

This item is the archived peer-reviewed author-version of:

Mountain roads shift native and non-native plant species' ranges

Reference:

Lembrechts Jonas, Alexander Jake M., Cavieres Lohengrin A., Haider Sylvia, Lenoir Jonathan, Kueffer Christoph, McDougall Keith, Naylor Bridgett J., Nuñez Martín A., Pauchard Aníbal,- Mountain roads shift native and non-native plant species' ranges

Ecography - ISSN 0906-7590 - 40:3(2017), p. 353-364

Full text (Publisher's DOI): <http://dx.doi.org/doi:10.1111/ECOG.02200>

To cite this reference: <http://hdl.handle.net/10067/1371010151162165141>

1 Mountain roads shift native and non-native plant species ranges

2 Jonas J. Lembrechts^{1*}, Jake M. Alexander², Lohengrin A. Cavieres³, Sylvia Haider^{4, 5}, Jonathan Lenoir⁶,
3 Christoph Kueffer², Keith McDougall⁷, Bridgett J. Naylor⁸, Martín A. Nuñez⁹, Aníbal Pauchard³, Lisa J.
4 Rew¹⁰, Ivan Nijs¹, Ann Milbau^{11, 12}

5

6 1 Centre of Excellence of Plant and Vegetation Ecology, University of Antwerp, 2610 Wilrijk, Belgium

7 2 Institute of Integrative Biology, Department of Environmental Systems Science, ETH Zürich, CH-

8 8092 Zürich, Switzerland

9 3 Laboratorio de Invasiones Biológicas, Universidad de Concepción and Institute of Ecology and

10 Biodiversity (IEB), Casilla 160-C, Concepción, Chile

11 4 Institute of Biology / Geobotany and Botanical Garden, Martin Luther University Halle-Wittenberg,

12 Halle (Saale), Germany ,

13 5 German Centre for Integrative Biodiversity Research (iDiv), Leipzig, Germany

14 6 UR "Ecologie et Dynamique des Systèmes Anthropisés" (EDYSAN, FRE 3498 CNRS-UPJV), Université

15 de Picardie Jules Verne, 1 Rue des Louvels, 80000 Amiens, France

16 7 Department of Ecology, Environment and Evolution, La Trobe University, PO Box 821, Wodonga,

17 Victoria, 3689, Australia

18 8 USDA Forest Service, Pacific Northwest Research Station, La Grande, OR 97850, United States of

19 America

20 9 Grupo de Ecología de Invasiones, Universidad Nacional del Comahue, INIBIOMA, CONICET, Quintral

21 1250, C.P. 8400, Bariloche, Argentina

22 10 Department of Land Resources and Environmental Sciences, Montana State University, Bozeman,

23 MT 59717, United States of America

24 11 Climate Impacts Research Centre (CIRC), Department of Ecology and Environmental Science,

25 Umeå University, SE-981 07 Abisko, Sweden

26 12 Research Institute for Nature and Forest INBO, Department of Biodiversity and Natural
27 Environment, 1070 Brussels, Belgium

28 **Abstract**

29 Roads are known to act as corridors for dispersal of plant species. With their variable microclimate,
30 role as corridors for species movement and reoccurring disturbance events, they show several
31 characteristics that might influence range dynamics of both native and non-native species. Previous
32 research on plant species ranges in mountains however seldom included the effects of roads. To
33 study how ranges of native and non-native species differ between roads and adjacent vegetation, we
34 used a global dataset of plant species composition along mountain roads. We compared average
35 elevation and range width of species, and used GLMMs to compile their range optimum and
36 amplitude. We then explored differences between roadside and adjacent plots based on a species'
37 origin (native vs. non-native) and nitrogen and temperature affinity.

38 Most non-native species had on average higher elevational ranges and broader amplitudes in
39 roadsides. Higher optima for non-native species were associated with high nitrogen and temperature
40 affinity. While native species with a lowland origin showed patterns comparable to those in non-
41 native species, native species from high elevations had significantly lower elevational ranges in
42 roadsides compared to the adjacent vegetation.

43 We conclude that roadsides indeed change the elevational ranges of a variety of species. These
44 changes are not limited to the expansion of non-native species along mountain roads, but also
45 include both upward and downward changes in ranges of native species. Roadsides may thus
46 facilitate upward range shifts, for instance related to climate change, and they could serve as
47 corridors to facilitate migration of alpine species between adjacent high-elevation areas. We
48 recommend including the effects of mountain roads in species distribution models to fine-tune the
49 predictions of range changes in a warming climate.

50 **Keywords:** Disturbance, mountain roads, native and non-native species, nitrogen and temperature
51 affinity, plant invasion, range shifts, species distributions.

52 **Introduction**

53 Mountain roads provide an important anthropogenic impact on global mountain ecosystems by
54 causing reoccurring disturbances, changing species compositions, fragmenting habitats, changing the
55 hydrology, soil ecology and nutrient availability, altering the microclimate, and funneling
56 anthropogenic effects into the most pristine environments (Forman and Alexander 1998, Forman et
57 al. 2003, Müllerová et al. 2011). In addition, roads might contribute to responses of vegetation to
58 global change, especially in mountains, where roads span steep climate gradients over short
59 distances and thus interact with sudden changes in environmental conditions (Pauchard et al. 2009).
60 Thorough knowledge of the effects of mountain roads on plant elevational ranges will be important
61 for mountain conservation in a future with a rapidly changing climate and increased anthropogenic
62 presence in mountains.

63 Previous research on plant species ranges in mountains have seldom included the effects of roads or,
64 if they did, focused on either native or non-native species or only studied general patterns of species
65 richness and composition. For non-native species, a general trend of upward movement in
66 mountains has been documented over time (Pyšek et al. 2011), and in most regions, non-native
67 species show a consistent pattern of declining abundance with elevation (Becker et al. 2005, Haider
68 et al. 2010, Alexander et al. 2011, Haider et al. 2011, Juvik et al. 2011). Non-native species
69 populations indeed seem to establish first in the lowlands and invade mountains from there, using
70 roads as their main vector (Haider et al. 2010, Alexander et al. 2011, McDougall et al. 2011). The
71 function of roads as corridors for non-native species has also been reported several times in other
72 ecosystems (Gelbard and Belnap 2003, Pauchard et al. 2009, Pollnac et al. 2012). Invasion away from
73 roadsides into the adjacent mountain vegetation has until now been limited (Leung et al. 2009,
74 Alexander et al. 2011, Lembrechts et al. 2014, Pollnac and Rew 2014, Seipel et al. 2015), which

75 suggests that disturbance might at this time be a more important explanatory variable than climate
76 to explain the observed patterns of non-native species distributions in mountains (Marini et al.
77 2012).

78 The effect of roads on native species' elevational ranges is poorly documented. Knowledge of range
79 changes of native terrestrial plants in mountain ecosystems is mostly limited to observations of
80 temporal upward range shifts in the light of contemporary climate change, unrelated to roads
81 (Grabherr et al. 1994, Walther et al. 2002, Pauli et al. 2007, Lenoir et al. 2008, Felde et al. 2012).
82 Several studies warn of rapid area loss for endemic high-elevation species (Pauli et al. 2007, Jump et
83 al. 2012), and a failure of lower elevation species to migrate upwards to track climate change
84 (Bertrand et al. 2011, Corlett and Westcott 2013). Recently, Lenoir et al. (2010) suggested that
85 unexpected downward shifts of species' lower elevational range limits (cf. the trailing edge) may be
86 caused by complex interactions between climate change and increased disturbance levels.
87 Knowledge of native species' distributions in mountain roadsides is fragmented and generally limited
88 to patterns of species richness (Paiaro et al. 2011, Lembrechts et al. 2014). A recent study in the
89 northern Scandes showed that at lower elevations, mostly competitive and ruderal species benefit
90 from roadside conditions, while in the alpine zone roadsides are mainly occupied by stress-tolerant
91 species (Lembrechts et al. 2014). Paiaro et al. (2011) suggested that roadsides may function as plant
92 species corridors both in upward and downward directions.

93 Roads combine several features that could potentially explain changes in plant species ranges in the
94 ecosystems they cross. They host a more variable and extreme microclimate than the surrounding
95 vegetation, affect soil hydrology, and improve nutrient availability through the addition of dissolved
96 nutrients and volatile nitrogen oxides, and through an increase in soil pH (Forman et al. 2003,
97 Johnston and Johnston 2004, Delgado et al. 2007, Müllerová et al. 2011). The role of vehicles and
98 hikers as vectors for travelling species and the related increased propagule pressure along roads can
99 also explain changes in the distribution of plant species (Forman and Alexander 1998, Forman et al.

100 2003, Ansong and Pickering 2013). Finally, roadsides are disturbed environments (Forman et al.
101 2003), characterized by repeated set-backs of succession to earlier stages (Güsewell and Klötzli 2012)
102 and they consequently have reduced levels of competition (Forman et al. 2003). These lower levels of
103 competition along roads might influence species distributions by allowing species to increase their
104 realised niche width (Bolnick et al. 2010). Based on these features and the known higher alpha
105 diversity of plant species in roadsides (Avon et al. 2010, Paiaro et al. 2011, Bergès et al. 2013,
106 Lembrechts et al. 2014), an expansion of plant elevational ranges in roadsides compared to the
107 surrounding vegetation can be expected in mountains. However, the sizes and directions of such
108 shifts likely depend on species-specific characteristics, as different species will profit or suffer
109 differently from the altered environment in roadsides.

110 In this paper we compare differences in the elevational range of species in roadsides and the
111 adjacent vegetation. Understanding the effects of mountain roads on species' elevational ranges is
112 not only important from a theoretical point of view, but also crucial to improve species distribution
113 models to forecast future climate change impacts on mountain biota and to decide on informed
114 management strategies for mountain ecosystems. We used a dataset based on a large-scale
115 monitoring effort of plant species distributions along roadsides and within adjacent natural
116 vegetation across elevation gradients in eight mountain regions (MIREN 2005), and applied two
117 different modelling approaches to study general and species-specific range patterns. The observed
118 patterns were then analysed for effects of a species' origin (native or non-native) and temperature
119 and nitrogen affinity (Landolt 2010). We hypothesized that (1) elevational ranges are in general
120 broader in roadsides than in the adjacent natural vegetation, (2) the difference in range amplitude
121 between roadsides and adjacent plots will be more positive for non-native than for native species
122 and (3), the magnitude and direction of differences for both native and non-native species will
123 depend on a species' ecological characteristics, with higher optima in roadsides compared to the
124 adjacent plots for lowland nutrient- and temperature-loving species, but lower optima for highland
125 species with opposite affinities.

126 **Materials and methods**

127 ***Survey design***

128 Vegetation surveys were performed during the summer of 2012 (2014 in AR) in eight regions within
129 MIREN (the Mountain Invasion Research Network) (MIREN 2005, McDougall et al. 2011, Kueffer et al.
130 2014): the Andes in Argentina (AR), the Alps in Australia (AU), the Andes in Central Chile (CLC),
131 Greater Yellowstone Ecosystem in Montana, USA (MT), the Northern Scandes in Norway (NO) and
132 the Blue Mountains in Oregon, USA (OR), the Andes in Southern Chile (CLS), the Alps in Switzerland
133 (SW), see Table 1.

134 In each region, three roads were selected (four in SW, one in CLC) that extended over a broad
135 elevation gradient (spanning 618 to 1715 elevational meters depending on the region) and were
136 open to vehicular traffic for at least part of the year. The lowest sampling point of a road was the
137 point below which there was no substantial change in elevation anymore, the highest sampling point
138 depended on regional constraints, such as roads ending, merging or substantially changing in
139 character. The elevational range covered by each road was divided into 19 equally spaced elevational
140 bands (20 in SW, 15 in CLC), giving 20 (21 in SW, 16 in CLC) sampling sites per road.

141 At each sampling site, two 2 × 50 m² rectangular plots were laid out, with one plot parallel to the
142 road (hereafter called 'roadside') and the other perpendicular to the centre of the first, with its
143 midpoint 75 m away from the roadside and thus ranging from 50 to 100 m from the roadside
144 (hereafter called 'adjacent plot'). In all plots, occurrence (presence/absence) of all vascular plant
145 species was recorded.

146 ***Elevational range differences between roadsides and adjacent plots***

147 Ranges based on the elevation of occurrence of species were calculated separately for roadsides and
148 adjacent plots. Although elevation differences might not have exactly the same ecological meaning in
149 different study regions, e.g. because of regional differences in adiabatic lapse rates and precipitation

150 gradients, elevation currently is the best available variable to study range shifts in mountains. The
151 use of climatic data would explain shifts in a more ecological way, but the current scale of globally
152 available climatic datasets is too coarse ($\sim 1 \text{ km}^2$) to explain differences in elevational ranges on a
153 scale of tens to hundreds of elevational meters in the mountains. Moreover, roadside-induced
154 elevational range changes might not be a pure climatological effect, as other factors, such as
155 disturbance and changes in nutrient levels, are likely to play an important role.

156 To assess elevational ranges in roadsides and adjacent plots we calculated range optima and
157 amplitudes for every species with at least ten occurrences per region, with a minimum of five in both
158 roadsides and adjacent plots. The range optimum is defined as the average elevation of occurrence,
159 or the top of the species' occurrence curve, while the amplitude specifies the whole elevational
160 range along which the species was observed (= range width). Differences in these values between
161 roadsides and adjacent plots were calculated with two complementary approaches, of which the first
162 one was coarse, allowing the use of a large species set and resulting in general and region-specific
163 conclusions, while the second one was more detailed and precise, resulting in an ecologically
164 meaningful grouping of a limited set of species based on the location of their optimum along the
165 elevational gradient.

166 In the first approach, average, minimum and maximum values of each species' elevational range in
167 the roadside and the adjacent plots were calculated per region (pooling all roads in a given region),
168 hereafter called "dataset A1" (N = 510 region-specific values, for 438 different species,
169 Supplementary material Appendix 1 Table. A1). The difference between a species' elevational
170 occurrence optima was defined as the difference between its average elevation of occurrence in the
171 roadside and in the adjacent plots. This resulted in positive values for species with a higher optimum
172 in roadsides than in the adjacent plots, and vice versa. Differences between range amplitudes were
173 defined as difference between ranges from maximum to minimum elevation of occurrence in
174 roadside plots and adjacent plots.

175 For the second approach, we compiled species- and region-specific generalised linear mixed models
176 (GLMMs). Species presence/absence per plot was modelled with a binomial distribution, as a
177 function of elevation and with or without an interaction term for distance to the road
178 (roadside/adjacent). **We distinguished between species with a second degree (quadratic) and first
179 degree (linear) binomial distribution. The former indicated a range optimum along the gradient
180 (negative quadratic function with optimum within the sampled range, “dataset A2”, see
181 Supplementary material Appendix A Table A2), the latter a linear distribution, for which the range
182 optimum lay above or below the gradient (positive or negative linear functions, monotonically
183 increasing or decreasing along the sampled gradient, “dataset A3”, see Supplementary material
184 Appendix A Table A3).** We acknowledged possible differences between roads within a region by
185 adding “road” as a random factor. Models were fitted in R with the function *glmer* from the package
186 *lme4* (Bates et al. 2013). The function *aictab* from the package *AICcmodavg* (Mazerolle 2015) was
187 used to select the model with the best fit based on the lowest AIC value. For details on the used
188 models and coefficients, see Supplementary material Appendix 2.

189 There were 171 species for which the model with the best fit was a second degree function of
190 elevation (dataset A2), of which 112 had next to this quadratic term a significant interaction between
191 the linear elevation term and distance to the road, and 59 had an additional interaction between the
192 quadratic elevation term and distance, hence showing a change in both optimum and amplitude
193 (dataset A2, Supplementary material Appendix 1 Table A2). The difference between species optima
194 was defined as the difference in elevational positions of the optimum information criteria (OPT) for
195 roadside and adjacent plots (ter Braak and Looman 1986, Lenoir et al. 2008), calculated based on the
196 coefficients from the GLMMs. Differences in range amplitudes were calculated by taking the
197 difference between the GLMM’s tolerance information criteria (AMP) (ter Braak and Looman 1986,
198 Lenoir et al. 2008, see Supplementary material Appendix 2 for detailed calculations). Only those
199 species that had an optimum elevation within the elevational range of the dataset were withheld.

200 For 44 species, the model with the best fit included only the linear elevation term, and a significant
201 interaction between elevation and distance (dataset A3, see Supplementary material Appendix 1
202 Table A3). In these cases, the range edge (EDG) was defined as the inflection point of the model, and
203 shifts in range edge between roadside and adjacent plots were examined (see Supplementary
204 material Appendix 2 for calculations).

205 ***Species origin and traits***

206 All species were marked as native or non-native for every region in which they occurred, based on
207 data available from the MIREN-network. Any species introduced after AD 1500 within a given region
208 was considered as non-native ($N_{\text{non-native}} = 99$).

209 To verify if changes in species ranges between roadsides and adjacent plots can be explained by
210 differences in species' affinity for temperature or nitrogen, we used indicator values for temperature
211 and nitrogen from the Flora Indicativa, available for a set of 184 unique species (Table 1, Landolt
212 2010). Landolt indicator values range from one to five and characterize the average air temperature
213 during the growing period of the species ("temperature") and a species preference for soil fertility
214 ("nitrogen"), with a value of one in both cases meaning a low affinity for the considered factor, and
215 five a high affinity.

216 Landolt values were available for 85 % of the species from the European regions (NO and SW), for 94
217 % of the non-native species in all regions, and for 18 % of North-American native species (OR and
218 MT) (Table 1). For native species from the southern hemisphere, Landolt value availability was
219 limited (on average 6 %). This implies that our analyses based on the Landolt values will be biased
220 towards regions with higher data availability. This bias does however not occur for non-native species
221 and is limited to native species from the southern hemisphere. The European regions (NO and SW)
222 had no non-native species with more than ten occurrences; the South-American datasets (AR, CLC,
223 CLS) contained fewer native species than the other regions.

224 Data for species origin and traits were added to each dataset in the Appendix and datasets were
225 grouped based on the species' origin (see Supplementary material Appendix 1 Table A1, A2 and A3).

226 **Statistical analysis**

227 Data from all three datasets (A1, A2, A3) were further tested with linear mixed models (LMMs) with
228 species nested in region as a random factor (package nlme (Pinheiro et al. 2013)). First, a null model
229 without any fixed effects was used, to test if the average optimum and amplitude (from datasets A1
230 and A2) differed from zero. Similar linear null models were used to analyse region-specific patterns
231 by testing each regional dataset separately. These models were recreated for native and non-native
232 species separately.

233 Next, LMMs with optimum, amplitude or edge as response variables, and species origin, species
234 nitrogen and temperature affinity and their interactions as explanatory variables were used to
235 explore correlations for all datasets, again with species nested in region as a random factor. For
236 dataset A3, the location of the optimum (based on the slope of the linear curve with a positive slope
237 indicating an optimum above the road fragment, and vice versa) was added as an extra fixed factor.
238 Model simplification was done based on the lowest AIC value and significance of variables, and only
239 the models with the best fit are shown.

240 A correlation test was used to test consistency in species patterns between regions, both with the
241 differences in optima and in range amplitudes. The same test was used to analyse the correlation
242 between differences in optima and amplitudes and the difference in amount of occurrences between
243 roadsides and adjacent plots, and to test the relation between regional patterns for native species
244 and the average nutrient affinity of a region's native species pool.

245 All data manipulations and analyses were performed in R (R Core Team 2013).

246 **Results**

247 ***General patterns***

248 There was no general significant difference in species' elevation optima or amplitudes between
249 roadsides and adjacent plots (LMMs, dataset A1, $df = 502$, optimum $P = 0.564$, amplitude $P = 0.373$).
250 Range amplitudes of non-native species in dataset A1 were however on average 192 elevational
251 meters broader in the roadsides than in the adjacent plots (Fig. 1, Table 2, right), which contrasted
252 with the observations for native species, for which no general trends could be observed (Table 2, Fig.
253 1A, C).

254 In dataset A2, differences in optima and amplitudes for non-native species with optima along the
255 studied road fragment were not significant (Fig. 1C, LMM, $df = 39$ (31 species), optimum: $P = 0.579$,
256 amplitude: $P = 0.538$), but the results from dataset A1 were supported by the regional trends (Fig. 1B
257 and 1D, Table 2). Indeed, for four out of the eight regions (AU, CLS, OR and MT) we observed broader
258 range amplitudes for non-native species in the roadsides in dataset A1. In OR and MT also, the
259 optima were higher in the roadsides, but they were lower in AU and not significant in CLS. Moreover,
260 in dataset A2, the one region (MT) with significant trends in non-native species showed on average
261 higher optima in the roadsides than the adjacent plots (Fig. 1D).

262 Native species on the other hand showed on a regional basis a trend towards lower optima in
263 roadsides, a trend significant in three regions (dataset A1; AU, SW, NO; Fig. 1B, Table 2). In two
264 regions, a smaller amplitude was recorded (AR, AU) and in SW the amplitude was broader in
265 roadsides than adjacent plots. In dataset A2, patterns for native species were marginally significant
266 for AU (smaller amplitude), SW (broader amplitude) and OR (higher optimum).

267 **Location of optimum along the gradient**

268 Species were classified based on the location of their elevational optimum by integration of dataset
269 A2 and A3 to unravel trends in range differences based on a species' location of origin that stay
270 hidden in the general trends discussed before.

271 The strongest range differences were observed for non-native species with an optimum below the
272 sampled road fragments (Fig. 2, “lowland species”). For these species, their upper range edge
273 occurred at higher elevations in the roadsides than in the adjacent plots (LMM, Estimate = 677.1, $P =$
274 0.021). Non-native species with optima along the sampled road fragments, on the other hand, did
275 not show a significant response (see also Fig. 1C), and non-native species with an optimum above the
276 sampled road fragment were not observed.

277 In native species, we observed different patterns for the three species groups: native species with
278 their optimum below the sampled road fragment had upper edges at higher elevations in roadsides
279 than adjacent plots and native species with an optimum along the sampled road fragment did not
280 show any response. The lower range edges of native species with a range optimum above the
281 sampled road fragments (“highland species”), on the other hand reached to lower elevations in the
282 roadsides than the adjacent plots (LMM, Highland = -299.0, Lowland = 472.5, $P = 0.002$). An example
283 of species with optimum along the roads (quadratic model) and below the sampled road fragment
284 (linear model) can be seen respectively in Figures 2C and 2D.

285 ***Temperature and nitrogen affinity***

286 Next to species origin (native or non-native), species’ affinity for temperature and nitrogen also
287 influenced how species ranges were affected by the presence of roads (Fig. 3, Table 3). In non-native
288 **species of European** origin (94 % of the 71 non-native species in dataset A1 and 92 % of the 37 non-
289 native species in dataset A2), high nitrogen affinity was correlated to higher range optima in the
290 roadside than in the adjacent plots, while low nitrogen affinity resulted in lower range optima (Fig.
291 3A and 3C). For the larger dataset A1, an additional trend related to temperature affinity was
292 observed, with the highest difference in optima between roadsides and adjacent plots for non-native
293 species with high indicator values for both nitrogen and temperature (upper right corner). It is
294 however noteworthy that non-native species with temperature affinities below 3 were not observed,
295 so almost no non-native species with lower roadside optima were recorded. In dataset A2, only the

296 correlation with nitrogen remained (Fig. 3C, LMM: Optima $\sim 1.78*OR_N$ ($P = 0.06$) + $0.61*N$ ($P = 0.01$) –
297 $0.55*OR_N*N$ ($P = 0.06$) – 1.90 ($P = 0.02$)). Non-native species with lower temperature affinity tended to have
298 broader range amplitudes than the more thermophilic non-natives (borderline significant in Table 3
299 for dataset A1). Range amplitudes did not correlate significantly with nitrogen affinity.

300 Range optima of native species of European origin (48 % of the the 439 native species in dataset A1
301 and 38 % of the 125 native species in dataset A2) showed the same correlation with nitrogen as
302 those from non-natives (Fig. 3B and 3D), with higher roadside optima for species with a high nitrogen
303 affinity and vice versa, as there was no significant interaction between species origin and nitrogen
304 (Table 3). The significant interaction of species origin with temperature affinity in dataset A1 resulted
305 in lower optima for native species with a higher temperature affinity. In dataset 2, again a positive
306 correlation of optima with nitrogen affinity could be observed, but it was less strong than in non-
307 native species (Fig. 3D, model see previous paragraph). Range amplitudes for native species were on
308 average always broader in roadsides. Patterns for temperature and nitrogen affinity in dataset A3
309 were not significant and are not shown.

310 Regional models supported the abovementioned patterns (Table 3), although regional datasets were
311 seldom large enough to allow the same model complexity. Differences in optima for native species
312 were smaller than those for non-natives in MT and OR and showed a positive correlation with
313 nitrogen affinity in SW. Differences in amplitudes were also larger for non-natives in AU, MT and OR,
314 while the observed positive correlations with temperature affinity could also be observed in AU, CLS
315 and SW. The regional differences in optima correlated significantly with the average nutrient affinity
316 of the species recorded in that region ($cor = 0.82$, $t = 3.539$, $df = 6$, $P = 0.012$), with relatively lower
317 roadside optima in regions with on average lower nitrogen affinities and vice versa.

318 Table 3 shows that sufficient regional data to get a significant model was available for both
319 parameters in three regions (MT, OR, SW) and for amplitude in an additional set of two regions (AU
320 and CLS). For CLS, origin was not significant, and the model only holds for non-native species. In SW,

321 model results only apply to native species. Patterns for species that occurred in at least two different
322 regions were consistent for changes in range amplitudes ($cor = 0.21$, $t = 2.033$, $df = 93$, $P = 0.045$), but
323 not for range optima ($cor = -0.021$, $t = -0.202$, $df = 93$, $P = 0.842$). The observed changes in range
324 amplitude in roadsides compared to the adjacent vegetation could be a statistical artefact of an
325 increase in the presence of the species in the roadsides. There was indeed a correlation between the
326 difference in the amount of occurrences and the difference in amplitude between roadsides and
327 adjacent plots ($cor = 0.465$, $df = 508$, $t = 11.830$, $P < 0.001$), but not with the differences in range
328 averages ($cor = -0.016$, $df = 508$, $t = -0.362$, $P = 0.718$).

329 Discussion

330 Non-native species

331 Elevational range amplitudes of non-native plant species were on average broader in the roadsides
332 than in the adjacent vegetation. Roadsides have often been shown to serve as a vector for non-
333 native species to higher elevations, as they combine the necessary propagule dispersal through
334 human traffic with locally improved abiotic conditions (Seipel et al. 2012, Barros and Pickering 2014,
335 Lembrechts et al. 2014). Concerning the latter, non-native species occurrence in roadsides has for
336 example been linked to the occurrence of road edge habitats with increased resource availability
337 (Paiaro et al. 2011, Pollnac et al. 2012), and in our survey, non-native species with high nitrogen
338 affinity indeed showed the largest increases in elevational optima in roadsides. The higher nutrient
339 levels that are commonly recorded in roadsides could thus serve as a trigger for the successful
340 establishment of non-native species in roadsides at higher elevations (Davis et al. 2000, Godefroid
341 and Koedam 2004, Müllerová et al. 2011, Paiaro et al. 2011). These higher nutrient levels might
342 especially be important facilitators of non-native species establishment at the highest elevations, as
343 alpine environments are often nutrient-limited.

344 Surprisingly, all observed non-native species had moderate to high temperature affinities (Landolt
345 values of three or more), indicating that adaptation to lowland climatic condition is a premise for

346 non-native species to invade mountain ecosystems (Alexander et al. 2011). Direct transportation of
347 cold-adapted species from one mountain region to the other is thus apparently until now a minor
348 process, although it remains a high risk as a driver of future mountain invasions (Pauchard et al.
349 2009).

350 The expansion of non-natives, especially lowland species with high nitrogen-affinity, along roadsides,
351 strengthens conclusions from other research that the distribution of non-native species in mountains
352 is currently more determined by the presence of suitable growing conditions (e.g. less competition
353 and more nutrients in roadsides) and the availability of propagules (facilitated by roads) than by
354 climatic or elevational limitations (Marini et al. 2012). Their roadside ranges indeed indicate that they
355 can occur at higher elevations in the mountains than they are currently found in the adjacent natural
356 vegetation. Our data hint that although all non-native species have broader ranges in the roadsides
357 than in the adjacent plots, non-native species better adapted to mountain climates (lower Landolt
358 temperature values) show the largest range expansion (Pauchard et al. 2009, Lembrechts et al.
359 2014). It should be noted, though, that the observed increases in range amplitudes could partially be
360 a statistical artefact of a higher occurrence of a species in the roadside. The directionality of the
361 observed shifts however indicates that the increased amplitudes are more than just directed by
362 chance.

363 Regional patterns for non-native species in our dataset were mostly consistent with the global
364 results. Non-native species for example showed broader roadside range amplitudes in all of the
365 regions (although only significantly in those regions where data availability was sufficient), which
366 strengthens the conclusion that a broader elevational range for non-native species in roadsides is a
367 global pattern (Seipel et al. 2012). The absence of non-native species with more than 10 occurrences
368 in Old World regions (NO and SW) is probably due to the Eurasian origin of many mountain invaders
369 (Seipel et al. 2012). The two regions (MT, OR) that showed a higher optimum for non-native species
370 in the roadsides than the adjacent vegetation were located in a temperate climate, while the one

371 negative optimum difference occurred in a Mediterranean climate (AU). In the latter system, drought
372 and heat – which are amplified in roadsides - might actually restrict invasion in lowlands more than
373 at intermediate elevations, which could explain the reversed pattern.

374 **Native species**

375 Native species also generally had broader range amplitudes in roadsides than in the adjacent
376 vegetation (Table 3), although the difference was less pronounced than for non-native species. We
377 could, however, not observe any general pattern for range changes, due to the presence of three
378 species groups with opposite trends. Indeed, lowland species had an upward increase in their upper
379 edge in roadsides, while the lower range edges of high elevation species reached to lower elevations,
380 with both patterns leveling each other out in the intermediate group. Native species with high
381 nitrogen affinity, but low temperature affinity, also showed higher range optima in the roadside,
382 confirming previous research (Godefroid and Koedam 2004, Müllerová et al. 2011, Lembrechts et al.
383 2014), while native species with low nitrogen affinity had relatively lower roadside range optima,
384 although these conclusions are only based on 48 % of the observed native species.

385 Trends in the direction of the optimum for native species varied between regions, although
386 differences were negative in all significant cases (Fig. 1B, Table 2). The final pattern depended on the
387 average nutrient affinity of the species in the regional dataset. Regions with native species with
388 lower nitrogen affinity showed lower optima in roadsides than in the natural vegetation, and vice
389 versa. This could either be an artefact of the limited availability of Landolt values for non-European
390 regions or link to varying patterns of soil fertility between regions.

391 **General effects of roads on native and non-native plant ranges**

392 Patterns were surprisingly similar between lowland native and lowland non-native species. Roads
393 thus serve as a vector for (both native and non-native) lowland plants and facilitate their invasion
394 towards higher elevations (Alexander et al. 2011, Taylor et al. 2012). That these patterns were not

395 limited to non-native species might indicate an additional use of roads as pathways for native species
396 expanding their ranges into mountains under climate change. This relates to the observed upward
397 spread of lowland species in mountains as so-called local invaders in a warming climate (Lenoir et al.
398 2010). Roads might promote the spread of such species triggered by climate change by providing an
399 easy pathway to reach elevations above their current climatic limits, from where they can start
400 colonising the adjacent natural vegetation. This process could accelerate climate change induced
401 range shifts as roads weaken barriers, such as biotic competition and low nutrient levels, experienced
402 by upward moving species (Walther et al. 2005, Lenoir et al. 2009, Lenoir et al. 2010, Zhu et al. 2012).
403 Roadside processes thus could increase the discrepancy in the upward moving speed of different
404 species under climate change, by facilitating the upward movement of fast-growing species with a
405 quick generation turn-over even more than already observed (Lenoir et al. 2008).

406 High-elevation species surprisingly showed an opposite trend, with lower reaching lower edges in
407 roadsides than in the adjacent vegetation. Our results suggest that those species might benefit from
408 the altered abiotic conditions and the competitive release in roadsides to expand their ranges
409 towards lower elevations, against the general uphill movement driven by climate change (Forman et
410 al. 2003, Lenoir et al. 2010, Lembrechts et al. 2014). As the lower realised range margin of alpine
411 species is often not defined by abiotic conditions but by their inability to compete with faster
412 growing lowland species (Lenoir et al. 2010, le Roux et al. 2012), this downward shift along disturbed
413 roadsides areas should not come as a surprise. Competitive release has earlier been suggested as a
414 driver of similar unexpected downward range shifts of plants as climate warms (Vetaas 2002, Lenoir
415 et al. 2010). Our results imply that roadsides could serve as corridors for native species movements,
416 bridging lowland gaps between separate populations of certain mountain species.

417 It has often been observed that mountain species have lower nitrogen affinity (Körner 2003), and in
418 our results lower optima in roadsides are similarly linked to lower nitrogen affinity. We thus observe
419 two contrasting nutrient-related patterns, with both species with low and high nitrogen affinity

420 showing broader ranges in the roadsides than in the adjacent vegetation. Species with low nitrogen-
421 affinity are not restricted to nutrient-poor environments, but microvariation in roadside habitats has
422 also been proven to result in a variety of abiotic conditions (e.g. edges versus fill slopes) (Paiaro et al.
423 2011), suggesting that highland species with low nitrogen affinity might use other parts of the
424 roadside than lowland species. Fill slopes for example have high resource availability and facilitate
425 fast-growing lowland species through resource enrichment, while rocky roadside substrates have
426 scarce soils and unstable hydrological and thermal conditions and thus favour the presence of stress-
427 tolerant species. This implies that roadsides host a large variety of plant species on a small surface
428 area, increasing their vulnerability for instability.

429 Several species occurred in more than one region and differences in their range amplitudes were
430 positively correlated between regions, implying that species ranges would in general either be
431 positively or negatively affected by roadsides, regardless of the region. Directions of changes in
432 optima did not show a significant correlation, indicating that there was still a significant portion of
433 regional variation in the effects of roads at species level, despite the general trends and the
434 consistency in their affinity for roadsides or not. Possible explanations for these differences could be
435 residence time of non-native species, regional climatic differences or region- or road-specific
436 variation such as levels of roadside disturbance.

437 It is clear from these results that the elevational range of a wide variety of plant species differs
438 between roadsides and the adjacent vegetation. Surprisingly, these range differences are not limited
439 to the well-documented expansion of non-native species along mountain roads, but also include
440 native species, which, depending on the species, show either higher or lower range optima in
441 roadsides. The consistent trend towards broader range amplitudes in roadsides for both native and
442 non-native plant species might find its main explanation in the reoccurring disturbance events in
443 roadsides that alter resource availability and biotic interactions, which have a known positive impact
444 on both ruderal native and non-native species, as well as stress-tolerant mountain species (le Roux et

445 al. 2012). Several other factors probably play a role, like the presence of vehicles that can serve as
446 vectors for species movement up and down mountain roads, thereby acilitating invasion at other
447 elevations (Von der Lippe and Kowarik 2007). Small-scale variation in abiotic conditions in close
448 proximity to roads could play an additional role in creating different niche spaces (Paiaro et al. 2011).

449 **Implications**

450 It is currently not possible to predict the stability of the range changes observed in roadsides because
451 source-sink dynamics might be more important drivers of the observed changes in elevational niches
452 on a long temporal scale. Thanks to the improved mobility in roadsides, species might indeed quickly
453 establish roadside populations at high or low elevations which are potentially outside of their longer-
454 term elevational niche. It is also important to keep in mind that roadside environments are highly
455 unstable and comprise only a small part of the mountain area, which means that a stable source
456 population might remain necessary to maintain the observed role as a refuge for these species
457 outside their current range in the natural vegetation. Our results however suggest that roads play a
458 more important role as drivers of range changes than previously assumed. They likely facilitate
459 climate-induced upward range shifts for both native and non-native plant species and they could
460 serve as corridors to facilitate exchange of alpine species between adjacent high-elevation mountain
461 sites and slow down the observed upward retreat of the trailing edge of these species under climate
462 change (Lenoir et al. 2010).

463 We conclude that roadsides indeed serve as corridors for species movements and as such trigger
464 range dynamics of species (whether native or non-native) into new climatic zones (Paiaro et al.
465 2011). Lowland species with high nutrient affinity profit the most from these altered conditions and
466 patterns are strongest for, but not limited to, non-native species. Roadsides can hence serve as an
467 important early detection system where shifts in species ranges will become visible first. These
468 monitoring systems in roadsides might however be sensitive to short-term population fluctuations,
469 but are nevertheless useful to finetune existing species distribution models. By adding roadsides as

470 an extra factor, the description of true realised elevational niches will be more accurate and
471 predictions of range changes under future climate conditions will be more reliable.

472 **Tables and figures**

473 *Table 1. Characteristics of the eight regions, including the coordinates, the number of roads sampled,*
 474 *the range from the minimum to the maximum elevation of the sampling plots, and the total number*
 475 *of non-native and native vascular plants with more than five occurrences in both roadside and*
 476 *adjacent plots recorded per region, with the number of species with known Landolt values in*
 477 *parentheses.*

Region	Coordinates	Roads	Elevational range (m a.s.l.)	Non-native species	Native species
Argentina (AR)	41°10' S 071°55' W	3	857-1678	6 (5)	32 (0)
Australia (AU)	36°06' S 148°18' E	3	410-2125	12 (11)	47 (3)
Central Chile (CLC)	33°54' S 070°18' W	1	1895-3585	2 (2)	5 (1)
Montana, USA (MT)	44°48' N 110°24' W	3	1803-3307	7 (7)	70 (12)
Norway (NO)	68°19' N 017°80' E	3	13-697	0 (0)	47 (34)
Oregon, USA (OR)	45°18' N 117°48' W	3	902-2265	25 (23)	121 (19)
Southern Chile (CLS)	36°58' S 071°24' W	3	274-1668	19 (18)	16 (0)
Switzerland (SW)	46°12' N 007°12' E	4	411-1802	0 (0)	101 (97)

478

479 Table 2. Estimates, P-values and degrees of freedom for general (all, bold) and regional linear mixed
 480 null models for range optima (left) and amplitudes (right), for non-native (top) and native (bottom)
 481 species. Significant P-values are marked with an asterisk (*) and P-values between 0.05 and 0.10 with
 482 a period (.). Data from dataset A1.

Non-natives	Optimum ~ 1			Amplitude ~ 1		
	<i>Estimate</i>	<i>P-value</i>	<i>df</i>	<i>Estimate</i>	<i>P-value</i>	<i>df</i>
All	38.9	0.326	65	191.5	<0.001 *	65
Argentina	-0.6	0.986	5	31.2	0.560	5
Australia	-99.8	0.039 *	11	304.6	0.074 .	11
Central Chile	113	0.408	1	193.5	0.500	1
Montana	142.0	<0.001 *	6	213	0.148	6
Norway	-	-	-	-	-	-
Oregon	110.9	<0.001 *	24	191.5	0.005 **	24
Southern Chile	-8.6	0.705	18	162.7	0.010 *	18
Switzerland	-	-	-	-	-	-
Natives						
All	-14.4	0.212	431	-14.3	0.670	431
Argentina	-29.4	0.187	31	-51.8	0.021 *	31
Australia	-97.3	0.010 *	46	-136.7	0.003 *	46
Central Chile	54.4	0.362	4	-136.4	0.376	4
Montana	23.8	0.061 .	69	-28.7	0.380	69
Norway	-29.8	0.002 *	46	0.872	0.970	46
Oregon	14.2	0.138	120	-8.7	0.678	120
Southern Chile	-32.3	0.126	15	13.94	0.789	15
Switzerland	-40.7	0.003 *	100	153.6	<0.001 *	100

483

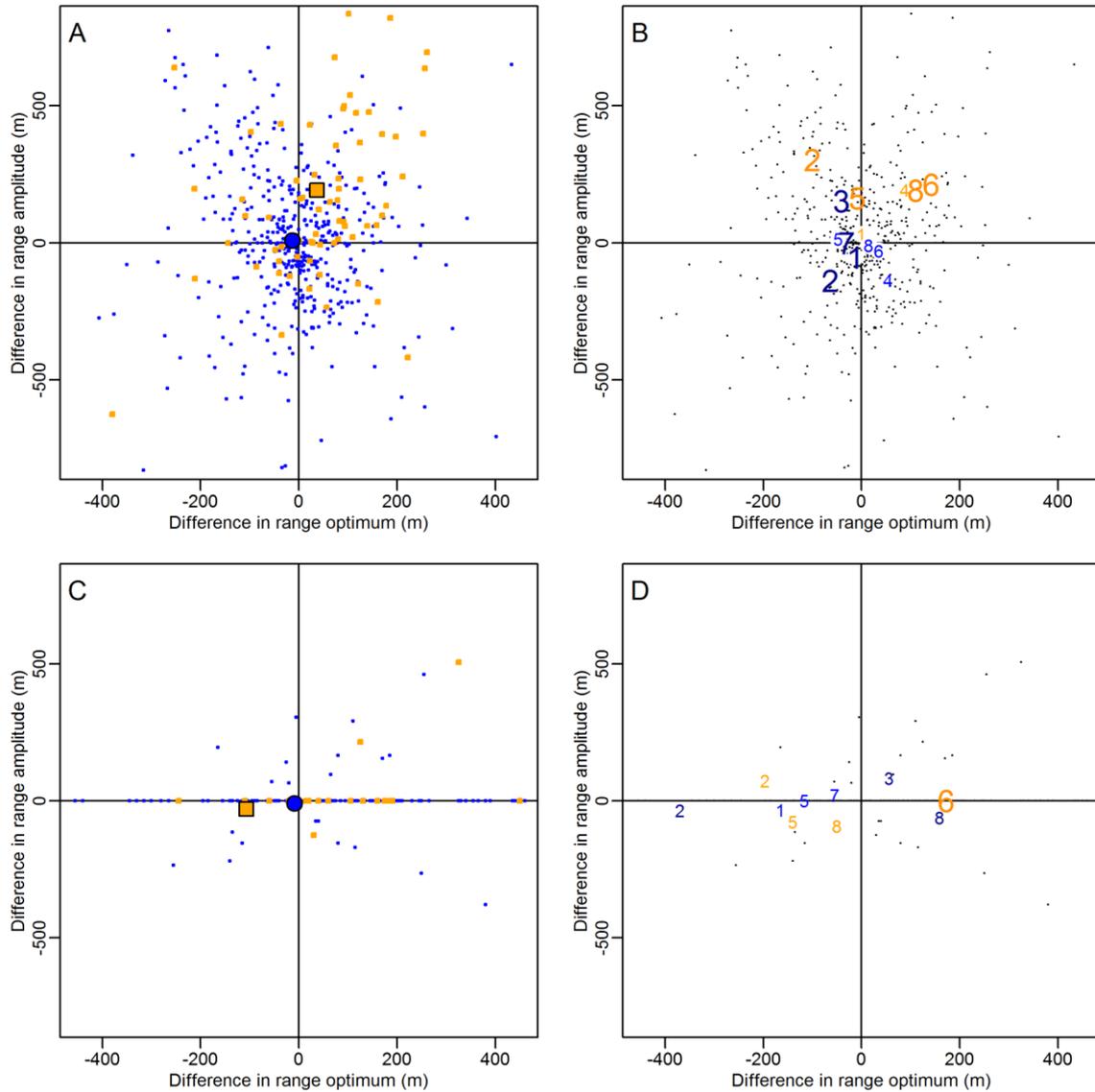
484 Table 3. Estimates and P-values for general (all, bold) and regional linear mixed models for range optima (top) and amplitudes (bottom) for species origin
 485 (OR_N = native, intercept is for non-native), nitrogen (N) and temperature (T) affinity and relevant two-way interactions. Only estimates and interactions
 486 shown for models with the best fit. Data from dataset A1.

<u>Optimum</u>	(Int)	P	OR_N	P	T	P	N	P	OR_N*T	P	T*N	P
All	-204.7	0.038	177.0	0.079	42.9	0.062	25.8	0.005	-65.4	0.014	-	-
Argentina	-	-	-	-	-	-	-	-	-	-	-	-
Australia	-	-	-	-	-	-	-	-	-	-	-	-
Central Chile	-	-	-	-	-	-	-	-	-	-	-	-
Montana	142.0	<0.001	-118.3	0.004	-	-	-	-	-	-	-	-
Norway	-	-	-	-	-	-	-	-	-	-	-	-
Oregon	110.9	<0.001	-96.7	<0.001	-	-	-	-	-	-	-	-
Southern Chile	-	-	-	-	-	-	-	-	-	-	-	-
Switzerland	-187.4	<0.001	-	-	-	-	50.1	0.001	-	-	-	-
<u>Amplitude</u>												
All	-586.2	0.007	-659.2	0.006	-89.6	0.103	-	-	108.7	0.086	-	-
Argentina	-	-	-	-	-	-	-	-	-	-	-	-

<i>Australia</i>	1806.6	0.013	-2084.7	0.022	-375.7	0.038	-	-	367.6	0.099	-	-
<i>Central Chile</i>	-	-	-	-	-	-	-	-	-	-	-	-
<i>Montana</i>	213.0	0.046	-241.7	0.031	-	-	-	-	-	-	-	-
<i>Norway</i>	-	-	-	-	-	-	-	-	-	-	-	-
<i>Oregon</i>	191.5	<0.001	-200.1	<0.001	-	-	-	-	-	-	-	-
<i>Southern Chile</i>	-4773.5	0.045	-	-	1150.2	0.044	1648.4	0.031	-	-	-387.3	0.037
<i>Switzerland</i>	-165.9	0.308	-	-	99.7	0.048	-	-	-	-	-	-

487

488



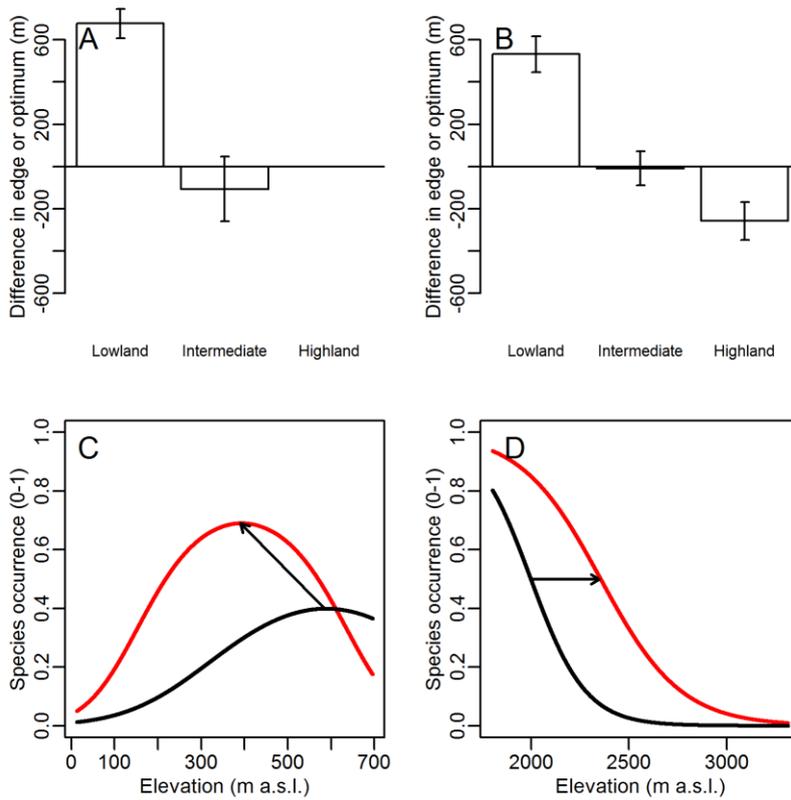
489

490 *Figure 1. Differences (in elevational meters) in range optima (x) and amplitudes (y) between roadsides*
 491 *and adjacent plots for dataset A1 (top) and A2 (bottom), and for the global dataset (left) and the*
 492 *regional subsets (right). Species- and region-specific values are marked with small dots. In A and C,*
 493 *non-native species are marked with orange squares, native species with blue circles, in B and D they*
 494 *are left black for clarity. Overall average optima and amplitude values for natives and non-natives are*
 495 *marked respectively with a large blue dot and an orange square (A, C) (only the range amplitude for*
 496 *non-native species from dataset A1 (Fig. 1A) differed significantly from zero). Regional averages (B,D)*
 497 *are marked with numbers, with larger fontsize for significant results. 1 = AR, Argentina, 2 = AU,*

498 *Australia, 3 = SW, Switzerland, 4 = CLC, Central Chile, 5 = CLS, Southern Chile, 6 = MT, Montana, 7 =*

499 *OR, Oregon, 8 = NO, Norway.*

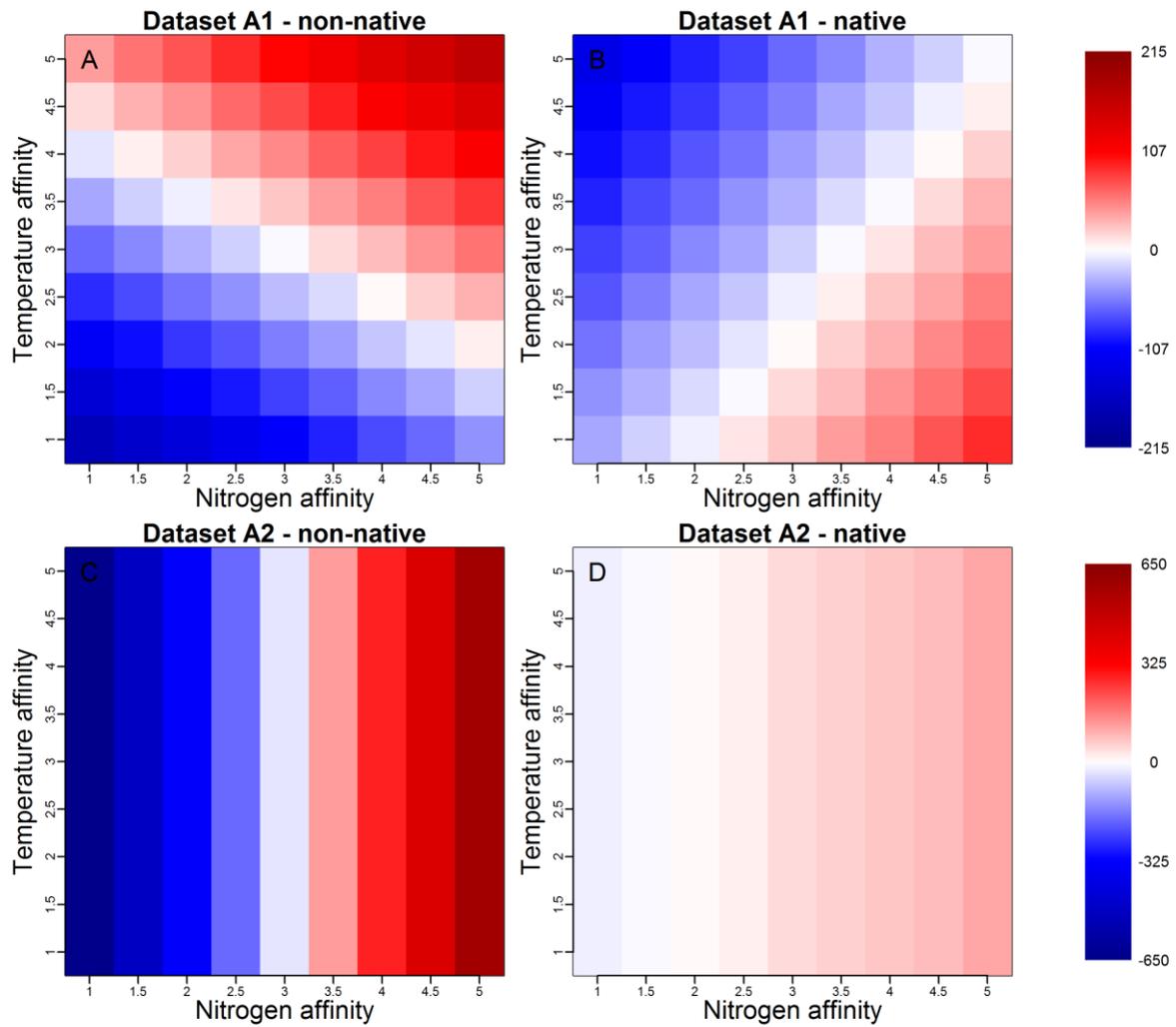
500



501

502 Figure 2. Top: Average elevational differences in edge (for species with an optimum below or above
 503 the sampled road fragment) or optimum (for species with their optimum along the road fragment) (+/-
 504 1 SD) between roadsides and adjacent plots for non-native (A) and native species (B) separately.
 505 Bottom: Example of a species with its optimum along the sampled road fragment, showing a
 506 downward shift (C, *Pinguicula vulgaris*, Norway) and one with its optimum below the road, with a
 507 higher range end in the roadside compared to the adjacent plots (D, *Tragopogon dubius*, Montana).
 508 Red line = roadside, black line = natural vegetation, black arrow connects optimum (C) or edge (D) in
 509 the natural vegetation with the corresponding value in the roadside. Data from dataset A2 and A3.

510



511

512 *Figure 3. Differences (in m) in elevational optima between roadside and adjacent plots for non-native*
 513 *(A, C) and native (B, D) species based on data from dataset A1 (A, B) and dataset A2 (C, D), as a*
 514 *function of nitrogen (x) and temperature (y) affinity. Graphs based on the general LMMs with the best*
 515 *fit (see Table 3). Red = positive values and thus higher optima in roadsides than in the natural*
 516 *vegetation, blue = negative values and thus lower optima, white = no clear trend.*

517

518 Acknowledgements

519 We express our gratitude to the data collectors in the different MIREN-regions and acknowledge the
520 input from two anonymous reviewers. We gratefully acknowledge the grants from the Research
521 Foundation - Flanders (FWO) to J.J. Lembrechts and the support from the Swedish Research Council
522 (VR 2012-6252) to A. Milbau, A. Pauchard and M. Nuñez.

523 Citations

- 524 Alexander, J. M. et al. 2011. Assembly of nonnative floras along elevational gradients explained by
525 directional ecological filtering. — *P Natl Acad Sci USA* 108: 656-661.
- 526 Ansong, M. and Pickering, C. 2013. Are weeds hitchhiking a ride on your car? A systematic review of
527 seed dispersal on cars. — *Plos One* 8:
- 528 Avon, C. et al. 2010. Does the effect of forest roads extend a few meters or more into the adjacent
529 forest? A study on understory plant diversity in managed oak stands. — *Forest Ecol Manag*
530 259: 1546-1555.
- 531 Barros, A. and Pickering, C. M. 2014. Non-native plant invasion in relation to tourism use of
532 Aconcagua Park, Argentina, the highest protected area in the Southern Hemisphere. — *Mt*
533 *Res Dev* 34: 13-26.
- 534 Bates, D. et al. 2013. lme4: Linear mixed-effects models using Eigen and S4.
- 535 Becker, T. et al. 2005. Altitudinal distribution of alien plant species in the Swiss Alps. — *Perspect*
536 *Plant Ecol* 7: 173-183.
- 537 Bergès, L. et al. 2013. Influence of forest road, road-surfacing material and stand age on floristic
538 diversity and composition in a nutrient-poor environment. — *Appl Veg Sci* 16: 470-479.
- 539 Bertrand, R. et al. 2011. Changes in plant community composition lag behind climate warming in
540 lowland forests. — *Nature* 479: 517-520.
- 541 Bolnick, D. I. et al. 2010. Ecological release from interspecific competition leads to decoupled changes
542 in population and individual niche width. — *Proceedings of the Royal Society B-Biological*
543 *Sciences* 277: 1789-1797.
- 544 Corlett, R. T. and Westcott, D. A. 2013. Will plant movements keep up with climate change? —
545 *Trends Ecol Evol* 28: 482-488.
- 546 Davis, M. A. et al. 2000. Fluctuating resources in plant communities: a general theory of invasibility.
547 — *Journal of Ecology* 88: 528-534.
- 548 Delgado, J. D. et al. 2007. Edge effects of roads on temperature, light, canopy cover, and canopy
549 height in laurel and pine forests (Tenerife, Canary Islands). — *Landscape Urban Plan* 81: 328-
550 340.
- 551 Felde, V. A. et al. 2012. Upward shift in elevational plant species ranges in Sikkildalen, central
552 Norway. — *Ecography* 35: 922-932.
- 553 Forman, R. T. T. and Alexander, L. E. 1998. Roads and their major ecological effects. — *Annu Rev Ecol*
554 *Syst* 29: 207-231.
- 555 Forman, R. T. T. et al. 2003. *Road Ecology. Science and solutions.* — Island Press.
- 556 Gelbard, J. L. and Belnap, J. 2003. Roads as conduits for exotic plant invasions in a semiarid
557 landscape. — *Conserv Biol* 17: 420-432.
- 558 Godefroid, S. and Koedam, N. 2004. The impact of forest paths upon adjacent vegetation: effects of
559 the path surfacing material on the species composition and soil compaction. — *Biol Conserv*
560 119: 405-419.

561 Grabherr, G. et al. 1994. Climate effects on mountain plants. — *Nature* 369: 448-448.

562 Güsewell, S. and Klötzli, F. 2012. Local plant species replace initially sown species on roadsides in the
563 Swiss National Park. — *Eco Mont-Journal on Protected Mountain Areas Research* 4: 23-33.

564 Haider, S. et al. 2010. The role of bioclimatic origin, residence time and habitat context in shaping
565 non-native plant distributions along an altitudinal gradient. — *Biol Invasions* 12: 4003-4018.

566 Haider, S. et al. 2011. Elevational distribution limits of non-native species: combining observational
567 and experimental evidence. — *Plant Ecology & Diversity* 4: 363-371.

568 Johnston, F. M. and Johnston, S. W. 2004. Impacts of road disturbance on soil properties and on
569 exotic plant occurrence in subalpine areas of the Australian Alps. — *Arct Antarct Alp Res* 36:
570 201-207.

571 Jump, A. S. et al. 2012. Rapid altitudinal migration of mountain plants in Taiwan and its implications
572 for high altitude biodiversity. — *Ecography* 35: 204-210.

573 Juvik, J. O. et al. 2011. "The upper limits of vegetation on Mauna Loa, Hawaii": a 50th-anniversary
574 reassessment. — *Ecology* 92: 518-525.

575 Körner, C. 2003. *Alpine plant life: functional plant ecology of high mountain ecosystems*. — Springer.

576 Kueffer, C. et al. 2014. The Mountain Invasion Research Network (MIREN) linking local and global
577 scales for addressing an ecological consequence of global change. — *Gaia-Ecological*
578 *Perspectives for Science and Society* 23: 263-265.

579 Landolt, E., Bäumler, B., Erhardt, A., Hegg, O., Klötzli, F., Lämmli, W., Nobis, M., Rudmann-Maurer,
580 F., Schweinsgruber, F.H., Theurillat, J.P., et al. 2010. *Flora indicativa*. — Haupt.

581 le Roux, P. C. et al. 2012. Biotic interactions affect the elevational ranges of high-latitude plant
582 species. — *Ecography* 35: 1048-1056.

583 Lembrechts, J. J. et al. 2014. Alien roadside species more easily invade alpine than lowland plant
584 communities in a subarctic mountain ecosystem. — *Plos One* 9(2):

585 Lenoir, J. et al. 2008. A significant upward shift in plant species optimum elevation during the 20th
586 century. — *Science* 320: 1768-1771.

587 Lenoir, J. et al. 2009. Differences between tree species seedling and adult altitudinal distribution in
588 mountain forests during the recent warm period (1986-2006). — *Ecography* 32: 765-777.

589 Lenoir, J. et al. 2010. Going against the flow: potential mechanisms for unexpected downslope range
590 shifts in a warming climate. — *Ecography* 33: 295-303.

591 Leung, G. P. C. et al. 2009. Exotic plant invasion in the highly degraded upland landscape of Hong
592 Kong, China. — *Biodivers Conserv* 18: 191-202.

593 Marini, L. et al. 2012. Alien and native plant life-forms respond differently to human and climate
594 pressures. — *Global Ecol Biogeogr* 21: 534-544.

595 Mazerolle, M. J. 2015. *AICcmodavg: Model selection and multimodel inference based on (Q)AIC(c)*.

596 McDougall, K. L. et al. 2011. Alien flora of mountains: global comparisons for the development of
597 local preventive measures against plant invasions. — *Divers Distrib* 17: 103-111.

598 MIREN 2005. *MIREN: The Mountain Invasion Research Network*.

599 Müllerová, J. et al. 2011. The impacts of road and walking trails upon adjacent vegetation: Effects of
600 road building materials on species composition in a nutrient poor environment. — *Sci Total*
601 *Environ* 409: 3839-3849.

602 Paiaro, V. et al. 2011. Altitudinal distribution of native and alien plant species in roadside
603 communities from central Argentina. — *Austral Ecol* 36: 176-184.

604 Pauchard, A. et al. 2009. Ain't no mountain high enough: plant invasions reaching new elevations. —
605 *Front Ecol Environ* 7: 479-486.

606 Pauli, H. et al. 2007. Signals of range expansions and contractions of vascular plants in the high Alps:
607 observations (1994-2004) at the GLORIA*master site Schrankogel, Tyrol, Austria. — *Global*
608 *Change Biol* 13: 147-156.

609 Pinheiro, J. et al. 2013. *nlme: linear and nonlinear mixed effects models*.

610 Pollnac, F. et al. 2012. Plant invasion at landscape and local scales along roadways in the
611 mountainous region of the Greater Yellowstone Ecosystem. — *Biol Invasions* 14: 1753-1763.

- 612 Pollnac, F. W. and Rew, L. J. 2014. Life after establishment: factors structuring the success of a
613 mountain invader away from disturbed roadsides. — *Biol Invasions* 16: 1689-1698.
- 614 Pyšek, P. et al. 2011. Colonization of high altitudes by alien plants over the last two centuries. — *P*
615 *Natl Acad Sci USA* 108: 439-440.
- 616 R Core Team 2013. R: a language and environment for statistical computing. — In: R Foundation for
617 Statistical Computing, V., Austria. (ed).
- 618 Seipel, T. et al. 2012. Processes at multiple scales affect richness and similarity of non-native plant
619 species in mountains around the world. — *Global Ecol Biogeogr* 21: 236-246.
- 620 Seipel, T. et al. 2015. Performance of the herb *Verbascum thapsus* along environmental gradients in
621 its native and non-native ranges. — *J Biogeogr* 42: 132-143.
- 622 Taylor, K. et al. 2012. Human-mediated long-distance dispersal: an empirical evaluation of seed
623 dispersal by vehicles. — *Divers Distrib* 18: 942-951.
- 624 ter Braak, C. F. and Looman, C. N. 1986. Weighted averaging, logistic regression and the Gaussian
625 response model. — *Vegetatio* 65: 3-11.
- 626 Vetaas, O. R. 2002. Realized and potential climate niches: a comparison of four *Rhododendron* tree
627 species. — *J Biogeogr* 29: 545-554.
- 628 Von der Lippe, M. and Kowarik, I. 2007. Long-distance dispersal of plants by vehicles as a driver of
629 plant invasions. — *Conserv Biol* 21: 986-996.
- 630 Walther, G. R. et al. 2002. Ecological responses to recent climate change. — *Nature* 416: 389-395.
- 631 Walther, G. R. et al. 2005. Trends in the upward shift of alpine plants. — *J Veg Sci* 16: 541-548.
- 632 Zhu, K. et al. 2012. Failure to migrate: lack of tree range expansion in response to climate change. —
633 *Global Change Biol* 18: 1042-1052.

634

635

636

637 Supplementary material (Appendix at www.oikosoffice.lu.se/appendix). Appendix 1-2.

638 Appendix 1: dataset A1, A2 and A3.

639 Appendix 2: Models used in model selection for individual regional GLMMs and calculations of
640 optimum and amplitude.

641