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Research article

Roadside disturbance promotes plant communities with arbuscular mycorrhizal associations in mountain regions worldwide

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We assessed the impact of road disturbances on the dominant mycorrhizal types in ecosystems at the global level and how this mechanism can potentially lead to lasting plant community changes. We used a database of coordinated plant community surveys following mountain roads from 894 plots in 11 mountain regions across the globe in combination with an existing database of mycorrhizal–plant associations in order to approximate the relative abundance of mycorrhizal types in natural and disturbed environments. Our findings show that roadside disturbance promotes the cover of plants associated with arbuscular mycorrhizal (AM) fungi. This effect is especially strong in colder mountain environments and in mountain regions where plant communities

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are dominated by ectomycorrhizal (EcM) or ericoid-mycorrhizal (ErM) associations. Furthermore, non-native plant species, which we confirmed to be mostly AM plants, are more successful in environments dominated by AM associations. These biogeographical patterns suggest that changes in mycorrhizal types could be a crucial factor in the worldwide impact of anthropogenic disturbances on mountain ecosystems. Indeed, roadsides foster AM-dominated systems, where AM-fungi might aid AM-associated plant species while potentially reducing the biotic resistance against invasive non-native species, often also associated with AM networks. Restoration efforts in mountain ecosystems will have to contend with changes in the fundamental make-up of EcM- and ErM plant communities induced by roadside disturbance.

Keywords: anthropogenic disturbance, arbuscular mycorrhiza, drivers of plant distributions, mountain ecology, mountain roads, mycorrhizal fungi, plant invasions

Introduction

Mycorrhizal associations are found in the majority of terrestrial plants (Wang and Qiu 2006, Kivlin et al. 2011) and are increasingly seen as fundamental drivers of plant community composition and ecosystem functioning (Klironomos et al. 2011, Wagg et al. 2014, Neuenkamp et al. 2018). Different mycorrhizal types have in general different nutrient provision traits: arbuscular mycorrhizas (AM) are usually more important in the uptake of inorganic nutrients, thereby improving nutrient and carbon cycling (Phillips et al. 2013), whereas many ectomycorrhizas (EcM) and ericoid mycorrhizas (ErM) can directly free up nutrients locked up in organic matter (Read et al. 2004, Sulman et al. 2017). Therefore, different ecosystems are dominated by different mycorrhizal types. The dominance of a certain mycorrhizal strategy is determined not only by environmental conditions and present plant species, but also by mycorrhiza-mediated feedbacks that result in relatively 'stable states' of a particular dominant mycorrhizal types (Averill et al. 2022). The latter implies that even relatively minor disturbances could cause lasting changes in mycorrhizal communities if they would tip over into another stable state (Averill et al. 2022, Carteron et al. 2022).

Existing studies in natural (Gerz et al. 2019, Clavel et al. 2020) and agricultural settings (Schnoor et al. 2011, van der Heyde et al. 2017) show a range of responses of mycorrhizal communities to different types of anthropogenic disturbances. However, these studies remain limited to local scales, and all took place in Europe or North America, and thus generalizing their results remains challenging (Öpik et al. 2010, Soudzilovskaia et al. 2017). Here, we explore the impact of anthropogenic disturbances on the dominant mycorrhizal types of mountain plant communities, using a global database from the Mountain Invasion Research Network (MIREN, www.mountaininvasions.org) (Haider et al. 2022) linked to a database of mycorrhizal associations (Soudzilovskaia et al. 2020).

Plants were surveyed both close to and away from 62 mountain roads covering large elevation gradients, and distributed across 11 mountain ranges from the Arctic tundra to the tropics (Haider et al. 2022). Mountains are highly valuable ecosystems, being home to a disproportionately large share of global biodiversity (Rahbek et al. 2019) and providing crucial ecosystem services (Grêt-Regamey et al. 2021), that are under increasing pressures from anthropogenic disturbances, ranging from increased tourism to intensified mining (Kohler et al. 2010, Dainese et al. 2017). Mountain roads are ideal systems to study the impact of human-induced disturbances as they have a strong but locally limited effect on their surroundings (O'Farrell and Milton 2006, Müllerová et al. 2011, Pollnac et al. 2012) while covering large elevational, and consequently, large climatic gradients.

The plant cover data from MIREN was combined with the FungalRoots database (Soudzilovskaia et al. 2020) to estimate the proportions of plant cover associated with each mycorrhizal type in disturbed roadsides and in the adjacent undisturbed vegetation. The FungalRoots database is a trait database that allows assigning the dominant mycorrhizal type to a species. Such trait databases have shown important merit, as they allow combining trait-based observations from studies across the globe, relieving the need to measure traits for all species in all focal study systems. Especially for mycorrhizal types, such an approach has value, as most species are relatively conservative in their preferred mycorrhizal associations, and only a small minority (2%) associates with multiple mycorrhizal types (Soudzilovskaia et al. 2020). Thus, while assessments of mycorrhizal status here are not based on direct measurements of mycorrhizal associations within the system, dominant mycorrhizal types can be reported with sufficient confidence thanks to such measurements elsewhere.

Our expectation was that the disturbance caused by roads would cause a shift in types of mycorrhizal associations, represented in the plant communities, as road disturbance is known to alter community composition (Lembrechts et al. 2016, McDougall et al. 2018). As roads tend to favour ruderal species, commonly AM or non-mycorrhizal (NM) plants, to the detriment of more perennial and woody plants, more likely to be associated with EcM and ErM fungi, we expected road disturbance to correlate with increased AM and NM representation and decreased EcM and ErM. As a result, the impact of roadsides on mycorrhizal dominance would be larger if the native vegetation is EcM or ErM-dominated, rather than AM-dominated.

As non-native plant species are typically AM or NM (Pringle et al. 2009) and non-native species are favored by disturbance, we hypothesized that high non-native plant species cover would be found in plots and regions with native communities dominated by AM- or NM-associated species.

In turn, non-native species presence should be higher along roadsides.

More specifically, we tested the following hypotheses:

1) Road disturbance is associated with changes in the distribution of mycorrhizal types in mountain plant communities, including both native and non-native plant species, at the global scale.
2) The strength of the disturbance effect on mycorrhizal type distribution depends on local environmental conditions and on the dominant mycorrhizal type of the region's native community.
3) Non-native plant success is highest in AM- and NM-dominated communities and in plots affected by road disturbance.

Material and methods

MIREN dataset

Vegetation composition along mountain roads has been recorded by the MIREN network across 18 mountain regions on five continents (Haider et al. 2022). For the current study we focused on eleven mountain regions, as the remaining seven did not offer plant cover data both along the roadside and in the neighboring natural vegetation at the time of analyses. These regions cover environmental gradients with elevations ranging from 0 to 4000 m a.s.l. and mean annual soil temperatures ranging from −5.8 to 27.9°C. The studied mountain regions were: the Argentine Andes; the Caucasus Mountains in Armenia; the Australian Alps; the Chilean Andes; the Changbai Mountains in China; the Himalayas in India; the northern Scandes in Norway; Mount Teide in the Canary Islands (Spain); the European Alps in Switzerland; the Rocky Mountains in Montana (USA); the Blue Mountains in Oregon (USA). In each of these 11 regions, three roads which covered large elevational gradients, were accessible by the local research teams, were asphalted or covered by gravel, and were actively used by motorized traffic were selected. The surveyed road edges were typically highly disturbed, with shallow soils and often altered surface material due to the road construction, and reduced vegetation cover (Müllerová et al. 2011) (see the Supporting information for examples). The surveys were first executed between 2007 and 2018, depending on the region. Surveys are repeated every five years, resulting in currently one (two regions), two (five regions) or three (four regions) repeated surveys depending on the region. As the covered time period is too short to assess meaningful trends, these repeated surveys are treated as repetitions rather than as time series.

Vegetation monitoring

Twenty sample sites were set up along each road at approximately equal elevational steps following the MIREN protocol (cf. Haider et al. 2022 for the detailed version of the protocol). Each of these sample sites was then divided in three 2 × 50 m plots organized in a T-shape. The first plot was laid out parallel to the road, encompassing the vegetation directly impacted by the road-associated disturbance, and both the second and third plots were set up perpendicular to the road, respectively from 2 to 52 m and from 52 m to 102 m, covering the less disturbed vegetation communities adjacent to the road. Henceforth, we will refer to the first plot as 'roadside plots' and the two latter plots as 'adjacent plots'. In total, our dataset included 1489 plots spread out across 32 separate mountain roads and 11 regions. 786 of these plots were sampled twice, 535 of them three times, resulting in a total of 3345 plot-level surveys.

While anthropogenic disturbance was almost always higher in the roadside plot, some of the adjacent plots were also subject to anthropogenic disturbances, especially so at lower elevations. The presence and total cover of all vascular plant species present in each plot were visually estimated and classified using the following semi-continuous scale: 1 = < 1%; 2 = 1–5%; 3 = 5–25%; 4 = 25–50%; 5 = 50–75%; 6 = 75–95%; and 7 = 95–100% (Lembrechts et al. 2017). Plant species were also categorized as either native or non-native following local and regional floras, with species introduced in the country or mountain region after AD 1500 considered to be non-native (Haider et al. 2022). Additionally, average yearly soil temperature was extracted from the SoilTemp global maps of soil temperature at a 1 km resolution (Lembrechts et al. 2022). While mycorrhizal dominance might respond to other environmental parameters such as drought and nutrient availability, we decided to limit ourselves to temperature, as our main aim was to focus on the impact of road disturbance.

Mycorrhizal type

Using the FungalRoot database (Soudzilovskaia et al. 2020), plant species were grouped according to their mycorrhizal types: arbuscular mycorrhizal (AM); ericoid mycorrhizal (ErM); ecto-mycorrhizal (EcM); orchid mycorrhizal (OM); or non-mycorrhizal (NM). Scores of 0, 0.5 or 1 were attributed to each plant species for each mycorrhizal type, depending on whether they were recorded as either associating (1) or not (0) with a certain mycorrhizal type, or associating with two different types (0.5) (e.g. AM and NM; there were no species associated with more than two types). We included plant species which were referred to in the FungalRoot database as 'AM, others not addressed' and 'EcM, others not addressed' simply as 'AM' and 'EcM', respectively. Indeed, this statement means that they were confirmed to associate with the respective mycorrhizal type, but that uncertainty remained regarding their potential to form associations with more than one mycorrhizal type. The potential resulting error is minimal, however, as amongst all the species for which mycorrhizal types were assessed, only 0.3% were found to associate with more than one type of mycorrhizal fungi, indicating that such instances of multiple associations are negligibly rare.

We could extract mycorrhizal types at the plant species level for 65.0% of all observations, ranging from a minimum of 30.2% in Argentina to a maximum of 93.2% in Norway. For the remaining species the dominant mycorrhizal type at the genus level was used instead, resulting in 98.4% of all observations being assigned a mycorrhizal type, ranging from a minimum of 94.2% in Argentina to a maximum of 99.8% in India. This categorization by genus was done by Soudzilovskaia et al. (2020), who assigned a mycorrhizal type or NM status to a genus if more than 2/3 of the available observations in that genus converged.

We multiplied the cover percentage for each species in a plot by its score for each mycorrhizal type (0, 0.5 or 1). The resulting percentages of total vegetation cover were added up for each mycorrhizal type and then divided by the total vegetation cover of the plot obtained by adding up the cover values of all species present. This resulted in a percentage of total plot vegetation cover associated with each mycorrhizal type (for example, 65% of all vegetation in a plot is associated with AM fungi) which was then converted into proportions between 0 and 1 by dividing by 100. These proportions were then used as the response variable in further analysis. This value is henceforth referred to as 'mycorrhizal type cover'. It is worth noting that this value is a proportion of a plots' total vegetation cover and not of the plot total surface. OM mycorrhizal type cover was excluded from further analysis as it represented less than 0.1% of total cover so it is unlikely to be relevant when looking at changes in mycorrhizal type distribution.

Statistical analysis

We fitted generalized linear mixed-effects models (GLMMs) for each mycorrhizal type to test for the effects of road disturbance (hypothesis 1), temperature and elevation, and their interactions with road disturbance (hypothesis 2) on the respective mycorrhizal type covers. As the response variable (i.e., proportion of total plant cover associated with a mycorrhizal type) was a continuous variable constrained between zero and one, we modelled it using beta regressions with a logit-link (Zuur et al. 2009), using the glmmTMB package (Brooks et al. 2017) in R (www.r-project.org). For this, we first transformed the response variable to avoid extreme values of 0 and 1, as beta regressions only handle data between, but excluding, 0 and 1: (response variable value × (number of observations – 1) + 0.5) / number of observations (Cribari-Neto and Zeileis 2010). The explanatory variables used were: 1) distance to the road as a proxy for disturbance, as a three-level simple factor for each plot (0–2 m from the road, 2–52 m from the road and 52 to a 102 m from the road); 2) mean annual soil temperature; 3) elevation; as well as 4) the two-way interactions between them. The elevation values used were relative to each region's elevation gradient obtained by scaling elevation individually for each region using the *scale* function in base R (resulting in gradients between −1 and 1 for all regions, with the lowest elevation of each gradient being the point at which the plot with the lowest elevation of that region is located and hence where the elevation gradient starts, and not sea level. We chose this because we were interested in the elevational distance relative to the bottom of the gradient and not in the absolute elevation of a region, as the latter is not easily comparable. The initial model contained both elevation and temperature, as elevation can serve as a measure of non-climate driven and more local gradients: roads, acting as linear disturbances, add a 'connection' between elevation bands, which can result in propagule exchange (both for plants and mycorrhizae) between them, independent of climate, and also often have a gradient in disturbance intensity and usage along the elevation gradient. Temperature, on the other hand, incorporates the macroclimatic differences between regions as well as large-scale climate-driven trends within a region. However, after testing for multicollinearity using the VIF (variable inflation factor; assesses the degree of multicollinearity among predictor variables in regression models by measuring how much the variance of an estimated coefficient increases due to correlation with other predictors) through the VIF function in R (Fox and Weisberg 2018), elevation and temperature were found to be too strongly correlated (VIF value of 5.812 for elevation). We consequently omitted the effect of elevation from the final model. However, to make sure that temperature and elevation patterns did indeed behave similarly we also ran the model selection strategy in parallel with elevation instead of temperature. The random intercept term of sample site nested in road nested in region was added to consider the hierarchical nature of our design, as well as a random intercept term for year of observation to consider repeated surveys, and a random slope term for plots. Candidate models with all possible combinations of fixed effects were then derived from the complete model and compared using AICc (Akaike information criterion, corrected for small sample sizes). Only models with a ΔAICc of less than 2 units compared to the best candidate model were retained (Zuur et al. 2009). We calculated the conditional and marginal pseudo-R^2 using the 'performance' package. These values provide a proxy for the amount of variance explained by fixed effects only (marginal) or fixed effects in combination with the random structure (conditional), yet differ slightly from R^2-values traditionally calculated for linear models, occasionally even rendering values above one.

We then applied a variation partitioning approach to the selected models using the performance package in R to determine the proportion of variation in mycorrhizal type cover explained by disturbance, mean annual soil temperature and elevation (Lüdecke et al. 2021). This approach calculates the total variance explained by each explanatory variable, including its role in interaction terms.

To investigate the differences between regions, we used a partial pooling approach, a statistical technique used to estimate group-level and individual-level effects simultaneously (Harrison et al. 2018). This was done using models derived from the aforementioned beta regressions for each mycorrhizal types with the same explanatory variables that were retained after model selection, i.e. temperature and disturbance, but with additional random slope terms for both of these terms. The addition of these random effects allows for the intercept and slope associated with each region and each variable to deviate while still capturing the overall trends from the larger dataset. We then extracted the coefficients associated with each variable for every region, allowing for comparisons of trends between these regions and the global models.

A similar beta regression modeling approach was then used to investigate how the proportion of plants associated with the different mycorrhizal types correlated with the proportion of non-native plant cover (hypothesis 3). While before, mycorrhizal type was used as a response trait, now we treat it as an effect trait (sensu Suding et al. 2008), testing if the prevalence of a certain mycorrhizal type in the native community can explain non-native plant success. The models included native cover percentage of a certain mycorrhizal type and mean annual soil temperature as well as their interaction as explanatory variables, and either roadside plot or adjacent plot non-native plant cover percentage as a response variable in order to distinguish between non-native species simply benefitting from the road disturbance and more established non-native species present in the surrounding vegetation. As previously, a random intercept of road nested into region was included to account for the survey's hierarchical design. Model selection was then performed by comparing AICc values as described above. We ran separate tests for the percentage of total non-native plant cover in the roadside plots (0–2 m from the road) and in the neighboring vegetation in the furthest adjacent plots (52–102 m from the road). The 2–52 m plots were left out for this particular analysis, because we know from previous studies (McDougall et al. 2018, Clavel et al. 2020) that using the 2–52 m adjacent plot could be misleading for non-native species as it in some cases still included roadside vegetation when the roadside was more than 2 m wide. As the presence of non-native species is linked to changes in the local balance of mycorrhizal association types, we used the percentage cover of vegetation associated to each given mycorrhizal type amongst native species only as a predictor instead of the proportion of total vegetation cover.

Results

Global patterns in mycorrhizal types

Over the whole dataset, we observed 3456 plant species (from 125 species in Armenia to 856 in Switzerland), 97.1% of which could be assigned a mycorrhizal status (of which 41.5% at the genus/family level). AM plants accounted for 71.3% of all plant species with an assigned mycorrhizal association, EcM plants accounted for 7.0%, ErM for 4.2%, NM for 15.8% and orchid mycorrhizas (OM) for 0.1%. These numbers are similar to the proportions per mycorrhizal type found by Soudzilovskaia et al. (2020) across the entire FungalRoot database (AM: 70%, EcM: 8%, ErM: 2%, OM: 1%, NM: 17%). The distribution of mycorrhizal types amongst native species in our data was likewise broadly similar to that of the FungalRoot database (AM: 79.3%, EcM: 6%, ErM: 3%, OM: 0.6%, NM: 10.3%). We observed 452 non-native species (from one in Armenia to 150 in Australia). As expected, the majority of non-native species were found to associate with AM or to be non-mycorrhizal (AM: 85.6%, EcM: 0.3%, ErM: 0%, OM: 0%, NM: 14.1%). Mycorrhizal type distribution also varied with region (Fig. 1): AM plant species made up more than half of the total vegetation in almost all regions except for Norway, where ErM vegetation was dominant. In Argentina, Armenia, Chile and India there was no or almost no EcM and ErM vegetation, with all plants being either AM or NM.

Globally, our models showed that both EcM and ErM vegetation cover decreased with increasing mean annual soil temperatures, while AM and NM vegetation cover increased (Table 1). This effect of temperature on EcM and ErM vegetation remained mostly consistent across regions while there was a high variability of responses for AM and NM vegetation (Table 2). In all but one (EcM) case, at least one of the best models included temperature, distance to the road and their two-way interactions. Models had on average conditional pseudo-R^2 values of 0.54, with values ranging between 0.182 and 1.058, yet the difference with the marginal R^2 (between 0.004 and 0.044) indicated that accounting for the hierarchical structure of the data was critical for the observed patterns to emerge (Table 1). All the patterns we describe regarding soil temperature remained the same when using elevation instead as the environmental explanatory variable (Supporting information).

Impact of mountain roads on mycorrhizal types

At the global scale, the percentage of vegetation cover associated with AM fungi was higher on average in the roadside plots than in the adjacent plots (Table 1, Fig. 2). Conversely, the proportion of EcM and ErM vegetation cover was lower on average in the roadside plots. In general, the proportion of EcM and ErM vegetation cover behaved in an opposite manner to that of AM plant cover where increased levels of AM vegetation cover corresponded to decreased levels of EcM and ErM vegetation cover and vice versa. NM vegetation cover did not significantly differ between the two environments (Table 1).

The impact of disturbance along the climatic gradient

The aforementioned effect of disturbance on mycorrhizal type distribution was strongest in plots with low mean annual soil temperature, as shown in Fig. 2 and as indicated by a positive interaction between disturbance and temperature (Table 1). While the percentage of AM vegetation cover was on average higher in roadsides, this pattern tended to be reversed at the upper ranges of the regional temperature gradients where the percentage of AM vegetation cover in high temperature plots was lower in the roadside when compared to the adjacent vegetation, with NM vegetation instead being higher in these roadside plots. This interactive effect between temperature and disturbance was less clear at the inter-regional level: while

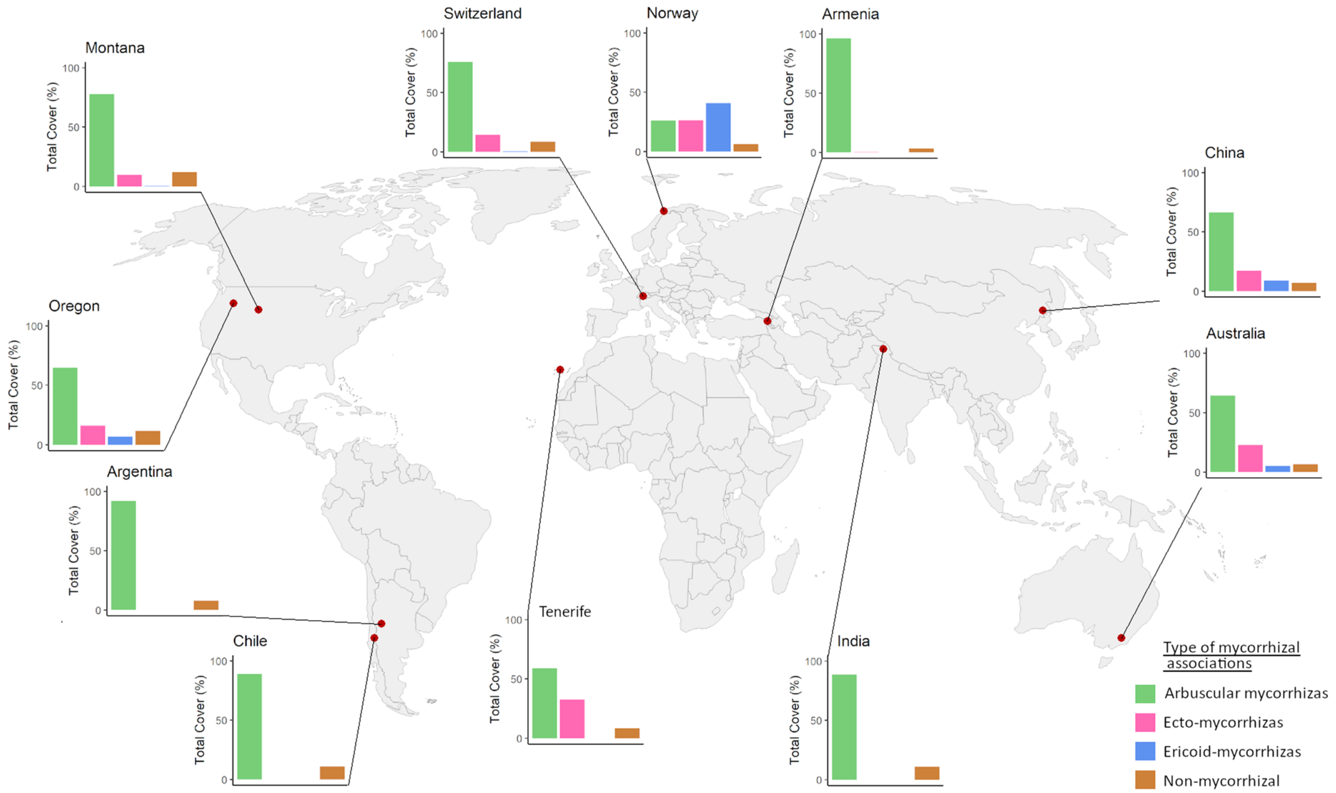

Figure 1. Map of mycorrhizal type associations in the 11 studied mountain regions. Percentage of total vegetation cover for plants associated with arbuscular mycorrhizas, ecto-mycorrhizas and ericoid-mycorrhizas, as well as non-mycorrhizal plants. For each region the total cover of plant species was recorded along multiple mountain roads as well as in the adjacent vegetation, plotted here are only the results from this adjacent vegetation independent of the road effect.

the effect of disturbance was mostly higher in cold regions compared to warmer regions, both Australia and especially Tenerife where outliers with comparatively high average temperatures as well as a strong effect of road disturbance on the proportion of mycorrhizal association types observed in the vegetation (Fig. 2, Table 3).

Overall, disturbance had larger and more consistent effects on the proportion of mycorrhizal association types than elevation or temperature, as shown using variation partitioning: we found that disturbance explained 9.8% of the total variation in AM vegetation cover and mean annual soil temperature 4.0%. For EcM, these numbers were 2.8% for disturbance and 2.2% for temperature, for ErM these were 21.6 against 7.9% respectively, and 1.0 against 0.6% for NM. Again, we found similar results when replacing mean annual soil temperature with elevation as the environmental explanatory variable: 8.9% for disturbance and 1.2% for elevation in AM vegetation and respectively 2.7 and 1.9% for EcM, 15.3 and 1.3% for ErM, 3.0 and 1.9% for NM. The direction of the temperature effect on the proportion of mycorrhizal association types also greatly varied across regions for all mycorrhizal types except ErM, while the disturbance effect was consistent in its direction across all regions for all four mycorrhizal types (Table 2).

Table 1. Selected models explaining percentage of vegetation cover associated with a certain mycorrhizal type: Coefficients and their p-values (between brackets) for each type of mycorrhizal association: arbuscular mycorrhizas (AM), ecto-mycorrhizas (EcM), ericoid mycorrhizas (ErM) and non-mycorrhizal (NM). Model selection was performed by selecting all models with a ΔAICc < 2 from the best model (i.e. Model 1). Explanatory variables were soil temperature (Temp), disturbance (Dist) as the three-level plot with 1: 52–102 m from the road, 2: 2–52 m from the road, and 3: 0–2 m from the road, and the interaction between temperature and disturbance. Blue and orange fields are respectively positive and negative correlations. Gray fields represent explanatory variables that were not retained in a given model.

Model		Intercept	Temp	Dist	Dist × Temp	Cond R^2	Marg R^2
AM	1	1.6177 ($p < 0.001$)	0.0132 ($p=0.178$)	0.3909 ($p=0.004$)	−0.0293 ($p < 0.001$)	1.058	0.044
EcM	1	−3.0698 ($p < 0.001$)	−0.0377 ($p < 0.001$)	−0.2520 ($p=0.010$)		0.679	0.022
ErM	1	−4.1528 ($p < 0.001$)	−0.0165 ($p=0.060$)	−0.2671 ($p=0.003$)	0.0111 ($p=0.098$)	0.241	0.038
	2	−4.1141 ($p < 0.001$)	−0.0378 ($p < 0.001$)			0.182	0.004
NM	1	−2.3977 ($p < 0.001$)	0.0079 ($p=0.412$)	−0.0022 ($p=0.978$)	0.0156 ($p=0.025$)	0.490	0.011
	2	−2.3341 ($p < 0.001$)		0.1103 ($p=0.130$)		0.487	0.008
	3	−2.2948 ($p < 0.001$)	−0.0051 ($p=0.498$)	0.1104 ($p=0.126$)		0.485	0.008

Table 2. Partial pooling results showing variation of mycorrhizal type cover responses across regions: Region-specific coefficients for each type of mycorrhizal association: arbuscular mycorrhizas (AM), ecto-mycorrhizas (EcM), ericoid mycorrhizas (ErM) and non-mycorrhizal (NM) across all regions where a given mycorrhizal type was present. Explanatory variables were mean annual soil temperature (Temp), disturbance (Dist) as the three-level plot with 1: 52–102 m from the road, 2: 2–52 m from the road, and 3: 0–2 m from the road and the interaction between disturbance and temperature. Blue and orange fields are respectively positive and negative correlations. Gray fields are factors that were not included in a given model following the results of model selection (Supporting information). Region abbreviations are as follows: ARC for Argentina, ARM for Armenia, AUN for Australia, CHE for Switzerland, CLC for Chile, CNN for China, TEN for Tenerife, IND for India, MTN for Montana, NOR for Norway and ORE for Oregon.

Region	Intercept	Temp	Dist	Temp × Dist
AM				
ARC	1.78	−0.01	0.00	0.03
ARM	2.28	0.00	0.25	0.01
AUN	2.11	−0.06	0.58	0.01
CHE	1.19	0.04	0.28	0.01
CLC	2.46	−0.19	0.10	0.12
CNN	1.05	0.06	0.52	0.01
TEN	0.09	0.04	1.16	0.04
IND	1.86	−0.03	0.13	0.03
MTN	2.40	−0.03	0.62	0.04
NOR	-0.15	0.06	0.47	−0.06
ORE	−0.54	0.23	0.39	0.04
EcM				
AUN	−3.54	0.16	−0.45	
CHE	−2.25	−0.05	−0.17	
CNN	−1.74	0.06	−0.10	
TEN	0.32	−0.13	−0.62	
MTN	−2.84	−0.03	−0.35	
NOR	−0.94	0.00	−0.05	
ORE	−0.57	−0.17	−0.14	
ErM				
AUN	−3.01	−0.03	−0.36	−0.02
CHE	−3.01	−0.03	−0.32	−0.03
CNN	−3.08	−0.05	−0.18	−0.05
NOR	−1.33	−0.10	−0.50	0.06
ORE	−1.89	−0.11	−0.20	−0.01
NM				
ARC	−2.00	0.00	0.16	−0.02
ARM	−2.02	−0.12	0.26	−0.01
AUN	−1.87	−0.12	−0.26	−0.02
CHE	−1.73	−0.06	0.02	−0.01
CLC	−3.89	0.52	−0.78	−0.15
CNN	−2.26	−0.08	0.25	0.00
TEN	−1.24	−0.19	0.39	0.01
IND	−2.07	0.05	−0.14	−0.03
MTN	−2.85	0.02	−0.45	−0.04
NOR	−2.02	−0.06	0.19	−0.02
ORE	−0.90	−0.21	0.07	0.00

Influence of regionally dominant mycorrhizal type

In spite of the wide variation in ecosystems, all eight regions where EcM and ErM associations occurred (all except India, Argentina and Chile) showed the pattern of increased AM vegetation cover and decreased EcM and ErM vegetation cover in roadside plots (Table 2). Importantly, however, the difference in proportion of mycorrhizal-type associations between the vegetation of the roadside plots and that of the adjacent plots was larger in plots (and regions) where AM plant species had a lower representation in the native natural vegetation (Fig. 3). In general, the lower the percentage cover of AM-dominated species in the natural vegetation, the higher the increase in AM-dominated species in the roadside plot (Fig. 1, as indicated by a flatter line above the 1:1 in Fig. 3). This effect mirrored the pattern we described for soil temperature, in plots for which the natural vegetation was in the upper range of AM vegetation cover we did observe a reversal of the general pattern: AM vegetation cover was lower in the roadside when compared to the adjacent vegetation with the vegetation being more NM instead (Fig. 3, regression line crossing the 1:1-line).

Non-native species

The proportion of mycorrhizal association types amongst the native vegetation was significantly correlated with the proportion of non-native species in the total vegetation cover, both in the roadside plots (Fig. 4, Table 3) and in the adjacent plots (Supporting information, Table 3). Coincident with the AM or NM status of almost all non-native species, we observed that higher proportions of AM and NM native plant cover correlated with a higher proportion of non-native cover both in the roadside plots (Fig. 4) and in the adjacent plots (Supporting information). The opposite pattern was true for EcM and ErM vegetation cover. Elevation was as expected also strongly correlated with non-native plant cover, with higher elevation plots being on average less colonized by non-native plant species. Finally, we observed weak (yet non-significant) support for an interaction between mycorrhizal type cover and temperature, with for example a stronger correlation between AM native plant cover and non-native cover in warmer plots, i.e. at lower elevations (Table 3).

Discussion

On average, roadsides harbored an increased share of AM plant species in the total vegetation cover and a decreased share of EcM and ErM vegetation (Fig. 2). This mostly followed our initial expectations as road conditions and management are known to be detrimental to the more perennial and often tall and/or woody vegetations types that commonly associate with EcM and ErM fungi, with these fungi themselves also being on average much more long-living than AM fungi (Verbruggen et al. 2017). More ruderal and opportunist plant species on the other hand are most often AM and tend to be more successful in these environments (Smith and Read 2010, Müllerová et al. 2011). These differences were especially true in colder environments, i.e. at high elevations and high latitudes, but were less pronounced or even reversed at the upper end of the temperature gradient where roadside vegetation showed lower AM vegetation cover than in

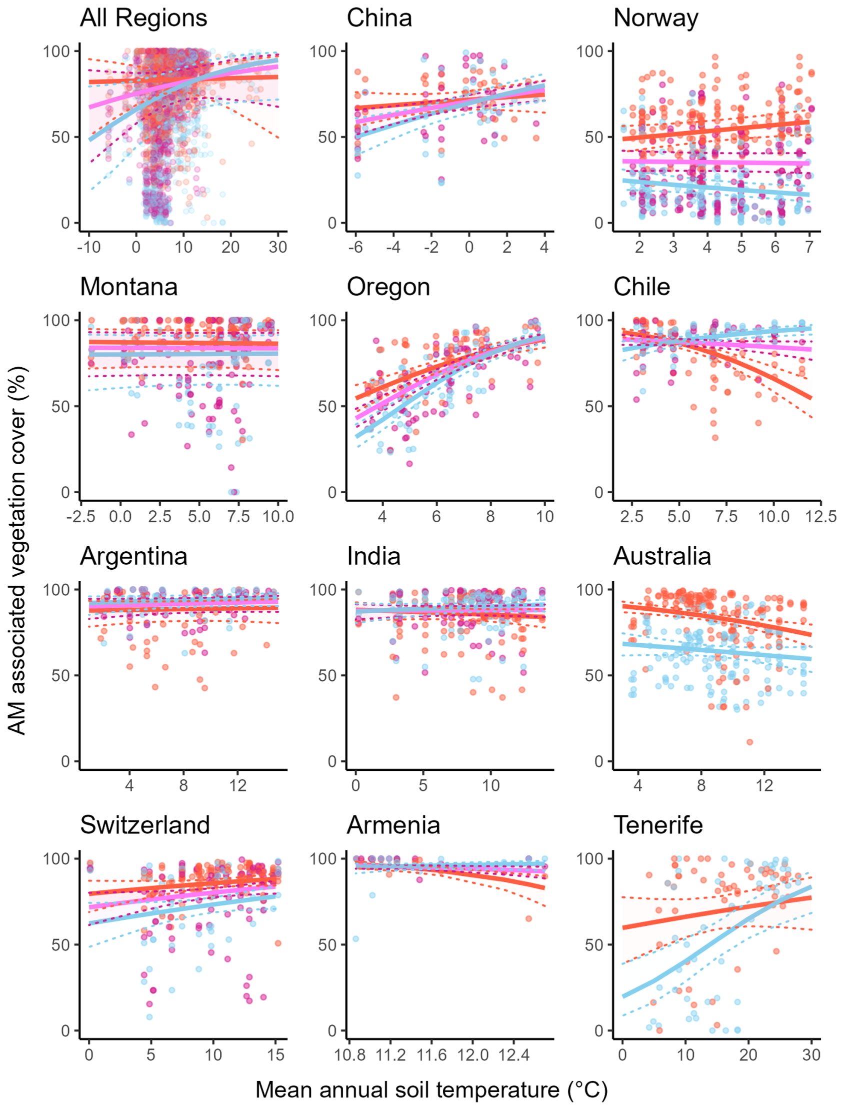

Figure 2. Effect of road disturbance on the proportion of total vegetation cover associated with arbuscular mycorrhizal (AM) fungi across regions and along temperature gradients. AM vegetation cover was measured along roadsides from 0 to 2 m (red) and in the adjacent vegetation both from 2 to 52 m away from the road (purple) and from 52 to 102 m (blue). Mean annual soil temperature was extracted from global maps of soil temperature at a 1 km resolution. The regions are plotted in order from lowest to highest average yearly soil temperature and confidence intervals are represented by the dotted lines. Trendlines come from a partial pooling approach on a linear mixed model.

the adjacent vegetation. The latter could be explained by the fact that disturbances also tend to promote NM plant species (Lambers and Teste 2013), albeit less strongly so than AM plant species (Table 2).

However, despite these intra-regional fluctuations, we did observe that for almost all regions the effect of disturbance on the regional scale followed the global trend of increased AM vegetation along roadsides coupled with decreased ErM and EcM vegetation (when present; Table 2). Only Argentina was an exception as we found no correlation between road disturbance and changes in mycorrhizal type, which was not the case in other regions where the vegetation was entirely or almost entirely AM associated or NM (yet in Argentina around 70% of mycorrhizal types had to be approximated at the plant genus level, making conclusions from this region potentially less trustworthy). These findings suggest that the impact of mountain road disturbance on mycorrhizal type distribution follows a systematic pattern that can be influenced, but is mostly not overruled by, local factors. As we observed in a recent study in the northern Scandes (Clavel et al. 2020), this change in AM vegetation cover is likely also reflected in the prevalence of the AM fungi themselves, as disturbance in these cold-climate mountains strongly promoted both the colonization of roots by arbuscular mycorrhizas as well as overall AM fungal diversity, at least partially due to the tendency of Scandinavian roadsides to have significantly less acidic soils.

While largely constant in its direction, the strength of the roadside disturbance effect on mycorrhizal types varied between regions (Table 2, Fig. 2–3) as it was lowest, but still

Table 3. Selected models explaining percentage of non-native plant species cover amongst roadside (a) and adjacent (b) vegetation for the different mycorrhizal types: coefficients and their p-values (between brackets) for each type of mycorrhizal associations: arbuscular mycorrhizas (AM), ecto-mycorrhizas (EcM), ericoid mycorrhizas (ErM) and non-mycorrhizal (NM). Model selection was performed by selecting all models with a ΔAICc < 2 from the best model (i.e. model 1) (in each case, there were two such models). Explanatory variables were mean annual soil temperature ('Temp'), the percentage cover of native vegetation associated to each given mycorrhizal type ('% cover') and the interaction between these two factors. Blue and orange fields are respectively positive and negative correlations. Gray fields represent explanatory variables that were not retained in a given model.

Model		Intercept	% Cover	Temp	% Cover × Temp
(a) Roadside non-native plant species					
AM	1	−3.29 ($p < 0.001$)	0.60 ($p=0.003$)	0.06 ($p < 0.001$)	
	2	−3.09 ($p < 0.001$)	0.34 ($p=0.279$)	0.03 ($p=0.212$)	0.03 ($p=0.305$)
EcM	1	−2.82 ($p < 0.001$)	−0.39 ($p=0.364$)	0.07 ($p < 0.001$)	−0.02 ($p=0.609$)
	2	−2.81 ($p < 0.001$)	−0.57 ($p=0.010$)	0.07 ($p < 0.001$)	
ErM	1	−2.87 ($p < 0.001$)	−0.54 ($p=0.050$)	0.07 ($p < 0.001$)	
	2	−2.90 ($p < 0.001$)	−0.04 ($p=0.920$)	0.07 ($p < 0.001$)	−0.12 ($p=0.139$)
NM	1	−2.99 ($p < 0.001$)	0.65 ($p=0.098$)	0.06 ($p < 0.001$)	
	2	−3.02 ($p < 0.001$)	1.09 ($p=0.160$)	0.08 ($p < 0.001$)	−0.06 ($p=0.517$)
(b) Adjacent vegetation non-native plant species					
AM	1	−3.10 ($p < 0.001$)	0.34 ($p=0.279$)	0.03 ($p=0.212$)	0.03 ($p=0.305$)
	2	−3.29 ($p < 0.001$)	0.60 ($p=0.003$)	0.06 ($p < 0.001$)	
EcM	1	−2.81 ($p < 0.001$)	−0.58 ($p=0.014$)	0.06 ($p < 0.001$)	
	2	−2.83 ($p < 0.001$)	−0.39 ($p=0.364$)	0.07 ($p < 0.001$)	−0.02 ($p=0.609$)
ErM	1	−2.91 ($p < 0.001$)	−0.04 ($p=0.920$)	0.07 ($p < 0.001$)	−0.12 ($p=0.139$)
	2	−2.87 ($p < 0.001$)	−0.54 ($p=0.050$)	0.07 ($p < 0.001$)	
NM	1	−2.98 ($p < 0.001$)	0.65 ($p=0.098$)	0.07 ($p < 0.001$)	
	2	−3.03 ($p < 0.001$)	1.08 ($p=0.160$)	0.08 ($p < 0.001$)	−0.06 ($p=0.517$)

present, in regions already dominated by AM and NM plants, and in warmer regions. This was most obvious in the three regions where EcM and ErM vegetation was entirely absent (Argentina, Chile and India) as could be expected since there is less margin for increases in AM vegetation cover when they already dominate the regional vegetation. Conversely, the regions with large proportions of EcM- and ErM vegetation cover, such as Norway or Tenerife, exhibited the largest differences in mycorrhizal associations between the vegetation of the roadside and of the adjacent plots (Fig. 3). In a similar fashion the effect of road disturbance on mycorrhizal type distribution was on average strongest in plots with lower average soil temperature, which is to be expected as EcM and ErM plant species are more common in colder conditions (Brundrett and Tedersoo 2018). The physical removal of these EcM and ErM plants, their associated mycorrhizal networks, and the competitive advantage that would otherwise keep their stable state (Averill et al. 2022), now creates opportunities for an increase in AM plant species. However, this pattern was less clear at a regional level with examples of warmer regions such as Tenerife and colder regions such as China not following the global pattern (Fig. 2). Despite these region-specific patterns, disturbance was overall the strongest predictor of mycorrhizal proportion, greater than the effects of elevation and temperature, and this for all mycorrhizal types. This prominence of disturbance as explanatory variable for community-level patterns is at the global level in line with other findings from previous regional studies showing that local anthropogenic disturbance predicts plant species composition better than macro-environmental drivers (Lembrechts et al. 2016, Fuentes-lillo et al. 2021). The distribution patterns of the different mycorrhizal types that we observed across our sites was overall consistent with those previously reported in the scientific literature across climate and elevation gradients (Soudzilovskaia et al. 2017, Barcelo et al. 2019).

The aforementioned relationship between disturbance and the different mycorrhizal types seems to suggest that ErM and EcM plant species are more sensitive to the effects of road disturbance when compared to AM plant species, thus resulting in increased success for AM plant species along roadsides in environments where they would usually be competing (for nutrients, light and other necessary resources) with an established EcM and ErM plant and fungal community (Segre et al. 2016). This would also help explain the discrepancies between our results of increased AM vegetation cover in disturbed roadside conditions and the results of previous studies on disturbance in agricultural settings, where physical disturbances in the form of tillage led to reduced colonization by AM fungi in largely AM-dominated systems (Schnoor et al. 2011, van der Heyde et al. 2017). This disparity would then be explained by the effect of altered biotic interactions outweighing the negative effects of physical disturbance in a setting that is not already entirely AM-dominated. Indeed, in our system, disturbance has a disproportionately high impact on the native EcM and ErM plants, as such creating opportunities for (ruderal) AM plants that would otherwise have a hard time colonizing a fully established native vegetation (Averill et al. 2022). Supporting this hypothesis is the fact that the proportion of AM vegetation cover in the roadside plots tended to be comparatively lower when the proportions of AM vegetation cover in the adjacent vegetation was high. This pattern also aligned with the relationship between soil temperature and road disturbance, i.e. the

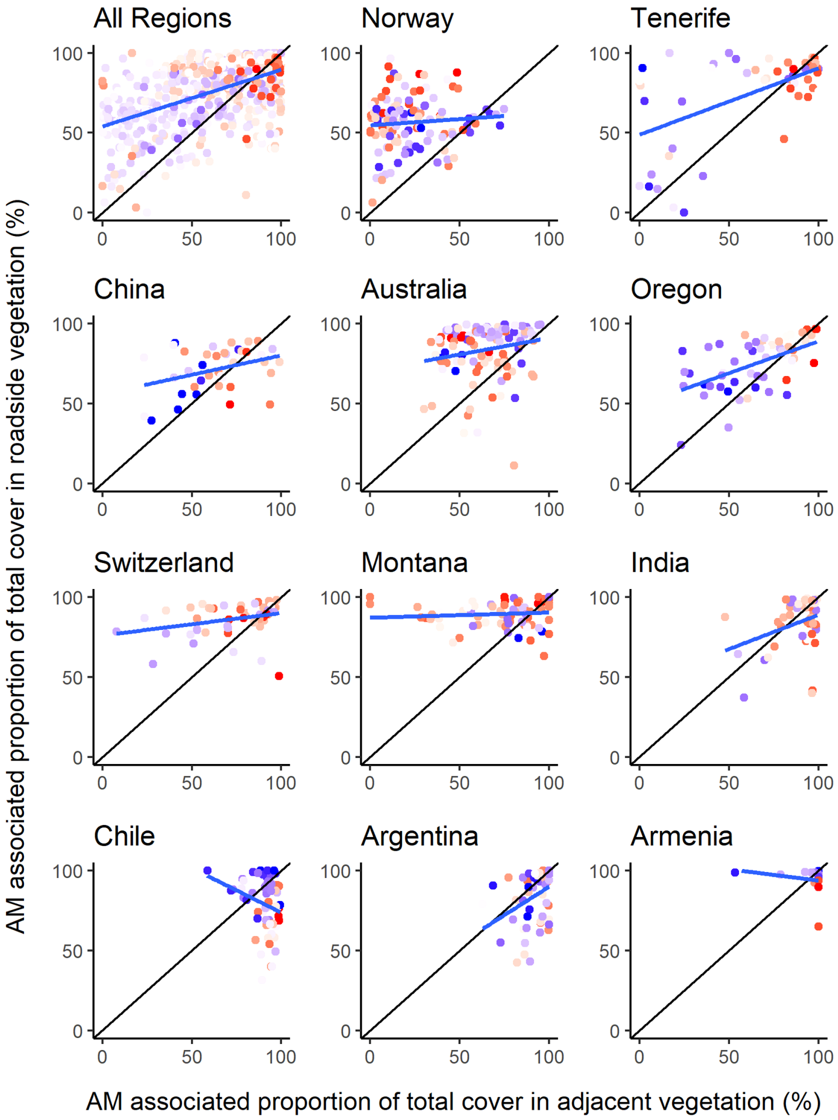

Figure 3. Pairwise comparison of arbuscular mycorrhizal (AM) proportions of total vegetation cover between disturbed (roadside plot) and undisturbed (adjacent plot) vegetation. For each region, every individual sample site along the studied mountain roads was plotted as the intersection between the percentage of AM vegetation cover in 2 × 50 m plots parallel to the road (0–2 m from the road) and in 2 × 50 m plots of adjacent vegetation perpendicular to the roadside (52–102 m from the road). Points above the identity line correspond to sample sites in which the AM proportion of the total vegetation cover was higher along the roadside compared to the proportion in the adjacent vegetation. The blue regression line was plotted using the results of linear models, highlighting that the relationships between AM vegetation cover proportion in the disturbed and undisturbed vegetation are different from what would be expected if disturbance had no effect (i.e. relative to the 1/1-line). Regions are ordered from lowest total proportion of AM vegetation cover (Norway) to highest (Armenia) and points are colored from low temperatures (blue) to high temperatures (red) scaled within region.

fact that the difference between mycorrhizal proportions in the roadside and in the adjacent plots grew smaller following the regional temperature gradients, and higher following the regional elevational gradients. In both cases, when reaching the warmer limits of the temperature gradients and at the highest saturation of AM natural vegetation, the effect of disturbance tended towards reversing, with lower proportions of AM vegetation cover along roadsides than in the adjacent vegetation (Fig. 2, roadside plot line in red crossing over the adjacent vegetation line in green; Fig. 3, points below the 1/1-line, blue line falling below 1/1-line). These congruent patterns are to be expected as EcM and ErM vegetation tends to be most common in cooler conditions and at higher elevations (Smith and Read 2010, Barcelo et al. 2019, Bueno et al. 2021). Understanding these interactions and the general patterns that result from them is a crucial first step in disentangling the nexus between disturbance and changes in mycorrhizal type distribution.

While we cannot come to a definitive conclusion as to the mechanisms driving the aforementioned increase in AM plants to the detriment of EcM and ErM plants due to the strictly observational nature of our study, a possible hypothesis would

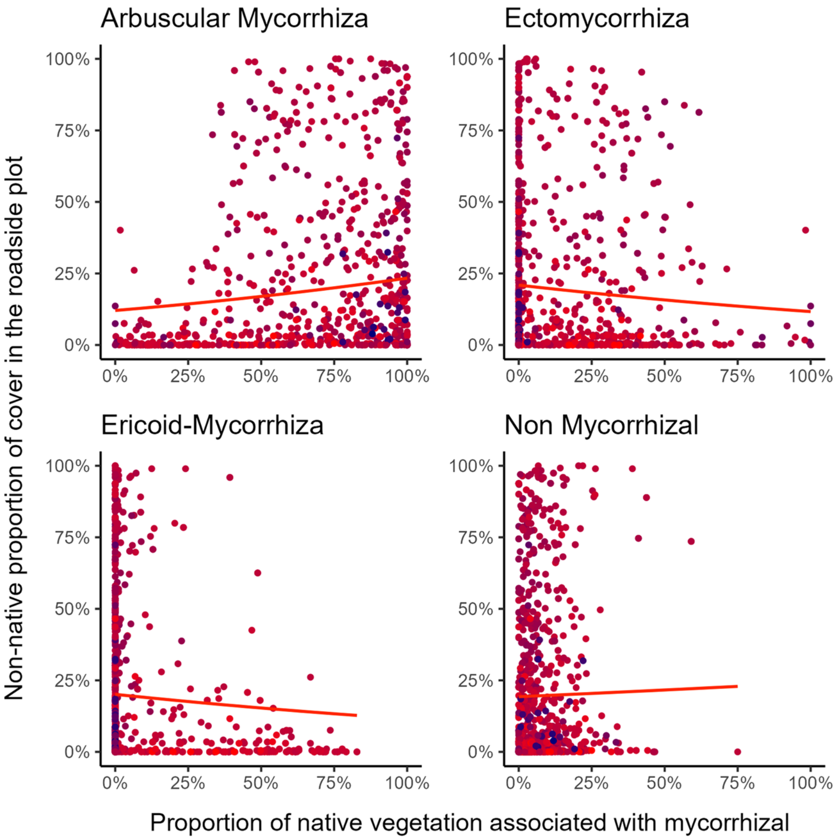

Figure 4. Correlation between native mycorrhizal associations and cover of non-native species. For each mycorrhizal-type association, the proportion of the vegetation cover in roadside plots (0–2 m from the road) which was of non-native origin was plotted against the proportion of the native vegetation in plots perpendicular and away from to the road (52–102 m from the road) which was associated with each mycorrhizal type. Each dot represents an individual pair of plots. Regression lines were plotted using the results of generalized linear models (Table 3) and individual dots were colored according to elevation from low elevation (blue) to high elevation (red).

be that roadside disturbance leads to increased soil nutrient mineralization (Müllerová et al. 2011) and/or reduced soil acidity (Ratier Backes et al. 2021) which AM-fungi are more apt at taking advantage of (Read et al. 2004, Sulman et al. 2017). Indeed, it is no coincidence that most ruderal plant species are associated with AM-fungi, with their relatively rapid colonization strategies, generalist nature, lower level of specialization for specific soil conditions, and preference for dynamic, disturbed habitats compared to most EcM and ErM fungi, leading ecto- or ericoid mycorrhizal associations to be less advantageous. The fact that these ruderal AM plant species (as well as NM species) are generally faster growing and more disturbance tolerant due to their ability to take advantage of vegetation gaps (García de León et al. 2016), thus could begin to explain the patterns we observed: increased nutrient availability, less extreme pH, more dynamic conditions and reduced competition in roadsides all act in favor of AM plant species.

Importantly, we also observed a clear difference in mycorrhizal association type between native and non-native plants species: almost all non-native plant species were NM or AM, with 0.2% of EcM non-native plant species being the exception. This matches the results of previous studies in the US that found non-native plant species to be mainly AM or NM (Pringle et al. 2009). Although as we saw earlier that EcM/ErM dominated vegetation showed a greater increase in AM plant abundance upon disturbance, increases in non-native vegetation were more pronounced in AM-dominated communities. Additionally, non-native species had greater potential for establishing in the native community when that native community was already dominated by AM-associated native plant species (Fig. 4, Supporting information). This suggests that plant communities that predominantly associate with the same mycorrhizal fungi as the non-native plant species are also more susceptible to potential invasions by these non-native plant species (Yang et al. 2013), either directly through interactions between mycorrhizal fungi, or indirectly through the selection for other associated plant traits, such as ruderality. The importance of anthropogenic disturbances in facilitating the success of non-native plant species outside of their natural range is well documented (Jauni et al. 2015, Lembrechts et al. 2016). However, the multiple possible mechanisms that link these disturbances to increased non-native success remain far from resolved. We suggest that anthropogenic disturbances being favorable to the most common types of mycorrhizal association amongst non-native species could partly help explain the pattern of increased non-native species success in roadside-adjacent environments, especially in communities already dominated by AM or NM-associated species. In these cases, indeed, disturbances as occurring in roadsides might alter native communities through their impacts on soil conditions (Müllerová et al. 2011, Ratier Backes et al. 2021), and as such shift them towards AM-dominated communities, while simultaneously increasing the propagule pressure of non-native species that associate with AM-fungi as well.

However, it remains important to keep the limitations of our study in mind when considering potential mechanisms that drive changes in plant species composition and non-native success. Indeed, due to the observational nature of our study, it is hard to be conclusive about which factors are driving and which are following the observed ecosystem changes. Moreover, our observations remain based on a proxy of mycorrhizal abundance shown previously to have limitations (Brundrett and Tedersoo 2019): aggregated datasets such as FungalRoot are bound to accumulate small errors and imprecisions and should be used with caution when looking at distribution patterns. This is partly why we limited our analyses to broad categories of mycorrhizal associations. Nevertheless, using large collections of datasets remains valuable as long as direct mycorrhizal measurements are not sufficiently available. Additionally, we have limited our assessment to temperature as the only one macro-ecological driver, while many other environmental gradients, such as drought, nutrients and pH will also play a role. Our results should thus be seen as a first investigation of global relationships between anthropogenic disturbances, mycorrhizal distribution and their potential impacts on non-native plant invasions, and the resulting observations as potential openings for further studies investigating how human activities can impact mycorrhizal communities and plant–fungal interactions.

Conclusion

Our results show a global pattern of anthropogenic disturbance influencing the distribution of plant cover associated with the different types of mycorrhizal fungi in mountains. AM and NM vegetation cover increased along mountain roads, while the cover of EcM and ErM vegetation decreased. This pattern was consistent across regions but varied in intensity along gradients of environmental factors and depending on the prevailing type of mycorrhiza in the natural vegetation. Indeed, cold-climate regions with higher representation of EcM and ErM vegetation showed greater increases in AM vegetation as a result of road disturbance. Non-native plants were almost exclusively associated with AM fungi or NM, and in turn more successful in environments strongly dominated by AM associations, suggesting that disturbance could be facilitating non-native plant invasion through changes in local mycorrhizal communities. While we hypothesize that this shifting effect of disturbance on the distribution of mycorrhizal types could be caused by changing abiotic factors and in particular by changes in nutrient availabilities and pH, further research with a focus on testing individual drivers associated with disturbance in an experimental setting would be required to truly understand which underlying processes drive the shifts we observed. Regardless, our results represent an important first global study of the role of anthropogenic disturbances in shaping plant communities through the mycorrhizal fungi they associate with. These findings have important implications for vegetation restoration worldwide, as they suggest that roadside disturbance can change the fundamental make-up of EcM- and ErM-dominated plant communities, potentially shifting communities between alternative stable states of mycorrhizal dominance that could be very difficult to reverse (Fukami et al. 2017, Averill et al. 2022).

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Data availability statement

Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.0p2ngf27s (Clavel et al. 2024).

Supporting information

The Supporting information associated with this article is available with the online version.

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