

MASTERTHESIS

THE EFFECT OF ROADBUILDING ON SUBARCTIC MOUNTAIN VEGETATION
AND THE INTRODUCTION OF NONNATIVE SPECIES

JONAS LEMBRECHTS

PROMOTOR: PROF. DR. IVAN NIJS

CO-PROMOTOR: DR. ANN MILBAU

RESEARCH GROUP ON PLANT AND VEGETATION ECOLOGY
FACULTY OF BIOLOGY
UNIVERSITY OF ANTWERP
BELGIUM
JONAS.LEMBRECHTS@STUDENT.UA.AC.BE

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Contents

ABSTRACT

This research focusses on the disturbance of a Northern Scandinavian mountain region through the building of roads. It tries to estimate the vulnerability of subarctic mountain vegetation to this specific kind of disturbance as reflected in changes in native species composition, introduction of nonnative species and species-specific changes in distribution on the mountain. Vegetation surveys were taken along transects stratified on roads and by elevation, with plots within the roadside and on a transect from 0 to 100 m away from it. The driving factors behind diversity and species richness of natives and nonnatives were entangled with multivariate statistics. Similarities with other studied mountain road systems around the world were observed, including the edge-effect, introduction of nonnatives, directional ecological filtering and enemy-release. Differences with other ecosystems (the unusual high resistance of the mountain vegetation, the higher diversity in roadside plots, the unclear relationship between native and nonnative diversity) stress the need to treat every ecosystem as a unique system, with its own specific reaction to anthropogenic disturbance. It can be a warning for conservation that measures should be adapted to the specific local situation. The new insight that alpine, natural species can profit from road building to expand their own growing range to lower elevations adds a new and highly interesting viewpoint to the study area. Future research on disturbances in mountains should take these positive effects on native species into account.

1. INTRODUCTION

Anthropogenic pressure on natural ecosystems is bigger than ever. Completely undisturbed areas are almost inexistent while the influences of the human society reaches the most remote areas. In order to preserve the last natural diamonds in the world, accurate knowledge of the dangers of anthropogenic influence is necessary. This research focusses on the disturbance of a Northern Scandinavian mountain region through the building of roads. It tries to estimate the vulnerability of subarctic mountain vegetation to this specific kind of disturbance as reflected in changes in native species composition, introduction of nonnative species and species-specific changes in distribution on the mountain. In this introduction, current knowledge on the subject is summarized, starting with the effects caused by roadbuilding. Subsequently, invasion by nonnatives and the factors making an ecosystem vulnerable to invasion and disturbance are discussed.

1.1. Disturbance by roadbuilding

Roadbuilding provides a classic example of the fragmentation of nature under human influence. Due to roadbuilding, habitats are fragmented, biodiversity is lost and habitats are homogenized, all on a global scale (Paiaro et al., 2011). Because of their linear structure, they allow dispersal of plant species. They hence homogenize the distribution of native species and provide a corridor for nonnatives, opening the door for plant invasion (Paiaro et al., 2011). Seeds of both natives and nonnatives are transported over often long distances by vectors, which can be cars (Taylor et al., 2012), footwear (Ware et al., 2011) or large herbivorous species (Mcdougall et al., 2005). Because roadsides are often highly disturbed areas due to the process of roadbuilding, the introduction of these traveling species is facilitated (Paiaro et al., 2011). Invasibility differs between different roadside habitats, as other factors play a role as well. Highly vegetated roadsides are invaded more easily than poorly vegetated sides (Paiaro et al., 2011).

1.1.1. *Edge effect*

Vegetation several tens of meters from a road verge feels the influence and can change dramatically, resulting in an edge effect. The exact depth of the edge effect can vary from some to almost hundred meters (MacQuarrie and Lacroix, 2003, LaPaix et al., 2012). The edge-effect consists out of changing abiotic conditions with distance from the roadside. Variations on a small scale are caused by the roadside and include light, temperature, humidity, wind, soil water content, dust, surface water, patterns of runoff and sedimentation (Trombulak and Frissel, 2013, Takahashi and Miyajima, 2010, LaPaix et al., 2012). Chemical conditions are altered within the edge, resulting in higher values of heavy metals, salts, organic molecules, ozone and nutrients (Trombulak and Frissel, 2013, Lee et al., 2012). An increase in pH results in a higher nutrient availability (Müllerová et al., 2011). The size of the edge effect correlates strongly with the roadside verge width, depending on the road improvement, with a larger depth of the edge effect when the roadside verge itself is larger (Gelbard and Belnap, 2003). This results in a higher nonnative species richness in the interior community when the road verge is larger.

1.1.2. *Changes in species composition*

The building of roads has a great impact on species composition in the influenced habitat. Because of the physical and chemical disturbance explained in the previous paragraph, local climax vegetation is put under high pressure (Gelbard and Belnap, 2003). In the meantime, anthropogenic vectors using the road import seeds of both natives and nonnatives with good dispersing qualities (see higher). The import of seeds, changing abiotic circumstances and setback in succession result in higher diversity of both natives and nonnative species in roadsides (Pauchard et al., 2004, Zeng et al., 2011, LaPaix et al., 2012). It is difficult to predict the range of these changes, but it unmistakably results in a different species composition.

1.1.3. *Roads in mountains*

The aforementioned effects caused by roads are not much studied in mountains. It is however stated by LaPaix et al. (2012) that the changing abiotic (climatic) and anthropogenic (disturbance) conditions change with increasing height in the mountains. The introduction of nonnative species declines significantly with increasing height in

the mountain, as does the depth of their penetration in the natural vegetation. The harsher climatic conditions and the lower frequency of passing vectors (cars and walkers) form two possible explanations for this decline in nonnative species (LaPaix et al., 2012, Pollnac et al., 2012, Seipel et al., 2012). However, a delay in the spread of nonnatives by the vectors is another explanation for this pattern (Paiaro et al., 2011).

1.2. Invasions

On purpose or not, people have moved thousands of plant species from everywhere in the world outside of their normal range. Some of them got established in their new environment and started to spread, often with detrimental effects on ecosystems (Mack et al., 2000, Bradley et al., 2010).

1.2.1. *Nonnatives in mountain regions*

Most of the research on introduction of nonnative plant species is performed in highly-populated lowlands, where large-scale invasions took place (Pauchard et al., 2009). High elevations are less affected by invasions, because of the harsh climatic conditions and the low human-mediated disturbance Barni et al. (2012), but as global temperatures rise and anthropogenic pressure increases, the risk for invasion in mountains is growing (Pauchard et al., 2009, Pyšek et al., 2011). Invasibility is lower on higher elevations, which is supported by observed lower numbers of nonnative species on a higher altitude (Alexander et al., 2011). This could however also be caused by a lower propagule pressure and less anthropogenic disturbances at high altitudes (Pyšek et al., 2011). It is not necessarily linked to differences in abiotic circumstances. Moreover, due to a reduced competition and higher small-scale heterogeneity, invasibility could even increase at high altitudes (Davies, 2011). Nonnative species are often introduced recently and still 'on their way to the top' (Pyšek et al., 2011). However, evidence shows that the speed of these invasions is increasing (Pyšek et al., 2011). Although the actual invasion rate in mountains is lower than in lowlands, they are not necessarily more resistant. Spread of nonnatives is prevented by three factors, as explained above: the paucity of nonnative species that are pre-adapted to harsh abiotic conditions, low nonnative propagule pressure, and low human disturbances (Pauchard et al., 2009). These restricting factors are changing rapidly. However, abiotic factors (e.g. climatic

conditions) often dominate over biotic factors (e.g. competition) in determining colonization or invasion success. On a global scale, highly similar processes are recorded, even when different species are involved. Nonnative species richness always declines with elevation, while native species richness peaks at mid-elevations (Seipel et al., 2012). Nonnatives are progressively filtered out by the increasingly harsh climatic conditions, a process called 'directional ecological filtering' (Pollnac et al., 2012). The lowland nonnative flora brings up the main determinant of a mountain region's nonnative species composition (Haider et al., 2010, Mcdougall et al., 2011) and only those species with a broad environmental tolerance survive on a gradient to higher elevations and species with a narrow elevational altitude drop out (Alexander et al., 2011). Directional ecological filtering depends on the relative and not the absolute difference in abiotic factors within mountains (Alexander et al., 2011). Hence, the relative temperature difference is the driver. Mid-European species are the dominant nonnative species on mountains everywhere in the world (Seipel et al., 2012). They occur on almost all continents and along the entire elevation gradient. This relates to their high propagule pressure, but also to their high climatic plasticity and their known association with agriculture (Mcdougall et al., 2011). Cold-adapted plants are not found to be invasive, although they cause a potential danger in mountain regions (Alexander et al., 2011). Plants adapted to a lowland environment may be more likely to establish than cold-adapted species and hence have a better chance to invade adjacent mountain regions (Haider et al., 2010). The change in elevation is not only the predictor of a change in climate, but also of a change in anthropogenic use. More intense anthropogenic use is accompanied with an increase in nonnatives, which partly explains the species richness of nonnatives in the lowlands (Pauchard et al., 2004). Questions remain about the combination of directional ecological filtering and the anthropogenic disturbance caused by roadbuilding. It is possible that nonnatives use the lower biotic competition in roadsides to get round the abiotic limits of ecological filtering and get above their normal elevational limit.

1.2.2. *Nonnatives in mountains under climate change*

Because of their steep environmental and climatic gradients, mountains are recognized as being especially sensitive to climate change (Mcdougall et al., 2011b). This will

probably increase the threat of invasive species on the system, even though the expected effects from climate change on invasive plants are not straightforward (Bradley et al., 2010). Warming has been proved to improve the growth and fertility of invasive plants (see for example Chuine et al. (2012)). As the climate in the Arctic mountains will change, lowland conditions will climb up on the mountain, possibly taking typical lowland nonnatives with them. Invaders will likely reach higher elevations, partly because of a longer growing season due to less snow cover and higher average mean temperature (Mcdougall et al., 2005). However, species movements will not necessarily be upward, because water availability for example can be more limiting. The changes in invasions are not limited to the 'traditional' invaders. Native species distribution patterns can alter to, with movements of native plant species to higher elevations (Mcdougall et al., 2011b). The changing patterns of native species are not fully understood.

Similar ideas about the limitations of invasion on high altitudes apply to higher latitudes. Even the most remote and harsh northern regions are not danger free (Rose and Hermanutz, 2004, Pauchard et al., 2009). The rapid warming in these regions and the predicted above average increase in future temperature will not only lead to a northward movement of native plant species, but also potentially increase the invasion rate in the future (Milbau et al., 2013).

1.3. Invasibility

1.3.1. *Invasion succes*

The previous sections summarized the ecological knowledge on roadsides, invasions in mountains and the combination of both. However, invasion success of a nonnative species depends on several other biotic and abiotic factors that can alter the straightforward patterns theoretically expected and explained above. Invasive success is determined by invasiveness, invasibility and propagule pressure. Invasiveness is the ability of exotic plants to enter an ecosystem, determined by their own plant traits. Invasibility is the susceptibility of an ecosystem to the entrance of new species (nonnatives or natives) and depends on the traits of the ecosystem (Milbau et al., 2009, 2013). The propagule pressure is the number of introduced seeds and/or number of

introduction events and depends on source populations and vectors (Colautti et al., 2006).

1.3.2. *Disturbance*

Biotic resistance of an ecosystem to invasion changes dramatically when the system is disturbed. Even small scale disturbances can create gaps, which creates opportunities for nonnative species (Milbau et al., 2013). Human disturbances show a higher correlation with nonnative diversity, compared to naturally disturbing processes (Haider et al., 2010). This correlation occurs because the change in the amount of disturbance, more than the disturbance itself, forms the trigger for invasion (Pauchard et al., 2004). Plant communities are adapted to their own disturbance regime, while recent changes in disturbance intensity and frequency are often caused by humans. Invasive species are ideal weeds, perfectly equipped to behave as opportunists when resources suddenly become available after a disturbing event (Burke and Grime, 2012). The building of roads is one of the biggest disturbing events in the Arctic mountain regions and the influence on both the native community and the spread of nonnatives can hardly be underestimated. Rose and Hermanutz (2004) proved for instance that disturbance is a prerequisite for nonnative plant establishment in boreal systems. Aikio et al. (2012) reported that no matter where a nonnative got recorded, it always ended up in the roadside vegetation, a clear indication of how roadsides can serve as an important entrance for nonnative species into a previously undisturbed habitat.

1.3.3. *Plant community*

Invasibility is strongly influenced by the plant community structure of the invaded ecosystems, as different plants and combinations of plants prevent or facilitate invasion. Diversity of native and non-native species is positively correlated, with more non-natives in more diverse communities (Levine and D'Antonio, 1999, Zeiter and Stampfli, 2012). There are several possible explanations for this. First, invaders and resident species could be similar and depending on the same environmental variables. Secondly, resistance could be correlated to vegetation structure and species composition, more than to productivity or diversity. Moreover, native species could facilitate the settlement of nonnatives and native and nonnative diversity can both correlate with heterogeneity of a plot (Zeiter and Stampfli, 2012, Milbau et al., 2013). Other

researchers however reported different correlations between natives and nonnatives, with anthropogenic disturbance as the most important explaining factor Tomasetto et al. (2013). Vegetation density can also be an explaining factor, with less invasion in habitats with high densities (Yager et al., 2011, LaPaix et al., 2012).

In subarctic ecosystems, it is known that rich *Empetrum*-heaths are highly resistant against invasions (Milbau et al., 2013). *Empetrum* is a strong competitor in nutrient-poor habitats. It immobilizes nutrients and secretes allelopathic compounds. It creates harsh circumstances for typical ruderal species that profit from quick releases of nutrients in a disturbed environment (Pellissier et al., 2010). The opposite holds true for *Salix*-shrublands or meadows (Milbau et al., 2013). Some boreal habitats like bogs, marshes and heath-lichen tundra are highly resistant against invasion, except after anthropogenic disturbance. Riparian areas, forests and alpine meadows can be invaded without anthropogenic disturbance (Rose and Hermanutz, 2004).

1.3.4. *Natives vs. nonnatives*

Eutrophication strongly facilitates invasion in previously nutrient-poor environments. The easiest establishment of nonnatives can be seen when there is a combination of an increased disturbance with high eutrophication (Burke and Grime, 2012). With increasing human influence, both disturbance and eutrophication are likely to increase, providing high risks in the future. Nonnatives occur more in lowlands and close to anthropogenic disturbance (Gonzalez-Moreno et al., 2012). Native species diversity is probably negatively associated with disturbance (Gonzalez-Moreno et al., 2012). It is also expected to decline with elevation, with a less rich vegetation higher in the mountains (Pauchard et al., 2009).

1.3.5. *Enemy release*

The enemy release hypothesis connects the better performance of nonnative species in a new habitat with the absence of their normal enemies and herbivores (Keane and Crawley, 2002, Liu and Stiling, 2006). The performance of a plant is often limited due to the consumption by herbivores. The release of enemies in the new system gives the alien the opportunity to increase its population size without fundamental constraints. This is for example shown by Alba and Hufbauer (2012) for *Verbascum thapsus*.

2. RESEARCH QUESTIONS

To reach conclusions about elevational trends in native and nonnative plant richness within road sides and the factors that determine them, we recorded species richness in transects placed at regular elevational intervals along three roads within the mountains. Our study addressed three main hypotheses, all three of them with several sub-hypotheses. We stated that (1) roads have a large influence on species composition in a natural subarctic mountain vegetation, with effects spanning over several tens of meters of edge. We expected diversity of natives as well as nonnatives to be larger in roadsides, with changed dominance compared to natural vegetation, due to the negative effect of the road on natural species of the climax vegetation. For native species, a change in their realized niche in the climate and elevation dimension will occur in roadsides. (2) We also expected a different ecological behavior of nonnatives, compared to natives. Species richness of nonnatives would go down faster with altitude than for natives, with directional ecological filtering acting on nonnatives. Species richness of nonnatives would be positively correlated with disturbance and high native species richness, but species richness of both natives and nonnatives would depend strongly on habitat type. Caterpillars probably preferred natives above nonnatives. (3) We hence expected to conclude that roads provide a danger for a natural mountain vegetation, creating significant changes in vegetation and transfer of aliens from the roadsides into the natural vegetation. The danger of nonnatives would be concentrated in the lower regions of the mountain gradient, but species with the broadest niche would reach the top.

3. MATERIAL AND METHODS

The methodology in this thesis is based on the MIREN-protocol (www.miren.ethz.ch), with some site-specific changes. The methodology is globally synchronized in order to draw globally relevant conclusions.

3.1. Location

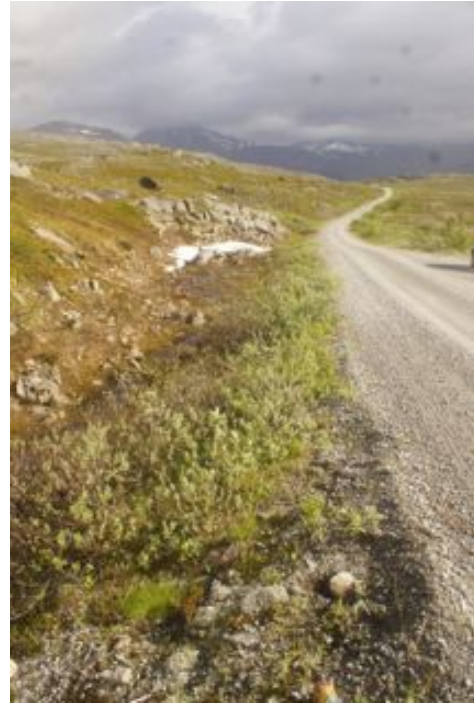
Data were collected in the Northern Scandes, which is in several ways relevant for the research. The region only recently received higher anthropogenic disturbance, visible as roads from the coast to hydropower centrals in the mountains. These recent disturbances (building of roads and hydropower installations occurred in the eighties) in an unspoiled area provide the opportunity to study the effects of the roads without disturbance of the data due to other disturbing events. The region is also still invasion-free, which gives conservation management the chance to take preventive measures.

3.1.1. Climate

By choosing the western side of the mountains on the edge between Sweden and Norway (in Narvik), a climatic gradient could be studied. The seaside of the Scandinavian peninsula profits from warm oceanic currents, which results in a wet, temperate climate, even in the northern parts. Lowland vegetation in this climate zone consists of productive rain forests with birch, willow, pine and an understory of mainly ferns. On the mountain slopes, climatic conditions become drier and colder. Vegetation changes accordingly to a poor open forests, with an understory dominated by *Vaccinium*-species and *Empetrum nigrum* L. The treeline is situated at ca. 600 m.a.s.l. There, vegetation is dominated by dwarf shrubs, with *Betula nana* L., *Vaccinium* sp., *Empetrum nigrum* L. The resulting climatic and vegetation gradients shifts from a productive, temperate lowland vegetation to a poor subarctic alpine vegetation over a span of 600 meters. An impression of the roadside vegetation in the area is shown in Fig. 1. Although altitude is not a perfect substitute for environmental harshness, the air temperature and the duration of the growing season usually decline with increasing elevation in high-latitude mountains, especially if other factors such as moisture regime are held constant (Milbau et al., 2013).



(A) Lowland vegetation



(B) Alpine vegetation

FIGURE 1. The typical roadside vegetation in the temperate forests of the lowlands (a) and the subarctic alpine vegetation above treeline (b).

3.1.2. Roads

Roads were chosen using the criteria from MIREN. They are open to general vehicular traffic during summer months and have a broad elevational range, so they capture the whole variation from lowland to alpine vegetation. The three roads are established in the '80s. They have a comparable size and traffic intensity and hence a similar influence on the vegetation (LaPaix et al., 2012). Traffic to the hydropower installations provides the main bulk of vehicles, with only some occasional tourists or locals. During winter, roads are blocked by snow, which limits road use to the summer half of the year. Roads are gravel roads with a road verge with drainage system. They were in good condition, on one road, gravel addition was going on during the sampling period. All roads start approximately at sea level ($\pm 10-20$ m.a.s.l.), along the coast of Narvik. Their location is indicated on the map in Figure 2.

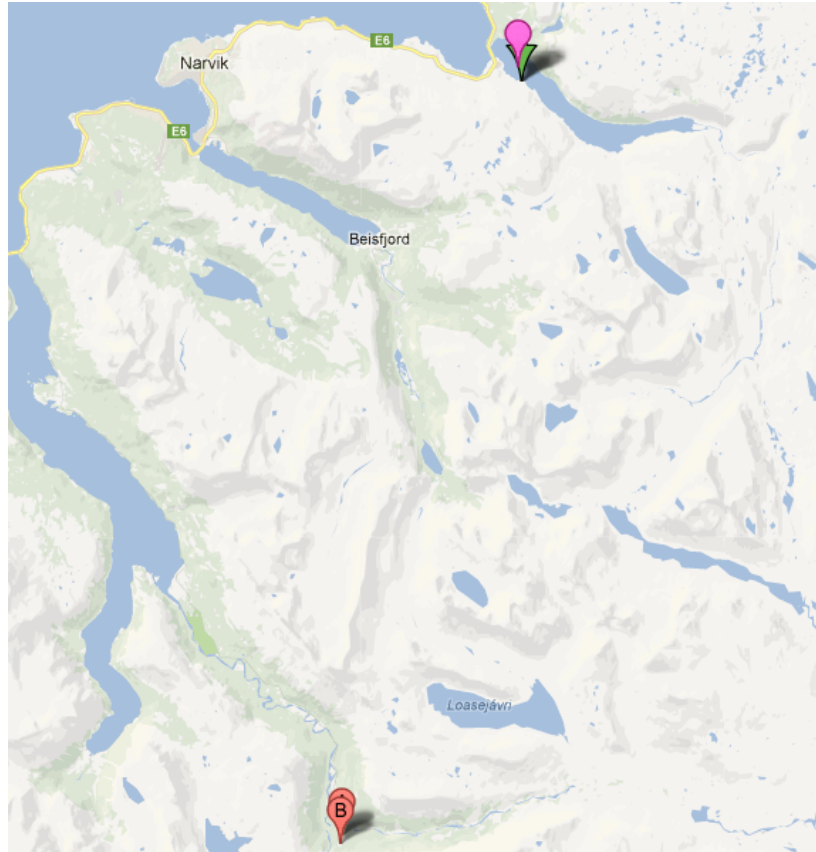


FIGURE 2. Map of the Narvik-area, with an indication of the location of the study roads. The first road lies in the north, starting at the green and pink symbol and winding on the mountain to the south. Road 2 and 3 start at the fjord northwest of the red dots, follow the river and split at the red dots. The second road follows the valley eastwards, the third road goes south.

3.2. Sampling design

The MIREN survey adopts a "targeted transect" approach. They use transects stratified on roads and by elevation. The developed design can be used for new and follow-up surveys and are similar all over the world. Some additions to the design, relevant for this thesis, were made. All fieldwork was performed within one month with the help of a field assistant, data processing comes completely on my own account.

3.2.1. *Transects*

Each of the 3 aforementioned roads was divided in 19 equal elevational portions, which resulted in 20 evenly spaced contour lines. At the intersection of the road with its

contour line, 20 times along a road, a transect was placed (Figure 3). When a road crossed the contour line more than once, the first section was used.

Three mountain gradients were used, each of them along a road going from the valley at the coast to approximately 700 m.a.s.l. Each gradient was divided in 19 equal elevational portions, which resulted in 20 evenly spaced contour lines (Figure 3). At the intersection of the road with its contour line, so 20 times along a road, a transect was placed. When the road crossed the contour line more than once, the first section was used. Each transect consisted of three plots, (each 2x50 m), one parallel to the road verge, the other two perpendicular, together forming a T (Figure 3). The outside edge of the roadside section of the transect was placed at the first occurrence of roadside vegetation. With GPS-coördinates and local markings, the location of the plot was saved for follow-up research. The side of the road was chosen randomly by flipping a coin in all cases where topography, impassable barriers (large rivers) or bends in the road didn't force us to choose one side. When the transect could not be placed at the target position, it was placed at the first permissible position uphill from the target position. Some overall observations were done (road verge width, traces of herbivores, the aspect of slope and trees (if present) and the chosen roadside (down, up, left or right)).

3.2.2. *Plots*

For each of the 3 plots in the transect (see Figure 3), present vegetation was recorded and several data values were noted (see Appendix for the definitions). We recorded mountain zone, habitat, disturbance type and intensity and the occurrence of fences (yes/no). Cover classes were used to estimate the amount of bare ground, vegetation and forest canopy. Cover classes were on a scale from 0 to 8, as shown in Table 1.

Some other factors, not part of the MIREN-protocol, were also recorded. A cover class was estimated for the moss cover at the surface, the vegetation cover without mosses and the aquatic area. We also indicated (yes/no) if there were moist patches in the plot. Mosses form an important part of the arctic vegetation, often covering all empty spots. This means that even in a very sparse vegetation, the options for invasion through gaps in the vegetation are very limited. Moist and aquatic areas (mostly marshes) are highly diverse, with a totally different species composition than drier spots with possible effects on invasibility. Species-specific data were also recorded

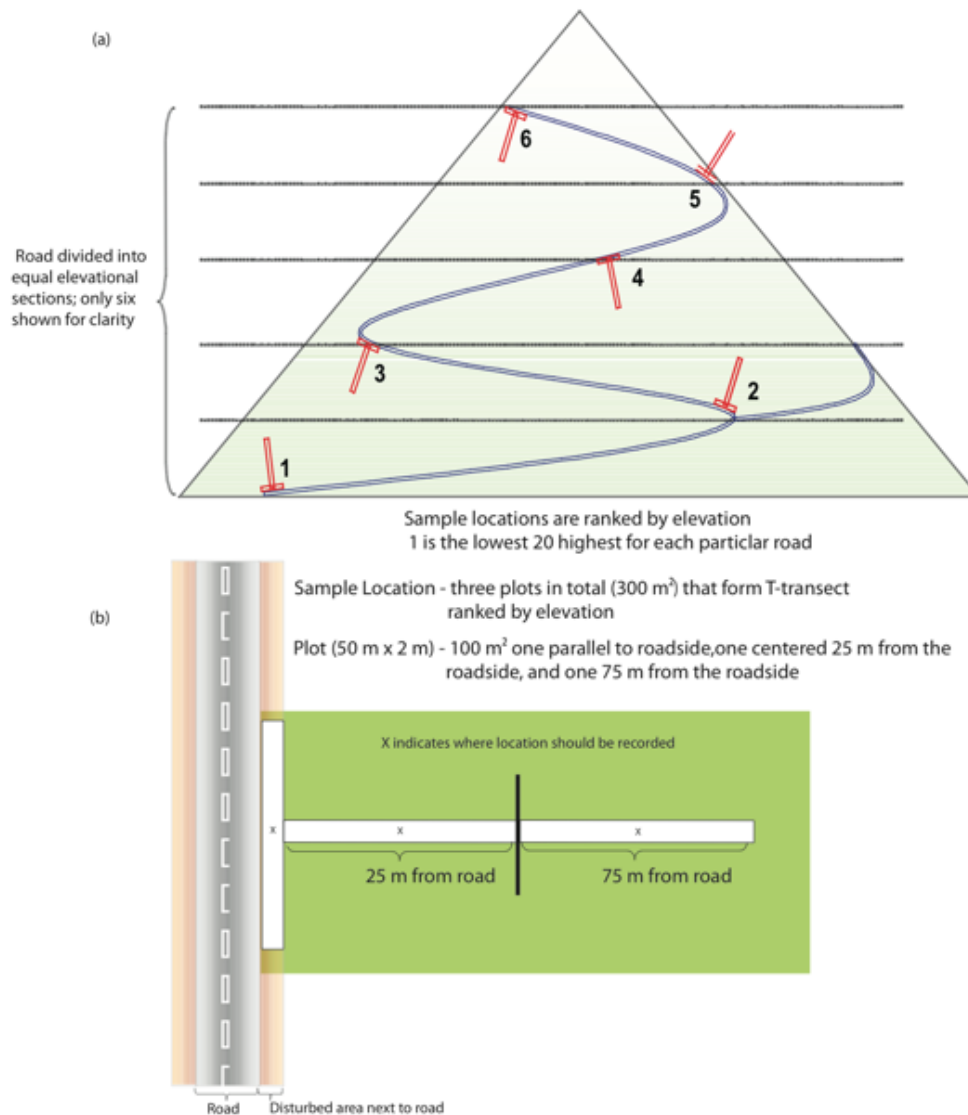


FIGURE 3. Details of transect placement and plot layout. The roadside plot is plot A, followed by plot B and C parallel from the road. B and C are each divided in 2 subplots: B1, B2, C1 and C2.

within each plot. Abundance, cover, herbivory and herbivore type were noted. For definitions and classes, see the Appendix. Species were verified with Den nya nordiska Floran (2010). Plot B and C, the plots in the natural vegetation, were divided in 2 more plots, resulting in plot B1, B2, C1 and C2, each of them 2x25 meters. For this change in the standard design was opted, because a steep gradient and changing species composition of natives and nonnatives could be expected, which was impossible to catch with only 2 plots of 50 meters. Only presence or absence of species was recorded to limit the input of extra man hours.

TABLE 1. Cover classes

Cover classes	Percentages
0	0
1	0–1
2	1–5
3	5–25
4	25–50
5	50–75
6	75–95
7	95–99
8	99–100

3.3. Nonnatives

The native or nonnative status of the species was determined by an expert in this field: Torbjörn Alm, from the University museum in Tromsø. Species were classified as nonnative if introduced from another region since 1492 Alexander et al. (2011). The biggest difficulty in this definition is the relevant scale for the region. There are different datasets on nonnative species, but often on the scale of a whole country. Norway spans a whole climatic gradient from south to north, and plants that occur naturally in one part are not necessarily natives in other parts. Because this research is performed in the absolute north of the country, it is relevant to include natives from the south of the country as nonnatives in the dataset if they are expanding their range to the north. So both nonnatives for Norway as for the mountains of Narvik are used.

3.4. Data processing and analysis

Species richness and species-specific coverage for all plots (which means 3 per transect, 60 per road, so 180 plots in total) were analyzed with a Detrended Correspondence Analysis (DCA) (Oksanen, 2013). This allowed visual interpretation of the multi-dimensional data. Graphs were created to show the two main axes of the DCA and compare them with plot-specific values. Ellipses and trend arrows were used to explore and test relationships between abiotic and biotic factors. Evolution of species diversity, bare ground, moss and vegetation coverage were compared visually with height and

distance from the road. Changes in species diversity with distance from the road were tested with a linear model, containing plots (or subplots) and roads as fixed factor. The same was done for nonnative species diversity with distance to the road. Dominance was tested with two-sample t-tests on species richness within each cover class in roadside plots versus plots in natural vegetation. Changes in species-specific niches with elevation and distance to the road are shown in a scatterplot containing plot numbers and height. Correlations between altitude and species richness, the concept of directional ecological filtering and the factors explaining diversity of natives and nonnatives and intensity of herbivory were all tested and visualized with linear models with all studied factors, which gave specific p-values or correlations.

4. RESULTS

Some very clear patterns emerged from our data, allowing to answer the 3 main research questions, formulated above. The influence of roads on the species composition is discussed first. A closer look will be given to changes in species richness of natives and nonnatives, changes in dominance and realized niche. Next, the different ecological behavior of nonnatives is examined and compared to the native vegetation. Finally, the dangers of roadbuilding for the flora are listed.

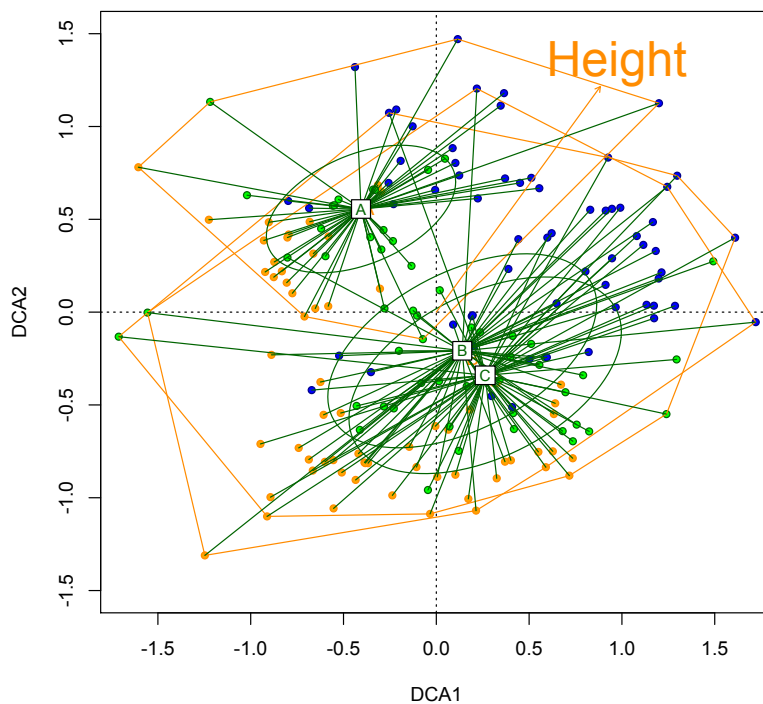


FIGURE 4. Graphical representation of the two main axes of the DCA-analysis of the community structure in all 180 plots (dots), with the outlines of the different types of plots shown. A = Roadside plots, B = plots from 2 to 52 m away from the road, C = plots from 52 to 102 m. Ellipses show standard deviation, spiderwebs connect all contributing plots and hulls give total spreading. Color of dots depending on altitude: orange = 0-200 m.a.s.l., green= 200-400 m.a.s.l., blue= 400-600 m.a.s.l. Eigenvalues of DCA1 and 2: 0.348 and 0.277 respectively.

4.1. The influence of roads on the species composition

Fig. 4 shows the DCA-analysis of the coverage of all species within the 180 plots. Coverage was marked with cover classes as a measure of the importance of the species in the plot. With ellipses, the roadside plot (A) and the two plots in the natural vegetation (B) and (C) are indicated. Roadside plots and natural vegetation had a significantly different vegetation (p-value of linear model <0.005 and non-overlapping ellipses in the DCA).

Fig. 5 shows other plot-specific factors and their correlation with either distance to the road or altitude (symbolizing the negative gradients in climate and anthropogenic pressure). Species diversity was slightly higher on higher elevations, but strongly correlated to distance to the road (Fig. 5a). Bare ground (Fig. 5b) and vegetation (Fig. 5d) showed an opposite trend, with more bare ground and less vegetation on higher elevations and in roadside plots. Moss cover (Fig. 5c) was much lower in roadside plots, where they covered less than 25 %, compared to 50 % in the natural vegetation. Moss cover did not seem to change with altitude.

TABLE 2. Species per cover class per plot. Comparison between the roadside plot (plot A) and the natural vegetation (plot C). Cover classes as a percentage of the total area, values show the mean of the amount of species within this cover class for each plot. P-values from a two-sample t-test.

Cover class	Plot A	Plot C	P-value	Significance
0–1 %	25.68	14.12	0.000	***
1–5 %	4.28	5.2	0.042	*
5–25 %	1.48	2.18	0.005	**
25–50 %	0.33	1.25	0.000	***
50–75 %	0.13	0.4	0.002	**
75–95 %	0	0.05	0.083	*

Dominant species were less omnipresent in roadside plots, which were put back in an earlier stage of succession. This shift in dominance is shown in Table 2, with fewer dominant species in the roadside plots than in the climax vegetation. Roadside plots contained on average 26 species with a coverage of less than 1 %, compared to 15 in the

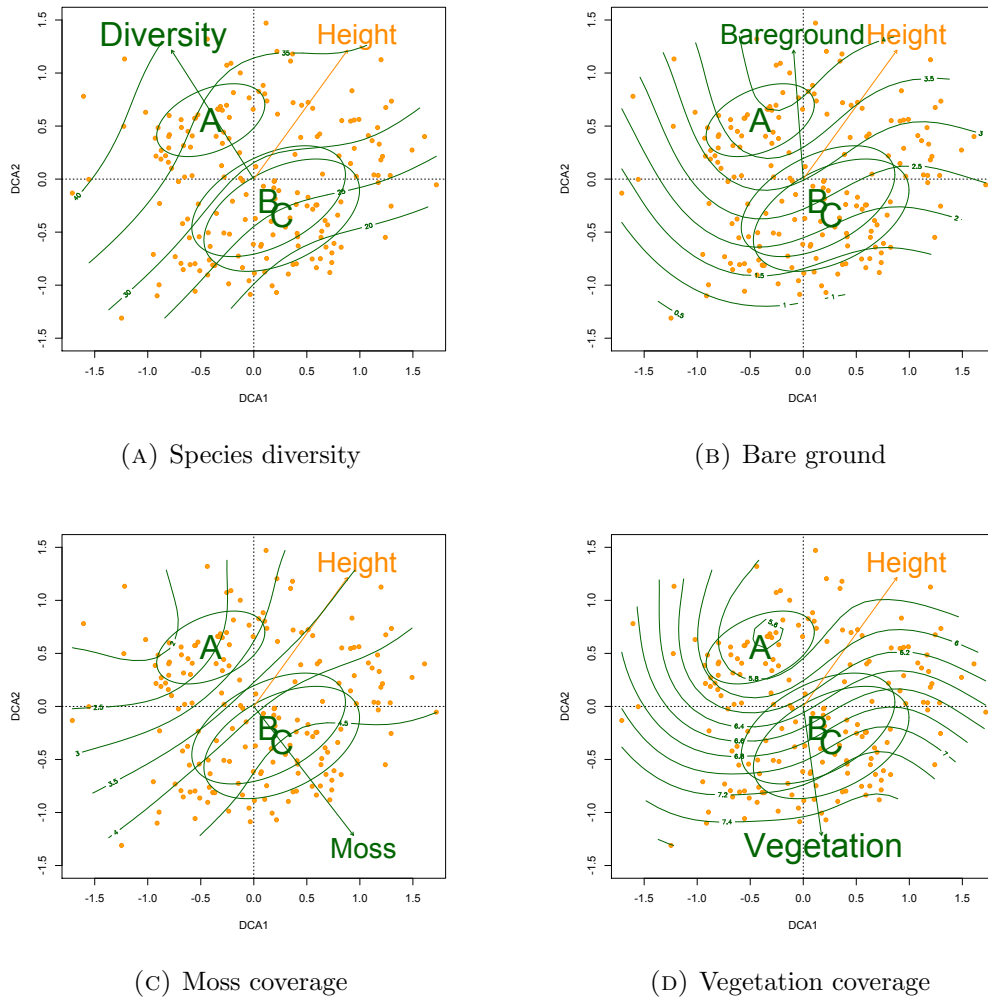


FIGURE 5. Factors correlating with the changes in community structure close to roads, as shown in Figure 4. The graphs show respectively species diversity (5a), the amount of bare ground in a plot (5b), the moss coverage (5c) and the vegetation coverage (5d). In each plot, the orange arrow shows the increasing elevation in the mountains. Contour lines and green arrows show the trends in the studied factor, ellipses the standard deviation for the plots.

natural vegetation. The amount of dominant species, with a coverage of 5 % or more, was however significantly higher in the natural vegetation for each cover class.

The species richness of the plot types apparently gradually went down from the roadside to the natural vegetation over the whole studied distance (Fig. 6a), with more than 30 species in the roadside plot, around 22 in the third plot and an intermediate

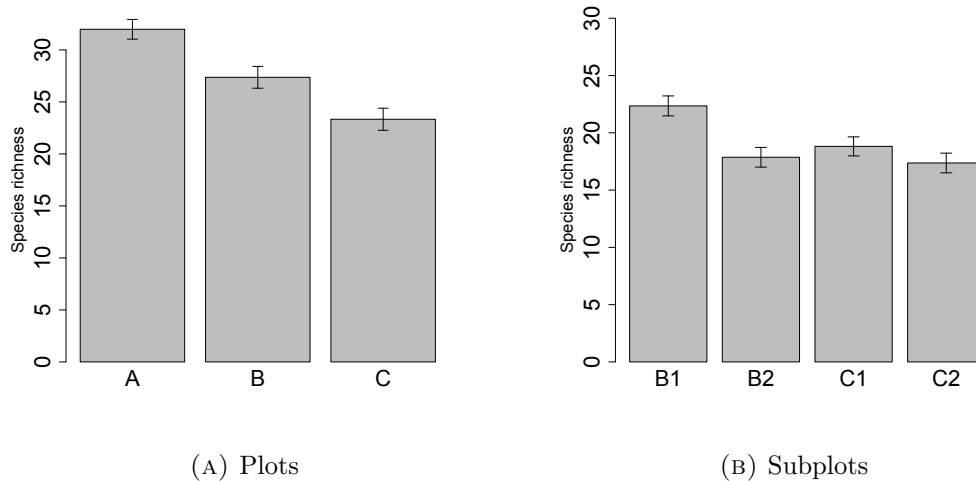


FIGURE 6. Species richness in plots and subplots along the roads. In Fig. 6A, the three main plots are shown, with A the roadside plot, B and C the plots in the natural vegetation, all differences tested with Anova and significant ($p < 0.000$). In Fig. 6B the subplots of plots B and C are shown. Diversity on the left = species/100m². B1 differs significantly from B2, C1 and C2 ($p=0.001$, 0.020 , 0.000 respectively), the other differences are not significant (Anova).

species richness in plot B. But the whole higher species richness in the second plot was due to B1 (Fig. 6b), which had a significantly higher richness than the 3 other subplots. B2 had a species richness level similar to the one in C (no significant differences noticed). As a conclusion, the changes in species richness due to the disturbance of the road is felt not further than 27 m from the road, probably even less, but our sampling design prevents us from narrowing the view even more. The species richness in this first subplot (B1) was not correlated with the width of the road verge (Anova, $p=0.414$, $F=0.676$), which means that the higher diversity exceeded at least the simple edges of the road verge, but reached not much further into the vegetation. Species richness in plots along the roads differed between the different elevations (Fig. 7). On the lowest elevations, roadside species richness differed significantly from species richness in natural vegetation. Between 200 and 400 m, species richness still differed between plot A and C, on the highest elevations, differences were not significant. The grouping of the plots on the 3 elevations is shown visually on (Fig. 8), with higher distances between ellipses indicating a higher difference in vegetation type.

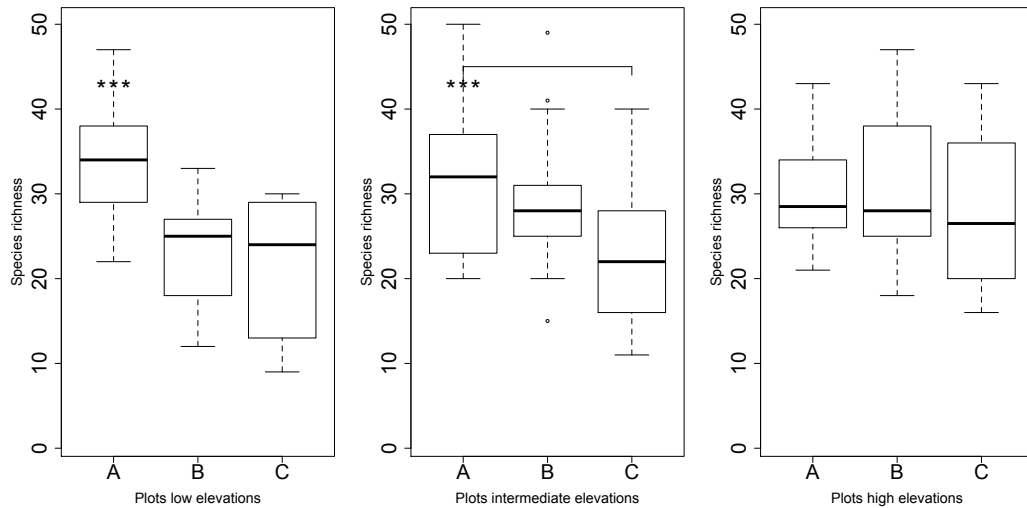


FIGURE 7. Species richness in plots along the roads, divided over lower, intermediate and higher elevations. X-axis: plot types as higher, Y-axis: species richness. Significance limited to left (A versus B and C: $p < 0.000$) and middle (A versus C: $p < 0.003$)

4.1.1. *Introduction of nonnatives*

Not only changes in the local species contributed to the changes in community structure along mountain roads. With the roads, nonnative species entered the ecosystem. Fig. 9 shows where the different nonnatives are situated in the DCA. A total of 14 nonnative species could be found. Almost all of them were situated in the left upper corner of Fig. 9, correlating with the direction of the roadside plots. The correlation between plot number and nonnatives was stronger than the one between nonnatives and altitude, because even on the lowest elevations, the diversity of nonnatives in the natural vegetation was almost zero.

The correlation between richness of nonnatives and plot type was highly significant. The results are shown in Fig. 10, with an average of ca. 3 species per roadside plot (plot A) and 0.5 or 0 nonnatives in plots B and C. The decline away from the roads was not linear, (Fig. 10G), with almost all nonnatives that escaped the roadside plot in the first part of the second plot (B1), occurrence of nonnatives more than 27 m from the roadside was very rare.

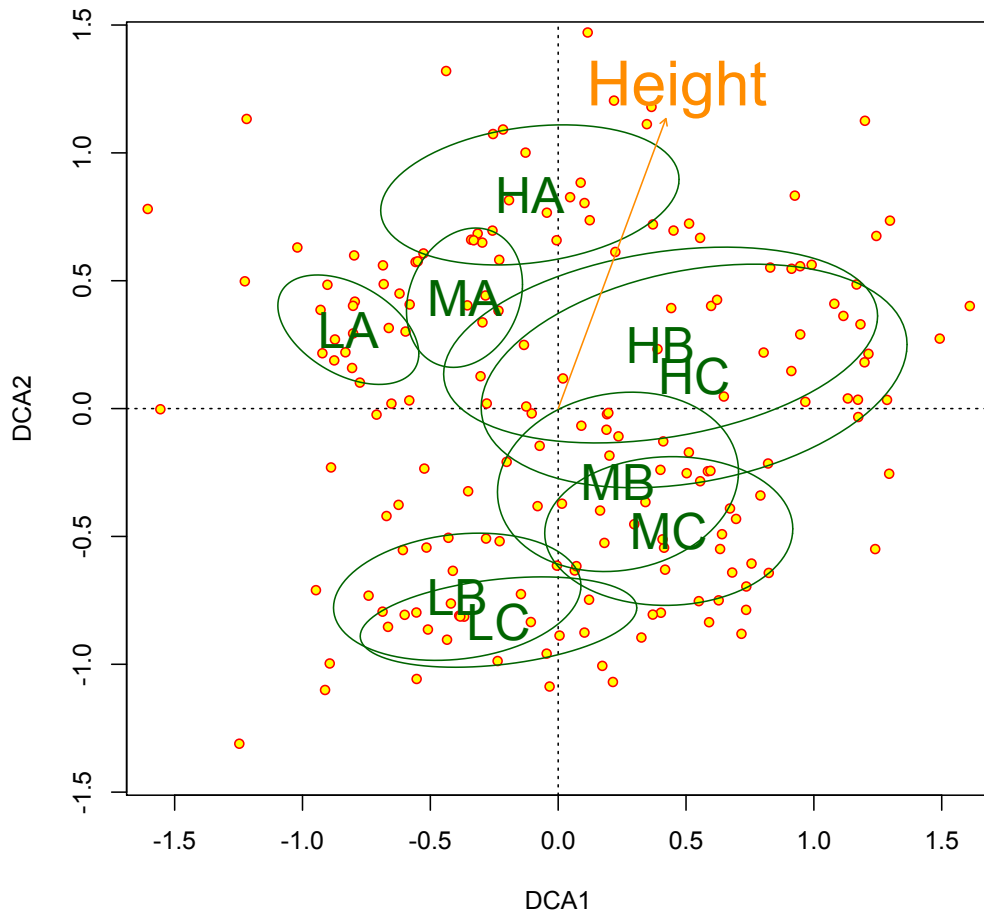


FIGURE 8. Species composition in plots along the roads, divided over lower (L), intermediate (M) and higher (H) elevations, on the representation of the DCA. A= roadside plot, B and C = natural vegetation

4.1.2. *Species-specific effects*

For each species, distribution over the elevational gradient and the different plots was studied. Fig. 11 gives six typical examples of the species-specific changes in realized niche on the mountain. A group of almost one third of the observed species only grew along the road and did not enter the native vegetation (Fig. 11A). A lot of the roadside species were typical weed species, with a large global distribution. Two other groups of species avoided the road, they lived on lower elevations (Fig. 11B) or higher elevations (Fig. 11C) and their distribution was negatively influenced by roads. Another group of species contained the generalists (Fig. 11D), plants that grew almost everywhere on the mountain, regardless of the elevation or the distance to the road. Fig. 11E

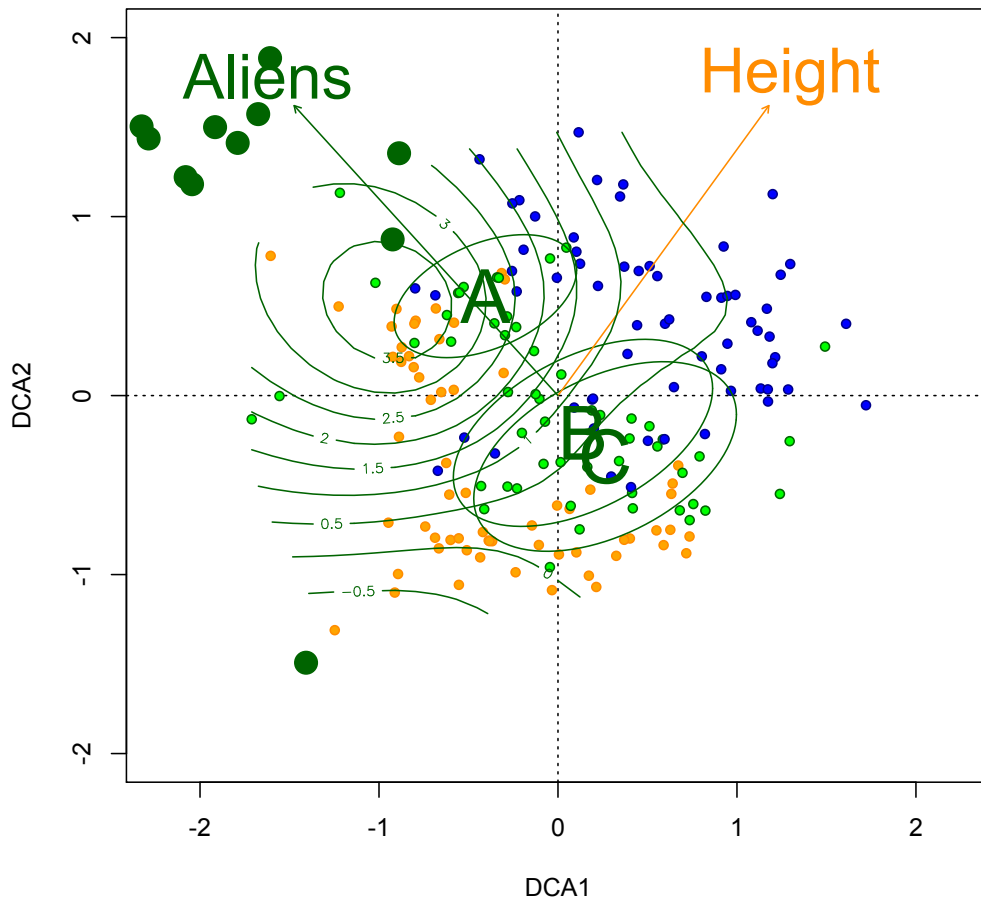


FIGURE 9. Graphical representation of nonnative species in the DCA of Fig. 4 . Small dots represent plots, green ovals and numbers represent plots at the roadside (1) and in the natural vegetation (2 and 3). Green isolines show changing diversity of nonnatives within plots, large green dots are nonnative species, long arrows show trends in nonnatives and altitude.

shows plant species from the natural, subarctic vegetation that expanded their realized niche to the lowlands in roadsides. These species had a much broader (and especially lower) realized niche on the climatic gradient in the roadside plots than in the natural vegetation. Only one species (Fig. 11F) from the natural, non-roadside vegetation was found that used the road in the other direction; to grow uphill.

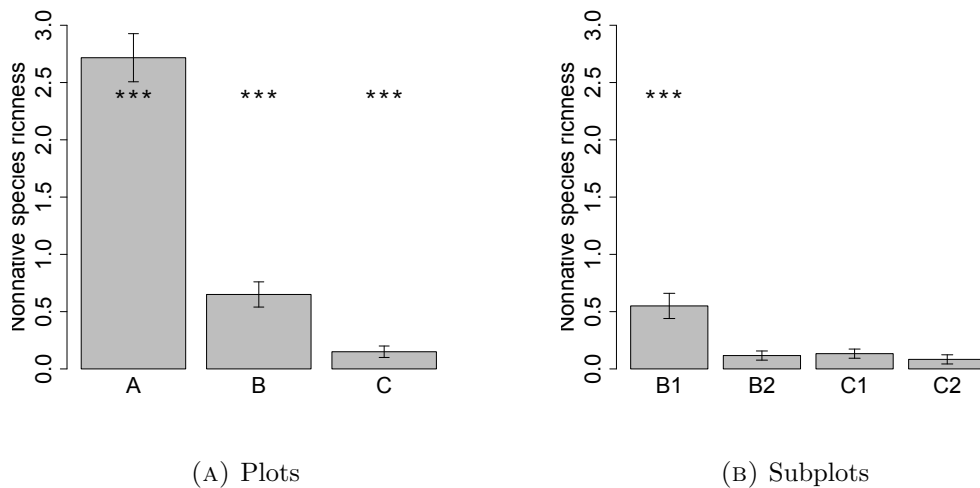


FIGURE 10. Species richness of nonnatives in plots and subplots, as average amount of nonnatives per plot. In Fig. 10a, the three main plots are shown, with A the roadside plot, B and C the plots in the natural vegetation. All differences significant ($p < 0.000$). In Fig. 10b, subplots of B and C, amount of nonnatives per subplot. B1 differs significantly from B2, C1 and C2 all p-values less than 0.000, other p-values more than 0.9.

4.2. Ecological behavior of nonnatives

4.2.1. *Nonnatives on the elevational gradient*

Trends in native and nonnative species richness were opposite over the climatic gradient in the mountain (Fig. 12). Native species richness increased from 38 species per plot with 2 species every 100 m to 50 species per plot on the highest elevations. Fig. 12B showed how the nonnative diversity went down over the mountainous gradient. In the lowland area, there were approximately 5 nonnative species per plot, with a loss of 0.5 species with an increase of 100 m altitude. All nonnatives were gone on a height of 700 m.a.s.l..

4.2.2. *Directional ecological filtering*

It is shown in Fig. 13 how the decline in nonnative species goes directional, with a progressive loss of species over the elevational gradient. Almost all species of nonnatives occurred on low elevations, but with increasing altitude, one after another, the

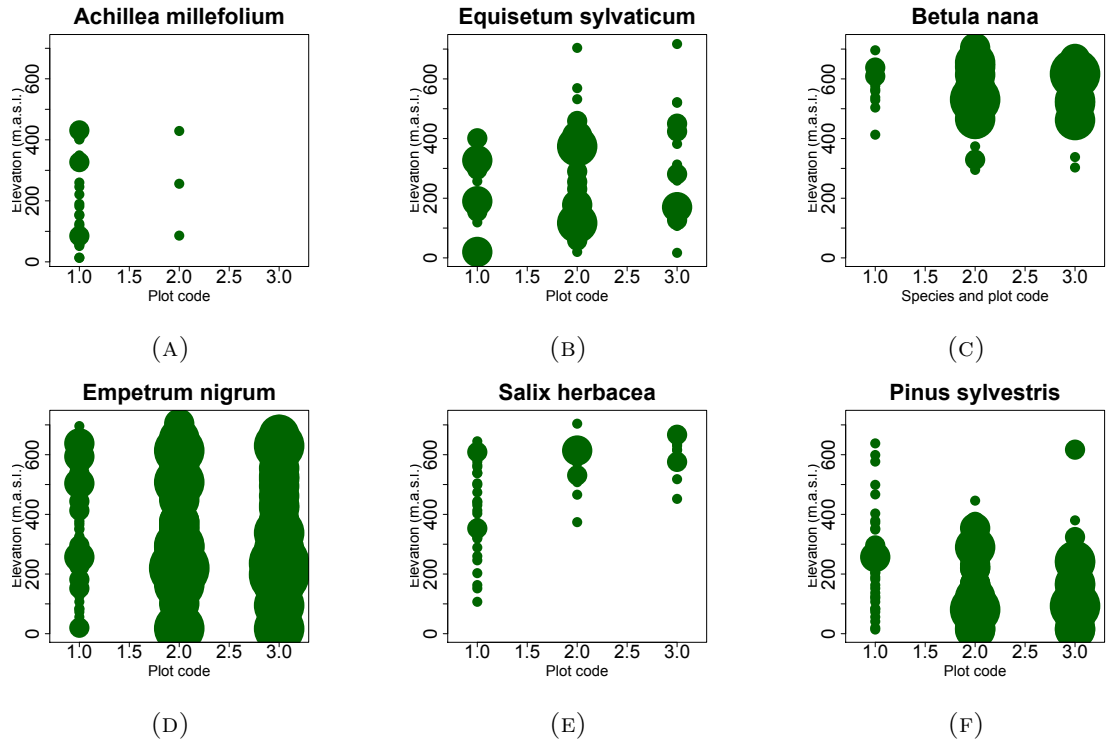


FIGURE 11. Typical examples of the interaction between roads and elevation and the different effect on species. *Achillea millefolium*, a typical roadside species, *Equisetum sylvaticum* lives concentrated in the lowlands, *Betula nana* will only be find higher up the mountains. *Empetrum nigrum* is a generalist, occurring everywhere on the mountain and as well close as far away from the road. *Calamagrostis lapponica* uses the road to broaden it's realized niche downwards from the mountain, *Pinus sylvestris* uses the road to migrate upwards. X: plot numbers, (1) = roadside plot, (2) = intermediate, (3) = natural vegetation. Y: elevation (m.a.s.l.). Size of the dots = cover class of the species.

species dropped out. This means that nonnative species that reached the top had the largest total range (which is shown in Fig. 13B). Only two species had a high maximum altitude but only a small total range, all other nonnative species accorded to the directional ecological filtering.

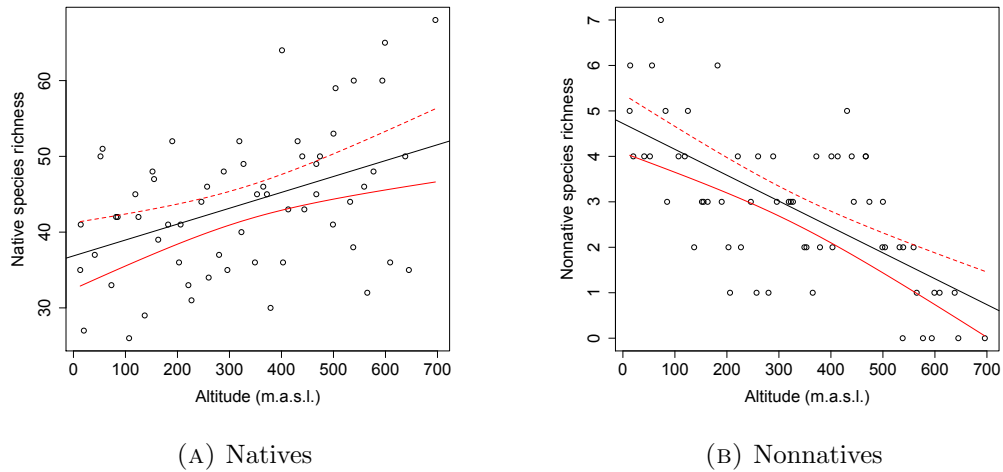


FIGURE 12. Diversity of natives (A) and nonnatives (B) as a function of elevation. Red lines show 95-percent confidence intervals for the linear model. ($P < 0.0001$ *** in both cases, for a regression coefficient of 2 natives per 100 m and -0.5 nonnatives per 100 m.

4.2.3. Factors explaining diversity

TABLE 3. Factors explaining diversity of natives and nonnatives. + = significant ($p < 0.5$) positive effect, +++ = strong ($P < 0.005$) significant positive effect, *** = strong significant effect without a clear direction, — = strong significant negative effect, . = no significant effect.

Factor	Natives	Nonnatives
Plot	.	—
Road	***	.
Elevation	+	—
Fresh water	+++	.
Moist	+++	.
Vegetation	+	.
Moss	—	—
Habitat	***	.
Canopy	.	—
Disturbance	.	.
Bareground	.	.

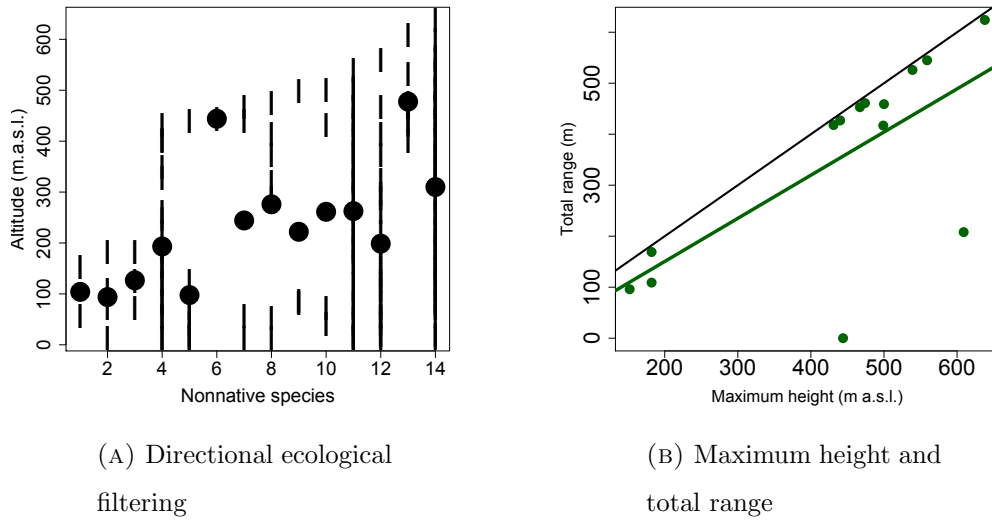


FIGURE 13. Directional ecological filtering in nonnative species. A: elevational range (lines) and mean elevation of occurrence (dots) of non-natives (numbers on the x-axis indicating different species). B: relationship between maximum elevation and total range for nonnative species. The black (highest) line indicates the maximum possible relationship, for a total range from sea-level to the maximum height, the green line underneath it gives the observed relationship.

Diversity of natives and nonnatives corresponded with different factors, as summarized in Table 3. Two linear models were created to check significance for all factors in the study, one for native diversity, the other for diversity of nonnatives. A distinction was made between the aforementioned factors (first part of the table; distance to road (plot), road (the 3 different roads in the mountains) and height (altitudinal gradient)) and plot-specific factors (second part of the table). Road had a significant effect on native diversity, which meant that the vegetation on the different gradients was clearly different. As expected, the occurrence of fresh water and moist soil strongly correlated with the diversity of natives. In the subarctic mountains, diversity is much higher in marshes and along creeks and rivers, probably because of a different phase in the succession. The amount of vegetation cover had a slightly positive effect too, with more species in more productive plots. The moss cover had a clearly significant negative effect on diversity of both natives and aliens. Habitat type proved to have a significant

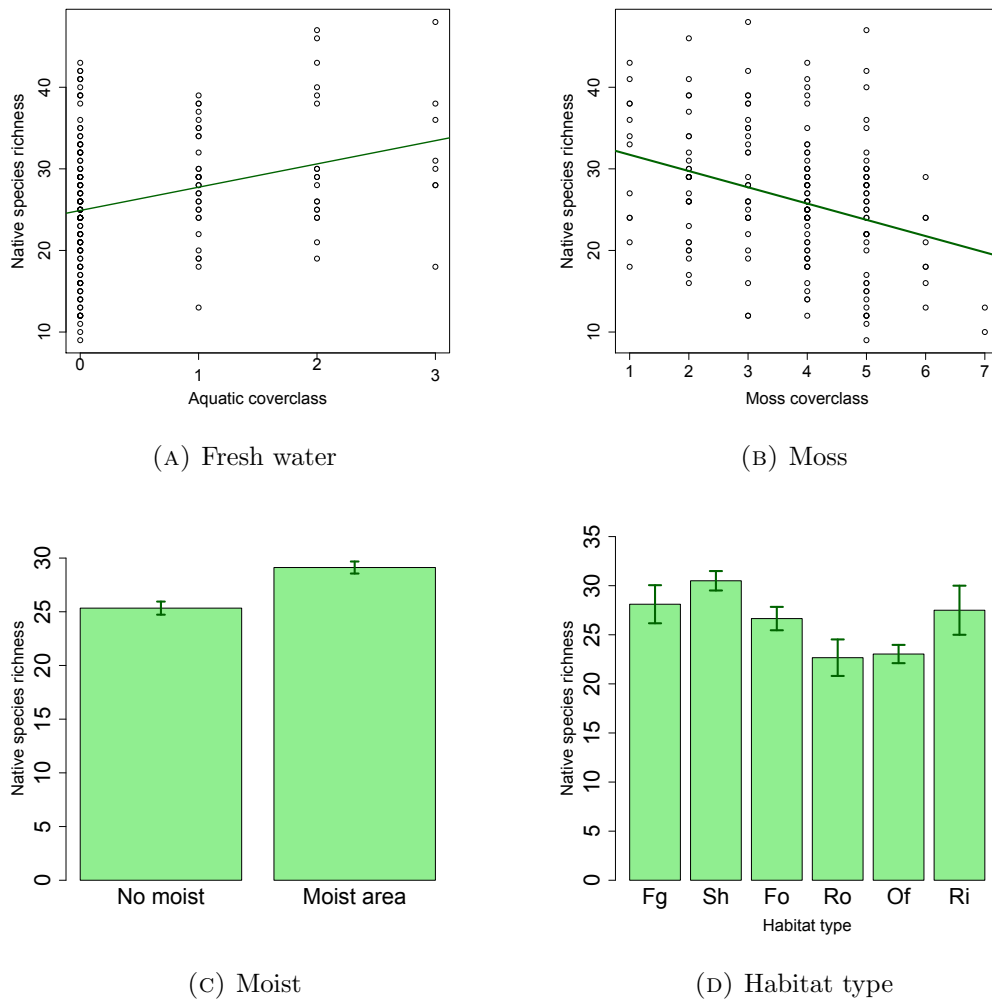


FIGURE 14. Factors correlating with native species diversity. Top left: fresh water cover classes, top right: moss cover classes (cover classes as explained in Materials and methods). Bottom left: presence or absence of moist areas, bottom right: habitat types (Fg = forb/grass, Sh = Shrubland, Fo = Forest, Ro = Rock/bare ground, Of = Open forest, Ri = Riparian.).

explanation for native diversity, but does not explain any additional variation in non-natives. Forest canopy negatively correlated with nonnative species richness, probably because roadsides are often much more open.

Fig. 14 shows the correlation between native species diversity and the most significant factors. Diversity increased with a larger coverage of fresh water in the plot (Fig. 14A). Although there was a lot of variation (especially in the dry plots, which could have a

high diversity too), the trend was unmistakable. The opposite trend for moss coverage (Fig. 14B) was even clearer. The occurrence of moisture (an indication of marshes in this region) resulted in on average an additional 5 species (Fig. 14C). The last graph (Fig. 14D) shows the mean species diversity in the different habitats. Shrublands, often willows occurring adjacent to creeks, contained the highest diversity, followed by riparian habitats (next to larger rivers), forb/grass-habitats and highly productive closed forests. The dry, open forests with an understory of dwarf shrubs and the bare rock habitats obviously had the lowest diversity. The same type of graphs for nonnative species richness are not relevant, because their diversity was much less influenced by plot-specific factors. They almost completely depended on distance to road verge and elevation, as explained earlier.

4.2.4. Herbivory

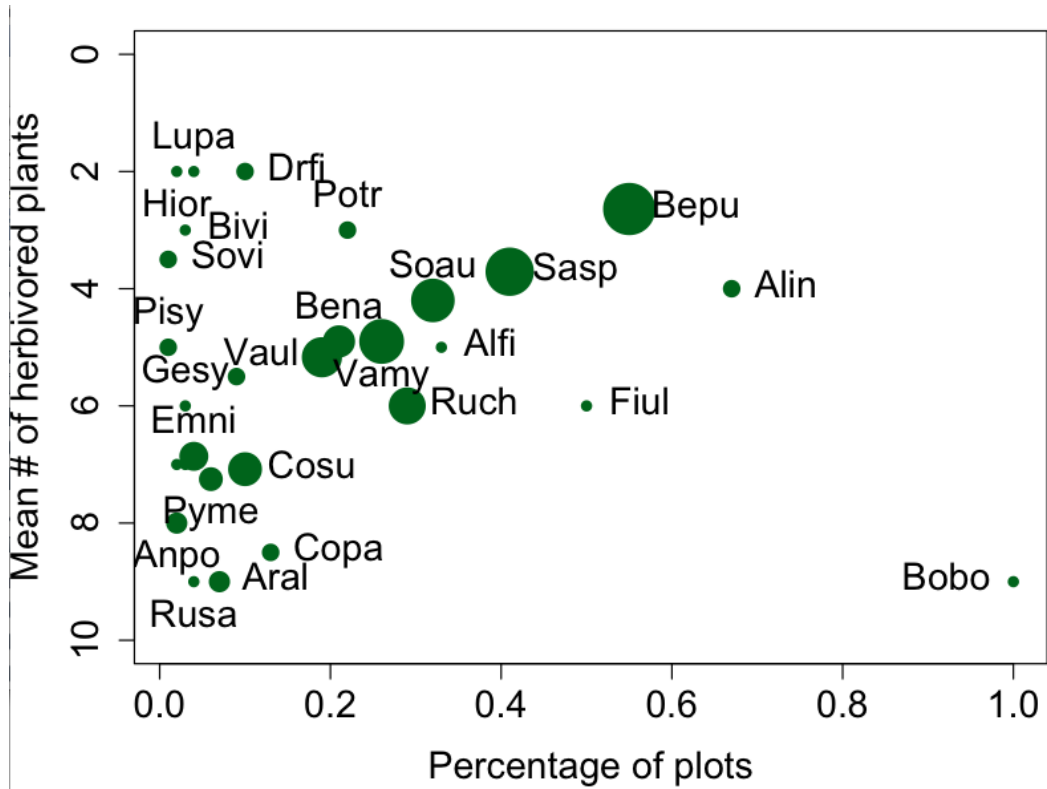


FIGURE 15. Species affected by *Epirrita autumnata*. x-axis shows the percentage of plots where the species occurs with herbivore damage. y-axis gives the mean amount of accompanying herbivored species, showing the preference of the caterpillar. The bigger the dot, the larger the absolute value of occurrence of damaged plants in a plot (with size of the dot = $\log(\text{absolute value})$).

The region under study experienced a plague of caterpillars of *Epirrita autumnata*, exactly at the time of observations (as observed by for example Tenow et al. (2004) and Heliasz et al. (2011)). This created the opportunity to make a thorough analysis of the effects of herbivory on nonnatives and natives. The resulting consumption of leaves could be spotted in 65 % of the plots. Caterpillar infection differed between the roads (with more infected plots on road RO), but this difference was not significant. The percentage of caterpillar infected roadside plots (52 %) however, was significantly lower than the percentage of infected plots in the natural vegetation (77 % plot 2, $P = 0.02$ *, 67 % plot 3, $P = 0.09$).

Fig. 15 shows the different species affected by herbivores. Species that occur more to the right of the graph were infected more often, relative to their occurrence. *Bothrychium borealis* (Bobo), for example, was infected in 100 percent of the plots it occurred in, but it only occurred in a very small amount of plots, which is why it has only a small dot.

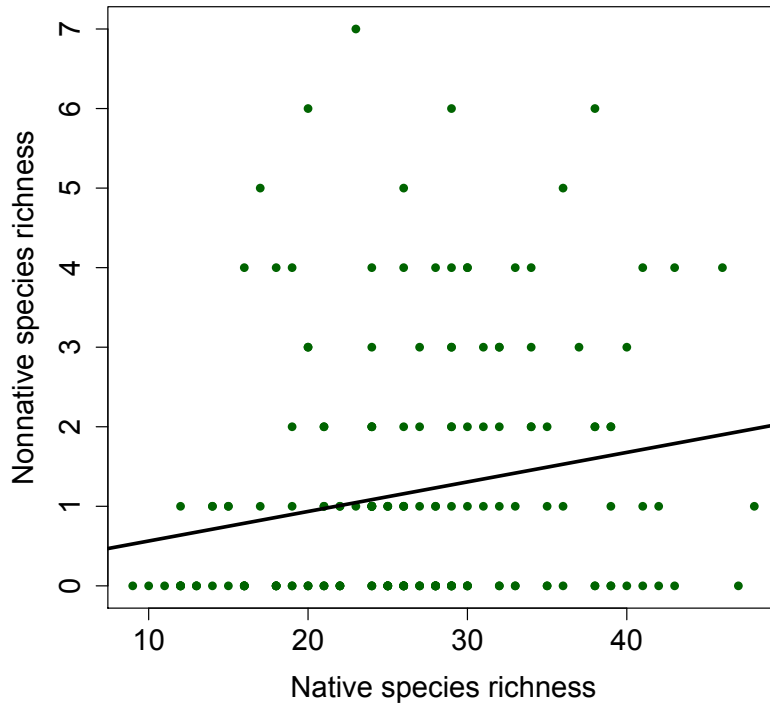


FIGURE 16. Correlation between native and nonnative species richness.
 $P=0.009$ **.

The larger the dots, the more plots (absolutely) with damage could be recorded. *Betula pubescens*, *Salix sp.*, *Sorbus aucuparia*, *Betula nana*, *Vaccinium uliginosum* and *Vaccinium myrtillus* were in absolute numbers damaged the most. To calculate the preference of the caterpillars, the mean amount of accompanying damaged plant species was calculated (y-axis). Species with a low value for this factor were found more often as the only damaged plants in a plot. The only species damaged in a plot is probably the preference species for the caterpillars. Species with a high score in all three dimensions could be expected to be the most important food source for the caterpillars. *Betula pubescens* came out of this analysis first, but *Salix*, *Sorbus aucuparia* and *Betula nana* were a clear second choice. Next in row were the *Vaccinium*-species and

Rubus chamaemorus. Consumption of all other species could be seen as 'collateral damage'. None of the determined nonnatives was eaten by the caterpillars, even not as collateral damage.

4.2.5. *Correlation between native and nonnative richness*

Native and nonnative species richness were positively correlated, with higher nonnative richness in plots with more native species ($P = 0.009$ **). The trend (Fig. 16) was however not clear and when only roadside plot diversity was used to compare with roadside diversity in nonnatives, no significant correlation was found.

4.3. **The danger of roadbuilding**

All information on roads, nonnatives and their danger is given in the first two sections. Analysis of the potential danger of roadbuilding will be explained later in the discussion section.

5. DISCUSSION

5.1. Influence of roads

The building of roads caused significant changes in the species composition on a small strip next to the road verge (Fig. 4). This distinct shift in species and abundance close to the road could be expected (Takahashi and Miyajima, 2010, LaPaix et al., 2012), because growing conditions were different in roadside plots. Vegetation cover was lower and more bare ground was exposed (Fig. 5B and 5D). The previous indicates a setback in succession through the physical disturbance caused by roadbuilding. Gaps were created and the dominance of dwarf shrubs was reduced, providing the opportunity for other species to establish. The decrease in dominance and increase in species with less coverage is shown in Table 2. The outcome was a vegetation with more and different species (Fig. 5 and 6B). A higher diversity along roadsides was encountered in other studies too (LaPaix et al., 2012). It can be explained with changing conditions in roadsides due to disturbance: more light, higher temperatures and changing chemical conditions (Zeng et al., 2011, Lee et al., 2012). An increase in biodiversity in subarctic roadsides corresponded with a loss of the typical species-poor vegetation that dominates in the undisturbed (dry) parts of the area. Such a habitat of open birch-forest with a dense cover of dwarf shrubs and mosses forms a typical example of a climax vegetation. It consists out of slow-growing species and changes almost nothing over the years. Due to disturbance, this climax vegetation was lost. The gaps created by the physical disturbance of the road created the opportunities for less dominant species to grow. Another indication for this is the loss of the moss cover (Fig. 5D). The importance of gaps through small disturbances is often shown in literature (for example Milbau et al. (2013)).

Although the effect on the species composition was unmistakable, it did not reach far in the vegetation. The difference between the plots from 2 to 52 (plot B) and 52 to 102 m (C) from the road was negligible, with only a slight shift from the first plot to the vegetation of the roadside plot (Fig. 4). The species richness in the three plot types was significantly different (Fig. 6a), with an intermediate richness in plot B. The results however indicate a large influence of species in the first few meters of the plot. When species richness was compared between the first and the second half of both plots B and C (Fig. 6b), only the first half of plot B had a significant higher diversity. The edge

effect was only visible on a short distance of 25 m, probably less. So that, the outcome was different than recorded in literature (LaPaix et al., 2012). Explanations for this can be found in the high resistance of the typical subarctic vegetation of *Empetrum*-heaths against changes (Pellissier et al., 2010, Milbau et al., 2013). Therefore, the impact of the building of roads occurred to be within the smallest range of recorded edge effects in literature (LaPaix et al., 2012). The subarctic mountain vegetation as a whole was quiet resistant against the disturbance by roads. The edge effect was even less important on the higher elevations than in the lowlands (Fig. 7 and 8). Species richness was significantly higher in roadside plots than in natural vegetation for the lower third of the transects and partly for the intermediate elevation. However, it stayed the same in the highest transects. Species composition also differed more between roadside plots and natural vegetation in the lowest two third of the transects, with a smaller difference on the higher elevations. Hence, the edge effect was much lower on higher elevations. This could be due to a higher resistance of the vegetation on these elevations or to a lower anthropogenic disturbance.

Nonnative species richness decreased faster with increasing distance to the road than overall species richness (Fig. 10 and 9). Species richness dropped immediately a few meters from the road. It was virtually zero 27 m away from the road. The natural vegetation seems resistant against the introduction of nonnatives, with only an occasional recording in plots B2 and C. The high vegetation densities in the natural vegetation could be one of the reasons (LaPaix et al., 2012) why invasion is limited. Resources are used more effectively in a denser vegetation (Pollnac et al., 2012). The resistance of the typical subarctic mountain vegetation, as explained above, can also prevent the introduction (Milbau et al., 2013).

Even though the natural vegetation is fairly resistant, the introduction of nonnatives along the roads is clearly a fact. This could be due to the provision of suitable habitat by altering conditions, the increase in invasion-probability through the increased stress on native species and the movement of seeds by anthropogenic vectors (Trombulak and Frissel, 2013). Moreover, most nonnative species are ruderals that are adapted for growing conditions in roadsides.

The movement of plant species along roads by anthropogenic vectors is not limited to nonnatives. The studied roads also showed a clear movement of native species up and

down the mountain, introducing them in areas outside their normal elevation range. Although a negative effect of road building on native species is expected (Trombulak and Frissel, 2013, Pollnac et al., 2012), this is not necessarily the case. A large group of ruderals, even natives, depend almost completely on roadsides. Without roadsides they would be very rare and only occur in disturbed plots (after avalanches, close to creeks etc.). Other species use the roadsides to expand their native range to higher elevations, as an example *Pinus sylvestris* was given. Its growing range along the roadside reached more than 200 m higher in the mountains. This species probably profits from the same factors that promote establishment of nonnatives along the road in the mountains: bare ground through disturbance, less coverage by dominant species and transport of seeds.

More surprisingly, plants native to the highest elevations are seen to expand their range to lower elevations along the road. This pattern is opposite to the normal patterns, where ruderals use the road to grow higher in the mountains. The results could be found in at least 20 different species (Fig. 11E). Explanations need to be searched in the set-back of succession. Most cold-adapted species from high elevations are outcompeted on lower elevations because of the better circumstances. Those support more competitive species. Building of roads sets back this succession and creates gaps. It even changes the abiotic circumstances in a way that can promote the growth of alpine species with a larger absolute niche than can be realized in normal last-stage-of-succession circumstances. Because roadsides are more exposed and growing conditions between the gravel are similar to conditions on higher elevations, alpine plants can colonize the gaps created by anthropogenic disturbance, in a similar way as ruderals from the lowlands. As long as disturbance stays large enough, both types of species can profit from the lower competition in roadsides to expand their growing range.

To summarize: roadbuilding in subarctic mountain regions drastically changes the species composition on a small scale. Species composition and species richness is much higher in roadsides on low and intermediate elevations. Because succession is put back to an earlier phase, resulting in expanding possibilities for native and nonnative ruderals to higher, and for Alpine species to lower elevations.

5.2. Ecological behavior of natives vs. nonnatives

A total of 14 non-native species could be found in the research. A global survey of alien flora in mountains (Mcdougall et al., 2011) reported between 64 and 272 alien species in comparable research (13 regions, all continents except Antarctica). The nonnative species richness in Northern Scandinavia is surprisingly low. The harsh conditions above the pole circle, the remote character of the region or the relatively recent construction of the roads may be the cause.

Native species richness increased with height, but an opposite negative trend was found for nonnatives (Fig. 12). Other researches reported a peak in native species diversity on mid-elevations, after which diversity went down again Alexander et al. (2011). The decrease in native species was not found here, probably because the elevational range (0-700 m.a.s.l.) was not high enough.

The steep decline in nonnative species can be explained by a process called directional ecological filtering Alexander et al. (2011)). Almost all nonnative species occurring on high elevations grew on low elevations too. Their first introduction in the area must hence be on the low elevations (where propagule pressure is relatively high), from where they dispersed into the mountains. The highest recordings of nonnatives were from good dispersers, occurring on the whole gradient from sea level to the top. Nonnatives that live high in mountains must always be generalists, able to start their invasion on the lowest elevations and spread over the whole gradient to the top. On the way to the top, nonnatives progressively drop out due to harsh abiotic conditions (Alexander et al., 2011). Native species richness shows a different trend. Species living in an area for a longer period of time have found their optimal niche in combination with competition with other species. Directional ecological filtering only occurs when an unidirectional propagule pressure (from abroad, entering the lowlands through anthropogenic influence) exists.

Distance to the road and height in the mountains were the main factors explaining variations in native species richness. Additional variation in native species richness occurred due to variations in the occurrence of fresh water, moisture (Table 3, Fig. 14) and different habitat types. Highest species richness was associated with marshes and riparian vegetation. There, the common species poor open forests are replaced by diverse vegetation. Gaps are created on the banks where the dominant species are

lacking, creating opportunities for less dominant species. Hence, the process is similar as for the diversity in road verges). The availability of water can also be seen as a positive effect. Although the western side of the Nordic mountains is known for its humid climate, water always easily runs off due to a lack of soil on the rocky surface and habitats limited by a shortage of water do exist. The strong negative correlation between moss cover and native and nonnative species diversity occurred due to the higher moss cover in the natural species-poor open forests. The occurrence of the moss limited the establishment of new seeds, limiting the recruitment of new species in these forests (Eckstein et al., 2011, Soudzilovskaia et al., 2011).

Nonnative species richness did not correlate strongly with other factors than roadside and elevation. There was a negative interaction with moss cover and forest canopy, but both factors are explained by distance to the road. Although a different invasibility could be expected in different habitats (Rose and Hermanutz, 2004, Pollnac et al., 2012, Milbau et al., 2013), there was no proof for it in the subarctics. A certain lack of proof corresponds with the previous observations that the system seemed to be highly resistant against invasion and that even the habitats or locations most likely to be invaded are still nonnative-free. Nonnative species richness was not significantly higher in roadside plots with higher native species richness, in contradiction to what is predicted in Levine and D'Antonio (1999) and Zeiter and Stampfli (2012). A possible reason could be the fact that trends in native and nonnative species richness are opposite, or because nonnative species richness in this ecosystem depends on other abiotic conditions than native species richness.

Nonnative species were not attacked by herbivores. Damage was done by a plague of one species of caterpillar, attacking 28 different species and 67 to 77 % of natural plots, with a large impact on the system (see Tenow et al. (2004) or Heliasz et al. (2011) for more information on the outbreaks. Roadside plots were less damaged (52 %), probably because of less forestation and vegetation cover. Caterpillars preferred trees and shrubs, switching to the typical dwarf shrubs of the open forest vegetation when density in trees was high (Fig. 15). Caterpillars consequently chose the most dominant species as main food source, only attacking less dominant species when density was high. The lack of damage to nonnatives could be a proof of the enemy-release hypothesis (Alba and Hufbauer, 2012) but is more likely explained by the low

density of nonnative species and the preference of nonnatives for roadside (and hence caterpillar-poor) plots.

5.3. The possible danger of roadbuilding and nonnatives

Road building has a large effect on natural systems (Forman (2000), Trombulak and Frissel (2013), LaPaix et al. (2012)). It disturbs the natural processes and interactions and dramatically increases uniform edge zones by fragmentation of the natural area. In Northern Scandinavia, roads and human disturbance are still relatively rare. But anthropogenic influences are creeping up the mountain and roads are cutting the previously undisturbed mountains ecosystem. For now, the ecosystem seems fairly resistant against these disturbances and damage stays small-scaled. It is true that the roads, moderately used gravel roads, completely alter the vegetation (Fig. 4), introduce new species (Fig. 10), shift dominance (Table 2) and change the natural distribution of other species (Fig. 11). But all these effects are limited to the few first meters next to the road verge and the lower parts of the mountains. Other research recorded how roads could be used as a stepping stone for nonnative species to invade the adjacent natural vegetation (for example Gelbard and Belnap (2003)), but here this invasion is limited to the first meters. But the threat for possible invasion is still here, so caution is needed and prevention of damage caused by invaders should be the main aim for conservation. Nonnatives do use the roads to expand their range in the mountains. If propagule pressure increases in a future with higher anthropogenic pressure on the region, higher invasion rates in the natural vegetation can be expected. After directional ecological filtering, there are still some species with a very broad environmental range that reach an altitude of 700 m.a.s.l. It is important to define the original cause of the directional ecological filtering. If abiotic conditions are too harsh, a grim scenario under climate change could be expected. With a warmer future climate, the filter will be weakened and nonnatives will be able to expand their range (Mcdougall et al., 2005). If not directional ecological filtering, but a temporal factor caused the trend in nonnatives, the expansion of the range is a matter of time. However, this hypothesis is unlikely (see Seipel et al. (2012)). The best answer is probably a combination of both, but in any way an increase in danger can be expected in the future. In a future with higher anthropogenic pressure in the mountains, high-altitude nonnative species could be introduced directly from other locations in the world and get round the limitations

caused by directional ecological filtering. If an immediate establishment on high elevations could result when the anthropogenic vector increases the propagule pressure on high altitudes, high-altitude nonnative species could become invasive. Because of their pre-adaptation, they could imply great danger.

The study design is useful for the global scale for which it is intended. However, the results it gave on the importance of the edge effect were not conclusive enough. The range is set somewhere between 2 and 27 meters from the road, but extra research is needed to create a smaller scope and define differences between habitats. Future research should use a larger elevational range. Although no higher elevation was needed for the questions on nonnatives, the effect from the road on the real Alpine vegetation should be studied too. (Takahashi and Miyajima (2010), for example, recorded no difference in roadside and natural vegetation anymore). The most important remark is that the definition of a nonnative species involves a scale which is arbitrary chosen. That complicates the comparison between natives and nonnatives, because it is a very wuzzy line. Species like *Salix herbacea* that use roads to expand their range to lower elevations are in fact nonnatives for these lower elevations, although they are nowhere recognized as such. It needs to be stated here that along with to the traditional nonnatives and their introduction along a road, we might often overlook major changes in native species richness along the road.

6. CONCLUSION

The unique ecosystem of Northern Scandinavia reacts different in a subtle way in comparison to other studied systems. This creates the opportunity to highlight the similarities (directional ecological filtering, edge effect, enemy-release) as global reoccurring principles. Differences with other ecosystems (the unusual high resistance of the mountain vegetation, the higher diversity in roadside plots, the unclear relationship between native and nonnative diversity) point out the need to treat every ecosystem as a unique system, with its own specific reaction to anthropogenic disturbance. It can be a warning that decisions concerning conservation should be specific for every local situation. Moreover, the new insight that alpine, natural species can profit from road building to expand their own growing range to lower elevations adds a new and highly interesting point of view to the study area. Future research on disturbances in mountains should take these positive effects on native species into account.

APPENDIX A. DEFINITION OF ENVIRONMENTAL DATA

A.1. Vegetation zones *Lowland* – A large land area with vegetation reflecting limits set by regional climate and soil/site conditions; an area where elevation is not the primary gradient affecting vegetation zonation.

Montane – The zone in mountainous regions where the influence of altitude (vertical relief) results in local climatic regimes that are sufficiently different from those in the adjacent lowlands as to cause a complex vertical climate-vegetation-soil zonation; includes vegetation at the base of a mountain when it is different from lowland vegetation.

Alpine – The zone on mountain tops between permanent snow and the cold limits of trees.

A.2. Habitat type (Definitions are based on the structure of the vegetation.)

Forb-grass – vegetation dominated by grasses and forbs.

Shrubland – vegetation often dominated by shrubs up to five meters tall.

Open forest – forest with an open canopy, where large gaps exist between trees.

Closed forest – forest where canopy cover is high and only a few small gaps exist the canopy.

Bare-rock – habitat dominated by bare ground or rock where the vegetation is sparse.

Riparian-wetland – riparian areas are contiguous to and affected by surface and sub-surface hydrologic features either perennial or intermittent

A.3. Disturbance type (The definitions are based on the major causes of disturbance.)

None – There is no visible sign of disturbance of any kind, vegetation is intact.

Human – Signs that humans have recently influenced the vegetation, these may include agriculture, forestry, mowing, digging, and construction.

Animal – grazing, trampling or disturbance caused by wild or domesticated animals.

Environmental – these include geomorphologic processes such as flooding, rock slides, erosion, fire.

A.4. Disturbance intensity. (The intensity to which the plot has been disturbed is based on disturbance type and the impact that the disturbance has on the plot.)

None – No visual impact to the vegetation or soil from a recent disturbance.

Some – Moderate amounts of disturbance to the vegetation and soil; the disturbance may have been severe but occurred more than 10 years ago and the plot is recovering.

A lot – Very recent disturbance that has altered a large proportion a plots soil properties and vegetation.

A.5. Species-specific data .

Abundance – 0 = absent; 1 = 1-10 individuals (or ramets); 2 = 11-100 individuals; 3 = >100 individuals.

Cover – 0= Absent ; 1= <1%, 2 = 1% – 5%, 3= 5% or more.

Herbivory – 0= none, 1= trace, 2 = >10% of plants, 4= 10–25% damage, 5= >25% damage

Herbivore type – i= invertebrate, v=vertebrate, b=both

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