Quantifying threats to biodiversity from invasive alien plants and other factors: a case study from the Cape Floristic Region

A.M. Latimer[a*], J.A. Silander Jr[a], A.E. Gelfand[b], A.G. Rebelo[c] and D.M. Richardson[d]

Nearly a third of the area of South Africa's Cape Floristic Region has been transformed by human land use and invasive alien plants. The vulnerability of remaining natural areas to transformation has been assessed, but less attention has been given to characterizing how different types of habitat transformation have affected features of natural communities. A comparison of the effects of invasive alien species with other forms of transformation, including agriculture, forestry and urbanization, can distinguish unique features of invasive alien species and inform responses to their effects. Using Bayesian hierarchical regression models, we predicted what the potential distributions of a set of species of Proteaceae would have been before transformation. We used these predictions to describe and compare the impacts of different forms of habitat transformation. Results show that: 1) agriculture is by far the most important agent of transformation, in area and in severity of species loss; 2) forestry and urbanization cause relatively high species loss where they occur; 3) invasive alien plants are widespread, but have the least severe effects on diversity where present; and 4) agriculture affects common species disproportionately, whereas forestry and invasive alien plants influence species in direct proportion to their prevalence. Invasive alien plants have thus had by many measures a smaller effect on diversity than other forms of habitat transformation. However, they may pose the greatest continuing threat to diversity and rare species if they are allowed to persist and spread to their full potential.

Introduction

It is often stated that biological invasions pose the second most pressing threat to biodiversity after direct habitat transformation.[1] Yet this assertion, which has crucial policy implications for conservation, land-use planning and restoration, has yet to be quantitatively tested, except on the basis of analysis of threatening factors listed for rare species.[2] A more detailed assessment of the spatial dynamics of biological invasions and other threat factors is needed to inform effective conservation management. South Africa's Cape Floristic Region offers opportunities to advance our understanding in this area. First, the area is spectacularly rich in plant species, very detailed distribution data are available for some key taxa, and there is excellent information on environmental factors, a key prerequisite for spatial modelling. Second, the extent of the main types of habitat transformation has been mapped. Although the vulnerability of remaining natural areas to transformation has been assessed,[3] less attention has been given to characterizing how different types of transformation, including agriculture, forestry, urbanization and invasive alien plants, have affected features of natural communities, including species richness and rare species representation. This paper presents a novel method for producing an essential prerequisite for such an analysis, a prediction of species distributions and species richness in the absence of transformation. Unlike standard approaches to quantifying past and potential effects of alien plant invasions,[4] the method presented here, using the output from Bayesian hierarchical regression models[5] together with maps of transformation derived primarily from satellite imagery, facilitates a description of the effects of different kinds of transformation on individual species distributions and species richness. One aim of this study was to assist in objective priority formulation for management programmes aimed at clearing invasive alien plants in natural and seminatural vegetation.[6]

This study used spatially explicit, hierarchical regression models to predict the distributions of a representative set of species in the protea family (Proteaceae), one of the characteristic families of fynbos vegetation in the Cape Floristic Region.[7] The models computed a 'potential range' for each species in the form of a probability surface that represents predicted probability of occurrence in the absence of habitat transformation.[8] This potential range was then adjusted by the percentage of each grid cell that has been transformed to obtain a 'transformed range'. Unlike previous efforts to model species distributions and richness,[9] the distributions of all the species were modelled simultaneously, enabling predictions for each species to be informed by a common spatial effect. By summing across species, a prediction of potential species richness was obtained.

Using the maps of habitat transformation prepared for the recent Cape Action Plan for the Environment,[3,10] we compared the effects of alien plant invasions with those of agriculture, forestry, and urbanization. We related the distributions of these impacts to patterns of potential richness and to individual species distributions to address three questions: 1) Where do the various types of habitat transformation occur in relation to areas of high species richness? 2) What have been the consequences of these changes so far on richness (using Proteaceae as surrogates) and on rare and common species? 3) What types of transformation present the most immediate threats to diversity and rare species?

Predicting diversity and distributions in the untransformed landscape

An effort to characterize the effects of past transformation must start by inferring what the characteristics of the natural vegetation would be in the absence of transformation. We focused on species richness and individual species distributions,

---

[a]Department of Ecology and Evolutionary Biology, University of Connecticut, 75 North Eagleville Road, Storrs, CT 06269-3043, U.S.A. E-mail: andrew.latimer@uconn.edu, john.silander@uconn.edu

[b]Institute of Statistics and Decision Sciences, Duke University, 223-A Old Chemistry Building, Box 90251, Durham, NC 27708-0251, U.S.A. E-mail: alan@stat.duke.edu

[c]Protea Atlas Project, National Botanical Institute, Kirstenbosch, Private Bag X7, Claremont 7735, South Africa. E-mail: rebelo@nbict.nbi.ac.za

[d]Leslie Hill Institute for Plant Conservation, Botany Department, University of Cape Town, Private Bag, Rondebosch 7701, South Africa. E-mail: rich@botzoo.uct.ac.za

*Author for correspondence.

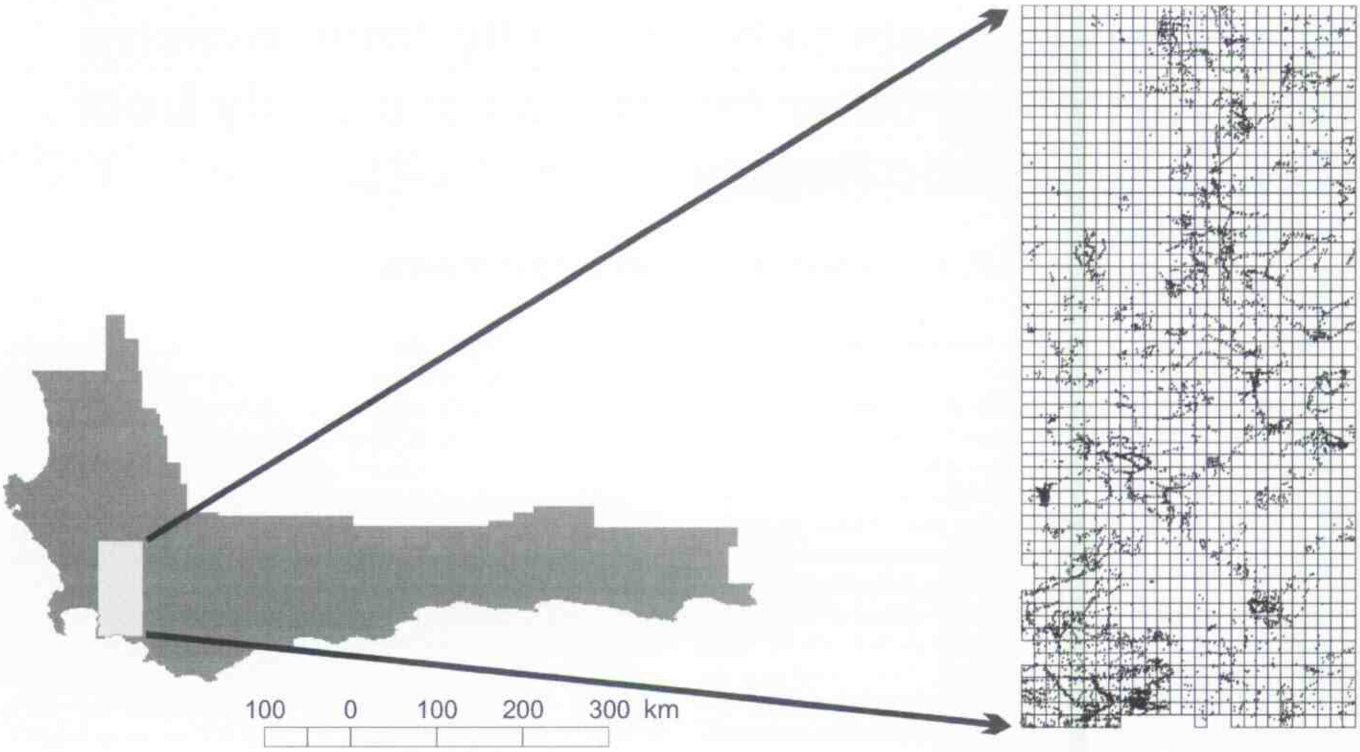

Fig. 1. The subregion selected for quantifying threats to biodiversity within the Cape Floristic Region, showing the localities of sites with species distribution data from the Protea Atlas Project.[15]

and predicted these using hierarchical regression models to relate observed species presence or absence to environmental variables and species attributes, explicitly considering spatial association through random effects. The Bayesian approach, in which the parameters of a fully specified probabilistic model are estimated based on new data and on prior information, enables more flexible and complicated models that can incorporate more features of the data than traditional single-level models.[5] An advantage of this approach is that it provides an explicit characterization of the uncertainty associated with the predictions, given our current state of knowledge about the climate and the species (that is, the data) and our understanding of the processes through which these are related (that is, the model). In this study, the first level of the model was a logistic regression that related the probability of species presence or absence at a particular site to environmental factors, and included a spatial random effect to capture spatial association in the species occurrences. This level of the model was thus similar in structure to other regression models now in widespread use for spatial ecological prediction.[11] The hierarchical models employed here, however, incorporated a second level that related species probability of occurrence at a site to the proportion of the site transformed by human activity, and a third level that related the sampling process to the actual presence or absence of a species through another logistic regression. A full specification of the modelling framework is presented elsewhere.[8]

The hierarchical structure of the models provided some major advantages over conventional, single-level regression techniques (whether logistic or tree-based). First, rather than simply accepting the sampling data (that is, which species are present at a site) as perfectly accurate, the model related these observations to an unobserved (latent) variable that represents true presence or absence. The relationship and the true state of the system could thus be explicitly modelled, and characteristics of the species that affected this relationship — here the probability of observing a species given that it is there — could be linked to relevant characteristics of species.[8,12] In addition to explicitly modelling the process of observation, the data sub-model handled differences in sampling intensity by treating the sampling data as a set of Bernoulli trials.

Second, by modelling individual species distributions simultaneously, the model can incorporate relevant species attributes (for instance, dispersal mode) and enable some 'borrowing' of distributional information across species. Thus the hierarchical structure enables reasonable prediction even for species that have been observed only a few times, while reducing the risk of overfitting.[5] Finally, the model is able to take into account human transformation of the landscape by incorporating data on the proportion of each grid cell that has been transformed.

The model likelihood was too complex to allow parameters to be estimated analytically, so the models had to be fitted using Markov Chain Monte Carlo methods. Because of the computational demands of this procedure, for model development and testing we focused on a subsection of the Western Cape. The area for which suitable data were available (Fig. 1) encompasses the Kogelberg Biosphere Reserve and Hawequas Reserve. This region was chosen for testing aspects of the modelling technique because it is spectacularly rich in species (with centres of species richness and endemism in key fynbos families such as Proteaceae, Ericaceae, and Restionaceae),[13] contains a range of habitats and topographical features. The area was also particularly well covered by Protea Atlas Project sampling (the Protea Atlas Project records the detailed distribution of plants in the family Proteaceae, to support research and conservation[15]). We modelled at a one-minute by one-minute scale, which is the finest resolution at which most climate data are available, yielding a total of 1554 grid cells for the subregion. We simultaneously modelled the distributions of 40 species of Proteaceae, selected to represent a range of genera, degrees of rarity and endemism, and ecological characteristics (species and attributes listed in

Appendix A). The 40 species included one alien species, *Hakea sericea*, which was modelled to investigate its potential range, but this species was excluded from calculations of species richness.

The model incorporated 24 environmental data layers, including information on rainfall and temperature level and variation from the *South African Atlas of Agrohydrology and Climatology*.[14] Topography was incorporated as altitude and altitudinal range, using a Digital Elevation Model from the same source. Soil characteristics were approximated by assigning ordinal values to geology types for fertility, texture, and pH of associated soils. Primary productivity was represented by a satellite-based chlorophyll index, or 'enhanced vegetation index'. The percentage of each cell that has been transformed was obtained from Cape Action for People and the Environment.[10] All layers were cut to the extent of the subregion. In addition to environmental characteristics, we also incorporated species attributes considered potentially relevant to species prevalence: height, typical observed local population size, post-fire regeneration capability, and pollination and dispersal mode. The number of times each species was observed in a grid cell and the sample size was obtained from Protea Atlas Project data.[15]

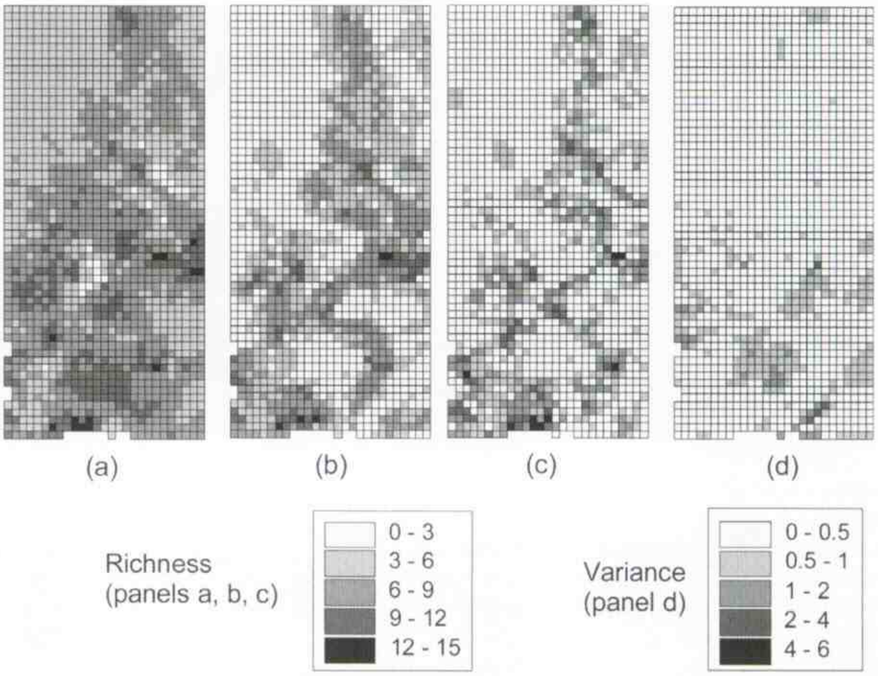

Fig. 2. Maps showing (**a**) predicted potential richness; (**b**) potential richness adjusted downward by percentage transformation (that is, 'transformed richness'); (**c**) observed richness based on Protea Atlas data; and (**d**) variance in potential richness. The units are number of protea species per grid cell, out of the 39 native species modelled.

We used the model to generate predictions for species distributions and richness in the absence of transformation, that is, potential range and richness, to project conditions for the subregion without habitat transformation (Fig. 2). The model predicts high and moderate diversity areas to have been much more widespread before transformation, and the transformed richness prediction matches well the general spatial pattern of observed species richness. Areas of high variance (that is, uncertainty) are concentrated in the southern part of the subregion, and include portions of the Elgin Basin and estuarine areas. Using these predictions as a baseline, it was possible to quantify the effects of different transformation types through a proportional adjustment by area. By multiplying predicted probabilities and richness for each grid cell by the proportion of each cell affected by each particular type of transformation, we obtained 'transformed' predictions for each species in each cell, which can be displayed or used to quantify level of impact. We then explored how the predicted distributions of individual species are spatially related to the locations of different types of impacts. We note that the relationship between the proportion of a grid cell transformed and a species' probability of occurrence in that cell might be better approximated by a properly fitted exponential function than by the simple linear function we used. But fitting such a function would be tricky because: 1) it would require additional information on how species' probability of occurrence decreases with changing patch area, keeping the environment constant; 2) the fit would presumably be different for different species; and 3) a non-linear function would present complications in cells in which multiple types of transformation co-occur, since the order in which different types of transformation arise would have to be specified. We accordingly applied a proportional linear adjustment as a reasonable proxy,[8] though we acknowledge that this method tends to exaggerate the loss of species predicted for cells with low to moderate proportions of transformation.

Forms of habitat transformation can be compared by plotting their mean effects on each species (that is, mean reduction in probability of occurrence across the subregion) against predicted prevalence of each species (calculated as mean probability of occurrence across the subregion). If the slope of this line is 1, species range reduction is directly proportional to prevalence, and rare and common species are affected strictly in proportion to their prevalence, whereas higher or lower slopes reflect bias toward common or rare species respectively. Note that because this comparison is based strictly on a comparison of the areal extent and location of the different types of transformation, it does not take into account possible interactions between species and transformation types, which could be a usefully explored through further modelling.

Discussion

Even in a part of the Western Cape not as affected by alien plant invasions as some,[3,16] invasive aliens have had impacts on natural vegetation patterns. But alien plants ranked only third as a cause of overall species loss, responsible for a mean reduction of 0.35 species per cell in the modelled subregion compared to 2.6 for agriculture, 0.46 for forestry, and 0.23 for urbanization. The total proportions of the study area that have been transformed are: 34.4% for agriculture, 4.1% for forestry, 3.6% for high and medium density aliens and 2.6% for urbanization. Alien plants have typically caused a less complete transformation of the areas they occupy than the direct forms of transformation, and thus have caused a smaller mean loss of species in cells in which they occur: a mean loss of 3.6 species per cell affected by agriculture (percentage transformed by agriculture >0), versus 2.1 for urbanization, 1.6 for forestry and 0.57 for aliens. Alien plants have accordingly had by many measures a smaller impact to date than other forms of transformation.

Maps of the distributions of the four types of habitat transformation and the magnitude of their effects on richness (Fig. 3) reveal some obvious features. Agriculture has overwhelmingly the greatest extent and, according to the model, has caused the greatest loss of species. This is despite the fact that many important agricultural areas, particularly in the northwestern corner of the subregion, are in the lowlands, where diversity in Proteaceae is low (compare Fig. 2 with Fig. 3). Species richness in lowlands is low for many fynbos taxa, although geophytes and associated renosterveld species are exceptions.[17] While each of the types of transformation has a clumped distribution, areas affected by invasive alien plants are relatively spatially dispersed, as the invaders can spread without human assistance, and invade fire-prone mountain fynbos areas.[3,16]

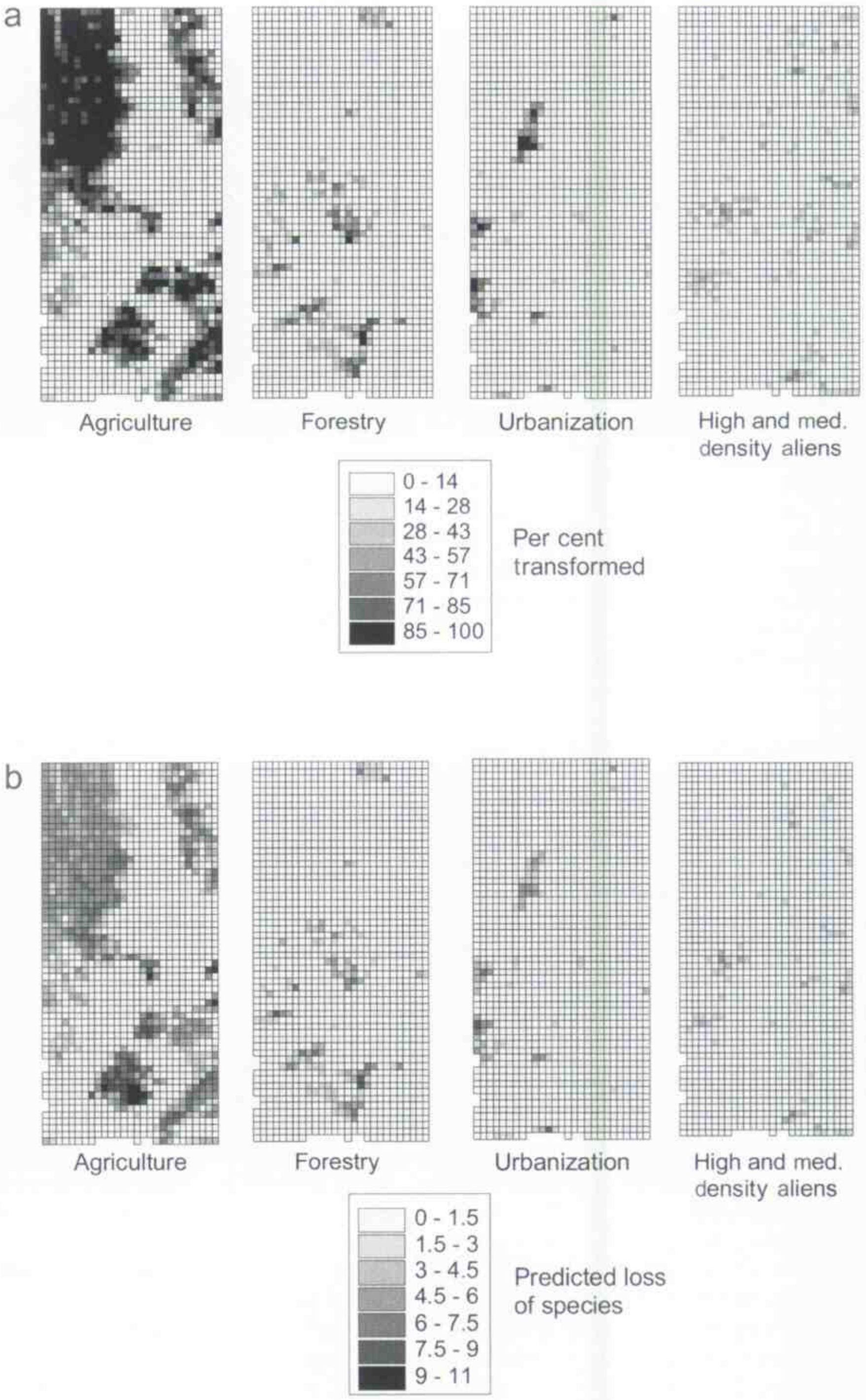

Fig. 3. The distribution of (**a**) different forms of land use / habitat transformation; and (**b**) their impact on potential species richness of Proteaceae.

Examination of the potential richness of cells in which different forms of habitat transformation occur reveal some characteristic spatial patterns. Histograms of potential richness in cells affected by each type of transformation show that alien plants and agriculture are by far the most widespread of the four impact types: agriculture affects 1106 cells out of a total of 1554, followed by alien plants (955 cells), forestry (453 cells) and urbanization (171 cells) (Fig. 4). Overall, forestry plantations occur in cells with higher mean potential richness than other impact types (mean potential richness 10.4 for forestry, 9.7 for urbanization, 9.1 for alien plants, and 8.5 for agriculture) (Fig. 4). Histograms of the levels of impact, defined as number of species expected to have been lost from individual grid cells in which the impact is present, show major differences between agriculture and aliens (Fig. 5). Though both types of transformation are evident in a large number of cells, where agriculture occurs, it tends to be almost completely transforming.

More strikingly, forestry is predicted to have caused, after agriculture, the largest number of severe impacts on diversity (200 cells with expected loss of more than 1 species, versus 173 cells for alien plants and 89 for urbanization) (see Fig. 5). This is because, as noted above, forestry tends to occur in cells with higher species richness (Fig. 4). Urbanization arises in few cells, but where it occurs, it has caused large species losses (Fig. 5). Across the subregion, agriculture is predicted to have caused the largest overall loss of species in cells in which it occurs, followed in order by urbanization, forestry, and aliens. Interestingly, rare species are not disproportionately affected by any of these types of transformation, but common species are disproportionately affected, due to their presence in low-elevation areas, by agriculture (slope = 1.14), and weakly (not statistically significantly) by urbanization (slope = 1.09) (Fig. 6). The highly linear, positive slopes of the fitted regression lines in Fig. 6 reflect the strong correlation between species prevalence and the absolute magnitude of the effect of transformation on their prevalence.

This study has demonstrated a method for estimating the natural composition and richness of a landscape that has been partially transformed, and for assessing the characteristics and 'signature' of different anthropogenic impacts. While results were limited to 40 species in a subregion of the Western Cape, some notable trends emerged. Agriculture clearly has had the greatest impact to date on diversity in the region. Perhaps more surprising are the findings on forestry and urbanization. Forestry has caused relatively high species loss relative to its extent due to its association with high-diversity areas; perhaps counter-intuitively, urbanization has not been restricted to areas

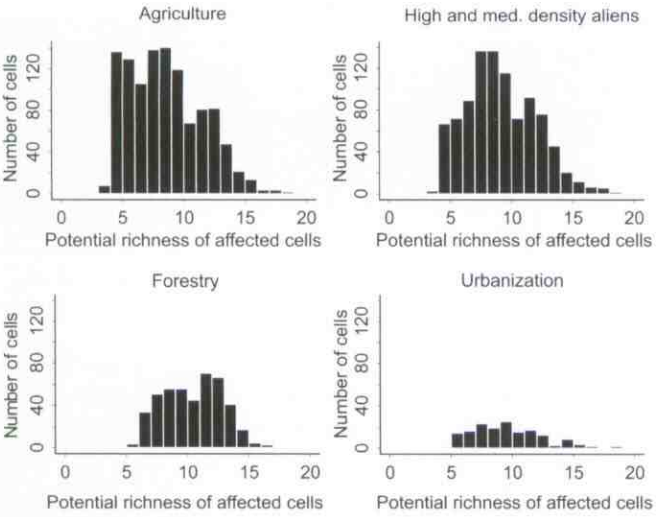

Fig. 4. The potential richness (number of species of the 39 modelled native Proteaceae) of cells affected by four types of land use / habitat transformation.

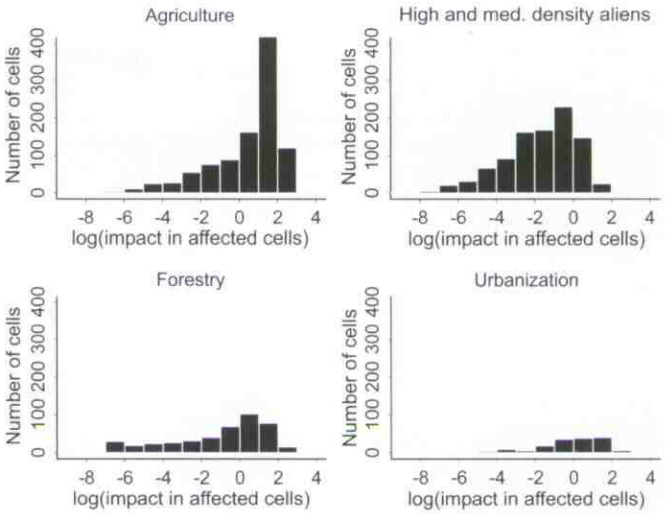

Fig. 5. The loss of species in modelled Proteaceae caused by four types of land use / habitat transformation.

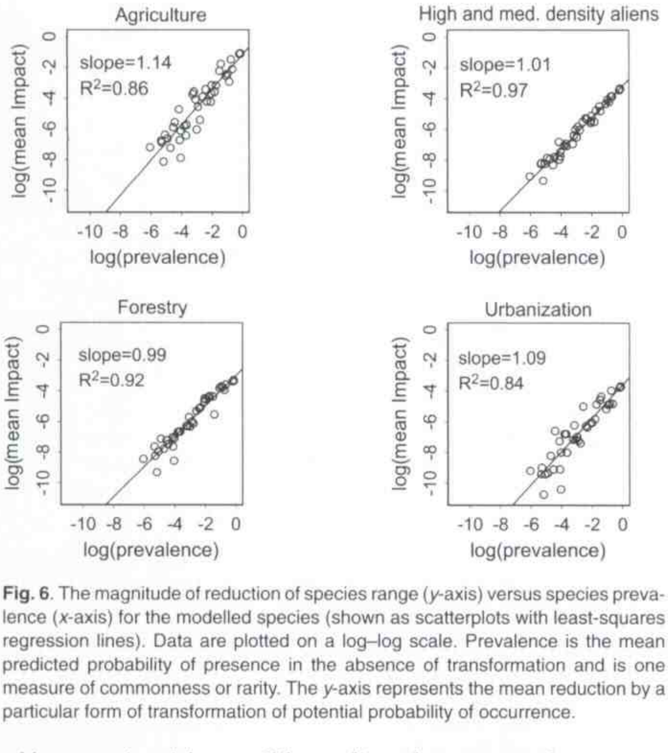

Fig. 6. The magnitude of reduction of species range (*y*-axis) versus species prevalence (*x*-axis) for the modelled species (shown as scatterplots with least-squares regression lines). Data are plotted on a log–log scale. Prevalence is the mean predicted probability of presence in the absence of transformation and is one measure of commonness or rarity. The *y*-axis represents the mean reduction by a particular form of transformation of potential probability of occurrence.

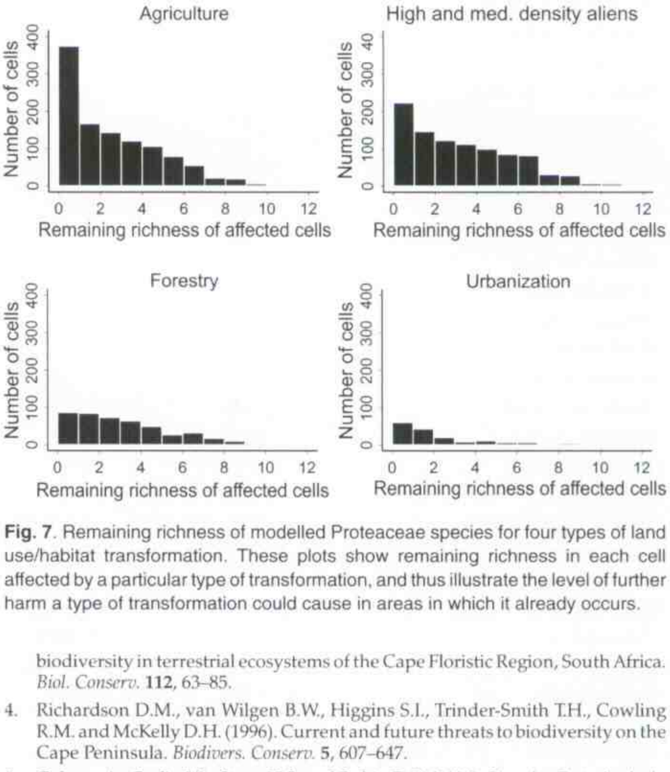

Fig. 7. Remaining richness of modelled Proteaceae species for four types of land use/habitat transformation. These plots show remaining richness in each cell affected by a particular type of transformation, and thus illustrate the level of further harm a type of transformation could cause in areas in which it already occurs.

of low species richness. Where alien plants occur, the average species loss has been lower than that for other forms of transformation. Because of their spatial dispersion and the high levels of remaining richness in affected cells (Fig. 7), alien plant invasions may pose a significant threat to rare species and diversity if their populations increase and become denser, particularly in remote, mountainous regions, and in protected areas. At this stage, we cannot say whether the resilience of Proteaceae to alien invasion is a result of competitive ability or escape (for instance, seed bank dynamics), or due to alien clearing efforts, or whether aliens may take longer to eliminate indigenous species than other anthropogenic factors.

---

1. Mooney H.A. and Hobbs R.J. (2000). *Invasive Species in a Changing World*. Island Press, Washington, DC.
2. Wilcove D.S., Rothstein D., Dubow J., Phillips A. and Losos E. (1998). Quantifying threats to imperiled species in the United States. *BioScience* **48**, 607–615.
3. Rouget M., Richardson D.M., Cowling R.M., Lloyd J.W. and Lombard A.T. (2003). Current patterns of habitat transformation and future threats to biodiversity in terrestrial ecosystems of the Cape Floristic Region, South Africa. *Biol. Conserv.* **112**, 63–85.
4. Richardson D.M., van Wilgen B.W., Higgins S.I., Trinder-Smith T.H., Cowling R.M. and McKelly D.H. (1996). Current and future threats to biodiversity on the Cape Peninsula. *Biodivers. Conserv.* **5**, 607–647.
5. Gelman A., Carlin J.B., Stern H.S. and Rubin D.B. (1995). *Bayesian Data Analysis*. Chapman and Hall, Boca Raton, Florida.
6. van Wilgen B.W., Little P.R., Chapman R.A., Görgens A.H.M., Willems T. and Marais C. (1997). The sustainable development of water resources: history, financial costs, and benefits of alien plant control programmes. *S. Afr. J. Sci.* **93**, 404–411.
7. Cowling R.M., Richardson D.M. and Mustart P.J. (1997). Fynbos. In *Vegetation of Southern Africa*, eds R.M. Cowling, D.M. Richardson and S.M. Pierce, pp. 99–130. Cambridge University Press, Cambridge.
8. Gelfand A.E., Schmidt A.M., Wu S., Silander J.A. Jr, Latimer A.M. and Rebelo A.G. (in press). Explaining species diversity through species level hierarchical modeling. *J. R. Stat. Soc. B.*
9. Guisan A. and Zimmermann N.E. (2000). Predictive habitat distribution models in ecology. *Ecol. Model.* **135**, 147–186.
10. Lloyd J.W., van den Berg E.C. and van Wyk E. (1999). *CAPE Project. The mapping of threats to biodiversity in the Cape Floristic Region with the aid of remote sensing and geographic information systems.* Report GW/A1999/54. Agricultural Research Council, Institute for Soil, Climate and Water, Pretoria.
11. Lehmann A., Overton J.M. and Leathwick J.R. (2002). GRASP: generalized regression analysis and spatial prediction. *Ecol. Model.* **157**, 189–207.
12. Wikle C.K. (2003). Hierarchical Bayesian models for predicting the spread of ecological processes. *Ecology* **84**, 1382–1394.

13. Goldblatt P. and Manning J. (2000). *Cape Plants: A conspectus of the Cape Flora of South Africa. Strelitzia* **9**, 1–722.
14. Schulze R.E. (1997). *South African Atlas of Agrohydrology and Climatology.* Water Research Commission Report TT 82/96, Water Research Commission. Pretoria.
15. Http://protea.worldonline.co.za/default.htm
16. Richardson D.M., Macdonald I.A.W., Holmes P.M. and Cowling R.M. (1992). Plant and animal invasions. In *The Ecology of Fynbos: Nutrients, fire and diversity,* ed. R.M. Cowling, pp. 271–308. Oxford University Press, Cape Town.
17. Low A.B. and Rebelo A.G. (1998). *Vegetation of South Africa, Lesotho and Swaziland.* Department of Environmental Affairs and Tourism, Pretoria.
18. Rebelo A.G. (2001). *Proteas: A field guide to the proteas of southern Africa,* 2nd edn. Fernwood Press, Cape Town.

Appendix A. Modelled species of Proteaceae and attributes included in the models. An asterisk (*) denotes alien species. Nomenclature follows Rebelo.[18]

Species	Height (mm)	Local population size	Re-sprouting ability?	Pollination mode	Dispersal mode
Aulax cancellata	1500	1–50	No	Insect	Wind
Aulax pallasia	2000	51–1000	Yes	Insect	Wind
Aulax umbellata	2000	>1000	No	Insect	Wind
Diastella myrtifolia	750	1–50	No	Insect	Ant
*Hakea sericea**	3500	>1000	No	Insect	Wind
Leucadendron comosum	1500	51–1000	No	Insect	Wind
Leucadendron corymbosum	1500	51–1000	No	Insect	Wind
Leucadendron daphnoides	1000	>1000	No	Insect	Ant or rodent
Leucadendron elimense subsp. *salteri*	1000	1–50	No	Insect	Wind
Leucadendron microcephalum	1250	>1000	No	Insect	Wind
Leucadendron rubrum	1500	>1000	No	Wind	Wind
Leucadendron sessile	1000	>1000	No	Insect	Ant or rodent
Leucadendron salicifolium	2000	>1000	No	Wind	Wind
Leucadendron salignum	500	>1000	Yes	Insect	Wind
Leucadendron spissifolium	1000	51–1000	Yes	Insect	Wind
Leucadendron tinctum	750	51–1000	No	Insect	Ant or rodent
Leucospermum bolusii	1000	>1000	No	Insect	Ant
Leucospermum grandiflorum	1500	1–50	No	Bird	Ant
Leucospermum oleifolium	750	5–1000	No	Bird	Ant
Mimetes arboreus	3000	1–50	Yes	Bird	Ant
Mimetes argenteus	2500	1–50	No	Bird	Ant
Mimetes cucullatus	1000	1–50	Yes	Bird	Ant
Mimetes hottentoticus	2000	1–50	No	Bird	Ant
Mimetes stokoei	1500	1–50	No	Bird	Ant
Orothamnus zeyheri	2900	1–50	No	Insect	Ant
Protea cynaroides	1000	1–50	Yes	Bird	Wind
Protea grandiflora	2000	51–1000	No	Bird	Wind
Protea lacticolor	4000	>1000	No	Bird	Wind
Protea mundii	4000	51–1000	No	Bird	Wind
Protea nana	1000	51–1000	No	Bird	Wind
Protea neriifolia	2500	>1000	No	Bird	Wind
Protea punctata	3000	>1000	No	Bird	Wind
Protea repens	2500	>1000	No	Bird	Wind
Protea restionifolia	300	51–1000	Yes	Bird	Wind
Protea rupicola	1000	1–50	No	Bird	Wind
Serruria elongata	1000	>1000	No	Insect	Ant
Serruria fasciflora	500	>1000	No	Insect	Ant
Serruria zeyheri	400	1–50	No	Insect	Ant
Sorocephalus imbricatus	1200	1–50	No	Insect	Ant
Spatalla curvifolia	650	51–1000	No	Insect	Ant