



Impacts of invasive alien trees on threatened lowland vegetation types in the Cape Floristic Region, South Africa



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ABSTRACT

This study investigated the autogenic recovery potential of native vegetation after clearing of dense stands of invasive alien trees in two critically endangered vegetation types in South Africa's Cape Floristic Region: Cape Flats Lowland Fynbos and Swartland Alluvium Fynbos. Sampling was done in areas previously occupied by the invasive tree *Acacia saligna* and plantations of *Pinus radiata* and in a fynbos reference site. Treatments varied in terms of the length of invasion and management histories.

Plots previously under pines recovered well in terms of indigenous perennial species richness, but indigenous species cover decreased with increasing number of planting rotations. Areas cleared of acacia recovered poorly in terms of indigenous species cover (after one cycle of invasion), and indigenous species richness exhibited a declining trend with increasing cycles of invasion. Proteoid overstorey was lost in all previously invaded/planted plots and this element will need to be re-introduced to areas after one cycle of invasion regardless of the invasive species. Acacias changed some abiotic variables after two cycles of invasion.

Follow-up clearing generally promoted better vegetation recovery in terms of overall species richness and structure but care should be taken not to damage indigenous ericoid shrubs. Overall, acacia invasion caused a greater change in biodiversity and vegetation structure than pine plantations.

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1. Introduction

Invasive alien plants can transform ecosystems by changing species composition, ecosystem structure and ecosystem functioning, and by fragmenting natural areas, driving degradation and negatively impacting biodiversity (Downey and Richardson 2016 and references therein). The magnitude and range of impacts of invasive alien species and the related investment of resources for research on invasive species impacts and ecosystem restoration are predicted to increase around the world (Walther et al. 2009; Sorte 2014) including South Africa (Van Wilgen et al. 1996, 2008).

Ecological restoration aims to speed up ecosystem recovery in terms of community composition, vegetation structure and ecosystem functioning (D'Antonio and Meyerson, 2002; Trabucchi et al. 2012). Clearing of invasive alien plants only (passive restoration) is sometimes not sufficient to allow ecosystems to recover adequately, and additional interventions such as re-introduction of native plant species (active restoration) may be needed (Holmes and Cowling 1997a; Crossman and Bryan 2006; Esler et al. 2008; Reid et al. 2009; Gaertner et al. 2012b).

Failing to restore ecosystems to their historical state (Whisenant 1999; Hobbs and Harris 2001; Suding et al. 2004) can often be attributed to ignoring the biotic and abiotic changes, and their interactions, that have occurred during invasions (Bakker and Berendse 1999; Zedler 2000; Suding et al. 2004). The removal of invasive alien species that have changed the properties of invaded ecosystems (i.e. transformer species sensu Richardson et al. (2000b)) can have unexpected results (Richardson et al. 2000b; Hobbs et al. 2006). Transformer species often leave legacy effects, such as increased nitrogen levels in the soil (Yelenik et al. 2004). These can lead to secondary invasions that capitalize on the increased soil nutrient availability left by the aliens (Loo et al. 2009).

A threshold model has been developed to explain the different stable states of ecosystems under different levels of invasion and the barriers separating these levels (Stringham et al. 2003). Two types of ecosystem thresholds—structural thresholds (e.g. decrease in species richness or changes in nutrient availability) and functional thresholds (i.e. changes in ecological processes such as greater fire intensity and changes in guild composition) (Beisner et al. 2003)—can be distinguished.

During alien plant invasions, structural biotic changes usually occur first (Gaertner et al. 2012a), followed by abiotic changes. However, abiotic structural changes can also occur alongside biotic structural changes. In recently invaded areas, some ecosystem functions might

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still operate similarly to those of uninvaded sites; in such cases, the system may recover without any further post-clearing interventions (Whisenant 1999; Archer et al. 2001; Stringham et al. 2003; Gaertner et al. 2012a). Once the invasion is dense, changes in re-enforcing ecosystem feedbacks (e.g. higher nutrient levels will lead to more invader biomass) will result in altered ecosystem functioning, facilitating further dominance of invasive alien species and eventually abiotic functional thresholds will be crossed (Gaertner et al. 2012a). In such instances, ecosystem resilience will decline and restoration interventions must aim to restore ecosystem functions and processes. In such extreme cases, active interventions (such as alleviating high soil nutrient levels) might be necessary (Holmes and Richardson 1999; Stringham et al. 2003; Marchante et al. 2009; Gaertner et al. 2012a).

In a biodiversity hotspot such as the Cape Floristic Region (encompassing the fynbos biome), it is crucial to identify possible barriers to restoration. The fynbos biome is one of the most invaded biomes in South Africa (Richardson et al. 1997). Especially in the lowlands, a high proportion of vegetation has been transformed or is threatened by agricultural and urban developments and invasion by alien plants (Rouget et al. 2003). Several species of acacias (*Acacia* spp.) and pines (*Pinus* spp.) are important transformer invaders of fynbos (Richardson et al. 1992; Wilson et al. 2014).

A conceptual approach, classifying categories of acacia and pine invasion in fynbos ecosystems and determining potential thresholds to native ecosystem recovery, has been developed but has not been empirically tested (Gaertner et al. 2012a). By identifying measurable indicators of invasion stages and related ecosystem changes, one can identify the risks and benefits of certain management actions but also estimate the restoration potential (Stringham et al. 2003; Briske et al. 2005).

Previous research on the impacts of alien plants and restoration potential has mostly focused on one dominant invasive species in riparian or mountain fynbos ecosystems (Musil 1993; Blanchard and Holmes 2008; Holmes 2008; Pretorius et al. 2008; Vosse et al. 2008; Le Maitre et al. 2011).

This study concentrated on two dominant invasive species in lowland fynbos, where restoration of highly threatened vegetation appears to be most challenging (Holmes 2002, 2008). *Pinus radiata* D. Don (Monterey pine) plantations and widespread invasions of *Acacia saligna* (Labill.) H.L. Wendl. (Port Jackson willow) are important threats to lowland fynbos vegetation types (Rebelo et al. 2006). Invasive trees have different traits and can impact communities and ecosystems differently. *A. saligna* has higher growth rates and attains greater heights than native fynbos shrubs, resprouts after fire and cutting, can fix soil nitrogen and maintains large and persistent dormant seed banks (Witkowski 1991a; Yelenik et al. 2004; Richardson and Kluge 2008). These features mean that *A. saligna* has a greater and longer-lasting impact on fynbos ecosystems than some other invasive trees, such as the serotinous tree *P. radiata*, which does not resprout or have a long-lived soil seed bank and which does not fix nitrogen (Richardson and Van Wilgen 1986; Holmes et al. 2000; Holmes and Foden 2001). The two species seldom co-invade, as pines are mainly invasive in mountain vegetation whereas *A. saligna* is most invasive in the lowlands (Richardson et al. 1992). However, the lowlands have been afforested with pines.

The aims of this study were: (1) to compare ecosystem impacts of acacia and pine invasion on lowland fynbos (2) to identify the most important management and invasion history variables that influence vegetation recovery and abiotic variables and (3) to assess the association between biotic and abiotic variables.

We examined the following hypotheses: (i) a greater change in biodiversity, and vegetation structure and ecosystem functioning (using guild composition and soil attributes as indicators) will occur in acacia-invaded than pine plantation areas; (ii) management and invasion history (including number of follow-up treatments and whether an area has been burned after clearing, number of fire cycles since invasion or rotations of pine plantings), will affect the ability for autogenic

recovery of cleared areas in terms of biodiversity, and vegetation structure and ecosystem functioning and (iii) changes in abiotic variables will affect biodiversity, and vegetation structure and ecosystem functioning, by influencing ecosystem-level feedbacks.

If the invasion history is important in explaining biodiversity and differences in vegetation structure and ecosystem functioning (i.e. guild composition and soil attributes) among invaded sites, this could indicate that some thresholds have been crossed and that active restoration measures could be required. Such insights are crucial for planning effective restoration efforts.

2. Materials and methods

2.1. Study sites

The study was conducted in two critically endangered vegetation types within the Cape Town, Stellenbosch and Drakenstein municipal areas, South Africa. Cape Flats Sand Fynbos (CFSF) landscapes consist of predominantly flat plains with acidic, sandy soils; mean annual rainfall is 576 mm, most of which falls in winter. More than 85% of the extent of CFSF is transformed (Rebelo et al. 2006). The main threats to this vegetation type are urban sprawl and invasive alien plants, with many remaining areas being small patches, surrounded by urban areas. CFSF is prone to invasion by *Acacia cyclops* A. Cunn. ex G. Don (rooikrans) and *A. saligna*, *Pinus* spp., *Eucalyptus* spp. (gums), *Hakea* spp. (hakeas), *Leptospermum laevigatum* (Gaertn.) F. Muell. (Australian myrtle) and to secondary invasion by alien annual grasses (Richardson et al. 2000a). Five study sites were sampled within this vegetation type: Tokai Park, Youngsfield Military Base, Blaauwberg Nature Reserve, Penhill, Haasendal Conservation Area and a reference site 7 km from the Blaauwberg site (Bas Ariesfontein) (Table 1).

The second vegetation type is Swartland Alluvium Fynbos (SAF). SAF landscapes occur next to mountains on slightly rolling plains with alluvial sands; mean annual rainfall is 656 mm, most of which falls in winter. The main threats to this vegetation type are pine plantations, vineyards, orchards and alien plants such as *A. saligna* (Rebelo et al. 2006). The three study sites were sampled within SAF: Wemmershoek, Victor Verster and Safariland (Table 1).

Study areas were previously invaded by *A. saligna* (>75% cover) or had previously been *P. radiata* plantations. These stands typically have no living fynbos plants, but after clearing, soil seed banks may passively return to fynbos. Reference plots were used to provide goals for recovery (Buijse et al. 2002; Blanchard and Holmes 2008) and to assess the degree of recovery success post-clearing. Comparisons were made with reference plots to indicate changes in vegetation structure and ecosystem function. Only one reference site could be sampled, since most remnants of both vegetation types are currently heavily invaded or were previously heavily invaded by alien plants. The highly threatened status of these two vegetation types and the urgent need to restore them dictated this study design, although more reference areas spread across the region would have been desirable. The reference site was characterized by mature fynbos and was initially only sparsely invaded (<25% canopy cover) by *A. saligna*. Initial clearing of the reference site was done in 2011 and the reference site has had yearly follow-up treatments, keeping it free of acacia invasions. The reference site is dominated by a proteoid overstorey, with restioids, asteraceous and ericoid shrubs forming important structural components. All other study sites had been cleared of alien trees, with some areas burnt after clearing, at least a year prior to this study.

Historical and management information data were collected from managers and other knowledgeable stakeholders (Table 1). Fire and invasion history data were inferred from satellite images obtained from Google Earth (2005–2014) and the Department of Rural Development and Land Reform (1938–2005). Treatments varied over time scales and management histories with the following variables accounted for: number of fire cycles since canopy closure or rotations

Table 1

Descriptive and management variables for study sites. Three different treatments were compared (a reference site—Bas Ariesfontein and sites cleared of dense (>75% cover) *Acacia saligna* and *Pinus radiata* stands) in terms of vegetation recovery. The extent of vegetation recovery takes into account the invasion history (no. cycles of invasion) and the management history (No. of FU = no. of follow-up treatments received and whether a site has burned or not after initial clearing) and environmental variables (vegetation type and MAP = mean annual precipitation). The reference site had a 25% canopy cover of acacia, but had been cleared and kept free of acacias since the initial clearing. UB = unburned; B = burned; CFSF = Cape Flat Sand Fynbos; SAF = Swartland Alluvium Fynbos.

Site	Elevation (m)	Invasive species	Latitude (decimal degrees)	Longitude (decimal degrees)	MAP (mm)	No. cycles of invasion	Years since initial clearing	Initial clearing method	Post-clearing burn	Vegetation type	No. of FU	Follow-up method
Bas Ariesfontein	178	<i>A. saligna</i>	33.719056	18.545167	422	0	N/A Age >20	Cut and herbicide	UB	CFSF	3	Cut and herbicide; hand pulling
Blaauwberg A	74	<i>A. saligna</i>	33.754444	18.486722	361	1	1	Block burn	B	CFSF	1	Cut below ground
Blaauwberg B	72	<i>A. saligna</i>	33.756528	18.483944	361	2	1	Stack burn	UB	CFSF	1	Cut below ground
Haasendal	85	<i>A. saligna</i>	33.919222	18.704417	580	2	4	Cut and herbicide	UB	CFSF	3	Cut, herbicide, foliar spray
Penhill	48	<i>A. saligna</i>	33.990333	18.727111	556	1	9	Cut and herbicide	B	CFSF	7	Cut, herbicide, foliar spray
Youngsfield	29	<i>A. saligna</i>	34.008417	18.487833	1018	1	5	Cut and herbicide	UB	CFSF	4	Hand pulling
Safariland	152	<i>P. radiata</i>	33.824667	18.999361	796	1	15	Clear felled	B	SAF	1	Cut, herbicide, foliar spray
Tokai block 7	55	<i>P. radiata</i>	34.051361	18.421889	974	3	6	Clear felled	UB	CFSF	1	Cut, herbicide, foliar spray
Tokai block 8	37	<i>P. radiata</i>	34.051333	18.424028	974	3	8	Clear felled	B	CFSF	1	Cut, herbicide, foliar spray
Tokai block 14	29	<i>P. radiata</i>	34.055306	18.429611	967	3	10	Clear felled	UB	CFSF	3	Hand pull (pine) and cut below ground (acacias)
Tokai block 17a	26	<i>P. radiata</i>	34.054361	18.434861	967	3	9	Clear felled	UB	CFSF	3	Hand pull (pine) and cut below ground (acacias)
Tokai block 17b	20	<i>P. radiata</i>	34.053306	18.435444	967	3	9	Clear felled	B	CFSF	3	Hand pull (pine) and cut below ground (acacias)
Victor Verster	161	<i>P. radiata</i>	33.855694	19.004333	797	3	4	Clear felled	UB	SAF	3	Cut, herbicide, foliar spray
Wemmershoek A	182	<i>P. radiata</i>	33.877833	19.048972	886	2	6	Clear felled	UB	SAF	4	Cut, herbicide, foliar spray
Wemmershoek B	182	<i>P. radiata</i>	33.875806	19.04775	836	1	12	Clear felled	B	SAF	8	Cut, herbicide, foliar spray

of planting, clearing method, time since initial clearing, time since last fire (vegetation age) and number of follow-up treatments. Areas that had not been burnt after the initial clearing treatment were classified as mature vegetation when fire data could not be inferred from satellite imagery.

2.2. Field sampling

Vegetation was sampled during September and October 2014. Three replicate 5 × 10 m plots were set up in each treatment per study site (Cape Flat Sand Fynbos, $n = 33$; Swartland Alluvium Fynbos, $n = 12$), spaced out as far as possible (at least 50 m apart in small areas but up to 200 m where possible) to ensure independence among sample plots. All species were identified either in the field or by collecting specimens for later identification and were categorized as indigenous or alien (naturalized and invasive) using published floras such as Manning and Goldblatt (2012) and Bromilow (2010). Total percentage projected species cover was estimated for each indigenous and alien species. Species richness was recorded for the whole plot. Soil sampling was done after vegetation sampling in October. Elevation and GPS coordinates were taken at the south-east corner of each plot with a Garmin GPS. Three litter samples were taken within the plot, by randomly placing a 25 × 25 cm quadrat on the ground and collecting all litter in the quadrat. Litter was oven-dried at 45 °C for 72 h and weighed. Three equal volume soil samples were taken per plot below soil litter, in the upper 10 cm of soil and bulked. Samples were sent for analyses at Bemlab (Pty) Ltd. (Somerset West, South Africa) for soil texture analysis, available phosphorus (P, mg/kg, P Bray II), mineral nitrogen (ammonium, NH₄-N, mg/kg, and nitrate; NO₃-N, mg/kg, extracted from soil with 1N KCl and determined calorimetrically on a SEAL AutoAnalyzer 3 after reaction with a sodium salicylate), percentage carbon (%C) and nitrogen (%N). Electrical conductivity and pH were analysed at Stellenbosch University. The soil electrical conductivity (EC) was measured using a 5 g soil sample mixed with deionized water (25 mL) to form a 1:5 ratio, and the supernatant was measured with an EC meter. Soil pH was also measured using the 1:5 ratio, using a 0.01 M CaCl₂·2H₂O solution (25 mL) and the pH of the supernatant was measured with a pH meter.

2.3. Analysis

To determine whether native vegetation had recovered after alien plant clearing, invaded plots were compared to the relatively uninvaded reference plots. To reduce the dimensionality of data, principal component analysis was performed during exploratory analysis (Hammer et al. 2001). Vegetation age was least informative and was therefore excluded from the models (Walker and Madden 2008; Osborne and Costello, 2009). The assumption that replicate plots are independent was tested by applying the Breusch–Godfrey test using 'lmtest' package to models (Hothorn et al. 2014).

Data were analysed using generalized linear models (GLM) in R statistical software (R Core Team 2015). Models were tested for homogeneity of residuals and collinearity of variables and for the assumption that residuals of response variables are normally distributed (Fox 2008; Hothorn et al. 2014). Percentages of C and NO₃-N were correlated with NH₄-N (0.61 and 0.76 Pearson's correlation coefficient, respectively) and were therefore removed as explanatory variables. Percentage N was correlated with available P (0.62 Pearson's correlation coefficient) and removed. If categorical variables were significant at $p < 0.1$, they were further analysed post hoc to determine differences. For post hoc analysis, the Games–Howell test was used as a multiple comparison test that takes into account heterogeneity of variances and unequal sample sizes (Games and Howell 1976; Kromrey and La Rocca 1995). Analyses were performed in R using 'userfriendlyscience' package (Peters 2015).

Predictor variables included environmental, invasion history and management variables and were used to determine which invasion and management-related variables are most important in determining

Table 2

Attributes used to classify species into functional guilds.

Plant species attribute	Range of possibilities
Origin	Indigenous or alien species
Growth form	Shrub, parasite, graminoid, geophyte, forb, restioid
Longevity	Annual or perennial
Shrubs	Ericoid or non-ericoid

Table 3
Results of post hoc test done on response variables used in GLMs. Treatments that were compared pairwise are indicated in two columns, along with their means and variances, appropriate test statistics (*t*-statistic, degrees of freedom (*df*) and significance level (*p*-value) are given. CFSF = Cape Flat Sand Fynbos; SAF = Swartland Alluvium Fynbos.

Response variable	Pairwise comparison variable 1	Mean; Variance 1	Pairwise comparison variable 2	Mean; variance 2	<i>t</i> -statistic	<i>df</i>	<i>p</i> value
Alien cover (%)	PineCFSF	0.44 0.029	PineSAF	0.25 0.012	3.4	24.1	0.011
	PineSAF	0.25 0.012	Reference	0.10 0.010	2.3	3.3	0.259
	AcaciaCFSF	0.64 0.068	Reference	0.10 0.010	6.1	8.7	<0.001
	PineCFSF	0.44 0.029	Reference	0.10 0.010	4.7	4.8	0.022
	Reference	0.10 0.010	Pine	0.36 0.030	3.9	3.5	0.049
	Reference	0.10 0.010	Acacia	0.64 0.068	6.1	8.7	<0.001
	Acacia	0.64 0.068	Pine	0.36 0.030	3.8	21	0.003
	Burned	0.36 0.031	Unburned	0.48 0.085	1.7	43	0.09
	One cycle of acacia invasion	1.00 0.0023	Two cycles of acacia invasion	0.55 0.0417	6.9	12.9	<0.001
	Woody alien cover (%)	Acacia	3.93 15.50	Pine	0.40 0.67	3.42	14.9
Acacia		3.93 15.50	Reference	0.33 0.33	3.37	15.9	0.01
Pine		0.40 0.67	Reference	0.33 0.33	0.18	3.4	0.98
Herbaceous alien cover (%)	Acacia	26 557	Pine	12 166	2.1	20	0.1248
	Acacia	26 557	Reference	1 1	4	14	0.0033
	Pine	12 166	Reference	1 1	3.7	20	0.0042
Indigenous cover (%)	PineCFSF	1.13 0.0296	PineSAF	1.32 0.0123	3.4	24.1	0.012
	PineSAF	1.32 0.0123	Reference	1.47 0.0097	2.3	3.4	0.253
	AcaciaCFSF	0.93 0.0670	Reference	1.47 0.0097	6.1	8.9	<0.001
	PineCFSF	1.13 0.0296	Reference	1.47 0.0097	4.7	4.9	0.021
	Reference	1.47 0.0097	Pine	1.21 0.0299	3.9	3.6	0.046
	Reference	1.47 0.0097	Acacia	0.93 0.0670	6.1	8.9	<0.001
	Acacia	0.93 0.0670	Pine	1.21 0.0299	3.8	21.1	0.003
	Burned	1.2 0.031	Unburned	1.1 0.084	1.7	43	0.093
	One cycle of acacia invasion	0.57 0.0022	Reference	1.47 0.0097	14.3	2.9	0.002
	Two cycles of acacia invasion	1.02 0.0407	Reference	1.47 0.0097	5.5	7	0.002
	One cycle of pine invasion	1.3 0.0118	Reference	1.47 0.0097	1.74	4.5	0.404
	Two cycles of pine invasion	1.2 0.0199	Reference	1.47 0.0097	2.49	3.6	0.214
	Three cycles of pine invasion	1.2 0.0319	Reference	1.47 0.0097	4.24	4.6	0.034
	One cycle of acacia invasion	0.57 0.0022	Two cycles of acacia invasion	1.02 0.0407	7	12.9	0.001
	Ammonium	PineCFSF	6.0 2.98	PineSAF	4.6 0.22	3.11	16.5
Reference		5.1 0.29	Acacia	8.9 39.76	2.3	14.9	0.091
Reference		5.1 0.29	Pine	5.6 2.19	1.2	6.4	0.496
EC	PineCFSF	24 10.51	PineSAF	31 50.73	3.24	15	0.026
pH	PineCFSF	4.0 0.1107	Reference	4.6 0.0067	6.5	14	<0.001
	PineSAF	4.2 0.3592	Reference	4.6 0.0067	2.4	12	0.140
	Reference	4.6 0.0067	Acacia	4.9 0.2300	2.4	16	0.072
	Reference	4.6 0.0067	Pine	4.1 0.2232	5.3	22	<0.001

Table 3 (continued)

Response variable	Pairwise comparison variable 1	Mean; Variance 1	Pairwise comparison variable 2	Mean; variance 2	t-statistic	df	p value
Perennial indigenous species richness	Acacia	4.9	Pine	4.1	5.6	29	<0.001
	Two cycles of acacia invasion	0.2300	One cycle of acacia invasion	0.2232	3.8	7.6	0.014
	Two cycles of acacia invasion	5.1	Reference	4.4	3.3	12.9	0.014
	Three cycles of pine invasion	0.1924	Reference	4.6	7.09	17.4	<0.001
	Three cycles of pine invasion	5.1	One cycle of pine invasion	0.0067	3.62	9.2	0.023
	Three cycles of pine invasion	3.9	Two cycle of pine invasion	0.0067	5.24	15.5	<0.001
	Reference	0.1611	Pine	0.0090	3.7	21.5	0.0032
	Reference	9.5	Pine	16.6	0.2	2.2	0.9775
	Burned	42	Unburned	20	1.9	32	0.067
	Burned	17.3	Acacia	9.5	2	3	0.2602
Ericoid shrub richness	Acacia	37	Pine	42	3.3	30.9	0.0065
	Burned	44	Unburned	13	0.97	42	0.34
	One cycle of acacia invasion	1.7	Reference	3.1	4.92	2.2	0.059
	Two cycles of acacia invasion	3.4	Reference	7.7	4.36	2.7	0.054
	Reference	4.9	Acacia	6.33	0.74	13.2	0.75
	Reference	1.3	Pine	8.7	1.76	23.8	0.21
Litter biomass	One cycle of pine invasion	0.33	Reference	6.33	1.37	6.8	0.41
	Two cycles of pine invasion	1.8	Reference	8.7	2.55	6.6	0.14
	Three cycles of pine invasion	4.15	Reference	6.33	4.78	4	0.03
	Reference	186	Acacia	213	0.23	9.5	0.996
	Acacia	1097	Pine	14274	3.06	8.1	0.037
	Reference	213	Pine	150	2.86	8.2	0.049
	One cycle of pine invasion	14274	Unburned	8867	1	32	0.32
	Two cycles of pine invasion	186	Reference	150	2.7	13	0.046
Available phosphorous	One cycle of acacia invasion	1097	Reference	8867	0.5	4.7	0.875
	Two cycles of acacia invasion	56	Reference	186	0.83	29	0.41
	Three cycles of pine invasion	1143	Reference	1097	3.16	5	0.086
	Reference	179	Reference	186	5	17	<0.001
	Reference	9380	Acacia	1097	1.7	36	0.1
	Burned	0.47	Pine	0.67	1.9		
Restioid richness	Reference	0.0054	Acacia	0.0331			
	Reference	0.47	Pine	0.65			
	Burned	0.0054	Unburned	0.0542			
	One cycle of acacia invasion	0.60	Reference	0.038			
Indigenous perennial grasses richness	Two cycles of acacia invasion	0.055	Reference	0.0054			
	Reference	4.5	Reference	0.47			
	Burned	2.32	Unburned	0.0054			

vegetation and soil nutrient responses and recovery post-clearing. Variables included both continuous and categorical data. Predictor variables were standardized (the mean of each variable was subtracted from each data point and divided by twice the standard deviation of the variable; see Schielzeth, (2010) and Grueber et al. (2011) for further explanation). This enables estimates of predictors to be comparable relative to one another (Schielzeth 2010).

As biotic response variables, richness of indigenous perennial plants and relative cover of alien and indigenous species were used. Functional guild richness was used as a response variable indicating the post-clearing guild recovery. To categorize functional guilds, plant attributes such as growth form, longevity and leaf type (Holmes and Richardson 1999; Holmes et al. 2000) were identified and assigned to species (see Table 2). Shrubs were subdivided into ericoid (fine-leaved shrubs) and

non-ericoid shrubs. Cyperaceae were included with the graminoids (grasses), and restioids were placed as a separate category.

Soil nutrients and litter biomass were analysed as abiotic response variables. Litter biomass was averaged and is expressed as grams of dry weight per m². Response variables consisted of continuous variables (P, NH₄-N, litter, EC, pH), count data (number of species of each guild: indigenous perennial species, restioids, indigenous perennial grasses, non-ericoid and ericoid shrubs) and percentage species cover data (relative cover of indigenous plants and relative alien cover). Appropriate error and link functions were chosen in models accordingly.

For biotic ecosystem components (ecosystem structure, biodiversity and guild richness) two sets of models were run, one containing management and invasion history variables as predictor variables and a second model was run using litter and soil variables as predictor variables.

To account for natural variation among sites, mean annual precipitation values (Schulze 2006) or soil depth were included as environmental variables when spatial autocorrelation was detected; the choice of variable depended on which one resulted in a model without spatial autocorrelation.

3. Results

Full output and results from GLM analysis are shown in Appendix A. Results from post hoc analyses and pairwise comparisons are presented in Appendix B. This includes the group sample sizes, means and variances, along with appropriate test statistics and significance levels. Test statistic of post hoc tests and GLMs referred to in the text are presented in Tables 3 and 4, respectively.

Models showed that there was no significant autocorrelation among samples and that replicate plots can be considered independent ($P > 0.05$). The only model that showed signs of autocorrelation according to the Breusch–Godfrey test was the management model for non-ericoid shrub richness ($P < 0.05$), and results for this model should be interpreted with caution. Other than those previously mentioned, no assumptions of models were violated. Swartland Alluvium Fynbos only harboured *P. radiata* plantations but no acacia-invaded sites. Significant differences between vegetation types occurred for indigenous and alien species cover, ammonium and EC. Alien species cover was significantly lower and indigenous species cover was significantly higher in SAF than CFSF. In all cases, except SAF plots, indigenous species cover was significantly lower and alien species cover significantly higher compared to reference plots. Ammonium was significantly lower and soil EC was significantly higher in SAF compared to CFSF pine plots. CFSF pine plots had significantly higher pH but SAF pine plots had a similar pH to the reference plots. All plots had a comparable sandy soil texture.

3.1. Ecosystem impacts of acacia versus pine invasion on lowland fynbos vegetation types

Overall, both cleared pine and acacia plots had significantly lower indigenous species cover than the reference plots and acacia had significantly lower indigenous species cover than pine plots (Fig. 1A). Acacia

and pine plots had significantly higher alien species cover than the reference plots, with acacia plots also having significantly more alien species cover than pine plots (Fig. 1B). When separating alien species cover into woody (Fig. 1C) and herbaceous species cover (Fig. 1D), there was overall very low cover of woody alien species, though significantly higher for acacia compared to pine and reference plots (both having a mean relative alien woody species cover close to zero). The majority of alien species cover were comprised of herbs and both acacia and pine plots had significantly more herbaceous alien species cover than the reference plots (Fig. 1D).

Acacia plots had significantly lower indigenous perennial species richness than pine and reference plots (Fig. 2A). The reference plots had the highest number of ericoid species (Fig. 2B) while acacia and pine plots were associated with a significantly lower ericoid shrub richness, with the number of ericoid species being significantly lower in acacia than pine plots. Non-ericoid shrub richness did not differ significantly among dominant invasive species treatments (Fig. 2C).

Mean litter biomass was highest in acacia, then reference and lastly pine plots but these differences were non-significant (Fig. 2D). Ammonium levels in the soil did not differ significantly between the dominant invasive species and the reference plots (Fig. 3A), even though the GLM results indicated a species effect. Plots invaded by acacia had the highest mean level of ammonium, with pine plots having lower mean ammonium levels than the reference plots. Soil was more basic in acacia plots than in reference plots, with pine plots being significantly more acidic than in the former two treatments (Fig. 3B). There was no significant difference in EC among treatments (Appendix B 3iii; Fig. 3C). Available phosphorus was elevated in both acacia and pine plots compared to the reference plots (Fig. 3D).

3.2. The response of biotic and soil nutrient factors to abiotic variables

The number of restioid species decreased with available phosphorus (Table 4: 5). Grass and non-ericoid richness increased with lower levels of soil ammonium whereas indigenous perennial species richness was significantly lower with increasing ammonium (Table 4: 2, 6 and 7). Non-ericoid richness significantly decreased with increasing soil EC

Table 4
Results of general linear models (GLMs) with response variables of GLMs listed and the relevant explanatory variable and associated test statistics. No of FU treatments = the number of follow-up treatments after initial alien clearing.

	Response variable	Explanatory variable	z-statistic	p value	95% CI
1	Ericoid shrub richness	Acacia invaded	−4.147	<0.001	−4.392 to −1.619
		Pine invaded	−3.268	0.001	−1.319 to −0.320
		Burned	−1.835	0.066	−0.732 to 0.024
		No FU treatments	0.997	0.319	−0.176 to 0.546
2	Non-ericoid shrub richness	Acacia invaded	−0.933	0.351	−2.435 to 0.889
		Pine invaded	0.455	0.649	−0.73 to 1.493
		Ammonium	−1.735	0.083	−1.586 to 0.054
		EC	−2.281	0.023	−1.804 to −0.168
		No FU treatments	−0.051	0.959	−0.555 to 0.517
3	Litter biomass	Acacia invaded	2.181	0.036	5.218 to 458.008
		Pine invaded	0.101	0.9203	−172.477 to 121.781
		No FU treatments	2.426	0.02	15.143 to 124.069
		Ammonium	2.086	0.044	0.019 to 9.472
4	Ammonium	Pine invaded	2.749	0.009	2.056 to 12.426
		Litter	−1.872	0.07	−2.944 to 0.134
		Available phosphorous	−1.661	0.097	−3.452 to 0.004
5	Restioid species richness	Burned	−1.63	0.103	−1.888 to 0.135
		Ammonium	−1.734	0.083	−1.22 to 0.047
6	Indigenous perennial grass richness	Burned	−1.692	0.091	−0.733 to 0.054
		Ammonium	−4.798	<0.001	−1.066 to −0.451
7	Indigenous perennial species richness	Burned	−2.515	0.012	−0.401 to −0.049
		No FU treatments	3.436	<0.001	0.130 to 0.472
		Burned	−3.34	0.002	0.289 to −0.076
8	Indigenous cover (%)	Burned	3.409	0.002	0.079 to 0.292
9	Alien cover (%)	Burned	2.99	0.005	0.003 to 0.689
10	Available phosphorous	Burned	2.321	0.026	1.106 to 9.909
11	EC	No FU treatments			

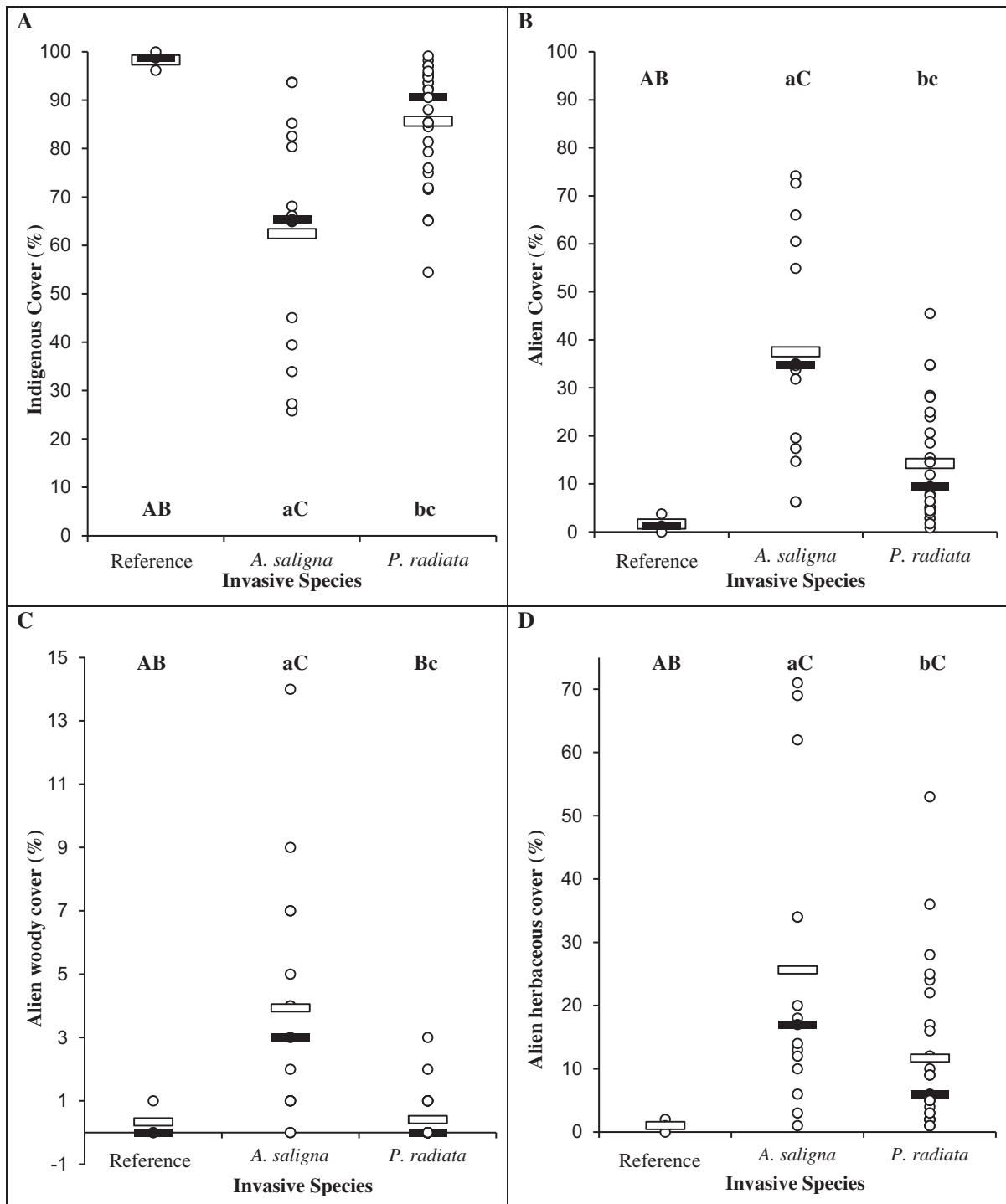


Fig. 1. A–D: Vegetation recovery was compared across previously invaded and a reference fynbos site. Relationship between biotic structural indicators as response variables (A) indigenous cover, (B) alien cover, (C) alien woody cover and (D) alien herbaceous cover and the dominant invasive species (reference, *A. saligna*, *P. radiata*). Solid bars indicate the median and open bars the mean. Open circles represent data points. Some points cannot be seen due to overlap in sample values. Response variables are represented untransformed. See Appendix B for corresponding statistics. Letters denote comparisons made between groups, where lowercase letters denote significant differences ($p < 0.05$). Graph template downloaded from Weissgerber et al. (2015).

(Table 4: 2). An increase in litter had a negative association with ammonium in the soil (Table 4: 4).

3.3. Associations between management and invasion history and vegetation recovery and abiotic variables

Areas that were burned had significantly higher indigenous species cover (Appendix C Fig. C 11i) and better guild recovery than those left

unburned: increased richness was observed for indigenous perennial species (Appendix C Fig. C 10i), restioids, ericoid shrubs and indigenous perennial grasses (Appendix C Fig. C 8i). Plots left unburned after clearing had significantly higher alien species cover.

There were larger amounts of litter in unburned areas (Appendix C Fig. C 5i). Unburned plots had more acidic soils than those burned after initial clearing (Appendix C Fig. C 2i) and higher mean available phosphorus (Appendix C Fig. C 4i).

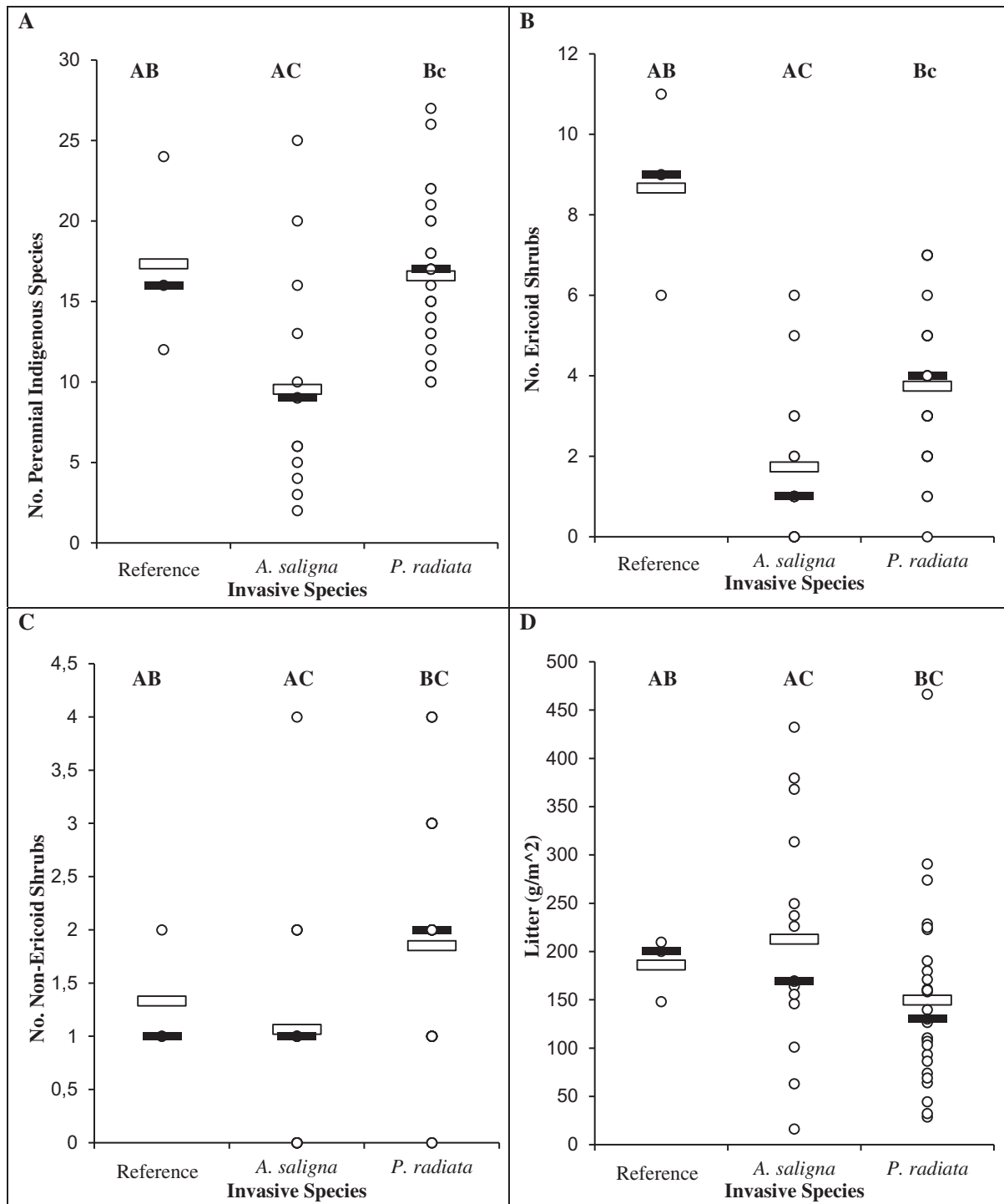


Fig. 2. A-D: Vegetation recovery was compared across previously invaded and a reference fynbos site. Relationship between biotic functional indicators as response variables (**A**) indigenous perennial grass richness, (**B**) ericoid shrub richness, (**C**) non-ericoid shrub richness and (**D**) between abiotic functional indicator, litter, as response variables and the dominant invasive species (reference, *A. saligna*, *P. radiata*). Solid bars indicate the median and open bars the mean. Open circles represent data points. Some points cannot be seen due to overlap in sample values. Response variables are represented untransformed. See Appendix B for corresponding statistics. Letters denote comparisons made between groups, where lowercase letters denote significant differences ($p < 0.05$). Graph template downloaded from [Weissgerber et al. \(2015\)](#).

Effect sizes show that the number of follow-up treatments received after clearing had a positive association with the richness of ericoid shrubs and a negative association with the richness of non-ericoid shrubs (Table 4: 1 and 2). The number of follow-ups that plots had received was associated with significantly higher richness of indigenous perennial species and higher litter biomass (Table 4: 3 and 7).

Increasing follow-up treatments were associated with a significant increase in EC (Table 4: 11).

For cycles of invasion, acacias and pines were separated for visualisation and analysis when a cycle of invasion was indicated as significant during GLM analysis (Appendix B, 1iv–12iv; Appendix C, Fig. 1iv–12iv). Increasing cycles of invasion were associated with

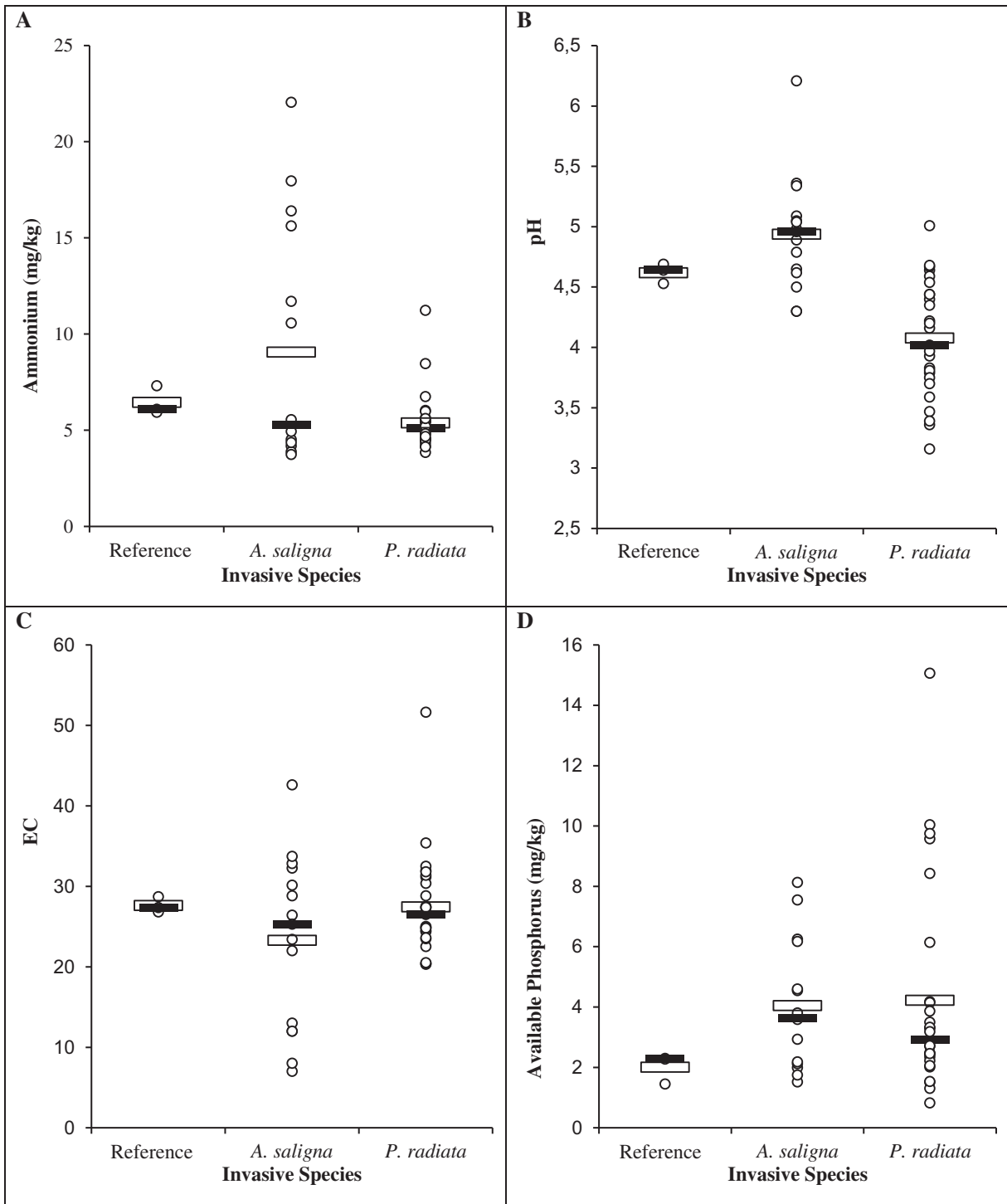


Fig. 3. A–D: Vegetation recovery was compared across previously invaded and a reference fynbos site. Relationship between abiotic functional indicators as response variables (A) ammonium, (B) pH, (C) EC and (D) available phosphorus and the dominant invasive species (reference, *A. saligna*, *P. radiata*). Solid bars indicate the median and open bars the mean. Open circles represent data points. Some points cannot be seen due to overlap in sample values. Response variables are represented untransformed. See Appendix B for corresponding statistics. Letters denote comparisons made between groups, where lowercase letters denote significant differences ($p < 0.05$). Graph template downloaded from Weissgerber et al. (2015).

poor indigenous species cover recovery. After one and two cycles of acacia invasion, indigenous species cover was significantly lower than in the reference plots. After one and two pine rotations, indigenous species cover recovered to a similar level as in reference plots. After three rotations of pine, indigenous species cover was significantly lower compared to the reference plots. The inverse trend

was shown for alien species cover. Acacia plots exhibited an unusual result, whereby after one cycle of invasion, indigenous species cover was lower and alien species cover higher when compared to two cycles of invasion. Both one and two cycles of acacia invasion resulted in a lower richness of ericoid shrubs compared to the reference plots. In pine plots, two rotations had lower restioid richness than

one rotation and significantly lower restioid richness than after three rotations.

In acacia plots, pH was significantly higher (more basic) after two cycles of invasion than after one cycle of invasion or in reference plots. Litter biomass did not differ significantly among the reference plots and the different cycles of acacia invasion. Available phosphorus did not show a clear pattern in terms of cycles of invasion: after one cycle of acacia invasion, level of available phosphorus was significantly higher than the reference plots, but another cycle of invasion did not lead to a significant increase. Soil pH in first and second rotation pine plots did not differ significantly from the reference plots. After three pine rotations, pH was significantly lower (more acidic) compared to the reference plots, and first and second pine rotation plots.

Electrical conductivity did not differ significantly between different pine rotations and the reference plots. Litter biomass was lower after one pine rotation and significantly lower after two rotations in comparison to the reference plots, while after three rotations, litter was similar to the reference plots.

4. Discussion

The main aim of this study was to compare ecosystem-level impacts of acacia and pine invasion on lowland fynbos recovery potential. The hypothesis that a greater change in biodiversity and vegetation structure and ecosystem functioning (including guild composition and soil attributes) will occur in acacia-invaded than pine plantation plots was supported. The study also attempted to identify the most important management and invasion history variables that influence vegetation recovery and abiotic variables. Some variables had much larger effects on ecosystem recovery. The study further aimed to assess feedback processes between biotic and abiotic variables. It was found that changes in abiotic variables affected ecosystem recovery.

4.1. Ecosystem impacts of acacia versus pine invasion on lowland fynbos vegetation types

4.1.1. Impacts on vegetation structure and functional guild and species richness recovery post-alien clearing

Plots dominated by pines did recover structurally (in terms of indigenous species cover) to levels close to the vegetation in reference plots, whereas plots dominated by acacia did not. A lack of post-clearing recovery in terms of indigenous vegetation cover, changes in vegetation structure and species richness following removal of invasive acacias has been found in other studies in the fynbos (Holmes and Marais 2000; Holmes et al. 2005; Blanchard 2008). The successful recovery of indigenous species cover, indigenous guilds and overall indigenous perennial richness in pine plots could be due to the persistence of the native seed bank beneath the canopies (Holmes and Richardson 1999; Moles and Drake 1999; Heelemann et al. 2013). Indigenous vegetation can persist beneath pine canopies for a long time since it can take up to 13 years for complete pine canopy closure, giving indigenous species a chance to establish and replenish seed banks (Cremer 1992; Holmes and Marais 2000). In terms of functional guilds, ericoid shrubs did not recover to the same level as reference plots.

Ericoid shrubs are a key guild in the lowland fynbos (Cowling and Holmes 1992; Rebelo et al. 2006) and may need to be re-introduced in cleared sites. Richness of non-ericoid shrubs did not differ significantly between acacia- and pine-invaded plots. The non-ericoid shrubs found in pine plots were widespread species, e.g. shrubs that could have been dispersed from the surrounding vegetation by birds. In all invaded areas, the protea overstorey was absent and would need to be re-introduced. The exclusion of ericoid and proteoid shrubs in pine- and acacia-invaded plots, and non-ericoid shrubs in the case of acacia-invaded plots, could be due to shrubs not having sufficient time to mature and set seed before canopy closure and shading out by the alien between fire events (Schwilk et al. 1997) or between rotations of

planting. The loss of key structural components is a common impact of plant invasions in the fynbos (Holmes and Richardson 1999; Blanchard 2008), especially for proteas which have canopy-stored, rather than soil-stored, seeds (Van Wilgen 1982; Richardson and Van Wilgen 1986; Holmes and Cowling 1997b; Schwilk et al. 1997). If certain functional guilds do not recover or are underrepresented, it could lead to a loss of overall diversity and ecosystem functioning (Parker-Allie et al. 2004; King and Hobbs 2006).

4.1.2. Impact of invasive species on abiotic variables

Producing large amounts of nutrient-rich litter is a known impact of invasive acacias (Le Maitre et al. 2011), and large amounts of litter can hinder the recovery of indigenous vegetation (Witkowski 1991a; Yelenik et al. 2004): where large amounts of litter burn in summer, the time required for vegetation recovery could be longer due to very hot, damaging fires (Holmes et al. 2000; Blanchard and Holmes 2008).

Surprisingly, areas with one and two cycles of pine rotation and all acacia invaded plots (i.e. all cycles of acacia invasion) had lower amounts of litter than the reference plots, but this could be due to the fact that the reference area is mature vegetation (>20 years post-fire age), having accumulated large amounts of litter and senescent plant material (Van Wilgen 1982). Thick litter layers can also prevent the germination of native seeds by insulating the soil from heat or acting as a physical obstruction to emerging seedlings (Friedman et al. 1996; Blanchard and Holmes 2008).

Litter has been linked to increased nutrient levels in the soil, where litter with a high phosphorus and nitrogen content could increase phosphorus release into the soil (Stock and Lewis 1986). This was not the case in our study plots, where litter had a negative association with soil nutrients and no statistically significant effect was observed; this could be due to the reference plots being mature and having large amounts of litter and low soil nutrient content, leading to a lack of expected pattern. Additionally, Fynbos litter biomass also decomposes slowly, taking a long time to release nutrients back into the ecosystem (Bengtsson et al. 2012; Witkowski 1991b).

It was expected that acacia-invaded plots would have larger amounts of mineral nitrogen but ammonium levels were not significantly higher than reference plots. However, it should be noted that the ammonium data was highly skewed: both invader species plots had a lower median level of ammonium compared to the reference plots. The lack of extreme changes in soil nutrients in invaded plots could be explained as follows: recently cleared plots contained the highest amount of ammonium due to a legacy effect of the acacias. Due to poor nutrient retention in sandy soils, excess nutrients could have leached out with time after clearing with rain infiltration or volatilized during fires (Stock and Lewis 1986; D'Antonio and Vitousek 1992). Witkowski (1991b) and Yelenik et al. (2004) similarly found no difference in ammonium in the soil between acacia-invaded and fynbos areas. They did find an increase in available phosphorus but no change in soil pH. In this study, invasive species did change soil acidity. Soil was more basic in acacia-invaded plots after two cycles of invasion. In pine plots, soil was significantly more acidic than reference plots and acacia-invaded plots and had increased levels of available phosphorus compared to reference plots, indicating a change in soil chemistry. Invasion and afforestation by pines usually lead to soil acidification (Scholes and Nowicki 2000) and an increase in available phosphorus from nutrient-rich litter (Heelemann et al. 2013). High levels of ammonium and available phosphorus were not detected at the same time, although both occurred at low levels simultaneously, high levels of the one soil nutrient, usually coincided with low levels of the other. The soil pH and the type of invasive species could explain this relationship between available phosphorus and ammonium.

High organic matter from litter content and high soil pH can favour soil nitrification in acacia-invaded plots, immobilizing available phosphorus (Witkowski and Mitchell 1987; Seeling and Zasoski 1993). On the other hand, high soil available phosphorus and low nitrogen can

be attributed to continued phosphorus input from decomposing litter and also lower available phosphorus uptake by pine trees, as reported on the sandy soils of southern Australia (Bekunda et al. 1990).

4.1.3. Invasive species effect on alien persistence and native species recovery

Acacia plots had the highest overall cover of alien species post-clearing, which will have a negative impact on vegetation recovery. The fact that acacias persisted following clearing is due to the vigorous resprouting ability of cut stumps and germination from the large persistent seed banks (Holmes et al. 2005). Woody alien species cover comprised only of acacia seedlings and resprouts, highlighting the importance of effective and thorough follow-up clearing by stump-herbicide application and hand pulling of seedlings during initial clearing treatments and subsequent follow-up treatments.

Both species pose a challenge to remove from sites because of their high propagule pressure but differ in germination and re-growth. Acacia seeds germinate en masse after a fire, but some germination can also take place between fires (Holmes et al. 1987; Tozer and Ooi 2014), making them persistent and effective competitors and ecosystem transformers (Moll et al. 1980; Pieterse and Boucher 1997; Foxcroft et al. 2013). Monterey pine on the other hand does not resprout after fire and seed release from serotinous cones is only stimulated by fire, and seeds are either consumed by predators or rot, and do not form seed banks in the soil (Reyes and Casal 2002).

The fact that alien herbaceous species dominated alien species cover indicates a serious problem of secondary invasions that follow initial woody alien species clearing (Richardson et al. 2000a; Yelenik et al. 2004; Blanchard and Holmes 2008). Secondary invasions were a bigger problem in acacia-invaded than pine plantation areas. This is due to the legacy effects in the soil after acacia invasions, with higher soil nutrients and altered soil chemistry promoting competitive herbaceous aliens and acting as a barrier to native species recovery and causing secondary changes in species composition (Yelenik et al. 2004).

High levels of available phosphorus, ammonium and soil EC could limit native vegetation performance and recovery because of strong competition from secondary invaders under high soil nutrient conditions (Yelenik et al. 2004; Marchante et al. 2008). Considering that fynbos is adapted to moderate amounts of disturbance by fires and low resources in terms of nutrients and summer drought, competition is usually considered to be of less importance (Huston 1979; Cowling 1987; Richards 1993), but as soon as the resources (increased nutrients and more water consumption by pines and acacias) and disturbance regimes change (increased biomass and altered fire regimes), competition with invaders and secondary invaders could become important mediators of fynbos recovery.

4.2. Association between management and invasion history and vegetation recovery and abiotic variables

4.2.1. The effect of fire on vegetation and abiotic variable recovery

Fire is a key driver of fynbos dynamics and is crucial for the regeneration of many indigenous species. Vegetation can become senescent if left unburned for too long (Van Wilgen 1982; Kraaij et al. 2013). The disturbance and regeneration triggered by fire causes an increase in species richness and indigenous cover directly following the fire event, both in South African fynbos (Kruger 1983) and Californian chaparral (Keeley et al. 1981). No statistically significant results in terms of the post hoc comparisons supported the improved effects of burning, although trends of improvement after burning were observed in GLMs. In other studies (e.g. Blanchard 2008), burned plots had higher indigenous species richness and cover than unburned plots. Species richness usually peaks one year after a fire and then declines, making richness comparisons between differently aged stands difficult (Schwilk et al. 1997). However, in this case, even though the reference plots were mature, indigenous species richness was still higher than in the

more recently disturbed (cleared) plots. If the reference plots had been younger, the difference in richness would probably have been more significant.

If biomass is present in large amounts, hot fires resulting from elevated fuel loads can damage indigenous seed banks and trigger the germination or resprouting of alien species (Holmes 2001). This does not seem to be the case in our study.

Native vegetation recovered well in burnt areas compared to areas that were not burnt after initial clearing. This is in contrast to other studies that found no difference between areas that were burnt or not after clearing (Fernández et al. 2015).

Nitrogen volatilizes during burning, and can be reduced by up to 50% (Stock and Lewis 1986). There was a large variance in ammonium and soil EC values, leading to an unrepresentative mean. The median level of ammonium and EC are lower at burned plots, as expected. This could be because some of the recently cleared plots had extremely high levels of ammonium and levels started to decrease through leaching out over time, especially in the sandy lowland soils (Stock and Lewis 1986). An increase in soil ammonium can be found directly after burning (accounting for some skewed data) because not all ammonium-containing compounds were released during combustion (DeBano et al. 1976, 1979). The uncombusted ammonium compounds can be leached down the soil through time (DeBano 1991). Available phosphorus responds differently, whereby it was either volatilized or phosphorus-containing compounds did not move down the soil profile, but were concentrated on the soil surface (which was not sampled in this case) (Stock and Lewis 1986; DeBano 1991). Fire has been linked to changes in soil chemistry (Stock and Lewis 1986; D'Antonio and Vitousek 1992), especially leading to increased pH after burning in the fynbos (Parker-Allie et al. 2004), but no significant effects of fire on pH were found in this study.

4.2.2. Management of sites after initial clearing of alien plants

The number of follow-up treatments had several effects on biotic and abiotic variables. There is a concern that indigenous species, specifically woody species, can be damaged during follow-up, especially where herbicide is applied (Parker-Allie et al. 2004); this could be why a wide range of responses were observed in the relationship between number of follow-up treatments and the richness of ericoid and non-ericoid shrubs. The number of follow-up treatments can also be used as a proxy for time since initial clearing as follow-ups are usually done annually. Even though guilds could be underrepresented after invasion or damaged by clearing or follow-up operations, diligent follow-ups over time resulted in improved richness of indigenous species indicating recovery in terms of biodiversity.

Litter increased with the number of follow-up treatments applied, even though there are fewer alien plants to contribute to litter production; litter can remain after clearing if not removed or burned, and recovering native species also add to the litter over time.

4.2.3. Impact of duration of invasion

Impacts of acacias and pines on the soil became more apparent when separating cycles of invasion or rotations of planting. After two cycles of invasion, acacia-invaded plots had significantly more basic soil than one-cycle and reference plots, indicating increasing impact after each cycle of invasion. After two cycles of acacia invasion, changes to soil properties were significant which could mean an abiotic structural or functional threshold is approached or has been crossed. For pine plots, rotations of planting are only important in terms of significantly lowered pH after three rotations after planting.

This study provides evidence that the impact of invasive species on abiotic and biotic variables increases with duration of invasion and supports the findings of other studies that have found increased negative impact on indigenous species recovery with longer duration of pine and acacia invasion (Holmes and Cowling 1997a; Privett et al. 2001; Le Maitre et al. 2011; Richardson and Gaertner 2013). An anomaly

was higher impact after one cycle of acacia invasion on ecosystem recovery; this could be due to high levels of human disturbance, which can promote alien invasions and prevent indigenous species recovery (Morgan 1998; Milton 2004).

4.3. Re-enforcing feedbacks between abiotic and biotic variables

Biotic variables and soil nutrients correlated to changes in abiotic variables, when comparing invaded plots to each other and to the reference plots. Functional guilds were associated with changes in soil nutrients. Restioid species richness responded negatively to an increase in available phosphorus in the soil; and indigenous perennial species, grass and non-ericoid richness decreased with increasing ammonium (and soil EC in the case of non-ericoid shrubs). These results indicate that increases in soil nutrients were associated with poor indigenous species recovery and this could be indicative of a re-enforcing feedback loop between higher nutrient levels and re-invasion or colonisation by secondary invaders, resulting in poor indigenous vegetation recovery (van der Putten et al. 2013).

An increase in soil nutrients has been linked to further changes in ecosystem functioning such as altered nutrient cycling and soil microbial processes (Marchante et al. 2008).

4.4. Comparisons between different vegetation types

Combining the two different vegetation types is justified because they are similar in dynamics and structure. Both vegetation types are dominated by proteoids and restioids, with ericaceous species common in wetter areas. An asteraceous component is dominant in SAF but only forms a major component of CFSF in drier areas (Rebello et al. 2006). All plots had similar sand soil texture.

However, caution should be taken when interpreting results because of the unbalanced study design: acacia invasions are not represented in the SAF vegetation type, there is no reference site for SAF and only one reference site was used for comparison. Only after the sample size of SAF is increased and compared to a completely uninvaded, unmanaged reference site, can more generalizations be made that apply to both vegetation types. Swartland Alluvium Fynbos does, however, seem to be more resistant in terms of overall vegetation structure, having significantly higher relative indigenous species cover and lower relative alien species cover than CFSF. Although not directly tested, this could be due to a higher mean number of follow-ups or more diligent follow-ups being done in old plantations in SAF. Some of the soil nutrients are also different between vegetation types: ammonium was lower and soil EC was higher in SAF compared to CFSF pine plots.

In summary, in terms of biotic and abiotic thresholds, acacias changed abiotic variables after two cycles of invasion (i.e. the number of fire cycles since canopy closure) and after one cycle in the case of indigenous species cover, whereas lowland fynbos is resilient up to three rotations of pine planting. In terms of vegetation structure, perennial species and guild richness: acacias more negatively impacted invaded plots, whereas pine plots recovered better in comparison to the reference plots. Follow-up clearing generally promoted better ecosystem recovery in terms of overall species richness and structure but care should be taken to not damage indigenous shrubs.

4.5. Management recommendations and priorities for future work

Future research should if possible separate vegetation types and locate a reference site suitable for SAF since the vegetation types differ in terms of soil ammonium and EC. There were not enough species in each functional guild and growth form to allow for a quantitative analysis of effects on native species recovery by regeneration mode, although this would be an important aspect to study. Future studies investigating the restoration of lowland fynbos should include measures of heterogeneity at different scales. Only alpha diversity was considered

in this study, while gamma and beta diversity might show more pronounced or different patterns of richness and diversity caused by invasive alien species (Cowling 1990; Richards 1993).

Most management of invasive alien plants in South Africa is co-ordinated by the national Working for Water (WfW) programme. WfW, funded by government, private and international organizations, manages invasive alien plants over large areas, especially in catchment areas, using mechanical, chemical and biological control measures. The programme does not currently incorporate active restoration measures in operations, but this study shows that further interventions are required in some cases, especially where the aim is to restore the original structure of fynbos, e.g. when the proteoid overstorey has been reduced or eliminated. This is particularly important in areas cleared of dense stands of invasive acacias. In terms of management, some measures should be taken to reduce soil nutrients or at least to reduce alien species cover and re-introduce indigenous species to assist indigenous vegetation recovery. Secondary invasion is a concern in areas cleared of acacias, as is the case with some other invasive woody plants in the fynbos (Ruwanza et al. 2013). Supplying local indigenous seed or propagules, to supplement depleted seed banks or diminished seed supply is a tractable way of setting ecosystems on a trajectory of recovery to a properly functioning ecosystem (Galatowitsch and Richardson 2005; Blanchard and Holmes 2008).

Supplementary data to this article can be found online at doi:10.1016/j.sajb.2016.10.014.

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References

- Archer, S., Boutton, T.W., Hibbard, K.A., 2001. Trees in grasslands: biogeochemical consequences of woody plant expansion. In: Schulze, E.-D., Heimann, M., Harrison, S., Holland, E., Lloyd, J., Prentice, I.C., Schimel, D.S. (Eds.), *Global Biogeochemical Cycles in the Climate System*. Academic Press, San Diego, pp. 115–137.
- Bakker, J.P., Berendse, F., 1999. Constraints in the restoration of ecological diversity in grassland and heathland communities. *Trends in Ecology & Evolution* 14, 63–68.
- Beisner, B.E., Haydon, D.T., Cuddington, K., 2003. Alternative stable states in ecology. *Frontiers in Ecology and the Environment* 1, 376–382.
- Bekunda, M.A., Smethurst, P.J., Khanna, P.K., Willett, I.R., 1990. Effects of post-harvest residue management on labile soil phosphorus in a *Pinus radiata* plantation. *Forest Ecology and Management* 38, 13–25. [http://dx.doi.org/10.1016/0378-1127\(90\)90082-M](http://dx.doi.org/10.1016/0378-1127(90)90082-M).
- Bengtsson, J., Janion, C., Chown, S.L., Leinaas, H.P., 2012. Litter decomposition in fynbos vegetation, South Africa. *Soil Biology and Biochemistry* 47, 100–105. <http://dx.doi.org/10.1016/j.soilbio.2011.11.023>.
- Blanchard, R., 2008. An Investigation of Riparian Vegetation Recovery Following Invasive Alien Tree Clearing in the Western Cape (Thesis–MSc). University of Cape Town, Cape Town.
- Blanchard, R., Holmes, P.M., 2008. Riparian vegetation recovery after invasive alien tree clearance in the Fynbos Biome. *South African Journal of Botany* 74, 421–431.
- Briske, D.D., Fuhlendorf, S.D., Smeins, F.E., 2005. State-and-transition models, thresholds, and rangeland health: a synthesis of ecological concepts and perspectives. *Rangeland Ecology & Management* 58, 1–10. [http://dx.doi.org/10.2111/1551-5028\(2005\)58<1:SMTARH>2.0.CO;2](http://dx.doi.org/10.2111/1551-5028(2005)58<1:SMTARH>2.0.CO;2).
- Bromilow, C., 2010. *Problem Plants and Alien Weeds of South Africa*. Briza, Pretoria.
- Buijse, A.D., Coops, H., Staras, M., Jans, L.H., Van Geest, G.J., Griff, R.E., Ibelings, B.W., Oosterberg, W., Roozen, F.C.J.M., 2002. Restoration strategies for river floodplains along large lowland rivers in Europe. *Freshwater Biology* 47, 889–907.

- Core Team, R., 2015. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.
- Cowling, R.M., 1987. Fire and its role in coexistence and speciation in Gondwanan shrublands. *South African Journal of Science* 83, 106–111.
- Cowling, R.M., 1990. Diversity components in a species-rich area of the Cape Floristic Region. *Journal of Vegetation Science* 1, 699–710.
- Cowling, R.M., Holmes, P.M., 1992. Flora and vegetation. In: Cowling, R.M. (Ed.), *The Ecology of Fynbos: Nutrients, Fire and Diversity*. Oxford University Press, Cape Town, pp. 23–61.
- Cremer, K.W., 1992. Relations between reproductive growth and vegetative growth of *Pinus radiata*. *Forest Ecology and Management, The Biology of Forest Growth Experiment* 52, 179–199. [http://dx.doi.org/10.1016/0378-1127\(92\)90501-Y](http://dx.doi.org/10.1016/0378-1127(92)90501-Y).
- Crossman, N.D., Bryan, B.A., 2006. Systematic landscape restoration using integer programming. *Biological Conservation* 128, 369–383. <http://dx.doi.org/10.1016/j.biocon.2005.10.004>.
- D'Antonio, C., Meyerson, L.A., 2002. Exotic plant species as problems and solutions in ecological restoration: a synthesis. *Restoration Ecology* 10, 703–713.
- D'Antonio, C.M., Vitousek, P.M., 1992. Biological invasions by exotic grasses, the grass/fire cycle, and global change. *Annual Review of Ecology and Systematics* 23, 63–87. <http://dx.doi.org/10.2307/2097282>.
- DeBano, L., 1991. The Effect of Fire on Soil Properties. General Technical Report INT-US Department of Agriculture. Forest Service, Intermountain Research Station (USA).
- DeBano, L., Savage, S., Hamilton, D., 1976. The transfer of heat and hydrophobic substances during burning. *Soil Science Society of America Journal* 40, 779–782.
- DeBano, L.F., Eberlein, G.E., Dunn, P.H., 1979. Effects of burning on chaparral soils: I. Soil nitrogen. *Soil Science Society of America Journal* 43, 504–509. <http://dx.doi.org/10.2136/sssaj1979.03615995004300030015x>.
- Downey, P.O., Richardson, D.M., 2016. Alien plant invasions and native plant extinctions: a six-threshold framework. *AoB PLANTS* 8, plw047. <http://dx.doi.org/10.1093/aobpla/plw047>.
- Esler, K.J., Holmes, P.M., Richardson, D.M., Witkowski, E.T.F., 2008. Riparian vegetation management in landscapes invaded by alien plants: insights from South Africa. *South African Journal of Botany* 74, 397–400. <http://dx.doi.org/10.1016/j.sajb.2008.01.168>.
- Fernández, C., Vega, J.A., Fonturbel, T., 2015. Does shrub recovery differ after prescribed burning, clearing and mastication in a Spanish heathland? *Plant Ecology* 216, 429–437. <http://dx.doi.org/10.1007/s11258-015-0447-y>.
- Fox, J., 2008. *Applied Regression Analysis and Generalized Linear Models*. 2nd ed. Sage Publications Inc, Thousand Oaks, CA, US.
- Foxcroft, L.C., Pyšek, P., Richardson, D.M., Pergl, J., Hulme, P.E., 2013. The bottom line: impacts of alien plant invasions in protected areas. In: Foxcroft, L.C., Pyšek, P., Richardson, D.M., Genovesi, P. (Eds.), *Plant Invasions in Protected Areas, Invading Nature—Springer Series in Invasion Ecology*. Springer Netherlands, pp. 19–41.
- Friedman, J.M., Osterkamp, W.R., Lewis Jr., W.M., 1996. Channel narrowing and vegetation development following a Great Plains flood. *Ecology* 77, 2167–2181. <http://dx.doi.org/10.2307/2265710>.
- Gaertner, M., Holmes, P.M., Richardson, D.M., 2012a. Biological invasions, resilience and restoration. In: Van Andel, J., Aronson, J. (Eds.), *Restoration Ecology: The New Frontier*. John Wiley & Sons Ltd, Chichester, UK, pp. 265–280.
- Gaertner, M., Nottebrock, H., Privett, S.D.J., Richardson, D.M., 2012b. Plant invasions, restoration, and economics: perspectives from South African fynbos. *Perspectives in Plant Ecology, Evolution and Systematics* 14, 341–353. <http://dx.doi.org/10.1016/j.ppees.2012.05.001>.
- Galatowitsch, S., Richardson, D.M., 2005. Riparian scrub recovery after clearing of invasive alien trees in headwater streams of the Western Cape, South Africa. *Biological Conservation* 122, 509–521. <http://dx.doi.org/10.1016/j.biocon.2004.09.008>.
- Games, P.A., Howell, J.F., 1976. Pairwise multiple comparison procedures with unequal n's and/or variances: a Monte Carlo study. *Journal of Educational and Behavioral Statistics* 1, 113–125.
- Grueber, C.E., Nakagawa, S., Laws, R.J., Jamieson, I.G., 2011. Multimodel inference in ecology and evolution: challenges and solutions. *Journal of Evolutionary Biology* 24, 699–711. <http://dx.doi.org/10.1111/j.1420-9101.2010.02210.x>.
- Hammer, Ø., Harper, D.A.T., Ryan, P.D., 2001. *Past: Paleontological Statistics Software Package for Education and Data Analysis*. *Palaeontologia Electronica* 4, 1–9.
- Heeleman, S., Krug, C.B., Esler, K.J., Reisch, C., Poschod, P., 2013. Soil seed banks of remnant and degraded Swartland Shale Renosterveld. *Applied Vegetation Science* 16, 585–597. <http://dx.doi.org/10.1111/avsc.12026>.
- Hobbs, R.J., Harris, J.A., 2001. Restoration ecology: repairing the earth's ecosystems in the new millennium. *Restoration Ecology* 9, 239–246. <http://dx.doi.org/10.1046/j.1526-100x.2001.009002239.x>.
- Hobbs, R.J., Arico, S., Aronson, J., Baron, J.S., Bridgewater, P., Cramer, V.A., Epstein, P.R., Ewel, J.J., Klink, C.A., Lugo, A.E., 2006. Novel ecosystems: theoretical and management aspects of the new ecological world order. *Global Ecology and Biogeography* 15, 1–7.
- Holmes, P.M., 2001. A comparison of the impacts of winter versus summer burning of slash fuel in alien-invaded fynbos areas in the Western Cape. *Southern African Forestry Journal* 192, 41–49.
- Holmes, P.M., 2002. Depth distribution and composition of seed-banks in alien-invaded and uninvaded fynbos vegetation. *Austral Ecology* 27, 110–120.
- Holmes, P.M., 2008. Optimal ground preparation treatments for restoring lowland Sand Fynbos vegetation on old fields. *South African Journal of Botany* 74, 33–40. <http://dx.doi.org/10.1016/j.sajb.2007.08.005>.
- Holmes, P.M., Cowling, R.M., 1997a. The effects of invasion by *Acacia saligna* on the guild structure and regeneration capabilities of South African fynbos shrublands. *Journal of Applied Ecology* 34, 317–332. <http://dx.doi.org/10.2307/2404879>.
- Holmes, P.M., Cowling, R.M., 1997b. Diversity, composition and guild structure relationships between soil-stored seed banks and mature vegetation in alien plant-invaded South African fynbos shrublands. *Plant Ecology* 133, 107–122.
- Holmes, P.M., Foden, W., 2001. The effectiveness of post-fire soil disturbance in restoring fynbos after alien clearance. *South African Journal of Botany* 67, 533–539.
- Holmes, P.M., Marais, C., 2000. Impacts of alien plant clearance on vegetation in the mountain catchments of the Western Cape. *Southern African Forestry Journal* 189, 113–117.
- Holmes, P.M., Richardson, D.M., 1999. Protocols for restoration based on recruitment dynamics, community structure, and ecosystem function: perspectives from South African fynbos. *Restoration Ecology* 7, 215–230.
- Holmes, P.M., Macdonald, I.A.W., Juritz, J., 1987. Effects of clearing treatment on seed banks of the alien invasive shrubs *Acacia saligna* and *Acacia cyclops* in the Southern and South Western Cape, South Africa. *Journal of Applied Ecology* 24, 1045–1051.
- Holmes, P.M., Richardson, D.M., Wilgen, B.W., Gelderblom, C., 2000. Recovery of South African fynbos vegetation following alien woody plant clearing and fire: implications for restoration. *Austral Ecology* 25, 631–639.
- Holmes, P.M., Richardson, D.M., Esler, K.J., Witkowski, E.T.F., Fourie, S., 2005. A decision-making framework for restoring riparian zones degraded by invasive alien plants in South Africa. *South African Journal of Science* 101, 553–564.
- Hothorn, T., Zeileis, A., Farebrother, R.W., Cummins, C., Mollo, G., Mitchell, D., Zeileis, M.A., 2014. Package "lme4".
- Huston, M., 1979. A general hypothesis of species diversity. *American Naturalist* 113, 81–101.
- Keeley, S.C., Keeley, J.E., Hutchinson, S.M., Johnson, A.W., 1981. Postfire succession of the herbaceous flora in southern California chaparral. *Ecology* 62, 1608–1621.
- King, E.G., Hobbs, R.J., 2006. Identifying linkages among conceptual models of ecosystem degradation and restoration: towards an integrative framework. *Restoration Ecology* 14, 369–378. <http://dx.doi.org/10.1111/j.1526-100X.2006.00145.x>.
- Kraaij, T., Cowling, R.M., van Wilgen, B.W., 2013. Fire regimes in eastern coastal fynbos: imperatives and thresholds in managing for diversity. *Koedoe* 55, 01–09.
- Kromrey, J.D., La Rocca, M.A., 1995. Power and type I error rates of new pairwise multiple comparison procedures under heterogeneous variances. *The Journal of Experimental Education* 63, 343–362.
- Kruger, F.J., 1983. *Plant Community Diversity and Dynamics in Relation to Fire*. In: Kruger, F.J., Mitchell, P.D.T., Jarvis, P.J.U.M. (Eds.), *Mediterranean-Type Ecosystems, Ecological Studies*. Springer, Berlin Heidelberg, pp. 446–472.
- Le Maitre, D.C., Gaertner, M., Marchante, E., Ens, E., Holmes, P.M., Pauchard, A., O'Farrell, P.J., Rogers, A.M., Blanchard, R., Blignaut, J., 2011. Impacts of invasive Australian acacias: implications for management and restoration. *Diversity and Distributions* 17, 1015–1029.
- Loo, S.E., Mac Nally, R., O'Dowd, D.J., Lake, P.S., 2009. Secondary invasions: implications of riparian restoration for in-stream invasion by an aquatic grass. *Restoration Ecology* 17, 378–385. <http://dx.doi.org/10.1111/j.1526-100X.2008.00378.x>.
- Manning, J., Goldblatt, P., 2012. *Plants of the Greater Cape Floristic Region. 1: The Core Cape flora, Strelitzia 29*. South African National Biodiversity Institute, Pretoria.
- Marchante, E., Kjølner, A., Struwe, S., Freitas, H., 2008. Short- and long-term impacts of *Acacia longifolia* invasion on the belowground processes of a Mediterranean coastal dune ecosystem. *Applied Soil Ecology* 40, 210–217. <http://dx.doi.org/10.1016/j.apsoil.2008.04.004>.
- Marchante, E., Kjølner, A., Struwe, S., Freitas, H., 2009. Soil recovery after removal of the N2-fixing invasive *Acacia longifolia*: consequences for ecosystem restoration. *Biological Invasions* 11, 813–823.
- Milton, S.J., 2004. Grasses as invasive alien plants in South Africa. *South African Journal of Science* 100, 69–75.
- Moles, A.T., Drake, D.R., 1999. Potential contributions of the seed rain and seed bank to regeneration of native forest under plantation pine in New Zealand. *New Zealand Journal of Botany* 37, 83–93.
- Moll, E.J., McKenzie, B., McLachlan, D., 1980. A possible explanation for the lack of trees in the fynbos, Cape Province, South Africa. *Biological Conservation* 17, 221–228. [http://dx.doi.org/10.1016/0006-3207\(80\)90057-9](http://dx.doi.org/10.1016/0006-3207(80)90057-9).
- Morgan, J.W., 1998. Patterns of invasion of an urban remnant of a species-rich grassland in southeastern Australia by non-native plant species. *Journal of Vegetation Science* 9, 181–190. <http://dx.doi.org/10.2307/3237117>.
- Musil, C.F., 1993. Effect of invasive Australian acacias on the regeneration, growth and nutrient chemistry of South African Lowland Fynbos. *Journal of Applied Ecology* 30, 361–372. <http://dx.doi.org/10.2307/2404637>.
- Osborne, J.W., Costello, A.B., 2009. Best practices in exploratory factor analysis: Four recommendations for getting the most from your analysis. *Pan-Pacific Management Review* 12 (2), 131–146.
- Parker-Allie, F., Richardson, D.M., Holmes, P.M., 2004. The effects of past management practices for invasive alien plant control on subsequent recovery of fynbos on the Cape Peninsula, South Africa. *South African Journal of Botany* 70, 804–815.
- Peters, G.-J., 2015. *userfriendlyscience: Quantitative Analysis Made Accessible*.
- Pieterse, P.J., Boucher, C., 1997. Is burning a standing population of invasive legumes a viable control method? Effects of a wildfire on an *Acacia mearnsii* population. *The Southern African Forestry Journal* 180, 15–21. <http://dx.doi.org/10.1080/10295925.1997.9631163>.
- Pretorius, M.R., Esler, K.J., Holmes, P.M., Prins, N., 2008. The effectiveness of active restoration following alien clearance in fynbos riparian zones and resilience of treatments to fire. *South African Journal of Botany, Riparian Vegetation Management in Landscapes Invaded by Alien Plants: Insights from South Africa* 74, 517–525. <http://dx.doi.org/10.1016/j.sajb.2008.01.180>.
- Privett, S.D.J., Cowling, R.M., Taylor, H.C., 2001. Thirty years of change in the fynbos vegetation of the Cape of Good Hope Nature Reserve, South Africa. *Bothalia* 31, 99–115.
- Rebello, A.G., Boucher, C., Helme, N., Mucina, L., Rutherford, M.C., Smit, W.J., Powrie, L.W., Ellis, F., Lambrechts, J.J.N., Scott, L., Radloff, F.G.T., Johnson, S.D., Richardson, D.M., Ward, R.A., Proche, S.M., Oliver, E.G.H., Manning, J.C., Jürgens, N., McDonald, D.J., Janssen, J.A.M., Walton, B.A., Roux, I.A., Skowno, A.L., Todd, S.W., Hoare, D.B., 2006.

- Fynbos Biome. In: Mucina, L., Rutherford, M.C. (Eds.), *The Vegetation of South Africa, Lesotho and Swaziland*. SANBI, Pretoria, South Africa, pp. 52–219.
- Reid, A.M., Morin, L., Downey, P.O., French, K., Virtue, J.G., 2009. Does invasive plant management aid the restoration of natural ecosystems? *Biological Conservation* 142, 2342–2349.
- Reyes, O., Casal, M., 2002. Effect of high temperatures on cone opening and on the release and viability of *Pinus pinaster* and *P. radiata* seeds in NW Spain. *Annals of Forest Science* 59, 327–334. <http://dx.doi.org/10.1051/forest:2002028>.
- Richards, M.B., 1993. *Soil Factors and Competition as Determinants of Fynbos Plant Species Distributions in the South Western Cape, South Africa* (Thesis—PhD). University of Cape Town, Cape Town.
- Richardson, D.M., Gaertner, M., 2013. Plant invasions as builders and shapers of novel ecosystems. In: Hobbs, R.J., Higgs, E.S., Hall, C.M. (Eds.), *Novel Ecosystems: Intervening in the New Ecological World Order*. John Wiley & Sons Ltd., Chichester, UK, pp. 102–114.
- Richardson, D.M., Kluge, R.L., 2008. Seed banks of invasive Australian acacia species in South Africa: role in invasiveness and options for management. *Perspectives in Plant Ecology, Evolution and Systematics* 10, 161–177. <http://dx.doi.org/10.1016/j.ppees.2008.03.001>.
- Richardson, D.M., Van Wilgen, B.W., 1986. Effects of thirty-five years of afforestation with *Pinus radiata* on the composition of mesic mountain fynbos near Stellenbosch. *South African Journal of Botany* 4, 309–315.
- Richardson, D.M., Macdonald, I.A.W., Holmes, P.M., Cowling, R.M., 1992. Plant and animal invasions. In: Cowling, R.M. (Ed.), *The Ecology of Fynbos. Nutrients, Fire and Diversity*. Oxford University Press, Cape Town, pp. 271–308.
- Richardson, D.M., Macdonald, I.A.W., Hoffmann, J.H., Henderson, L., 1997. Alien plant invasions. In: Cowling, R.M., Richardson, D.M., Pierce, S.M. (Eds.), *Vegetation of Southern Africa*. Cambridge University Press, Cambridge, pp. 535–570.
- Richardson, D.M., Bond, W.J., Dean, W.R.J., Higgins, S.I., Midgley, G.E., Milton, S.J., Powrie, L.W., Rutherford, M.C., Samways, M.J., Schulze, R.E., 2000a. Invasive alien species and global change: a South African perspective. In: Mooney, H.A., Hobbs, R.J. (Eds.), *Invasive Species in a Changing World*. Island Press, Washington, DC, pp. 303–349.
- Richardson, D.M., Pyšek, P., Rejmánek, M., Barbour, M.G., Panetta, F.D., West, C.J., 2000b. Naturalization and invasion of alien plants: concepts and definitions. *Diversity and Distributions* 6, 93–107.
- Rouget, M., Richardson, D.M., Cowling, R.M., Lloyd, J.W., Lombard, A.T., 2003. Current patterns of habitat transformation and future threats to biodiversity in terrestrial ecosystems of the Cape Floristic Region, South Africa. *Biological Conservation* 112, 63–85. [http://dx.doi.org/10.1016/S0006-3207\(02\)00395-6](http://dx.doi.org/10.1016/S0006-3207(02)00395-6).
- Ruwanza, S., Gaertner, M., Esler, K.J., Richardson, D.M., 2013. The effectiveness of active and passive restoration on recovery of indigenous vegetation in riparian zones in the Western Cape, South Africa: a preliminary assessment. *South African Journal of Botany* 88, 132–141. <http://dx.doi.org/10.1016/j.sajb.2013.06.022>.
- Schielzeth, H., 2010. Simple means to improve the interpretability of regression coefficients. *Methods in Ecology and Evolution* 1, 103–113. <http://dx.doi.org/10.1111/j.2041-210X.2010.00012.x>.
- Scholes, M.C., Nowicki, T.E., 2000. Effects of pines on soil properties and processes. In: Richardson, D.M. (Ed.), *Ecology and Biogeography of Pinus*. Cambridge University Press, Cambridge, UK, p. 341.
- Schulze, R.E., 2006. *South African Atlas of Climatology and Agrohydrology*.
- Schwilk, D.W., Keeley, J.E., Bond, W.J., 1997. The intermediate disturbance hypothesis does not explain fire and diversity pattern in fynbos. *Plant Ecology* 132, 77–84. <http://dx.doi.org/10.1023/A:1009755320731>.
- Seeling, B., Zasoski, R.J., 1993. Microbial effects in maintaining organic and inorganic solution phosphorus concentrations in a grassland topsoil. *Plant and Soil* 148, 277–284.
- Sorte, C.J.B., 2014. Synergies between Climate Change and Species Invasions: Evidence from Marine Systems. In: Ziska, L.H., Dukes, J.S. (Eds.), *Invasive Species and Global Climate Change*, 4. CABI, Oxfordshire, UK; Boston, USA, pp. 101–116.
- Stock, W.D., Lewis, O.A.M., 1986. Soil nitrogen and the role of fire as a mineralizing agent in a South African coastal fynbos ecosystem. *The Journal of Ecology* 74, 317–328.
- Stringham, T.K., Krueger, W.C., Shaver, P.L., 2003. State and transition modeling: an ecological process approach. *Journal of Range Management* 56, 106–113.
- Suding, K.N., Gross, K.L., Houseman, G.R., 2004. Alternative states and positive feedbacks in restoration ecology. *Trends in Ecology & Evolution* 19, 46–53.
- Tozer, M.G., Ooi, M.K.J., 2014. Humidity-regulated dormancy onset in the Fabaceae: a conceptual model and its ecological implications for the Australian wattle *Acacia saligna*. *Annals of Botany* 114, 579–590. <http://dx.doi.org/10.1093/aob/mcu144>.
- Trabucchi, M., Ntshotsho, P., O'Farrell, P.J., Comín, F.A., 2012. Ecosystem service trends in basin-scale restoration initiatives: a review. *Journal of Environmental Management* 111, 18–23. <http://dx.doi.org/10.1016/j.jenvman.2012.06.040>.
- van der Putten, W.H., Bardgett, R.D., Bever, J.D., Bezemer, T.M., Casper, B.B., Fukami, T., Kardol, P., Klironomos, J.N., Kulmatiski, A., Schweitzer, J.A., Suding, K.N., Van de Voorde, T.F.J., Wardle, D.A., 2013. Plant–soil feedbacks: the past, the present and future challenges. *Journal of Ecology* 101, 265–276. <http://dx.doi.org/10.1111/1365-2745.12054>.
- Van Wilgen, B.W., 1982. Some effects of post-fire age on the above-ground plant biomass of fynbos (macchia) vegetation in South Africa. *Journal of Ecology* 70, 217–225. <http://dx.doi.org/10.2307/2259874>.
- Van Wilgen, B.W., Cowling, R.M., Burgers, C.J., 1996. Valuation of ecosystem services. *BioScience* 46, 184–189.
- Van Wilgen, B.W., Reyers, B., Le Maitre, D.C., Richardson, D.M., Schonegevel, L., 2008. A biome-scale assessment of the impact of invasive alien plants on ecosystem services in South Africa. *Journal of Environmental Management* 89, 336–349.
- Vosse, S., Esler, K.J., Richardson, D.M., Holmes, P.M., 2008. Can riparian seed banks initiate restoration after alien plant invasion? Evidence from the Western Cape, South Africa. *South African Journal of Botany* 74, 432–444.
- Walker, J., Madden, S., 2008. Factor analysis, path analysis, and structural equation modeling. *Statistics in Criminology and Criminal Justice: Analysis and Interpretation*. 3rd ed. Jones & Bartlett Publishers, USA, pp. 325–351.
- Walther, G.-R., Roques, A., Hulme, P.E., Sykes, M.T., Pyšek, P., Kühn, I., Zobel, M., Bacher, S., Botta-Dukát, Z., Bugmann, H., Czúcz, B., Dauber, J., Hickler, T., Jarošík, V., Kenis, M., Klotz, S., Minchin, D., Moora, M., Nentwig, W., Ott, J., Panov, V.E., Reineking, B., Robinet, C., Semchenko, V., Solaz, W., Thuiller, W., Vilà, M., Vohland, K., Settele, J., 2009. Alien species in a warmer world: risks and opportunities. *Trends in Ecology & Evolution* 24, 686–693. <http://dx.doi.org/10.1016/j.tree.2009.06.008>.
- Weissgerber, T.L., Milic, N.M., Winham, S.J., Garovic, V.D., 2015. Beyond Bar and Line Graphs: Time for a New Data Presentation Paradigm. *PLOS Biology* 13. <http://dx.doi.org/10.1371/journal.pbio.1002128> e1002128.
- Whisenant, S., 1999. *Repairing Damaged Wildlands: A Process-Oriented, Landscape-Scale Approach*. 1st edition. Cambridge University Press, Cambridge, UK; New York, NY, USA.
- Wilson, J.R., Gaertner, M., Griffiths, C.L., Kotzé, I., Le Maitre, D.C., Marr, S.M., Picker, M.D., Spear, D., Stafford, L., Richardson, D.M., van Wilgen, B.W., Wannenburg, A., 2014. Biological invasions in the Cape Floristic Region: history, current patterns, impacts, and management challenges. In: Allsopp, N., Colville, J.F., Verboom, G.A. (Eds.), *Fynbos: Ecology, Evolution, and Conservation of a Megadiverse Region*. Oxford University Press, pp. 273–298.
- Witkowski, E.T.F., 1991a. Growth and competition between seedlings of *Protea repens* (L.) L. and the alien invasive, *Acacia saligna* (Labill.) Wendl. in relation to nutrient availability. *Functional Ecology* 5, 101–110.
- Witkowski, E.T.F., 1991b. Effects of invasive alien acacias on nutrient cycling in the coastal lowlands of the Cape fynbos. *Journal of Applied Ecology* 28, 1–15. <http://dx.doi.org/10.2307/2404109>.
- Witkowski, E.T.F., Mitchell, D.T., 1987. Variations in soil phosphorus in the fynbos biome, South Africa. *Journal of Ecology* 75, 1159–1171.
- Yelenik, S.G., Stock, W.D., Richardson, D.M., 2004. Ecosystem level impacts of invasive *Acacia saligna* in the South African fynbos. *Restoration Ecology* 12, 44–51.
- Zedler, J.B., 2000. Progress in wetland restoration ecology. *Trends in Ecology & Evolution* 15, 402–407.