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1 **Railways redistribute plant species in mountain landscapes**

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14

15 **Abstract**

16 1. The significant portion of global terrestrial biodiversity harbored in mountains is under
17 increasing threat from a variety of anthropogenic impacts. Protecting fragile mountain
18 ecosystems requires understanding how these human disturbances affect biodiversity. As roads
19 and railways are extended further into mountain ecosystems, understanding the long-term
20 impacts of this infrastructure on community composition and diversity gains urgency.

21 2. We used railway corridors constructed across the mountainous landscapes of the Kashmir
22 Himalaya from 1994-2013 to study the effects of anthropogenic disturbance on species'
23 distributions and community dynamics. In 2014 and 2017, we collected vegetation data along

24 31 T-shaped transects laid perpendicular to the railway line, adopting the MIREN (Mountain
25 Invasion Research Network) road survey methodology.

26 3. Plant communities shifted significantly from 2014 to 2017, potentially as a result of ongoing
27 species' redistribution after railway construction, mostly driven by declines in both native and
28 non-native species richness, and increasing abundance of a few non-native species, especially
29 in areas away from the railway track.

30 4. These patterns indicate an advancing succession, where initially – rare – pioneer species are
31 replaced by increasingly dominant and often non-native competitors, and potentially suggest a
32 trend towards delayed local extinctions after the disturbance event. Native and non-native
33 species richness were negatively correlated with elevation, but that relationship diminished
34 over time, with the abundance of non-natives significantly increasing at higher elevations.

35 5. Synthesis and applications: Transport corridors seem to facilitate the spread of non-native
36 species to higher elevations, which has serious implications in light of the warming mountain
37 tops. Our results indicate that plant communities next to railways do not reach equilibrium
38 quickly after disturbance. More than 10 years after railway establishment succession
39 continued, and signs pointed in the direction of a landscape increasingly dominated by non-
40 native species. Our study indicates that the single disturbance event associated with
41 construction of a railway in this Himalayan region had large and long-lasting effects on plant
42 communities at and around this transport corridor and suggests the need for a long-term region-
43 wide coordinated monitoring and management program.

44 **KEY WORDS:** biodiversity, disturbance, elevation, invasion, mountain, railways, Himalaya

45

46

47 1 | INTRODUCTION

48 Mountain ecosystems contribute disproportionately to the global species pool of
49 terrestrial biodiversity, with diverse assemblages of small-ranged species constituting montane
50 centers of endemism (Rahbek et al., 2019). The unique biodiversity in these fragile ecosystems
51 is threatened by the upslope spread of non-native species, mainly driven by unbridled land use
52 changes associated with ever-increasing human activities, and now aided by a rapidly warming
53 climate (Marini, Gaston, Prosser, & Hulme, 2009; Petitpierre et al., 2016; Dainese et al., 2017;
54 Guo et al., 2018). As biological invasions are an outcome of the human-mediated transportation
55 of species beyond their natural distribution ranges (Essl et al., 2018), the fast-increasing footprint
56 of transport infrastructure in the form of roads and railways in mountain landscapes acts as a
57 dispersal corridor for the invasion of non-native species (Bacaro et al., 2015; Lembrechts et al.
58 2017; Haider et al., 2018; Medvecká et al., 2018). These linear infrastructures facilitate the
59 dispersal of non-native species across physical and environmental barriers, and by transforming
60 nearby habitats to be suitable for initial establishment and subsequent spread of invasive species
61 (McDougall et al., 2018).

62 During the past two decades, research on biological invasions in mountainous regions
63 has gained momentum (Pauchard & Alaback, 2004; Pauchard et al., 2009; Alexander et al., 2011,
64 Seipel et al., 2012; Lembrechts et al., 2017; Ahmad, Khuroo, Hamid, Malik, & Rashid, 2019;
65 Liedtke et al., 2020). However, most of what we currently know about the role of transport
66 infrastructure in facilitating invasions in mountains across the globe comes from road ecology
67 studies (Lázaro-Lobo & Ervin, 2019). The role of railways as conduits for plant invasions
68 remains little investigated (but *see* Hansen and Clevenger, 2005; Wang, Gillespie, Liang,
69 Mushkin, & Wu, 2015; Benedetti & Morelli, 2017), and only a few studies have been conducted

70 in mountains (e.g., Becker, Dietz, Billeter, Buschmann, & Edwards, 2005; Deng et al., 2020).
71 The basic scientific understanding about the relative role of this transport system in the dispersal
72 of non-native species within mountain ecosystems, and on how this can be better managed, is
73 therefore still poorly known. Nonetheless, railways clearly act as dispersal corridors that exert
74 considerable effects on the biodiversity and ecosystem functioning of surrounding natural areas
75 (Fahrig, 2003; Penone, Machon, Julliard, & Le Viol, 2012).

76 A fundamental ecological consequence of railways, as with other kinds of linear transport
77 corridors, is the suite of changes that occur in adjacent natural vegetation (Hansen &
78 Clevenger, 2005; Wilkomirski et al., 2012, Wang, Gillespie, Liang, Mushkin, & Wu, 2015;
79 Pollock, Nielsen, & St. Clair, 2017). These transport infrastructures all result in large gains and
80 losses of species, creating new interaction networks among the novel set of species that establish
81 in that location (Lembrechts et al., 2017; Dornelas et al., 2019). The re-mixed sets of species
82 interact ecologically, evolve in relation to the new physical environment and co-evolve in
83 relation to one another, changing the biodiversity of the affected region (Ellis, 2018). How far
84 these novel ecosystems extend, and how fast these changes take place, is however still
85 unresolved.

86 As railway networks filter through various land-use types (e.g., agricultural, urban, areas
87 with high natural value, intact forests), they enhance the dispersion of non-native species into more
88 pristine habitat types, thereby inducing changes in the species composition, particularly in adjacent
89 communities (Hansen & Clevenger, 2005). However, to the best of our knowledge no study has
90 so far investigated the impact of this transport infrastructure on species' redistributions. Here,
91 we try to fill this knowledge gap by sampling T-shaped transects perpendicular to railway
92 stations – as hotspots of introduction of new species – and along the railway tracks located

93 between these stations in the mountainous region of Kashmir Himalaya, by adapting the road
94 survey methodology from the Mountain Invasion Research Network (MIREN). Surveys were
95 performed during the summer of 2014 and 2017. We hypothesize that the railway (both
96 construction and use) would significantly shift both native and non-native plant species
97 distributions in the region, resulting in the establishment of novel ecosystems dominated by an
98 increasingly large proportion of non-native species, while native species are gradually pushed
99 towards extinction. These shifts towards novel ecosystems are expected to be particularly strong
100 at low elevations, where anthropogenic disturbance is traditionally higher, yet they would
101 gradually worsen over time along the entire elevation gradient as traffic, and therefore species
102 dispersal, increases. Thus, our study sheds light on how railways act as conduits for non-native
103 species into mountainous areas, where non-native species may percolate from disturbed areas
104 into adjacent natural ecosystems.

105 **2 | MATERIALS AND METHODS**

106 **2.1 | Study area**

107 Kashmir Himalaya, located in the northwestern side of the Himalayan biodiversity hotspot, is a
108 mountainous valley bounded by the Pir Panjal range of Lesser Himalaya in the south and south-
109 west, and the Zaskar range of the Greater Himalaya in the north and north-east (Dar & Khuroo,
110 2020). The climate of the region, marked by well-defined seasonality, resembles that of
111 mountainous and continental parts of the temperate latitudes. It receives an annual precipitation of
112 about 1,050 mm, mostly in the form of snow during the winter months. Temperatures range from
113 an average daily maximum of 31°C and minimum of 15°C during summer to an average daily
114 maximum of 4°C and minimum of -4°C during winter. The future climate change projections of
115 the region (under two Representative Concentration Pathways, RCP 8.5 and RCP 4.5) point

116 towards more severe temperature changes than the global average, with a median value of 2.1°C
117 and 2.8°C as compared to 1.5°C and 2.0°C global temperature rise (GTR) respectively
118 (Yaduvanshi, Zaroug, Bendapudi, & New, 2019). The lowlands of this region are known to be
119 heavily invaded by non-native species (Khuroo, Rashid, Reshi, Dar, & Wafai, 2007; Mehraj et al.,
120 2018; Muzafar et al., 2019; Mehraj et al., 2021), which have also been shown to move to higher
121 elevations along roads in this Himalayan region (Dar, Reshi, & Shah, 2018).

122 To ensure a reliable transportation system for the Kashmir region, and its connection with
123 the Indian Railways, the construction of 345 km of railway was started in 1994. The Jammu—
124 Udhampur—Katra—Quazigund—Baramulla (JUSBRL) railways is divided into four sections, out
125 of which leg 3 of the line traverses the Kashmir valley. The connection to the Indian Railway is
126 planned for December 2022, but the Baramulla to Banihal (~135 km) part of this leg was
127 completed in 2013. The present study was carried out along the operational leg 3 of Kashmir
128 railway (130 km) — the only railway line of the region — that starts from Baramulla on the
129 northwestern edge of the Kashmir, passing through the Pir Panjal tunnel, connecting the south and
130 southwest Bichleri valley of Banihal through the Qazigund area of the Kashmir region (Fig. 1).
131 The Kashmir railway became operational between Anantnag and Mazhom stations in October
132 2008. The service was extended beyond Mazhom to Baramulla in February 2009, and in the south,
133 Anantnag was connected to Qazigund in October 2009. In December 2012, Qazigund was
134 connected to Banihal, but this leg 3 still remains disconnected from the rest of the Indian railways.
135 Thus, the main source of propagules of non-native species could be most likely from the alien
136 species pool already present in cities falling along its length and seldom at the southern border of
137 the Kashmir valley from mainland India.

138

139 2.2 | Sampling design and data collection

140 Several field reconnaissance surveys were carried out during the year 2014 to get a good idea about
141 the area, its species composition and distribution, and approachability of the railway track. The
142 entire stretch of the railway (130 km) going through the Kashmir region was divided into 31 sites
143 consisting of 16 stations (STN) and 15 between-station (BTN) sites within a narrow elevational
144 belt from 1591 to 1741 m a.s.l (Appendix-1). All sites were first sampled during 2014 and then
145 resampled during 2017. The sampling for BTN sites was carried out at the midpoints between the
146 stations. The upper surface of the railway track was flat and raised from the adjacent interior plots
147 with an embankment. All the filling material (e.g., stones, sand, soil, etc.) used for construction of
148 track and embankments has been locally procured.

149 At each site, four transects were laid out with one plot parallel to the track edge and the
150 other three plots perpendicular to it, together forming a “T” (Fig. 1, Modified from Seipel et al.,
151 2012). The head of the ‘T’ was 50 x 2 m with a total length of 50 m, between the railway tracks,
152 and the remaining three plots (embankment, interior 1 and interior 2) were perpendicular to the
153 track, ending ca. 150 m from the track. A hand-held GPS (Garmin eTrex, Garmin International,
154 Inc., Olathe, KS) was used for recording the elevation and geo-coordinates of each plot. Within
155 each of the plots (4 x 31 = 124 plots), we recorded all vascular plant species, and at each site,
156 twelve 1 x 1m quadrants were laid out for recording species abundance. In total, we recorded 123
157 species, 75 of which were native and 48 non-native (Appendix-2).

158 The selected sites, as introduced above, were first sampled during 2014 and then resampled
159 during 2017. Plant specimens of all the vascular species sampled were collected and processed
160 following standard herbarium methods (Forman & Bridson, 1989). The specimens were identified
161 by comparing the housed herbarium samples at the Centre for Biodiversity and Taxonomy,

162 University of Kashmir and consulting relevant taxonomic literature (Stewart, 1972;
163 www.efloras.org/Pakistan). The specialized taxonomic database of The Plant List
164 (www.theplantlist.org) was used for the nomenclature of all the collected species. During field
165 sampling, the life and growth form data pertaining to each plant species was recorded. On the basis
166 of available scientific literature (Khuroo, Rashid, Reshi, Dar, & Wafai, 2007; Mehraj et al., 2018;
167 Muzafar et al., 2019) and specialized websites such as GRIN (Germplasm Resource Information
168 Network, www.ars-grin.gov), plant species were categorized into native and non-native species.

169 **2.3 | Statistical analysis**

170 All analyses were done in R (R Core Team 2015). To test for trends at the community level, we
171 analyzed total, non-native, and native species richness and abundance (summed abundance of
172 all species) separately, as a function of year (2014 or 2017), elevation (continuous variable),
173 track age (continuous variable) or plot type [categorical variable; track, embankment, interior 1
174 or interior 2, separately for at station (STN) and between station (BTN) sites], and all their two-
175 way interactions. We used generalized linear models with a Poisson-distribution for species
176 richness, and linear models with a logarithmic correction ($\ln(x+0.1)$) for species abundance to
177 conform with normality of model residuals. We used the function *dredge* from the package
178 MuMIn (Barton 2016) to create all potential sub-models and to select the best model (i.e., the
179 model with the lowest AIC).

180 Next, we tested for changes in the abundance of the most common native and non-native species
181 (i.e., all species with more than 10 occurrences out of the 124 plots, for a total of 81 species)
182 using species-specific linear models [with a logarithmic correction ($\ln(x+0.1)$)], following the
183 procedure in Lembrechts et al. (2017). We modeled each species as a function of year, elevation,
184 distance to the railway and their two-way interactions, created all sub-models and selected the

185 model with the lowest AIC. Then, we analyzed all the coefficients of these best models for each
186 species as a function of species' characteristics [status (native vs alien), life form (annual vs
187 perennial), growth form (herb vs grass)]. This analysis allowed us to study trends across different
188 groups of species with related functional traits.

189 Finally, we analyzed shifts in the community as a whole using Non-Metric Multidimensional
190 Scaling [NMDS, function *metaMDS* in the vegan package (Oksanen et al. 2013)]. We plotted
191 the first two dimensions of this NMDS and super-imposed a polygon delineating the year-effect
192 (function *ordihull*) and a contour plot (function *ordisurf*) delineating the native and non-native
193 species richness. We also plotted arrows showing the shifts in the center of the community for
194 each plot type (tracks, embankments, interior 1 and 2) from 2014 to 2017, separately for sites at
195 and between stations.

196 **3 | RESULTS**

197 **3.1 | Species richness**

198 On average, total plant species richness across all the sites, as well as richness of both native and
199 non-native species, declined between 2014 and 2017 (Fig. 2; Table 1). Species richness declined
200 slightly more in the plots between the tracks and those on the embankment at the station, with a
201 higher decline in non-native species richness on the embankments at the station. Total species
202 richness, and species richness of both natives and non-natives, was highest in the plots on the
203 embankments and lowest for those between the tracks. Importantly, richness of native and non-
204 native species was similar, ranging from on average 3 species on the tracks to close to 15 species
205 per plot on the embankments.

206 Both native and non-native species richness were negatively correlated with elevation. The
207 reduction in species richness from 2014 to 2017 was larger at lower elevations than at higher

208 elevations for both native and non-native species, resulting in less steep elevational declines in all
209 the plots in 2017 than in 2014 (Fig. 3; Table 1).

210 **3.2 | Species abundance**

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

223 **3.3 | Individual species-specific patterns**

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

230 On an individual species basis, most common non-native species on average showed a
231 slight increase in abundance in all the plot types (even though the total non-native abundance
232 decreased in some plot types as shown before). However, there was large variation in their
233 abundance, and thus overall changes over time did not differ significantly from zero (Fig. 6). On
234 the other hand, most common native species showed a significant decrease in abundance on an
235 individual species basis in all the plot types, although the total native species abundance has been
236 shown to increase in some. Native species like *Artemisia absinthium*, *Astragalus grahamianus*,
237 *Butomus umbellatus*, *Colchicum luteum* and *Indigofera heterantha* saw the strongest decline in
238 abundance between 2014 and 2017, while non-native species like *Arundo donax*, *Centaurea*
239 *iberica*, *Conium maculatum*, *Convolvulus arvensis*, *Melilotus albus*, *Medicago lupulina*,
240 *Saccharum spontaneum*, *Sigesbeckia orientalis*, *Solanum nigrum* and *Trifolium fragiferum*
241 increased most in abundance during the resurvey (Rashid et al., 2021). On the other hand, few
242 native species like *Cichorium intybus*, *Lactuca serriola* and *Senecio chrysanthemoides* increased
243 in abundance, while the abundance of some non-native species like *Anthemis cotula*, *Amaranthus*
244 *caudatus*, *Cirsium arvense* declined (Rashid et al., 2021).

245 In some cases, species-specific patterns for time, elevation and their interaction were best
246 explained by the status of the species, while trends in distance from the railway track, and the
247 interaction between time and distance were better explained by life and growth form (Table 3). In
248 general, non-native species had a positive change in abundance over time, while native species
249 had a negative one (Table 3). Common non-native species on average related slightly positively
250 — yet not significantly — with elevation, while native species related negatively. The interaction
251 between time and elevation indicated a decrease in the positive and negative elevation effects for

252 non-native and native species in 2017, respectively. Finally, we found more perennial grasses and
253 fewer perennial herbs closer to the railway tracks; although these patterns decreased over time.

254 **3.4 | Shifts in community composition**

255 Communities showed a general shift from 2014 to 2017 across all the plot types (Fig.7), with all
256 the plots shifting in the same direction, yet with increasing distance between communities over
257 time (the polygon of 2017 is larger than the one from 2014). Species composition of communities
258 at station and between station sites mostly differed on the tracks only.

259 **4 | DISCUSSION**

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

272 Railways modify environmental conditions via two basic actions: 1) an initial intense
273 disturbance of the local natural landscapes, and 2) continuous modifications of the habitat due to
274 traffic and railway maintenance. Understanding how plant communities reassemble post-

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

291 In addition, it is important to note that species extirpations, after any ecosystem
292 disturbance, seldom manifest immediately; some populations persist for extended periods below a
293 minimum viable population size or an extinction threshold, contributing to an extinction debt
294 (Figueiredo et al., 2019). Previous studies have synthesized the evidence for extinction debts in a
295 variety of environments and/or organisms (Kuussaari et al., 2009; Essl et al., 2015). Both abiotic
296 (e.g., disturbance intensity) and biotic factors (species' life-history traits), as well as environmental
297 stochasticity have been shown to influence how many local extinctions happen and how long they

298 will take (Kuussaari et al., 2009). The observed decreases in species richness, especially of native
299 species such as *Indigofera heterantha* and *Cirsium wallichii*, several years after the disturbance
300 event could also indicate that the community is paying these extinction debts. This decrease in
301 species richness was most obvious at the stations, where more persistent disturbance can actually
302 speed up the species loss.

303 Parallel to the process of native species decline (Fig. 2), a higher abundance of non-natives,
304 and to a certain extent native species in the natural vegetation may suggest firmer establishment
305 of more competitive ‘second-wave’ species such as *Convolvulus arvensis*, *Medicago lupulina* and
306 *Melilotus albus* (Fig. 4; Table 2). A favorable local habitat that helps non-native species to shift
307 from ‘naturalized’ to ‘invasive’ allows them to make efficient use of their inherent abilities to
308 invade and reduce the extent of native species. Besides the invasive abilities of non-native species
309 (‘species invasiveness’), the structure of native community and the non-native propagule pressure
310 can determine the degree to which a community becomes invaded. In the absence of favorable
311 local habitat or at low propagule pressure, non-native species may remain naturalized, coexisting
312 with natives for a longer period of time without causing significant shifts in the community. In the
313 present situation, the interior plots represent the natural habitats with least disturbance from
314 railway construction. Seeing the abundance of non-natives significantly increase there, especially
315 at higher elevations, provides an indication that the natural vegetation is vulnerable to invasion by
316 non-native species, and that the effect of the railway over time thus extends far beyond the visual
317 disturbance of tracks and embankment. Seeing this increase in abundance, especially at the
318 stations, suggests that a continuous influx of seeds of common non-natives could have sustained
319 their spread.

320 Importantly, this increased abundance of non-native species in the natural vegetation goes
321 together with a persistent decline, on average, in the abundance of the most common native species
322 in all plots (Fig. 6, even though increases in general native species abundance were found in Fig.
323 4, suggesting expansion of a small set of ‘native weed species’, potentially well-adapted to
324 disturbance, e.g., *Capsella bursa-pastoris* and *Cichorium intybus*). Studies examining changes in
325 species richness following human-driven disturbances are common in the ecological literature
326 (Vellend et al., 2013; Dornelas et al., 2014; Newbold et al., 2015), and the declines in species
327 richness have often served as ecological indicators of biodiversity loss. Our results suggest that in
328 most plots, a continuous shift is occurring away from the native community, towards more
329 common non-native species. The latter are increasing most significantly in the vegetation away
330 from the railway track. These patterns, combined with the reduction in species richness of both
331 native and non-native species as discussed above, suggests that the vegetation may be gradually
332 losing many of its rarer native species. This combined with the increased abundance of non-native
333 species in particular in the interior natural vegetation, hints towards a community that is slowly
334 evolving towards a novel ecosystem. These negative impacts on the native plant community are
335 observed despite the fact that the Himalaya is a mountainous region with active orogenesis (Najma,
336 2006), with the native species pool thus adapted to more active disturbance than in paleo-
337 mountains (Lázaro-Lobo & Ervin, 2020).

338 Even though our survey covered a relatively shorter elevational gradient of 150 meters
339 only, both native and non-native species were negatively correlated with elevation, in harmony
340 with studies conducted elsewhere in the world (Pauchard & Alaback, 2004; Becker, Dietz, Billeter,
341 Buschmann, & Edwards, 2005; Kalwij, Robertson, & van Rensburg, 2008; Haider et al., 2010;
342 Pollnac, Seipel, Repath, & Rew, 2012; Medvecká et al., 2018). Among different factors that have

343 been proposed to explain elevational species-richness patterns, climate conditions (e.g., water-
344 energy theory) (Hawkins et al., 2003), area size (Rosenzweig, 1995), mid-domain effect (Colwell,
345 Rahbek, & Gotelli, 2004) and biotic processes (Shmida & Wilson, 1985) have been widely
346 explored. In a study on non-native species distribution at railway stations and along roadsides in
347 the Swiss Alps, Becker, Dietz, Billeter, Buschmann, and Edwards (2005) suggest that the decrease
348 in the number of non-native plants with increasing elevation is probably due to poor adaptation to
349 conditions at higher elevations combined with low propagule pressure. In the Kashmir valley, one
350 might expect such a combination of factors as well, especially given the fact that those highest
351 elevation parts of the railway track were also the most recently constructed. Even though track age
352 was not withheld in the final models for non-native species, one can assume through its partial
353 correlation with elevation that it contributed to the observed decline at higher elevations.

354 Interestingly, the reduction in species richness from 2014 (dashed, Fig. 3) to 2017 (full
355 lines) was larger at lower elevations than at higher elevations, resulting in a less steep relation with
356 elevation in 2017 than in 2014. Higher compositional turnover through time at low-elevation sites
357 than at high elevation sites has been widely reported (Aplet & Vitousek, 1994; Taverna, Peet, &
358 Phillips, 2005), and a number of factors that are often associated with elevation have been shown
359 or hypothesized to determine these temporal changes within communities (Chase & Leibold, 2002;
360 Yurkonis & Meiners, 2004; Taverna, Peet, & Phillips, 2005; White et al., 2006). Additionally, one
361 could hypothesize that disturbances at low elevations recur more often, as these areas are
362 commonly associated with a greater human presence – as is the case here as well. As such, lower
363 elevation areas might have experienced a stronger setback in succession than high elevation areas,
364 reflected in the fact that non-native species abundance on the embankments along the railway
365 declined dramatically at low elevations, yet increased at high elevations (Fig. 4). Finally, we could

366 be seeing an ongoing biotic homogenization of the vegetation: with extinctions more common at
367 lower elevations, and non-native species expanding towards higher elevations. Such
368 homogenization is a common effect of linear disturbances on plant species communities, as has
369 been shown for mountain roads (Lembrechts et al. 2017, Haider et al. 2018; Medvecká et al.,
370 2018). Nevertheless, future studies along railway covering larger elevational gradients are
371 necessary to see if plant communities along them follow the same distributional patterns as are
372 known from along the mountain roads.

373 **5 | CONCLUSION**

374 Our results indicate that the disturbance associated with building a railway has wide implications
375 for plant communities at and around the railway corridor, with natural communities remaining far
376 from equilibrium more than 10 years after its establishment. We observed declines in both native
377 and non-native species richness, and increasing abundance of common non-native species,
378 especially in areas away from the railway track. Both these patterns indicate an advancing
379 succession, where initially – rare – pioneer species are replaced by increasingly dominant and often
380 non-native competitors. These results also hint that delayed local extinctions may occur well after
381 the disturbance event. While longer-term monitoring is necessary to get a better grip on the
382 community dynamics at hand, these results do indicate an emerging risk of plant invasions caused
383 by the construction of railways for the native biodiversity in the mountainous region of Kashmir
384 Himalaya.

385 While this railway line is currently separated from the rest of the country (mainland India),
386 a connection with the Indian Railway network is planned for December 2022 (from Banihal further
387 south to Jammu). With this connection, the chances of mechanical introduction of propagules of

388 non-native species will likely increase along the railway corridor (Lemke, Kowarik & von der
389 Lippe, 2019), further tipping the balance in favor of non-native species. A major concern of
390 connecting the railway with the national system is the potential for the transport of large amounts
391 of construction and filling material, carrying propagules of species that are, up to now, absent in
392 the area. This study can serve as a baseline study to assess and monitor future invasions along the
393 Kashmir railway network once this connectivity increases. It should also serve as a warning that
394 this increased connectivity is likely to have detrimental effects on the native vegetation in the
395 vicinity of these railways in the long run. A simple but consistent biosecurity protocol could reduce
396 the risk of new introductions into the area and should be considered within the environmental
397 mitigation plan for the railway expansion.

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

- 401 • A comprehensive Environmental Management Plan should be developed to address the
402 environmental management requirements of the railway line, especially in regard to the
403 connection of the railroad to the Indian Railway network.
- 404 • The land managers, in collaboration with Railway authorities should monitor the natural
405 vegetation in the interior natural areas and eradicate invasive species at an early stage.
406 Management should at least focus on those species shown here to be expanding most
407 rapidly (e.g., *Arundo donax*, *Conium maculatum*, *Saccharum spontaneum*, *Solanum*
408 *nigrum*, *Trifolium fragiferum*), yet also monitor for species currently not yet present in the
409 region.

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

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

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434 **Conflict of Interest**

435 **Author Contributions**

436 *IR and AAK conceived the ideas and designed methodology; SMH collected the data; JJJ analysed*
437 *the data. All authors led the writing of the manuscript and contributed critically to the drafts and*
438 *gave final approval for publication.*

439 **Data Availability Statement**

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

442 **Figures**

443 **References**

- 444 Ahmad, R., Khuroo, A.A., Hamid, M., Malik, A.H., & Rashid, I. (2019). Scale and season
445 determine the magnitude of invasion impacts on plant communities. *Flora*, 260, 151481.
- 446 Alexander, J.M., Kueffer, C., Daehler, C.C., Edwards, P.J., Pauchard, A., Seipel, T., &
447 Consortium, M. (2011). Assembly of nonnative floras along elevational gradients
448 explained by directional ecological filtering. *Proceedings of the National Academy of*
449 *Sciences of the United States of America*, 108, 656–661.
- 450 Aplet, G.H., & Vitousek, P.M. (1994). An age-altitude matrix analysis of Hawaiian rain forest
451 succession. *Journal of Ecology*, 82, 137–147.
- 452 Arévalo, J. R., Delgado, J. D., Otto, R., Naranjo, A., Salas, M., & Fernández-Palacios, J. M. (2005).
453 Distribution of alien vs. native plant species in roadside communities along an altitudinal
454 gradient in Tenerife and Gran Canaria (Canary Islands). *Perspectives in Plant Ecology,*
455 *Evolution and Systematics*, 7(3), 185-202.
- 456 Bacaro, G., Maccherini, S., Chiarucci, A., Jentsch, A., Rocchini, D., Torri, D., Gioria, M., Tordoni,
457 E., Martellos, S., Altobelli, A. & Otto, R. (2015). Distributional patterns of endemic, native
458 and alien species along a roadside elevation gradient in Tenerife, Canary
459 Islands. *Community Ecology*, 16(2), 223-234.
- 460 Barton, K. (2016) MuMIn: Multi-Model Inference. R package version 1.15.6
- 461 Becker, T., Dietz, H., Billeter, R., Buschmann, H., & Edwards, P.J. (2005). Altitudinal distribution
462 of alien plant species in the Swiss Alps. *Perspectives in Plant Ecology, Evolution and*
463 *Systematics*, 7(3), 173-183.
- 464 Benedetti, Y. & Morelli, F. (2017). Spatial mismatch analysis among hotspots of alien plant
465 species, road and railway networks in Germany and Austria. *Plos one*, 12(8), e0183691.

466 Forman, L. & Bridson, D. (1989). *The Herbarium Handbook*. (Revised edition). Royal Botanic
467 Gardens, Kew, UK.

468 Chase, J.M., & Leibold, M.A. (2002). Spatial scale dictates the productivity-biodiversity
469 relationship. *Nature*, 416: 427–430.

470 Colwell, R. K., Rahbek, C., & Gotelli, N. J. (2004). The mid-domain effect and species richness
471 patterns: what have we learned so far?. *The American Naturalist*, 163(3), E1-E23.

472 Dainese M, Aikio S, Hulme PE, Bertolli A, Prosser F, Marini L. (2017). Human disturbance and
473 upward expansion of plants in a warming climate. *Nature Climate Change*, 7:577-580.

474 Dar, G. H., Khuroo, A. A. (Eds.). (2020). *Biodiversity of the Himalaya: Jammu and Kashmir State*
475 (Vol. 18). Springer Nature.

476 Dar, P.A., Reshi, Z.A., & Shah, A.B. (2018). Altitudinal distribution of native and alien plant
477 species along roadsides in Kashmir Himalaya, India. *Tropical Ecology*, 59(1), 45-55.

478 Deng, H., Ju, W., Gao, Y., Zhang, J., Li, S., Gao, X. & Xu, B. (2020). The species composition and
479 distributional characteristics of invasive alien plants along the Sichuan-Tibet Railway
480 (Ya'an to Changdu section). *Biodiversity Science* 18(10), 1174-1181.

481 Dornelas, M., Gotelli, N. J., McGill, B., Shimadzu, H., Moyes, F., Sievers, C., & Magurran, A.
482 E. (2014). Assemblage time series reveal biodiversity change but not systematic
483 loss. *Science*, 344, 296–299.

484 Dornelas, M., Gotelli, N.J., Shimadzu, H., Moyes, F., Magurran, A.E., & McGill, B.J. (2019). A
485 balance of winners and losers in the Anthropocene. *Ecology Letters*, 22(5), 847-854.

486 Ellis, E.C. (2018). *Anthropocene: a very short introduction*. Oxford, UK: Oxford University Press.

487 Essl, F., Bacher, S., Genovesi, P., Hulme, P.E., Jeschke, J.M., Katsanevakis, S., ... Schindler, S.,
488 (2018). Which taxa are alien? Criteria, applications, and uncertainties. *BioScience*, 68(7),
489 496-509.

490 Essl, F., Dullinger, S., Rabitsch, W., Hulme, P.E., Pyšek, P., Wilson, J.R., & Richardson, D.M.,
491 (2015). Historical legacies accumulate to shape future biodiversity in an era of rapid global
492 change. *Diversity and Distributions*, 21(5), 534-547.

493 Fahrig, L., 2003. Effects of habitat fragmentation on biodiversity. *Annual Review in Ecology,*
494 *Evolution and Systematics*, 34, 487–515.

495 Figueiredo, L., Krauss, J., Steffan-Dewenter, I. & Cabral, J.S., (2019). Understanding extinction
496 debts: spatio-temporal scales, mechanisms and a roadmap for future
497 research. *Ecography*, 42(12), 1973-1990.

498 Götzenberger, L., de Bello, F., Bråthen, K.A., Davison, J., Dubuis, A., Guisan, A., ... Pellissier,
499 L., (2012). Ecological assembly rules in plant communities - approaches, patterns and
500 prospects. *Biological Reviews*, 87(1), 111-127.

501 Guo, Q., Fei, S., Shen, Z., Iannone III, B.V., Knott, J., & Chown, S.L., 2018. A global analysis of
502 elevational distribution of non-native versus native plants. *Journal of Biogeography*, 45(4),
503 793-803.

504 Haider, S., Alexander, J., Dietz, H., Trepl, L., Edwards, P. J., & Kueffer, C. (2010). The role of
505 bioclimatic origin, residence time and habitat context in shaping non-native plant
506 distributions along an altitudinal gradient. *Biological Invasions*, 12, 4003-4018.

507 Haider, S., Kueffer, C., Bruelheide, H., Seipel, T., Alexander, J.M., Rew, L.J., ... Naylor, B.J.,
508 (2018). Mountain roads and non-native species modify elevational patterns of plant
509 diversity. *Global Ecology and Biogeography*, 27(6), 667-678.

510 Hansen, M.J., & Clevenger, A.P., (2005). The influence of disturbance and habitat on the presence
511 of non-native plant species along transport corridors. *Biological conservation*, 125(2), 249-
512 259.

513 Hawkins, B.A., Field, R., Cornell, H.V., Currie, D.J., Guégan, J.F., Kaufman, D.M., ... Porter,
514 E.E., (2003). Energy, water, and broad-scale geographic patterns of species
515 richness. *Ecology*, 84(12), 3105-3117.

516 Kalwij, J.M., Robertson, M.P., & van Rensburg, B.J., (2008). Human activity facilitates altitudinal
517 expansion of exotic plants along a road in montane grassland, South Africa. *Applied*
518 *Vegetation Science*, 11(4), 491-498.

519 Khuroo, A.A., Rashid, I., Reshi, Z., Dar, G.H., & Wafai, B.A., (2007). The alien flora of Kashmir
520 Himalaya. *Biological Invasions*, 9(3), 269-292.

521 Kuussaari, M., Bommarco, R., Heikkinen, R.K., Helm, A., Krauss, J., Lindborg, R., ... Stefanescu,
522 C., (2009). Extinction debt: a challenge for biodiversity conservation. *Trends in Ecology*
523 *and Evolution*, 24(10), 564-571.

524 Lázaro-Lobo, A., & Ervin, G.N., (2019). A global examination on the differential impacts of
525 roadsides on native vs. exotic and weedy plant species. *Global Ecology and*
526 *Conservation*, 17, p.e00555.

527 Lázaro-Lobo, A., & Ervin, G.N. (2020). Native and exotic plant species respond differently to
528 ecosystem characteristics at both local and landscape scales. *Biological Invasions*, 1-14.

529 Lembrechts, J.J., Alexander, J.M., Cavieres, L.A., Haider, S., Lenoir, J., Kueffer, C., ... Rew, L.J.,
530 (2017). Mountain roads shift native and non-native plant species'
531 ranges. *Ecography*, 40(3), 353-364.

532 Lemke, A., Kowarik, I., & von der Lippe, M. (2019). How traffic facilitates population expansion
533 of invasive species along roads: the case of common ragweed in Germany. *Journal of*
534 *Applied Ecology*, 56(2), 413-422.

535 Liedtke, R., Barros, A., Essl, F., Lembrechts, J.J., Wedegärtner, R.E., Pauchard, A., & Dullinger,
536 S., 2020. Hiking trails as conduits for the spread of non-native species in mountain
537 areas. *Biological Invasions*, 22(3), 1121-1134.

538 Marini, L., Gaston, K.J., Prosser, F., & Hulme, P.E. (2009). Contrasting response of native and
539 alien plant species richness to environmental energy and human impact along alpine
540 elevation gradients. *Global Ecology and Biogeography*, 18, 652–661.

541 McDougall, K.L., Lembrechts, J., Rew, L.J., Haider, S., Cavieres, L.A., Kueffer, C.,
542 ... Alexander, J.M. (2018). Running off the road: roadside non-native plants invading
543 mountain vegetation. *Biological Invasions*, 20, 3461–3473.

544 Medvecká, J., Zaliberová, M., Májeková, J., Senko, D., & Jarolímek, I., (2018). Role of
545 infrastructure and other environmental factors affecting the distribution of alien plants in
546 the Tatra Mts. *Folia Geobotanica*, 53(3), 349-364.

547 Mehraj, G., Khuroo, A.A., Hamid, Muzafar, I., Rashid, I., & Malik, A.H. (2021) Floristic diversity
548 and correlates of naturalization of alien flora in urban green spaces of Srinagar city. *Urban*
549 *Ecosystems*, <https://doi.org/10.1007/s11252-021-01105-7>

550 Mehraj, G., Khuroo, A.A., Qureshi, S., Muzafar, I., Friedman, C.R., & Rashid, I. (2018) Patterns
551 of alien plant diversity in the urban landscapes of global biodiversity hotspots: a case study
552 from the Himalayas. *Biodiversity and Conservation*, 27, 1055-1072.

553 Muzafar, I., Khuroo, A.A., Mehraj, G., Hamid, M., Rashid, I., & Malik, A.H., (2019). Floristic
554 diversity along the roadsides of an urban biodiversity hotspot in Indian Himalayas. *Plant*
555 *Biosystems*, 153(2), 222-230.

556 Najman, Y. (2006). The detrital record of orogenesis: A review of approaches and techniques used
557 in the Himalayan sedimentary basins. *Earth Science Reviews*, 74(1-2),1-72.

558 Newbold, T., Hudson, L.N., Hill, S.L., Contu, S., Lysenko, I., Senior, R.A., Börger, L., Bennett,
559 D.J., Choimes, A., Collen, B., & Day, J., (2015). Global effects of land use on local
560 terrestrial biodiversity. *Nature*, 520(7545), 45-50.

561 Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., et al... (2013) vegan:
562 Community Ecology Package. R package version 2.0-8. Available: CRAN.R-
563 project.org/package=vegan

564 Pauchard, A., & Alaback, P.B. (2004). Influence of elevation, land use, and landscape context on
565 patterns of alien plant invasions along roadsides in protected areas of South-Central
566 Chile. *Conservation Biology*, 18(1), 238-248.

567 Pauchard, A., Kueffer, C., Dietz, H., Daehler, C.C., Alexander, J., Edwards, P.J., ... Jakobs, G.
568 (2009). Ain't no mountain high enough: plant invasions reaching new elevations. *Frontiers*
569 *in Ecology and the Environment*, 7(9), 479-486.

570 Penone, C., Machon, N., Julliard, R., & Le Viol, I., (2012). Do railway edges provide functional
571 connectivity for plant communities in an urban context?. *Biological Conservation*, 148(1),
572 126-133.

573 Petitpierre, B., McDougall, K., Seipel, T., Broennimann, O., Guisan, A., & Kueffer, C. (2016).
574 Will climate change increase the risk of plant invasions into mountains?. *Ecological*
575 *Applications*, 26(2), 530-544.

576 Pollnac, F., Seipel, T., Repath, C. & Rew, L.J. (2012). Plant invasion at landscape and local scales
577 along roadways in the mountainous region of the Greater Yellowstone
578 Ecosystem. *Biological Invasions*, 14(8), 1753-1763.

579 Pollock, S.Z., Nielsen, S.E. & St. Clair, C.C. (2017). A railway increases the abundance and
580 accelerates the phenology of bear-attracting plants in a forested, mountain
581 park. *Ecosphere*, 8(10), p.e01985.

582 R Core Team (2015). R: a language and environment for statistical computing. R Foundation for
583 Statistical Computing.

584 Rahbek, C., Borregaard, M.K., Antonelli, A., Colwell, R.K., Holt, B.G., Nogues-Bravo, D., ...
585 Fjeldså, J., (2019). Building mountain biodiversity: Geological and evolutionary
586 processes. *Science*, 365(6458), 1114-1119.

587 Rashid, I., Shiekh, M., Lembrechts, J., Khuroo, A., Pauchard, A. & Dukes, J. (2021). Species
588 abundance along the railway of Kashmir Himalaya, Dryad, Dataset.
589 <https://doi.org/10.5061/dryad.0pngf20h>

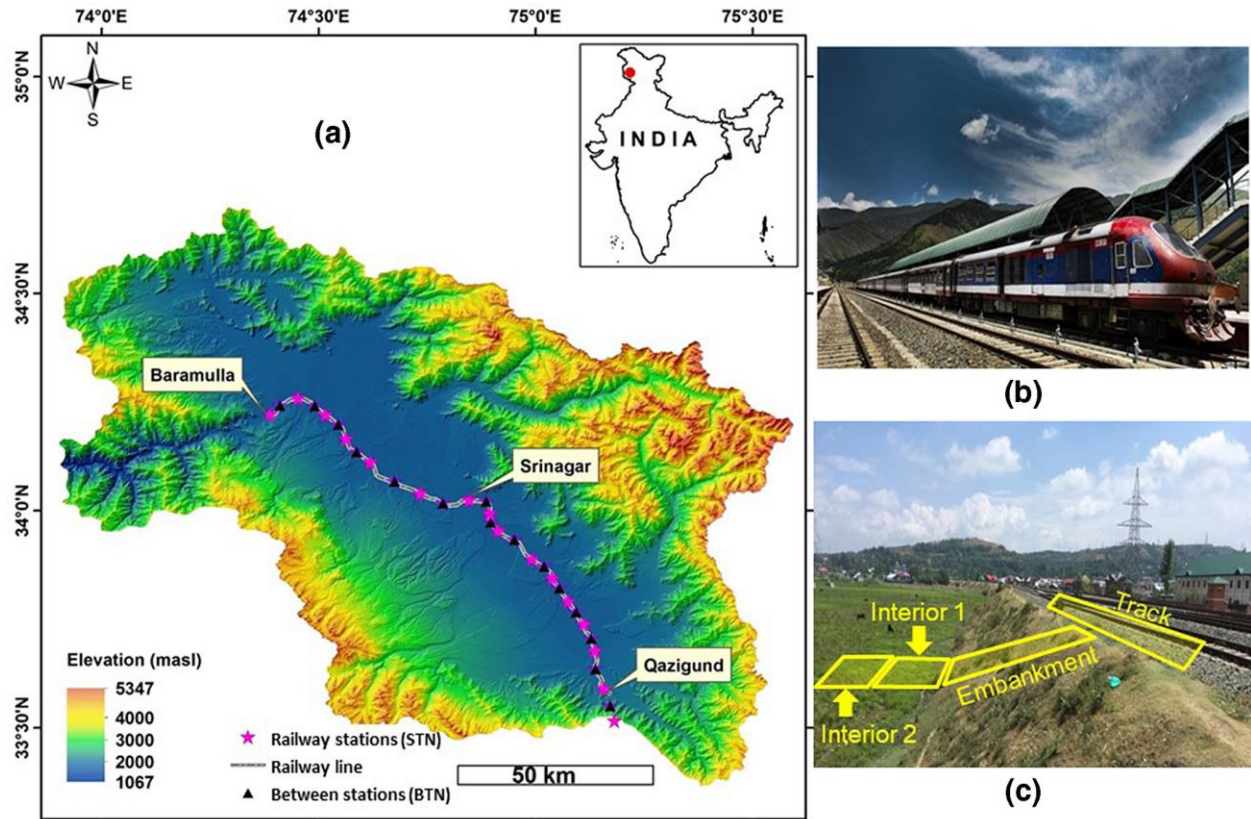
590 Rosenzweig, M.L. (1995) Species diversity in space and time. Cambridge University
591 Press, Cambridge, UK.

592 Rutkovska, S., Pučka, I., Evarts-Bundersanta, P. & Paidere, J. (2013). The role of railway lines in
593 the distribution of alien plant species in the territory of Daugavpils City (Latvia). *Estonian*
594 *Journal of Ecology*, 62, 212–225.

595 Seipel, T., Kueffer, C., Rew, L.J., Daehler, C.C., Pauchard, A., Naylor, B.J., ... Cavieres, L.A.,
596 (2012). Processes at multiple scales affect richness and similarity of non-native plant
597 species in mountains around the world. *Global Ecology and Biogeography*, 21(2), 236-
598 246.

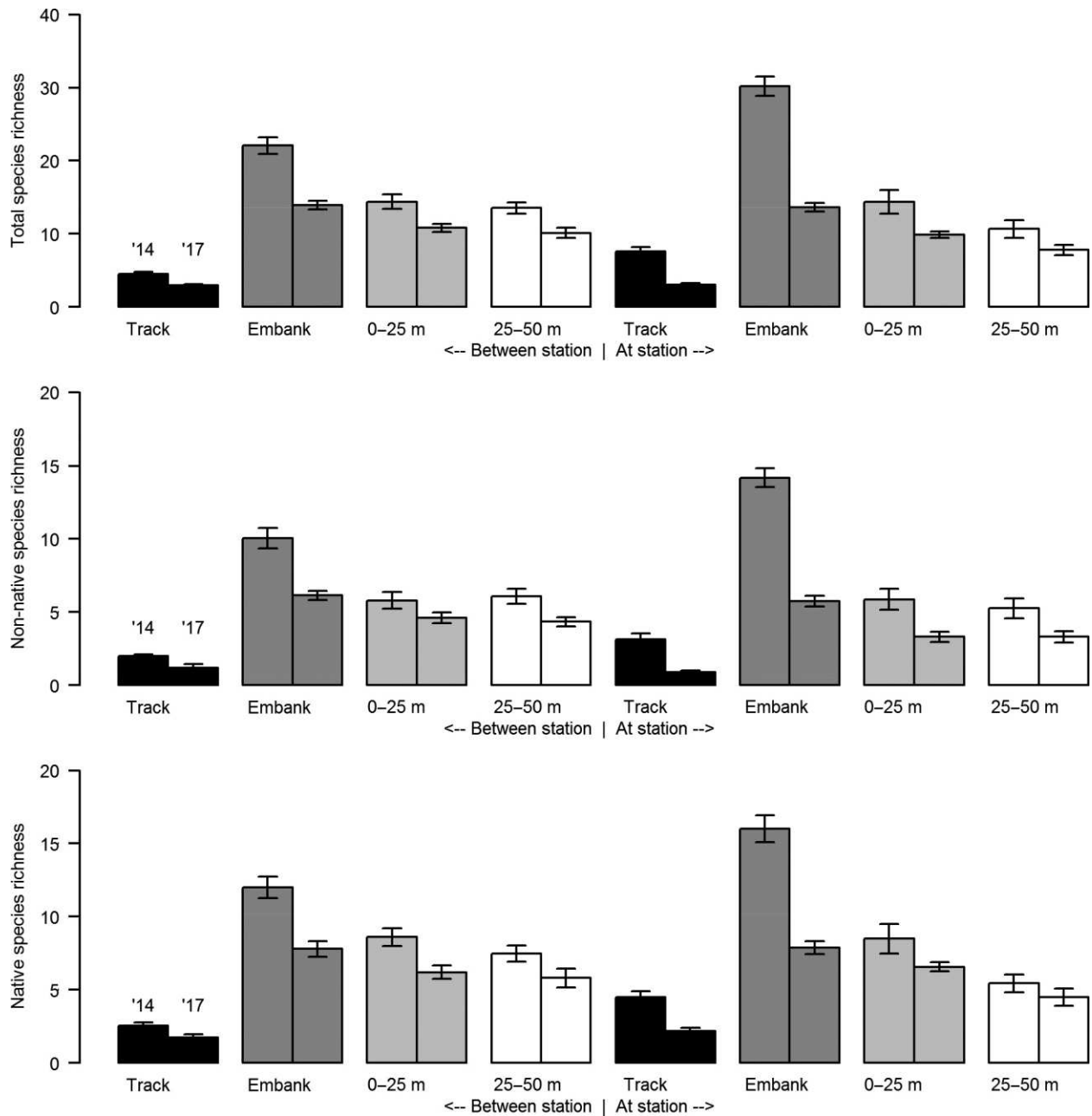
599 Shmida, A.V.I., & Wilson, M.V. (1985). Biological determinants of species diversity. *Journal of*
600 *Biogeography*, 12, 1-20.

- 601 Stewart RR (1972) An annotated catalogue of the vascular plants of West Pakistan and Kashmir.
602 Fakhri Press, Karachi, Pakistan
- 603 Taverna, K., Peet, R.K., & Phillips, L.C., (2005). Long-term change in ground-layer vegetation of
604 deciduous forests of the North Carolina Piedmont, USA. *Journal of Ecology*, 93(1), 202-
605 213.
- 606 Vellend, M., Baeten, L., Myers-Smith, I. H., Elmendorf, S. C., Beauséjour, R., Brown, C. D.,
607 ... Wipf, S.M. (2013). Global meta-analysis reveals no net change in local-scale plant
608 biodiversity over time. *Proceedings of the National Academy of Sciences of the United*
609 *States of America*, 110, 19456–19459.
- 610 Wang, G., Gillespie, A.R., Liang, S., Mushkin, A., & Wu, Q. (2015). Effect of the Qinghai–Tibet
611 Railway on vegetation abundance. *International Journal of Remote Sensing*, 36(19-20),
612 5222-5238.
- 613 White P.S. & Pickett S. T. A. (1985) Natural disturbance and patch dynamics: an introduction. The
614 ecology of natural disturbance and patch dynamics (ed. & Pickett S. T. A.). Orlando,
615 FL: Academic Press.
- 616 White, E.P., Adler, P.B., Lauenroth, W.K., Gill, R.A., Greenberg, D., Kaufman, D.M., Rassweiler,
617 A., Rusak, J.A., Smith, M.D., Steinbeck, J.R., & Waide, R.B., (2006). A comparison of the
618 species–time relationship across ecosystems and taxonomic groups. *Oikos*, 112(1), 185-
619 195.
- 620 Wiłkomirski, B., Galera, H., Sudnik-Wójcikowska, B., Staszewski, T., & Malawska, M., (2012).
621 Railway tracks-habitat conditions, contamination, floristic settlement – a
622 review. *Environment and Natural Resources Research*, 2(1), 86.
- 623 Yaduvanshi, A., Zaroug, M., Bendapudi, R., & New, M. (2019). Impacts of 1.5°C and 2°C global
624 warming on regional rainfall and temperature change across India. *Environmental*
625 *Research Communications*, 1(12), 125002.
- 626 Yurkonis, K.A. & Meiners, S. J. (2004). Invasion impacts local species turnover in a successional
627 system. *Ecology Letters*, 7, 764-769.
- 628

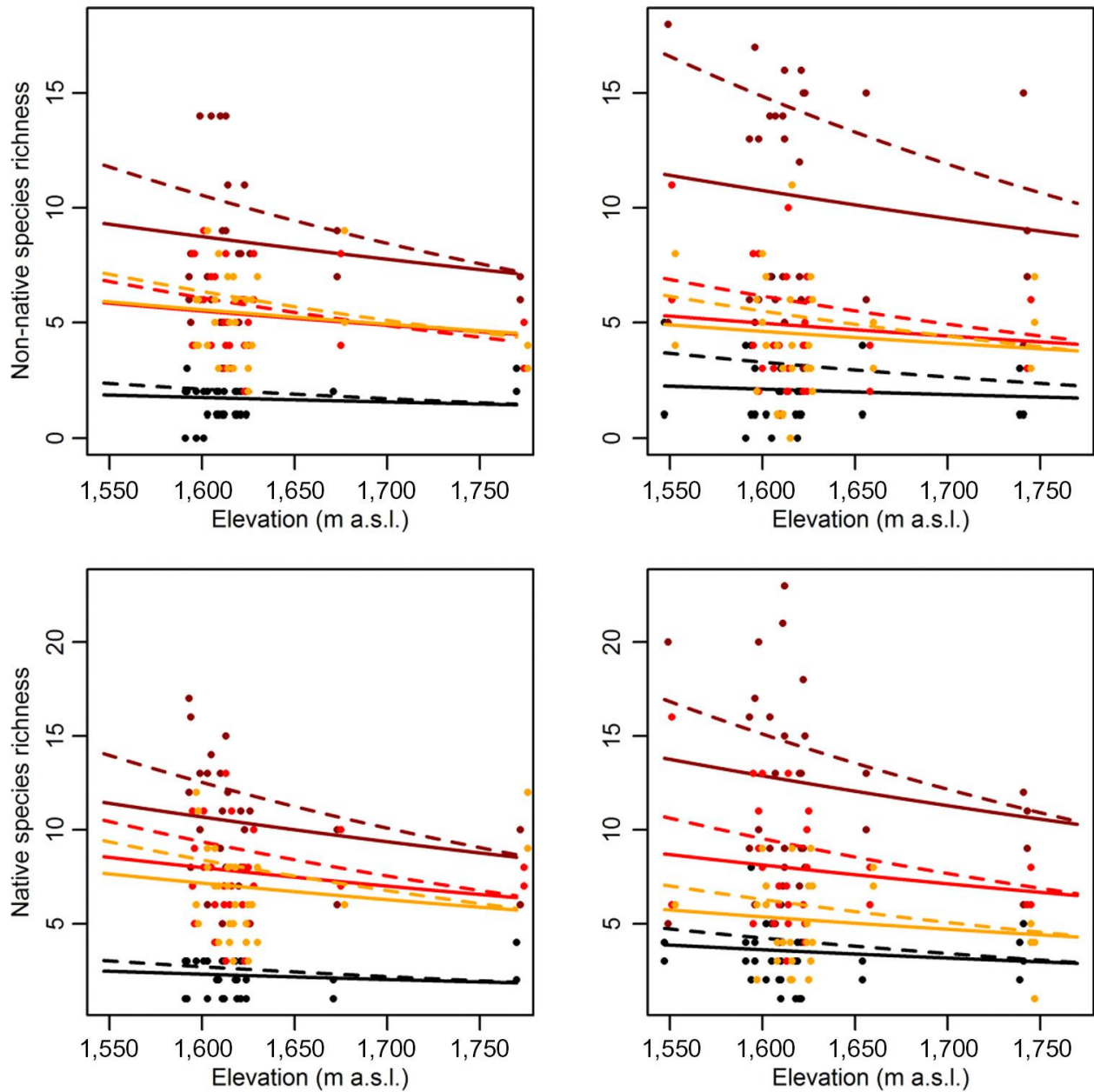


629
 630 Figure 1: Railway of Kashmir Himalaya: (a) map with marked localities of the sampling sites,
 631 (b) a view of the railway station (STN), (c) a sampling site between stations (BTN) illustrating
 632 the sampling design with four 2×50 m plots laid down in form of a 'T' (plots not drawn to
 633 scale)

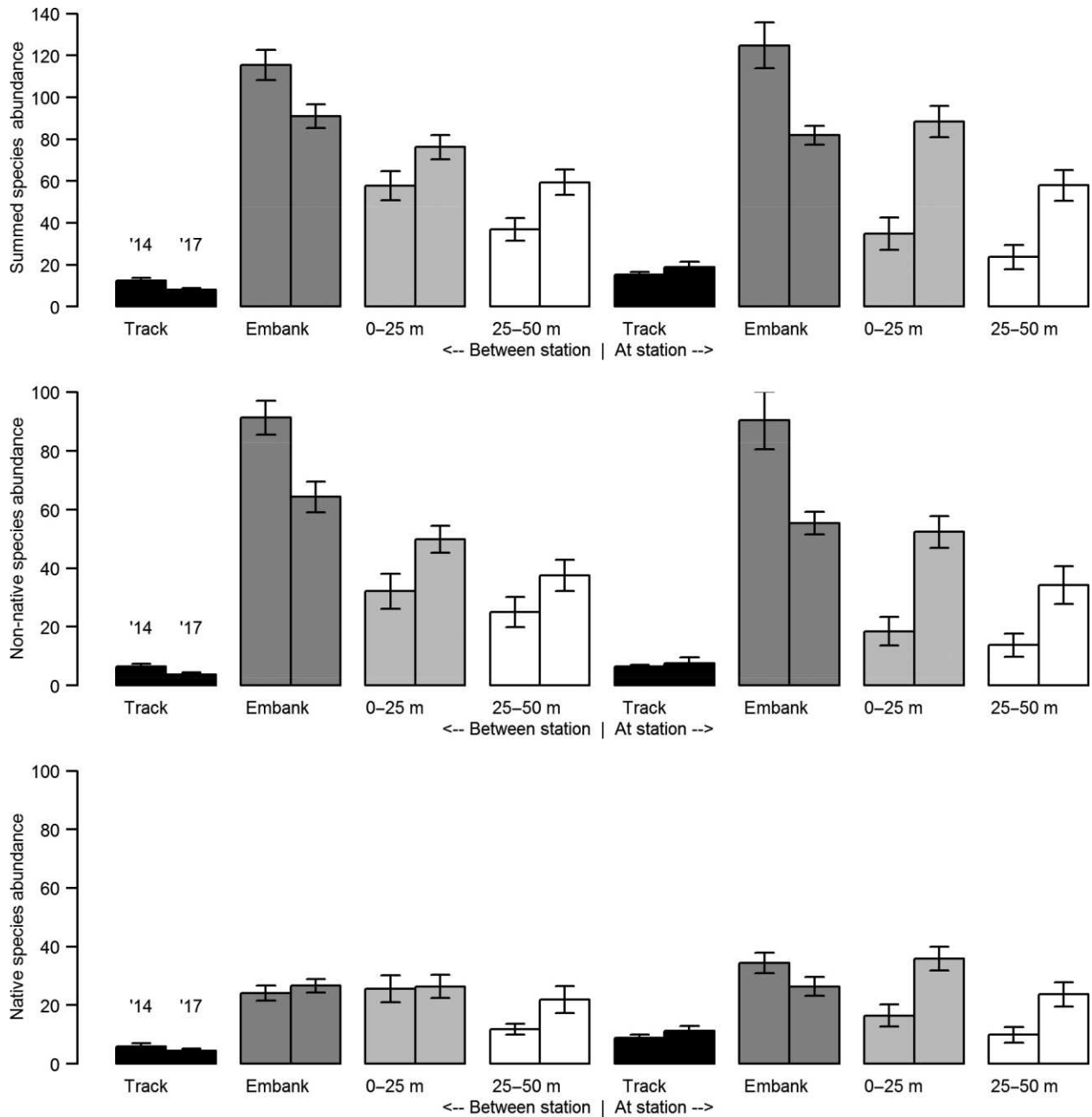
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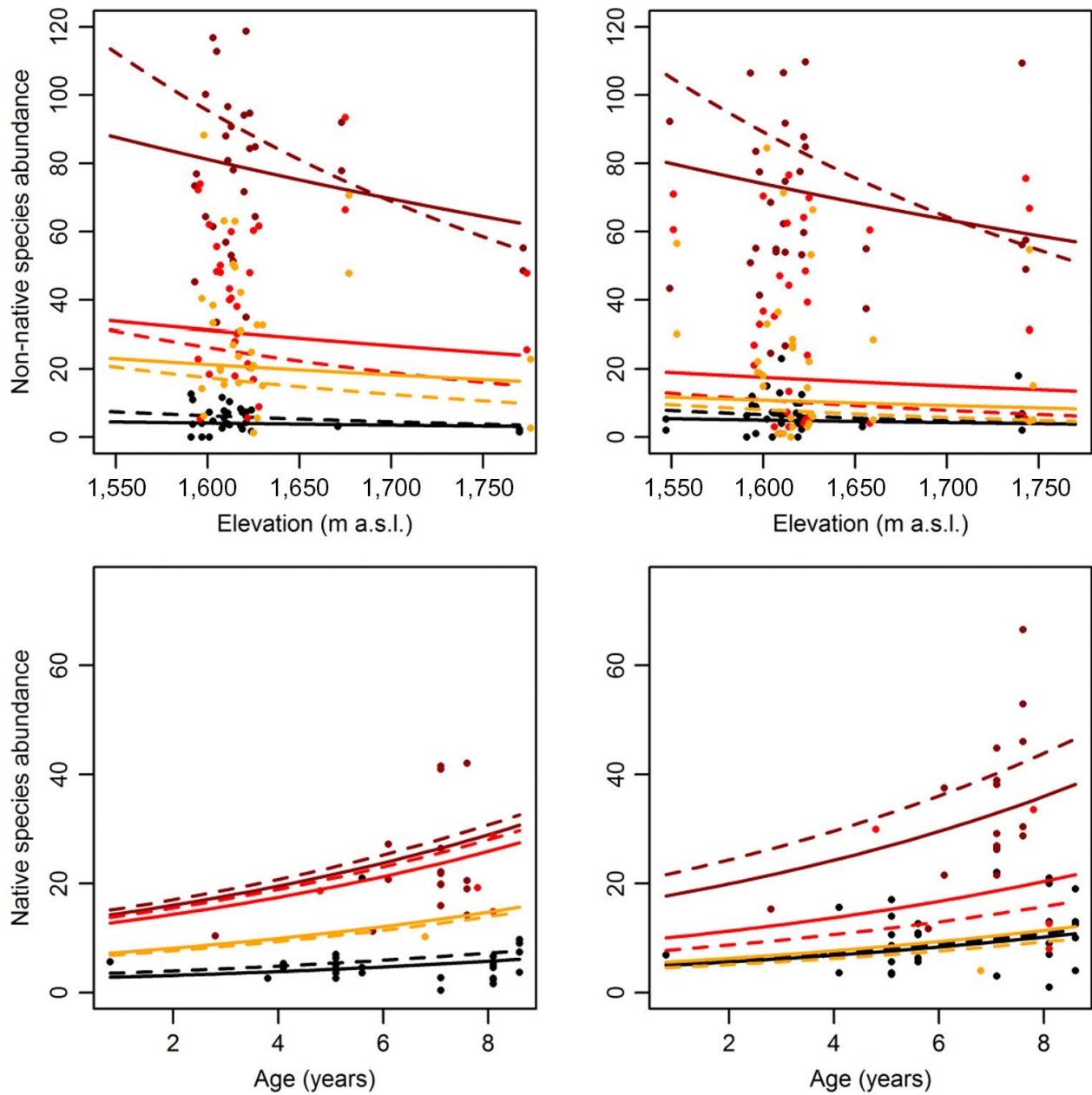
637
 638 Figure 2: Average (with standard error) of total (top), non-native (middle) and native (bottom)
 639 species richness for each plot type in 2014 and 2017. For outcomes of the models, see Table 1
 640



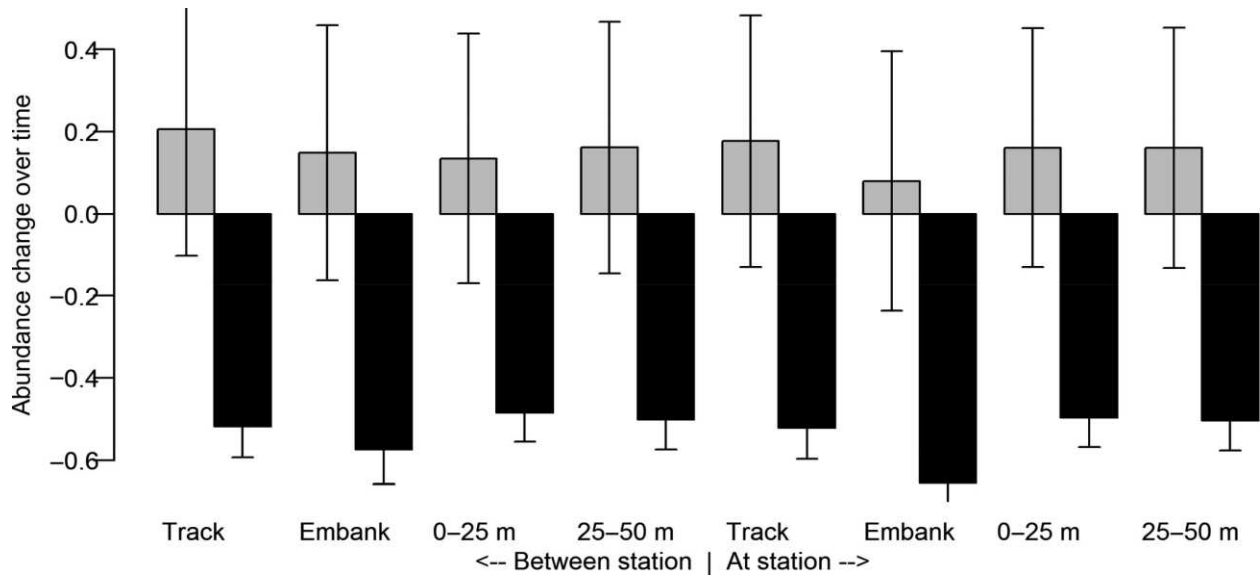
641
 642 Figure 3: Non-native and native species richness as a function of elevation (x -axis), year
 643 (2014 = dashed line and 2017 = full line) and plot type (left = between station, right = at station:
 644 track (black), embankment (dark red), 0–25 m (red) and 25–50 m (orange)). Results from the
 645 best (i.e. lowest AIC) GLM with a Poisson distribution (see Table 1)
 646



647
 648 Figure 4: Average (with standard error) of summed abundances for all (top), non-native-only
 649 (middle) and native-only (bottom) species abundance for each plot type in 2014 (left bar) and
 650 2017 (right bar). For outcomes of the models, see Table 2
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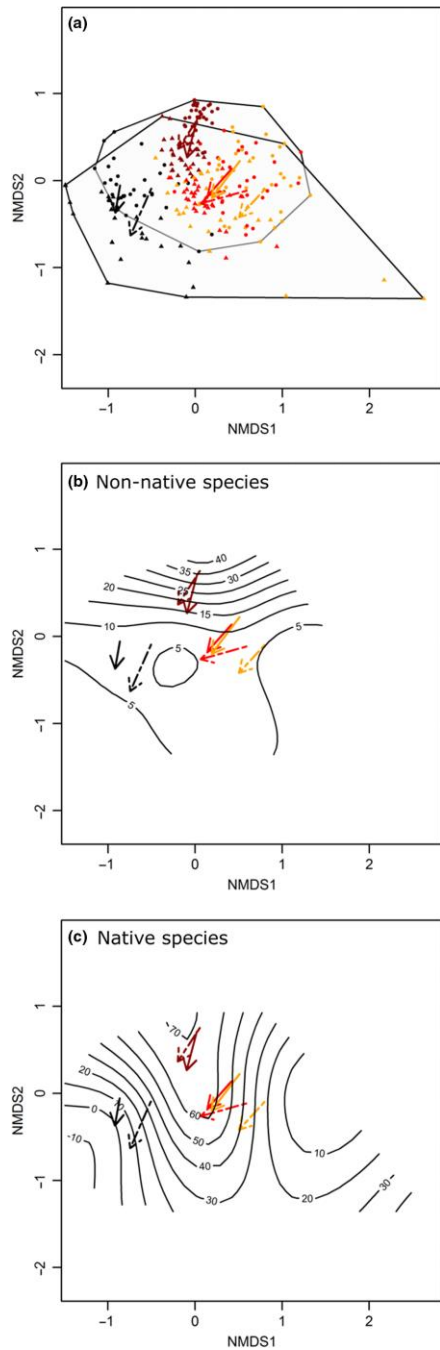


652
 653 Figure 5: Non-native (top) and native (bottom) species richness as a function of elevation (top)
 654 or railway age (bottom), year (2014 = dashed line and 2017 = full line) and plot type
 655 (left = between station, right = at station: track (black), embankment (dark red), 0–25 m (red) and
 656 25–50 m (orange)). Results from the linear models with the best fit (i.e. lowest AIC) of
 657 $\ln(x + 0.1)$ (see Table 2)
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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



665
 666 Figure 7: (a) First two dimensions of a non-metric dimensional scaling (NMDS)-analysis on
 667 species composition. Coloured symbols indicate plots (circles = 2014, triangles = 2017;
 668 black = tracks, dark red = embankments, red = 0–25 m and orange = 25–50 m), with smaller
 669 distances between dots indicating higher similarity. The two polygons indicate the spread in plots
 670 in 2014 (connecting circles, the small circular polygon) and 2017 (connecting triangles, the
 671 larger one). Arrows indicate the shift in average species composition per plot type from 2014 to
 672 2017 (colours see earlier; full lines = between stations and dashed lines = at stations). Averages
 673 in non-native (b) and native (c) species abundance super-imposed on the time shifts per plot type
 674 from the first graph
 675