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Human activity facilitates altitudinal expansion of exotic plants along a road in montane grassland, South Africa

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Abstract

Question: Do anthropogenic activities facilitate the distribution of exotic plants along steep altitudinal gradients?

Location: Sani Pass road, Grassland biome, South Africa.

Methods: On both sides of this road, presence and abundance of exotic plants was recorded in four 25-m long road-verge plots and in parallel 25 m × 2 m adjacent land plots, nested at five altitudinal levels: 1500, 1800, 2100, 2400 and 2700 m a.s.l. Exotic community structure was analyzed using Canonical Correspondence Analysis while a two-level nested Generalized Linear Model was fitted for richness and cover of exotics. We tested the upper altitudinal limits for all exotics along this road for spatial clustering around four potential propagule sources using a *t*-test.

Results: Community structure, richness and abundance of exotics were negatively correlated with altitude. Greatest invasion by exotics was recorded for adjacent land at the 1500 m level. Of the 45 exotics, 16 were found at higher altitudes than expected and observations were spatially clustered around potential propagule sources.

Conclusions: Spatial clustering of upper altitudinal limits around human inhabited areas suggests that exotics originate from these areas, while exceeding expected altitudinal limits suggests that distribution ranges of exotics are presently underestimated. Exotics are generally characterised by a high propagule pressure and/or persistent seedbanks, thus future tarring of the Sani Pass may result in an increase of exotic species richness and abundance. This would initially result from construction-related soil disturbance and subsequently from increased traffic, water run-off, and altered fire frequency. We suggest examples of management actions to prevent this.

Keywords: Alien; Dispersal; Disturbance; Gradient analysis; Grassland; Multivariate; Spatial analysis; Transect.

Nomenclature: Germishuizen & Meyer (2003).

Introduction

Invasion of exotic plants depends on a variety of factors, e.g. habitat conditions, competition, or propagule pressure (Richardson et al. 2005; Pyšek & Richardson 2006). Ecosystem invasibility normally decreases with altitude as fewer exotic plants can invade high altitude habitats due to the harsh climatic conditions at high altitudinal levels (Keeley et al. 2003; Arévalo et al. 2005). However, a high propagule pressure, defined as a composite measure of introduction events and number of released propagules, facilitates and increases an exotic species' ability to overcome invasion-limiting barriers (Richardson et al. 2000; Von Holle & Simberloff 2005). Roads have been suggested to facilitate the spread of exotics (Ullmann et al. 1998; Johnston & Johnston 2004; Pauchard & Alaback 2004), and could therefore increase the altitudinal limit at which an exotic plant is invasive. However, the influence of roads on the distribution of exotics at high altitudinal levels (> 1500 m a.s.l.), has received little attention to date (Becker et al. 2005).

Roads may reduce local biodiversity due to habitat destruction, ecosystem fragmentation, and anthropogenic disturbance (Meunier et al. 1999; Gelbard & Belnap 2003; Spooner et al. 2004). Road verges are also susceptible to invasion by exotic plants due to soil disturbance and increased water run-off (Gelbard & Belnap 2003; Johnston & Johnston 2004; Pauchard & Alaback 2004). The effect of a road depends on its design and construction (Sýkora et al. 2002; Gelbard & Belnap 2003).

As compared to gravel roads, verges of tarred roads are usually associated with a higher number and cover of exotics due to more anthropogenic disturbance and a higher propagule pressure (Gelbard & Belnap 2003; Kalwij et al. in press). However, in steep areas with a high precipitation, exotics may be more abundant along gravel roads due to water run-off (Paterson 1996). To our knowledge, however, to date no studies have compared the distribution of exotics along an altitudinal gradient between gravelled and tarred roads while taking confounding covariables into account. Ecological studies at a landscape scale often have to deal with variation in climatic conditions, preventing a direct comparison between tarred and gravel roads (Hurlbert 1984). We therefore suggest that a repetition in time would be more appropriate to ensure that all covariables are comparable.

The aim of this study was to examine the present altitudinal distribution of exotic plants along the Sani Pass road, to determine the present status of invasion by exotics and to discuss the possible effects of an eventual sealing of the Sani Pass road on invasion by exotic plants. The outcome of this study can be used by the managers for control of exotic plants that currently occur in the study area and to prevent a further spread of exotics, and as baseline data for an eventual repetition in time after sealing of the road.

Methods

Study area

The study area was located in the Cobham region of the Ukhahlamba-Drakensberg Park (29°17-39' E, 29°35-39' S). This park has a rich diversity of plant and animal species, a large number of endemic species, and several globally threatened species (Branch 1988; Skelton et al. 1995; Bond et al. 2003; Carbutt & Edwards 2004, 2006). Its vegetation, part of the grassland biome (Mucina & Rutherford 2006), receives an annual precipitation of 990-1180 mm (Lynch 2003). The Sani Pass road is the major arterial road between the South African province of KwaZulu-Natal and Lesotho: entering the Cobham region at an altitude of 1562 m and winding its way up to the top of Sani Pass at 2873 m (the border between South Africa and Lesotho; Fig. 1). This road forms an important trade link between the Lesotho highlands and South Africa.

Sampling of exotic plants

We recorded the presence and abundance of exotics at five altitudinal levels: 1500, 1800, 2100, 2400 and 2700 m a.s.l along the Sani Pass road in January 2007. At each level, we randomly selected four locations. At each location we sampled plots of two sample categories (disturbed road-verge plots or adjacent pristine land plots) nested within road side (mountain side or valley side plots) in order to represent the aspect of the pass. Thus a total of 80 vegetation plots were surveyed in a three-level nested hierarchical design: plots within sample category, within road side, within altitudinal level. Verge plots were 25 m long and immediately adjacent to the road surface. The width of these plots was determined by the extent of road-related disturbance such as soil disturbance or water run-off. In accordance with a Environmental Impact Assessment report, the width of the future road and verge will not exceed the present extent (Anon. 2006). Therefore, adjacent land plots were 25 m × 2 m in size and located parallel to the verge plot at a distance of 5 - 7 m from the road edge to ensure that adjacent land plots are unlikely to be affected by future road construction. Within each plot, cover/abundance of exotics was recorded with the extended Braun-Blanquet scale (van der Maarel 1979). In addition, we visually estimated the percentage (1) bare soil, (2) total exotic vegetation cover, and (3) total indigenous vegetation cover as environmental variables to be included in the data analysis.

To determine the upper altitudinal limit of exotic species, seven observers walked from the top of the pass down to 1500 m along the Sani Pass road and recorded the first location of every exotic plant encountered. We used a hand-held GPS (Garmin 12XL) to record the position of these locations along the road (length ca. 20 km). Elevation data were determined for each observation from a digital elevation model with a spatial resolution of three arc seconds (ca. 80 m × 92.5 m) (Anon. 2004).

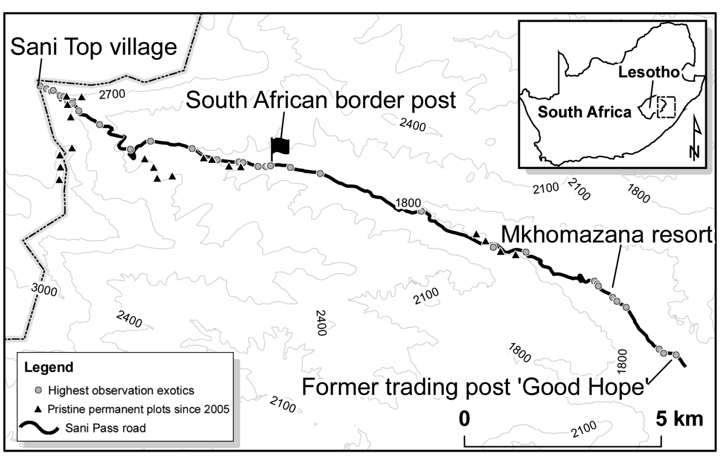

Fig. 1. Location of the study area in South Africa (inset), the locations of potential nearest sources of exotic propagules, and the positions of the highest observed exotic plants along the Sani Pass road.

Data analysis

The relation between environmental variables – road side, sample category, verge width, or altitudinal level – with abundance of exotic plants was analysed with Detrended Correspondence Analysis (DCA) from CANOCO 4.5 (ter Braak & Šmilauer 2002). The heterogeneity of samples based on the number of exotic species and the occurrence of potential outliers were assessed (Lepš & Šmilauer 1999). As DCA showed no evident gradient or distinct sample clusters, a Canonical Correspondence Analysis (CCA) was used to quantify the contribution of environmental variables to variation in exotic species.

To determine if exotic species richness within plots ($n = 80$) could be attributed to specific habitat conditions, we fitted nested Generalized Linear Models (GLM) assuming a Poisson distribution and using a logistic link function in S-Plus 6.0 (Anon. 2001).We adopted the quasi-likelihood method to estimate the dispersion parameter from the data to adjust for overdispersion of errors (Morton 1987). This method is used to estimate the dispersion of errors as scale parameters while fitting the model instead of assuming the dispersion *a priori* (Myers et al. 2002). GLM included the following variables: verge width, road side, sample category, and altitudinal level. The variable road side was nested within sample category, in turn nested within altitudinal level. A similar GLM was fitted to test for the effect of the environmental variables on total exotic vegetation cover. We used *F*-tests to determine which variables contributed significantly to each model and to test the statistical differences in model fit (McCullagh & Nelder 1989).

To determine the upper altitudinal distribution of exotics we calculated the cumulative number of exotics across the altitudinal gradient. We supplemented this list with exotics found in 20 plots of 4 m × 4 m in pristine vegetation that have been monitored annually since September 2005. These plots were located in groups of four plots along five altitudinal contours (1800, 2100, 2400, 2700 and 3000 m; see Fig. 1) at distances of 26 - 1523 m from the Sani Pass road. To assess the present altitudinal status of invasion in our study area we compared each highest observation with the expected altitudinal limit for each species according to Germishuizen & Meyer (2003) supplemented with data of specimens from the Natal University Herbarium (NU).

We also studied clustering of exotic plants around human-inhabited or formally inhabited dwellings as potential dispersal sources. For this we compared the mean distance between observations and nearest potential source, d_{obs}, with mean distance between 1000 randomly plotted points along the Sani Pass road and nearest potential source, d_{ran}, using a one-sided modified two-sample *t*-test to adjust for unequal variances (Quinn & Keough 2002).

Results

We found a total of 25 exotic plant species in the plots examined and a further 20 species along the entire gradient of the Sani Pass road (Table 1). One additional species was identified as a possible hybrid between the indigenous bramble *Rubus rigidus* and the exotic *R. cuneifolius* (pers. comm. Charles Stirton, bramble specialist). This species was observed at very high densities at some places, especially at the 1500 m altitudinal level. We excluded this species from statistical data analysis because of the lack of flowers at the time of data collection prevented us from reliably identifying *Rubus* species in the field. Of the confirmed exotic plants, six species were listed as declared invasive alien species (Henderson 2001): *Acacia dealbata*, *A. mearnsii*, *A. melanoxylon*, *Cirsium vulgare*, *Datura stramonium*, and *Solanum mauritianum*.

The observed altitudinal distribution of exotic species differed strongly with what was expected based on their known altitudinal upper limits. Twenty-seven (61%) exotic species were observed at a higher altitude than was expected from the literature, mostly located in the higher (> 2200 m) altitudinal levels (Fig. 2). Moreover, all declared invasive aliens, with the exception of *D. stramonium*, were found at higher altitudes than expected from Germishuizen & Meyer (2003). The NU Herbarium contained 723 specimens for 84% of the observed exotic species. Ten of these specimens were collected on average 151 m (± 40 s.e.) above their upper altitudinal limits as suggested by Germishuizen & Meyer (2003).

The CCA showed that the community structure of the 25 exotic plant species found in the plots was primarily correlated to an altitudinal gradient, while the width of the verge was of secondary importance (Fig. 3). Neither bare soil nor total exotic vegetation cover contributed significantly to exotic plant community structure. Exotic

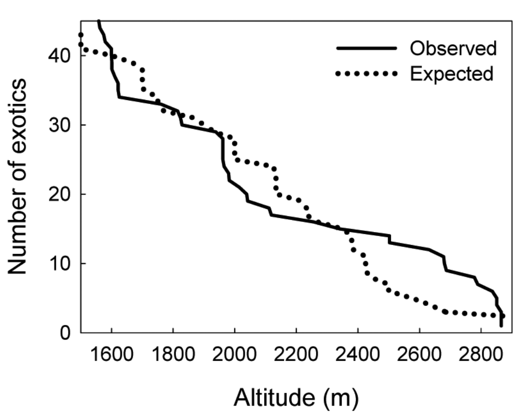

Fig. 2. Observed (—) and expected (---) cumulative number of exotic plant species against the altitudinal gradient of the Sani Pass road. The expected gradient was constructed for the same exotic species using the altitudinal distribution limits from Table 1.

Table 1. List of exotic plant species observed along the Sani Pass road between 1500-2873 m a.s.l., listing the highest observation and known upper altitudinal limit (m a.s.l.) following Germishuizen & Meyer (2003) or a specimen of the Natal University Herbarium (indicated with an asterisk (*)). The national invasion status followed the South African Biodiversity Act No.10 of 2004, indicating IAS for Invasive Alien Species and E for exotic species (Bromilow 2001).

Species name	Family	Status	Highest observation	Expected limit of occurrence
Agave americana	*Agavaceae*	E	1961	2500
Acanthospermum australe	*Asteraceae*	E	1824	1600
Bidens pilosa	*Asteraceae*	E	2503	1770
Cirsium vulgare	*Asteraceae*	IAS	2687	2134
Conyza canadensis	*Asteraceae*	E	2678	2125
Cosmos bipinnatus	*Asteraceae*	E	1558	2000
Hypochaeris radicata	*Asteraceae*	E	1980	2350*
Tagetes minuta	*Asteraceae*	E	2789	2425*
Taraxacum officinale	*Asteraceae*	E	2866	2500
Sisymbrium turczaninowii	*Brassicaceae*	E	2851	2450
Canna indica	*Cannaceae*	E	1579	1065
Chenopodium album	*Chenopodiaceae*	E	2681	2575
Acacia dealbata	*Fabaceae*	IAS	2015	1750
Acacia melanoxylon	*Fabaceae*	IAS	2112	1900
Acacia mearnsii	*Fabaceae*	IAS	2042	1700
Medicago polymorpha	*Fabaceae*	E	2256	2000
Trifolium repens	*Fabaceae*	E	1961	2233*
Hypericum forrestii	*Hypericaceae*	E	1599	2216
Hibiscus trionum	*Malvaceae*	E	1599	2635
Eucalyptus spec.1	*Myrtaceae*	E	1938	1500
Eucalyptus spec.2	*Myrtaceae*	E	1574	1500
Phytolacca octandra	*Phytolaccaceae*	E	1982	2134
Pinus spec.	*Pinaceae*	E	1829	1700
Plantago lanceolata	*Plantaginaceae*	E	2640	2425
Plantago major	*Plantaginaceae*	E	1601	1705
Avena fatua	*Poaceae*	E	2778	2233*
Bromus catharticus	*Poaceae*	E	2836	3000
*Bromus pectinatu*s	*Poaceae*	E	2851	2000
Cynodon dactylon	*Poaceae*	E	2503	2000
Lolium perenne	*Poaceae*	E	1961	2425*
Paspalum dilatatum	*Poaceae*	E	2342	2267*
Paspalum notatum	*Poaceae*	E	1760	1867*
Pennisetum clandestinum	*Poaceae*	E	2039	1700
Persicaria lapathifolia	*Polygonaceae*	E	1621	2385
Rumex crispus	*Polygonaceae*	E	2866	2380
Agrimonia procera	*Rosaceae*	E	1610	2134
Malus domestica	*Rosaceae*	E	1601	?
Prunus persica	*Rosaceae*	E	1965	1750
Richardia brasiliensis	*Rubiaceae*	E	1815	1667*
Salix babylonica	*Salicaceae*	E	1961	1933*
Salix fragilis	*Salicaceae*	E	1625	2440
Solanum mauritianum	*Solanaceae*	IAS	1621	1500
Datura stramonium	*Solanaceae*	IAS	1562	2380
Urtica urens	*Urticaceae*	E	2866	2685
Verbena bonariensis	*Verbenaceae*	E	2119	2135

community structure of plots differed only partially between the verge and adjacent land sample categories, as the community structure of these two groups was largely overlapping (Fig. 3). However, there was no difference in exotic plant community structure between plots uphill (on the mountain side) and downhill (on the valley side) of the road (results not shown).

Both richness and total exotic vegetation cover were related to verge width, altitudinal level, and sample category as each of these three variables had a significant effect on the model fit (Table 2). Adding road side (nested within sample category) as a term did not improve the model fit for either richness (three-level nested GLMs; $P > 0.05$) or total exotic vegetation cover ($P > 0.05$). Exotic species richness was higher in the verge category than in the adjacent land category (Fig. 4a). Plots in both road-verge and adjacent land categories showed a decrease in exotic richness with increasing altitude. In contrast, the total exotic vegetation cover in the adjacent land category of the lowest altitudinal level was three times higher than the verge category (Fig. 4b). At higher altitudes, however, total exotic vegetation cover was relatively low for all plots while no exotic species were observed in any of the pristine, annually monitored plots.

Four potential point sources of exotic propagules were identified along the current Sani Pass road: (1) old trading post 'Good Hope', (2) Mkhomazana resort, (3) South African border post, and (4) Sani Top vil-

Table 2. Nested analysis of deviance tables of the F-tests on the effects of predictor variables verge width, altitudinal level, and sample category (road-verge or adjacent land) on exotic plant species richness and total exotic vegetation cover (n = 80).

Response variable	res. deviance/df	df	F	P	Terms included	df	deviance % explained	F	P
Richness	30.64	3	34.83	< 0.0001	Verge width	1	17.19	32.71	< 0.0001
					Altitudinal level	1	26.77	50.94	< 0.0001
					Sample category (alt. level)	1	10.95	20.84	< 0.0001
Cover	185.50	3	35.96	< 0.0001	Verge width	1	22.45	37.28	< 0.0001
					Altitudinal level	1	37.70	62.61	< 0.0001
					Sample category (alt. level)	1	4.82	8.00	0.0060

lage (Lesotho border post) (Fig. 1). The mean distance d_{obs} between highest exotics observations (n = 45) and potential sources was 891 m (± 140 s.e.); significantly lower (modified one-sided t-test: t = 5.6166, df = 49.487, P < 0.0001) than the mean distance d_{ran} between 1000 randomly plotted points and nearest potential sources (1699 m ± 34), and therefore spatially clustered around the potential sources.

Discussion

Exotic plant species had invaded the verges of the Sani Pass road to a far greater degree than the adjacent landscape. We observed upper altitudinal limits for exotics that were often much higher than our expectation based on Germishuizen & Meyer (2003), or based on the specimens. As Germishuizen & Meyer (2003) is principally based on herbarium collections of the South African National Biodiversity Institute, an underestimation of the distribution range is to be expected as introduced species may not have had sufficient time to occupy all suitable areas (Welk 2004; Wilson et al. 2007), or due to low sampling effort (Wilson et al. 1992; Robertson & Barker 2006). Nevertheless, from an invasion biology and management perspective the observation of well-studied invasive alien species such as *Acacia dealbata* and *A. mearnsii* above their currently known altitudinal range is cause for concern, as it suggests that these species may have a larger potential habitat than expected or planned for, e.g., in the selection of suitable biological control agents (Olckers 2004). On the other hand, knowing that some exotic species have not reached their maximum altitudinal limit means that these exotics have the potential to expand their current distribution even further. Adequate management actions may be able to prevent exotics from establishing in the currently uninvaded

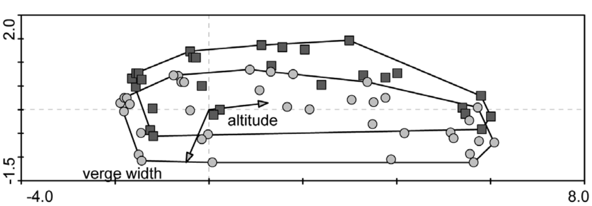

Fig. 3. Canonical Correspondence biplot of the exotic plant community structure model for plots and the significant environmental variables altitudinal level, verge width, and sample category. Sample symbols are shaped and enveloped according to sample category whereby circles represent plots located in the road verge and squares plots located in the adjacent land.

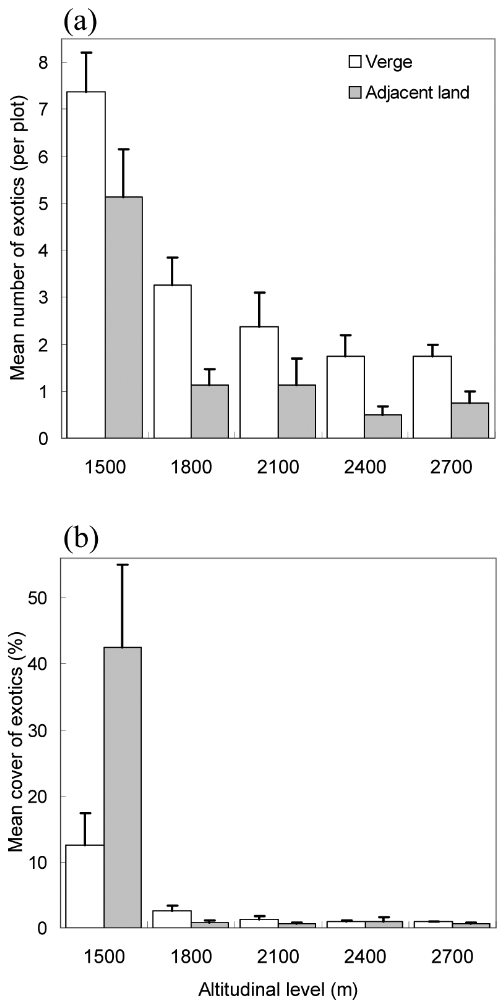

Fig. 4. (**a**) Exotic plant species richness and (**b**) total exotic vegetation cover per plot (top row) along the altitudinal levels, grouped by sample category. Error bars (n = 8) represent mean ± SE.

adjacent areas (Nel et al. 2004).

The clustering of exotics around potential sources suggests that exotic propagules may originate from human inhabited areas. Whether exotics are intentionally or accidentally introduced, anthropogenically disturbed habitats tend to facilitate the establishment and subsequent dispersal of exotics (Barton et al. 2004; Hill et al. 2005). A high propagule pressure of exotics could subsequently result in successful persistence outside the human inhabited areas, much like the dynamics of a metapopulation (Sax & Brown 2000; Guisan & Thuiller 2005). Although our results showed that successful establishment had mainly occurred in the relatively disturbed verges, the longevity and/or density of exotic propagules may cause future exotics to establish outside the verge or in the currently uninvaded pristine plots following disturbance events such as fire or erosion (Mooney et al. 2005).

Vehicles are potential sources of exotic propagules (Lonsdale & Lane 1994; Zwaenepoel et al. 2006; Von der Lippe & Kowarik 2007). Presently, the gravelled Sani Pass road is already a major scenic attraction for tourists visiting the Drakensberg region (Briggs 2006). The road is also an important link for trade between the relatively isolated town of Mokhotlong in Lesotho and the cities of Pietermaritzburg and Durban in South Africa, but is due to be tarred by 2009 (Radebe 2006). This anticipated tarring of the Sani Pass road will offer a unique opportunity to investigate the distribution of exotics along an altitudinal gradient after the sealing of the road surface. However, if the South African Ministry of Transport's intention of tarring this road by 2009 materializes (Radebe 2006), traffic volume is likely to increase substantially.

Increased traffic volumes should result in increased propagule pressure of established exotics, which could result in more exotics invading the adjacent landscape and reaching even higher altitudes. Moreover, vehicles are capable of introducing new exotic species into an area (Von der Lippe & Kowarik 2007). Although various measures, such as the prevention of exotic plant establishment and an annual exotic eradication programme, are planned to prevent the currently occurring exotic plants from spreading as a result of construction activities (ACER 2006), a long-term exotic control programme should be considered to ensure that this increased exotic propagule pressure does not result in more established populations of exotics, such as Pompom weed *Campuloclinium macrocephalum* (Henderson 2007), as a result of increased traffic volumes.

Although excluded from our statistical analysis, the observed high abundances of *Rubus* species in the 1500 m altitudinal level suggests an anthropogenic type of disturbance (Edees & Newton 1988). In the grassland biome, increases in the abundance of exotic *Rubus* spp. are associated with unnaturally high disturbance regimes (O'Connor 2005). Most *Rubus* spp. are adapted to resprout swiftly following disturbance events and, as a result, may subsequently outcompete slower developing species. As the tarring of the Sani Pass will increase traffic volumes, fire frequency in this area is also likely to increase with subsequent negative effects on local biodiversity (Fynn et al. 2004, 2005). If a future investigation confirms that the unidentified *Rubus* species recorded in the study area is a putative hybrid between the indigenous *R. rigidus* and the North American exotic *R. cuneifolius*, the possibility of this hybrid developing into an evolutionary adapted strain is a serious cause for concern (Facon et al. 2006).

Conclusion

We showed that exotic species composition, richness and total exotic vegetation cover are mostly explained by altitudinal level, followed by verge width and sample category, whereby verge width is regarded a surrogate for the extent of local disturbance, and road side as the direction of water run-off. This combination of explanatory variables confirms that the invasion status of the study area is predominantly negatively correlated with altitude (Arévalo et al. 2005; Becker et al. 2005), and that local disturbance increases the extent of the invasion status (Gelbard & Harrison 2005).

Single disturbance events and increased water run-off may already cause verges to become entirely and persistently invaded by exotics (Kalwij et al. in press). It is therefore of critical ecological importance that future road construction minimizes disturbance and erosion caused by water run-off onto adjacent land by using a drainage system of sufficient capacity to handle downpours in this region (Anon. 2003). Construction work must be succeeded by a habitat restoration programme that includes the eradication of exotics at an early stage of their development, as an established seedbank of exotics will negatively affect future vegetation succession (Pakeman & Small 2005). If such an early-stage control programme is not properly implemented, financial costs and environmental effects of the road construction are likely to be long-lasting and of high impact on biodiversity (Rejmánek & Pitcairn 2002; Stohlgren & Schnase 2006), especially in areas characterised by unique ecosystems such as the Ukhahlamba-Drakensberg region (Carbutt & Edwards 2004, 2006). In addition, an effective long-term exotic control programme should be implemented to prevent exotics from building up seedbanks. Finally, fire control infrastructure and public awareness programmes must reduce the frequency of wildfires, especially outside the natural fire season (Fynn et al. 2004).

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