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- 1 **Running off the road: roadside non-native plants invading mountain vegetation**
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- 3 **Keith L. McDougall**, 1) Office of Environment and Heritage, PO Box 733, Queanbeyan, NSW, 2620,
4 Australia; 2) Department of Ecology, Environment and Evolution, La Trobe University, Wodonga 3690,
5 Victoria, Australia
- 6 **Jonas Lembrechts**, Centre of Excellence on Plant and Vegetation Ecology, CDE C.007- University of
7 Antwerp, Belgium
- 8 **Lisa J. Rew**, Department of Land Resources and Environmental Sciences, Montana State University,
9 Bozeman, Montana 59717, USA
- 10 **Sylvia Haider**, 1) Institute of Biology / Geobotany and Botanical Garden, Martin Luther University Halle-
11 Wittenberg, Halle (Saale), Germany; 2) German Centre for Integrative Biodiversity Research (iDiv) Halle-
12 Jena-Leipzig, Leipzig, Germany
- 13 **Lohengrin A. Cavieres**, Departamento de Botánica, Facultad de Ciencias Naturales y Oceanográficas,
14 Universidad de Concepción, Concepción, Chile and Instituto de Ecología y Biodiversidad (IEB), Santiago,
15 Chile
- 16 **Christoph Kueffer**, Institute of Integrative Biology, Department of Environmental Systems Science, ETH
17 Zurich, CH-8092 Zürich, Switzerland
- 18 **Ann Milbau**, Research Institute for Nature and Forest – INBO, Havenlaan 88 bus 73, 1000 Brussels, Belgium
- 19 **Bridgett J. Naylor**, USDA Forest Service, Pacific Northwest Research Station, La Grande, Oregon 97850, USA
- 20 **Martin A. Nuñez**, Grupo de Ecología de Invaciones, Universidad Nacional del Comahue, INIBIOMA,
21 CONICET, Av. Pionero, 2335 C.P. 8400, Bariloche, Argentina
- 22 **Anibal Pauchard**, 1. Laboratorio de Invaciones Biológicas (LIB), Facultad de Ciencias Forestales, Universidad
23 de Concepción, Casilla 160-C, Concepción, Chile, 2. Institute of Ecology and Biodiversity (IEB), Santiago,
24 Chile
- 25 **Tim Seipel**, Department of Land Resources and Environmental Sciences, Montana State University,
26 Bozeman, Montana 59717, USA

27 **Karina L. Speziale**, Grupo de Biología de la Conservación, Laboratorio Ecotoño, INIBIOMA (CONICET-
28 UNCOMA), Bariloche, Argentina
29 **Genevieve T. Wright**, Office of Environment and Heritage, PO Box 733, Queanbeyan, NSW, 2620, Australia
30 **Jake M. Alexander**, Department of Ecology and Evolution, University of Lausanne, 1015 Lausanne,
31 Switzerland
32
33 Corresponding author: Keith L. McDougall, email: K.Mcdougall@latrobe.edu.au, phone: 61 2 6229 7111, 61
34 435 065 438; orcid.org/0000-0002-8288-6444.
35
36 **Abstract**
37 Prevention is regarded as a cost-effective management action to avoid unwanted impacts of non-native
38 species. However, targeted prevention can be difficult if little is known about the traits of successfully
39 invading non-native species or habitat characteristics that make native vegetation more resistant to
40 invasion. Here, we surveyed mountain roads in seven regions worldwide, to investigate whether different
41 species traits are beneficial during primary invasion (i.e. spread of non-native species along roadside
42 dispersal corridors) and secondary invasion (i.e. percolation from roadsides into natural adjacent
43 vegetation), and to determine if particular habitat characteristics increase biotic resistance to invasion. We
44 found primary invasion up mountain roads tends to be by longer lived, non-ruderal species without seed
45 dispersal traits. For secondary invasion, we demonstrate that both traits of the non-native species and
46 attributes of the receiving natural vegetation contribute to the extent of invasion. Non-native species that
47 invade natural adjacent vegetation tend to be shade and moisture tolerant. Furthermore, non-native
48 species invasion was greater when the receiving vegetation was similarly rich in native species. Our results
49 show how mountain roads define which non-native species are successful; first by favouring certain traits in
50 mountain roadsides (the key dispersal pathway to the top), and secondly by requiring a different set of
51 traits when species invade the natural adjacent vegetation. While patterns in species traits were observed
52 at a global level, regional abiotic and biotic variables largely generated region-specific levels of response,
53 suggesting that management should be regionally driven.

54 **Keywords**

55 Biotic resistance, elevation gradient, management, primary invasion, secondary invasion, traits

56 **Introduction**

57 Plant invasions in natural vegetation can cause impacts on biodiversity, ecosystem services and ecological
58 processes, including nutrient cycling (Simberloff 2011), water production (LeMaitre et al. 1996), and fire
59 regimes (Mack and D'Antonio 1998; Ehrenfeld 2010; Simberloff 2011). Prevention of new invasions is
60 typically regarded as the most cost-effective management action to avoid these impacts (Leung et al.
61 2002). To pursue this strategy, land managers can make use of the fact that the spread of non-native
62 species follows typical dispersal pathways, like roads and railways tracks, and from there they invade into
63 natural vegetation (McDougall et al. 2011; Pollnac et al. 2012; Seipel et al. 2012). However, in reality it is
64 impossible to monitor such pathways in a whole region and manage or eradicate all newly established
65 populations of non-native species. Therefore, management may be more effective if it is targeted at 1) the
66 species possessing traits that are likely to increase their invasiveness in natural vegetation and 2) the
67 characteristics of natural vegetation that make it less resistant to invasion.

68 A long-standing goal of invasion research has been to identify species traits that increase the
69 invasiveness of a species, starting with Baker's idea of the 'ideal weed' in the 1960s (Baker 1965). Since
70 then, numerous studies have compared traits between native and non-native species (Daehler 2003; van
71 Kleunen et al. 2010a), or between non-native and invasive species, and, several consistent patterns have
72 been identified. For instance, van Kleunen et al. (2010b) reported in their meta-analysis of over 100 field or
73 common-garden studies that invasive non-native species scored higher in performance-related traits than
74 non-invasive species. But a limitation of these studies is that they do not distinguish between traits
75 favouring establishment and spread in anthropogenically disturbed habitats such as dispersal corridors, and
76 traits that enable a non-native species to percolate from there into natural vegetation. Indeed, favourable
77 species traits are likely to differ between "primary" (anthropogenically disturbed habitat) and "secondary"
78 (natural habitat) phases of the invasion process (Dietz and Edwards 2006). During primary invasion, usually
79 in resource-rich and disturbed environments, species with a ruderal ecological strategy (*sensu* Grime 1977)
80 possessing traits that promote establishment and spread along invasion corridors, such as short (i.e.
81 annual) generation times, highly dispersive seeds and tolerances for open dry conditions, are hypothesised
82 to have an advantage (Dietz and Edwards 2006). In contrast, species with traits conferring greater

83 competitive ability or higher stress-tolerance, such as clonality, perennial life history or shade tolerance,
84 are expected to be more successful during secondary invasion (Dietz and Edwards 2006). That different
85 selection pressures operate at different stages of invasion might help explain why research results
86 sometimes seem to be contradictory and the process of invasion has been regarded as idiosyncratic
87 (Lockwood et al. 2005; Dietz and Edwards 2006; Kueffer et al. 2013a).

88 Beside species traits, characteristics of the receiving site can play an important role in determining
89 invasibility, with some vegetation types in a region typically being more resistant to invasion than others
90 (e.g. Vilà et al. 2007; Milbau et al. 2013; Speziale and Ezcurra 2011). This may be explained by the
91 frequency and magnitude of disturbances, which affect the availability of resources (e.g. Davis et al. 2000;
92 Lake and Leishman 2004; Lembrechts et al. 2017), and facilitation (e.g. Cavieres et al. 2007) or competition
93 (Cavieres et al. 2018) by resident native plants. At a local scale, vegetation structure may be important
94 with, for instance, natural gaps in forest being entry points for invasive species (e.g. Knapp and Canham
95 2000; Knight et al. 2008). Vegetation that is species diverse tends to be more resistant to invasion (Elton
96 1958; McCann 2000), although there are inconsistencies across spatial extents and habitats (Fridley et al.
97 2007).

98 Even though these and other drivers of invasibility and invasiveness have been extensively
99 explored, little is known about how the relative importance of different drivers varies between regions with
100 differing environmental contexts. For example, the meta-analysis of van Kleunen et al. (2010b) showed that
101 in tropical climates the difference in growth rates between invasive and non-invasive species is much
102 greater than in temperate climates. Similarly, drivers of invasibility and invasiveness might be expected to
103 change across environmental gradients within regions (Pauchard et al. 2009). For example, traits associated
104 with stress tolerance might become increasingly important for non-native species establishment as
105 environmental harshness increases (Zefferman et al. 2015), even in anthropogenically disturbed habitats.
106 Furthermore, factors promoting the invasibility of natural habitats might increase or decrease in
107 importance depending on environmental severity. For example, if disturbance acts to reduce competitive
108 pressure from native species, then disturbance might be an especially important driver of non-native
109 species establishment under benign environmental conditions (Pauchard et al. 2009; Lembrechts et al.

110 2014). To address these questions, and so achieve a more complete picture of the determinants of invasion
111 success, the challenge is to obtain data on non-native species establishment in both anthropogenically
112 disturbed and natural vegetation, across environmental gradients and in multiple regions.

113 Mountains offer ideal conditions for investigating the spread of non-native species from dispersal
114 corridors into adjacent vegetation along environmental gradients. Non-native species are typically
115 introduced at low elevation and spread towards higher elevation along roads (Alexander et al. 2011; Haider
116 et al. 2018). Once established along the disturbed road edges, non-native species may then move into the
117 adjacent vegetation that is typically less affected by humans and dominated by native plant species. A
118 strong decline in non-native species richness away from mountain roads has been observed (Seipel et al.
119 2012), indicating that invasion does occur beyond roads but that there are substantial barriers that limit it
120 (Pollnac et al. 2012). An advantage of this study system is that the geographical distance between pathway
121 and natural vegetation is short. This excludes the possibility that propagule availability and climate are the
122 limiting factors and potential barriers, because non-native species have already established along the
123 roadsides. Furthermore, the decline in non-native species richness away from roads is increasingly steep at
124 higher elevations (Seipel et al. 2012), suggesting that climate interacts with other community or species
125 characteristics to affect invasion into natural vegetation. Finally, these patterns have been observed in
126 multiple mountain regions around the world, providing the opportunity to assess the extent to which
127 particular correlates of habitat invasibility and species' invasiveness are region-specific.

128 In this paper, using data from widely separated global regions, we investigate which species traits
129 promote invasion along roadsides (i.e. primary invasion) and from there into natural vegetation (i.e. during
130 secondary invasion), and which characteristics of the habitat away from the roads influence resistance to
131 invasion. In addition, we analyse for the first time whether factors influencing non-native species secondary
132 invasion change along steep elevation gradients. We predict that (1) particular traits and ecological
133 attributes will be associated with higher levels of invasion, specifically that long-lived species, with good
134 competitive abilities, and the ability to tolerate shadier, cooler and moister conditions are more likely to
135 invade natural vegetation. In addition, we expect that seed traits related to dispersal adaptation are not
136 relevant to spread from roadsides into adjacent vegetation, due to the environmental and species trait

137 filters associated with primary invasion and the availability of propagules over the short distances involved.
138 Further we predict that (2) natural vegetation has a higher invasion resistance if it has a high native species-
139 richness, with a high proportion of tree species that compete for light and resources with the invader, and
140 a low level of disturbance.

141 With the use of our systematic sampling approach along elevation gradients we explore the
142 importance of factors influencing non-native species richness in natural vegetation not only along
143 environmental gradients within regions, but also the variation of these patterns between regions, asking
144 what generalizations emerge across regions.

145

146 **Methods**

147 *Study areas and survey design*

148 We sampled roads and their adjacent vegetation in seven mountain regions: Nahuel Huapi National Park in
149 Argentina; Kosciuszko National Park in Australia; south-central Andes in Chile; northern Scandes in Norway;
150 Canton Valais in Switzerland; two regions in the United States – the Greater Yellowstone Ecosystem in
151 Montana and Wyoming, and the Wallowa Mountains in north-eastern Oregon (Table 1).

152 In these seven regions, we selected three roads that extended over broad elevational gradients
153 (Table 1) and were open to vehicular traffic for at least part of the year. The roads sampled ranged from
154 low use, gravel roads to asphalt highways. The road edges typically had shallow soils, reduced tree canopy
155 cover (compared to adjacent vegetation) and much bare ground. In many cases the surface soils of the road
156 edge were heavily altered, or not native to the area having been imported for road-making. The adjacent
157 vegetation was less or un-disturbed, had native soils, and plants native to the region dominated. All
158 sampling was conducted between 2011 and 2015.

159 Twenty locations were selected on each road at approximately equal elevational intervals (see also
160 Seipel et al. (2012) and Haider et al. (2018)). The highest sample was generally at the highest point that
161 could be reached by road and the bottom was the point below which there was no substantial change in
162 elevation or further sampling became impractical (e.g. because of land tenure). At each location, three 2 m
163 x 50 m (100 m²) plots were sampled; one in road habitat at the edge of the road surface and with the long

164 side parallel to it, one perpendicular to it in adjacent vegetation, from 50 m to 100 m away from the road
165 and a third (not used in this paper because it represents an ecotone between disturbed roadsides and more
166 natural vegetation), 0 m to 50 m from the road. Topographic constraints (e.g. cliffs) and cultivated farmland
167 prevented the sampling of some plot pairs in two regions (Table 1). The covers of all vascular plant species
168 and bare ground were recorded in each plot using the following ordinal scale: 1 = <1%, 2 = 1 to <5%, 3 = 5
169 to <25%, 4 = 25 to <50%, 5 = 50 to <75%, 6 = 75 to <95%, 7 = 95 to 100%. Taxonomy was standardised
170 between regions using the Taxonomic Name Resolution Service v4.0 (Boyle et al. 2013;
171 <http://tnrs.iplantcollaborative.org/TNRSapp.html>, accessed April 2015) and local published floras. Species
172 were classified as either native or non-native according to local and regional floras (for details see Haider et
173 al. 2018).

174

175 *Species traits*

176 Intra-specific trait variation can be remarkably high along elevation gradients for some traits (e.g. specific
177 leaf area, see Rosbakh et al. 2015), and in such cases species' average trait values would not be appropriate
178 for our study design. Therefore, we chose to use species traits that are or are more likely to be spatially
179 invariant: 1) life history (obtained from local floras and personal knowledge); 2) ecological traits: Grime
180 strategy (Grime 1977) obtained from the BiolFlor database (Klotz et al. 2002) and Ellenberg indicator values
181 for moisture, light and temperature (Ellenberg and Leuschner 2010); and 3) seed characters relating to
182 dispersal, obtained from the D³ database (Hintze et al. 2013) (Table 2). These traits are indirectly related to
183 plant performance (e.g. perenniability or competitive behaviour, differential dispersal capacity, and habitat
184 preference). For some species, trait data were not available; availability ranged from 45 to 100% of species
185 (Table 2).

186

187 *Data analysis*

188 Do trait patterns of non-native species differ along elevation gradients and between roadside and adjacent
189 vegetation?

190 We modelled the proportion of non-native species in a plot possessing particular traits as a function of the
191 elevation of the plot, and whether it was located in roadside or natural adjacent vegetation. We calculated
192 the proportion of species with a certain trait at the plot level by dividing the number of non-native species
193 with that trait in each plot by the total number of non-native species in that plot. Then, we fitted models
194 across all regions for the proportion of each trait, using generalized linear mixed models with a binomial
195 distribution (GLMMs, function glmer, package lme4; Bates et al. 2011), with elevation (regionally scaled
196 with mean = 0 and standard deviation = 1), plot type (roadside vs. adjacent) and their interaction as fixed
197 effects, and including 'road' nested in 'region' as random effects. We also fitted models including random
198 effects of transect (nested in road), but these were not supported based on a comparison of Akaike
199 Information Criterion values (AICc, corrected for small sample sizes; Zuur et al. 2009), and so were dropped
200 from the models. For each trait, we then made a set of models with all possible combinations of the
201 abovementioned fixed factors as explanatory variables. Next, we used model averaging of the estimates of
202 all models in which the AICc differed less than 2 from the best model (function model.avg, package MuMIn;
203 (Barton 2015)), and weighted the estimates based on the support for each model, with more weight given
204 to models with a lower AICc (Burnham and Anderson 2002). Such an approach has been advocated to
205 result in more robust model fitting than single-model methods and stepwise model selection, as it provides
206 a quantitative measure of relative support for competing hypotheses and the uncertainty surrounding each
207 predictor (Burnham and Anderson 2002).

208

209 Which biotic and abiotic plot-level factors increase non-native species richness in adjacent vegetation?

210 We investigated the effect of five environmental factors collected at the plot level on non-native species
211 richness in the adjacent vegetation plots using GLMMs. In preliminary analyses with region and road
212 (nested) as random effects, models were uninformative because of large regional differences and so, unlike
213 the trait analysis, models were fitted for each region separately. The following factors were assessed for
214 each adjacent vegetation plot:

215 a) Non-native species richness in the corresponding roadside plot, as a proxy for propagule availability at
216 the roadside;

217 b) Native species richness in the adjacent vegetation plot;
218 c) Disturbance: the cover of bare ground in adjacent plots (on the ordinal classes outlined above);
219 d) Elevation recorded in the adjacent plot. Elevation in all regions was strongly inversely correlated with
220 mean annual temperature and mean temperature of the warmest quarter and so this variable is reflective
221 of climate at the plot scale (Table S1). Elevation was also positively correlated with annual precipitation and
222 precipitation in the warmest quarter in all regions except in Argentina and Chile where it was negatively
223 correlated (though weakly so in Chile);
224 e) Tree cover rank in adjacent plots: the rank in tree cover from lowest (1) to highest (equal to the number
225 of plots in a region). To calculate tree rank for a plot, the median covers of the ordinal values for tree
226 species in each plot were summed and the total was then ranked from lowest to highest.

227 Our approach to fitting the GLMMs here involved two steps. Firstly, we fitted models containing
228 only main effects of the five explanatory variables listed above to estimate their overall effect sizes within
229 each region. An exception was Switzerland, where due to lower sample size we only included three
230 variables (native species richness, bare ground, elevation) in the models to avoid overfitting. Secondly, we
231 fitted models including elevation and variables associated with properties of the adjacent vegetation (i.e.
232 native species richness, bare ground and tree cover rank, but excluding roadside non-native species
233 richness) and their two-way interactions with elevation (but only with bare ground in the case of
234 Switzerland). In all cases we fitted the GLMMs for each region separately, with non-native species richness
235 in adjacent plots as the response variable and “road” included as a random factor. Models were fitted
236 assuming a Poisson distribution and log link function. All explanatory variables were standardised by region
237 prior to analysis (with mean = 0 and standard deviation = 1) so that model estimates could be interpreted
238 as relative effect sizes. Estimates and 95% confidence intervals were calculated for each explanatory
239 variable. Variables for which the confidence intervals did not include zero were regarded as significant. The
240 mixed model analyses were performed using the lme4 package (Bates et al. 2011), and all analyses were
241 performed using in R version 3.4.3 (R Development Core Team 2014).

242

243 **Results**

244 Most non-native species on roadsides were recorded in Australia (114) and fewest in Norway and
245 Switzerland (14; Table 3). Despite this, Australia had the second lowest percentage of non-native species
246 reaching adjacent vegetation at a regional scale (37%); Oregon had the highest (92%). There were large
247 regional differences at the plot scale. In Norway for instance, on average only 7% of non-native species in
248 roadside plots were found in the adjacent plots while in Chile on average more than half of the species in
249 roadside plots (55%) were present in the adjacent plots. Most non-native species recorded on roads (63%)
250 were only recorded in one region, making it difficult to generalise at the species level.

251

252 Do trait patterns of non-native species differ between roadside and adjacent vegetation, along elevation
253 gradients?

254 Both along roadsides and in the adjacent vegetation, the proportion of all perennial non-native species
255 significantly increased with increasing elevation, while the proportion of all annuals decreased (Fig. 1). The
256 proportion of ruderal non-natives increased significantly with increasing elevation in adjacent vegetation
257 but remained relatively constant along the roadsides (Fig. 1, Supplementary Material Table S2). Contrarily,
258 the proportion of non-ruderals decreased with elevation in adjacent vegetation, but slightly increased
259 along the roadsides. Overall, we found a higher proportion of non-ruderal species in adjacent vegetation
260 compared to roadside plots (Table S2). Across the whole elevation gradient, we found higher proportions of
261 non-native species preferring moister (Ellenberg values for moisture M5-10) and shadier conditions (values
262 L4-7) in the adjacent vegetation (Fig. 1). The proportion of species invading adjacent vegetation preferring
263 cooler sites (values T3–5) increased with elevation, while the proportion of non-native species preferring
264 warmer sites (values T6–8) decreased in proportion with increasing elevation, with some support for a
265 relative increase in cold-adapted species in the adjacent vegetation across the whole elevation gradient
266 (Fig. 1). The proportion of non-native species with seeds adapted for dispersal (Fig. 1, see Table 2 for
267 adaptations included) decreased with elevation, while the proportion of non-native species without
268 dispersal-adapted seeds increased with elevation (Fig. 1).

269

270 Which biotic and abiotic plot-level factors influence non-native species richness away from roadsides?

271 Non-native richness on roadsides had an effect on non-native richness in adjacent vegetation in only two
272 regions: Argentina (negative) and Australia (positive) (Fig. 2a). Native species richness in adjacent
273 vegetation was significantly positively related to non-native richness in adjacent vegetation in all regions
274 except Switzerland (Fig. 2a). In Argentina and Australia, these positive effects of native species richness
275 became stronger with increasing elevation (Fig. 2b). Bare ground had a positive influence on non-native
276 species richness in adjacent vegetation in three regions (Argentina, Australia and Oregon) but a negative
277 effect in Chile (Fig. 2a). However, these effects depended on elevation, decreasing in Chile and Argentina
278 and increasing in Australia and Oregon with increasing elevation (Fig. 2b). Elevation had a negative effect
279 on non-native species richness in adjacent vegetation in five regions (Argentina, Chile, Montana, Oregon
280 and Switzerland). Tree cover had a negative effect on non-native richness in adjacent vegetation in three
281 out of six regions (Australia, Chile and Montana).

282

283 Discussion

284 While it is by now well established that non-native species richness declines with elevation in mountains
285 around the world (Alexander et al. 2016), less is known about the ability of these species to spread away
286 from disturbed roadside corridors into natural adjacent vegetation. Here we show that both traits of the
287 non-native species and attributes of the receiving natural vegetation contribute to the extent of invasion.
288 Interestingly, we had consistent results regarding the species traits which support secondary invasion away
289 from the roads, however, biotic and abiotic plot-level characteristics varied strongly across regions.

290

291 Do trait patterns of non-native species differ between roadside and adjacent vegetation, along elevation
292 gradients?

293 We identified several species traits that varied in proportion either along elevation gradients within
294 regions, or between roadside and natural adjacent habitat. This suggests the presence of two filters
295 operating on non-native species in mountain environments (Dietz and Edwards 2006): one acting on the
296 species pool as species spread upwards along the elevation gradient (Alexander et al. 2011), and a second
297 related to the subsequent invasion into natural vegetation away from roads (Lembrechts et al. 2014). The

298 increase in the proportion of perennial species with increasing elevation – and corresponding reduction in
299 the proportion of annuals – is consistent with global trends and explained by the difficulty of completing
300 the life-cycle within a single growing season at high elevation (Körner 2003). However, the proportion of
301 perennial species was not higher in adjacent vegetation compared to roadsides as we expected. Thus, we
302 assume that short-lived species are not only filtered out through biotic, competition-related mechanisms
303 during secondary invasion, but that environmental filtering during primary invasion limits the spread of
304 non-perennial species. We did not find an increase of cold-adapted species at higher elevations,
305 strengthening the assumption that species need to establish first under lowland conditions and from there
306 spread to high-elevations. Interestingly, the proportion of species with dispersal abilities decreased with
307 increasing elevation. This suggests that the overall low invasion rate in most mountain regions is not due to
308 dispersal limitation, but that other species traits (e.g. climatic pre-adaptation) might be more important.

309 Other species traits were disproportionately associated with non-native species that established
310 away from roadsides. In particular, these species tended to show a preference for moister and shadier
311 habitats, in contrast to the open and well-drained conditions typical of many roadside habitats (Forman
312 and Alexander 1998). While the traits that appear to be disproportionately affected by elevation and
313 habitat filters make intuitive sense, our analyses also suggested that these filters only rarely interact. The
314 only exception was the proportion of species with a ruderal strategy, which strongly increased with
315 elevation in adjacent vegetation, while it was rather constant along roadsides. Likely, this refers to a
316 decrease of competition levels in natural adjacent vegetation with increasing elevation, which allows
317 ruderal species to establish. However, it is counter-intuitive that the proportion of ruderal species at high-
318 elevations is lower in roadside compared to adjacent plots. In this case, we might expect that the few
319 species that do spread away from roadsides are ecological opportunists. Contrarily, the species attributes
320 that were associated with successful establishment away from roadsides rarely changed with elevation (i.e.
321 proportion of moist- and shade-adapted species). While the limited amount of interactions between
322 elevation and habitat filters suggests that, for example, an ability to tolerate higher elevation environments
323 does not necessarily trade-off with attributes (such as shade-tolerance) that would promote invasion of
324 higher elevation habitats away from roadsides, it is likely that the number of species with traits necessary

325 for both primary and secondary stages of spread is limited. The additive effect of these filters thus helps
326 explain why the number of non-native species decreases with both elevation and distance from roads
327 (Seipel et al. 2012).

328 That elevation and climate gradients serve as a directional filter for non-native species with certain
329 traits was already known (Alexander et al. 2011). However, our results reveal how mountain roads also
330 define which non-native species are successful; first by favouring certain traits in mountain roadsides (the
331 key dispersal pathway to the top), and secondly by providing a secondary filter – requiring a different set of
332 traits - when species invade the natural adjacent vegetation.

333

334 Which biotic and abiotic plot-level factors influence non-native species richness away from roadsides?

335 Invasion success into adjacent vegetation was also influenced by the characteristics of the receiving
336 vegetation, though not always in ways we expected. We expected invasion resistance in natural vegetation
337 to occur where there was high native species-richness, a high cover of tree species that compete for light
338 and resources with the invader, and a low level of disturbance. However, only the last two of these were
339 supported by our analyses and then not in all regions and not in consistent ways. In all but one region,
340 there was greater invasion where native species richness was higher in the adjacent vegetation. Greater
341 invasibility of species-rich habitat has been observed at coarser spatial scales (Fridley et al. 2007). Native
342 species-rich habitat might indicate good resource availability so that many species can co-exist. Such
343 communities will tend to have greater capacity to accept additional, non-native species than resource-poor
344 habitat. Our study plots of 100 m², might indicate that the positive effect of microhabitat variability on
345 species richness operate at this relatively fine scale. Light is an important resource for invading species, and
346 native tree cover had a negative impact on invasion in three of the six regions. Knight et al. (2008) found a
347 negative relationship between tree cover and invasibility but a positive relationship between native species
348 richness and non-native cover, concluding that native species and non-native species respond similarly to
349 resource availability (in this case light) where the resource is limited. The positive relationship we observed
350 between non-native and native species richness may thus simply reflect natural processes associated with

351 tree death, with opportunistic native and non-native species colonising canopy gaps, at least in plots below
352 the tree line.

353 Bare ground is typically associated with disturbance and had a significant positive effect on invasion
354 in three regions but in Chile the effect was negative. There is little doubt that disturbance can aid invasion
355 of natural vegetation by non-native plant species (e.g. Petryna et al. 2002; Lake and Leishman 2004; Hansen
356 and Clevenger 2005; Lembrechts et al. 2016). Disturbances such as fire (e.g. Keeley et al. 2003) and animal
357 digging (e.g. Larson 2003) typically create room for establishment of non-native species by seed. The lack of
358 an effect of bare ground in some regions is perhaps temporal. Many disturbances causing bare ground are
359 ephemeral (e.g. fire, landslides, flood, road maintenance). If the time since disturbance was long, bare
360 ground might already have been covered by regenerating and establishing plants. The negative effect of
361 bare ground on the richness of non-native species in Chile is likely explained by the dry Mediterranean-type
362 climate generating a patchy vegetation, as bare ground was typically highest in areas with a high cover of
363 rock. It is possible that the shallow and dry soils of these sites, although exposed, were not conducive to
364 plant establishment in general.

365 While climatic conditions (as represented by elevation) and habitat characteristics were important
366 drivers of non-native species richness away from roadsides in most regions; the effect of non-native species
367 richness on the roadside was only significant in Argentina and Australia. If non-native richness at roadsides
368 can be taken as a proxy for propagule availability, this suggests that plant invasion away from the roadside
369 in mountains is not just a stochastic process driven by the roadside non-native species pool, but that it
370 depends on a match between species traits and habitat characteristics (Pollnac and Rew 2014; Lembrechts
371 et al. 2018).

372

373 Management implications

374 We found that there are large differences within and between regions in the degree of invasion away from
375 roadsides. Some of this variation might be attributable to differences in management between regions,
376 with considerable control of non-native species occurring in some regions (e.g. Australia and the US) but

377 barely in others (e.g. Chile). Yet although herbicides are used to reduce non-native species abundance in
378 Australia and the US, the level of invasion was low in Australia and high in Oregon.

379 Our results can help identify good practices for management. At the most general level, the study
380 makes a strong case for the importance of multiple filters in mountain invasions: only species that are both
381 successful in primary invasions at disturbed sites and along broad elevational gradients, and in secondary
382 invasions into natural vegetation, will eventually become invasive. This supports the idea that direct human
383 introduction of mountain-adapted species to high elevations, which surpasses the primary invasion filters,
384 can greatly increase invasion risks in mountains through non-native species that are filtered out at present
385 in the primary invasion phase (McDougall et al. 2011; Kueffer et al. 2013b). As a result, many novel invasive
386 species not yet present in mountains might emerge in coming years (McDougall et al. 2011).

387 The region-specificity of many of the observed patterns suggests that it will be difficult to globally
388 target individual species, a group of species or general habitat types for management of non-native species
389 based on the combined data. Indeed, while the non-native species pool in high elevation adjacent
390 vegetation showed some specific traits that could be targeted (for example cold-, moist- and shade-
391 adapted), the degree to which these species escape into the natural vegetation was largely habitat-specific,
392 and the large overlap in species in roadsides and natural adjacent vegetation suggests invasion into the
393 adjacent vegetation might be largely idiosyncratic though ultimately inevitable. Targeted management may
394 still be possible region by region, however, and some of our study regions have already identified priority
395 species for control (e.g. Kueffer et al. 2013a). The regional patterns observed in this study might help in
396 that regard, as we do report several region-specific habitat characteristics that were related with higher
397 non-native species richness. In Australia at least, the positive relationship between non-native species
398 richness on roads and non-native species richness in adjacent habitat suggests that a simple approach to
399 non-native species management will be to reduce non-native species richness on roads. This might be
400 achieved with regular application of herbicide or mechanical removal, and vehicle and visitor hygiene
401 where practicable (Rew et al. 2018). Where herbicides are frequently applied, managers should be mindful
402 of secondary invasion; i.e. removing one non-native species may simply create space for another (Kuebbing
403 and Nuñez 2016; Pearson et al. 2016). Habitat restoration using native species or sterile non-native species,

404 in combination with herbicide application, is likely to be a better long-term solution in most cases.
405 Whatever the approach to management of non-native species on roads, adaptive management (e.g.
406 vigilance, rapid response and monitoring) is required to deal with future, possibly unpredictable, threats
407 from non-native species.

408

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418

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- 554

555 Table 1. Characteristics of the seven regions: location, the number of sampled plots, the range from the
556 minimum to the maximum elevation of the sampling plots, and the range of mean annual temperature and
557 rainfall (extracted from downscaled 30 arc second Worldclim data (Hijmans *et al.* 2005)).

558

Region	Coordinates (approx.)	Sample pairs	Elevation range (m a.s.l.)	Mean annual temperature range (°C)	Annual rainfall range (mm)
Argentina	41°S, 72°W	60	857 – 1678	3.6 – 7.5	883 – 1240
Australia	36°S, 148°E	60	410 – 2125	3.9 – 13.2	856 – 1842
Chile	37°S, 71°W	51	378 – 1666	6.5 – 11.6	1150 – 2285
Norway	68°N, 18°E	60	13 – 696	-4.3 – 1.9	700 – 862
Switzerland	46°N, 7°E	29	411 – 1800	0.3 – 8.8	780 – 1770
USA: Montana	45°N, 110°W	60	1803 – 3315	-3.1 – 4.7	487 – 777
USA: Oregon	45°N 118°W	60	902 – 2264	0.5 – 8.6	462 – 715

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571 Table 2. Species trait data analysed, the categories (attributes) within each trait, and the percentage of
572 species for which trait data were available. The Grime strategy category was compressed from the original
573 data to the three key components (C, R and S; i.e. a species regarded as CR was included in both
574 categories). The Ellenberg indicator values were grouped so that there was an approximately equal number
575 of species in each category. The last column indicates for how many species (in %) trait data were available.
576

Species traits	Categories	Species (%)
Life history	Annual / perennial	100
Grime strategy	Competitive (C species) / not competitive (Ruderal (R species) and Stress tolerant (S species))	70
Ellenberg moisture	Indicator values: M2–4 (drier) / M5–9 (moister)	52
Ellenberg temperature	Indicator values: T3–5 (cooler) / T6–8 (warmer)	45
Ellenberg light	Indicator values: L4–7 (shadier) / L8–9 (brighter)	56
Seed dispersal characters	Present (seeds are nutritious, flat, elongated, hooked or mucilaginous) / absent (no dispersal adaptations)	84

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581 Table 3. The minimum - median - maximum numbers of non-native species per plot in roadside and
582 adjacent vegetation, and the total number of species recorded (in parentheses) in the seven regions.

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Region	Roadside	Adjacent vegetation	Non-native species reaching adjacent vegetation (total % for region)	Non-native species reaching adjacent vegetation (mean % by plot)
Argentina	0 – 7 – 15 (45)	0 – 0 – 9 (23)	51	28
Australia	2 – 18 – 38 (114)	0 – 2 – 13 (42)	37	17
Chile	2 – 7 – 19 (62)	0 – 4 – 14 (37)	60	55
Norway	0 – 3 – 6 (14)	0 – 0 – 1 (3)	21	7
Switzerland	0 – 1 – 8 (14)	0 – 0 – 4 (7)	50	24
USA: Montana	0 – 6 – 12 (37)	0 – 0 – 11 (23)	60	24
USA: Oregon	0 – 11 – 27 (63)	0 – 2 – 31 (58)	92	42

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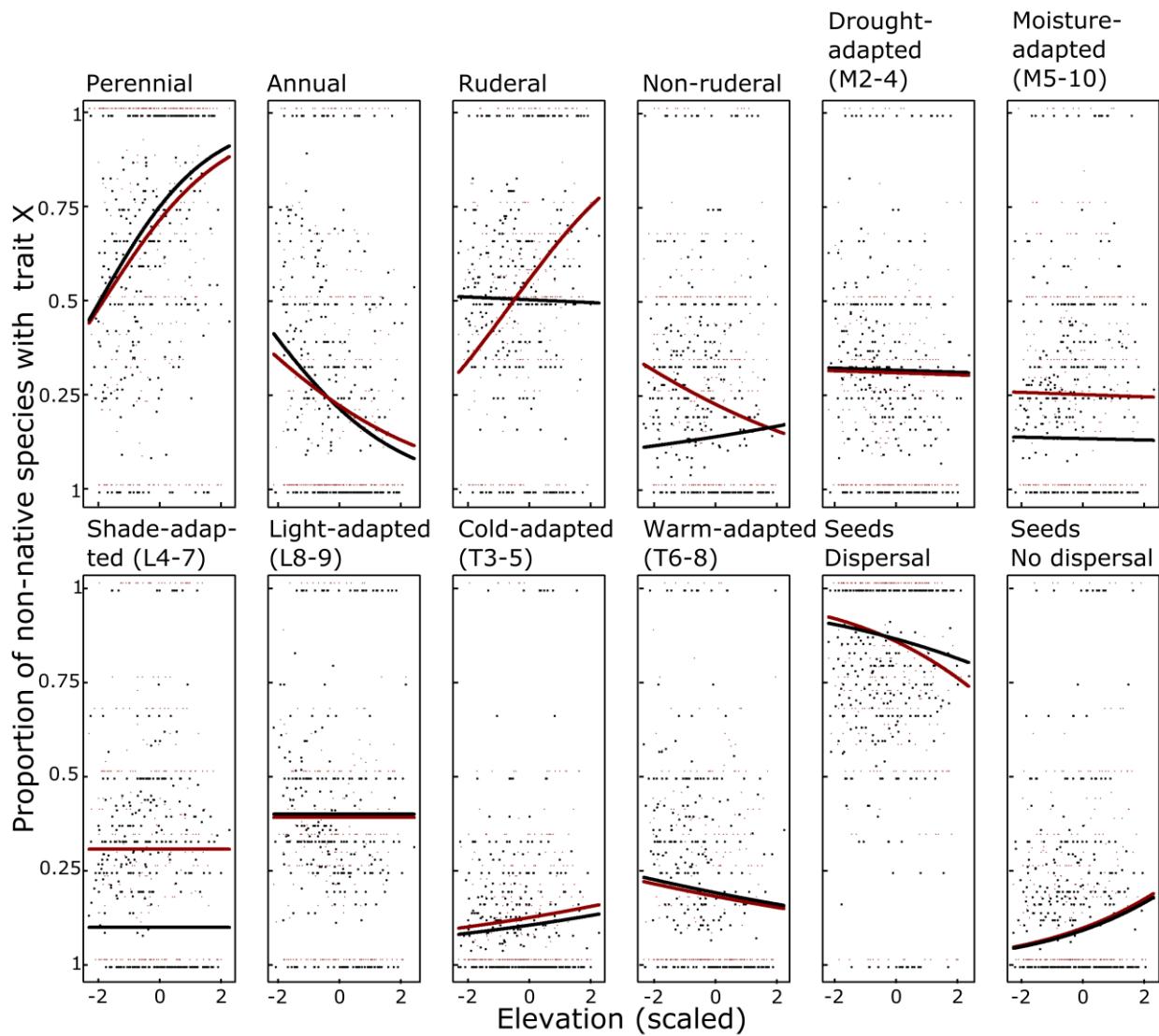
586

587 FIGURE CAPTIONS

588

589 Fig. 1. Model predictions (weighted averages of all models with $\Delta AIC_c < 2$, see Supplementary Material

590 Table S2 for model support) for the proportion of non-native species with a certain trait (panel header) as a
 591 function of elevation (x-axis, scaled with mean = 0 and sd = 1), plot type (roadside = black line, adjacent
 592 vegetation = red line). Ruderal: Grime-strategy = R; Non-ruderal: Grime-strategy = C or S; Drought-adapted:
 593 Ellenberg moisture values of 2 to 4; Moist-adapted: Ellenberg moisture values of 5 to 10; Shade-adapted:
 594 Ellenberg light values of 4 to 7; Light-adapted: Ellenberg light values of 8-9; Cold-adapted: Ellenberg
 595 temperature values of 3 to 5; Warm-adapted: Ellenberg temperature values of 6 to 8; Seeds dispersal:
 596 seeds with traits adapted for dispersal (see Table 2 for adaptations included); Seeds no dispersal: seeds
 597 without dispersal-adaptations.



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600 Fig. 2. Effect size (estimate) and 95% confidence intervals for a) variables in generalised linear mixed effects
 601 models of non-native species richness in adjacent vegetation and b) interactions between elevation and
 602 selected variables. Significantly positive estimates are indicated in red (with full dots), negative in blue
 603 (open dots).

