

Railways redistribute plant species in mountain landscapes

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Abstract

1. The significant portion of global terrestrial biodiversity harboured in the mountains is under increasing threat from various anthropogenic impacts. Protecting fragile mountain ecosystems requires understanding how these human disturbances affect biodiversity. As roads and railways are extended further into mountain ecosystems, understanding the long-term impacts of this infrastructure on community composition and diversity gains urgency.
2. We used railway corridors constructed across the mountainous landscapes of the Kashmir Himalaya from 1994 to 2013 to study the effects of anthropogenic disturbance on species distributions and community dynamics. In 2014 and 2017, we collected vegetation data along 31 T-shaped transects laid perpendicular to the railway line, adopting the MIREN (Mountain Invasion Research Network) road survey methodology.
3. Plant communities shifted significantly from 2014 to 2017, potentially because of an ongoing species redistribution after railway construction, driven mainly by declines in both native and non-native species richness, and an increasing abundance of a few non-native species, especially in areas away from the railway track.
4. These patterns indicate an advancing succession, where initially—rare—pioneer species are replaced by increasingly dominant and often non-native competitors, and potentially suggest a trend towards delayed local extinctions after the disturbance event. Native and non-native species richness was negatively correlated with elevation, but that relationship diminished over time, with the abundance of non-natives significantly increasing at higher elevations.
5. *Synthesis and applications.* Transport corridors seem to facilitate the spread of non-native species to higher elevations, which has serious implications considering the warming mountain tops. Our results indicate that the plant communities next to railways do not reach equilibrium quickly after a disturbance. More than 10 years after railway establishment within Kashmir Himalaya, succession continued, and signs pointed towards a landscape increasingly dominated by non-native species. Our study indicates that the single disturbance event associated with constructing

railway in this Himalayan region had large and long-lasting effects on plant communities at and around this transport corridor and suggests the need for a long-term region-wide coordinated monitoring and management program.

KEYWORDS

biodiversity, disturbance, elevation, Himalaya, invasion, mountain, railways

1 | INTRODUCTION

Mountain ecosystems contribute disproportionately to the global species pool of terrestrial biodiversity, with diverse assemblages of small-ranged species constituting montane centres of endemism (Rahbek et al., 2019). The unique biodiversity in these fragile ecosystems is threatened by the upslope spread of non-native species, mainly driven by unbridled land-use changes associated with ever-increasing human activities, and now aided by a rapidly warming climate (Dainese et al., 2017; Guo et al., 2018; Marini et al., 2009; Petitpierre et al., 2016). As biological invasions are an outcome of the human-mediated transportation of species beyond their natural distribution ranges (Essl et al., 2018), the fast-increasing footprint of transport infrastructure in the form of roads and railways in mountain landscapes acts as a dispersal corridor for the invasion of non-native species (Bacaro et al., 2015; Haider et al., 2018; Lembrechts et al., 2017; Medvecká et al., 2018). These linear infrastructures facilitate the dispersal of non-native species across physical and environmental barriers and by transforming nearby habitats to be suitable for the initial establishment and subsequent spread of invasive species (McDougall et al., 2018).

During the past two decades, research into biological invasions in mountainous regions has gained momentum (Ahmad et al., 2019; Alexander et al., 2011; Lembrechts et al., 2017; Liedtke et al., 2020; Pauchard & Alaback, 2004; Pauchard et al., 2009; Seipel et al., 2012). However, most of what we currently know about the role of transport infrastructure in facilitating invasions in the mountains across the globe comes from road ecology studies (Lázaro-Lobo & Ervin, 2019). The role of railways as conduits for plant invasions remains little investigated (but see Benedetti & Morelli, 2017; Hansen & Clevenger, 2005; Wang et al., 2015), and only a few studies have been conducted in the mountains (e.g. Becker et al., 2005; Deng et al., 2020). The basic scientific understanding about the relative role of this transport system in the dispersal of non-native species within mountain ecosystems and on how this can be better managed is, therefore, still poorly known. Nonetheless, railways clearly act as dispersal corridors that exert considerable effects on the biodiversity and ecosystem functioning of surrounding natural areas (Fahrig, 2003; Penone et al., 2012).

A fundamental ecological consequence of railways, as with other kinds of linear transport corridors, is the suite of changes that occur in adjacent natural vegetation (Hansen & Clevenger, 2005; Pollock et al., 2017; Wang et al., 2015; Wiłkomirski et al., 2012). These transport infrastructures all result in large gains and losses of species,

creating new interaction networks among the novel set of species that establish in that location (Dornelas et al., 2019; Lembrechts et al., 2017). The remixed sets of species interact ecologically, evolve in relation to the new physical environment and co-evolve in relation to one another, changing the biodiversity of the affected region (Ellis, 2018). However, how far these novel ecosystems extend and how fast these changes take place is still unresolved. As railway networks filter through various land-use types (e.g. agricultural, urban, areas with high natural value, intact forests), they enhance the dispersion of non-native species into more pristine habitat types, thereby inducing changes in the species composition, particularly in adjacent communities (Hansen & Clevenger, 2005). However, to the best of our knowledge, no study has so far investigated the impact of this transport infrastructure on species' redistributions. Here, we try to fill this knowledge gap by sampling T-shaped transects perpendicular to railway stations—as hotspots of introduction of new species—and along the railway tracks located between these stations in the mountainous region of Kashmir Himalaya by adapting the road survey methodology from the Mountain Invasion Research Network (MIREN). Surveys were performed during the summer of 2014 and 2017. We hypothesize that the railway (both construction and use) would significantly shift both native and non-native plant species distributions in the region, resulting in the establishment of novel ecosystems dominated by an increasingly large proportion of non-native species, while native species are gradually pushed towards extinction. These shifts towards novel ecosystems are expected to be particularly strong at low elevations, where anthropogenic disturbance is traditionally higher, yet they would gradually worsen over time along the entire elevation gradient as traffic, and therefore species dispersal, increases. Thus, our study sheds light on how railways act as conduits for non-native species into mountainous areas, where non-native species may percolate from disturbed areas into adjacent natural ecosystems.

2 | MATERIALS AND METHODS

2.1 | Study area

Kashmir Himalaya, located in the north-western side of the Himalayan biodiversity hotspot, is a mountainous valley bounded by the Pir Panjal range of Lesser Himalaya in the south and south-west, and the Zaskar range of the Greater Himalaya in the north and northeast (Dar & Khuroo, 2020). The climate of the region, marked

by well-defined seasonality, resembles that of mountainous and continental parts of the temperate latitudes. It receives annual precipitation of about 1,050 mm, mainly in the form of snow during the winter months. Temperatures range from an average daily maximum of 31°C and minimum of 15°C during summer to an average daily maximum of 4°C and minimum of -4°C during winter. The future climate change projections of the region (under two Representative Concentration Pathways, RCP 8.5 and RCP 4.5) point towards more severe temperature changes than the global average, with a median value of 2.1 and 2.8°C as compared to 1.5 and 2.0°C global temperature rise (GTR) respectively (Yaduvanshi et al., 2019). The lowlands of this region are known to be heavily invaded by non-native species (Khuroo et al., 2007; Mehraj et al., 2018, 2021; Muzafar et al., 2019), which have also been shown to move to higher elevations along roads in this Himalayan region (Dar et al., 2018).

To ensure a reliable transportation system for the Kashmir region, and its connection with the Indian Railways, the construction of 345 km of railway was started in 1994. The Jammu–Udhampur–Katra–Quazigund–Baramulla (JUSBRL) railway is divided into four sections, out of which leg 3 of the line traverses the Kashmir valley. The connection to the Indian Railway is planned for December 2022, but the Baramulla to Banihal (~135 km) part of this leg was completed in 2013. The present study was carried out along the operational leg 3 of Kashmir railway (130 km)—the only railway line of the region—that starts from Baramulla on the north-western edge of the Kashmir, passing through the Pir Panjal tunnel, connecting the south and south-west Bichleri valley of Banihal through the Qazigund area of the Kashmir region (Figure 1). The Kashmir railway became operational between Anantnag and Mazhom stations in October 2008. The service was extended beyond Mazhom to Baramulla in February 2009, and in the south, Anantnag was connected to Qazigund in October 2009. In December 2012, Qazigund was connected to Banihal, but this leg 3 still remains disconnected from the rest of the Indian railways. Thus, the main source of propagules of non-native species could be most likely from the alien species pool already

present in cities falling along its length and seldom at the southern border of the Kashmir valley from mainland India.

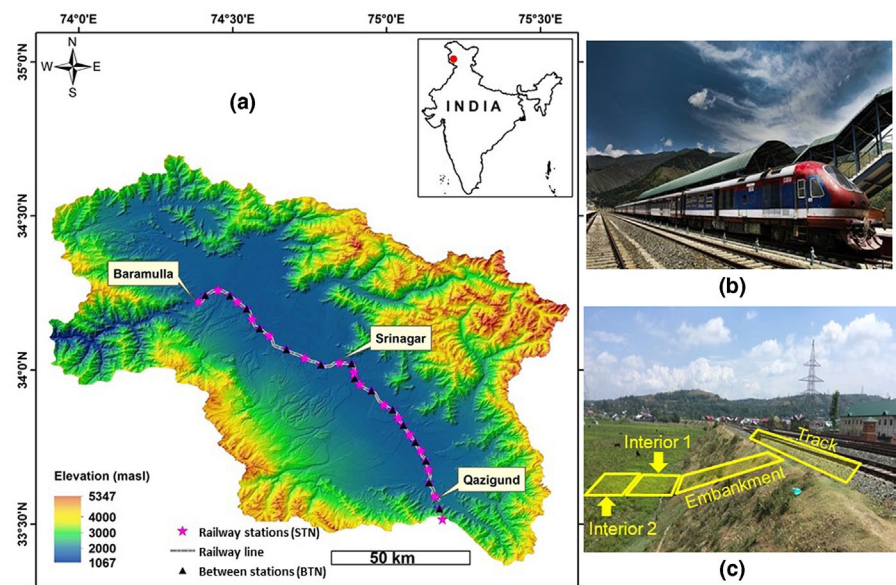
2.2 | Sampling design and data collection

Several field reconnaissance surveys were carried out during the year 2014 to get a good idea about the area, its species composition and distribution, and the approachability of the railway track. The entire stretch of the railway (130 km) going through the Kashmir region was divided into 31 sites consisting of 16 stations (STN) and 15 between-station (BTN) sites within a narrow elevational belt from 1,591 to 1,741 m a.s.l. (see Appendix S1). All sites were first sampled during 2014 and then resampled during 2017. The sampling for BTN sites was carried out at the midpoints between the stations. The upper surface of the railway track was flat and raised from the adjacent interior plots with an embankment. All the filling materials (e.g. stones, sand, soil, etc.) used to construct track and embankments have been locally procured.

At each site, four transects were laid out with one plot parallel to the track edge and the other three plots perpendicular to it, together forming a 'T' (Figure 1, Modified from Seipel et al., 2012). The head of the 'T' was 50 × 2 m with a total length of 50 m, between the railway tracks, and the remaining three plots (embankment, interior 1 and interior 2) were perpendicular to the track, ending ca. 150 m from the track. A handheld GPS (Garmin eTrex; Garmin International, Inc.) was used for recording the elevation and geo-coordinates of each plot. Within each of the plots (4 × 31 = 124 plots), we recorded all vascular plant species, and at each site, twelve 1 × 1 m quadrants were laid out for recording species abundance. In total, we recorded 123 species, 75 of which were native and 48 non-native (see Appendix S2).

The selected sites, as introduced above, were first sampled during 2014 and then resampled during 2017. Plant specimens of all the vascular species sampled were collected and processed following

FIGURE 1 Railway of Kashmir Himalaya: (a) map with marked localities of the sampling sites, (b) a view of the railway station (STN), (c) a sampling site between stations (BTN) illustrating the sampling design with four 2 × 50 m plots laid down in form of a 'T' (plots not drawn to scale)



standard herbarium methods (Forman & Bridson, 1989). The specimens were identified by comparing the housed herbarium samples at the Centre for Biodiversity and Taxonomy, University of Kashmir, and consulting relevant taxonomic literature (Stewart, 1972; www.efloras.org). The specialized taxonomic database of The Plant List (www.theplantlist.org) was used for the nomenclature of all the collected species. During field sampling, the life- and growth-form data pertaining to each plant species were recorded. On the basis of available scientific literature (Khuroo et al., 2007; Mehraj et al., 2018; Muzafar et al., 2019) and specialized websites such as GRIN (Germplasm Resources Information Network, www.ars-grin.gov), plant species were categorized into native and non-native species.

2.3 | Statistical analysis

All analyses were done in R (R Core Team, 2015). To test for trends at the community level, we analysed total, non-native and native species richness and abundance (summed abundance of all species) separately, as a function of year (2014 or 2017), elevation (continuous variable), track age (continuous variable) or plot type [categorical variable; track, embankment, interior 1 or interior 2, separately for at STN and BTN sites] and all their two-way interactions. We used GLMs with a Poisson distribution for species richness, and linear models with a logarithmic correction ($\ln(x + 0.1)$) for species abundance to conform

to normality of model residuals. We used the function *dredge* from the package *MuMIn* (Barton, 2016) to create all potential submodels and to select the best model (i.e. the model with the lowest AIC).

Next, we tested for changes in the abundance of the most common native and non-native species (i.e. all species with more than 10 occurrences out of the 124 plots, for a total of 81 species) using species-specific linear models [with a logarithmic correction ($\ln(x + 0.1)$), following the procedure in Lembrechts et al. (2017)]. We modelled each species as a function of the year, elevation, distance to the railway and their two-way interactions; created all submodels; and selected the model with the lowest AIC. Then, we analysed all the coefficients of these best models for each species as a function of species' characteristics [status (native vs. alien), life-form (annual vs. perennial) and growth-form (herb vs. grass)]. This analysis allowed us to study trends across different groups of species with related functional traits.

Finally, we analysed shifts in the community as a whole using non-metric multidimensional scaling [NMDS, function *metaMDS* in the *vegan* PACKAGE (Oksanen et al., 2013)]. We plotted the first two dimensions of this NMDS and super-imposed a polygon delineating the year-effect (function *ordihull*) and a contour plot (function *ordisurf*) delineating the native and non-native species richness. We also plotted arrows showing the shifts in the centre of the community for each plot type (tracks, embankments, interiors 1 and 2) from 2014 to 2017, separately for sites at STN and BTN.

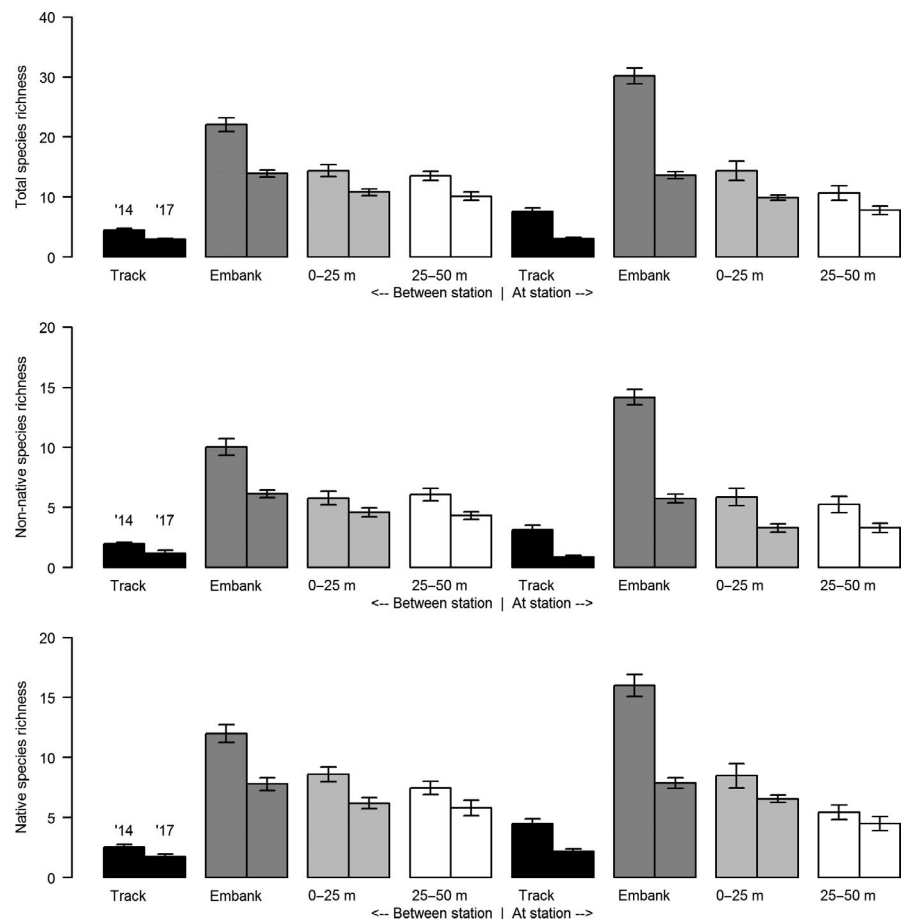


FIGURE 2 Average (with standard error) of total (top), non-native (middle) and native (bottom) species richness for each plot type in 2014 and 2017. For outcomes of the models, see Table 1

TABLE 1 Estimate and *p*-value of the best (i.e. lowest AIC) GLMs with a Poisson distribution of total, non-native and native species richness against plot type, year and their interactions. Significant values ($p < 0.05$) are in bold, borderline significant values ($0.05 < p < 0.1$) are in bold and italics

	Total richness		Non-native richness		Native richness	
	Estimate	<i>p</i> -value	Estimate	<i>p</i> -value	Estimate	<i>p</i> -value
(Intercept)	5.055	<0.001	4.286	0.002	4.461	<0.001
Year	-1.634	<0.001	-1.821	0.010	-1.516	0.012
Elevation	-0.002	<0.001	-0.002	0.008	-0.002	0.003
Between station						
Embank	1.583	<0.001	1.616	<0.001	1.535	<0.001
0–25 m	1.156	<0.001	1.065	<0.001	1.244	<0.001
25–50 m	1.094	<0.001	1.110	<0.001	1.134	<0.001
At station						
Track	0.520	<0.001	0.446	0.054	0.449	0.004
Embank	1.896	<0.001	1.959	<0.001	1.722	<0.001
0–25 m	1.154	<0.001	1.077	<0.001	1.261	<0.001
25–50 m	0.857	<0.001	0.965	<0.001	0.845	<0.001
Interactions						
Year × Elevation	0.001	0.001	0.001	0.018	0.001	0.022
Between station						
Year × Embank	-0.008	0.908	0.005	0.963		
Year × 0–25 m	0.049	0.501	0.093	0.410		
Year × 25–50 m	0.049	0.509	0.058	0.608		
At station						
Year × Track	-0.159	0.064	-0.254	0.073		
Year × Embank	-0.120	0.086	-0.131	0.224		
Year × 0–25 m	0.020	0.784	-0.021	0.857		
Year × 25–50 m	0.041	0.590	0.017	0.884		

3 | RESULTS

3.1 | Species richness

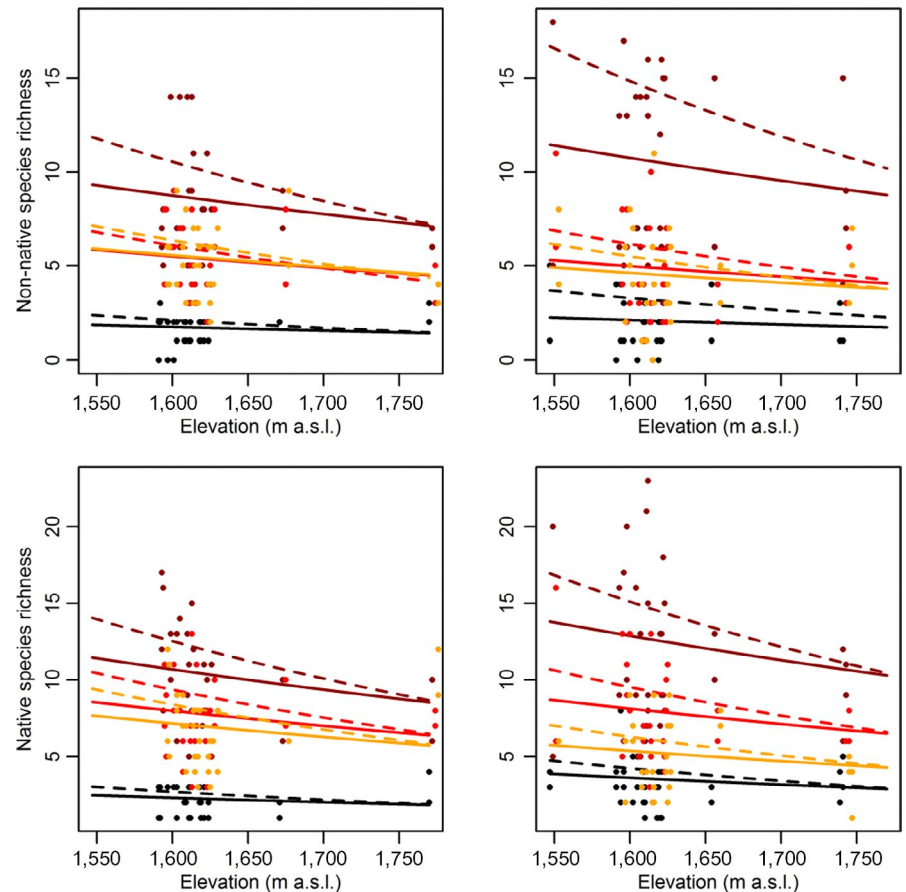
On average, total plant species richness across all the sites, as well as the richness of both native and non-native species, declined between 2014 and 2017 (Figure 2; Table 1). Species richness declined slightly more in the plots between the tracks and those on the embankment at the station, with a higher decline in non-native species richness on the embankments at the station. Total species richness, and species richness of both natives and non-natives, was highest in the plots on the embankments and lowest for those between the tracks. Importantly, the richness of native and non-native species was similar, ranging from, on average, three species on the tracks to close to 15 species per plot on the embankments.

Both native and non-native species richness was negatively correlated with elevation. The reduction in species richness from 2014 to 2017 was larger at lower elevations than at higher elevations for both native and non-native species, resulting in less steep elevational declines in all the plots in 2017 than in 2014 (Figure 3; Table 1).

3.2 | Species abundance

Despite the observed decline in total species richness across all the plots between 2014 and 2017, the summed species abundance increased in several of the plot types over the same period, especially further away from the tracks and at higher elevations (Figures 4 and 5). The decline on the embankments was driven by a decrease in non-native species abundance at lower elevations, while the increase in species abundance in the interior natural vegetation plots was mostly due to an increase in non-native species abundance, yet secondarily also in native species. Importantly, non-native species had on average a much higher abundance than native species, especially on the embankments (Figure 4; Table 2). Non-native species abundance was better explained as a function of elevation than of track age, while native species abundance correlated better with the latter, significantly increasing with increasing track age. Interestingly, increases in species abundance in the natural vegetation were much stronger at the STN than BTN plots, largely (yet not only) driven by non-native species.

FIGURE 3 Non-native and native species richness as a function of elevation (x-axis), year (2014 = dashed line and 2017 = full line) and plot type (left = between station, right = at station: track (black), embankment (dark red), 0–25 m (red) and 25–50 m (orange)). Results from the best (i.e. lowest AIC) GLM with a Poisson distribution (see Table 1)



3.3 | Individual species-specific patterns

Some of the native species such as *Achillea millefolium*, *Calamintha umbrosa*, *Fumaria indica*, *Lotus corniculatus*, *Malva neglecta*, *Nasturtium officinale*, *Potentilla reptans*, *Ranunculus laetus*, *Tussilago farfara* and *Veronica beccabunga*, which were common in 2014, were not found during the resurvey of 2017. On the other hand, several new non-native species like *Arundo donax*, *Conium maculatum*, *Solanum nigrum* and *Trifolium fragiferum* were reported for the first time during the resurvey (Rashid et al., 2021).

On an individual species basis, the most common non-native species, on average, showed a slight increase in abundance in all the plot types (even though the total non-native abundance decreased in some plot types, as shown before). However, there was a large variation in their abundance, and thus overall changes over time did not differ significantly from zero (Figure 6). On the other hand, most common native species showed a significant decrease in abundance on an individual species basis in all the plot types, although the total native species abundance has been shown to increase in some. Native species like *Artemisia absinthium*, *Astragalus grahamianus*, *Butomus umbellatus*, *Colchicum luteum* and *Indigofera heterantha* saw the strongest decline in abundance between 2014 and 2017, while non-native species like *Arundo donax*, *Centaurea iberica*, *Conium maculatum*, *Convolvulus arvensis*, *Melilotus albus*, *Medicago lupulina*, *Saccharum spontaneum*, *Sigesbeckia orientalis*, *Solanum nigrum* and *Trifolium fragiferum* increased most in abundance during the

resurvey (Rashid et al., 2021). On the other hand, few native species like *Cichorium intybus*, *Lactuca serriola* and *Senecio chrysanthemoides* increased in abundance, while the abundance of some non-native species like *Anthemis cotula*, *Amaranthus caudatus* and *Cirsium arvense* declined (Rashid et al., 2021).

In some cases, species-specific patterns for time, elevation and their interaction were best explained by the status of the species, while trends in the distance from the railway track and the interaction between time and distance were better explained by life- and growth-form (Table 3). In general, non-native species had a positive change in abundance over time, while native species had a negative one (Table 3). Common non-native species on average related slightly positively—yet not significantly—with elevation, while native species related negatively. The interaction between time and elevation indicated a decrease in the positive and negative elevation effects for non-native and native species in 2017 respectively. Finally, we found more perennial grasses and fewer perennial herbs closer to the railway tracks, although these patterns decreased over time.

3.4 | Shifts in community composition

Communities showed a general shift from 2014 to 2017 across all the plot types (Figure 7), with all the plots shifting in the same direction, yet with increasing distance between communities over time (the polygon of 2017 is larger than the one from 2014). Species

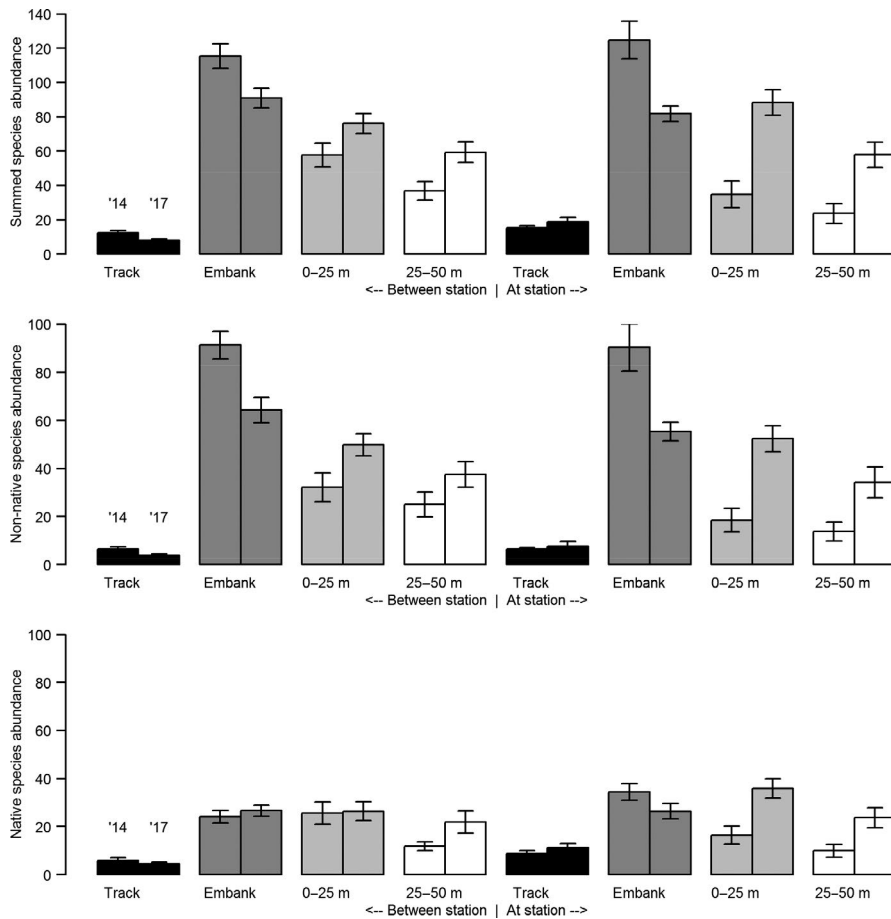


FIGURE 4 Average (with standard error) of summed abundances for all (top), non-native-only (middle) and native-only (bottom) species abundance for each plot type in 2014 (left bar) and 2017 (right bar). For outcomes of the models, see Table 2

composition of communities at the STN and BTN sites mostly differed on the tracks only.

4 | DISCUSSION

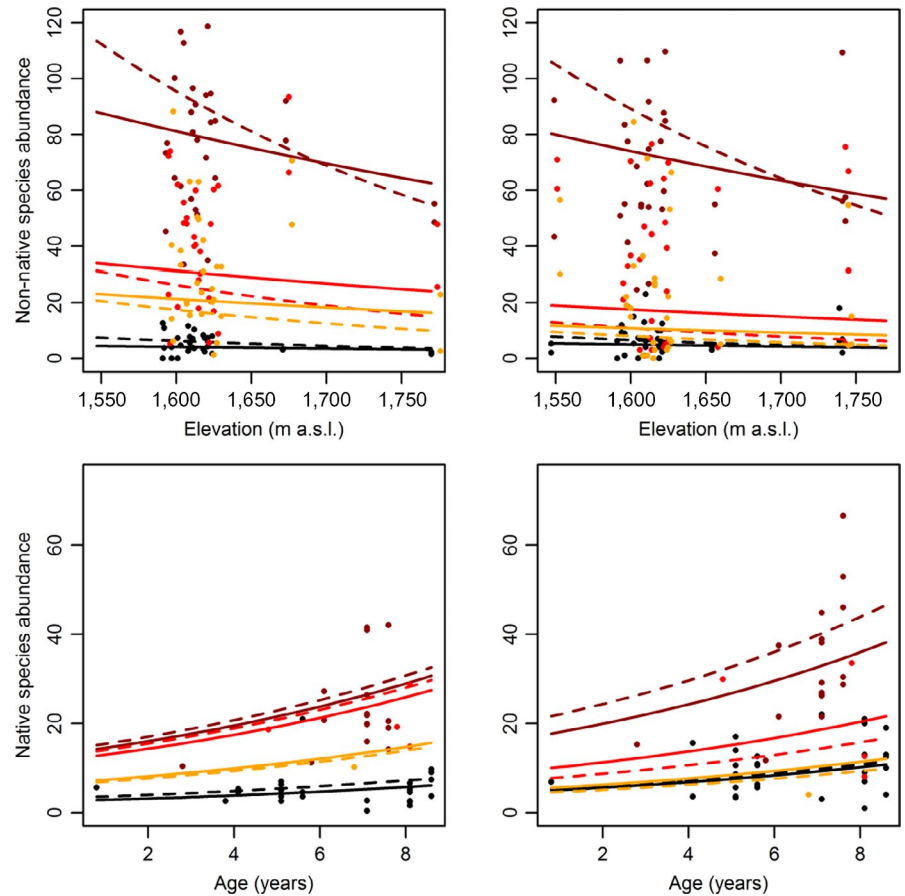
As hypothesized, the construction of a railway drastically changed community composition in Kashmir Himalaya. First of all, half of the species—and more so on the railway embankments—were non-native in origin (Figure 2). Even more importantly, these non-native species dominated the communities in abundance, especially at lower elevations (Figures 4 and 5). These results are in accordance with other studies, showing that at least the lowland areas from the Kashmir Himalaya are known to be heavily invaded by non-native species (Khuroo et al., 2007; Mehraj et al., 2018; Muzafar et al., 2019) and that the linear disturbances like railway and roads are often hotspots of non-native species (Lembrechts et al., 2017; McDougall et al., 2018; Seipel et al., 2012). Interestingly, however, both non-native species and native species decreased in richness and abundance over the studied time period of 3 years (2014–2017). These surprising declines could indicate that the system is still in a transition period after building the railway less than a decade earlier.

Railways modify environmental conditions via two basic actions: (a) an initial intense disturbance of the local natural landscapes and (b) continuous modifications of the habitat due to traffic and railway

maintenance. Understanding how plant communities reassemble post-disturbance has since long been a central question in ecology (Götzenberger et al., 2012). Disturbances are discrete events that change resources or the physical environment, disrupt ecosystem structure (White & Pickett, 1985) and play a key role in the community dynamics. In the case of railways, species propagules, coming from multiple local and regional sources, may arrive at the disturbed site, interacting ecologically and adapting to the new physical environment, and potentially changing the biodiversity of the affected region (Ellis, 2018; Rutkowska et al., 2013). The communities gain species through immigration, lose others through continued extirpations and consequently stabilize at a new equilibrium. In our study, the major railway construction activities in the region were completed in 2013, and the only remaining disturbance associated with this transport corridor was the movement of trains and travellers. One would thus expect the system to be in an ongoing process of succession. In the period under study here (5–8 years after railway establishment), the study system seems to have moved into the second phase of this succession, in which the native and non-native species introduced initially are disappearing again, resulting in a reduced native and non-native species richness between 2014 and 2017. Indeed, several species that disappeared were typical pioneering weed species such as *Potentilla reptans* and *Tussilago farfara*.

In addition, it is important to note that species extirpations, after any ecosystem disturbance, seldom manifest immediately; some

FIGURE 5 Non-native (top) and native (bottom) species richness as a function of elevation (top) or railway age (bottom), year (2014 = dashed line and 2017 = full line) and plot type (left = between station, right = at station: track (black), embankment (dark red), 0–25 m (red) and 25–50 m (orange)). Results from the linear models with the best fit (i.e. lowest AIC) of $\ln(x + 0.1)$ (see Table 2)



populations persist for extended periods below a minimum viable population size or an extinction threshold, contributing to an extinction debt (Figueiredo et al., 2019). Previous studies have synthesized the evidence for extinction debts in a variety of environments and/or organisms (Essl et al., 2015; Kuussaari et al., 2009). Both abiotic (e.g. disturbance intensity) and biotic factors (species' life-history traits), as well as environmental stochasticity, have been shown to influence how many local extinctions happen and how long they will take (Kuussaari et al., 2009). The observed decreases in species richness, especially of native species such as *Indigofera heterantha* and *Cirsium wallichii*, several years after the disturbance event could also indicate that the community is still paying these extinction debts. This decrease in species richness was most obvious at the stations, where more persistent disturbance can actually speed up the species loss.

Parallel to the process of native species decline (Figure 2), a higher abundance of non-natives, and to a certain extent native species in the natural vegetation may suggest the firmer establishment of more competitive 'second-wave' species such as *Convolvulus arvensis*, *Medicago lupulina* and *Melilotus albus* (Figure 4; Table 2). A favourable local habitat that helps non-native species to shift from 'naturalized' to 'invasive' allows them to make efficient use of their inherent abilities to invade and reduce the extent of native species. Besides the invasive abilities of non-native species ('species invasiveness'), the structure of the native community and the non-native propagule pressure can determine the degree to which a community becomes

invaded. In the absence of favourable local habitat or at low propagule pressure, non-native species may remain naturalized, coexisting with natives for a longer period of time without causing significant shifts in the community. In the present situation, the interior plots represent the natural habitats with the least disturbance from railway construction. As the abundance of non-natives significantly increase there, especially at higher elevations, it indicates that the natural vegetation is vulnerable to invasion by non-native species, and that the effect of the railway over time thus extends far beyond the visual disturbance of tracks and embankment. Seeing this increase in abundance, especially at the stations, suggests that a continuous influx of seeds of common non-natives could have sustained their spread.

Importantly, this increased abundance of non-native species in the natural vegetation goes together with a persistent decline, on average, in the abundance of the most common native species in all plots (Figure 6, even though increases in general native species abundance were found in Figure 4, suggesting the expansion of a small set of 'native weed species', potentially well-adapted to disturbance, e.g. *Capsella bursa-pastoris* and *Cichorium intybus*). Studies examining changes in species richness following human-driven disturbances are common in the ecological literature (Dornelas et al., 2014; Newbold et al., 2015; Vellend et al., 2013), and the declines in species richness have often served as ecological indicators of biodiversity loss. Our results suggest that in most plots, a continuous shift is occurring away from the native community towards more common non-native species. The latter are increasing most significantly in the vegetation

	Total abundance		Non-native abundance		Native abundance	
	Estimate	<i>p</i> -value	Estimate	<i>p</i> -value	Estimate	<i>p</i> -value
(Intercept)	1.678	<0.001	7.077	0.023	1.206	<0.001
Year	-0.321	0.002	-3.181	0.030	-0.227	0.010
Elevation			-0.003	0.086		
Age	0.167	0.037			0.098	0.007
Between station						
Embank	2.589	<0.001	2.710	<0.001	1.438	<0.001
0–25 m	2.191	<0.001	1.422	<0.001	1.346	<0.001
25–50 m	1.191	0.039	1.013	0.005	0.648	0.007
At station						
Track	0.630	0.273	0.050	0.886	0.399	0.093
Embank	2.676	<0.001	2.641	<0.001	1.793	<0.001
0–25 m	1.900	0.001	0.548	0.119	0.774	0.001
25–50 m	0.227	0.693	0.245	0.484	0.249	0.294
Interactions						
Year × Elevation			0.002	0.050		
Between station						
Year × Embank	0.149	0.298	0.252	0.134	0.167	0.141
Year × 0–25 m	0.430	0.003	0.587	<0.001	0.148	0.193
Year × 25–50 m	0.392	0.007	0.614	<0.001	0.285	0.013
At station						
Year × Track	0.273	0.055	0.138	0.406	0.168	0.134
Year × Embank	0.108	0.447	0.228	0.168	0.029	0.798
Year × 0–25 m	0.835	<0.001	0.885	<0.001	0.481	<0.001
Year × 25–50 m	0.542	<0.001	0.709	<0.001	0.429	<0.001
Between station						
Age × Embank	-0.073	0.519				
Age × 0–25 m	-0.155	0.172				
Age × 25–50 m	-0.047	0.678				
At station						
Age × Track	-0.088	0.436				
Age × Embank	-0.082	0.467				
Age × 0–25 m	-0.256	0.024				
Age × 25–50 m	0.007	0.950				

TABLE 2 Estimate and *p*-value of the linear models with the best fit (i.e. lowest AIC) of $\ln(x + 0.1)$, with *x* the summed total, non-native and native species abundance against plot type, year, elevation and their interactions. Significant values ($p < 0.05$) are in bold, borderline significant values ($0.05 < p < 0.1$) are in bold and italics

away from the railway track. These patterns, combined with the reduction in species richness of both native and non-native species as discussed above, suggest that the vegetation may be gradually losing many of its rarer native species. This, combined with the increased abundance of non-native species in particular in the interior natural vegetation, hints towards a community that is slowly evolving towards a novel ecosystem. These negative impacts on the native plant community are observed despite the fact that the Himalaya is a mountainous region with active orogenesis (Najma, 2006), with the native species pool thus adapted to more active disturbance than in palaeo-mountains (Lázaro-Lobo & Ervin, 2021).

Even though our survey covered a relatively shorter elevational gradient of 150 m only, both native and non-native species were negatively correlated with elevation, in harmony with studies conducted elsewhere in the world (Becker et al., 2005; Haider et al., 2010; Kalwij et al., 2008; Medvecká et al., 2018; Pauchard & Alaback, 2004; Pollnac et al., 2012). Among different factors that have been proposed to explain elevational species richness patterns, climate conditions (e.g. water–energy theory; Hawkins et al., 2003), area size (Rosenzweig, 1995), mid-domain effect (Colwell et al., 2004) and biotic processes (Shmida & Wilson, 1985) have been widely explored. In a study on non-native species distribution at railway stations and

FIGURE 6 Average abundance changes over time (from 2014 to 2017) for all non-native (grey) and native (black) species in the different plot types, based on the coefficients of species-specific models. Species-specific models were created for all species with more than 10 occurrences. For each species ($N = 81$), the best model was selected based on the lowest AIC

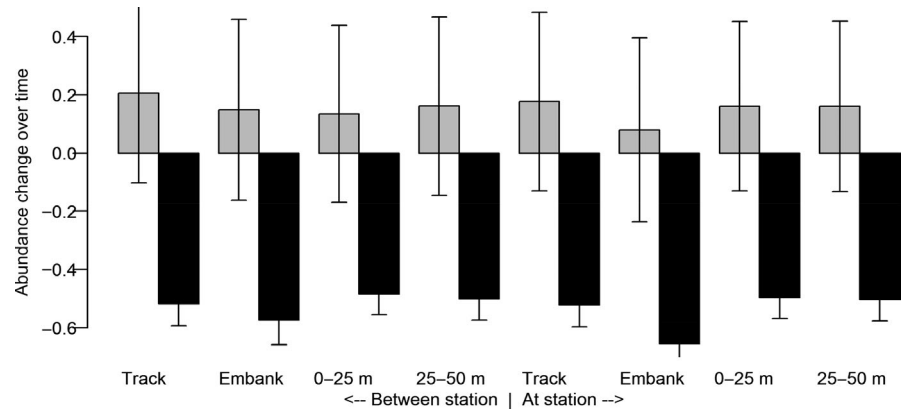


TABLE 3 Patterns in the average coefficients of the species-specific models, results from species-specific linear models including time (2014 vs. 2017), elevation (1,500–1,800 m a.s.l.) and distance from the trail (1–3, from the embankment till 50 m away from the road) on all 81 assessed species. Plots between tracks were excluded from this analysis to simplify the system to a linear decrease with distance to the railway. Significant values ($p < 0.05$) are in bold

	Time		Elevation		Time × elevation	
	Estimate	<i>p</i> -value	Estimate	<i>p</i> -value	Estimate	<i>p</i> -value
(Intercept)	0.370	0.265	0.001	0.100	-0.0003	0.109
Status _{Native}	-1.027	0.019	-0.002	0.008	0.0006	0.015
	Distance		Time × distance			
	Estimate	<i>p</i> -value	Estimate	<i>p</i> -value	Estimate	<i>p</i> -value
(Intercept)	-0.052	0.781	-0.029	0.526		
Life-form _{perennial}	-0.824	0.009	0.205	0.008		
Growth-form _{herb}	-0.195	0.354	0.084	0.104		
Life-form _p × growth-form _h	0.927	0.007	-0.229	0.006		

along roadsides in the Swiss Alps, Becker et al. (2005) suggest that the decrease in the number of non-native plants with increasing elevation is probably due to poor adaptation to conditions at higher elevations combined with low propagule pressure. In the Kashmir valley, one might expect such a combination of factors as well, especially given the fact that those highest elevation parts of the railway track were also the most recently constructed. Even though track age was not withheld in the final models for non-native species, one can assume through its partial correlation with elevation that it contributed to the observed decline at higher elevations.

Interestingly, the reduction in species richness from 2014 (dashed lines, Figure 3) to 2017 (full lines) was larger at lower elevations than at higher elevations, resulting in a less steep relation with elevation in 2017 than in 2014. Higher compositional turnover through time at low-elevation sites than at high-elevation sites has been widely reported (Aplet & Vitousek, 1994; Taverna et al., 2005), and a number of factors that are often associated with elevation have been shown or hypothesized to determine these temporal changes within communities (Chase & Leibold, 2002; Taverna et al., 2005; White et al., 2006; Yurkonis & Meiners, 2004). Additionally, one could hypothesize that disturbances at low elevations recur more often, as these areas are commonly associated with a greater human presence—as is the case here as well. As such,

lower elevation areas might have experienced a stronger setback in succession than higher elevation areas, reflected in the fact that non-native species abundance on the embankments along the railway declined dramatically at low elevations, yet increased at high elevations (Figure 4). Finally, we could be seeing an ongoing biotic homogenization of the vegetation: with extinctions more common at lower elevations and non-native species expanding towards higher elevations. Such homogenization is a common effect of linear disturbances on plant species communities, as has been shown for mountain roads (Haider et al., 2018; Lembrechts et al., 2017; Medvecká et al., 2018). Nevertheless, future studies along railways covering larger elevational gradients are necessary to see if plant communities along them follow the same distributional patterns as are known from along the mountain roads.

5 | CONCLUSIONS

Our results indicate that the disturbance associated with building a railway has wide implications for plant communities at and around the railway corridor, with natural communities remaining far from equilibrium more than 10 years after its establishment. We observed declines in both native and non-native species richness and

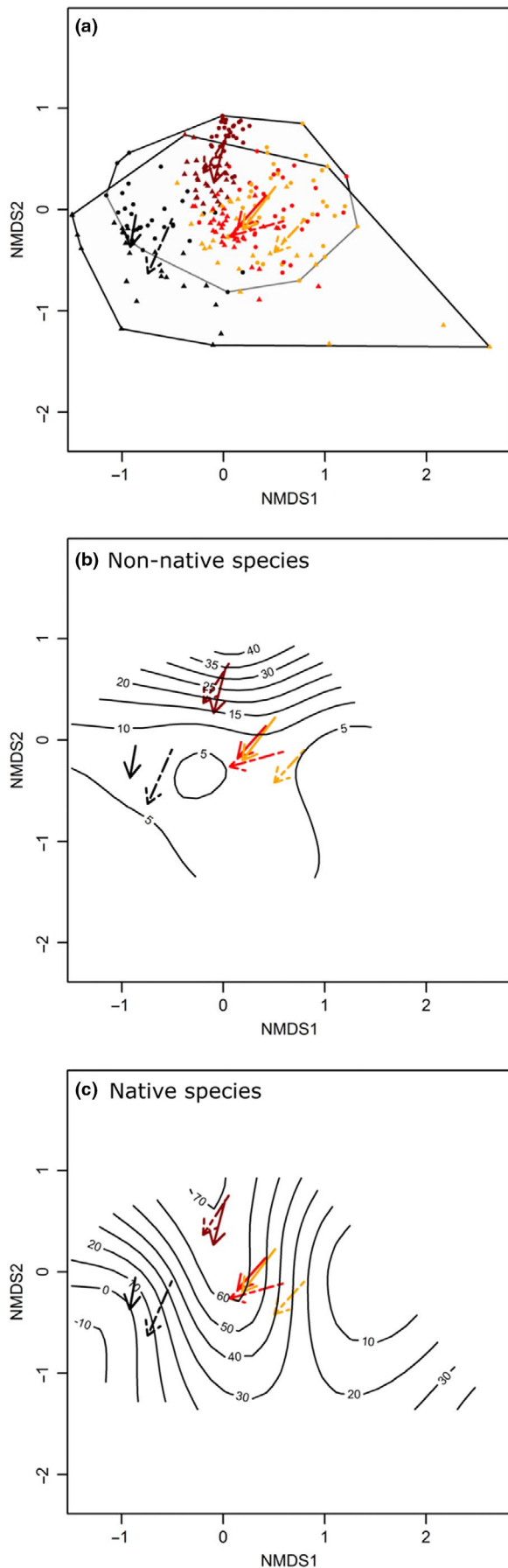


FIGURE 7 (a) First two dimensions of a non-metric dimensional scaling (NMDS)-analysis on species composition. Coloured symbols indicate plots (circles = 2014, triangles = 2017; black = tracks, dark red = embankments, red = 0–25 m and orange = 25–50 m), with smaller distances between dots indicating higher similarity. The two polygons indicate the spread in plots in 2014 (connecting circles, the small circular polygon) and 2017 (connecting triangles, the larger one). Arrows indicate the shift in average species composition per plot type from 2014 to 2017 (colours see earlier; full lines = between stations and dashed lines = at stations). Averages in non-native (b) and native (c) species abundance super-imposed on the time shifts per plot type from the first graph

increasing abundance of common non-native species, especially in areas away from the railway track. Both these patterns indicate an advancing succession, where initially—rare—pioneer species are replaced by increasingly dominant and often non-native competitors. These results also hint that delayed local extinctions may occur well after the disturbance event. While longer term monitoring is necessary to get a better grip on the community dynamics at hand, these results do indicate an emerging risk of plant invasions caused by the construction of railways for the native biodiversity in the mountainous region of Kashmir Himalaya.

While this railway line is currently separated from the rest of the country (mainland India), a connection with the Indian Railway network is planned for December 2022 (from Banihal further south to Jammu). With this connection, the chances of mechanical introduction of propagules of non-native species will likely increase along the railway corridor (Lemke et al., 2019), further tipping the balance in favour of non-native species. A major concern of connecting the railway with the national system is the potential for the transport of large amounts of construction and filling materials, carrying propagules of species that are, up to now, absent in the area. This study can serve as a baseline study to assess and monitor future invasions along the Kashmir railway network once this connectivity increases. It should also serve as a warning that this increased connectivity is likely to have detrimental effects on the native vegetation in the vicinity of these railways in the long run. A simple but consistent biosecurity protocol could reduce the risk of new introductions into the area and should be considered within the environmental mitigation plan for the railway expansion.

Based on our findings, we provide the following recommendations to reduce the invasion of non-native species and secure the recovery of local plant communities along the Kashmir railway network:

- A comprehensive Environmental Management Plan should be developed to address the environmental management requirements of the railway line, especially in regard to the connection of the railroad to the Indian Railway network.
- The land managers, in collaboration with Railway authorities, should monitor the natural vegetation in the interior natural areas and eradicate invasive species at an early stage. Management

should at least focus on those species shown here to be expanding most rapidly (e.g. *Arundo donax*, *Conium maculatum*, *Saccharum spontaneum*, *Solanum nigrum*, *Trifolium fragiferum*), yet also monitor for species currently not yet present in the region.

- The governmental departments entrusted with natural resource management in the region (Agriculture, Horticulture, Forests) should undertake regular monitoring and surveillance of propagules/seedlings of potential invasive species on tracks and embankments so that these species do not move into the interior natural areas.
- Ecological restoration of the embankments dominated by invasive species should be undertaken, using a hardy species pool of native species that can withstand competition with non-native species.
- Railway staff, particularly at the stations, should be sensitized and trained for potential ecological risks, and timely information should be shared with the natural resource managers in the region.
- Future research should focus on monitoring the natural vegetation much beyond the last plot of the present study (i.e. more than 150 m away from the railway track) in order to understand species range shifts across spatial and elevational gradients in the light of rapid climate warming in the Himalayas (Yaduvanshi et al., 2019).

Our findings from the Kashmir Himalaya help to shed light into how other mountain regions are likely affected by the increasing density, extent and connectivity of railways and other physical infrastructure. Nevertheless, it is important that studies like this must be conducted on railway networks in other mountain regions across the world to understand the importance of local factors in driving these processes.

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AUTHORS' CONTRIBUTIONS

I.R. and A.A.K. conceived the ideas and designed the methodology; S.M.H. collected the data; J.J.L. analysed the data. All authors led the writing of the manuscript and contributed critically to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository <https://orcid.org/0000-0002-9304-228X> (Rashid et al., 2021).

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SUPPORTING INFORMATION

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

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