EXAMINING THE SPATIOTEMPORAL DYNAMICS OF EXOTIC PLANTS IN A MONTANE GRASSLAND: MECHANISMS AND MANAGEMENT
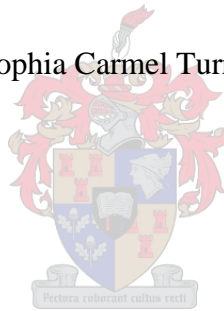
by

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Tesis ingelewer ter gedeeltelike voldoening aan die vereistes vir die graad Magister in Natuurwetenskappe aan die Universiteit van Stellenbosch

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Declaration

By submitting this thesis electronically, I declare that the entirety of the work contained therein is my own, original work, that I am the sole author thereof (save to the extent explicitly otherwise stated), that reproduction and publication thereof by Stellenbosch University will not infringe any third party rights and that I have not previously in its entirety or in part submitted it for obtaining any qualification.

Sophia Carmel Turner

April 2019

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Dedication

To all those curious minds that dared to keep asking: "But why?"

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This project is the product of collective support from several parties. Firstly, the DST-NRF Centre of Excellence for Invasion Biology (C·I·B) and its hub staff. Never have I ever had so many people backing me on a single goal. Thank you for allowing me to divert my attention from my primary role as Iimbovane Outreach Project Assistant Officer (Outreach), to further   my studies. Thank you for the funding and mobility to expand my skillset and challenge myself through taking the BDE212 module at Stellenbosch University, as well as attending conferences to better my communication and networking skills. The support has been far beyond financial. Thank you to Dave Richardson and John Wilson for integrating me in your lab working group, providing the opportunity to interact with other students regularly, attend discussion groups and working group retreats, and experience working on a joint paper. It was inspirational. Any academic successes that I achieve in the future are linked to my foundation at the C·I·B, I am but a mere by-product of your brilliance. Thank you.

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I am incredibly grateful to my family and friends. Thank you to my parents for always thinking I am better than I am. Thanks to all my siblings for your endless support shown in various ways. And my friends – my comrades in this common pursuit, thank you for always understanding when I was constantly "too busy". I am extremely grateful to AN and CM for advising on different sections of this thesis. MC, for all your motivation and words of wisdom, I am indebted to you always. I do not know what I would have done without you.

Finally, I would like to thank my examiners for taking the time to review my work.

Summary

Despite a surge of research on exotic species in alpine habitats, a lack of reliable baseline data has inhibited long-term understanding about exotic species dynamics in mountain ecosystems across the world. A long-term study of species invasion in the Drakensberg region of South Africa provides an important exception. Making use of historical data collected in this system, vegetation surveys and online sources, this thesis investigates the underlying mechanisms resulting in exotic species establishment in mountain ecosystems, and whether prioritizing invasion introduction pathways is an optimal management strategy for the area.

To investigate the change in exotic plant species richness and composition in and adjacent to a mountain pass road verge; and explore the role of the road verge in exotic species establishment, I complemented data collected ten years prior with a re-survey of road verge and adjacent transects in semi-natural habitat (N = 80; 25x2m) across an elevational gradient of 1500-2874 m a.s.l.. Along all transects, exotic species richness, exotic species cover, indigenous species cover and bare soil cover was estimated. Generalized Linear Models were fitted to test whether exotic richness, vegetation cover and bare soil had changed over time, and a Canonical Correspondence Analysis was used to estimate changes in exotic species composition. Since the initial survey, exotic species richness increased significantly across the entire elevational gradient, particularly in the mid-elevational zones. This distribution pattern indicates small-scale jump dispersal, which is likely driven by human-mediated activities, rather than gradual range expansion. Exotic species composition became more homogenous between road verge and semi-natural transects, showing that exotic species are spreading into natural habitat. It is likely that propagule pressure is key for colonization success, while disturbance in the road verges fosters spread both in elevation and expansion into the natural area. Further expansion of exotic species into the natural area can be expected.

Invasive species management can be executed either through prioritizing species, sites or introduction pathways. Pathway management is particularly useful when propagule pressure is the dominant driver of invasion success. Knowing the important role of propagule pressure in this study system, I then investigated whether prioritizing introduction pathways would be an efficient approach to reduce exotic species richness and expansion. I did this by identifying the likely vectors and introduction pathways of exotic species along the Sani Pass, to see if successful exotic species made use of a specific vector or pathway.

The likely introduction pathways of all the exotic species was categorized using information from online sources. Generalized linear models (GLMs) were used to test whether

successful exotic species were associated with specific introduction pathways. Extent of exotic species' presence in the natural area was used as a proxy for success. I also tested whether the number of pathways used by exotic species was related to their success, using GLMs. Successful species in the area do not utilise multiple introduction pathways, and only unintentional transport stowaways are significantly associated with presence in the natural area. These results show that successful species enter through vectors such as vehicles, people and livestock. Adopting stringent control of these vectors at the border posts will likely reduce the introduction of new exotic species in the area.

Opsomming

Ten spyte van die groeiende navorsing in uitheemse spesies in hoë berg-alpiene gebiede, beperk die gebrek aan betroubare basislyndata die langtermyn begrip van uitheemse spesiesdinamika in berg-ekosisteme. 'N uitsondering is egter die langtermyn studie van indringerspesies in die Drakensberg streek van Suid-Afrika. Deur gebruik te maak van historiese data wat in hierdie stelsel ingesamel is, plantegroei opnames en aanlynbronne, ondersoek hierdie proefskrif die onderliggende meganismes wat tot uitheemse indringer spesies in bergekosisteme lei, en of die prioritering van die oorspronklikke verspreidings meganismes 'n optimale bestuurstrategie vir die gebied is.

Deur die verandering te ondersoek in die uitheemse spesierykheid en samestelling van die plantegroei in en aangrensend tot die bergpas; en die ondersoek van die rol van die padrand in uitheemse spesie vestiging, het ek die volgende gebruik. Data wat tien jaar gelede versamel is, is gekomplimenteer deur 'n heropname van die padrand en aangrensende transekte in die semi- natuurlikke habitat (N = 80; 25x2m) oor 'n hoogtegradient van 1500- 2874 meter bo seespieël. Langs elke transekt is alle uitheemse spesies en die algehele inheemse spesie-dekking aangeteken. Algemene Lineêre Modelle is toegepas om te toets of uitheemse spesie rykheid, plantbedekking en kaal grond oor tyd verander het, en 'n Canonical Correspondence Analysis is gebruik om veranderinge in uitheemse spesiesamestelling te bepaal. Sedert die aanvanklike opname het uitheemse spesiesrykheid aansienlik toegeneem oor die hele hoogtegradiënt, veral in die sones van middel ligging. Hierdie verspreidingspatroon dui op sprong-verspreiding, wat waarskynlik deur mensgemedieerde aktiwiteite gedryf word, eerder as geleidelike verspreiding. Uitheemse spesiesamestelling het meer homogeen tussen padrand en semi- natuurlike transekte geword, wat bewys het dat uitheemse spesies in die natuurlike habitat indring. Dit is waarskynlik dat propagule druk (saad beskikbaarheid) die sleutel tot indringing is, terwyl versteuring in die padrandte beide verspreiding in die natuurlike gebied en verspreiding in hoogte be seespiël bevorder. Verdere verspreiding van uitheemse spesies in die natuurlike gebied kan dus verwag word.

Indringerbestuur kan uitgevoer word deur die priotiseering van spesies, òf gebiede òf verspreidings meganismes. Laasgenoemde is veral handig wanneer propagule druk die dominante aanvoerder van indringing sukses is. Weens die belangrikke rol van propagule druk in hierdie studiestelsel, het ek dan ondersoek ingestel of die bestuur van plaaslike skaal inbringingsweë 'n effektiewe benadering sou wees om uitheemse spesiesrykheid te verminder.

Die waarskynlike inbringingsweë van elke uitheemse spesie is gekategoriseer met behulp van inligting uit aanlynbronne. Algemene lineêre modelle is gebruik om te toets of suksesvolle uitheemse spesies geassosieer word met spesifieke inbringingsweë. Die omvang van uitheemse spesieteenwoordigheid in die natuurlike gebied is as 'n proxy vir sukses gebruik. Ek het ook getoets of die aantal indringingsweë wat deur uitheemse spesies gebruik word, met hul sukses verband hou deur middel van algemene lineêre modelle. Suksesvolle indringerspesies in die omgewing gebruik nie veelvuldige inbringingsweë nie, en slegs toevallige vervoersaamryers word aanmerklik geassosieer met die teenwoordigheid in die natuurlike omgewing. Hierdie resultate toon dat suksesvolle indringerspesies deur vektore soos voertuie, mense en vee die gebied binne kom. Met die toepassing van streng beheer van hierdie vektore by die grensposte, sal die waarskynlikheid van die inbring van nuwe uitheemse spesies in die gebied verminder.

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Definitions

Exotic species: (synonyms: non-native, introduced, non-indigenous species) species present in an area beyond their native range, through human-mediated dispersal.

Hinterland: the natural area adjacent to the roadside, considered semi-natural.

MIREN: Mountain Invasion Research Network

Mountain Ecosystems: synonymous with "high elevation areas" and "montane ecosystems"

MRI: Mountain Research Initiative

NOP: Number of Pathways

Introduction pathway: the human-mediated processes that result in the introduction of exotic species from one geographical region to another.

PINT: Presence in Natural Area

POI: Points of Introduction

Ruderal: opportunistic weedy plant species that thrives in disturbed areas

Transect categories used in study:

— Adjacent natural: Transects occurring in the natural area immediately adjacent to the roadside. These transects are not directly affected by road activities and are considered semi-natural –pristine transects. Also called "natural transects".

— Road verge: Also called roadside verge transects. Transects present within the roadside. These are considered disturbed transects.

Vector: dispersal mechanisms that can be natural (wind, water, birds, mammals, amphibians, etc.) and human-mediated. It is synonymized with mode, transport mechanism, carrier, and bearer.

Verge: also called roadside, the area directly adjacent to the road, and still effected by road activities (i.e. considered disturbed).

ZIP models: Zero-inflated Poisson regression models. Such models are used for count data that has too many zero counts. Theoretically, zeros and counts can be modelled separately since they are generated from different processes. Therefore, ZIP models consist of two models, a Poisson model, for counts as well as a logit model, for excess zeros.

References:

Ansong, M., Hons, B. S., & Sc, M. (2015). Unintentional human dispersal of weed seed, (September).

Richardson, D. M., editor. 2011. *Fifty Years of Invasion Ecology: The Legacy of Charles Elton.* Wiley-Blackwell, Oxford.

Zero-inflated Poisson Regression: R Data Analysis Examples. UCLA: Statistical Consulting Group. Retrieved from: https://stats.idre.ucla.edu/r/dae/zip/

CHAPTER 1: GENERAL INTRODUCTION

Mountain ecosystems serve as important study systems for ecological studies. The natural gradient present can provide insights into how a given plant species or community responds to variables, such as UV radiation, precipitation, altitude and air pressure (Alexander et al. 2009, Alexander at al. 2016). For this reason, the patterns and underlying mechanisms of indigenous vegetation in mountain ecosystems are well-studied, however, comparatively less is known about exotic plants in mountain systems (Guo et al. 2018). One reason for mountain ecosystems being relatively understudied in invasion science is that the "boom" in invasion science research only occurred once invasive species began causing environmental and socioeconomic problems (Blackburn et al. 2011, Hill et al. 2016). Concerted research efforts were then undertaken to understand the ecology of invasive species, and further developed to look at prevention, management and restoration (Thuiler et al. 2006, Blackburn et al. 2011). These efforts lead to most studies taking place in heavily invaded areas, such as in lowlands and near water sources (Pauchard, *et al.* 2009, Chamier *et al.* 2012). Mountain ecosystems were a low priority in invasion science, since it was perceived that the harsh growing conditions and low propagule pressure were sufficient in hindering invasions (Millennium Ecosystem Assessment, 2003).

Globalisation and free trade progression have greatly enhanced the opportunity for species movement beyond their native ranges (Lockwood *et al.* 2009, van Wilgen *et al.* 2014). Indeed, the movement of exotic species is on the rise, and showing no signs of saturation (Van Kleunen et al. 2015, Seebens *et al.* 2017). Exotic species are introduced to new areas through a range of activities including horticulture, agriculture, forestry, interconnected waterways and as stowaways on vehicles (van Wilgen *et al.* 2014. Cadotte et al. 2018). Therefore, exotic species are progressively expanding into mountainous areas, and increasingly seen as a threat to such regions (Bacaro *et al.* 2015, Pauchard *et al.* 2009).

In the last two decades, there has been an upsurge of research on mountain invasions (Lembrechts et al. 2016, Alexander et al. 2016), including the creation of dedicated research networks, such as the Mountain Invasion Research Network (henceforth, MIREN) (http://www.mountaininvasions.org/) (Dietz *et al.* 2005), and the Mountain Research Initiative (MRI) (http://www.mountainresearchinitiative.org/en/). While such global initiatives have established a strong foundation on the distributional patterns and dynamics of exotic vegetation in mountain ecosystems, some questions remain unanswered. Factors inhibiting research on mountain invasions thus far include a dearth of reliable baseline data for temporal studies, and sampling biases due to the limitations of conducting surveys in challenging, mountainous terrain.

This thesis is comprised of two data chapters (Figure 1.1). The first data chapter investigates the mechanisms behind the spatiotemporal change in exotic species richness and composition along a mountain roadside and the adjacent natural area. The second data chapter focuses on the management of exotic species in the same study area, by using data collected in the first data chapter, in unison with information acquired from various online sources.

While we know that anthropogenic disturbance and propagule pressure are the likely causes of exotic species spread in mountain ecosystems (McDougall et al. 2011, Pauchard et al. 2009, Haider et al. 2018), how these mechanisms change in importance through space and time is less apparent (Guo et al. 2018). Many of the studies in mountain ecosystems focus on species richness change and expansion beyond upper elevational range limits (Lenoir et al. 2008, Dainese et al. 2017, Lembrechts et al. 2017). Yet, no known studies to date have investigated the spatiotemporal change in exotic species composition. Considering this gap, my first data chapter (Chapter 2) investigates the spatiotemporal change in exotic species richness and composition along the road verges and adjacent natural area of the Sani Pass, a well-travelled gravel mountain road in the Drakensberg Mountains, South Africa. This chapter makes use of historical data collected in the study system (Kalwij et al. 2008), coupled with a re-survey conducted 10 years later to answer the following research questions, (i) How has exotic plant species richness and composition changed in and adjacent to a montane road verge over a 10-year period? And (ii) Are montane road verges conduits of exotic species dispersal?
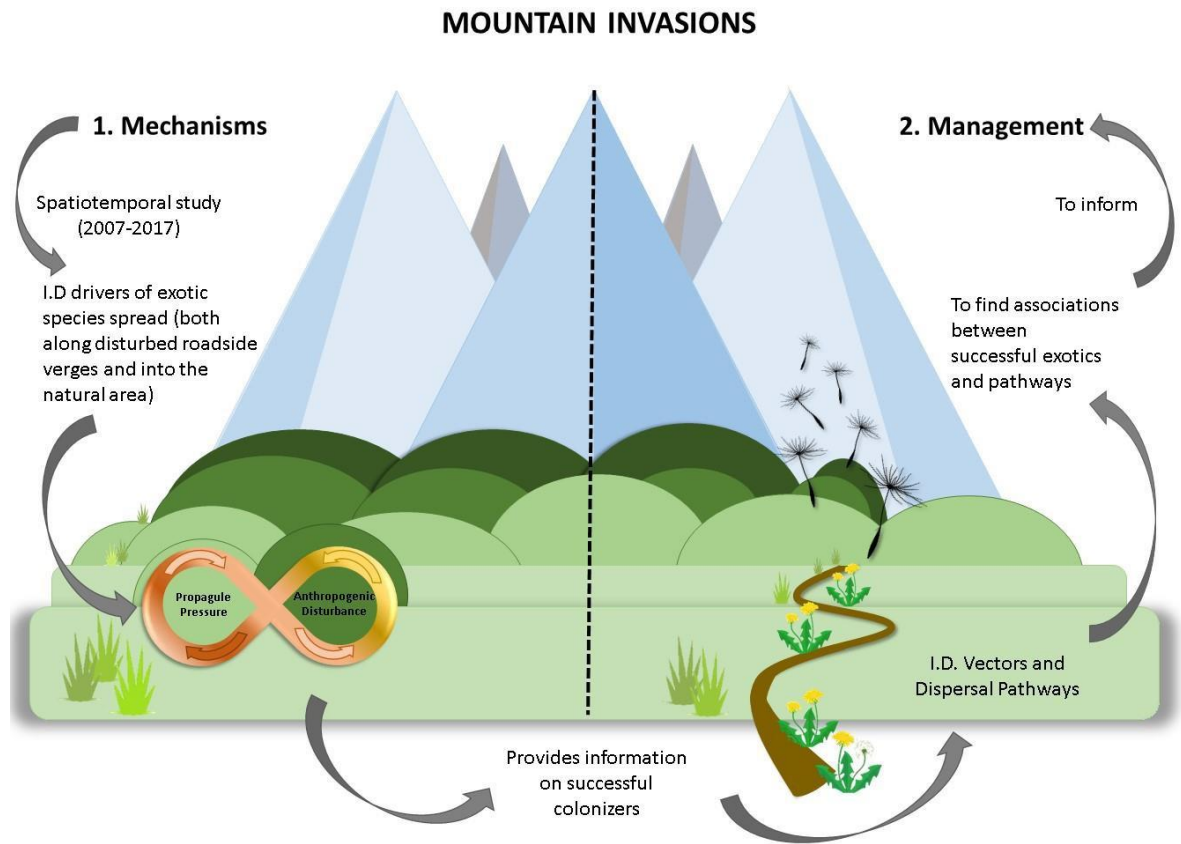
Pathways are defined as the various mode(s) that aid a species entry and spread throughout a region (FAO, 2007). Managing pathways is essential to reduce the introduction of new, potentially harmful exotic species (Faulkner et al. 2014, Essl et al. 2015, Keller et al. 2018). Local-scale pathway identification and management is less common than global- and national-scale management propositions. However, understanding how to manage local pathways of invasives is useful since regions and countries are heterogeneous and the type of species and their associated pathways are likely to differ between regions (Faulkner et al. 2016, Robertson et al. 2017). Prioritizing pathways instead of species or areas is an efficient management tool against species with a high propagule pressure, this has been shown with freshwater and marine invaders (McGeoch et al. 2016, Keller et al. 2018). Since propagule pressure is a key contributor to the success of exotic vegetation, particularly in mountain ecosystems (Johnston et al. 2008, Kalwij et al. 2015), my second data chapter identifies the various pathways of exotic species into the Sani Pass and investigates whether successful species are associated with particular pathways. The aims of this chapter were to test (i) whether different pathways are associated with a higher or lower probability of introducing successful exotic species, and (ii) whether there is a

relationship between successful species and the number of pathways through which a species has been introduced.

Conducting such research has specific requirements. Firstly, spatiotemporal studies require reliable, and relevant data on the exotic species present in a mountain system. The area needs to cover a large enough gradient to provide meaningful results. To measure the change both in elevation and spread into the natural area, transects need to be situated both in the roadside verges and the adjacent natural area. Reducing bias by having a researcher from the original survey present is ideal. Secondly, to understand the introductory pathways to invasive species in mountain ecosystems, one needs a system where there is sound data on the exotic species present in the area. The introductory pathways need to be easily identifiable. Complex anthropogenic development can make it difficult to derive conclusions. Fitting the physical requirements, being a well-studied area with available historical data makes the Sani Pass, a mountain pass in the Drakensberg region of South Africa a suitable setting to answer the above research questions (Bishop et al. 2014, Steyn et al. 2016).

The final chapter of this thesis collates the main findings of the two data chapters into a general conclusion. Please note that the two data chapters were written with the intention of submission as separate publications, therefore some overlap is evident in particular sections, and referencing style differs. Additionally, since these intended manuscripts include co-authors, pronoun use changes from "I" to "we" for Chapters two and three.

Figure 1.1. A conceptual graphic depicting the two data chapters of this thesis and how they are linked. Chapter 2 uses a spatiotemporal study (2007-2017) to identify the drivers of exotic species spread, and the role of road verges in this. Information from chapter 2 on which species are present in the area, as well as which species that have spread into the adjacent natural area is used in addition to information of the likely, local dispersal pathways of each species, to investigate if there are any associations between successful colonizers and particular pathways. The purpose of Chapter 3 is to identify whether pathway prioritization is a feasible tool for conservation management in the area.

References:

Alexander, J. M., Edwards, P. J., Poll, M., Parks, C. G., & Dietz, H. (2009). Establishment of parallel altitudinal clines in traits of native and introduced forbs. *Ecology*, *90*(3), 612– 622. https://doi.org/10.1890/08-0453.1

Alexander, J. M., Lembrechts, J. J., Cavieres, L. A., Daehler, C., Haider, S., Kueffer, C., … Seipel, T. (2016). Plant invasions into mountains and alpine ecosystems: current status and future challenges. *Alpine Botany*. https://doi.org/10.1007/s00035-016-0172-8

Bacaro, G., Maccherini, S., Chiarucci, A., Jentsch, A., Rocchini, D., Torri, D., … Arévalo, J.R. (2015). Distributional patterns of endemic, native and alien species along a roadside elevation gradient in Tenerife, Canary Islands. *Community Ecology*, *16*(2), 223–234. https://doi.org/10.1556/168.2015.16.2.10

Bishop, T. R., M. P. Robertson, B. J. van Rensburg, and C. L. Parr. 2014. Elevation-diversity patterns through space and time: ant communities of the Maloti-Drakensberg Mountains of southern Africa. Journal of Biogeography **41**:2256-2268.

Blackburn, T.M. Pysek, P. Bacher, S. Carlton, J. Duncan, R.P. Jarosik, V. Wilson, J.R.U. Richardson, D.M. 2011. A proposed unified framework for biological invasions. *Trends in Ecology & Evolution,* 26(7): 333-339.

Cadotte, M. W., Campbell, S. E., Sodhi, D. S., & Mandrak, N. E. (2018). Preadaptation and Naturalization of Nonnative Species : Darwin's Two Fundamental Insights into Species Invasion, (February), 1–24.

Chamier, J. Schachtschneider, K. le Maitre, D.C. Ashton, P,J. & van Wilgen, B.W. 2012. Impacts of invasive alien plants on water quality, with particular emphasis on South Africa. *Water SA*, *38*(2): 345-356

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, (July). https://doi.org/10.1038/NCLIMATE3337

Dietz, H. Kueffer, C. & Parks. C.G. 2006. MIREN: A new research network concerned with plant invasion into mountain areas. Mountain Research and Development 26: 80-81.

[FAO] Food and Agriculture Organization of the United Nations. 2007. International Standards for Phytosanitary Measures: Glossary of Phytosanitary Terms. FAO. ISPM no. 5. (02 December 2018; *http://agriculture. gouv.fr/IMG/pdf/ispm_05_version_2007_ang.pdf*)

Faulkner, K. T., Robertson, M. P., Rouget, M., & Wilson, J. R. U. (2016). Understanding and managing the introduction pathways of alien taxa : South Africa as a case study, 73– 87. https://doi.org/10.1007/s10530-015-0990-4

Faulkner, K. T., Robertson, M. P., Rouget, M., & Wilson, J. R. U. (2014). A simple, rapid methodology for developing invasive species watch lists, *179*, 25–32.

Guo, Q., Knott, J., Fei, S., Shen, Z., Iannone, B. V, & Chown, S. L. (2018). A global analysis of elevational distribution of non-native versus native plants, 793–803. https://doi.org/10.1111/jbi.13145

Haider, S., Kueffer, C., Bruelheide, H., Seipel, T., Alexander, J. M., Rew, L. J., … Milbau, A. (2018). Mountain roads and non-native species modify elevational patterns of plant diversity, (April 2017), 667–678. https://doi.org/10.1111/geb.12727

Hill, M.P., Clusella-Trullas, S., Terblanche, J.S., Richardson, D.M. 2016. Drivers, impacts mechanisms and adaptions in insect invasions. *Biol Invasions* 18:883-891.

Johnston, E.L. Piola, R.F. Clarke, G.F. 2008. The Role of Propagule Pressure in invasion success. In Rivlov, G. Crooks, J.A. (eds). *Biological Invasions in Marine Ecosystems,* Ecological Studies 204, pp 133-151. Berlin, Heidelberg, Springer-Verlag.

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*(12), 3517–3529. https://doi.org/10.1007/s10530-015-0975-3

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*(12), 3517–3529. https://doi.org/10.1007/s10530-015-0975-3

Keller, R. P., Ermgassen, P. S. E. Z., & Aldridge, D. C. (2018). Vectors and Timing of Freshwater Invasions in Great Britain Vectors and Timing of Freshwater Invasions in Great Britain, *23*(6), 1526–1534.

Lembrechts, J.J. Alexander, J.M. Cavieres, L.A. Haider, S. Lenoir, J. Keuffer, C. McDougall, K. Naylor, B.J. Nuñez, M.A. Pauchard, A. Rew, L.J. Nijs, I. Milbau, A. 2016. Mountain roads shift native and non-native plant species'range. *Ecography* 39: 001-012.

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.

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*(5), 904–910. https://doi.org/10.1111/j.1472- 4642.2009.00594.x

McDougall, K.L. Khuroo, A.A. Loope, L.L. Parks, C.G. Pauchard, A. Reshi, Z.A. Rushworth, Keuffer, C. 2011. Plant Invasions in mountains: Global Lessons for Better Management. *Mountain Research and Development,* 31 (4): 380-387.

McGeoch, M. A., Genovesi, P., Bellingham, P. J., Costello, M. J., McGrannachan, C., &

Sheppard, A. (2016). Prioritizing species, pathways, and sites to achieve conservation targets for biological invasion. *Biological Invasions*, *18*(2). https://doi.org/10.1007/s10530-015-1013-1

Millennium Ecosystem Assessment. 2003. Ecosystems and human well-being: a framework for assessment. Island Press, Washington, DC.

Pauchard, A., Kueffer, C., Dietz, H., Daehler, C. C., Alexander, J., Edwards, P. J., … Seipel, T. (2009). Ain't no mountain high enough: Plant invasions reaching new elevations. *Frontiers in Ecology and the Environment*, *7*(9), 479–486. https://doi.org/10.1890/080072

Robertson, M. P. (2017). The balance of trade in alien species between South Africa and the rest of Africa, 1–16.

Seebens, H., Blackburn, T. M., Dyer, E. E., Genovesi, P., Hulme, P. E., Jeschke, J. M., … Essl,F. (2017). No saturation in the accumulation of alien species worldwide. *Nature Communications*, *8*. https://doi.org/10.1038/ncomms14435

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*(2), 337–346. https://doi.org/10.1111/jvs.12477

Thuiler, W. Richardson, DM. Rouget, M. Procheş, Ş & Wilson, JR. (2006). Interactions between environment, species trait, and human uses describe patterns of plant invasions. *Ecology,* 87(7): 1755-1769. https://doi.org/0012-9658

Van Kleunen, M., Dawson, W., Essl, F., Pergl, J., Winter, M., Weber, E., … Pyšek, P. (2015). Global exchange and accumulation of non-native plants. *Nature*, *525*(7567). https://doi.org/10.1038/nature14910

Van Wilgen, B.W. Davies, S. J. Richardson, D.M. 2014. Invasion science for society: A decade of contributions from the Centre for Invasion Biology. *S Afr J Sci,* 110 (7/8): 1-12.

Wilson, J. R. U., Richardson, D. M., Faulkner, K. T., Rahlao, S. J., Zengeya, T. A., & Wilgen, B. W. Van. (2018). Indicators for monitoring biological invasions at a national level, (June), 2612–2620. https://doi.org/10.1111/1365-2664.13251

CHAPTER 2: ROAD VERGES FACILITATE EXOTIC SPECIES EXPANSION INTO A NATURAL UNDISTURBED MONTANE GRASSLAND

Introduction

Mountain ecosystems are increasingly recognised as susceptible to colonization by exotic species (Pauchard et al. 2009, Alexander et al. 2016). Despite the fact that harsh environmental conditions and low propagule pressure were thought to sufficiently hinder exotic species from establishing and becoming invasive in these ecosystems (Pauchard et al. 2016). These environmental barriers were assumed to ensure that mountain ecosystems remain relatively pristine (Millennium Ecosystem Assessment 2003). Evidence of the growing presence of exotic plant species in mountain ecosystems has been observed at a global scale (Alexander et al. 2016, (Haider et al. 2018). Not only are exotic species successfully moving into mountain ecosystems, they are also spreading to higher elevations, and in some cases, 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). While such studies show that exotic species are increasingly found at high elevations, due to a deficiency in historical data, none provide information on the rate of change in abundance and composition.

Several environmental variables have been attributed to explain the introduction and establishment of exotic species in mountain ecosystems, with propagule pressure and disturbance generally considered as the primary short-term, small-scale drivers (Pauchard and Shea 2006, Lembrechts et al. 2016). Propagule pressure is the number of individuals and/or number of introductions of a species to an area, whereby species with high propagule pressure are more likely to become invasive than species exhibiting low propagule pressure (Lockwood et al. 2009). Habitat disturbance, whether of anthropogenic origin (e.g., trampling, verge maintenance) or due to natural processes (e.g., mudslides, rock falls, water run-off) facilitates the introduction and subsequent establishment of exotic pioneer species (Hierro et al. 2006, Pauchard and Shea 2006). Mountain ecosystems are subject to lower levels of propagule pressure and higher levels of disturbance than densely populated areas at lower elevations (McDougall et al. 2011). However, since biotic resistance to exotics decreases with elevation (Pauchard et al. 2009), habitat disturbance is considered to be the most significant factor facilitating exotic species establishment in mountain ecosystems (Lembrechts et al. 2016, Dainese et al. 2017, Sandoya et al. 2017). This is particularly true for exotic species with a ruderal life strategy (Hierro et al. 2006). Therefore, the rate at which new populations of exotic

species colonize mountain ecosystems is likely to largely depend on the frequency and intensity of human activities.

A major indicator of human activity is the presence of roads. Indeed, roads have completely altered global ecology (Ibisch et al. 2016). Roads are well-known pathways for biological invasions due to, amongst others, the persisting disturbance of adjacent habitats, habitat fragmentation, disruption of soil ecology, and changed hydrology (Ansong and Pickering 2013). While roadside verges can, through careful conservation management, act as habitat refugia in strongly converted habitats, they can also play the opposite role in more pristine areas (Procheş et al. 2005). By and large, road verges are subject to recurring anthropogenic disturbance, which can lead to the establishment of exotic plant populations (Lembrechts et al. 2016). Since traffic density is associated with habitat disturbance and potential propagule pressure, road verges with a high traffic density have a substantial richness and abundance of exotic species as compared to low traffic density roads (Hansen and Clevenger 2005, Benedetti and Morelli 2017). Indeed, vehicles are an important driver in the long-distance dispersal of exotic plants (Von der Lippe and Kowarik 2007, Taylor et al. 2012), especially of annual forbs and perennial graminoids (Ansong and Pickering 2013, Khan et al. 2018). In mountain ecosystems, the richness and composition of exotic vegetation is primarily influenced by anthropogenic modifications, particularly in the lowlands and close to roads (Bacaro et al. 2015). Therefore, 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 (Pauchard et al. 2009, Lembrechts et al. 2016).

Despite the recent increase of research on alpine invaders, a lack of reliable baseline data on exotic species has inhibited our understanding of the temporal dynamics of these plant communities in pristine montane areas adjacent to road verge habitats (Kalwij et al. 2015, Seipel et al. 2016). 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 and Macek 2015). A long-term monitoring project on exotic species along a mountain pass in the Drakensberg region of South Africa provides such prerequisites. This is a well-utilised area for biodiversity studies, subject to both short-term and long-term projects on insects and vegetation (Bishop et al. 2014, Steyn et al. 2017). Baseline data collected during an earlier study (Kalwij et al. 2008), and supplemented with annual survey data on the upper elevational range limits of exotic plant species (Kalwij et al. 2015), therefore provided a suitable opportunity to measure the spatiotemporal trends of exotic plant

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composition in a mountain ecosystem.

The aim of this study is to quantify the spatiotemporal patterns of exotic plant species richness and composition along road verges and within adjacent natural grassland of a mountain ecosystem, and to determine the underlying ecological mechanisms driving spatiotemporal compositional trends. Based on the amount of time that has passed since the initial survey in 2007, and the increase in upper elevational limits of exotics over time (Kalwij et al. 2015), we expected the richness and abundance of exotic species to have increased. We also anticipated that this increase has occurred predominantly in the road side verges, but with some exotic species expanding to the adjacent grassland due to persistent propagule pressure and repeated habitat disturbance. To test this hypothesis, we re-surveyed 80 transects across an elevational gradient, 10 years after the original survey, and compared the two datasets. Kalwij et al. (2008) identified four points of introduction (POI) for propagules along the Sani Pass road: (1) old trading post 'Good Hope', (2) Mkhomazana resort, (3) South African border post, and (4) Sani Top village (Lesotho border post). In the 2007 study, the distance of transects to these POI was directly related to exotic species richness. Due to the known importance of propagule pressure in exotic species introduction, we related the temporal change in exotic species richness to the distance of the closest of four points of introduction (POI) of propagules identified in 2007. We posit that an eventual increase in exotic richness or cover is related to the distance from these POI. We then discuss the various ecological mechanisms that contributed to our results as well as the future expectations and how this study parallels global perspectives on mountain invasions.

Methods

Study area

The Drakensberg Alpine Centre (DAC) is a 40'000 km² range of mountains situated in the west KwaZulu-Natal, South Africa, on the eastern flank of Lesotho (Carbutt and Edwards 2004). The DAC is the southernmost tip of the Afromontane regional centre for endemism (Carbutt and Edwards 2004). Within the DAC is uKhahlamba-Drakensberg Park, a UNESCO World Heritage site, which is well known for its incredibly high plant and animal diversity. This entire area falls within the grassland biome and has an annual rainfall of 990–1180 mm (Mucina and Rutherford 2006).

The study site was a mountain pass located at the cusp of uKhahlamba-Drakensberg Park, called Sani Pass (29°17–39' E, 29°35–39' S). This 20-km stretch of gravel road extends from 1500–2874 m a.s.l., offering a steep elevational gradient leading up to Lesotho. Sani Pass

is the only road in an otherwise pristine grassland. This road is an important trade route and border crossing between South Africa and Lesotho, with daily movement of locals, both in vehicles and on foot with livestock. Plans to upgrade sections of the road were implemented in the months leading up to the second survey season of this study (in 2017). This resulted in the presence of road construction along the study site during the 2017 plant surveys.

In these grasslands, disturbance includes natural and anthropogenic fires and low-intensity grazing. Natural disturbance by torrential rains is also common, and causes soil erosion, which can create deep rifts in sections of the road verges. The exceptionally diverse plant and animal life, and compelling setting makes this area a well-known tourist destination. Four consecutive years of data between 2007 and 2017 showed the traffic density of the area has remained constant, with an estimated 10'000 people crossing the border from South Africa and back per annum (Kalwij et al. 2015).

Sampling

Data collection occurred in January 2017, ten years after a study conducted by Kalwij et al. (2008). Sampling followed the protocol set out in Kalwij et al. (2008). The first author was present in this second sampling; this ensured sampling remained consistent with the initial survey and avoided bias. The road was divided into five elevational bands in 300-m intervals: 1500 m, 1800 m, 2100, 2400 m, and 2700 m a.s.l. In 2007, four locations were randomly chosen within each band. Each location consisted of four transects: a road verge transect and an adjacent natural grassland transect and the same on the opposite side of the road. Therefore, eighty transects were surveyed in total, following a nested split-plot design. In 2017, a handheld GPS was used to relocate these locations. The verge was defined as the area directly alongside the road and affected by road-related disturbance. Verge width varied between <1 and 7 m. Road verge transects were 25 m long and 2 m wide where possible. The adjacent natural grassland transects were all 50×2 m. In each transect, we estimated the cover of each exotic species, as well as the overall indigenous and bare soil cover using the Braun-Blanquet scale (Van der Maarel 1979).

Quantifying disturbance and propagule pressure

Considering the important role of disturbance and propagule pressure in exotic species success, we quantified them as follows: bare soil cover percentage was used as a proxy for disturbance. Kalwij et al. (2008) identified four points of introduction (POI) for propagules along the road (Figure 1). The distance between each location and these POI were calculated

using a geographical information system.

Data analysis

To quantify if exotic species richness and cover had changed over time, we calculated the difference between 2007 and 2017 whereby positive values indicate an increase. We then fitted Generalized Linear Models (quasi-distribution to adjust for overdispersion and identity link) to test if these changes were significant and to determine which environmental variables contributed significantly to the model. Environmental variables tested were elevation, roadside, transect type (verge or adjacent natural grassland), distance to PPOI, and verge width. We nested roadside (mountain or valley side) within elevation and transect type (verge or hinterland) in roadside to create a model with a hierarchical design. In cases where a variable proved to be insignificant, we subsequently removed it from the analyses. We used the final model as it was the most parsimonious model (Table 1). An Analysis of Variance (ANOVA) model was fitted to test which variable contributed to the significance of each model and to what degree. ANOVAs were also used to compare each model to a null model.

A Canonical Correspondence Analysis (CCA) was used to determine which variables explained the variation in exotic species composition over time. The CCA incorporated elevational band, year, transect type (verge or hinterland), bare soil cover, roadside (mountain or valley), distance to PPOI, as well as indigenous and exotic vegetation cover as explanatory variables. We also ran CCAs for each year separately to see if any of the variables had changed in importance over time. R was used for all the data analyses.

Results

The number of exotic species along the elevational gradient more than doubled, from 25 species in 2007 to 60 in 2017. All elevational bands displayed a higher number of exotic species, particularly the lower and mid elevational bands (1500–2100 m a.s.l; Figure 2a). The verge transects displayed a higher increase in species richness than adjacent natural transects (Figure 2b). All species observed in 2007 still occurred within our transects in 2017, except three species (*Agrimonia procera, Prunus persica* and *Rapistrum rugosum*). However, annual monitoring of exotic species presence along the elevational gradient indicates that these species still occur in the study area (Kalwij et al. 2015).

The GLM model explained 51.8% of the overall change in exotic species richness (F = 5.992, P < 0.0001). This change was primarily attributed to elevational band (F = 8.727, P =

0.0002) and transect type (road verge or adjacent natural area) nested within roadside (F = 9.532, P < 0.0001). Roadside (mountain or valley side) nested within elevational band and verge width were also significant contributors to the model, however to a lesser degree, and are therefore of secondary importance (% dev. = 9.10%, F = 2.568, P = 0.0347 and & dev. = 3.45%, F = 4.862, P = 0.0309 respectively). The most parsimonious model for overall change in exotic species cover attributed 6.31% of the visible change to transect type (road verge or adjacent natural area) (F = 5.252, P = 0.0246). No other variables showed any significance. Some 24.9% of the change in indigenous cover could be explained by transect type nested within elevation (F = 2.577, P = 0.0127). None of our variables could explain change in soil cover.

A biplot of the canonical correspondence analysis showed that the variation in exotic species composition was best explained by elevation (elevational band as categorical variable), transect type (verge or hinterland transect), total cover of indigenous species, total cover of exotics, and the year in which sampling took place. The permutation tests showed that the location of transects along the elevational gradient contributed most to the overall model (F = 7.82, P < 0.0001), closely followed by distance from nearest potential point of introduction (F = 4.04, P < 0.0001), and that the shift in species composition over time was significant (F = 3.78, P < 0.0001) but not closely correlated to elevation. Total cover of exotics only became a significant explanatory variable by 2017 (F = 2.40, P = 0.0092). Other explanatory variables, such as road verge width, and road side (valley or mountain side) did not contribute significantly in either year or to the overall model (all P-values > 0.05). Cover of indigenous plant species was excluded from this analysis as it was a colinear variable to cover of exotics and bare soil.

Discussion

To the best of our knowledge, this study is the first to systematically repeat an inventory on exotic species composition in roadside verge and adjacent undisturbed natural grassland transects along an elevational gradient in a mountain ecosystem, over a 10-yr time-span. In spite of this relatively short time-span, our data showed an increase in exotic species richness, especially in the mid-elevational range. This pattern is in line with that predicted by global patterns on exotic plants invading mountain ecosystems (Guo et al. 2018, Haider et al. 2018). Notably, we observed that exotic species composition of adjacent plots had become similar to the roadside plots, indicating that exotic species have also spread into the adjacent natural grassland. This homogenizing effect shows that exotic species are not confined to road verges,

and that this spread can take place within a relatively short period. Here, we discuss how the arrival of new exotic species to the mid-elevational range could be the result of either gradual range expansion or of jump dispersal (Wilson et al. 2009), we also discuss which ecological mechanisms, such as propagule pressure and habitat disturbance, may have facilitated a subsequent spread of exotics into the hinterland.

Gradual range expansion is the process of a species extending its range by colonising new areas on the edge of its range (Wilson et al. 2009). In the face of warming climatic conditions, species gradually shifting or expanding to higher elevations has been observed globally (Chown et al. 2012, Dainese et al. 2017, Freeman et al. 2018). Indeed, gradual range expansion could be expected in a model system such as the one we explored. The lower reaches of the pass are where the exotic species richness and abundance are the highest, providing a pool of species to slowly creep up to higher elevations, so we would expect to see the largest increase in exotic species at the lowest elevation (1500m a.s.l). Thus, displaying the common pattern of exotic species richness decreasing with elevation. However, our data shows that the most prominent increase in exotic species was experienced at the mid-elevational zone (2100m a.s.l.). This shows that the exotic species pool is not undergoing range expansion from the lower elevations upwards, but rather that their proliferation is human-induced, so we can surmise that jump dispersal is a more likely explanation. Jump dispersal is long distance dispersal, usually with a connection between the original and new ranges (Wilson et al. 2009). In road verge habitats jump dispersal is typically the result of several underlying mechanisms such as propagules being carried in by animals or anthropogenic vectors, for example, vehicles and people (Kalwij et al. 2007, Joly et al. 2011). Propagule dispersal via animals would result in a stochastic spatial pattern of exotic species distribution. Whereas, anthropogenic dispersal would result in exotic species richness being spatially associated with places where vehicles stop and people walk around, such as viewpoints, picnic spots and tourist information centres (Taylor et al. 2012, Ware et al. 2012, Khan et al. 2018). Indeed, distance of transects from potential points of introduction was a significant explanatory variable in our model system, and also supports the observations of a longitudinal study along the entire gradient (Kalwij et al. 2015). The significance of this explanatory variable for both the 2007 and the 2017 survey, shows that these anthropogenic centres serve as points of introduction and dispersal of exotic species, and are key to their prevalence (Anderson et al. 2015).

Habitat disturbance has also been shown to foster exotic species expansion along road verges (Kalwij et al. 2008), particularly in high elevation environments. Considering that many of the exotic species that we observed were ruderal weeds, it is likely that habitat disturbance

was a primary driver of their spread in elevation (Lembrechts et al. 2016). Furthermore, anthropogenic disturbance has been shown to favour exotic ruderals over native ruderals (Chiuffo et al. 2018), and the effects of disturbance have also been found to be stronger in introduced ranges than native ranges (Hierro et al. 2006). Construction and maintenance of roads such as grading is another human activity known to facilitate the intermediate dispersal of species (Rauschert et al. 2017), and so it is likely that the known construction in the area has facilitated the spread of exotics in the road verges.

The advantage of our longitudinal study and survey design, is that not only can we quantify an increase in exotic species richness in elevation, we are also able to detect spread from the disturbed roadside verges into the natural area, over time. Here again, the points of introduction played an important role in increasing the propagule pressure to the area, such that exotic species were able to expand further into the natural area. Disturbance in the road verges fostered establishment of exotic species, allowing them to then spread into the natural area. So, while the dominant increase in richness and abundance of exotics was experienced in the road verges, an increase was also seen in the natural area, as predicted. The robustness of our results is emphasized by similar patterns being observed by other studies globally, across multiple survey designs and scales. For example, it has been inferred that roads homogenize plant communities between roadside verges and adjacent natural areas in mountains (Haider et al. 2018), our data supports this observation.

Conclusion

The unique survey design allows us to quantify the change in exotic plant species patterns over time, not only in elevation, but also away from the disturbed roadside. The notable spread of exotic species into adjacent natural grassland along the entire elevational gradient of this Afromontane study system is primarily caused by anthropogenic influences in the area. Four points of introduction along the mountain pass have continued to introduce new exotic species, while disturbance in the road verges fosters their establishment and spread, both in elevation and into the adjacent natural area. This study shows that exotic plant communities in mountain ecosystems are primarily shaped by human activities, and that exotic species are not confined to disturbed areas, close to their points of introduction.

References

Anderson, L. G., Rocliffe, S., Haddaway, N. R., & Dunn, A. M. 2015. The Role of Tourism and Recreation in the Spread of Non-Native Species : A Systematic Review and Meta-Analysis, 1– 15. https://doi.org/10.1371/journal.pone.0140833

Alexander, J. M., J. J. Lembrechts, L. A. Cavieres, C. Daehler, S. Haider, C. Kueffer, G. Liu, K. McDougall, A. Milbau, A. Pauchard, L. J. Rew, and T. Seipel. 2016. Plant invasions into mountains and alpine ecosystems: current status and future challenges. Alpine Botany **126**:89- 103.

Ansong, M., and C. Pickering. 2013. Are weeds hitchhiking a ride on your car? A systematic review of seed dispersal on cars. PLoS One **8**:e80275.

Bacaro, G., S. Maccherini, A. Chiarucci, A. Jentsch, D. Rocchini, D. Torri, M. Gioria, E. Tordoni, S. Martellos, A. Altobelli, R. Otto, C. G. Escudero, S. Fernández-Lugo, J.M. Fernández-Palacios, and J. R. Arévalo. 2015. Distributional patterns of endemic, native and alien species along a roadside elevation gradient in Tenerife, Canary Islands. Community Ecology **16**:223-234.

Benedetti, Y., and F. Morelli. 2017. Spatial mismatch analysis among hotspots of alien plant species, road and railway networks in Germany and Austria. PLoS One **12**:13.

Bishop, T. R., M. P. Robertson, B. J. van Rensburg, and C. L. Parr. 2014. Elevation-diversity patterns through space and time: ant communities of the Maloti-Drakensberg Mountains of southern Africa. Journal of Biogeography **41**:2256-2268.

Carbutt, C., and T. J. Edwards. 2004. The flora of the Drakensberg Alpine Centre. Edinburgh Journal of Botany **60**:581-607.

Chiuffo, M. C., & Cock, M. C. 2018. Response of native and non-native ruderals to natural and human disturbance, *9*, 2915–2925. https://doi.org/10.1007/s10530-018-1745-9

Chown, S. L., P. C. le Roux, T. Ramaswiela, J. M. Kalwij, J. D. Shaw, and M. A. McGeoch. 2012. Climate change and elevational diversity capacity: do weedy species take up the slack? Biology Letters **9**:1-4.

Dainese, M., S. Aikio, P. E. Hulme, A. Bertolli, F. Prosser, and L. Marini. 2017. Human disturbance and upward expansion of plants in a warming climate. Nature Climate Change **7**:577-580.Freeman, B. G., J. A. Lee-Yaw, J. M. Sunday, and A. L. Hargreaves. 2018. Expanding, shifting and shrinking: The impact of global warming on species' elevational distributions. Global Ecology and Biogeography **27**:1268-1276.

Guo, Q., S. Fei, Z. Shen, B. V. Iannone, J. Knott, and S. L. Chown. 2018. A global analysis of elevational distribution of non-native versus native plants. Journal of Biogeography:n/a-n/a.

Haider, S., C. Kueffer, H. Bruelheide, T. Seipel, J. M. Alexander, L. J. Rew, J. R. Arévalo, L.A.

Cavieres, K. L. McDougall, A. Milbau, B. J. Naylor, K. Speziale, and A. Pauchard. 2018. Mountain roads and non- native species modify elevational patterns of plant diversity. Global Ecology and Biogeography **27**:667-678.

Hansen, M. J., and A. P. Clevenger. 2005. The influence of disturbance and habitat on the presence of non-native plant species along transport corridors. Biological Conservation **125**:249-259.

Hierro, José L., D. Villarreal, Ö. Eren, Jon M. Graham, and Ragan M. Callaway. 2006. Disturbance facilitates invasion: the effects are stronger abroad than at home. Am Nat **168**:144-156.

Ibisch, P. L., M. T. Hoffmann, S. Kreft, G. Pe'er, V. Kati, L. Biber-Freudenberger, D. A. DellaSala, M. M. Vale, P. R. Hobson, and N. Selva. 2016. A global map of roadless areas and their conservation status. Science **354**:1423-1427.

Joly, M., P. Bertrand, R. Y. Gbangou, M. C. White, J. Dube, and C. Lavoie. 2011. Paving the way for invasive species: road type and the spread of common ragweed (*Ambrosia artemisiifolia*). Environmental Management **48**:514-522.

Kalwij, J. M., S. J. Milton, and M. A. McGeoch. 2007. Road verges: corridors for plant invasions - a spatial hierarchical approach. South African Journal of Botany **73**:293- 294.

Kalwij, J. M., M. P. Robertson, and B. J. Van Rensburg. 2008. Human activity facilitates altitudinal expansion of exotic plants along a road in montane grassland, South Africa. Applied Vegetation Science **11**:491-498.

Kalwij, J. M., M. P. Robertson, and B. J. van Rensburg. 2015. Annual monitoring reveals rapid upward movement of exotic plants in a montane ecosystem. Biological Invasions **17**:3517-3529.

Khan, I., S. Navie, D. George, C. O'Donnell, and S. W. Adkins. 2018. Alien and native plant seed dispersal by vehicles. Austral Ecology **43**:76-88.Koide, D., K. Yoshida, C. C. Daehler, and D. Mueller-Dombois. 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.

Kopecký, M., and M. Macek. 2015. Vegetation resurvey is robust to plot location uncertainty. Diversity and Distributions **21**:322-330.

Lembrechts, J. J., A. Pauchard, J. Lenoir, M. A. Nuñez, C. Geron, A. Ven, P. Bravo-Monasterio, E. Teneb, I. Nijs, and A. Milbau. 2016. Disturbance is the key to plant invasions in cold environments. Proceedings of the National Academy of Sciences **113**:14061-14066.

Lenoir, J., J. C. Gégout, P. A. Marquet, P. de Ruffray, and H. Brisse. 2008. A significant upward shift in plant species optimum elevation during the 20th century. Science **320**:1768-1771.

Lindenmayer, D. B., G. E. Likens, A. Andersen, D. Bowman, C. M. Bull, E. Burns, C. R. Dickman, A. A. Hoffmann, D. A. Keith, M. J. Liddell, A. J. Lowe, D. J. Metcalfe, S.R. Phinn, J. Russell-Smith, N. Thurgate, and G. M. Wardle. 2012. Value of long-term ecological studies. Austral

Ecology **37**:745-757.

Lockwood, J. L., P. Cassey, and T. M. Blackburn. 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.

Lomolino, M. V. 2001. Elevation gradients of species-density: historical and prospective views. Global Ecology and Biogeography **10**:3-13.

McDougall, K. L., J. M. Alexander, S. Haider, A. Pauchard, N. G. Walsh, and C. Kueffer. 2011. Alien flora of mountains: global comparisons for the development of local preventive measures against plant invasions. Diversity and Distributions **17**:103-111.

Millennium Ecosystem Assessment. 2003. Ecosystems and human well-being: a framework for assessment. Island Press, Washington, DC.

Mucina, L., and M. C. Rutherford. 2006. The vegetation of South Africa, Lesotho and Swaziland. South African National Biodiversity Institute, Pretoria, South Africa.

Pauchard, A., C. Kueffer, H. Dietz, C. C. Daehler, J. Alexander, P. J. Edwards, J. R. Arévalo, A. Cavieres, A. Guisan, S. Haider, G. Jakobs, K. McDougall, C. I. Millar, B. J. Naylor, C. G. Parks, L. J. Rew, and T. Seipel. 2009. Ain't no mountain high enough: plant invasions reaching new elevations. Frontiers in Ecology and the Environment **7**:479-486.

Pauchard, A., A. Milbau, A. Albihn, J. Alexander, T. Burgess, C. Daehler, G. Englund, F. Essl, B. Evengård, G. B. Greenwood, S. Haider, J. Lenoir, K. McDougall, E. Muths, A. Nuñez, J. Olofsson, L. Pellissier, W. Rabitsch, L. J. Rew, M. Robertson, N. Sanders, and C. Kueffer. 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.

Pauchard, A., and K. Shea. 2006. Integrating the study of non-native plant invasions across spatial scales. Biological Invasions **8**:399-413.

Procheş, Ş., J. R. U. Wilson, R. Veldtman, J. M. Kalwij, D. M. Richardson, and S. L. Chown. 2005. Landscape corridors: Possible dangers? Science **310**:779.

Rauschert, E.S.J., Mortensen, D.A. & Bloser, S.M. 2017. Human-mediated dispersal via rural road maintenance can move invasive propagules. *Biol Invasions* **19**:2047-2058.

Sandoya, V., A. Pauchard, and L. A. Cavieres. 2017. Natives and non-natives plants show different responses to elevation and disturbance on the tropical high Andes of Ecuador. Ecology and Evolution **7**:7909-7919.

Seipel, T., J. M. Alexander, P. J. Edwards, and C. Kueffer. 2016. Range limits and population dynamics of non-native plants spreading along elevation gradients. Perspectives in Plant Ecology,

Evolution and Systematics **20**:46-55.

Steyn, C., M. Greve, M. P. Robertson, J. M. Kalwij, and P. C. le Roux. 2017. Alien plant species that invade high elevations are generalists: support for the directional ecological filtering hypothesis. Journal of Vegetation Science **28**:337-346.

Taylor, K., T. Brummer, M. L. Taper, A. Wing, and L. J. Rew. 2012. Human-mediated long- distance dispersal: an empirical evaluation of seed dispersal by vehicles. Diversity and Distributions **18**:942-951.

Van der Maarel, E. 1979. Transformation of cover-abundance values in phytosociology and its effect on community similarity. Vegetatio **39**:97-114.

Von der Lippe, M., and I. Kowarik. 2007. Long-distance dispersal of plants by vehicles as a driver of plant invasions. Conservation Biology **21**:986-996.

Ware, C., D. M. Bergstrom, E. Müller, and I. G. Alsos. 2012. Humans introduce viable seeds to the Arctic on footwear. Biological Invasions **14**:567-577.

Wilson, J. R. U., E. E. Dormontt, P. J. Prentis, A. J. Lowe, and D. M. Richardson. 2009. Something in the way you move: dispersal pathways affect invasion success. Trends in Ecology & Evolution **24**:136-144.

Table 2.1. Overview of the *F*-tests on the parsimonious generalized linear models fitted to the respective response variables. Each response variable was calculated as the paired difference between 2007 and 2017 (N = 80).

Response variable	res.deviance	df	*F*	*P*	Term included	df	% dev. explained	*F*	*P*
Exotic richness change	331.294	12	6.173	<0.0001	elevational level	4	25.33%	8.933	<0.0001
					verge width	1	3.45%	4.862	0.0309
					roadside (elevation)	5	9.10%	2.568	0.0347
					transect type(roadside)	2	14.63%	10.319	0.0001
Exotic species cover change	6701.9	1	5.252	0.0246	transect type	1	6.31%	5.252	0.0246
Indigenous species cover change	41385	9	2.577	0.0127	transect type (elevational level)	9	24.89%	2.577	0.0127
Bare soil cover change	47060	9	1.642	0.1204	transect type (elevational level)	9	17.43%	1.642	0.1204

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Figure 2.1. Position of the study are in South Africa (inset), and the plot locations along the Sani Pass road. The point colours indicate the elevational band of the respective plots (transects), while the triangles indicate the location of the four potential points of introduction (PPOI).
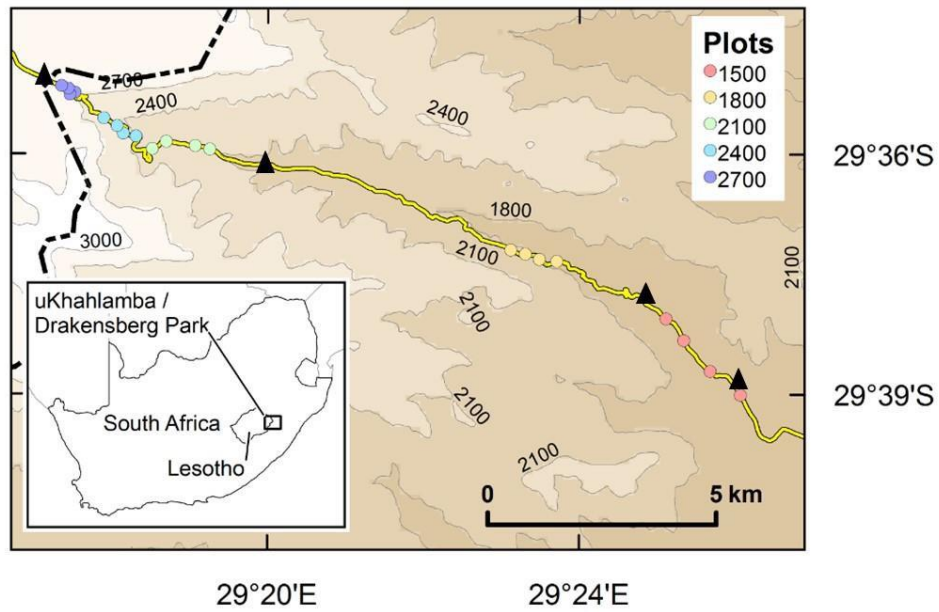
Figure 2.2. Boxplots of the exotic species richness for each elevation band for 2007 and 2017 (upper panel), and the change in exotic species richness over time along the elevational gradient for both disturbed road verge and adjacent natural transects (lower panel).
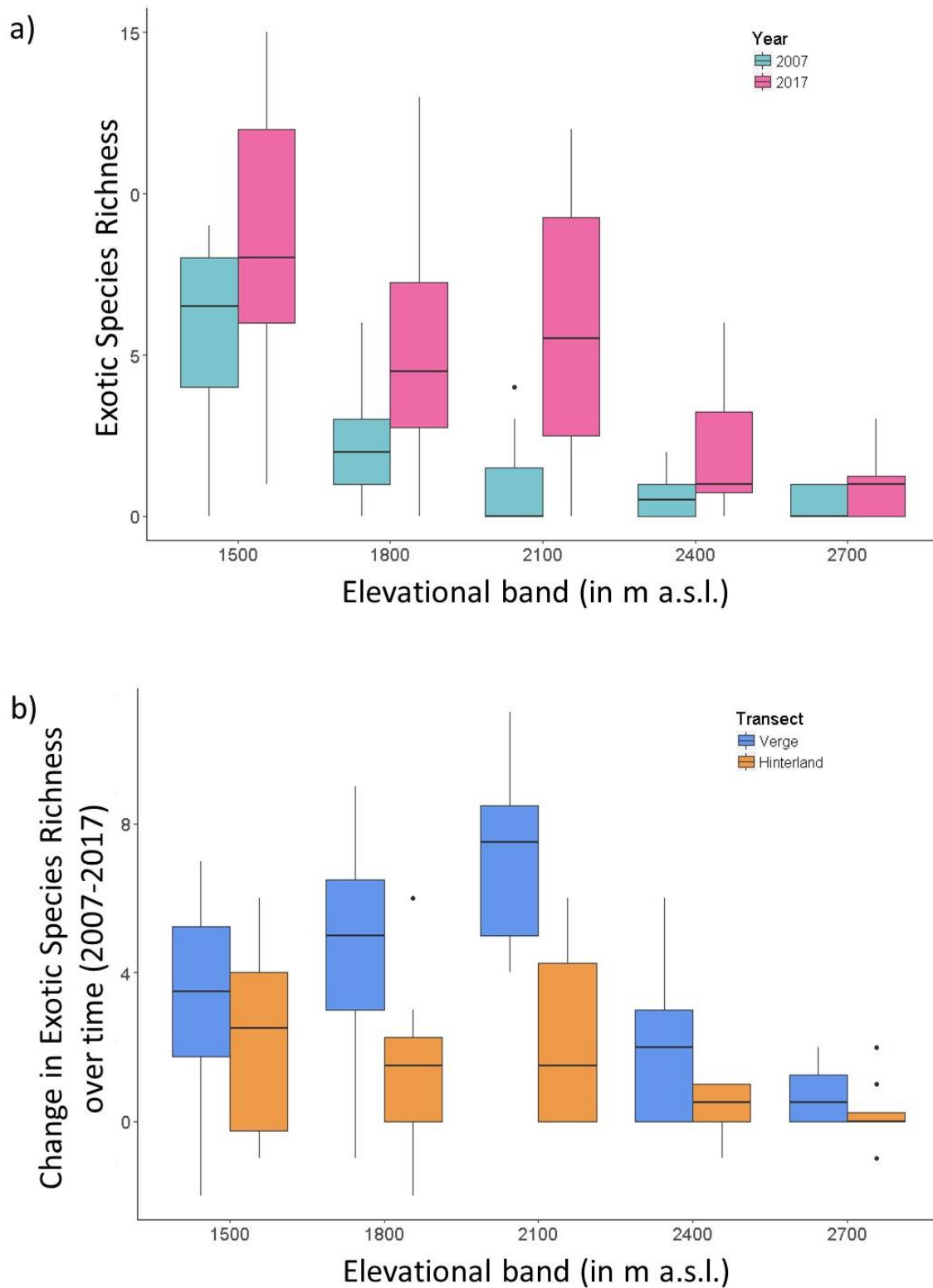
Figure 3.3. Biplots of the Canonical Correspondence Analysis of the exotic plant composition structure and the significant environmental variables, for the two sample years, a) 2007 and b) is 2017. The blue circles = adjacent natural (hinterland) transects, and the orange triangles = road verge transects. Width_m: transect wirdth, NearestPOI: nearest point of introduction, TransectTypeVerge: road verge transects, Cov_Ex_per: exotic species cover expressed as a percentage.
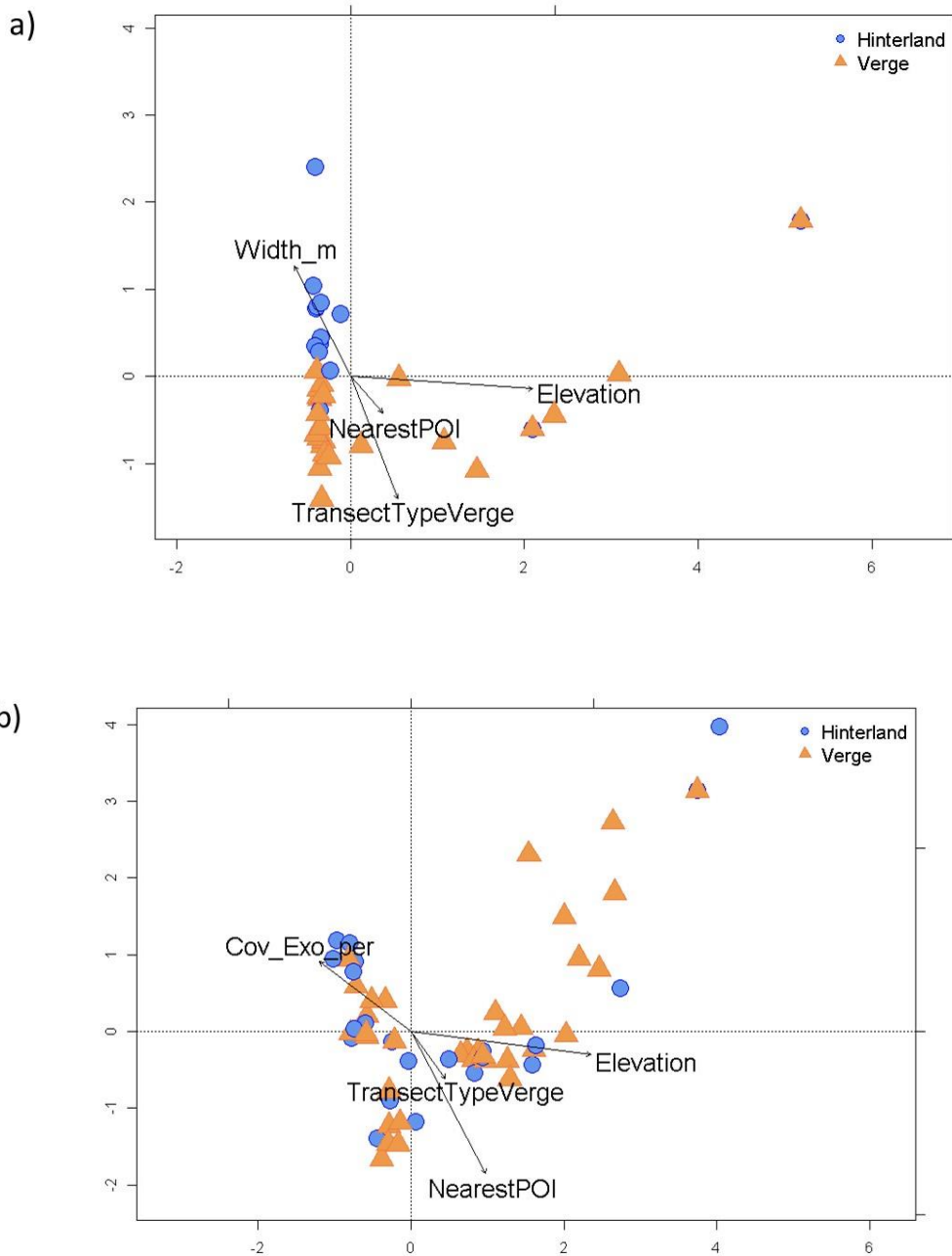
CHAPTER 3: LOCAL-SCALE IDENTIFICATION AND PRIORITIZATION OF VECTORS AND INTRODUCTION PATHWAYS OF EXOTIC PLANTS FOR MANAGEMENT

Introduction

Despite concerted management efforts, exotic species are increasing in number globally, with no prospects of their movement slowing down (Hulme et al. 2009, Seebens et al. 2017). This continued acceleration shows that current management strategies are insufficient in hindering the spread of species across borders and regions (Kaplan at al. 2017). Of these species, there are various estimates of how many become invasive (5-20%) (Lockwood et al. 2013, McGeoch et al. 2016). Species that are able to successfully invade an area often have large economic and ecological implications (Jeschke et al. 2014, Cadotte et al. 2018). Now more than ever, effective management strategies to minimise spread and impact of exotic species need to be created and implemented (McGeoch et al. 2010, Faulkner et al. 2016).

The management of invasive and exotic species can follow many strategies, from complex, science-based models, to basic, practical plans, but broadly, they target either species, sites or introduction pathways (Faulkner et al. 2016a, Mcgeoch et al. 2016). Species prioritization is usually adopted when a particular species has become highly invasive and causing ecological or socioeconomic harm (McGeoch et al. 2016). Site prioritization is implemented when certain areas, usually of a protected status, or hosting a high number of rare or endemic species, are under threat by an invasive species (Faulkner et al. 2016). Species and site management usually occur once a species has become invasive or has been prioritized, through risk assessment, as a potential invader (McGeoch et al. 2016). Introductory pathways are defined as the suite of means, by which a species is moved from one area to another (Pysek et al. 2011, IUCN 2017). Introduction pathways can consist of multiple vectors. Vectors are a physical object that a species uses as a mode of introduction and dispersal, such as vehicles, humans, a host species etc. (Genovesi and Shine (2004).

Pathway management is the control of how new species enter an area, with the purpose of preventing the introduction and spread of potentially harmful species (Essl et al. 2015). By focusing on the pathways and vectors that species use to enter and spread to an area, it is possible to decrease the complications that arise once a species has established and become invasive, making for more efficient risk management (Woodford et al. 2016). Not only does

pathway management prevent new species from entering an area, it also reduces colonization pressure of species that have already been introduced to the area, thereby reducing the exotic species prospects of outcompeting native species.

A key contributor to the success of exotic species invasion is propagule pressure (Lockwood et al. 2009, Simberloff et al. 2009). It is generally accepted that a higher number and frequency of propagules leads to a higher chance of success as an invasive species (Cassey et al. 2018). One of the most efficient ways to control exotic species in an area is therefore to manage their introductory pathways, as opposed to targeting species or areas for eradication (Mcgeoch et al. 2016). By managing pathways, one can prevent or at least reduce both the number and abundance of species entering an area (Faulkner et al. 2016). This is a particularly useful management strategy in situations where propagule pressure is the dominant contributor to the success of a species, for example in the case of aquatic invasions (Faulkner, Robertson, Rouget, & Wilson, 2017; Harvey, 2014). Pathway management is integral for aquatic invasions, because once an invader is in an aquatic environment they are very difficult to control, since there are marginally less control methods for aquatic invaders than terrestrial. Therefore, we posit that since exotic weeds are driven by propagule pressure and difficult to control once introduced, adopting an introduction pathway management scheme is an optimal solution, in our study system. While global plant introduction pathway studies have been conducted (Pergl et al. 2017, Saul et al. 2017), local- scale exotic plant pathway identification for management is less studied.

Prioritising introductory pathways for alien species is not a new strategy (Essl et al. 2015). However, such research has focused on national and global scales (Faulkner et al. 2016, Pergl et al. 2017). A global study by Pergl et al. (2017) sought to identify which introduction pathways are associated with ecologically harmful species, across all major taxa. While we acknowledge the value in such a study, we suggest there is also value in studies at local scales. Our motivation for this is that landscapes are heterogeneous, and the type of species that are able to invade areas are likely to differ spatially; therefore, context-dependent studies are needed (Faulkner et al. 2016, Saul et al. 2017).

Here, we assess the possibility of prioritising introduction pathways at a local-scale, as a conservation management tool, using Sani Pass, South Africa as a case study. This is a well-utilised area for biodiversity studies (Bishop et al. 2014, Steyn et al. 2017). Annual monitoring of exotic species along the pass shows that exotic species richness is continuing to increase (Kalwij et al. 2015). Exotic species are also spreading from the disturbed road verge, where

they were introduced, into adjacent natural areas (Chapter 2 of this thesis). The aims of this chapter are to test (i) whether different introduction pathways are associated with a higher or lower probability of introducing successful exotic species, and (ii) whether there is a relationship between successful species and the number of pathways through which a species has been introduced. We defined success as the extent to which a species was present in the natural area, by using a count of their presence in transects within the natural area. The reason why species present in the natural transects was used as a measure of success, was because those are the species that were able to expand from the disturbed road verge into the natural vegetation. The purpose of this study is to investigate whether local-scale pathway management is an optimal solution for non-native species management. We hypothesise that vehicles and natural dispersal are likely associated with successful exotic species establishment. Due to the variety of introductory pathways and possible vectors, we also hypothesise that successful species make use of multiple pathways.

Methods

Study area

The Sani Pass is a gravel mountain Pass in the Drakensberg Alpine Centre, ascending from 1500m a.s.l to 2874m a.s.l, and is a suitable area for such a study for a few reasons (Drakensberg, 2017). Firstly, the Pass is situated within the uKhuhlamba-Drakensberg Park, which is a well-renowned World Heritage Site, within the Afromontane grasslands of South Africa. Not only is this a protected area, it is also one of the border crossings and important trade routes between South Africa and Lesotho (Drakensberg, 2017). As a result, the Sani Pass has a far higher traffic density than other mountain passes in the area. The unique nature of the landscape has allowed for the introduction of exotic species which are spread through a compendium of dispersal methods such as livestock, wind, water, clothing, and vehicles (Carbutt, 2012). Furthermore, the Sani Pass is well-utilised for biodiversity studies (Bishop et al. 2014), including exotic vegetation (Kalwij et al. 2015), thus providing useful baseline biodiversity information. Annual monitoring in the area has shown that over 100 exotic species are present in the road verge of the pass (Kalwij et al. 2015). Chapter 1 of this thesis shows that at least one third of these have spread into the adjacent natural area. At this stage, no active measures are in place to control for these exotic species, which are predominantly ruderal weeds, common in many disturbed areas across the world. Indeed, the number of exotic species present in the area is underestimated by local authorities (EIA report, 2011).

Data collection

This chapter follows the concept used by Pergl et al. (2017), whereby various databases holding information about exotic species within all major taxa are used to identify associations between introduction pathways and ecologically harmful species, on a global scale. Our methods are related, however, instead of identifying introduction pathways of multiple taxa on a global scale, we refined the scope to a local scale, examined pathways and vectors used by exotic plant species present along the Sani Pass. Data from Chapter 2 were used as a source of information on which species occur in the study area, as well as which species had successfully established in the natural area adjacent to the disturbed roadside verge. It is worth noting that these data are from 80 transects spread across the Pass (40 in the roadside verges and 40 in the adjacent natural area). While these transects provide information on the dominant exotic species in the area, the data are not a complete representation of all exotic species in the area. The reason these data were used instead of a full species list, is that data on the species occurring in the adjacent natural area were needed as a proxy of successful establishment. Various databases and online searches were used to acquire information on each species' method of dispersal. The main two databases used were the "CABI Invasive Species Compendium" (https://www.cabi.org/isc), and SANBI's "Invasive Species South Africa" (http://invasives.org.za/) website. In cases where no or insufficient information was provided on a species, an online search was used, and information from other web-based sources and scientific articles was used to categorise the introductory pathways of species (Appendix C). This dispersal information was used to assign likely vectors and pathways of introduction to each exotic species recorded in the transects. The classification of introduction pathways was based on the scheme originally created by Hulme et al. (2008), and later adopted by the IUCN (2014) (Appendix B-1). Only pathways relevant to the study were used in the analyses (Figure 3.1). It is important to note that some species had additional known introductory pathways, however if this pathway was not relevant to the study area, it was not added. The motivation for this was that we wanted to investigate trends on a local scale and thus only analysed pathways specific to the study area. For example, some species were introduced as an ornamental species in other countries, but not in South Africa, therefore it is an irrelevant introductory pathway at the local scale. It is assumed that the online search was sufficient for vector and pathway identification, based on information provided and knowledge of the study area. Each species was assigned to one or more of the following pathways: Corridor and Dispersal (Natural dispersal, Waterways), Unintentional (Transport Stowaway), Intentional (Escape from Confinement). Within each of these categories, species were further sub-

categorized by their likely vectors, as follows: Natural Dispersal and Waterways (Corridor and Dispersal); Vehicles, Livestock, Cultivation, and Clothes and Shoes   (Unintentional); and Ornamental, Release into Nature and Forage (Intentional). Since natural   dispersal is beyond the scope of management (Essl et al. 2015), we did not separate the different   natural dispersal pathways (i.e. wind, insect, mammals). However, we suspect that this has the potential to further elucidate trends, and we consider it a venture for further analyses.

Measure of success

We used the presence of a species in the natural area as a proxy for invasion success, as it implies exotic species are not confined to the disturbed roadside verges and have the ability to spread. Thus, splitting the species into two groups: those that are present in the study area, yet unsuccessful at spreading at this point, and those that are present and successful colonizers in the area. In an effort to explore additional trends, we later redefined success as the extent of spread into the natural area, using the number of transects in the natural area that each species was present in.

Statistical analyses

Vector analyses

To test which vectors are associated with species that have become successful along the pass, we used Generalized Linear Models (GLMs). Both a full model, including all vectors was used, as well as models testing associations between individual vectors and successful species. GLMs were also used to test whether there was an association between Families that species belong to and vectors used; as well as successful species within families and vectors. Analyses on a family level were conducted to see if successful exotic species were within the same family as indigenous species. Since the data are binary, a binomial distribution was used (with a log link function). Chi square test of independence was used to test for a relationship between successful species and the number of vectors used. We then changed the measure of success to include the extent of presence in the natural area, making our data count data, as opposed to being binary presence/absence data. We re-ran analyses under a Poisson distribution, unless over dispersion was apparent, in which case quasi-Poisson distribution was used (Crawley, 2015). A GLM was then used to test for a relationship between successful species and number of pathways used (Poisson family, log link)

Introduction pathway analyses

Since this study is on a local-scale, some vectors did not include enough species, or proportions were too skewed to derive meaningful statistical outputs. For this reason, we

broadened the scope to focus on the introduction pathway level. Three introduction pathways were identified in the study area, Natural, Unintentional and Intentional (Figure 3.1). GLMs were also used to first test for associations between number of pathways used and extent of presence in the natural area (i.e. the measure of success used). We also tested if successful exotic species were associated with particular pathways. A full model including all three pathways was used, this was then narrowed down to the most parsimonious model. Our data displayed an excess of zeros, thus we used Zero-inflated Poisson (ZIP) models to analyse data (UCLA). Vuong tests were used to test if the ZIP model was an improvement on the standard Poisson model. Significant test statistic in the Vuong test indicates that the ZIP model is better. All analyses were performed in the statistical environment R (R Core Team 2016).

Results

Sixty-three species occurred in the study area. Three pathways of introduction, using nine vectors within these pathways were identified. Table 3.1 shows the total number and percentage of species introduced via each pathway. The most common vector was "Natural dispersal". The most common unintentional vector was "Livestock". Of the 63 exotic species occurring in the transects, 33 had spread to the adjacent natural area, at varying extents, ranging between presence in one transect to twelve.

Vectors

Table 3.2 shows the mean counts of successful and unsuccessful species for each vector, as proportions. This is used as a quick visual to see if there are significant differences between successful and unsuccessful species, if mean effects are similar, then it is unlikely that there are any significant associations. Small differences are noted for Natural, Ornamental, Release into Nature and Forage. However, GLMs showed no significant associations (Appendix D and F). The Chi square test of independence showed that there is a marginally significant association between the number of vectors and the success of a species in the study area (P=0.06) (Figure 3.3). Additionally, no associations were found between introduction pathways and families (Appendix D). All tests on vectors did not hold enough statistical vigour to yield any ecologically meaningful results, since many vectors did not have enough species attached to them to hold value, and in many cases the data was disproportionately skewed. For this reason, we focus on the introduction pathways in the discussion.

Introduction pathways

There was no association between presence in the natural area and number of pathways

used (P = 0.08) (Table 3.3). Species that entered and spread in the area as unintentional transport stowaways had a significant association with presence in the natural transects (P = 0.046) (Table 3.4). While intentional introductions and corridor dispersal had no significant associations with success (P = 0.91 and P= 0.99, respectively). Table 3.4 shows the models used as well as the strength of each model.

Discussion

Exotic species introduced as unintentional transport stowaways are significantly associated with presence in natural areas away from road verges, the proxy for success in this study. This is unlike pathway patterns seen on a national and global scale, where the most common introduction pathway is escape from confinement (Pyšek, Jarošík, & Pergl, 2011, Faulkner et al. 2016, Pergl et al. 2017, Saul et al. 2017). Surprisingly, the use of multiple vectors or pathways was not associated with successful species. The use of a single introduction pathway causing spread of exotics into the natural area suggests that local-scales favour specific pathways. Unintentional introductions, being the dominant pathway for successful species in this study, shows that despite the presence of the border crossing at the top and bottom of the study area, exotic species are still able to enter the area through unintentional means, such as vehicles tyres, clothes and shoes and livestock. This suggests that current biosecurity measures at the border crossings in the area are insufficient, and that managing this pathway more efficiently could reduce the extent of exotic species presence in the area.

The strategy of a stowaway

Many exotic species in the area are fast-growing, early successional species, since they are able to exploit resources and open space post disturbance (Alexander et al. 2011, Catford et al. 2012). Roadsides are subject to continual disturbance and interference from road related activities, resulting in novel plant communities, largely comprised of such weedy species (Procheş et al. 2005). These disturbance effects appear to be heightened in mountain ecosystems, where anthropogenic disturbance, such as recreation centres and roadsides, shape exotic plant communities (Pauchard et al. 2009, Bacaro et al. 2016, Anderson et al. 2015, Chapter 2). For this reason, common exotic species in mountain ecosystems are those with a ruderal strategy, that respond well to disturbance (Kalwij et al. 2015, Dainse et al. 2017, Yang et al. 2018). Our study system was no exception, with anthropogenic activities being a key contributor to exotic species richness and abundance of a dominantly weedy exotic species pool (Kalwij et al. 2008, Chapter 2). For example, species from the *Bidens* genus (commonly known as Blackjacks), a widespread weed both globally and in the study area, have seeds with

barbs that allow for attachment to people, animals and vehicles. *Verbena bonariensis*, a common invader throughout South Africa, produces thousands of tiny seeds per plant, which are easily carried far distances by wind, water and animals (ISSA). It is often found along roadsides, disturbed areas and grasslands. The Poaceae family, often spread through cultivation, but increasingly via unintentional introductions (Visser et al. 2017), has increased in our study system, and South Africa as a whole, over the past decade. Many grass species thrive in disturbed areas, such as roadsides, and are easily transported in tyre treads (Ansong & Pickering, 2013, 2014; Seebens et al., 2018).

Similarly, species that make use of unintentional pathways are often ruderals (favour disturbed areas) (Pyšek et al., 2011). To attach to a vector, withstand travel, and survive once dropped off in a new area, species need to be resilient and display characteristic traits of a weed (Van Kleunen et al. 2015). Such traits include having seeds that can attach to a vector easily, for example, being sticky, have burrs present, or barbed appendages; they need to have a strong outer coating or ability to survive for potentially long periods in changeable condition before germination; and they need to be quick-growing to optimise resources (Ansong & Pickering 2013). Therefore, we can surmise that the reason unintentional stowaways are the most successful exotic species in the area, is that conditions needed to withstand the pathway have many parallels with those needed to survive in mountain ecosystems.

Management of unintentional stowaways in the study area

It is far more effective to prevent the introduction of weedy species than to control infestations (Faulkner et al. 2016). Simple strategies can be implemented that would substantially reduce their propagule pressure and therefore chance of survival in new areas (Khan et al. 2017, Ansong & Pickering, 2013). General strategies include having stringent biosecurity and border assessments, creating buffer zones between protected areas and human populated areas, systematic cleaning of vehicles, equipment and shoes to remove seeds before permitting entry into protected areas, and promotion of compliance through awareness posters, articles and media (Kueffer et al. 2014, Buckley & Catford 2016). A strategy to optimise resources, is to prioritize border control checks based on seasons when species with a high probability of establishing, are introduced (Faulkner et al. 2016b)

While such strategies are logical and useful, some are difficult to achieve in the study system that we explored. For example, it is not possible to create a buffer between the reserve and human activities, as the Sani Pass area serves as both a border crossing and protected area. Implementing cleaning of vehicles and equipment is also likely to be met with dissention, since

cleaning takes time, and many visitors to the area, such as hikers and holiday makers, are on strict or limiting time schedules, which are often dependent on the variable weather conditions experienced in the area. Additionally, based on literature and local Environmental Impact Assessment reports, the extent of exotic species in the area is underestimated (Carbutt, 2012; Gibb, 2011; Report, 2011). Therefore, since exotic species are not perceived as a threat by management in the area, motivating the need for stricter border control is difficult. Considering these idiosyncrasies unique to the study area, we suggest scenario planning as an initial step forward (Hulme 2012). Scenario planning collates relevant stakeholders to develop a few hypothetical management plans for the area, with each scenario capturing a keystone uncertainty about the future of an area. The intent of such planning is for decision-makers to assess which management strategy would work be optimal across the different scenarios presented. Scenario planning would be a useful way to communicate the results of this study and to motivate the need for proactive management.

Role of multiple pathways

Contrary to our hypothesis, we found no relationship between the success of a species and the number of introductory pathways used. This negates the assumption that a higher number of pathways results in a higher propagule pressure, more opportunities to spread to new habitats (Pergl et al.2017), and therefore more chances for species to establish. However, it does show us that successful exotic species in our study system use a specific pathway (i.e. unintentional transport stowaways). This finding implies that the dominant introduction pathway used on a local scale will be the one that favours species that are able to withstand local conditions. Thus, identifying the type of exotic species that an area favours is important for introduction pathway identification and management. This is key, as it shows we cannot rely on national-scale pathway identifications alone, since new patterns emerge at local scales (Saul et al. 2017). The pathways identified on a local scale are those that should dictate management decisions. For example, mountain ecosystems favour ruderal weeds, therefore successful species are likely to be those that use a pathway that also favours ruderal weeds, such as unintentional transport stowaways; as was the case in our study system. This is not to say that global and national scale pathway identification is unimportant. On the contrary, this is vital for the identification of introduction pathways used by invasive and threatening exotic species, to aid risk management (Essl et al. 2015, Pergl et al. 2017, Saul et al. 2017). However, it is important to be cognizant that landscapes are heterogeneous, and different local-scale areas will favour specific pathways (Faulkner et al. 2016). Thus, local

scale pathway identification is needed for efficient local-scale management.

Conclusion

Transport stowaways (unintentional) is increasingly becoming a popular pathway of introduction; indeed, it is the main driver of exotic species success in our study system. Therefore, by implementing simple methods to manage this pathway, such as those suggested, in this chapter, it may be possible to reduce propagule pressure and halt the influx of potentially harmful species to the area. The dominant use of a single pathway on a local scale infers that specific conditions favour certain pathways, this highlights the need for local-scale pathway identification to dictate management decisions.

References

Africa, S. (2016). Grasses as invasive plants in South Africa revisited : Patterns, pathways and management.

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, *108*(2). https://doi.org/10.1073/pnas.1013136108

Anderson, L. G., Rocliffe, S., Haddaway, N. R., & Dunn, A. M. (2015). The Role of Tourism and Recreation in the Spread of Non-Native Species : A Systematic Review and Meta-Analysis, 1–15. https://doi.org/10.1371/journal.pone.0140833

Ansong, M., & Pickering, C. (2013). Are Weeds Hitchhiking a Ride on Your Car ? A Systematic Review of Seed Dispersal on Cars, *8*(11), 1–11. https://doi.org/10.1371/journal.pone.0080275

Ansong, M., & Pickering, C. (2014). Weed seeds on clothing : A global review. *Journal of Environmental Management*, *144*, 203–211. https://doi.org/10.1016/j.jenvman.2014.05.026

Bacaro, G., Maccherini, S., Chiarucci, A., Jentsch, A., Rocchini, D., Torri, D., … Arévalo, J. R. (2015). Distributional patterns of endemic, native and alien species along a roadside elevation gradient in Tenerife, Canary Islands. *Community Ecology*, *16*(2), 223–234. https://doi.org/10.1556/168.2015.16.2.10

Buckley YM. & Catford J. (2016). Does the biogeographic origin of species matter? Ecological effects of native and non-native species and the use of origin to guide management.

Buckley, Y. M., & Catford, J. (2016). Does the biogeographic origin of species matter? Ecological effects of native and non-native species and the use of origin to guide management. *Journal of Ecology*, *104*(1). https://doi.org/10.1111/1365-2745.12501

Buckley, Y. M., & Catford, J. (2016). Does the biogeographic origin of species matter? Ecological effects of native and non-native species and the use of origin to guide management. *Journal of Ecology*, *104*(1). https://doi.org/10.1111/1365-2745.12501

CABI. (2018). Invasive Species Compendium. Wallingford, UK: CAB International. Retrieved from: www.cabi.org/isc.

Carbutt, C. (2012). The emerging invasive alien plants of the Drakensberg Alpine Centre,

Southern Africa. *Bothalia*, *42*(2), 71–85.

Cassey, P., Delean, S., Lockwood, J. L., Sadowski, J., & Blackburn, M. (2018). Dissecting the null model for biological invasions : A meta-analysis of the propagule pressure effect, 1–16.

Catford, J. A., Daehler, C. C., Murphy, H. T., Sheppard, A. W., Hardesty, B. D., Westcott, D. A., … Hulme, P. E. (2012). The intermediate disturbance hypothesis and plant invasions: Implications for species richness and management. *Perspectives in Plant Ecology, Evolution and Systematics*. https://doi.org/10.1016/j.ppees.2011.12.002

Crawley MJ. (2015). Statistics: An Introduction using R. Wiley, Chichester

Drakensberg, N. (2017). THE FLORA OF THE DRAKENSBERG ALPINE C E NT RE, *60*(3), 581–607.

Essl, F., Bacher, S., Blackburn, T. I. M. M., Booy, O., Brundu, G., Brunel, S., … Zenetos, A. (2018). Crossing Frontiers in Tackling Pathways of Biological Invasions, *65*(8), 769–782. https://doi.org/10.1093/biosci/biv082

Faulkner, K. T., Robertson, M. P., Rouget, M., & Wilson, J. R. U. (2016). Border control for stowaway alien species should be prioritised based on variations in establishment debt, *180*, 301–309.

Faulkner, K. T., Robertson, M. P., Rouget, M., & Wilson, J. R. U. (2016). Understanding and managing the introduction pathways of alien taxa : South Africa as a case study, 73–87. https://doi.org/10.1007/s10530-015-0990-4

Faulkner, K. T., Robertson, M. P., Rouget, M., & Wilson, J. R. U. (2017). Prioritising surveillance for alien organisms transported as stowaways on ships travelling to South Africa. *PLoS ONE*, *12*(4), 1–20. https://doi.org/10.1371/journal.pone.0173340

Gibb, A. (2011). ECONOMIC IMPACT STUDY OF SURFACING THE SANI PASS ROAD Prepared for :, (August).

Guidance for interpretation of CBD categories on introduction pathways. (2018), (07), 1–100.

Guo, Q., Knott, J., Fei, S., Shen, Z., Iannone, B. V, & Chown, S. L. (2018). A global analysis of elevational distribution of non-native versus native plants. https://doi.org/10.1111/jbi.13145

Haider, S., Kueffer, C., Bruelheide, H., Seipel, T., Alexander, J. M., Rew, L. J., … Milbau, A. (2018). Mountain roads and non-native species modify elevational patterns of plant diversity, (April 2017), 667–678. https://doi.org/10.1111/geb.12727

Harvey, B. C. (2014). Local-scale invasion pathways and small founder numbers in introduced Sacramento pikeminnow (Ptychocheilus grandis), 1–9. https://doi.org/10.1007/s10592-013-0516-5

Hulme, E., Bacher, S., Kenis, M., Klotz, S., Kühn, I., Minchin, D., … Pergl, J. (2008).

Grasping at the routes of biological invasions :, 403–414. https://doi.org/10.1111/j.1365-2664.2007.01442.x

Hulme, P. E. (2012). Weed risk assessment : a way forward or a waste of time ?, 10–19. https://doi.org/10.1111/j.1365-2664.2011.02069.x

ISSA (2018). Invasive Species South Africa. Retrieved from: http://invasives.org.za/

Jeschke, J. M., Bacher, S., Blackburn, T. M., Dick, J. T. A., Essl, F., Evans, T., … Kumschick, S. (2014). Defining the impact of non-native species. *Conservation Biology*, *28*(5). https://doi.org/10.1111/cobi.12299

Kalwij, J. M., Milton, S. J., & McGeoch, M. A. (2008). Road verges as invasion corridors? A spatial hierarchical test in an arid ecosystem. *Landscape Ecology*, *23*(4), 439–451. https://doi.org/10.1007/s10980-008-9201-3

Kalwij, J. M., Robertson, M. P., & Rensburg, B. J. (2008). Human activity facilitates altitudinal expansion of exotic plants along a road in montane grassland, South Africa. *Applied Vegetation Science*, *11*(4), 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*(12), 3517–3529. https://doi.org/10.1007/s10530-015-0975-3

Khan, I., Navie, S., George, D., O 'donnell, C., & Adkins, A. S. W. (n.d.). Alien and native plant seed dispersal by vehicles. https://doi.org/10.1111/aec.12545

Kueffer, C., Mcdougall, K., Alexander, J., Daehler, C., Edwards, P., Haider, S., … Mcdougall, K. (2014). Plant Invasions into Mountain Protected Areas: Assessment, Prevention and Control at Multiple Spatial Scales. https://doi.org/10.1007/978-94-007-7750-7_6

Mcdougall, K. L., Khuroo, A. A., Loope, L. L., Parks, C. G., Pauchard, A., Reshi, Z. A., … Reshi, Z. A. (n.d.). Plant Invasions in Mountains : Global Lessons for Better Management Plant Invasions in Mountains : Global Lessons for Better Management, *31*(4), 380–387.

McGeoch, M. A., Genovesi, P., Bellingham, P. J., Costello, M. J., McGrannachan, C., & Sheppard, A. (2016). Prioritizing species, pathways, and sites to achieve conservation

targets for biological invasion. *Biological Invasions*, *18*(2). https://doi.org/10.1007/s10530-015-1013-1

Pauchard, A., Kueffer, C., Dietz, H., Daehler, C. C., Alexander, J., Edwards, P. J., … Seipel, T. (2009). Ain't no mountain high enough: Plant invasions reaching new elevations. *Frontiers in Ecology and the Environment*, *7*(9), 479–486. https://doi.org/10.1890/080072

Pergl, J., Pyšek, P., Bacher, S., Essl, F., Genovesi, P., Harrower, C. A., … Nentwig, W. (2017). Troubling travellers: are ecologically harmful alien species associated with particular introduction pathways? *NeoBiota*, *32*. https://doi.org/10.3897/neobiota.32.10199

Procheş, Ş., J. R. U. Wilson, R. Veldtman, J. M. Kalwij, D. M. Richardson, and S. L. Chown. 2005. Landscape corridors: Possible dangers? Science **310**:779.

Pyšek, P. et al. 2011. Colonization of high altitudes by alien plants over the last two centuries. — P Natl Acad Sci USA 108: 439-440.

Pyšek, P., Jarošík, V., & Pergl, J. (2011). Alien plants introduced by different pathways differ in invasion success: Unintentional introductions as a threat to natural areas. *PLoS ONE*, *6*(9). https://doi.org/10.1371/journal.pone.0024890

R Core Team (2016). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Report, F. S. (2011). Environmental Impact Assessment for the Proposed Upgrade of the Sani Pass Road (P318): Phase 2, (October).

Robertson, M. P. (2017). The balance of trade in alien species between South Africa and the rest of Africa, 1–16.

Saul, W. C., Roy, H. E., Booy, O., Carnevali, L., Chen, H. J., Genovesi, P., … Jeschke, J. M. (2017). Assessing patterns in introduction pathways of alien species by linking major invasion data bases. *Journal of Applied Ecology*, *54*(2). https://doi.org/10.1111/1365-2664.12819

Seebens et al. 2018. Global rise in emerging alien species results from increased accessibility of new source pools. PNAS

Seebens, H., Blackburn, T. M., Dyer, E. E., Genovesi, P., Hulme, P. E., Jeschke, J. M., … Essl, F. (2017). No saturation in the accumulation of alien species worldwide. *Nature Communications*, *8*. https://doi.org/10.1038/ncomms14435

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*(2), 337–346. https://doi.org/10.1111/jvs.12477

Van Kleunen, M., Dawson, W., & Maurel, N. (2015). Characteristics of successful alien plants. *Molecular Ecology*, *24*(9). https://doi.org/10.1111/mec.13013

Wilson, J. R. U., Richardson, D. M., Faulkner, K. T., Rahlao, S. J., Zengeya, T. A., & Wilgen, B. W. Van. (2018). Indicators for monitoring biological invasions at a national level, (June), 2612–2620. https://doi.org/10.1111/1365-2664.13251

Yang et al (2018). Distribution of non-native plant species along elevational gradients in a protected area in the eastern Himalayas, China.

Zero-inflated Poisson Regression: R Data Analysis Examples. UCLA: Statistical Consulting Group. Retrieved from: https://stats.idre.ucla.edu/r/dae/zip/

Tables

Table 3.1. Table showing the total number (species counts) and percentage of species introduced by each vector. Since many species use multiple vectors, the percentage total is not summed to 100.

Introduction Pathways	Corridor & Dispersal		Unintentional				Intentional		
	Natural	Corridor	Transport stowaway				Escape from confinement		
Vectors	Natural (wind, birds, insects)	Waterways	Livestock	Clothes & shoes	Vehicles	Cultivation	Ornamental	Release into nature	Forage
Total	59	27	28	19	18	18	4	1	1
Percentage	93,65	42,86	44,44	30,16	28,57	28,57	6,35	1,59	1,59

Table 3.2. The mean counts for successful and unsuccessful species for each vector. Here we see that there does not appear to be any substantial differences in the mean counts for any pathways. Ones that have some difference are Natural, Ornamental, (Intentional) Release into Nature and Forage.

Vector	Unsuccessful	Successful
Natural	0.75	0.51
Waterways	0.50	0.56
Livestock	0.51	0.54
Clothes & Shoes	0.50	0.58
Vehicles	0.47	0.67
Cultivation	0.47	0.67
Ornamental	0.51	0.75
Release into Nature	0.53	0.00
Forage	0.53	0.00

Table 3.3. Results of GLM testing association between Presence in Natural Transect (PINT) and Number of Pathways (NOP). First a model using a Poisson distribution is generated (log link), followed by a ZIP model (binomial family with logit link). A vuong test is used to compare the zero-inflated Poisson model to the standard Poisson model.

Response Variable	Estimate	SE	z	P
NOP	-0.4052	0.2327	-1.741	0.0816
Zero-inflated	0.4524	0.5665	0.798	0.425
Vuong	Raw		2.235345	0.012697
	AIC-corrected		2.043671	0.020493
	BIC-corrected		1.838279	0.033011

Table 3.4. Results of GLM testing association between Presence in Natural Transect (PINT) and unintentional and intentional pathways. First a model using a Poisson distribution is generated (log link), followed by a ZIP model (binomial family with logit link). A vuong test is used to compare the zero-inflated Poisson model to the standard Poisson model.

Response Variable	Estimate	SE	z	P
Unintentional	-1.2398	0.9551	-1.298	0.194
Intentional	-0.4651	0.2331	-1.995	**0.046 ***
Zero-inflation model				
Unintentional	-0.1507	1.9245	-0.078	0.938
Intentional	0.1773	0.5733	0.309	0.757
Vuong	Raw		2.251322	0.012183
	AIC-corrected		1.961139	0.024931
	BIC-corrected		1.650188	0.049452

Figures

Figure 3.1. Schematic depicting the relevant pathways based on Hulme et al (2008) and IUCN (2014). Only pathways relevant to the study area were analysed and no distinction was made between dispersal into and within the area. See Appendix B (Table B-1) for details.
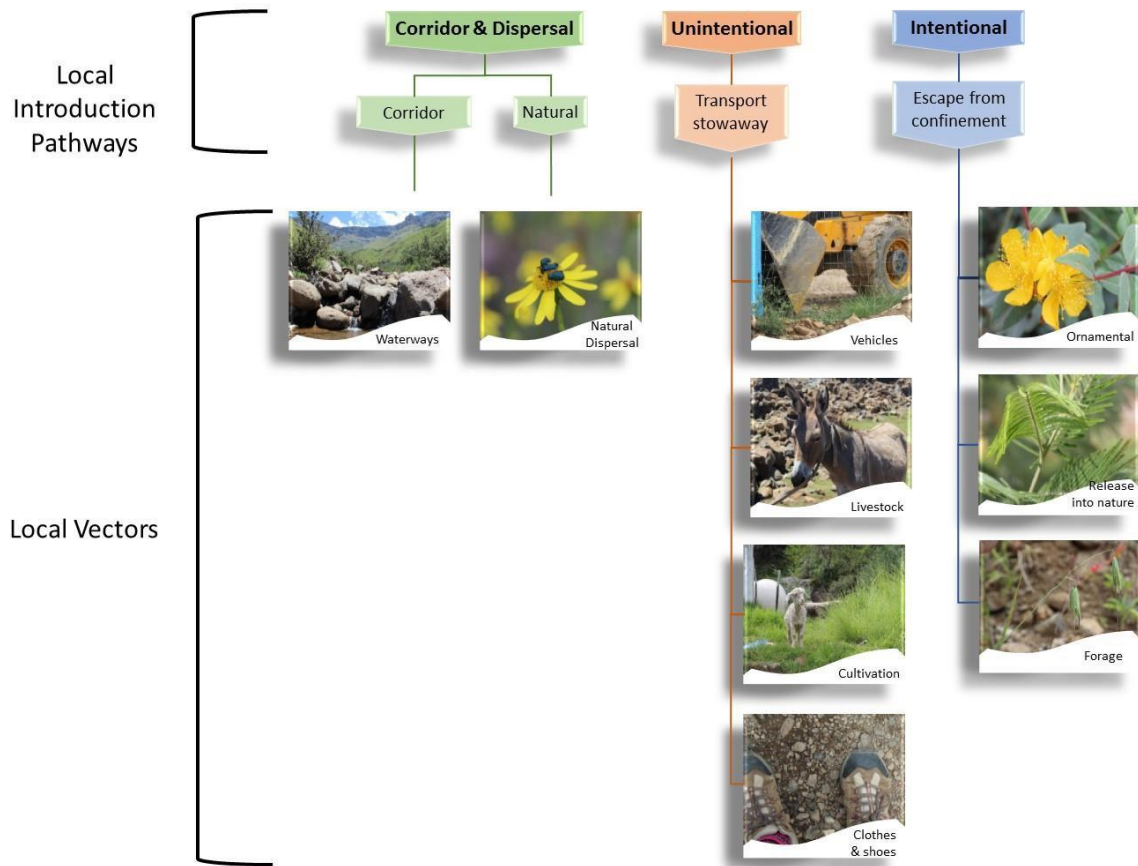
Figure 3.2. A collage showing examples of the species that occur in the study area, a) *Papaver aculeatum*, an ornamental, which also makes use of natural dispersal (insects), b) *Plantago lanceolata*, a cosmopolitan weed that spreads naturally, as well as through human-mediated means (livestock and agriculture), b) *Medicago polymorpha*, a Fabaceae occurring at high elevations (>2000m a.s.l.), with prickly burrs that attach to clothing, animal fur and vehicles, allowing for expansion of its geographic range, d) *Acacia dealbata*, a common invasive species in South Africa, occurring in the lower elevations of the study area, spread via seed dispersal, e) *Cirsium vulgare* -unintentionally introduced to the roadside, higher than its conventional upper elevational range limit.

Figure 3.3. Bar graph depicting the percentage of successful exotic species (y-axis) in relation to the number of vectors they utilise (x-axis) (Chi square test: P=0.06).
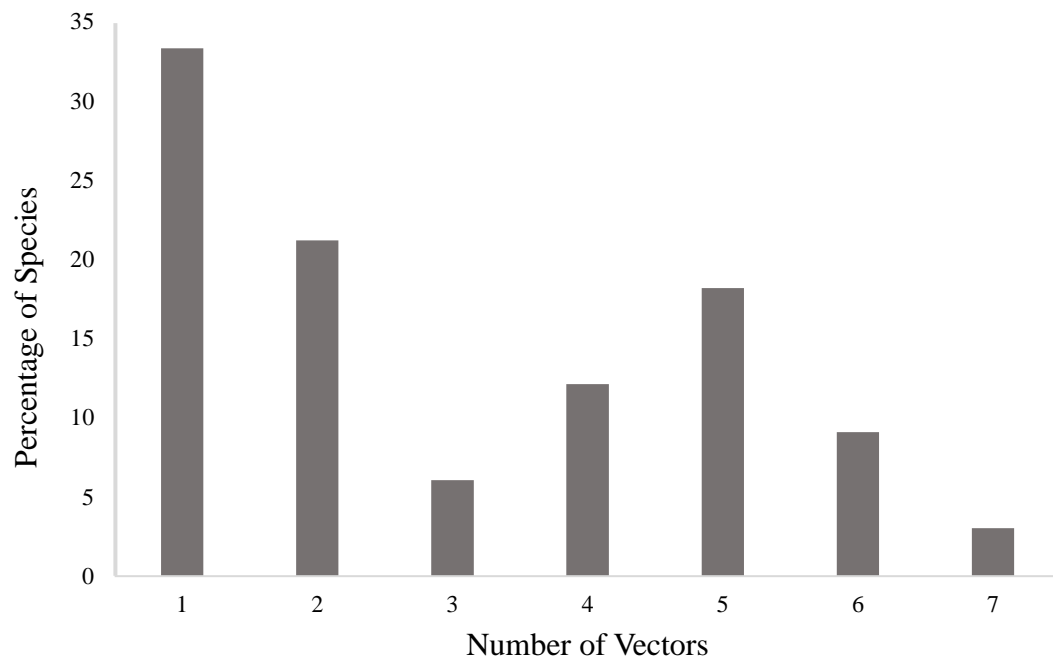
CHAPTER 4: GENERAL CONCLUSION

This study quantified the spatiotemporal change in exotic species richness and abundance within roadside and adjacent natural transects, across an elevation gradient (1500-2874m a.s.l), in Afromontane grassland, South Africa. A re-survey method was used, which showed that over ten years, exotic species richness increased significantly across the entire elevation gradient, both in the disturbed roadside and in the adjacent natural area. This increase occurred predominantly in the low- to mid-elevational ranges, suggesting that range extension of exotics into mountain ecosystem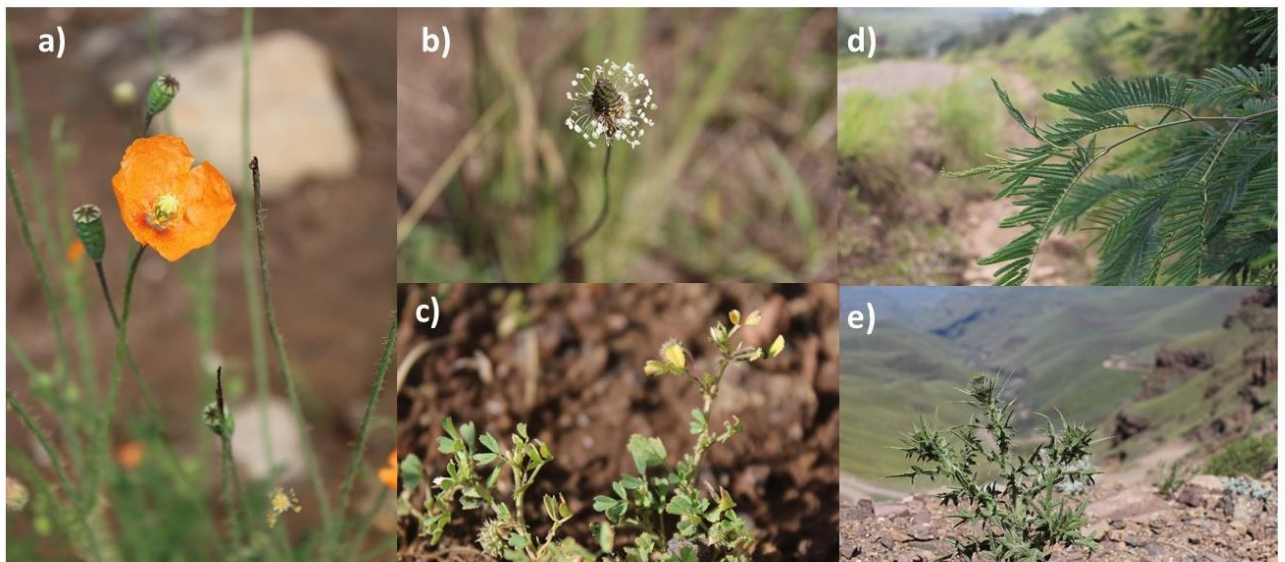s is human mediated, rather than by gradual range expansion from the lowlands. This finding supports observed patterns globally (Haider et al., 2018). Exotic species composition in roadside and adjacent natural transects homogenised over time, indicating that exotic species are increasingly moving into the hinterland. These results show that mountain roadside verges are far better conduits for the dispersal of exotic species than previously assumed (Millennium Ecosystem Assessment 2003), and that further colonisation of the natural area by exotics can be expected.

I then tested whether specific introduction pathways were associated with successful exotic species in the area, using the extent of their presence in the natural area as a proxy for invasion success. Exotic species made use of three pathways and within those, nine vectors. The only pathway that was significantly associated with successful exotic species, was unintentional transport stowaways. I found that unlike global and national-scale studies, the use of multiple pathways was not associated with successful species. This is a key finding, as it highlights the value of local-scale pathway identification. Global and national scale pathway studies show that exotic species that enter through multiple pathways are successful (Faulkner, Robertson, Rouget, & Wilson, 2016; Pergl et al., 2017). Here, I show that on a local-scale, specific pathways are favoured, based on the system. In this case, mountain ecosystems favour species of a ruderal strategy. Therefore, unintentional transport stowaways, which have the ability to utilise vectors such as people, livestock and vehicles as means of introduction are favoured. For this reason, managers should consider employing more stringent control at the border posts in the study area.

Using unique methods, such as re-surveying two sample category transects, with a

combination of data sources, this thesis provides important insights into the patterns and pathways, which facilitate exotic species expansion, in mountain ecosystems, as well as the management thereof. It highlights the influential role of anthropogenic developments (i.e. roads and tourism centres) in shaping exotic species composition and expansion in such ecosystems. Additionally, it shows the importance of local-scale pathway management (Saul et al., 2017). These findings are of use to conservation managers, particularly in mountain ecosystems, as well as researchers interested in biosecurity and risk management of exotic species.

References

Faulkner, K. T., Robertson, M. P., Rouget, M., & Wilson, J. R. U. (2016). Understanding and managing the introduction pathways of alien taxa : South Africa as a case study, 73–87. https://doi.org/10.1007/s10530-015-0990-4

Haider, S., Kueffer, C., Bruelheide, H., Seipel, T., Alexander, J. M., Rew, L. J., … Milbau, A. (2018). Mountain roads and non-native species modify elevational patterns of plant diversity, (April 2017), 667–678. https://doi.org/10.1111/geb.12727

Millennium Ecosystem Assessment. 2003. Ecosystems and human well-being: a framework for assessment. Island Press, Washington, DC.

Pergl, J., Pyšek, P., Bacher, S., Essl, F., Genovesi, P., Harrower, C. A., … Rabitsch, W. (2017). NeoBiota Troubling travellers : are ecologically harmful alien species associated with particular introduction pathways? *20*(October2016), 1–20. https://doi.org/10.3897/neobiota.32.10199

Saul, W. C., Roy, H. E., Booy, O., Carnevali, L., Chen, H. J., Genovesi, P., … Jeschke, J. M. (2017). Assessing patterns in introduction pathways of alien species by linking major invasion data bases. *Journal of Applied Ecology*, *54*(2). https://doi.org/10.1111/1365- 2664.12819

APPENDICES

Appendix A. Chapter 2 Additional information

Figure A-1 Chapter 2 sampling design, following the exact protocol of Kalwij et al. (2008). The Pass was divided into five elevational bands, 300m in elevation apart, from 1500m a.s.l to 2876m a.s.l. Within each band, four locations were randomly chosen in 2007. A GPS was used to locate them for sampling in 2017. At each location, four transects were sampled, in a nested design. Two sample categories were used – disturbed road verge and adjacent natural transects. The verge is defined as the area directly alongside the road that is affected by the road related disturbance. The natural area is the area beyond the verge that is considered pristine. Two transects were on the valley side and two on the mountain side. Therefore, eighty plots were surveyed along the Pass. Transects were 25m in length. The verge transects varied in width, depending on the width of the verge. The transects in the natural area were 2m in width.

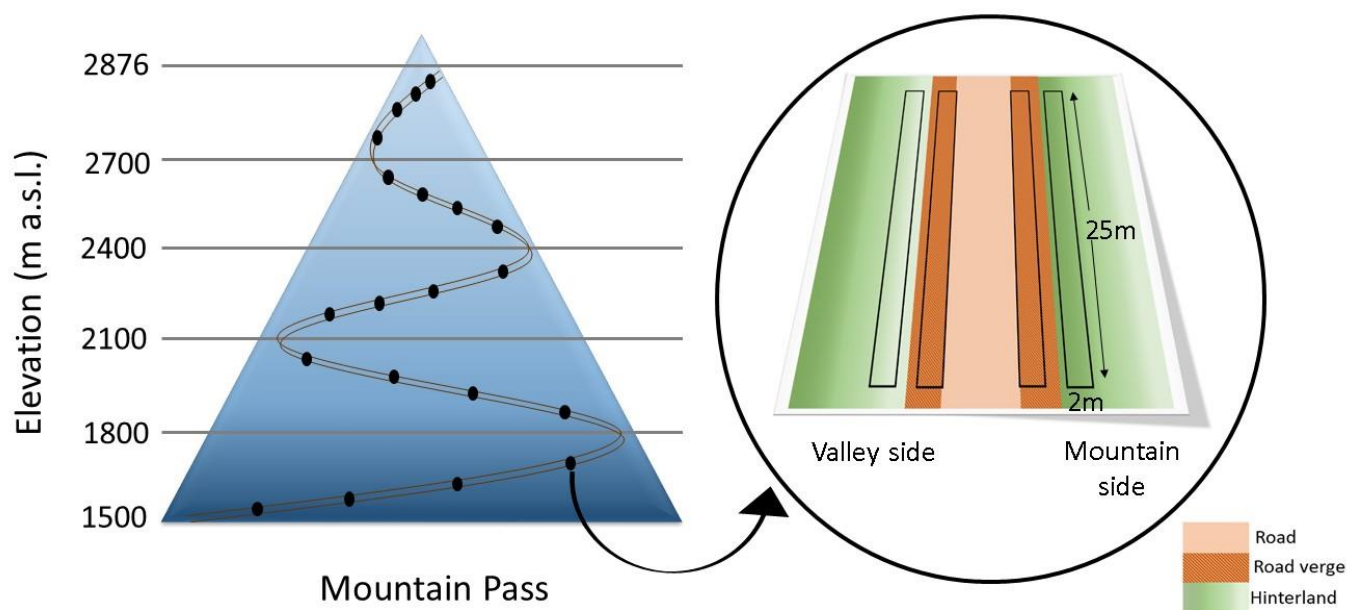**Figure A-2** Boxplots showing an overall increase in bare soil cover (Paired t-test: t= 4.8; P < 0.001) and decrease in indigenous vegetation (t= 5.21; P < 0.001) – indicative of disturbance (Hinterland = adjacent natural transects)
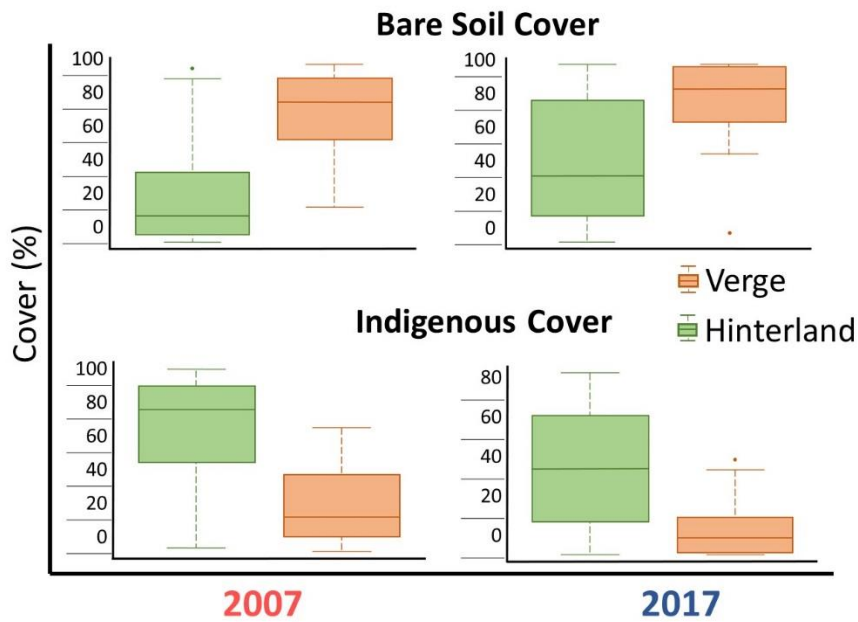

Figure A-3 Bar Graph depicting a significant increase in exotic species across the entire elevational gradient, over the ten-year time span (Paired t-test: t= 5.52; P < 0.001).
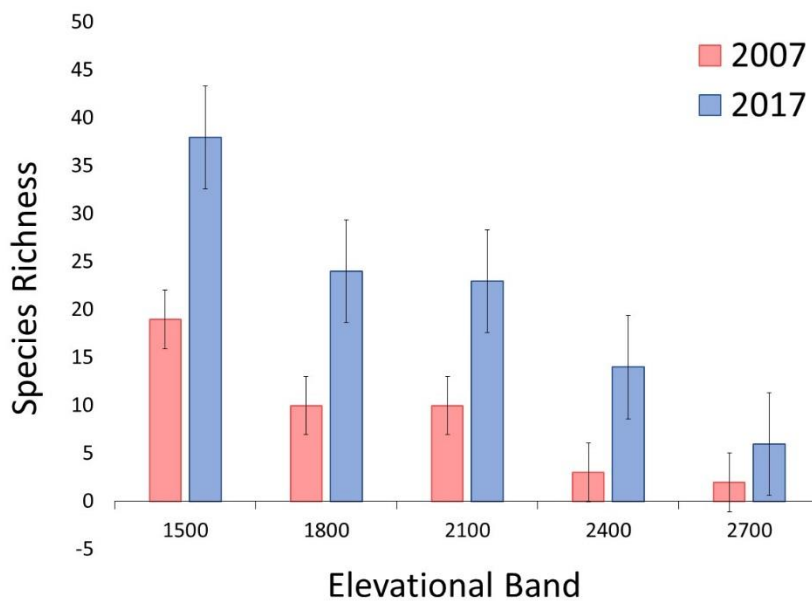
Table A-1 Table showing all the species present within the 80 transects surveyed in 2007 and 2017, and within which elevational band (1500, 1800, 2100, 2400, and 2700), as well as the family to which each species belongs. Species that only occurred in 2007, and not in 2017 are noted with an asterisk (*). Please note, this table indicates presence/absence, not abundance. Total number of species are 68, from 22 families. In 2007 there were 25 species from 11 families and in 2017 there were 63 species present from 20 families.

Year		2007					2017				
Species name	Family	1500	1800	2100	2400	2700	1500	1800	2100	2400	2700
Alternathera puguns	Amaranthaceae								X		
Amaranthus viridis	Amaranthaceae									X	
Chenopodium album	Amaranthaceae						X		X	X	X
Chenopodium carinatum	Amaranthaceae						X				
Salsola kali	Amaranthaceae						X				
Cyclospermum leptophyllum	Apiaceae						X				
Achillea millefolium	Asteraceae						X				
Bidens bipinnata	Asteraceae							X	X	X	X
Bidens pilosa	Asteraceae	X	X	X			X	X	X	X	
Cirsium vulgare	Asteraceae	X	X				X				
Conyza bonariensis	Asteraceae							X			
Conyza canadensis	Asteraceae	X	X				X	X	X	X	
Conyza sumatrensis	Asteraceae							X			
Cosmos bipinnatus	Asteraceae						X				
Galinsoga parviflora	Asteraceae						X				
Hypochaeris radicata	Asteraceae	X	X	X			X	X	X		
Pseudognaphalium luteoalbum	Asteraceae							X			
Schkuria pinnata	Asteraceae								X		
Tagetes minuta	Asteraceae	X	X	X			X	X	X	X	X
Taraxacum officinale	Asteraceae			X			X				
Xanthium strumarium	Asteraceae								X		
Rapistrum rugosum	Brassicaceae				X						
Canna indica	Cannaceae	X					X				
Stellaria media	Caryophyllaceae										X
Crepis hypochoeridea	Compositae							X			
Acacia mearnsii	Fabaceae	X					X				
Acacia dealbata	Fabaceae	X	X				X	X			
Acacia decurrens	Fabaceae						X				
Acanthospermum australe	Fabaceae							X			
Medicago falcata	Fabaceae								X		
Medicago polymorpha	Fabaceae			X					X		
Trifolium repens	Fabaceae						X				
Hypericum pseudohenryi	Hypericaceae						X				
Juncus bufonius	Juncaceae							X	X	X	
Juncus tenuis	Juncaceae								X	X	
Gagea	Liliaceae							X			
Oenothera rosea	Onagraceae						X		X	X	
Oenothera sp.2	Onagraceae						X				
Papaver aculeatum	Papaveraceae			X	X	X					

Year		2007					2017				
Species name	Family	1500	1800	2100	2400	2700	1500	1800	2100	2400	2700
Plantago lanceolata	Plantaginaceae	X		X			X	X	X		
Plantago major	Plantaginaceae	X						X			
Avena fatua	Poaceae								X		
Bromus catharticus	Poaceae	X		X	X				X	X	
Bromus sp.	Poaceae							X			
Dactylis glomerata	Poaceae						X				
Paspalum dilatatum	Poaceae	X	X	X			X	X	X		
Paspalum notatum	Poaceae							X			
Paspalum urvillei	Poaceae						X	X	X		
Pennisetum clandistinum	Poaceae	X					X				
Poa annua	Poaceae					X			X	X	X
Fallopia convolvulus	Polygonaceae									X	
Persicaria lapathifolia	Polygonaceae						X			X	
Polygonum aviculare	Polygonaceae								X		X
Rumex acetosella	Polygonaceae						X	X	X		
Agrimonia procera	Rosaceae	X									
Cotoneaster sp.1	Rosaceae						X				
Prunus persica	Rosaceae		X	X							
Pyracantha sp.	Rosaceae						X				
Rubus cuneifolius	Rosaceae	X	X				X	X			
Richardia brasiliensis	Rubiaceae	X	X				X	X			
Salix fragilis	Salicaceae						X				
Datura stramonium	Solanaceae	X					X		X		
Solanum mauritianum	Solanaceae	X					X				
Solanum pseudo-capsicum	Solanaceae						X	X			
Verbena bonariensis	Verbenaceae	X					X				
Verbena brasiliensis	Verbenaceae							X			

Appendix B. Pathway Classification

Table B-1 Categorization of pathways for the introduction of exotic species [Excerpt from CBD (2014)]

	Category	Subcategory
Movement of COMMODITY	**RELEASE** IN NATURE (1)	Biological control
		Erosion control/ dune stabilization (windbreaks, hedges, …) Fishery in the wild (including game fishing)
		Hunting
		Landscape/flora/fauna "improvement" in the wild
		Introduction for conservation purposes or wildlife management
		Release in nature for use (other than above, e.g., fur, transport, medical use) Other intentional release
	ESCAPE FROM CONFINEMENT (2)	Agriculture (including Biofuel feedstocks) Aquaculture / mariculture
		Botanical garden/zoo/aquaria (excluding domestic aquaria) Pet/aquarium/terrarium species (including live food for such species) Farmed animals (including animals left under limited control) Forestry (including afforestation or reforestation)
		Fur farms Horticulture
		Ornamental purpose other than horticulture Research and *ex-situ* breeding (in facilities) Live food and live bait
		Other escape from confinement
	TRANSPORT – **CONTAMINANT** (3)	Contaminant nursery material Contaminated bait
		Food contaminant (including of live food)
		Contaminant on animals (except parasites, species transported by host/vector) Parasites on animals (including species transported by host and vector) Contaminant on plants (except parasites, species transported by host/vector) Parasites on plants (including species transported by host and vector)
		Seed contaminant Timber trade
		Transportation of habitat material (soil, vegetation, etc.)
VECTOR	TRANSPORT - **STOWAWAY** (4)	Angling/fishing equipment
		Container/bulk
		Hitchhikers in or on airplane
		Hitchhikers on ship/boat (excluding ballast water and hull fouling)
		Machinery/equipment
		People and their luggage/equipment (in particular tourism)
		Organic packing material, in particular wood packaging
		Ship/boat ballast water
		Ship/boat hull fouling
		Vehicles (car, train, …)
		Other means of transport
SPREAD	**CORRIDOR** (5)	Interconnected waterways/basins/seas Tunnels and land bridges
	UNAIDED (6)	Natural dispersal across borders of invasive alien species that have been introduced through pathways 1 to 5

Table B-2 Percentage of species within each Family that use each dispersal method, with the actual counts in brackets. Note, species often use multiple dispersal methods, therefore percentages will not total 100.

Family	Dispersal Method								
	Natural	Waterways	Livestock	Clothes & shoes	Vehicles	Cultivation	Ornamental	Release into nature	Forage
Amaranthaceae	100 (5)	20 (1)	20 (1)	20 (1)	20 (1)	0 (0)	0 (0)	0 (0)	0 (0)
Apiaceae	100 (1)	100 (1)	100 (1)	100 (1)	100 (1)	100 (1)	0 (0)	0 (0)	0 (0)
Asteraceae	100 (15)	33.33 (5)	33.33 (5)	26.67 (4)	26.67 (4)	26.67 (4)	13.33 (2)	0 (0)	0 (0)
Brassicaceae	100 (1)	0 (0)	0 (0)	0 (0)	0 (0)	100 (1)	0 (0)	0 (0)	0 (0)
Cannaceae	100 (1)	100 (1)	0 (0)	0 (0)	0 (0)	0 (0)	100 (1)	0 (0)	0 (0)
Caryophyllaceae	100 (1)	0 (0)	100 (1)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Fabaceae	71.43 (5)	57.14 (4)	42.86 (3)	42.86 (3)	0 (0)	28.57 (2)	0 (0)	14.29 (1)	0 (0)
Hypericaceae	100 (1)	100 (1)	100 (1)	100 (1)	100 (1)	0 (0)	0 (0)	0 (0)	0 (0)
Juncaceae	50 (1)	0 (0)	0 (0)	50 (1)	50 (1)	0 (0)	0 (0)	0 (0)	0 (0)
Papaveraceae	100 (1)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	100 (1)	0 (0)	0 (0)
Phytolaccaceae	100 (1)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Plantaginaceae	100 (2)	0 (0)	100 (2)	100 (2)	0 (0)	100 (2)	0 (0)	0 (0)	0 (0)

Family	Dispersal Method								
	Natural	Waterways	Livestock	Clothes & shoes	Vehicles	Cultivation	Ornamental	Release into nature	Forage
Poaceae	100 (9)	55.56 (5)	88.89 (8)	44.44 (4)	55.56 (5)	55.56 (5)	0 (0)	0 (0)	11.11 (1)
Polygonaceae	100 (4)	100 (4)	50 (2)	50 (2)	100 (4)	75 (3)	0 (0)	0 (0)	0 (0)
Rosaceae	100 (5)	60 (3)	20 (1)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Rubiaceae	100 (1)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Salicaceae	0 (0)	100 (1)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Solanaceae	100 (3)	33.33 (1)	33.33 (1)	0 (0)	33.33 (1)	0 (0)	0 (0)	0 (0)	0 (0)
Verbenaceae	100 (2)	0 (0)	100 (2)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)

Appendix C. Database Information for Exotic Species Dispersal Methods

Appendix C-1 Table displaying the name of each species present in transects, Family of each exotic species, the name of the sources where information about each species' dispersal mechanisms and means of movement was acquired, and the type of source. References to the sources are below the table.

Species	Family	Source	Source Type
Alternathera puguns	Amaranthaceae	CABI/Herbiguide	Online database
Amaranthus viridis	Amaranthaceae	SAHRA	EMP
Chenopodium album	Amaranthaceae	FloraBase	Online database
Chenopodium carinatum	Amaranthaceae	SAHRA	EMP
Salsola kali	Amaranthaceae	CABI	Online database
Cyclospermum leptophyllum	Apiaceae	Lucid Key Server	Online database
Achillea millefolium	Asteraceae	CABI	Online database
Bidens bipinnata	Asteraceae	CABI /Plantwise	Online database
Bidens pilosa	Asteraceae	CABI /Plantwise	Online database
Cirsium vulgare	Asteraceae	CABI	Online database
Conyza bonariensis	Asteraceae	CABI	Online database
Conyza canadensis	Asteraceae	CABI	Online database
Conyza sumatrensis	Asteraceae	CABI	Online database
Cosmos bipinnatus	Asteraceae	Illinois Wildflowers	Website
Galinsoga parviflora	Asteraceae	CABI	Online database
Hypochaeris radicata	Asteraceae	CABI	Online database
Pseudognaphalium luteoalbum	Asteraceae	Herbiguide	Online database
Schkuria pinnata	Asteraceae	SAHRA	EMP
Tagetes minuta	Asteraceae	ISSA	Online database
Taraxacum officinale	Asteraceae	CABI	Online database
Xanthium strumarium	Asteraceae	ISSA	Online database

Species	Family	Source	Source Type
Rapistrum rugosum	Brassicaceae	Herbiguide	Online database
Canna indica	Cannaceae	CABI	Online database
Stellaria media	Caryophyllaceae	ISSA	Online database
Acacia dealbata	Fabaceae	CABI	Online database
Acacia decurrens	Fabaceae	CABI	Online database
Acacia mearnsii	Fabaceae	CABI	Online database
Acanthospermum australe	Fabaceae	CABI	Online database
Medicago falcata	Fabaceae	USDA	US Government Resource
Medicago polymorpha	Fabaceae	CABI	Online database
Trifolium repens	Fabaceae	OGTR	AU Government Resource
Hypericum pseudohenryi	Hypericaceae	FEIS	Online Resource
Juncus bufonius	Juncaceae	PNAS	Journal Article (supplementary information)
Juncus tenuis	Juncaceae	CABI	Online database
Papaver aculeatum	Papaveraceae	ISSA	Online database
Phytolacca octandra	Phytolaccaceae	ISSA	Online database
Plantago lanceolata	Plantaginaceae	CABI	Online database
Plantago major	Plantaginaceae	CABI	Online database
Avena fatua	Poaceae	CABI	Online database
Bromus catharticus	Poaceae	Blood (2001)	Journal article
Bromus sp.	Poaceae	CABI	Online database
Dactylis glomerata	Poaceae	CABI	Online database

Species	Family	Source	Source Type
Paspalum dilatatum	Poaceae	CABI	Online database
Paspalum notatum	Poaceae	CABI	Online database
Paspalum urvillei	Poaceae	CABI	Online database
Pennisetum clandistinum	Poaceae	CABI	Online database
Poa annua	Poaceae	CABI	Online database
Fallopia convolvulus	Polygonaceae	CABI	Online database
Persicaria lapathifolia	Polygonaceae	UAA	Online Resource
Polygonum aviculare	Polygonaceae	CABI	Online database
Rumex acetosella	Polygonaceae	CABI	Online database
Agrimonia procera	Rosaceae	ISSA	Online database
Cotoneaster sp.1	Rosaceae	ISSA	Online database
Prunus persica	Rosaceae	CABI	CABI
Pyracantha sp.	Rosaceae	Lucid Key Server	Online database
Rubus cuneifolius	Rosaceae	CABI	Online database
Richardia brasiliensis	Rubiaceae	ISSA	Online database
Salix fragilis	Salicaceae	CABI	Online database
Datura stramonium	Solanaceae	ISSA	Online database
Solanum mauritianum	Solanaceae	CABI	Online database
Solanum pseudo-capsicum	Solanaceae	Lucid Key Server	Online database
Verbena bonariensis	Verbenaceae	ISSA	Online database
Verbena brasiliensis	Verbenaceae	ISSA	Online database

References:

Australian Government Office of the Gene Technology Regulator. (2018).Retrieved from: http://www.ogtr.gov.au/

Blood K. (2001) Environmental Weeds: A Field Guide for SE Australia. CH Jerram & Associates – Science Publishers. Mt Waverley.

CABI. (2018). Invasive Species Compendium. Wallingford, UK: CAB International. Retrieved from: www.cabi.org/isc.

Gray, R. S. F., Small, P. L., Reed, M. C. F., Stein, P., Meisn, S., Fern, P., … Schrank, P. (1974). Spotted ladysthumb (Polygonum persicaria L . or Persicaria maculosa Gray) Curlytop knotweed (Polygonum lapathifolium L . or Persicaria lapathifolia (Linnaeus), 3–6.

Herbiguide. (1998).Retrieved from: http://herbiguide.com.au/

ISSA (2018). Invasive Species South Africa. Retrieved from: http://invasives.org.za/ John Hitly. (2002-2018). Illinois Wildflowers. Retrieved from: https://www.illinoiswildflowers.info/

Leach, M.C.; Hobbs, S.L.A. Plantwise knowledge bank: delivering plant health information to developing country users. Learned Publishing (2013) 26 (3) 180-185. Retrieved from: https://www.plantwise.org/KnowledgeBank/

Lucid Key Server. (2018). Lucidcentral. Retrieved from: http://www.lucidcentral.com/ South African Heritage Resources Agency (2018). Retrieved from: https://www.sahra.org.za/

USDA. (2018). United States Department of Agriculture Natural Resources Conservation Service Plant Database. Retrieved from: https://plants.sc.egov.usda.gov/java/

Western Australian Herbarium (1998-2018). Floarabase –the Western Australian Flora. Department of Biodiversity, Conservation and Attractions. Retrieved from: https://florabase.dpaw.wa.gov.au/

Wotton, D. M., & McAlpine, K. G. (2015). Seed dispersal of fleshy-fruited environmental weeds in New Zealand. *New Zealand Journal of Ecology*, *39*(2). https://doi.org/10.2307/26198707

Appendix D. Vectors: descriptive and multivariate analyses

Figure D-1. Scatterplot showing association between the number of introductory pathways used by exotic species and the number of natural transects that they are present in.
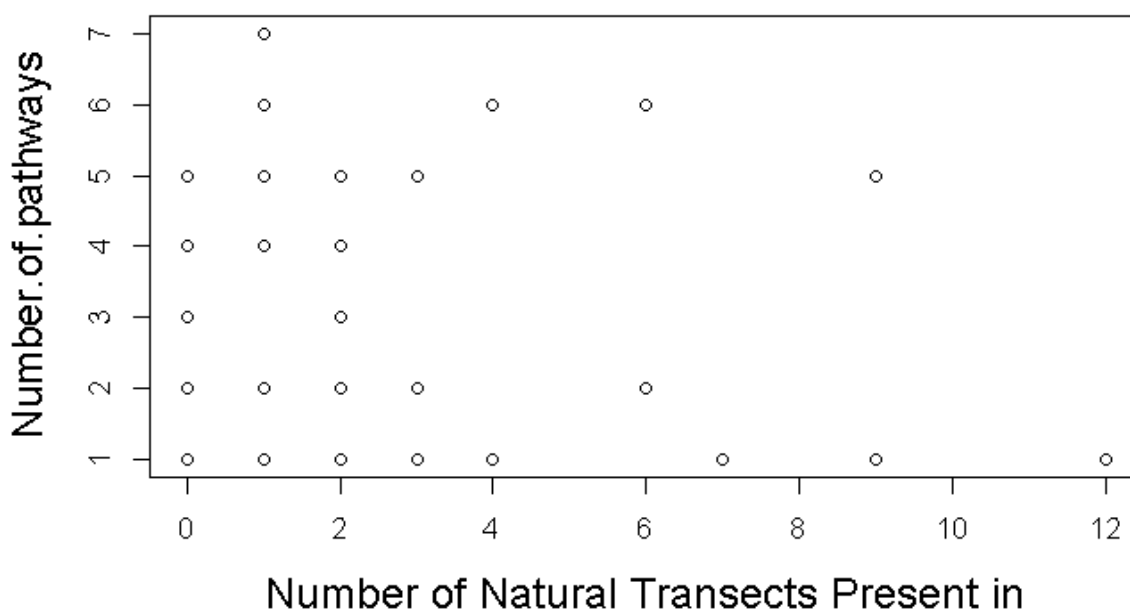

Table D-1 Results of a GLM testing associations between Presence in the natural transects and particular families. Initially generated with a Poisson distribution (log link), however overdispersion was present, thus it was regenerated with a quasi-Poisson distribution.

```
Call:
glm(formula = Natural.transects ~ Family + Number.of.pathways,
    family = poisson(), data = df)

Deviance Residuals:
    Min       1Q   Median       3Q      Max
-2.4495  -1.8184  -0.0003   0.4092   4.8800

Coefficients:
                      Estimate Std. Error z value Pr(>|z|)
(Intercept)           -0.99635    0.72274  -1.379   0.1680
FamilyApiaceae         0.73391    1.26907   0.578   0.5631
FamilyAsteraceae       1.60533    0.73304   2.190   0.0285 *
FamilyBrassicaceae   -16.39372 3467.85861  -0.005   0.9962
FamilyCannaceae        1.55828    1.00418   1.552   0.1207
FamilyCaryophyllaceae  0.90887    1.22480   0.742   0.4581
FamilyFabaceae         0.32375    0.86803   0.373   0.7092
FamilyHypericaceae   -16.52493 3467.85862  -0.005   0.9962
FamilyJuncaceae        1.84679    0.83713   2.206   0.0274 *
FamilyPapaveraceae   -16.39372 3467.85861  -0.005   0.9962
FamilyPhytolaccaceae   0.95261    1.22670   0.777   0.4374
FamilyPlantaginaceae   0.82139    1.01465   0.810   0.4182
FamilyPoaceae          1.38968    0.77340   1.797   0.0724 .
FamilyPolygonaceae     0.78841    0.89674   0.879   0.3793
FamilyRosaceae         1.79293    0.76378   2.347   0.0189 *
FamilyRubiaceae        2.05122    0.91549   2.241   0.0251 *
FamilySalicaceae       0.95261    1.22670   0.777   0.4374
```

```
FamilySolanaceae          -16.39259 2000.40131  -0.008   0.9935
FamilyVerbenaceae           2.00748    0.81657   2.458   0.0140 *
Number.of.pathways          0.04374    0.08033   0.545   0.5861
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

(Dispersion parameter for poisson family taken to be 1)

    Null deviance: 200.65  on 62  degrees of freedom
Residual deviance: 159.28  on 43  degrees of freedom
AIC: 280.04

Number of Fisher Scoring iterations: 15




Call:
glm(formula = Natural.transects ~ Family + Number.of.pathways,
    family = quasipoisson(), data = df)

Deviance Residuals:
    Min      1Q   Median      3Q      Max
-2.4495  -1.8184  -0.0003   0.4092   4.8800

Coefficients:
                          Estimate Std. Error t value Pr(>|t|)
(Intercept)               -0.99635    1.45529  -0.685    0.497
FamilyApiaceae             0.73391    2.55536   0.287    0.775
FamilyAsteraceae           1.60533    1.47604   1.088    0.283
FamilyBrassicaceae       -16.39372 6982.80659  -0.002    0.998
FamilyCannaceae            1.55828    2.02199   0.771    0.445
FamilyCaryophyllaceae      0.90887    2.46622   0.369    0.714
FamilyFabaceae             0.32375    1.74784   0.185    0.854
FamilyHypericaceae       -16.52493 6982.80661  -0.002    0.998
FamilyJuncaceae            1.84679    1.68563   1.096    0.279
FamilyPapaveraceae       -16.39372 6982.80659  -0.002    0.998
FamilyPhytolaccaceae       0.95261    2.47005   0.386    0.702
FamilyPlantaginaceae       0.82139    2.04308   0.402    0.690
FamilyPoaceae              1.38968    1.55731   0.892    0.377
FamilyPolygonaceae         0.78841    1.80566   0.437    0.665
FamilyRosaceae             1.79293    1.53792   1.166    0.250
FamilyRubiaceae            2.05122    1.84341   1.113    0.272
FamilySalicaceae           0.95261    2.47005   0.386    0.702
FamilySolanaceae         -16.39259 4027.96568  -0.004    0.997
FamilyVerbenaceae          2.00748    1.64423   1.221    0.229
Number.of.pathways         0.04374    0.16175   0.270    0.788

(Dispersion parameter for quasipoisson family taken to be 4.0545)

    Null deviance: 200.65  on 62  degrees of freedom
Residual deviance: 159.28  on 43  degrees of freedom
AIC: NA

Number of Fisher Scoring iterations: 15
```

Please note: GLMs were generated for each vector individually, Poisson distribution (log link).

No models showed any significant results and were therefore removed.

Appendix E. Introduction pathways: descriptive and multivariate analyses

Figure E-1 Boxplot depicting the number of pathways (NOP) used and presence in natural transects (PINT). A factor with 2 levels was used, where 1 = one pathway, 2 = more than one pathway.
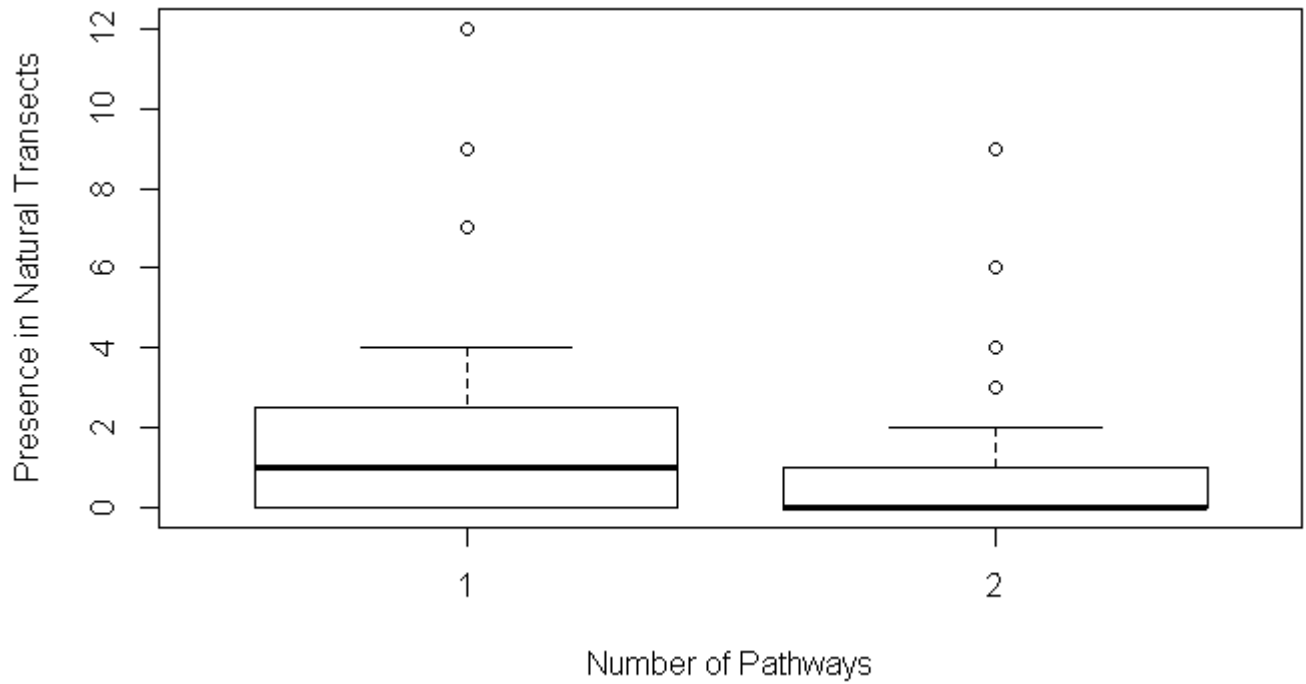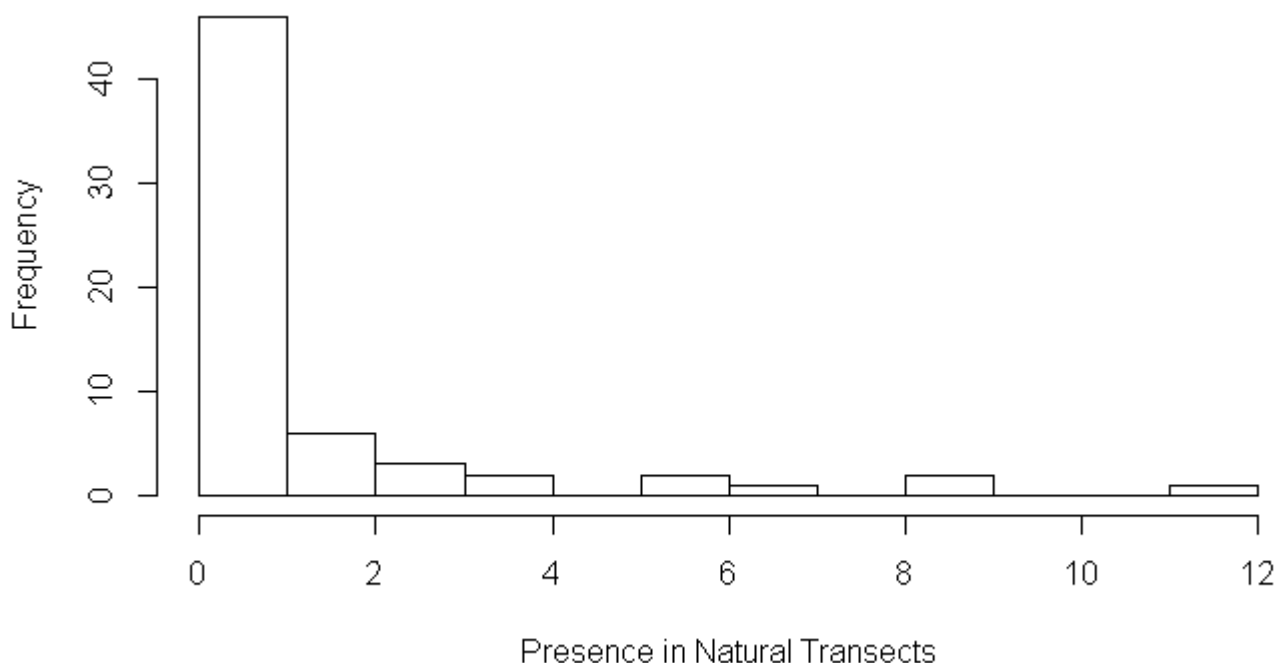
Figure E-2. A histogram depicting the frequency of exotic species presence in natural transects (PINT) (i.e. how many transects species occurred in, in the natural transects). This graph shows a zero-inflated count.

Tables E-(1-3) Results of GLMs testing association between Presence in Natural Transect (PINT) and individual pathways (E-1- Unintentional introductions, E-2- Corridor dispersal, and E-3- intentional introductions). First a model using a Poisson distribution was generated (log link), followed by a ZIP model (binomial family with logit link). A Vuong test was used to compare the zero-inflated Poisson model to the standard Poisson model.

Response Variable	Estimate	SE	z	P
Unintentional	-0.4597	0.2339	-1.965	**0.0494 ***
Zero-inflated	-0.4597	0.2339	-1.965	**0.0494 ***
Vuong	Raw		2.169883	0.015008
	AIC-corrected		2.169883	0.015008
	BIC-corrected		2.169883	0.015008

Response Variable	Estimate	SE	z	P
Corridor dispersal	1.11E+00	7.16E-01	1.545	0.122
Zero-inflated	16.68	2864.06	0.006	0.995
Vuong	Raw		2.108959	0.017474
	AIC-corrected		2.108959	0.017474
	BIC-corrected		2.108959	0.017474

Response Variable	Estimate	SE	z	P
Intentional	-1.2276	0.9509	-1.291	0.197
Zero-inflated	-0.22012	1.94997	-0.113	0.91
Vuong	Raw		2.108959	0.017474
	AIC-corrected		2.108959	0.017474
	BIC-corrected		2.108959	0.017474

Appendix F. Analyses using presence in hinterland as a proxy for success.

Please note that these analyses use presence/absence of species in the natural transects as a proxy for success and were later discarded and replaced with the extent of PINT (i.e. number of transects). The reason being that just using presence/absence was too simple to draw meaningful conclusions.

Figure F-1. Boxplot showing the number of pathways used by species that are absent and present in the natural area.
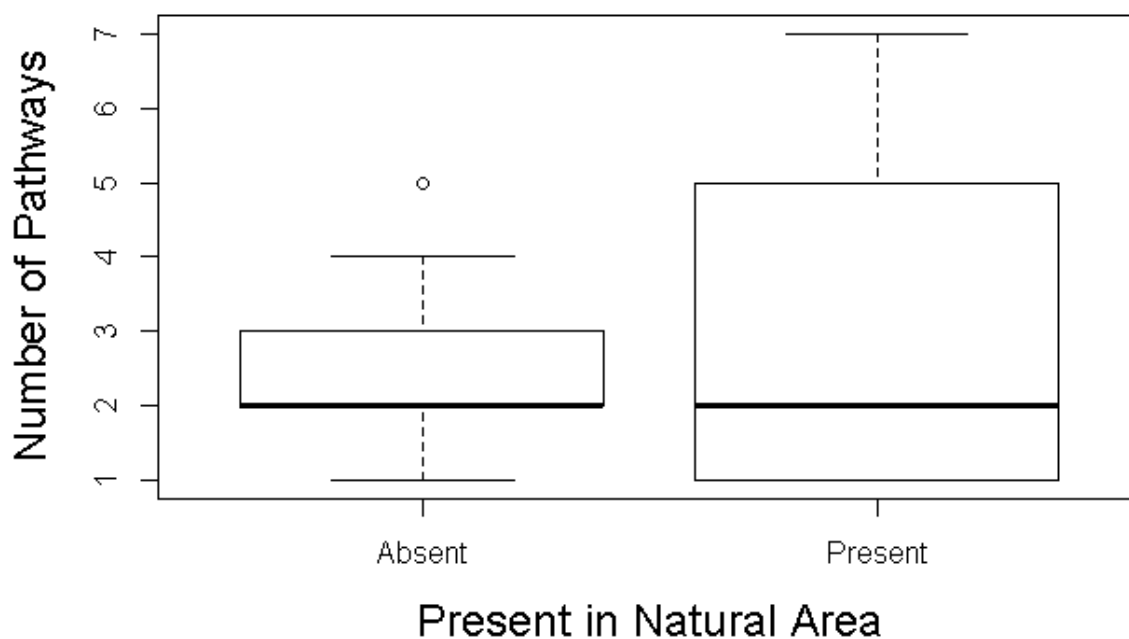
Table F-1. Logistic regression (using a binomial distribution) results showing no significant relationship between successful species and number of pathways used, where the presence of species in the natural area (hinterland) is a proxy for success.

```
Call:
glm(formula = Present.in.hinterland ~ Number.of.pathways, family = binomial
',
    data = df)

Deviance Residuals:
    Min       1Q    Median        3Q       Max
-1.3735  -1.1666    0.9321    1.1883    1.2565

Coefficients:
                   Estimate Std. Error z value Pr(>|z|)
(Intercept)         -0.3427     0.5084  -0.674    0.500
Number.of.pathways   0.1586     0.1606   0.987    0.324

(Dispersion parameter for binomial family taken to be 1)

    Null deviance: 87.194  on 62  degrees of freedom
Residual deviance: 86.197  on 61  degrees of freedom
AIC: 90.197

Number of Fisher Scoring iterations: 4
```

Table F-2. Counts of the number of species present or absent in the natural area, for whether it makes use of the pathways (Y) or not (N).

Pathway	Natural Area	Use Pathway	
		No	Yes
Natural	Absent	1	29
	Present	3	30
		No	Yes
Waterways	Absent	18	12
	Present	18	15
		No	Yes
Livestock	Absent	17	13
	Present	18	15
		No	Yes
Clothes & Shoes	Absent	22	8
	Present	22	11
		No	Yes
Vehicles	Absent	24	6
	Present	21	12
		No	Yes
Cultivation	Absent	24	6
	Present	21	12
		No	Yes
Ornamental	Absent	29	1
	Present	30	3
		No	Yes
Release into Nature	Absent	29	1
	Present	33	0
		No	Yes
Forage	Absent	29	1
	Present	33	0

Pathways that had less than 10 species in either N or Y were then excluded, as below 10 is not enough observations to tell us whether having that pathway increases the chances of being present or not (i.e. successful).

Figure F-2. Bar plots displaying the proportion of species that use each pathway (excluding pathways with no meaningful data).
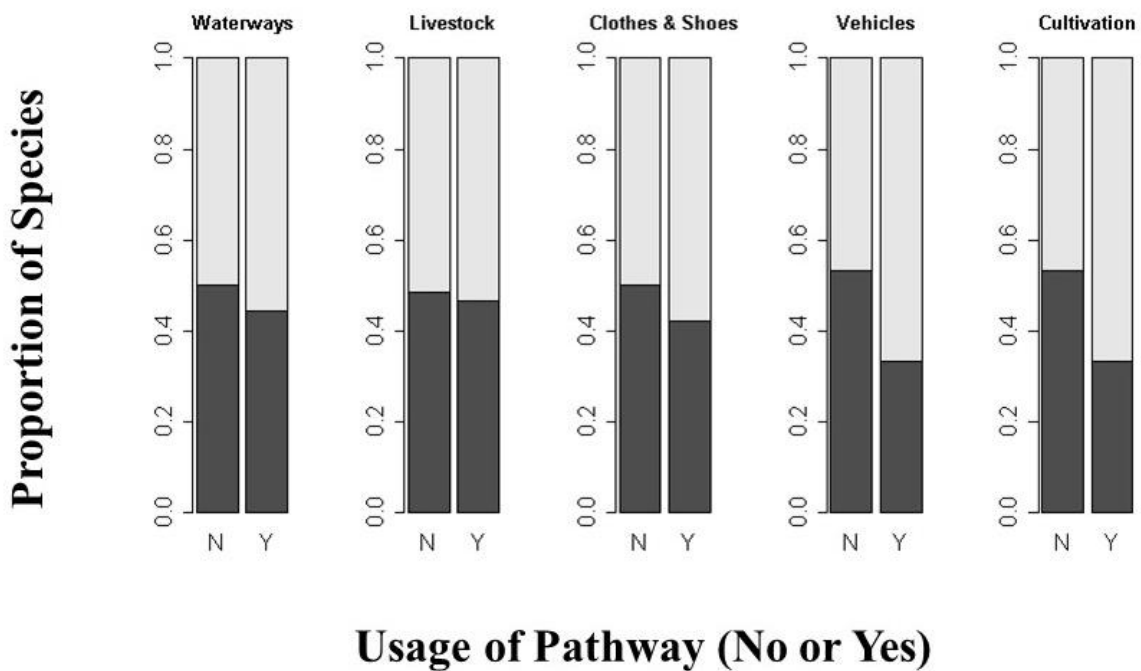

Figure A2 shows little difference in the proportion of successful versus unsuccessful species for "Waterways", "Livestock", and "Clothes and Shoes". There appears to be some difference in pathways "Vehicles" and "Cultivation". Chi square test of independence was used to test if there was a significant difference for the latter two pathways. Results of Chi square test of independence, where Vtable refers to "Vehicles", and Ctable refers to "Cultivation".

Table F-3. Results of the Chi square test of independence, show no significant association between both pathways (Vehicles and Cultivation) and number of successful species. Vtable refers to "Vehicles" and Ctable refers to "Cultivation".

```
> chisq.test(Vtable)

        Pearson's Chi-squared test with Yates' continuity correction

data:  Vtable
X-squared = 1.338, df = 1, p-value = 0.2474
```

```
> chisq.test(Ctable)

        Pearson's Chi-squared test with Yates' continuity correction

data:  Ctable
X-squared = 1.338, df = 1, p-value = 0.2474
```

Table F-4. Logistic regression (using a binomial distribution) incorporating all pathways to see if any are associated with successful species. This shows no significance.

```
Call:
glm(formula = Present.in.hinterland ~ Waterways + Livestock +
    Vehicles + Cultivation + Clothes.shoes, family = binomial,
    data = df)

Deviance Residuals:
   Min      1Q  Median      3Q     Max
-1.711  -1.143   0.760   1.212   1.466

Coefficients:
               Estimate Std. Error z value Pr(>|z|)
(Intercept)    -0.08043    0.40601  -0.198    0.843
WaterwaysY     -0.22207    0.59148  -0.375    0.707
LivestockY     -0.32851    0.67139  -0.489    0.625
VehiclesY       0.83035    0.77110   1.077    0.282
CultivationY    0.69814    0.64204   1.087    0.277
Clothes.shoesY -0.02541    0.78542  -0.032    0.974

(Dispersion parameter for binomial family taken to be 1)

    Null deviance: 87.194  on 62  degrees of freedom
Residual deviance: 83.678  on 57  degrees of freedom
AIC: 95.678

Number of Fisher Scoring iterations: 4
```