

Road verges facilitate exotic species' expansion into undisturbed natural montane grasslands

Sophia Carmel Turner^{1,2}  | Karen Joan Esler²  | Jesse Machiel Kalwij^{3,4} 

¹Department of Ecology and Evolutionary Biology, University of Tennessee, Knoxville, Tennessee, USA

²DSI-NRF Centre of Excellence for Invasion Biology, Department of Conservation Ecology and Entomology, Stellenbosch University, Matieland, South Africa

³Institute of Geography and Geoecology, Karlsruhe Institute of Technology, Karlsruhe, Germany

⁴Centre for Ecological Genomics and Wildlife Conservation, Department of Zoology, University of Johannesburg, Auckland Park, South Africa

Correspondence

Jesse M. Kalwij, Institute of Geography and Geoecology, Karlsruhe Institute of Technology, Karlsruhe, Germany.
Email: jessek@uj.ac.za

Funding information

This project was funded by the DSI-NRF Centre of Excellence for Invasion Biology.

Co-ordinating Editor: Lauchlan Fraser

Abstract

Questions: How has exotic plant species richness and composition changed in and adjacent to a montane road verge over a 10-year period? Are montane road verges conduits of exotic species' dispersal into adjacent, undisturbed hinterland?

Location: Montane grassland, Maloti-Drakensberg Transfrontier Conservation Area, South Africa.

Methods: We surveyed road verge and adjacent hinterland transects (25 × 2 m; N = 80) across an elevational gradient of 1,500–2,874 m a.s.l. in 2007 and 2017. In each transect, we estimated the cover of each exotic plant species and the total cover of indigenous species. Generalised Linear Models were fitted to test if exotic species' richness and cover had changed over time. A Canonical Correspondence Analysis was used to determine if exotic species' composition had changed over time.

Results: Ten years onwards, exotic species richness had increased significantly across the entire elevational gradient, predominantly in the low- to mid-elevational range. Road verge and adjacent hinterland transects differed in species composition in 2007, but no longer in 2017.

Conclusion: Exotic species richness and composition displayed a high spatiotemporal rate of change. Over time, exotic species increasingly moved into the hinterland from the verges as a result of human-mediated colonisation pressure. These results indicate that montane road verges are far better conduits for the dispersal of exotic species than previously assumed, and that further colonisation of the hinterland by exotics can be expected.

KEYWORDS

alien species, biodiversity monitoring, high-elevation environments, montane grasslands, neobiota, non-native species, road construction, road verge

1 | INTRODUCTION

Mountain ecosystems are increasingly recognised as susceptible to colonisation by exotic plant species (Alexander et al., 2016). Exotics are successfully moving into mountain ecosystems at a global scale

(Haider et al., 2018), occasionally beyond their conventional upper elevational range limits (Lenoir et al., 2008; Kalwij et al., 2015; Pauchard et al., 2016; Dainese et al., 2017; Koide et al., 2017). Exotic species are particularly common in montane road verges, which often harbour more exotics than the adjacent hinterland (Pauchard

This is an open access article under the terms of the Creative Commons Attribution-NonCommercial-NoDerivs License, which permits use and distribution in any medium, provided the original work is properly cited, the use is non-commercial and no modifications or adaptations are made.

© 2021 The Authors. *Applied Vegetation Science* published by John Wiley & Sons Ltd on behalf of International Association for Vegetation Science.

et al., 2009; Pollnac et al., 2012); similar patterns are also found along hiking tracks (Liedtke et al., 2020). While such studies show that exotic species are increasingly found at high elevations, information on spatiotemporal trends is still scarce due to a deficiency in historical data.

Several factors have been attributed to the introduction and establishment of exotic species in mountain ecosystems. Propagule pressure and habitat disturbance in particular are considered as primary drivers for short-term changes at a local scale (González-Moreno et al., 2014; Lemke et al., 2019; Corcos et al., 2020). Propagule pressure is the number of individuals and/or number of introductions to an area, whereby species with a high propagule pressure are more likely to become invasive (Lockwood et al., 2009). Habitat disturbance can be of anthropogenic origin, such as trampling, road construction, and verge maintenance, or due to natural processes such as mudslides, rock falls, and water run-off. Both factors are, therefore, important environmental drivers facilitating exotic species in montane ecosystems (Pauchard et al., 2009; Alexander et al., 2016). This is particularly true for exotic species with a ruderal life strategy (Hierro et al., 2006). For example, construction vehicles and road verge infill material can be contaminated with exotic seeds (Johnston & Johnston, 2004), or newly constructed verges are revegetated with exotic seed mixtures (McDougall, 2001). Therefore, the rate at which such species colonise mountain ecosystems largely depends on the frequency and intensity of human activities (Kalwij et al., 2015; Haider et al., 2018).

Roads are a major indicator of human activity and ecosystem impact. Indeed, the access that roads provide has completely altered global ecology (Ibisch et al., 2016). While roadside verges can act as habitat refugia in strongly converted habitats (Cousins, 2006), they may also act as conduits in the dispersal of exotic species (Procheş et al., 2005; Zwaenepoel et al., 2006; Kalwij et al., 2008a). Accordingly, roads are widely associated with biological invasions due to, among other factors, the persisting disturbance of adjacent habitats, habitat fragmentation, disruption of soil ecology, and changed hydrology (Ansong & Pickering, 2013). The importance of vehicles as potential dispersal vector also applies to mountain ecosystems (Kalwij et al., 2008b), especially in the lower elevational range and close to roads, where the richness and composition of exotic vegetation is primarily influenced by anthropogenic modifications (Jakobs et al., 2010; Bacaro et al., 2015). Consequently, the development, maintenance, and usage of roads in mountain ecosystems results in propagule pressure and habitat disturbance, facilitating a further spread and establishment of exotic species (Lembrechts et al., 2016; Haider et al., 2018).

Despite the recent increase of research on mountain invaders, a lack of reliable baseline data still inhibits our understanding of the temporal dynamics of exotic plant communities in relatively pristine montane areas adjacent to road verge habitats (Kalwij et al., 2015; Seipel et al., 2016; McDougall et al., 2018). Conducting such a study requires data from an elevational gradient of sufficient length and time span to acquire meaningful results (Lomolino, 2001; Lindenmayer et al., 2012). Measuring trends also requires adequate

baseline data to be resampled as accurately as possible (Kopecký & Macek, 2015). A mountain pass in the Drakensberg region of South Africa provides such prerequisites. This area has been subject to a range of short- and long-term studies on plant and insect communities (Kalwij et al., 2008b; Bishop et al., 2014; Steyn et al., 2017). For example, baseline data on the abundance of exotic and native plant species of roadside verges and adjacent natural grassland (hereafter referred to as hinterland) were collected in 2007 (Kalwij et al., 2008b), and annually supplemented with observations on the upper elevational range limits of exotic plant species (Kalwij et al., 2015). Such longitudinal monitoring programmes provide a unique opportunity to study spatiotemporal trends in exotic species.

In this study, we test which environmental drivers determine spatiotemporal trends in exotic species composition in roadside verges of a mountain ecosystem. We hypothesise that richness and abundance of exotic species increase in elevation and over time, while indigenous species abundance decreases. We also hypothesise that exotic species increase is higher in the road verges than in the hinterland. To test these hypotheses, we determined if and how exotic species' abundance changed over a 10-year period by resurveying road verge and hinterland transects, and by quantifying potential explanatory environmental variables such as road verge width, degree of road verge disturbance, and distance from potential points of exotic propagule introduction.

2 | METHODS

2.1 | Study area

Our study area was located in the Drakensberg Alpine Centre (DAC), a mountain range of some 40,000 km² situated in South Africa and Lesotho. The DAC is the southernmost tip of the Afromontane regional centre for endemism (Carbutt & Edwards, 2004). This entire area falls within the grassland biome and has an annual rainfall of 990–1180 mm (Mucina & Rutherford, 2006; Nel & Sumner, 2008). Within the DAC lies the Maloti-Drakensberg Park, a UNESCO World Heritage site characterised by its high plant and animal diversity and compelling setting, making this area a key tourist destination (UNESCO, 2013).

Sampling was done along a mountain pass located in the Maloti-Drakensberg Park (Figure 1a; 29°17'–39' E, 29°35'–39' S). This 20-km stretch of gravel road — the Sani Pass road — is the only road in an otherwise pristine grassland and covered an elevational gradient of 1,500–2,874 m a.s.l. The Sani Pass was established as a bridal path in 1913, and upgraded for four-wheel drives in the 1940s (Dobbs, 1975). Presently, this road is an important trade route and border crossing between South Africa and Lesotho. Movement of tourists, locals, and livestock — either by vehicle or on foot — amounts to about 10,000 people crossing the border from South Africa and back annually (Kalwij et al., 2015). At the time of sampling, road surface material ranged from gravel in the lower elevational range, to rocks and small boulders in the higher elevational range. This road surface

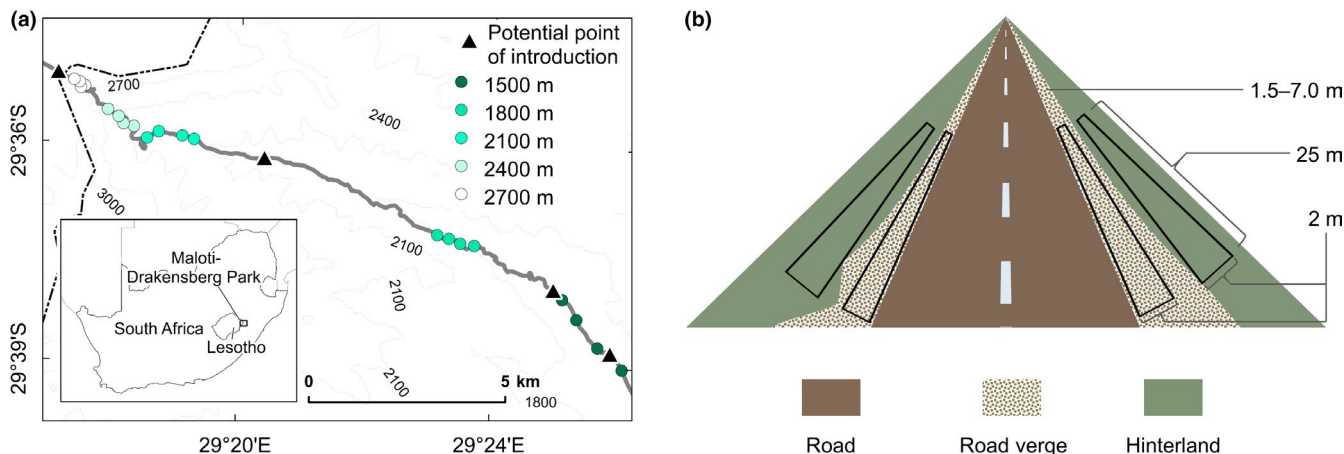


FIGURE 1 The left panel (a) shows an overview of the study area, its location in South Africa (inset), the plot locations along the Sani Pass road, and the locations of the four potential points of introduction. The colour of the plot symbol indicates the elevational level of the observations ($N = 80$ transects). Map projection: UTM 35S. The right panel (b) shows a schematic of transect layout at each plot

needs regular and continuous maintenance, especially at places where water run-off regularly causes severe erosion, making construction vehicles commonplace along the Sani Pass.

2.2 | Data collection

Data collection was conducted at five levels along the elevational gradient: 1,500 m, 1,800 m, 2,100 m, 2,400 m, and 2,700 m a.s.l. At each level, four locations were randomly selected based on accessibility and habitat representativeness, as replicates within the respective elevational level. At each location, one pair of plots was laid out. Since the hydrology and erosion of mountain road verges likely depends on verge slope, plots were placed on both sides of the road resulting in mountain-side and valley-side plots (Figure 1b). We defined the road verge as the area directly alongside the road surface and affected by road-related disturbance. Each plot consisted of a road verge transect and a hinterland transect in the adjacent natural grassland. Following this nested split-plot design, a total of 80 transects were surveyed. The first field survey was conducted in January 2007 (Kalwij et al., 2008b), and repeated in January 2017.

All transects were 25 m long, parallel to the road axis (Figure 1b). Hinterland transects were located immediately adjacent to road verge transects, in a paired transect design, and were always 2 m wide. Since road verge width varied (average width: 2.5 m; range: 1.5–7.0 m), road verge transects were up to 2 m wide. A handheld GPS (GPS 12XL in 2007, GPSMap 64st in 2017; Garmin Ltd., Olathe, Kansas, USA) was used to record the centre point of each location. In each transect, we recorded the abundance of exotic species using the Braun-Blanquet scale (van der Maarel, 1979), and we estimated the total percentage cover of exotic species, indigenous species and bare soil. We adopted the nomenclature of Germishuizen and Meyer (2003) where possible, and otherwise that of The Plant List (Kalwij, 2012).

To test if the presence or abundance of exotic species was related to areas of intense anthropogenic activity – where exotic propagule

pressure is high – we included the distance of transects from such areas as an explanatory variable (Kalwij et al., 2015). These areas of intense anthropogenic activity were: (a) Lesotho border post at the Sani Top village; (b) South African border post; (c) a tourist accommodation area; and (d) a public transport transfer area at the ruins of a former trading post. The Euclidean distance (in m) between transects and these four areas was calculated using ArcGIS (Version 10.5; ESRI, Redlands, California, USA), and included as the explanatory variable 'distance from nearest potential point of introduction'.

2.3 | Data analysis

To quantify a temporal change in exotic species richness and cover, we calculated the absolute difference between 2007 and 2017, whereby positive values indicated an increase over time. We then fitted Generalised Linear Models (GLMs) with an identity link function to test if these changes were significant, and to determine which environmental variables contributed significantly to the model. To estimate the model parameters, we adopted the quasi-likelihood method to adjust for overdispersion of errors. Explanatory variables tested were elevational level, roadside (mountain or valley side), transect type (verge or hinterland), distance from nearest potential point of introduction, and verge width. We nested roadside within elevation and transect type within roadside to ensure that variables fitted the nested design of the sampling strategy. In case a variable proved to be non-significant, we excluded it in the next step of our backward-selecting model building. We adopted the most parsimonious model as final model. For each model, we used an F test to determine the overall model fit and the degree to which each significant variable contributed (Crawley, 2013).

To determine which variables best explained variation in exotic species composition over time, we conducted a Canonical Correspondence Analysis (CCA) followed by a Monte Carlo permutation test with 9,999 runs. The CCA incorporated elevational level,

year, transect type (verge or hinterland), bare soil cover, roadside (mountain or valley), distance from nearest potential point of introduction, and vegetation cover as explanatory variables. Vegetation cover was recorded as total percentage cover of indigenous species, exotic species, and bare soil. Bare soil cover was automatically excluded from these analyses, as it was a colinear variable to indigenous and exotic species' cover. We also ran CCAs for each year separately to see if any of the variables had changed in importance over time. We excluded transects of the 2,400 m and 2,700 m elevational levels of 2007, because these transects had a single exotic species only. We used stepwise backward exclusion of non-significant variables until a model with only significant explanatory variables remained. Data on species abundance and environmental variables are available in Appendix S1. All data analyses were done in R version 4.1.1 (R Core Team, 2020), using the *vegan* v 2.5-7 package (Oksanen et al., 2020).

3 | RESULTS

The total number of exotic species more than doubled: from 24 species in 2007 to 56 in 2017, most of which belonged to Asteraceae or Poaceae. All species observed in 2007 were observed again in 2017, except for three: *Agrimonia procera*, *Prunus persica* and *Rapistrum rugosum*. Each elevational level displayed an increase in exotic species richness over time, particularly the lower and mid-elevational levels (1,500–2,100 m a.s.l.; Figure 2a). This increase was not limited to the verge transects. Indeed, exotic species richness increased in both verge and hinterland transects, although verge transects displayed a higher increase (Figure 2b). This pattern was confirmed by the GLM analysis. The most parsimonious GLM explained 58.9% of variation in exotic species richness change, with elevational level and transect type within elevational level as most important explanatory variables (Table 1). In spite of the overall increase in exotic species richness, the total cover of exotics only increased in the verge transects at the lower elevational range (Figure 2c). The most parsimonious GLM model fitted to exotic species' cover explained 20.6% of variation with transect type nested within elevation as the most important explanatory variable (Table 1). The most parsimonious GLM fitted to indigenous species cover change showed a similar combination of explanatory variables. Bare soil cover, however, was not explained by any of these explanatory variables.

A biplot of the CCA showed that in the year 2007 variation in exotic species composition was best explained by a combination of elevational level, transect type (verge or hinterland transect), and the distance from nearest potential point of introduction (Figure 3a). The Monte Carlo permutation tests confirmed that elevational level contributed most to the overall model ($F_{\text{elevational level}} = 4.49$, $p < 0.0001$), followed by distance from nearest potential point of introduction ($F_{\text{nearest PPOI}} = 2.62$, $p = 0.0022$) and transect type ($F_{\text{transectType}} = 2.53$, $p = 0.0020$), and finally by total cover of indigenous species ($F_{\text{Cover_Indigenous}} = 2.10$, $p = 0.0088$). A similar analysis showed that in the year 2017, this pattern had not changed

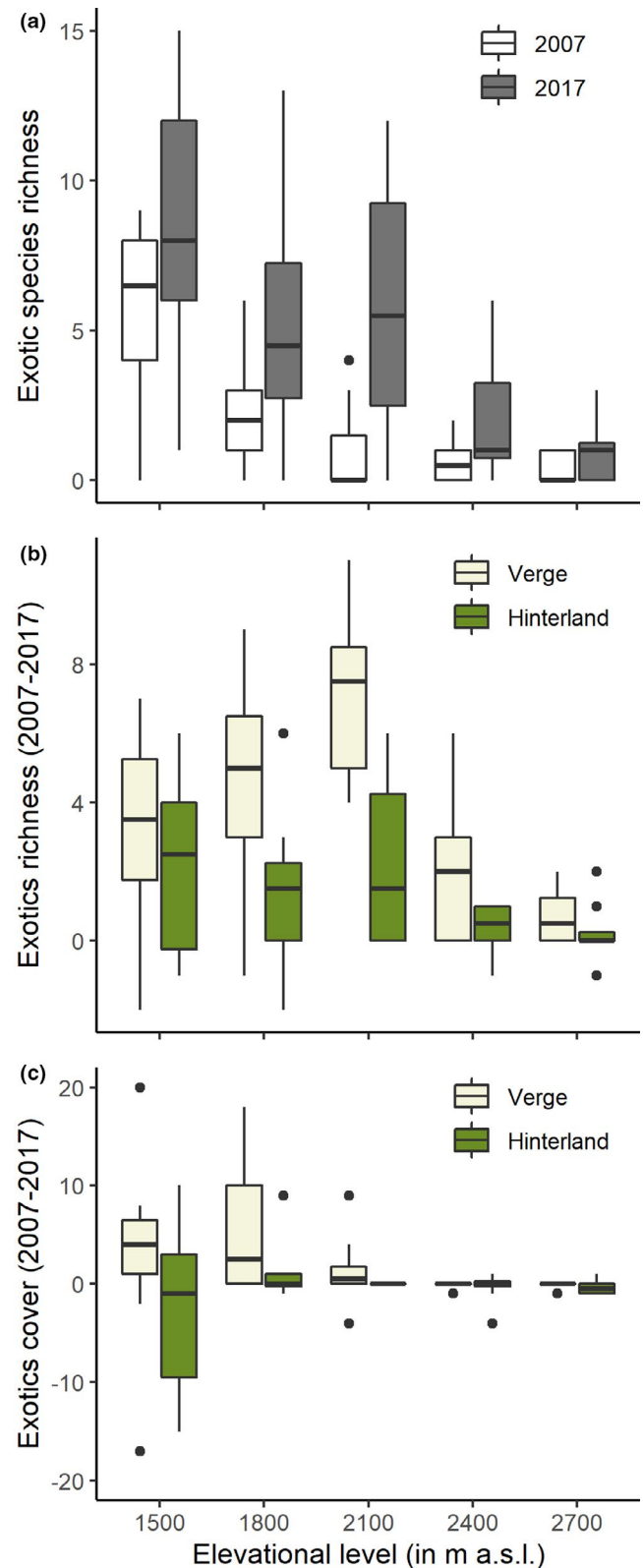


FIGURE 2 Boxplots of: (a) the exotic species richness for each elevation level in 2007 and 2017; (b) the change in exotic species richness; and (c) exotic species' cover between 2007 and 2017 along the elevational gradient for verge and hinterland transects

TABLE 1 Overview of the F tests on the most parsimonious generalized linear models fitted to the respective response variables. Each response variable was calculated as the paired difference between the observations ($N = 80$) in 2007 and 2017. Parentheses indicate within which variable the preceding variable is nested

Response variable	Residual deviance	df	F	p	Terms included	df	% deviance explained	F	p
Exotic richness change	286.7	14	6.6532	<0.0001	Elevational level	4	25.3%	10.014	<0.0001
					Verge width	1	3.4%	5.450	0.0227
					Elevational level \times verge width	4	8.2%	3.260	0.0169
Exotic species' cover change	5,677.5	9	2.022	0.0494	Transect type (elevational level)	5	21.9%	6.921	<0.0001
					Elevational level	4	2.1%	0.471	0.7568
Indigenous species cover change	41,385	9	2.577	0.0127	Transect type (elevational level)	5	18.5%	3.262	0.0105
					Elevational level	4	3.6%	0.8332	0.5087
Bare soil cover change	47,060	9	1.642	0.1204	Transect type (elevational level)	5	21.3%	3.9719	0.0031
					Elevational level	4	1.6%	0.3325	0.8552
					Transect type (elevational level)	5	15.9%	2.6887	0.0279

with elevational level as the most important variable (Figure 3b; $F_{\text{elevational level}} = 5.51$, $p < 0.0001$), followed by distance from nearest potential point of introduction ($F_{\text{nearestPPOI}} = 3.13$, $p < 0.0001$), transect type ($F_{\text{transectType}} = 1.61$, $p = 0.0083$), and total cover of exotic species ($F_{\text{CoverExotics}} = 2.47$, $p = 0.0020$). The CCA of both datasets combined confirmed that elevation level remained the most important explanatory variable ($F_{\text{elevational level}} = 7.08$, $p < 0.0001$), but also that species composition had changed over time (Figure 3c; $F_{\text{year}} = 3.78$, $p < 0.0001$). Other explanatory variables, such as road verge width and road side, did not contribute significantly in either year or to the overall model (all p values > 0.05).

4 | DISCUSSION

To the best of our knowledge, this is the first mountain plant invasion study to systematically repeat a survey of plots along an elevational gradient ten years later (cf. Seipel et al., 2016; Haider et al., 2018). Even within this relatively short time span, exotic species richness increased, especially in the verges of the mid-elevational range. This pattern is consistent with expectations of global predictions on exotic plants invading mountain ecosystems (Guo et al., 2018; Haider et al., 2018). Two potential explanations for this pattern are gradual range expansion and human-mediated dispersal. The subsequent spread of exotics into the hinterland, on the other hand, was more likely facilitated by mechanisms such as propagule pressure and habitat disturbance. In the discussion below, we explore the degree to which each of these mechanisms contributed to the increase of exotic plants in a relatively undisturbed montane grassland.

Gradual range expansion describes a species extending its distribution range by colonising new areas on the edge of its range (Wilson et al., 2009). Exotic species richness and abundance was highest in the lower elevational range, providing a pool of species with the potential to expand to higher elevations. This pattern fits the directional ecological filtering hypothesis in that we found a unidirectional range expansion of exotics from low elevations, and with less-adaptable species gradually dropping out with increasing elevation due to environmental conditions (Alexander et al., 2011; Steyn et al., 2017). However, if gradual range expansion was the only primary driver, the largest increase in exotic species would have been observed at the lower elevations. Here, the most prominent increase in exotic species was observed at the mid-elevational range (Figure 2b). This indicates that the exotic species pool is not merely expanding its range gradually, but that additional factors are aiding long-distance dispersal (Higgins et al., 2003; Jordano, 2017). Typically, the introduction of exotic propagules to montane road verges is attributed to anthropogenic dispersal vectors such as adhesion to vehicles (Taylor et al., 2012; Ansong & Pickering, 2013; Khan et al., 2018) and, to a lesser extent, footwear (Liedtke et al., 2020). Indeed, for both the 2007 and 2017 survey, distance from potential points of introduction was an important explanatory variable for exotic species richness and composition (Table 1; Figure 3). Therefore, we surmise that

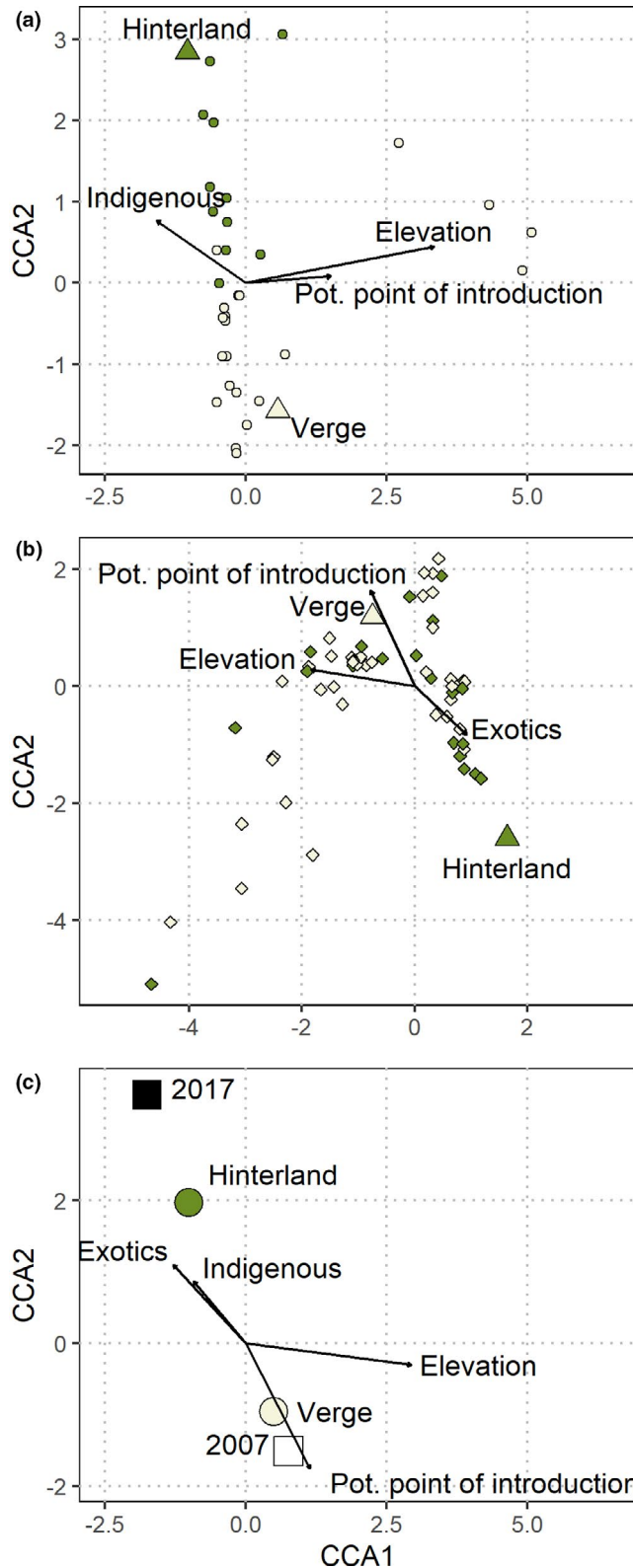


FIGURE 3 Canonical Correspondence Analysis (CCA) of exotic species composition and significant environmental variables for: (a) 2007; (b) 2017; and (c) both observation years. The colour and shape of the larger symbols indicate the sampling category (hinterland or verge transects) and sampling year (2007 or 2017). Significant explanatory variables included: (i) distance from nearest potential point of introduction (Pot. point of introduction); (ii) total cover of indigenous species (Indigenus); (iii) total cover of exotic species (Exotics); and (iv) elevation in m a.s.l. (Elevation). The smaller symbols in panels a and b indicate site scores. For aesthetic reasons these site scores were omitted from panel c

hinterland became colonised (Procheş et al., 2005; Kalwij et al., 2008a; Seipel et al., 2016). Exotic species' cover remained low at the time of the most recent survey, especially in the hinterland transects. Whereas exotic species composition of hinterland and verge transects showed a high degree of dissimilarity in 2007, this dissimilarity was reduced in 2017 (Figure 3), indicating that exotic species had moved into the hinterland across the entire elevational gradient. A low cover of exotic species in montane ecosystems is typically explained by the biotic resistance hypothesis for the low and mid-elevational range (McDougall et al., 2018; Popp & Kalwij, 2021), and by physiological limitation in the high-elevation range (Averett et al., 2016; McDougall et al., 2018). Therefore, despite their increase, the ecological impact of exotics on indigenous species composition remained rather limited at the time of the latest survey.

Of particular note is the high rate of change in exotic species richness and abundance, considering the relatively short time span of 10 years. A lack of equivalent repeated ecological surveys makes direct comparisons difficult. Irrespective, a change in climatic conditions does not play an important role since the rate of change was too rapid to be attributed to climate change (Koide et al., 2017; Carboni et al., 2018). The potential role of climate change as a driver of upward range expansion was addressed by Kalwij et al. (2015). This longitudinal study showed that exotic species' range expansion was much faster than would be expected by climate change-related rising temperatures, and the pattern was primarily explained by range expansion of annuals. Moreover, global metastudies suggest that ongoing disturbance of road verges is the primary environmental driver here (Lembrechts et al., 2016; Lázaro-Lobo & Ervin, 2019). For example, routine road maintenance – at a low frequency but with a high disturbance intensity – intermittently invigorates the seedbank for ruderal, pioneer species (Kalwij et al., 2008a; Rauschert et al., 2017). Such high levels of road verge disturbance favours exotic over native ruderals (Hiero et al., 2006; Chiuffo et al., 2018), particularly in high-elevation environments (Lembrechts et al., 2016). For this reason, exotic species composition in montane ecosystems globally is remarkably similar (McDougall et al., 2011). Interestingly, none of our disturbance proxies (verge width, percentage of bare ground) contributed significantly in our statistical models, while traffic density remained stable over time (Kalwij et al., 2015). The increase in exotic species is, nevertheless, a clear indication that anthropogenic vectors continuously introduce more and new exotic propagules.

human-mediated dispersal, rather than gradual range expansion, is the most likely explanation for the increase of exotic species in the road verges of the mid-elevational range.

As predicted, exotic species richness increased in the hinterland across the entire elevational gradient over time, indicating that the road verge acted as the primary source from where the

Each new invasion starts with a single propagule. For example, we observed a *Parthenium hysterophorus* (Asteraceae) individual at an active construction site – the first observation of this invasive alien species in the study area (GBIF, 2021). Since these construction vehicles originated from an area where *P. hysterophorus* is particularly abundant (Richards Bay, South Africa; approximately 400 km from the study area), it is a plausible assumption that a construction vehicle was the dispersal vector in this case. Since private vehicles are frequently cleaned, the actual number of attached propagules is usually quite low (Lonsdale & Lane, 1994; Khan et al., 2018). Moreover, remaining propagules are predominantly dispersed in close vicinity to home (Taylor et al., 2012). While heavy construction vehicles such as bulldozers and excavators are generally subject to standard cleaning protocols (e.g., DiVittorio et al., 2010), awareness of the necessity to have such protocols in place varies between population groups (Potgieter et al., 2019). Moreover, heavy construction vehicles are generally transported on a low-bed trailer, so that remaining propagules are predominantly dispersed at the final destination. Therefore, while tourist and tour guide vehicles are potential dispersal vectors (Ansong & Pickering, 2013), the role of road construction vehicles is not to be underestimated (Rauschert et al., 2017).

5 | CONCLUSIONS

Our study shows that exotic plant communities in this Afrotropical mountain ecosystem are primarily shaped by human activities, and that the impact of these species is not confined to disturbed areas or their distance from points of introduction. The spread of exotic species into the adjacent hinterland occurs along the entire elevational gradient, primarily caused by anthropogenic drivers. Specifically, a handful of sites of high anthropogenic activity along the mountain pass continue to act as points of introduction for new and existing exotic species, while managed road verges foster their establishment and subsequent spread across elevation and into the adjacent hinterland, irrespective of road verge width or level of disturbance.

ACKNOWLEDGEMENTS

This project was supported by the University of Johannesburg. We are indebted to Lisa Schwarz for field assistance, and to Tom R. Bishop for logistic support and final comments on the manuscript. Open access funding enabled and organized by ProjektDEAL.

AUTHOR CONTRIBUTIONS

SCT and JMK conceived of the research idea, and collected and analysed data; SCT and JMK, with contributions from KJE, wrote the paper; all authors discussed the results and commented on the manuscript.

DATA AVAILABILITY STATEMENT

The data set used in this paper is available as Supporting Information (Appendix S1).

ORCID

Sophia Carmel Turner  <https://orcid.org/0000-0003-1237-0562>

Karen Joan Esler  <https://orcid.org/0000-0001-6510-727X>

Jesse Machiel Kalwij  <https://orcid.org/0000-0002-8685-9603>

REFERENCES

- Alexander, J.M., Kueffer, C., Daehler, C.C., Edwards, P.J., Pauchard, A. & Seipel, T. (2011) Assembly of nonnative floras along elevational gradients explained by directional ecological filtering. *Proceedings of the National Academy of Sciences of the United States of America*, 108, 656–661. <https://doi.org/10.1073/pnas.1013136108>
- Alexander, J.M., Lembrechts, J.J., Cavieres, L.A., Daehler, C., Haider, S., Kueffer, C. et al. (2016) Plant invasions into mountains and alpine ecosystems: current status and future challenges. *Alpine Botany*, 126, 89–103. <https://doi.org/10.1007/s00035-016-0172-8>
- Ansong, M. & Pickering, C. (2013) Are weeds hitchhiking a ride on your car? A systematic review of seed dispersal on cars. *PLoS One*, 8, e80275. <https://doi.org/10.1371/journal.pone.0080275>
- Averett, J.P., McCune, B., Parks, C.G., Naylor, B.J., DelCurto, T. & Mata-Gonzalez, R. (2016) Non-native plant invasion along elevation and canopy closure gradients in a Middle Rocky Mountain ecosystem. *PLoS One*, 11, e0147826. <https://doi.org/10.1371/journal.pone.0147826>
- Bacaro, G., Maccherini, S., Chiarucci, A., Jentsch, A., Rocchini, D., Torri, D. et al. (2015) Distributional patterns of endemic, native and alien species along a roadside elevation gradient in Tenerife, Canary Islands. *Community Ecology*, 16, 223–234. <https://doi.org/10.1556/168.2015.16.2.10>
- Bishop, T.R., Robertson, M.P., van Rensburg, B.J. & Parr, C.L. (2014) Elevation-diversity patterns through space and time: ant communities of the Maloti-Drakensberg Mountains of southern Africa. *Journal of Biogeography*, 41, 2256–2268. <https://doi.org/10.1111/jbi.12368>
- Carboni, M., Gueguen, M., Barros, C., Georges, D., Boulangeat, I., Douzet, R. et al. (2018) Simulating plant invasion dynamics in mountain ecosystems under global change scenarios. *Global Change Biology*, 24, e289–e302. <https://doi.org/10.1111/gcb.13879>
- Carbutt, C. & Edwards, T.J. (2004) The flora of the Drakensberg Alpine Centre. *Edinburgh Journal of Botany*, 60, 581–607. <https://doi.org/10.1017/S0960428603000428>
- Chiuffo, M.C., Cock, M.C., Prina, A.O. & Hierro, J.L. (2018) Response of native and non-native ruderals to natural and human disturbance. *Biological Invasions*, 20, 2915–2925. <https://doi.org/10.1007/s10530-018-1745-9>
- Corcos, D., Nascimbene, J., Campesan, M., Donadello, D., Segat, V., Marini, L. et al. (2020) Establishment dynamics of native and exotic plants after disturbance along roadsides. *Applied Vegetation Science*, 23, 277–284. <https://doi.org/10.1111/avsc.12481>
- Cousins, S.A.O. (2006) Plant species richness in midfield islets and road verges - The effect of landscape fragmentation. *Biological Conservation*, 127, 500–509. <https://doi.org/10.1016/j.biocon.2005.09.009>
- Crawley, M.J. (2013) *The R Book*. 2nd Edition, West Sussex, UK: John Wiley & Sons, Ltd. <https://doi.org/10.1002/9781118448908>
- Dainese, M., Aikio, S., Hulme, P.E., Bertolli, A., Prosser, F. & Marini, L. (2017) Human disturbance and upward expansion of plants in a warming climate. *Nature Climate Change*, 7, 577–580. <https://doi.org/10.1038/nclimate3337>
- DiVittorio, J., Grodowitz, M. & Snow, J. (2010) *Inspection and cleaning manual for equipment and vehicles to prevent the spread of invasive species*. Denver, Colorado: U.S. Department of the Interior, Bureau of Reclamation.
- Dobbs, D.A. (1975) *A cradle of rivers: The Natal Drakensberg*. Cape Town, Johannesburg: Purnell.

- GBIF. (2021). *GBIF occurrence download of Parthenium hysterophorus L.* <https://doi.org/10.15468/dl.hqu9zx>
- Germishuizen, G. & Meyer, N.L. (2003) *Plants of southern Africa: an annotated checklist*. Pretoria, South Africa: National Botanical Institute.
- González-Moreno, P., Diez, J.M., Ibáñez, I., Font, X. & Vilà, M. (2014) Plant invasions are context-dependent: multiscale effects of climate, human activity and habitat. *Diversity and Distributions*, 20, 720–731. <https://doi.org/10.1111/ddi.12206>
- Guo, Q., Fei, S., Shen, Z., Iannone, B.V., Knott, J. & Chown, S.L. (2018) A global analysis of elevational distribution of non-native versus native plants. *Journal of Biogeography*, 45, 793–803. <https://doi.org/10.1111/jbi.13145>
- Haider, S., Kueffer, C., Bruehlheide, H., Seipel, T., Alexander, J.M., Rew, L.J. et al. (2018) Mountain roads and non-native species modify elevational patterns of plant diversity. *Global Ecology and Biogeography*, 27, 667–678. <https://doi.org/10.1111/geb.12727>
- Hierro, J.L., Villarreal, D., Eren, Ö., Graham, J.M. & Callaway, R.M. (2006) Disturbance facilitates invasion: the effects are stronger abroad than at home. *American Naturalist*, 168, 144–156. <https://doi.org/10.1086/505767>
- Higgins, S.L., Nathan, R. & Cain, M.L. (2003) Are long-distance dispersal events in plants usually caused by nonstandard means of dispersal? *Ecology*, 84, 1945–1956. <https://doi.org/10.1890/01-0616>
- Ibisch, P.L., Hoffmann, M.T., Kreft, S., Pe'er, G., Kati, V., Biber-Freudenberger, L. et al. (2016) A global map of roadless areas and their conservation status. *Science*, 354, 1423–1427. <https://doi.org/10.1126/science.aaf7166>
- Jakobs, G., Kueffer, C. & Daehler, C.C. (2010) Introduced weed richness across altitudinal gradients in Hawai'i: humps, humans and water-energy dynamics. *Biological Invasions*, 12, 4019–4031. <https://doi.org/10.1007/s10530-010-9816-6>
- Johnston, F.M. & Johnston, S.W. (2004) Impacts of road disturbance on soil properties and on exotic plant occurrence in subalpine areas of the Australian Alps. *Arctic, Antarctic, and Alpine Research*, 36, 201–207. [https://doi.org/10.1657/1523-0430\(2004\)036\[0201:ORDO S\]2.0.CO;2](https://doi.org/10.1657/1523-0430(2004)036[0201:ORDO S]2.0.CO;2)
- Jordano, P. (2017) What is long-distance dispersal? And a taxonomy of dispersal events. *Journal of Ecology*, 105, 75–84. <https://doi.org/10.1111/1365-2745.12690>
- Kalwij, J.M. (2012) Review of 'The Plant List, a working list of all plant species'. *Journal of Vegetation Science*, 23, 998–1002. <https://doi.org/10.1111/j.1654-1103.2012.01407.x>
- Kalwij, J.M., Milton, S.J. & McGeoch, M.A. (2008a) Road verges as invasion corridors? A spatial hierarchical test in an arid ecosystem. *Landscape Ecology*, 23, 439–451. <https://doi.org/10.1007/s10980-008-9201-3>
- Kalwij, J.M., Robertson, M.P. & Van Rensburg, B.J. (2008b) Human activity facilitates altitudinal expansion of exotic plants along a road in montane grassland, South Africa. *Applied Vegetation Science*, 11, 491–498. <https://doi.org/10.3170/2008-7-18555>
- Kalwij, J.M., Robertson, M.P. & Van Rensburg, B.J. (2015) Annual monitoring reveals rapid upward movement of exotic plants in a montane ecosystem. *Biological Invasions*, 17, 3517–3529. <https://doi.org/10.1007/s10530-015-0975-3>
- Khan, I., Navie, S., George, D., O'Donnell, C. & Adkins, S.W. (2018) Alien and native plant seed dispersal by vehicles. *Austral Ecology*, 43, 76–88. <https://doi.org/10.1111/aec.12545>
- Koide, D., Yoshida, K., Daehler, C.C. & Mueller-Dombois, D. (2017) An upward elevational shift of native and non-native vascular plants over 40 years on the island of Hawai'i. *Journal of Vegetation Science*, 28, 939–950. <https://doi.org/10.1111/jvs.12549>
- Kopecký, M. & Macek, M. (2015) Vegetation resurvey is robust to plot location uncertainty. *Diversity and Distributions*, 21, 322–330. <https://doi.org/10.1111/ddi.12299>
- Lázaro-Lobo, A. & Ervin, G.N. (2019) A global examination on the differential impacts of roadsides on native vs. exotic and weedy plant species. *Global Ecology and Conservation*, 17, 13. <https://doi.org/10.1016/j.gecco.2019.e00555>
- Lembrechts, J.J., Pauchard, A., Lenoir, J., Nuñez, M.A., Geron, C., Ven, A. et al. (2016) Disturbance is the key to plant invasions in cold environments. *Proceedings of the National Academy of Sciences of the United States of America*, 113, 14061–14066. <https://doi.org/10.1073/pnas.1608980113>
- Lemke, A., Kowarik, I. & Von der Lippe, M. (2019) How traffic facilitates population expansion of invasive species along roads: The case of common ragweed in Germany. *Journal of Applied Ecology*, 56, 413–422. <https://doi.org/10.1111/1365-2664.13287>
- Lenoir, J., Gégout, J.C., Marquet, P.A., De Ruffray, P. & Brisse, H. (2008) A significant upward shift in plant species optimum elevation during the 20th century. *Science*, 320, 1768–1771. <https://doi.org/10.1126/science.1156831>
- Liedtke, R., Barros, A., Essl, F., Lembrechts, J.J., Wedegärtner, R.E.M., Pauchard, A. et al. (2020) Hiking trails as conduits for the spread of non-native species in mountain areas. *Biological Invasions*, 22, 1121–1134. <https://doi.org/10.1007/s10530-019-02165-9>
- Lindenmayer, D.B., Likens, G.E., Andersen, A., Bowman, D., Bull, C.M., Burns, E. et al. (2012) Value of long-term ecological studies. *Austral Ecology*, 37, 745–757. <https://doi.org/10.1111/j.1442-9993.2011.02351.x>
- Lockwood, J.L., Cassey, P. & Blackburn, T.M. (2009) The more you introduce the more you get: the role of colonization pressure and propagule pressure in invasion ecology. *Diversity and Distributions*, 15, 904–910. <https://doi.org/10.1111/j.1472-4642.2009.00594.x>
- Lomolino, M.V. (2001) Elevation gradients of species-density: historical and prospective views. *Global Ecology and Biogeography*, 10, 3–13. <https://doi.org/10.1046/j.1466-822x.2001.00229.x>
- Lonsdale, W.M. & Lane, A.M. (1994) Tourist vehicles as vectors of weed seeds in Kakadu National Park, Northern Australia. *Biological Conservation*, 69, 277–283. [https://doi.org/10.1016/0006-3207\(94\)90427-8](https://doi.org/10.1016/0006-3207(94)90427-8)
- McDougall, B.K.L. (2001) Colonization by alpine native plants of a stabilized road verge on the Bogong High Plains, Victoria. *Ecological Management & Restoration*, 2, 47–52. <https://doi.org/10.1046/j.1442-8903.2001.00068.x>
- McDougall, K.L., Alexander, J.M., Haider, S., Pauchard, A., Walsh, N.G. & Kueffer, C. (2011) Alien flora of mountains: global comparisons for the development of local preventive measures against plant invasions. *Diversity and Distributions*, 17, 103–111. <https://doi.org/10.1111/j.1472-4642.2010.00713.x>
- McDougall, K.L., Lembrechts, J., Rew, L.J., Haider, S., Cavieres, L.A., Kueffer, C. et al. (2018) Running off the road: roadside non-native plants invading mountain vegetation. *Biological Invasions*, 20, 3461–3473. <https://doi.org/10.1007/s10530-018-1787-z>
- Mucina, L. & Rutherford, M.C. (2006) In: Mucina and Rutherford (Ed.) *The vegetation of South Africa, Lesotho and Swaziland*. Pretoria: South African National Biodiversity Institute.
- Nel, W. & Sumner, P. (2008) Rainfall and temperature attributes on the Lesotho-Drakensberg escarpment edge, southern Africa. *Geografiska Annaler: Series A, Physical Geography*, 90, 97–108. <https://doi.org/10.1111/j.1468-0459.2008.00337.x>
- Oksanen, J., Blanchet, F.G., Friendly, M., Kindt, R., Legendre, P., McGinn, D. et al. (2020) *vegan: Community Ecology Package. Version 2.5-6*. Available at <https://cran.r-project.org/web/packages/vegan/> [Accessed 1 September 2021].
- Pauchard, A., Kueffer, C., Dietz, H., Daehler, C.C., Alexander, J., Edwards, P.J. et al. (2009) Ain't no mountain high enough: plant invasions reaching new elevations. *Frontiers in Ecology and the Environment*, 7, 479–486. <https://doi.org/10.1890/080072>

- Pauchard, A., Milbau, A., Albiñ, A., Alexander, J., Burgess, T., Daehler, C. et al. (2016) Non-native and native organisms moving into high elevation and high latitude ecosystems in an era of climate change: new challenges for ecology and conservation. *Biological Invasions*, 18, 345–353. <https://doi.org/10.1007/s10530-015-1025-x>
- Pollnac, F., Seipel, T., Repath, C. & Rew, L.J. (2012) Plant invasion at landscape and local scales along roadways in the mountainous region of the Greater Yellowstone Ecosystem. *Biological Invasions*, 14, 1753–1763. <https://doi.org/10.1007/s10530-012-0188-y>
- Popp, M.R. & Kalwij, J.M. (2021) Abiotic conditions shape the relationship between indigenous and exotic species richness in a montane biodiversity hotspot. *Plant Ecology*, 222, 421–432. <https://doi.org/10.1007/s11258-021-01116-6>
- Potgieter, L.J., Gaertner, M., O'Farrell, P.J. & Richardson, D.M. (2019) Perceptions of impact: Invasive alien plants in the urban environment. *Journal of Environmental Management*, 229, 76–87. <https://doi.org/10.1016/j.jenvman.2018.05.080>
- Proches, S., Wilson, J.R.U., Veldtman, R., Kalwij, J.M., Richardson, D.M. & Chown, S.L. (2005) Landscape corridors: Possible dangers? *Science*, 310, 779. <https://doi.org/10.1126/science.310.5749.779>
- R Core Team (2020) *R: A language and environment for statistical computing*. R version 4.0.2. Available at <https://www.R-project.org/> [Accessed 1 September 2021].
- Rauschert, E.S.J., Mortensen, D.A. & Bloser, S.M. (2017) Human-mediated dispersal via rural road maintenance can move invasive propagules. *Biological Invasions*, 19, 2047–2058. <https://doi.org/10.1007/s10530-017-1416-2>
- Seipel, T., Alexander, J.M., Edwards, P.J. & Kueffer, C. (2016) Range limits and population dynamics of non-native plants spreading along elevation gradients. *Perspectives in Plant Ecology, Evolution and Systematics*, 20, 46–55. <https://doi.org/10.1016/j.ppees.2016.04.001>
- Steyn, C., Greve, M., Robertson, M.P., Kalwij, J.M. & Le Roux, P.C. (2017) Alien plant species that invade high elevations are generalists: support for the directional ecological filtering hypothesis. *Journal of Vegetation Science*, 28, 337–346. <https://doi.org/10.1111/jvs.12477>
- Taylor, K., Brummer, T., Taper, M.L., Wing, A. & Rew, L.J. (2012) Human-mediated long-distance dispersal: an empirical evaluation of seed dispersal by vehicles. *Diversity and Distributions*, 18, 942–951. <https://doi.org/10.1111/j.1472-4642.2012.00926.x>
- UNESCO (2013) *Maloti-Drakensberg Park* [Online]. UNESCO. Available: <http://whc.unesco.org/en/list/985> [Accessed 1 October 2020].
- van derMaarel, E. (1979) Transformation of cover-abundance values in phytosociology and its effect on community similarity. *Vegetatio*, 39, 97–114. <https://doi.org/10.1007/BF00052021>
- Wilson, J.R.U., Dormontt, E.E., Prentis, P.J., Lowe, A.J. & Richardson, D.M. (2009) Something in the way you move: dispersal pathways affect invasion success. *Trends in Ecology & Evolution*, 24, 136–144. <https://doi.org/10.1016/j.tree.2008.10.007>
- Zwaenepoel, A., Roovers, P. & Hermy, M. (2006) Motor vehicles as vectors of plant species from road verges in a suburban environment. *Basic and Applied Ecology*, 7, 83–93. <https://doi.org/10.1016/j.baae.2005.04.003>

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

Appendix S1. Data on species abundance and environmental variables.

How to cite this article: Turner, S.C., Esler, K.J. & Kalwij, J.M. (2021) Road verges facilitate exotic species' expansion into undisturbed natural montane grasslands. *Applied Vegetation Science*, 24, e12615. <https://doi.org/10.1111/avsc.12615>