriculture (e.g. *Parthenium hysterophorous*, *S. tora* and *X. strumarium*). Anthropogenic disturbances like fire and forest loss facilitated invasive plant richness across all forest types, while disturbance like human infrastructure strongly influenced their richness in wet forests. Hence, irrespective of the forest types, PAs should be managed for minimal anthropogenic modifications, in terms of habitat change (e.g. plantation), changing natural fire regime, livestock grazing and infrastructure development (e.g. road, railways, power lines etc.).

A potential limitation of our study is our definition of native plant richness, wherein we include all trees, shrubs and herbs but exclude grasses. Our exclusion of grasses was because of our inability for definitive taxonomic identification in the absence of inflorescence during the sampling period. However, in our defence, we argue that large-scale field studies can rarely include all taxa of native flora that can potentially contribute to biotic resistance (inclusive of pteridophytes, bryophytes, etc.). We believe that by defining what constitutes native richness, we allow our study to remain relevant for comparisons with other studies. Besides, we interpret our results conservatively, inclusion of Poaceae would only strengthen the reported pattern on biotic resistance of different forest systems. A strong point of our study is that we take advantage of manipulative experiments wherein large
**TABLE 3** The coefficients (standard error) of the best models explaining the relationship of invasive plant abundance and ecological covariates. Color shades are representative of the forest types in which these invasive plants are found, where increasing wetness of the forest is represented by darker green shades. Values in bold are statistically significant ($p < 0.1$).

| Species, $R^2$; $p$ value | I     | NR         | C         | NR*C     | T         | R         | HD        | FD         | FLD         |
|---------------------------|-------|------------|-----------|----------|-----------|-----------|-----------|------------|-------------|
| Chromolaena odorata ($R^2$: 0.43; $p < 0.001$) | 8.1 (±11.31) | 8.24 (±9.85) | 7.56 (±11.99) | -10.41 (±11.8) | -12.58 (±6.76) | - | -15.38 (±3.25) | - | - |
| Mikania micrantha ($R^2$: 0.50; $p < 0.001$) | -18.73 (±10.12) | 9.02 (±9.35) | 27.02 (±10.78) | -24.85 (±11.62) | -20.26 (±6.05) | - | -7.24 (±2.97) | - | - |
| Ageratina adenophora ($R^2$: 0.26; $p < 0.01$) | 9.18 (±2) | -2.13 (±1.39) | - | - | - | 9.17 (±5.59) | - | -6.08 (±2.73) | - |
| Ageratum conyzoides ($R^2$: 0.19; $p < 0.001$) | 8.09 (±1.73) | -4.74 (±1.61) | - | - | 6.24 (±2.35) | 3.74 (±1.96) | - | -6 (±2.25) | -6.23 (±2.23) |
| Lantana camara ($R^2$: 0.13; $p < 0.01$) | 12.64 (±1.51) | 6.82 (±1.57) | -4.22 (±1.69) | -4.46 (±1.63) | -1.21 (±1.53) | -2.01 (±1.62) | - | - | - |
| Senna tora ($R^2$: 0.53; $p < 0.001$) | 8.08 (±2.27) | - | -3.01 (±1.72) | - | 6.22 (±2.28) | -8.56 (±3.54) | - | 3.75 (±1.6) | 7.22 (±1.73) |
| Parthenium hysterophorus ($R^2$: 0.23; $p < 0.001$) | 3.91 (±2.39) | -3.63 (±1.93) | - | - | 6.87 (±2.48) | -10.81 (±3.62) | -2.88 (±1.82) | - | - |
| Hyptis suaveolens ($R^2$: 0.26; $p < 0.001$) | 5.41 (±2.25) | 5.05 (±1.69) | - | - | 5.75 (±2.2) | -7.58 (±3.48) | 4.09 (±1.67) | -4.35 (±1.73) | - |
| Prosopis juliflora ($R^2$: 0.38; $p < 0.01$) | -6.63 (±5.05) | - | -5.99 (±2.62) | - | 9.18 (±3.06) | -14.8 (±5.22) | - | - | 3.06 (±2.06) |
| Xanthium strumarium ($R^2$: 0.47; $p < 0.001$) | -9.1 (±6.77) | - | -12.74 (±3.47) | - | 23.41 (±3.94) | -14.11 (±6.76) | -4.79 (±2.66) | - | - |

Abbreviations: C, average canopy density; FD, distance from fire; FLD, distance from lost forest; HD, distance from human infrastructure; I, intercept; NR, richness of native plants; R, annual rainfall; T, mean temperature of warmest quarter.
parts of forest systems were devoid of human use (PAs) and conclusively show the detrimental effect of human use by increasing invasive species richness and abundance. Our study could be further extended by quantifying and manipulating propagule availability and quantification of their establishment in florally rich versus impoverished forests and in protected versus multi-use forests.

Our results bring in a better comprehension of the theory of biotic resistance within tropical systems. We found that this hypothesis holds true in systems that had high resistance and low resilience (wet tropical forests; Isbell et al., 2015); areas that are of paramount importance for targeting conservation investments. Whereas the relationship between native plant richness and invasive plant richness and abundance was less pronounced or inverse within systems that were known to have low resistance but higher resilience (dry tropical forests; Isbell et al., 2015). This result was further compounded by high human impacts in these drier forests. Human impacts opened up all systems to invasive species. Our results show the importance of protecting forests from anthropogenic modifications. Protection of hyperdiverse tropical forests results in a positive feedback, since they reduce biological invasions, which will in turn safeguard native species richness and abundance, ensuring their continued ecosystem services (IPBES, 2019b). Our results are timely, as tropical forests worldwide are being destroyed and degraded by unsustainable human uses and fragmented by infrastructure (Curtis et al., 2018; Song et al., 2018). Hence, there is an urgent need of making large tracts of tropical wet forests free of human modifications globally, to protect their ecological integrity and services.

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**FIGURE 4** Using the canonical correspondence analysis, abundance of invasive plants was found to best ordinate along the rainfall and temperature gradient in tropical forests of India. The distribution of these species can be compared with the forest type gradient, which is also determined by the rainfall and temperature gradient.
CONFLICT OF INTEREST
None of the authors have a conflict of interest.

AUTHORS’ CONTRIBUTIONS
Q.Q., Y.V.J. and N.A.M. conceived the study, N.A.M. collated the data; Y.V.J. and N.A.M. analysed the data and wrote the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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DATA AVAILABILITY STATEMENT
Data available from the Dryad Digital Repository https://doi.org/10.5061/dryad.b866tl1r4 (Mungi et al., 2021).

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**SUPPORTING INFORMATION**

Additional Supporting Information may be found online in the Supporting Information section.