Progress in Physical Geography 33(3) (2009) pp. 319–338

Impacts of alien plant invasions on species richness in Mediterranean-type ecosystems: a meta-analysis

Mirijam Gaertner,* Alana Den Breeyen, Cang Hui and David M. Richardson

Centre for Invasion Biology, Department of Botany and Zoology, Stellenbosch University, Private Bag X1, Matieland 7602, South Africa

Abstract: Besides a general consensus regarding the negative impact of invasive alien species in the literature, only recently has the decline of native species attributable to biological invasions begun to be quantified in many parts of the world. The cause-effect relationship between the establishment and proliferation of alien species and the extinction of native species is, however, seldom demonstrated. We conducted a meta-analysis of studies in Mediterranean-type ecosystems (MTEs) to examine: (1) whether invasion of alien plant species indeed causes a reduction in the number of native plant species at different spatial and temporal scales; (2) which growth forms, habitat types and areas are most affected by invasions; and (3) which taxa are most responsible for native species richness declines. Our results confirm a significant decline in native species richness attributable to alien invasions. Studies conducted at small scales or sampled over long periods reveal stronger impacts of alien invasion than those at large spatial scales and over short periods. Alien species from regions with similar climates have much stronger impacts, with the native species richness in South Africa and Australia declining significantly more post-invasion than for European sites. Australian *Acacia* species in South Africa accounted for the most significant declines in native species richness. Among the different growth forms of alien plants, annual herbs, trees and creepers had the greatest impact, whereas graminoids generally caused insignificant changes to the native community. Native species richness of shrublands, old fields and dune vegetation showed significant declines, in contrast to insignificant declines for forest habitats.

Key words: biodiversity, biological invasions, exotic species, growth form, habitat type, spatial and temporal scale.

I Introduction

Invasive alien species are considered a threat to biodiversity and ecosystem stability, and are widely held to be responsible for the decline of native species richness and the local extinction of certain species (Richardson

*Author for correspondence. Email: gaertnem@sun.ac.za

 DOI: 10.1177/0309133309341607

et al., 1989; Wilcove *et al*., 1998; Davis, 2003). However, it is often difficult to demonstrate the cause-effect relationship between the establishment and proliferation of alien plant species and the extinction of native species (Brown and Sax, 2004; Davis, 2009). Recently, the broadly accepted connection between invasive species and native diversity declines has been debated (Houlahan and Findlay, 2004; Hejda and Pyšek, 2006; Richardson *et al*., 2007). Perceptions on the negative impacts of invasions on native plant communities are, to a certain degree, affected by the spatial scales of studies. This has been widely recognized in the discussion about the 'invasion paradox' which describes the co-occurrence of independent lines of support for both a negative and a positive relationship between native biodiversity and the invasions of invasive alien species depending on the spatial scale of investigation (Fridley *et al*., 2007). Another factor which must be considered when evaluating impacts of alien invasions on native species richness is the different timescales involved in invasions and extinctions (Sax *et al*., 2002; Richardson *et al*., 2007). Although some species may be doomed to extinction due to disruptions caused by invasions (eg, Traveset and Richardson, 2006), extinction can be delayed (Tilman *et al*., 1994). With plant species especially, the process of extinction takes much longer (decades or longer) than naturalizations or invasion (rates easily measured in years). It is likely that many plant species will eventually be driven to extinction as a direct consequence of current processes. Therefore, we would expect a stronger signal of negative impact of invasions from studies that capture effects over longer periods. It is also important to consider that although invasions of alien species may not result in extinctions of entire species (over the typically short timescale captured in a field study) this does not mean that they are not reducing biodiversity. They may still be causing declines in the abundance of native species or the elimination of some populations which may reduce genetic diversity (Davis, 2009). Nevertheless, the above generalizations have emerged from isolated case studies and it is difficult to synthesize results from different spatial and temporal scales. Besides these scale-effects on the observed impact of alien invasions, features of the invading species and the invaded habitat must also be taken into account when considering the impact of alien invasions on native species richness.

We investigated how different spatial and temporal scales and factors (such as taxa, growth forms, habitat types and countries) affect the impact of invasions on native species richness. We chose to study the impact of invasions on native species richness in Mediterranean-type ecosystems (MTEs) which have similar climates and other environmental drivers. Several studies have addressed the importance of comparing alien plant invasions in similar climatic regions (Kruger *et al*., 1989; Sax, 2002; Pauchard *et al*., 2004), as comparing ecosystems with widely diverging climates, disturbance regimes and other factors may reduce our ability to isolate the effects of particular stressors. Mediterranean-climate zones are considered to be especially appropriate for global-scale 'natural experiments' as they differ less in key aspects than other biome types that occur at multiple localities around the world, eg, savannas (Pauchard *et al*., 2004). Invasions in MTEs have been well studied for decades (Groves and Di Castri, 1991; Richardson *et al*., 1992; Rejmánek and Randall, 1994) and the problem of alien plant invasions is widely recognized as a major threat to biodiversity in all MTEs today (Rejmánek and Randall, 1994; Rouget *et al*., 2003; Seabloom *et al*., 2006; Underwood *et al*., 2009).

We conducted a meta-analysis to quantify the impact of alien invasion on native plant species richness. This approach allowed us to examine: (1) whether invasion of alien plant species indeed causes a reduction in the number of native plant species at different localities and at different spatial and temporal scales; (2) which growth forms, habitat types and areas are most affected by invasions; and (3) which taxa are most responsible for native species richness declines.

II Methods

1 Mediterranean-type ecosystems

Mediterranean-type ecosystems (MTEs) are found between latitudes 32° and 40° north and south of the equator on the west coast of continents in five regions of the world, namely South Africa, Australia, California, Chile and the Mediterranean Basin (Aschmann, 1973). The defining factors for the Mediterranean-type climate are summer drought and winter rainfall (Köppen, 1923). Annual rainfall ranges from below 90 mm to 1500 mm; annual mean temperature ranges from about 11°C to 17°C; mean seasonal temperatures are 8°C in the coldest month and up to 25°C in the hottest month (Aschmann, 1973). The vegetation of MTEs is characterized by chaparral-like shrublands, coastal scrub, woodland and forest (Dallman, 1998). MTEs have remarkable plant diversity. Covering less than 5% of the Earth's surface, they contain nearly 20% of the planet's known plant species (Cowling *et al*., 1996).

2 Data

We confined our search to MTEs in five regions covering South Africa, Australia, Europe, California and Chile. The first criterion for our literature search was that the focus of the study should be an invasive plant species alien to the area under investigation (*sensu* Richardson *et al*., 2000; *sensu* Pyšek *et al*., 2004). Second, we only included studies that directly compared invaded ecosystems dominated by invasive alien species with corresponding, relatively intact, ecosystems in terms of native species richness. Third, we also required that species richness was quantified (or where this could be computed from presented data) as mean number of native species with standard error (SE) and sample size. In some cases, where such data were not provided, we obtained the data from the authors.

We searched for papers using combinations of the terms 'exotic', 'invasive', 'invasion', 'alien species', 'species richness' and 'biodiversity' on 'Web of Science', 'JSTOR' and 'Google Scholar'. Additional literature was obtained through conventional searches of the bibliographies of papers and reports. We did not limit the review to papers in a set of journals published during a certain period. This method allowed us to include a wider range of literature than if we had limited the survey to only certain journals or a certain timeframe.

3 Analysis

We summarized data from all the studies that fulfilled our criteria in a table including information about study area and habitat, origin and growth form of the invading species, and temporal and spatial scale, defined by extent of study area and unit size (grain) (Table 1). Eleven studies (three from South Africa, four from Europe, three from California and one from Australia) including 24 species (Figure 1) met our criteria. Some studies investigated species at different sites and in different seasons this left us with 47 cases for the meta-analysis. Chile was not included in the meta-analysis at all as none of the studies met our criteria.

For the meta-analysis, we recorded the number of native species (mean and SE) in invaded and natural reference sites for each study. The meta-analysis is a technique of quantitative research synthesis (Smith and Glass, 1977) and has been widely used in ecology (eg, Ashton *et al*., 2005). In this study, we used the comprehensive meta-analysis software (CMA version 2.0; Borenstein *et al*., 2005) to conduct a two-group comparison (native versus invaded) with additional moderators as defined by, for example, taxa, temporal scale, spatial scale, growth form, habitat, origin or invaded country. Cohen's (1988) mean difference

Table 1a Information on studies used in the meta-analysis to determine impacts of invasive plants on native plant species richness in Mediterranean-type ecosystems

Case study	Species	Country of origin	Invaded country	Timescale[4]	Unit size (m^2)	Extent (km^2)	Growth form	Habitat	Reference
1	*Acacia saligna*	Australia	South Africa	s	1	0.00012	tree	shrubland	Holmes and Cowling, 1997
2	*Acacia saligna*	Australia	South Africa	s	1	0.00012	tree	shrubland	Holmes and Cowling, 1997
3	*Acacia saligna*	Australia	South Africa	s	1	0.00012	tree	shrubland	Holmes and Cowling, 1997
4	*Acacia longifolia*	Australia	Portugal	s	25	0.003	tree	dune vegetation	Marchante *et al*., 2003
5	*Acacia longifolia*	Australia	Portugal	s	25	0.003	tree	dune vegetation	Marchante *et al*., 2003
6	*Acacia longifolia*	Australia	Portugal	s	25	0.003	tree	dune vegetation	Marchante *et al*., 2003
7	*Acacia longifolia*	Australia	Portugal	s	25	0.003	tree	dune vegetation	Marchante *et al*., 2003
8	*Acacia longifolia*	Australia	Portugal	s	25	0.003	tree	dune vegetation	Marchante *et al*., 2003
9	*Acacia longifolia*	Australia	Portugal	s	25	0.003	tree	dune vegetation	Marchante *et al*., 2003
10	*Acacia longifolia*	Australia	Portugal	s	25	0.003	tree	dune vegetation	Marchante *et al*., 2003
11	*Acacia longifolia*	Australia	Portugal	s	25	0.003	tree	dune vegetation	Marchante *et al*., 2003
12	*Acacia longifolia*	Australia	Portugal	s	25	0.003	tree	dune vegetation	Marchante *et al*., 2003
13	*Acacia longifolia*	Australia	Portugal	s	25	0.003	tree	dune vegetation	Marchante *et al*., 2003
14	*Acacia longifolia*	Australia	Portugal	s	25	0.003	tree	dune vegetation	Marchante *et al*., 2003
15	*Acacia longifolia*	Australia	Portugal	s	25	0.003	tree	dune vegetation	Marchante *et al*., 2003
16	*Acacia melanoxylon*	Australia	South Africa	s	4	0.01	tree	shrubland	Richardson *et al*., 1989
17	*Pinus pinaster*	Europe	South Africa	s	4	0.01	tree	shrubland	Richardson *et al*., 1989
18	different species[1]	South Africa/ Australia/Europe	South Africa	s	4	0.01	tree	different types	Richardson *et al*., 1989
19	*Asparagus asparagoides*	South Africa	Australia	s	10	0.0004	creeper	shrubland	Turner *et al*., 2008
20	*Ailanthus altissima*	China	Europe	s	4	302	tree	different types	Vilà *et al*., 2006
21	*Ailanthus altissima*	China	Europe	s	4	3656	tree	different types	Vilà *et al*., 2006
22	*Ailanthus altissima*	China	Europe	s	4	8682	tree	different types	Vilà *et al*., 2006
23	*Ailanthus altissima*	China	Europe	s	4	24090	tree	different types	Vilà *et al*., 2006
24	*Ailanthus altissima*	China	Europe	s	4	8700	tree	different types	Vilà *et al*., 2006
25	*Carpobrotus* spp.	South Africa	Europe	s	4	3656	succulent	different types	Vilà *et al*., 2006

26	*Carpobrotus* spp.	South Africa	Europe	s	4	302	succulent	different types	Vilà *et al*., 2006
27	*Carpobrotus* spp.	South Africa	Europe	s	4	6	succulent	different types	Vilà *et al*., 2006
28	*Carpobrotus* spp.	South Africa	Europe	s	4	12	succulent	different types	Vilà *et al*., 2006
29	*Carpobrotus* spp.	South Africa	Europe	s	4	24090	succulent	different types	Vilà *et al*., 2006
30	*Carpobrotus* spp.	South Africa	Europe	s	4	8700	succulent	different types	Vilà *et al*., 2006
31	*Oxalis pes-caprae*	South Africa	Europe	s	4	3656	perennial herb	different types	Vilà *et al*., 2006
32	*Oxalis pes-caprae*	South Africa	Europe	s	4	302	perennial herb	different types	Vilà *et al*., 2006
33	*Oxalis pes-caprae*	South Africa	Europe	s	4	1632	perennial herb	different types	Vilà *et al*., 2006
34	*Oxalis pes-caprae*	South Africa	Europe	s	4	12	succulent	different types	Vilà *et al*., 2006
35	*Oxalis pes-caprae*	South Africa	Europe	s	4	24090	perennial herb	different types	Vilà *et al*., 2006
36	*Oxalis pes-caprae*	South Africa	Europe	s	4	8700	perennial herb	different types	Vilà *et al*., 2006
37	*Cortaderia jubata*	Southern America	California	s	2500	0.025	graminoid	shrubland	Lambrinos, 2000
38	*Cortaderia jubata*	Southern America	California	s	2500	0.025	graminoid	shrubland	Lambrinos, 2000
39	*Cortaderia jubata*	Southern America	California	s	2500	0.025	graminoid	shrubland	Lambrinos, 2000
40	*Cortaderia jubata*	Southern America	California	s	2500	0.025	graminoid	shrubland	Lambrinos, 2000
41	*Delairea odorata*	South Africa	California	s	2,25	1	perennial herb	shrubland	Alvarez and Cushman, 2002
42	*Delairea odorata*	South Africa	California	s	2,25	1	perennial herb	shrubland	Alvarez and Cushman, 2002
43	*Delairea odorata*	South Africa	California	s	2,25	1	perennial herb	shrubland	Alvarez and Cushman, 2002
44	*Fallopia japonica*	Europe	Belgium	s	6	10	perennial herb	forest	Vanderhoeven *et al*., 2005
45	different species[2]	California	California	l	10	0.01	annual herb	shrubland	Stylinski and Allen, 1999
46	*Oxalis pes-caprae*	Greece/South Africa	Europe	s	0,25	0.004	perennial herb	old field	Petsikos *et al*., 2007
47	exotic annual species[3]	South Africa/ Europe	South Africa	s	1	625	annual herb	shrubland	Vlok, 1988

[1]*Pinus* spp., *P. pinaster*, *P. radiata*, *Hakea sericea*, *Acacia saligna*, *Acacia melanoxylon*
[2]*Hypochaeris glabra*, *Bromus* spp., *Erodium botry*, *Avena* spp.
[3]*Bromus diandrus*, *Hordeum murinum* ssp. *glaucum*, *Lolium perenne*, *Lolium rigidum*, *Lolium temulentum*, *Phalaris canariensis*, *Vulpia bromoides*
[4]s = short-term study (2–3 yrs); l = long-term study (>10 yrs)

Table 1b Effect sizes of all 47 studies. g = Cohen's (1988) mean difference effect size; SE = standard error; Lower CI95 = lower confidence interval (95%); Upper CI95 = upper confidence interval (95%); Z value = two-tail Z-test. Details for case studies are given in Table 1a

		Effect size and 95% confidence interval				Test of null (2–tail)			
Case study	Species	g[a]	SE[b]	Lower CI95[c]	Upper CI95[d]	Z–value[e]	p–value	Weight	Residual
1	*Acacia saligna*	–4.627734781	0.428776816	–5.4681219	–3.7873477	–10.792875	0	2.245591114	–3.1245763
2	*Acacia saligna*	–5.699759745	0.503036164	–6.6856925	–4.713827	–11.330716	0	2.13363434	–3.9637791
3	*Acacia saligna*	–3.106208205	0.33211942	–3.7571503	–2.4552661	–9.3526847	0	2.378228061	–1.8376697
4	*Acacia longifolia*	–0.787238207	0.599296254	–1.9618373	0.38736087	–1.3136044	0.188979361	1.982095738	0.2420421
5	*Acacia longifolia*	–1.082990516	0.618225568	–2.2946904	0.12870933	–1.7517724	7.98E-02	1.951984239	–2.34E-03
6	*Acacia longifolia*	–0.723057872	0.595917104	–1.8910339	0.44491819	–1.2133531	0.224994845	1.987468499	0.2954859
7	*Acacia longifolia*	–0.877865514	0.604519364	–2.0627017	0.30697067	–1.452171	0.146454052	1.973788928	0.1667936
8	*Acacia longifolia*	–0.487264088	0.585855012	–1.6355188	0.66099064	–0.8317145	0.405570134	2.003457533	0.4926155
9	*Acacia longifolia*	–1.598928254	0.663217271	–2.8988102	–0.2990463	–2.4108664	1.59E-02	1.880517309	–0.4173606
10	*Acacia longifolia*	–0.282437234	0.58022161	–1.4196507	0.85477622	–0.4867748	0.62641796	2.012401134	0.6643126
11	*Acacia longifolia*	–0.996434003	0.612130185	–2.1961871	0.20331911	–1.6278139	0.103564359	1.961681662	6.88E-02
12	*Acacia longifolia*	9.92E-02	0.577705547	–1.0330411	1.23152306	0.1717847	0.863606764	2.016393334	0.9831613
13	*Acacia longifolia*	–0.669646514	0.593310854	–1.8325144	0.49322139	–1.1286605	0.259041086	1.991611414	0.340045
14	*Acacia longifolia*	0.123452682	0.577899954	–1.0092104	1.25611578	0.2136229	0.830841116	2.016084926	1.0032665
15	*Acacia longifolia*	–2.12E-02	0.57736652	–1.1528391	1.11039606	–3.68E-02	0.970679778	2.016931145	0.8828609
16	*Acacia melanoxylon*	–7.689849727	1.832127026	–11.280753	–4.0989467	–4.1972252	2.70E-05	0.65930125	–3.1291088
17	*Pinus pinaster*	–0.730112887	0.540120758	–1.7887301	0.32850435	–1.3517586	0.176452548	2.075776324	0.2961463
18	different species[l]	–2.391637231	0.826301885	–4.0111592	–0.7721153	–2.8943868	3.80E-03	1.629195873	–0.9808011
19	*Asparagus asparagoides*	–2.11805426	0.558707299	–3.2131004	–1.0230081	–3.7909909	1.50E-04	2.046478466	–0.8717965
20	*Ailanthus altissima*	–0.551552832	0.330553971	–1.1994267	9.63E-02	–1.6685712	9.52E-02	2.380211081	0.4796395
21	*Ailanthus altissima*	–0.510541237	0.299649294	–1.0978431	0.07676059	–1.7037959	8.84E-02	2.418064758	0.5210482
22	*Ailanthus altissima*	–0.405798429	0.274952393	–0.9446952	0.13309836	–1.4758862	0.139974458	2.44641305	0.6205587
23	*Ailanthus altissima*	0.16	0.283294899	–0.3952478	0.7152478	0.5647825	0.572221715	2.437036677	1.1389876

24	*Ailanthus altissima*	–0.233020691	0.409631406	–1.0358835	0.56984211	–0.5688546	0.569454848	2.273261814	0.7507966
25	*Carpobrotus* spp.	–0.951036586	0.298403596	–1.5358969	–0.3661763	–3.1870815	1.44E-03	2.419536639	0.1181356
26	*Carpobrotus* spp.	–1.108831906	0.310065655	–1.7165494	–0.5011144	–3.5761197	3.49E-04	2.405589427	–2.62E-02
27	*Carpobrotus* spp.	–0.753789476	0.405922467	–1.5493829	4.18E-02	–1.8569789	6.33E-02	2.278552727	0.2895865
28	*Carpobrotus* spp.	–0.430497602	0.312160829	–1.0423216	0.18132638	–1.3790891	0.167867279	2.403044521	0.592375
29	*Carpobrotus* spp.	–0.877876225	0.270349568	–1.4077516	–0.3480008	–3.2471893	1.17E-03	2.45149631	0.1863298
30	*Carpobrotus* spp.	–1.802995743	0.448226538	–2.6815036	–0.9244879	–4.02251	5.76E-05	2.216915397	–0.6324912
31	*Oxalis pes-caprae*	3.08E-02	0.301529268	–0.5601461	0.62182686	0.1022798	0.918534583	2.415835244	1.0158044
32	*Oxalis pes-caprae*	–0.574818031	0.416593721	–1.3913267	0.24169066	–1.3798048	0.167646743	2.263267402	0.4468551
33	*Oxalis pes-caprae*	–0.739783497	0.266884488	–1.2628675	–0.2166995	–2.7719239	5.57E-03	2.455280116	0.3137921
34	*Oxalis pes-caprae*	–0.197900922	0.28938089	–0.765077	0.3692752	–0.683877	0.494052868	2.430066559	0.8090904
35	*Oxalis pes-caprae*	–4.07E-02	0.258225636	–0.5468254	0.46540052	–0.1576622	0.874722968	2.464571341	0.9601597
36	*Oxalis pes-caprae*	–1.613956446	0.514899393	–2.6231407	–0.6047722	–3.1345083	1.72E-03	2.115229984	–0.456009
37	*Cortaderia jubata*	–3.291858008	0.970472286	–5.1939487	–1.3897673	–3.3920165	6.94E-04	1.425972414	–1.5458383
38	*Cortaderia jubata*	–0.61588591	0.647275654	–1.8845229	0.65275106	–0.9515048	0.341348169	1.905801075	0.3760385
39	*Cortaderia jubata*	1.065397325	0.675835463	–0.2592158	2.39001049	1.5764152	0.114930138	1.860553922	1.72E+00
40	*Cortaderia jubata*	0.884877794	0.662684265	–0.4139595	2.18371509	1.3352932	0.181780403	1.881361639	1.5811996
41	*Delairea odorata*	–1.014466119	0.475108975	–1.9456626	–8.33E-02	–2.1352283	3.27E-02	2.176471766	5.69E-02
42	*Delairea odorata*	–0.900591374	0.469336362	–1.8204737	1.93E-02	–1.9188613	5.50E-02	2.185228031	0.1559506
43	*Delairea odorata*	–0.766964989	0.463363661	–1.6751411	0.1412111	–1.6552118	9.79E-02	2.194248208	0.2725882
44	*Fallopia japonica*	–0.684650429	0.514439811	–1.6929339	0.32363307	–1.330866	0.183233122	2.11594498	0.3379019
45	different species[2]	–2.997706948	0.505159926	–3.9878022	–2.0076117	–5.9341741	2.95E-09	2.130347783	–1.6440377
46	*Oxalis pes-caprae*	–1.832082371	0.284812292	–2.3903042	–1.2738605	–6.4325959	1.25E-10	2.435308994	–0.6903597
47	exotic annual species[3]	–1.637793969	0.270102937	–2.167186	–1.1084019	–6.0635918	1.33E-09	2.451766852	–0.5137536
		–1.080139574	0.172083842	–1.4174177	–0.7428614	–6.2768216	3.46E-10		

[1]*Pinus* spp., *P. pinaster*, *P. radiata*, *Hakea sericea*, *Acacia saligna*, *Acacia melanoxylon*
[2]*Hypochaeris glabra*, *Bromus* spp., *Erodium botry*, *Avena* spp.
[3]*Bromus diandrus*, *Hordeum murinum* ssp. *glaucum*, *Lolium perenne*, *Lolium rigidum*, *Lolium temulentum*, *Phalaris canariensis*, *Vulpia bromoides*

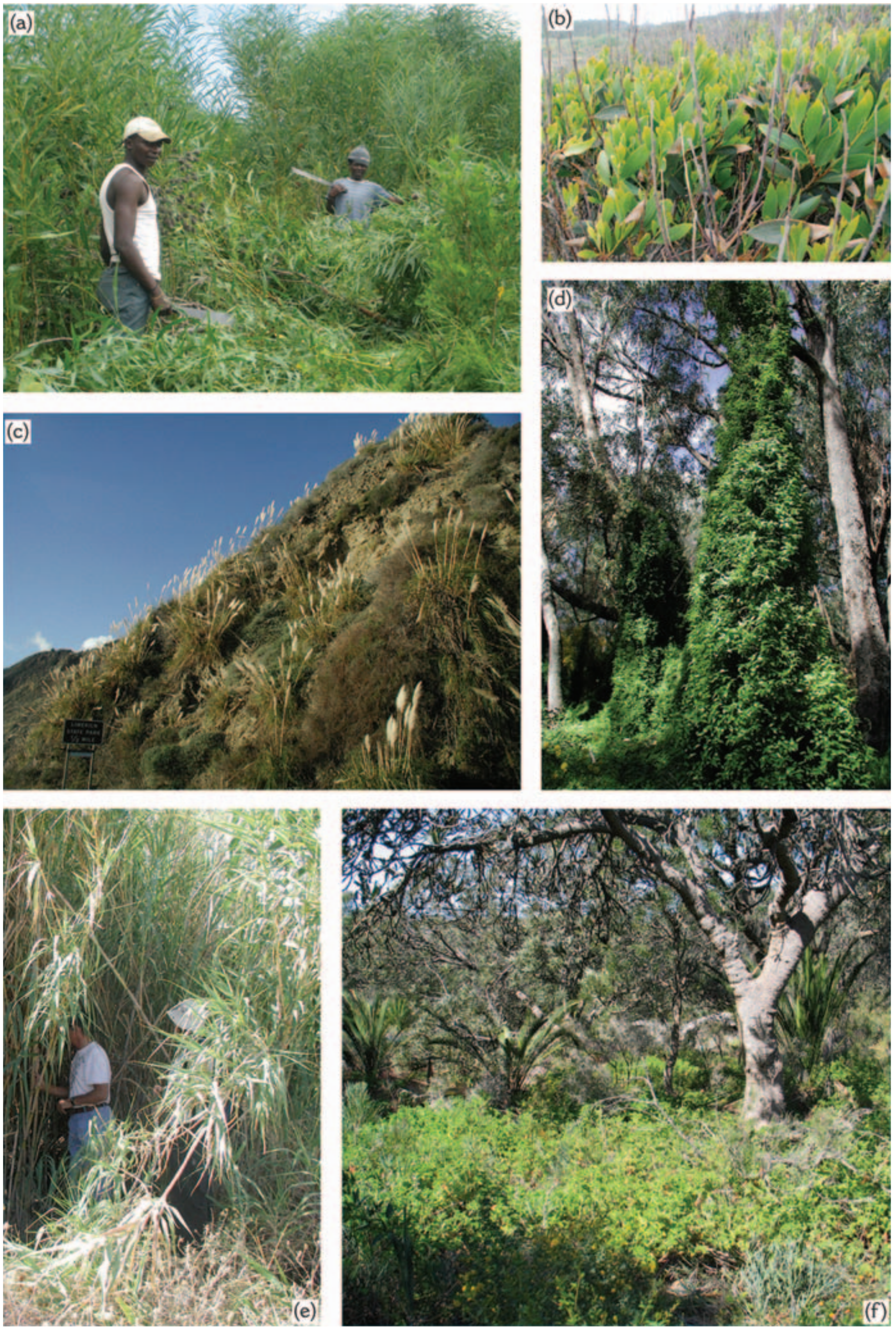

Figure 1 The impacts of invasive alien plants on native plant diversity have been investigated in many Mediterranean-type ecosystems around the world. Examples are: (a) *Acacia saligna* in South Africa; (b) *Acacia longifolia* in Portugal; (c) *Cortaderia jubata* in California, USA; (d) *Asparagus asparagoides* in Western Australia; (e) *Arundo donax* in California, USA; (f) *Pelargonium capitatum* in Western Australia (photo credits: (a) M. Gaertner; (b–f) D.M. Richardson)

effect size, g (Lipsey and Wilson, 2001; Borenstein *et al.*, 2005), and a mixed (random) effects model was used. A two-tail Z-test was used to examine the null hypothesis (ie, the effect size equals zero) and a Q-test was used for the heterogeneity analysis. Meta-analysis can largely alleviate the bias of favouring significant results in literature by weighing each case according to its sampling variance and size, and, as a result, can present a more robust synthesis than traditional literature review.

III Results

The meta-analysis revealed an overall significant decline of species richness after invasion. In five of the 47 cases invasion had a positive effect on native species richness (species richness increased after invasion). In the remaining 42, invaded sites had lower native species richness. Eighteen cases (38.3%) had a negative effect size, indicating a significant decline of species richness after invasion, while 29 cases (61.7%) had effect sizes not significantly different from zero (ie, 95% CI includes 0), indicating no significant decline of species richness after invasion (Figure 2; Table 2). According to Cohen's (1988) standard, 48.9% of the cases had large effect sizes (>0.8), 36.2% had medium effect sizes (0.2~0.8), and 14.9% had small effect sizes.

Effect size of invasion on native species richness declined significantly with increasing unit size. Cases with unit size <1 m^2, 1–10 m^2 and 10–100 m^2 had effect sizes significantly different from zero (Z= –4.78; $p < 0.001$; Z= –5.97; $p < 0.001$; Z= –3.33; $p < 0.001$, respectively). Cases with unit sizes >100 m^2 had effect sizes not significantly different from zero (Z = –0.45; p = 0.65) (Figure 3a). The same pattern was evident for increasing extent of study area. Effect size was highest for case studies where the extent of the study area was less than 0.01 km^2, and decreased with increasing extent of study area, except for studies with areal extent of 100–10 000 km^2. Cases with study area extent <0.01 km^2, 1–100 km^2 and 100–10 000 km^2 had effect sizes significantly different from zero (Z = –4.61; $p < 0.001$; Z= –2.46; p = 0.014; Z = –5; $p < 0.001$, respectively), whereas cases with extent of study area 0.01–1 km^2 and >10 000 km^2 had effect sizes not significantly different from zero (Z = –1.43; p = 0.153; Z = –0.81; p = 0.419, respectively) (Figure 3b). The time of investigation (temporal scale) also had a significant influence on effect size. Long-term investigations showed a significant higher effect size, with plant invasions having a stronger impact on native species richness than short-term investigations (Q = 13.51; $p < 0.001$).

Shrublands, old fields and dune vegetation showed significantly different effect sizes between groups (Q = 24.31; $p < 0.001$) with shrublands and old fields having largest declines in species richness attributable to alien invasion. Invaded sites in forest habitats, in contrast, showed no significant declines in species richness (Z = –1.33; p = 0.18). Among the different growth forms of alien plants reviewed, annual herbs, trees and creepers had the greatest impact on species richness decline (Z = –3.33; $p < 0.001$; Z = –3.78; $p < 0.001$; Z = –3.97; $p < 0.001$, respectively), whereas graminoids generally caused insignificant damage to the native communities (Z = –0.45; p = 0.65) (Figure 4a). An investigation of the different taxa included in the meta-analysis showed the highest effect size of invasion on species richness for two Australian *Acacia* species (*A. melanoxylon* and *A. saligna*) (Figure 4b; Table 2). Among the different countries investigated in the meta-analysis, South Africa had the highest declines of native plant species richness due to alien invasion followed by Australia (Figure 5a). Species with origin in Australia and Europe caused the largest declines in plant species richness (Figure 5b).

Table 2 Summary of the meta-analysis. SE = standard error; Lower CI95 = lower confidence interval (95%); Upper CI95 = upper confidence interval (95%); Z value = two- tail Z-test; Q-value = Q-test for heterogeneity

Model	Case study	Effect size		95% confidence interval		Test of null (2–tail)		Heterogeneity		
		Point estimate	SE[a]	Lower CI95[b]	Upper CI95[c]	Z–value[d]	p–value	Q–value[e]	df (Q)	p–value
Random effects	47	–1.080139574	0.172083842	–1.417418	–0.742861441	–6.276821588	3.5E-10			
Mixed effects analysis of unit size (m^2)										
<1	5	–3.337534451	0.697625712	–4.704856	–1.970213181	–4.784133373	1.7E-06			
1~10	26	–0.825721512	0.138366075	–1.096914	–0.55452899	–5.967658728	2.4E-09			
10~100	12	–0.574693192	0.172489573	–0.912767	–0.236619841	–3.331756125	0.00086			
>100	4	–0.381051267	0.851828047	–2.050604	1.288501026	–0.447333553	0.65463			
Total between								15.1847909	3	0.002
Overall	47	–0.782161057	0.105835916	–0.989596	–0.574726474	–7.390317864	1.5E-13			
Mixed effects analysis of extent (km^2)										
<0.01	21	–1.706183548	0.370467508	–2.432287	–0.980080574	–4.605487687	4.1E-06			
0.01~1	7	–0.582461722	0.408150694	–1.382422	0.217498939	–1.427075172	0.15356			
1~100	4	–0.435016063	0.176635013	–0.781214	–0.0888178	–2.462796342	0.01379			
100~10000	12	–0.811400437	0.162402514	–1.129704	–0.49309736	–4.996230783	5.8E-07			
>10000	3	–0.25454333	0.315088266	–0.872105	0.363018324	–0.807847695	0.41918			
Total within										
Total between								12.1306208	4	0.016
Overall	47	–0.677172027	0.1035127	–0.880053	–0.474290862	–6.541922146	6.1E-11			
Mixed effects analysis of temporal scales										
long-term	1	–2.997706948	0.505159926	–3.987802	–2.007611687	–5.9341741	3E-09			
short-term	46	–1.037141369	0.171330016	–1.372942	–0.701340708	–6.05347149	1.4E-09			
Total between								13.5088574	1	2E-04
Overall	47	–1.239398647	0.162252084	–1.557407	–0.921390406	–7.63872253	2.2E-14			
Mixed effects analysis of species										
Acacia saligna	3	–4.443252655	0.772123062	–5.956586	–2.929919261	–5.754591299	8.7E-09			
Acacia longifolia	12	–0.574693192	0.172489573	–0.912767	–0.236619841	–3.331756125	0.00086			
Acacia melanoxylon	1	–7.689849727	1.832127026	–11.28075	–4.09894674	–4.197225201	2.7E-05			
Pinus pinaster	1	–0.730112887	0.540120758	–1.78873	0.328504346	–1.351758613	0.17645			
Different	3	–2.256375532	0.49438226	–3.225347	–1.287404107	–4.564030132	5E-06			
Asparagus asparagoides	1	–2.11805426	0.558707299	–3.2131	–1.023008075	–3.790990851	0.00015			
Ailanthus altissima	5	–0.298376486	0.138759776	–0.570341	–0.026412323	–2.150309655	0.03153			
Carpobrotus spp.	6	–0.933931414	0.158401473	–1.244393	–0.623470231	–5.89597681	3.7E-09			
Oxalis pes-caprae	7	–0.677334604	0.283398874	–1.232786	–0.121883017	–2.390039852	0.01685			

Cortaderia jubata	4	−0.381051267	0.851828047	−2.050604	1.288501026	−0.447333553	0.65463			
Delairea odorata	3	−0.891940192	0.270890519	−1.422876	−0.36100453	−3.2926224	0.00099			
Fallopia japonica	1	−0.684650429	0.514439811	−1.692934	0.323633072	−1.330865953	0.18323			
Total between								65.9736814	11	7E-10
Overall	47	−0.732265113	0.076846942	−0.882882	−0.581647875	−9.528877702	0			
Mixed effects analysis of origin country										
Australia	16	−1.632729308	0.501253496	−2.615168	−0.650290509	−3.25729261	0.00112			
Europe	3	−1.47721098	0.774734357	−2.995662	0.041240456	−1.906732247	0.05656			
Others	3	−1.765041586	0.190694969	−2.138797	−1.391286315	−9.255837203	0			
South Africa	16	−0.777383315	0.136888616	−1.04568	−0.509086558	−5.678947892	1.4E-08			
China	5	−0.298376486	0.138759776	−0.570341	−0.026412323	−2.150309655	0.03153			
Southern America	4	−0.381051267	0.851828047	−2.050604	1.288501026	−0.447333553	0.65463			
Total between								42.4013174	5	5E-08
Overall	47	−0.822482264	0.084567953	−0.988232	−0.656732121	−9.725696683	0			
Mixed effects analysis of invaded country										
South Africa	7	−3.409153546	0.710910135	−4.802512	−2.015795286	−4.795477487	1.6E-06			
Europe	30	−0.566066113	0.089512527	−0.741507	−0.390624784	−6.323875908	2.6E-10			
Australia	1	−2.11805426	0.558707299	−3.2131	−1.023008075	−3.790990851	0.00015			
California	9	−1.039802653	0.412460063	−1.84821	−0.231395784	−2.520977778	0.0117			
Total within										
Total between								23.7111967	3	3E-05
Overall	47	−0.664560877	0.085791756	−0.83271	−0.496412125	−7.746209056	9.5E-15			
Mixed effects analysis of growth forms										
tree	23	−1.287094996	0.340359632	−1.954188	−0.620002374	−3.781573586	0.00016			
creeper	1	−2.11805426	0.558707299	−3.2131	−1.023008075	−3.790990851	0.00015			
succulent	7	−0.825590489	0.174204444	−1.167025	−0.484156054	−4.739204538	2.1E-06			
perennial herb	10	−0.786027168	0.221188511	−1.219549	−0.352505653	−3.553652788	0.00038			
graminoid	4	−0.381051267	0.851828047	−2.050604	1.288501026	−0.447333553	0.65463			
annual herb	2	−2.250749497	0.676647396	−3.576954	−0.924544971	−3.326325515	0.00088			
Total between								10.529787	5	0.062
Overall	47	−0.968281736	0.120569681	−1.204594	−0.731969504	−8.030889112	8.9E-16			
Mixed effects analysis of habitat types										
shrubland	15	−2.049044039	0.474893787	−2.979819	−1.118269319	−4.314741726	1.6E-05			
dune vegetation	12	−0.574693192	0.172489573	−0.912767	−0.236619841	−3.331756125	0.00086			
Different	18	−0.604948437	0.121655475	−0.843389	−0.366508088	−4.972636354	6.6E-07			
forest	1	−0.684650429	0.514439811	−1.692934	0.323633072	−1.330865953	0.18323			
old field	1	−1.832082371	0.284812292	−2.390304	−1.273860537	−6.432595869	1.3E-10			
Total between								24.3058357	4	7E-05
Overall	47	−0.775960769	0.09064049	−0.953613	−0.598308672	−8.560862425	0			

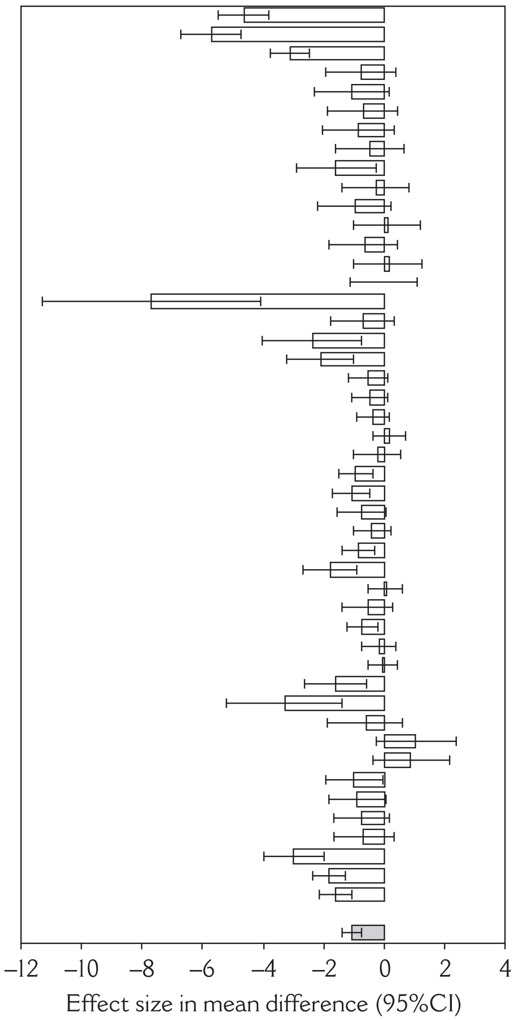

Figure 2 Meta-analysis of species richness of sites invaded by alien species and their natural reference community in four different Mediterranean-type ecosystems. Mean difference effect size, g, and a mixed (random) effects model (indicated in grey) were used. Case studies 1–47 are arranged from top to bottom (see Table 1)

IV Discussion

The impact of biological invasions on native ecosystems is the subject of ongoing debate in the literature. Many authors associate invasions with biodiversity declines (Pyšek and Pyšek, 1995; Higgins *et al.*, 1999; Seabloom *et al.*, 2003; French *et al.*, 2008; Hejda *et al.*, 2009). However, some authors argue that the number of naturalized species far exceeds the number of extinctions and that, on balance, introductions over the past few centuries has increased regional biodiversity levels (Rosenzweig, 2001; Davis, 2003; Brown and Sax, 2004; Gurevitch and Padilla, 2004; Houlahan and Findlay, 2004).

The studies reviewed in this paper show that plant invasions are often associated with a significant decline of native plant species richness. This decline varies according to different spatial and temporal scales. The impact of invasive alien species on native species richness is stronger at small spatial scales and decreases with increasing extent of study area and unit size, respectively. The reason for this is that studies at small scales are more likely to detect effects of competition (Huston, 1999) whereas studies conducted over larger areas are more likely to detect the effects of extrinsic factors (mean site-wide biotic or abiotic factors that covary with biodiversity) (Levine and D'Antonio, 1999). Some theories predict that at larger scales increased heterogeneity in resource availability and site conditions may favour the coexistence of native and invasive alien species, provided that they have different functional traits, competitive ability and resource optima (Davies *et al.*, 2005; Smith and Shurin, 2006; Melbourne *et al.*, 2007). Taking this theory further, one could argue that high heterogeneity at large spatial scales promotes diversity of both native and alien species. However, patterns of species diversity at larger scales (ie, regional or subglobal scales) do not necessarily reflect the impact on local biotic interactions (Smith and Shurin, 2006). Our meta-analysis clearly shows that invasions can reduce species richness at small scales.

Another important factor is temporal scale. Investigations in areas with a long invasion history revealed a much stronger impact of invasive alien species on native species

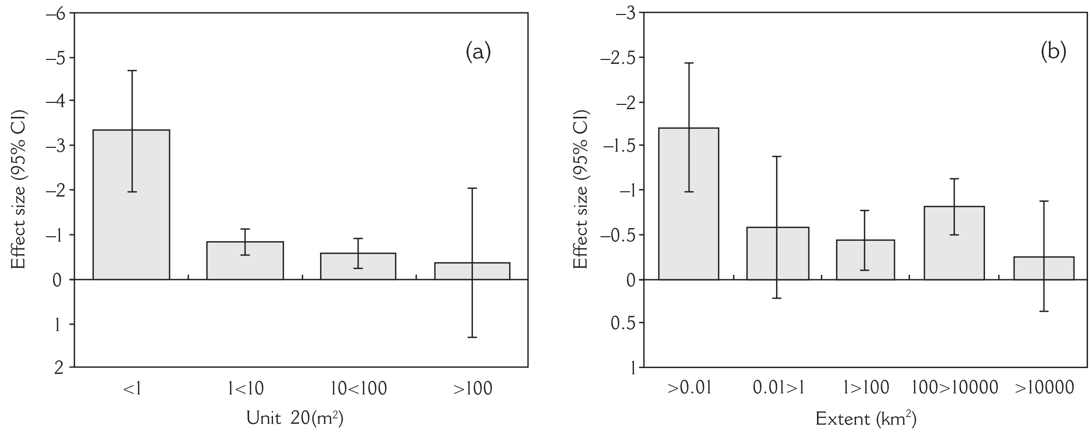

Figure 3 Effect size (95% CI) of invasion on species richness for different (a) unit sizes (m^2) and (b) extents (km^2) in Mediterranean-type ecosystems. Q-test shows significant different effect sizes (heterogeneity) between groups (a: $Q = 15.18$, $p < 0.01$; b: $Q = 12.13$, $p = 0.02$)

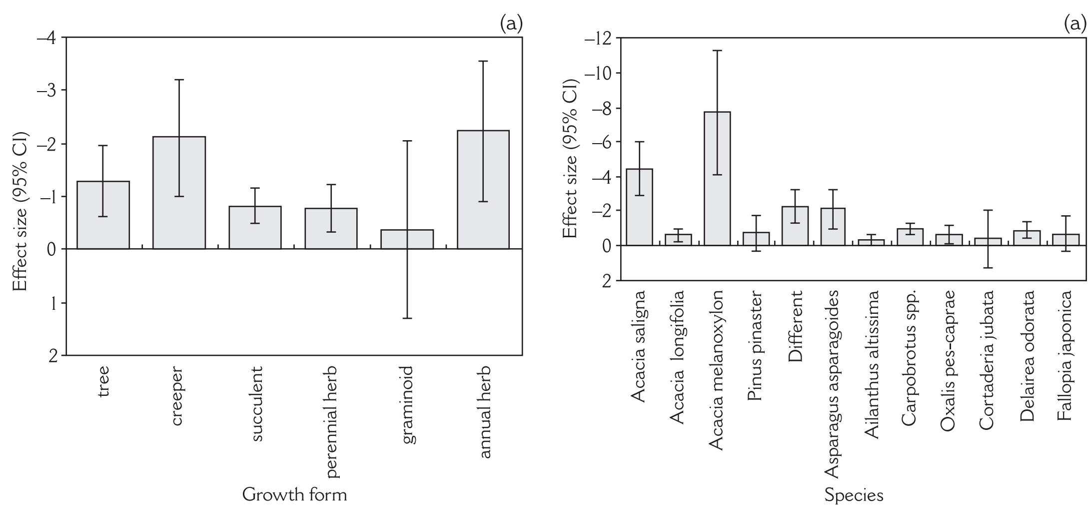

Figure 4 Comparison of the effect size (95% CI) on species richness from species with different (a) growth forms and (b) taxonomical groups in Mediterranean-type ecosystems. Q-test shows no significant different among growth forms ($Q = 10.53$; $p = 0.062$), but significant difference of effect sizes (heterogeneity) between species ($Q = 65.97$; $p < 0.001$)

richness than studies in recently invaded areas. This finding is supported by a long-term study from permanent plots which demonstrates a decline of plant species richness over a 10-year timeframe of *Lonicera japonica* invasion (Yurkonis and Meiners, 2004). Richardson *et al*. (2007) argued that a timelag between invasions and extinctions could be the reason for the temporary increase of species richness after invasions. Timelags in extinctions could create, and have already created, a large extinction debt which could

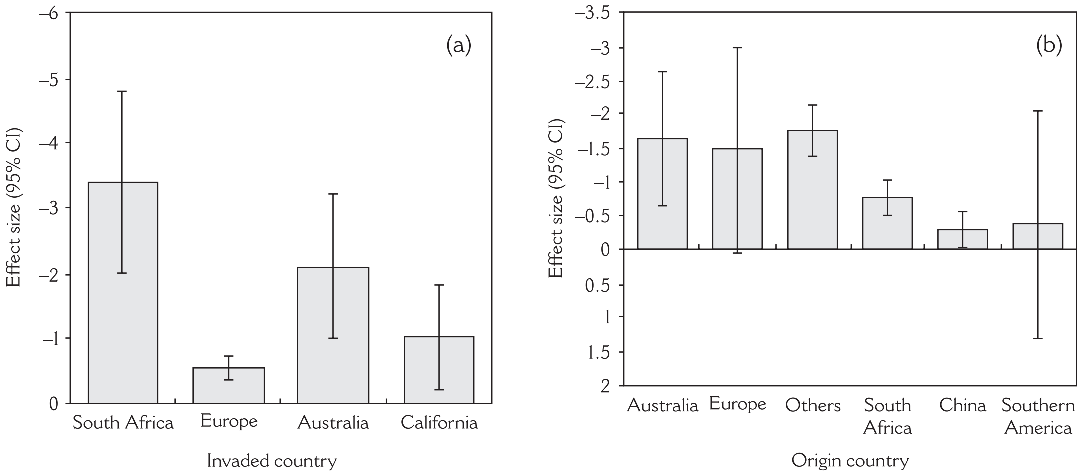

Figure 5 Comparison of the effect size (95% CI) of invasion on species richness in (a) different invaded countries and (b) the effect size of invasion from species with different countries of origin in Mediterranean-type ecosystems. Q-test shows significant different effect sizes (heterogeneity) between groups (a: $Q = 23.7$, $p < 0.001$; b: $Q = 42.4$, $p < 0.001$)

be paid in future even with no further introduction of alien plant species (Tilman *et al*., 1994; Sax and Gaines, 2008). Processes of extinction debt have also been recorded for extinctions related to habitat destruction or fragmentation (Helm *et al*., 2006). Another interesting aspect is that invasive alien species might not have a direct impact on extinction rates through competitive displacement of established plant species but rather influence colonization rates, thus leading to declines of local diversity (Yurkonis and Meiners, 2004).

Levine *et al*. (2003), in their review of mechanisms underlying the impact of alien plant invasions, posit that it is very difficult to uncover simple rules concerning which invaders or functional groups are most likely to exert large impacts across systems, or which communities will be most susceptible to impacts. Hejda *et al*. (2009) found that a decrease in species richness after alien invasion was largely driven by the identity of the invading species. We could detect patterns relating to the most successful growth forms among invaders and relating to the types of native habitats most affected by invaders. Shrublands were significantly affected by alien invasion. Trees are the growth form with the highest impact on native species richness, whereas graminoids caused insignificant reductions. These results are consistent with findings from Mason *et al*. (2009), who found a strong negative effect of woody invaders but little effect of graminoids on shrub species richness. Shrublands in MTEs generally lack tree species and therefore a decline of species richness might be caused by canopy-level changes due to tree invasions. Tree invasion results in higher canopy cover (Rejmánek, 1989), which might lead to species declines through shading effects. Investigations in the South African fynbos and Australian kwongan suggest that even high densities of indigenous overstorey shrubs (Proteaceae species) lead to a decrease in species richness of native plant species (Specht and Specht, 1989; Cowling and Gxaba, 1990; Vlok and Yeaton, 2000). The comparatively low impact of graminoids on native species richness in our meta-analysis was unexpected. Invasive alien grasses are seen as a serious challenge, especially in North America (Seabloom *et al.*, 2003; Callaway and Ridenour, 2004; Moyes *et al.*, 2005; Seastedt and Suding, 2007) but also in other parts of the world (Clarke *et al.*, 2005; Musil *et al.*, 2005). The decline of plant species richness is obviously only one measure of the impact of invasions on invaded ecosystems. The indirect effect of invasive grasses on floristic composition by changing fire regimes is widely recognized as a significant ecological factor (Brooks *et al.*, 2004; Clarke *et al.*, 2005; Rossiter-Rachor *et al.*, 2008).

Old fields showed significant declines in species richness after invasion. Anthropogenically disturbed habitats have been described as habitats with highest frequency and number of alien species (Vilà *et al.*, 2007). Invasions in old fields often hamper successional dynamics and old fields remain in a degraded state once invaded as alien species establish persistent communities that prevent the establishment of native species (Cramer *et al.*, 2008).

Forest habitats were less affected by alien invasions than other habitat types. In general, undisturbed and successionally advanced communities are less invasible than other habitats (Rejmánek, 1989). This finding is supported by studies in Poland (Knight *et al.*, 2008) and Australia (Mason *et al.*, 2009). Introduced Australian *Acacia* species caused the most severe decline of native species richness, with South Africa being the most affected country. Invasions of Australian *Acacia* species in fynbos are of particular concern. Australian *Acacia* species have a huge invasive potential and strong persistence due to enormous loads of long-lived seeds (Richardson and Kluge, 2008). They therefore have radically increased biomass and changed fuel properties in fynbos ecosystems (van Wilgen and Richardson, 1985). Apart from this, *Acacia* species have massive influences due to nitrogen fixation (Yelenik *et al.*, 2004). These factors in combination have wreaked havoc on fynbos communities.

One could conclude that species introduced from regions with similar climates within MTEs have much stronger impacts, with the native species richness in South Africa declining most severely due to invasion by Australian *Acacia* species. However, this conclusion might be premature as this cohesion could simply be caused by the fact that Australian *Acacia* species were not distributed equally to all the investigated countries.

When investigating declines of native species richness due to alien invasions one has to consider that in many instances invasive alien species have been found to be symptomatic of land-use change (Maskell *et al.*, 2006). In other words, many invaded systems are heavily impacted by habitat loss and disturbance (MacDougall and Turkington, 2005). This led to the reasoning that invasive species might be 'passengers' of degraded ecosystems rather than acting as drivers of degradation. One theory of invader success is that alien species fill unoccupied niches after extinction of native species due to degradation (Shea and Chesson, 2002). Because there might be pre-existing differences prior to invasion, it is difficult to attribute extinctions exclusively to the influence of alien plants.

Indeed most threatened species face more than one threat. It is difficult to disentangle the proximate and ultimate causes of decline or interactions between threats and to evaluate their relative importance (Gurevitch and Padilla, 2004). For example, habitat loss has been identified as the primary cause of extinctions at local and meta community levels in most areas of the world (Davis, 2003). Furthermore, an assessment of threats on biodiversity in the Mediterranean biome showed that both threatened mammals and plants had a negative correlative relationship with the amount of available natural area, with more species threatened when less area remained (Underwood *et al.*, 2009). The question of which factor is most responsible for species declines and which of the factors are drivers or passengers is secondary as ultimately global biodiversity is changing at an unprecedented rate (Sala *et al*., 2000) and it is crucial to minimize any impacts.

To understand impacts of alien invasions on native ecosystems it is important to investigate underlying mechanisms. Studies on impacts of invasive species on ecosystem processes concentrate mainly on one mechanism at a time. There are studies which investigate changes of above-ground vegetation due to alien plant invasion (Holmes, 1990; D'Antonio and Mahall, 1991; Blanchard and Holmes, 2008). Other studies concentrate on changes in the soil seed bank (Wearne and Morgan, 2006; Fourie, 2008; Vosse *et al*., 2008), or changes of soil chemical properties (Witkowski, 1991; Musil, 1993; Yelenik *et al*., 2004; Lindsay and French, 2005). A range of papers look at competitive interactions between native and invasive plant species (D'Antonio and Mahall, 1991; Sans *et al*., 2004; Garcia-Serrano *et al*., 2007; French *et al*., 2008), while others focus on allelopathic mechanisms (Ridenour and Callaway, 2001; Bais *et al*., 2003) or a change in soil microorganisms (Allsopp and Holmes, 2001). Assumptions about correlations between changes of vegetation structure and composition and the above-mentioned factors have been made (Holmes, 1990; Musil, 1993). However, our understanding about the interactions between the different mechanisms remains rudimentary. Further research should concentrate on mechanisms underlying alien plant invasions to get a better understanding about which factors are ultimately responsible for a decrease of native species richness.

The meta-analysis approach, although most useful for uncovering the patterns described above, clearly has some limitations that must be considered when evaluating the patterns that have emerged in this study. One problem relates to a potential publication bias in favour of studies that show strong negative impacts on biodiversity: we suggest that studies demonstrating significant impacts are more likely to be published overall than those reporting insignificant impacts. We feel that we have reduced the effect of this potential bias to some extent by including studies from a wide range of journals (ranging from top-tier publications to those with low impact factors), rather than limiting the review to papers in a specific set of journals (high-impact journals are more likely to report dramatic effects, whereas studies with non-significant effects are more likely to be published in journals with lower impact factors). Furthermore, meta-analysis, to a large degree, eliminates bias caused by significant studies with low sample sizes and high sample variance. Nonetheless, some invasive plant species have little or no de-tectable impact (examples of such 'benign invaders' are listed in Richardson *et al*. (2000: 101), which contribute much weight to the meta-analysis, especially when species richness shows little variation over a large number of samples. Given that, we feel that meta-analysis can improve the robustness of syntheses and should be used in further studies on the mechanisms causing biodiversity decline and biotic homogenization.

Another limitation which has to be considered is the fact that the studies which were included in the meta-analysis all use space for time substitution. The comparison of invaded and uninvaded sites introduces some uncertainty regarding the character of the invaded site prior to invasion.

V Conclusions

We have confirmed that in most cases where the effects of plant invasions on native plant diversity have been assessed in Mediterranean-type ecosystems, there are clear negative impacts. It has often been acknowledged that the type and magnitude of impacts depend on the spatial and temporal scale (Sax *et al*., 2002; Davies *et al*., 2005). However, our study highlights the importance of the growth form of the invading species, the invaded habitat, as well as the area of investigation. Our study confirmed that invasions indeed cause a marked decline of native plant species richness. Since most of the invasions that were included in our meta-analysis are fairly recent (mostly a few decades) and the results show that the magnitude of impacts increases markedly over time, there is no doubt that declines in species richness is likely to escalate rapidly. These results provide further motivation for urgent action to reduce the extent of alien plant invasions in Mediterranean-type ecosystems.

Acknowledgements
We thank the DST-NRF Centre of Excellence for Invasion Biology for financial support and Petr Pyšek and Marcel Rejmanek for helpful comments.

References

Allsopp, N. and **Holmes, P.M.** 2001: The impact of alien plant invasion on mycorrhizas in mountain fynbos vegetation. *South African Journal of Botany* 67, 150–56.

Alvarez, M.E. and **Cushman, J.H.** 2002: Community-level consequences of a plant invasion: effects on three habitats in coastal California. *Ecological Applications* 12, 1434–44.

Aschmann, H. 1973: Distribution and peculiarity of Mediterranean ecosystems. In Di Castri, F. and Mooney, H.A., editors, *Mediterranean type ecosystems*, London: Chapman and Hall, 391.

Ashton, I.W., Hyatt, L.A., Howe, K.M., Gurevitch, J. and **Lerdau, M.T.** 2005: Invasive species accelerate decomposition and litter nitrogen loss in a mixed deciduous forest. *Ecological Applications* 15, 1263–72.

Bais, H.P., Vepachedu, R., Gilroy, S., Callaway, R.M. and **Vivanco, J.M.** 2003: Allelopathy and exotic plant invasion: from molecules and genes to species interactions. *Science* 301, 1377–80.

Blanchard, R. and **Holmes, P.M.** 2008: Riparian vegetation recovery after invasive alien tree clearance in the fynbos biome. *South African Journal of Botany* 74, 421–31.

Borenstein, M., Hedges, L., Higgins, J. and **Rothstein, H.** 2005: *Comprehensive meta-analysis, version 2*. Englewood, NJ: Biostat.

Brooks, M.L., D'Antonio, C.M., Richardson, D.M., Grace, J.B., Keeley, J.E., Di Tomaso, J.M., Hobbs, R.J., Pellant, M. and **Pyke, D.** 2004: Effects of invasive alien plants on fire regimes. *BioScience* 54, 677–88.

Brown, J.H. and **Sax, D.F.** 2004: An essay on some topics concerning invasive species. *Austral Ecology* 29, 530–36.

Callaway, R.M. and **Ridenour, W.M.** 2004: Novel weapons: invasive success and the evolution of increased competitive ability. *Frontiers in Ecology and the Environment* 2, 436–43.

Clarke, P.J., Latz, P.K. and **Albrecht, D.E.** 2005: Long-term changes in semi-arid vegetation: invasion of an exotic perennial grass has larger effects than rainfall variability. *Journal of Vegetation Science* 16, 237–48.

Cohen, J. 1988: *Statistical power analysis for the behavioral sciences*. New York: Academic Press.

Cowling, R.M. and **Gxaba, T.** 1990: Effects of a fynbos overstorey shrub on understorey community structure: implications for the maintenance of community wide species richness. *South African Journal of Ecology* 1, 1–7.

Cowling, R.M., Rundel, P.W., Lamont, B.B., Arroyo, M.K. and **Arianoutsou, M.** 1996: Plant diversity in Mediterranean-climate regions. *Trends in Ecology and Evolution* 11, 362–66.

Cramer, V.A., Hobbs, R.J. and **Standish, R.J.** 2008: What's new about old fields? Land abandonment and ecosystem assembly. *Trends in Ecology and Evolution* 23, 104–12.

Dallman, P.R. 1998: *Plant life in the world's mediterranean climates*. Oxford: Oxford University Press.

D'Antonio, C.M. and **Mahall, B.E.** 1991: Root profiles and competition between the invasive, exotic perennial, *Carpobrotus edulis*, and two native shrub species in California coastal scrub. *American Journal of Botany* 78, 885–94.

Davies, K.F., Chesson, P., Harrison, S., Inouye, B.D., Melbourne, B.A. and **Rice, K.J.** 2005: Spatial heterogeneity explains the scale dependence of the native-exotic diversity relationship. *Ecology* 86, 1602–10.

Davis, M.A. 2003: Biotic globalization: does competition from introduced species threaten biodiversity? *Bioscience* 53, 481–89.

— 2009: *Invasion biology*. Oxford: Oxford University Press.

Fourie, S. 2008: Composition of the soil seed bank in alien-invaded grassy fynbos: potential for recovery after clearing. *South African Journal of Botany* 74, 445–53.

French, K., Ens, E., Gosper, C.R., Lindsay, E., Mason, T., Owers, B. and **Sullivan, N.** 2008: Management implications of recent research into the effect of bitou bush invasion. *Plant Protection Quarterly* 23, 24–28.

Fridley, J.D., Stachowicz, J.J., Naeem, S., Sax, D.F., Seabloom, E.W., Smith, M.D., Stohlgren, T.J., Tilman, D. and **von Holle, B.** 2007: The invasion paradox: reconciling pattern and process in species invasions. *Ecology* 88, 3–17.

Garcia-Serrano, H., Sans, F.X. and **Escarre, J.** 2007: Interspecific competition between alien and native congeneric species. *Acta Oecologica* 31, 69–78.

Groves, R.H. and **Di Castri, F.** 1991: *Biogeography of Mediterranean invasions*. Cambridge: Cambridge University Press.

Gurevitch, J. and **Padilla, D.K.** 2004: Are invasive species a major cause of extinctions? *Trends in Ecology and Evolution* 19, 470–74.

Hejda, M. and **Pyšek, P.** 2006: What is the impact of *Impatiens glandulifera* on species diversity of invaded riparian vegetation? *Biological Conservation* 132, 143–52.

Hejda, M., Pyšek, P. and **Jarošík, V.** 2009: Impact of invasive plants on the species richness, diversity and composition of invaded communities. *Journal of Ecology* 97, 393–403.

Helm, A., Hanski, I. and **Partel, M.** 2006: Slow response of plant species richness to habitat loss and fragmentation. *Ecology Letters* 9, 72–77.

Higgins, S.I., Richardson, D.M., Cowling, R.M. and **Trinder-Smith, T.H.** 1999: Predicting the landscape-scale distribution of alien plants and their threat to plant diversity. *Conservation Biology* 13, 303–13.

Holmes, P.M. 1990: Dispersal and predation in alien *Acacia*. *Oecologia* 83, 288–90.

Holmes, P.M. and **Cowling, R.M.** 1997: The effects of invasion by *Acacia saligna* on the guild structure and regeneration capabilities of South African fynbos shrublands. *Journal of Applied Ecology* 34, 317–32.

Houlahan, J.E. and **Findlay, C.S.** 2004: Effect of invasive plant species on temperate wetland plant diversity. *Conservation Biology* 18, 1132–38.

Huston, M.A. 1999: Local processes and regional patterns: appropriate scales for understanding variation in the diversity of plants and animals. *Oikos* 86, 393–401.

Knight, K.S., Oleksyn, J., Jagodzinski, A.M., Reich, P.B. and **Kasprowicz, M.** 2008: Overstorey tree species regulate colonization by native and exotic plants: a source of positive relationships between understorey diversity and invasibility. *Diversity and Distributions* 14, 666–75.

Köppen, W. 1923: *Die Klimate der Erde*. Berlin: Bornträger.

Kruger, F.J., Breytenbach, G.J., Macdonald, I.A.W. and **Richardson, D.M.** 1989: Characteristics of invaded Mediterranean-type regions. In Drake, J., Di Castri, F., Groves, R., Kruger, F.J., Mooney, H.A., Rejmánek, M. and Williamson, M., editors, *Biological invasions: a global synthesis,* Chichester: Wiley, 181–213.

Lambrinos, J.G. 2000: The impact of the invasive alien grass *Cortaderia jubata* (Lemoine) Stapf on an endangered Mediterranean-type shrubland in California. *Diversity and Distributions* 6, 217–31.

Levine, J.M. and **D'Antonio, C.M.** 1999: Elton revisited: a review of evidence linking diversity and invasibility. *Oikos* 87, 15–26.

Levine, J.M., Vila, M., D'Antonio, C.M., Dukes, J.S., Grigulis, K. and **Lavorel, S.** 2003: Mechanisms underlying the impacts of exotic plant invasions. *Proceedings of the Royal Society of London Series B – Biological Sciences* 270, 775–81.

Lindsay, E.A. and **French, K.** 2005: Litterfall and nitrogen cycling following invasion by *Chrysanthemoides monilifera* ssp *rotundata* in coastal Australia. *Journal of Applied Ecology* 42, 556–66.

Lipsey, M.W. and **Wilson, D.B.** 2001: *Practical meta-analysis*. London: Sage.

MacDougall, A.S. and **Turkington, R.** 2005: Are invasive species the drivers or passengers of change in degraded ecosystems? *Ecology* 86, 42–55.

Marchante, H., Marchante, E. and **Freitas, H.** 2003: Invasion of the Portuguese dune ecosystems by the exotic species *Acacia longifolia* (Andrews) Willd.: effects at the community level. *Plant invasions: ecological threats and management solutions*. Leiden: Backhuys, 75–85.

Maskell, L.C., Bullock, J.M., Smart, S.M., Thompson, K. and **Hulme, P.E.** 2006: The distribution and habitat associations of non-native plant species in urban riparian habitats. *Journal of Vegetation Science* 17, 499–508.

Mason, T.J., French, K. and **Lonsdale, W.M.** 2009: Do graminoid and woody invaders have different effects on native plant functional groups? *Journal of Applied Ecology* 46, 426–33.

Melbourne, B.A., Cornell, H.V., Davies, K.F., Dugaw, C.J., Elmendorf, S., Freestone, A.L., Hall, R.J., Harrison, S., Hastings, A., Holland, M., Holyoak, M., Lambrinos, J., Moore, K. and **Yokomizo, H.** 2007: Invasion in a heterogeneous world: resistance, coexistence or hostile takeover? *Ecology Letters* 10, 77–94.

Moyes, A.B., Witter, M.S. and **Gamon, J.A.** 2005: Restoration of native perennials in a California annual grassland after prescribed spring burning and solarization. *Restoration Ecology* 13, 659–66.

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, 361–72.

Musil, C.F., Milton, S.J. and **Davis, G.W.** 2005: The threat of alien invasive grasses to lowland Cape floral diversity: an empirical appraisal of the effectiveness of practical control strategies. *South African Journal of Science* 101, 337–44.

Pauchard, A., Cavieres, L.A. and **Bustamante, R.O.** 2004: Comparing alien plant invasions among regions with similar climates: where to from here? *Diversity and Distributions* 10, 371–75.

Petsikos, C., Dalias, P. and **Troumbis, A.Y.** 2007: Effects of *Oxalis pes-caprae* L. invasion in olive groves. *Agriculture Ecosystems and Environment* 120, 325–29.

Pyšek, P. and **Pyšek, A.** 1995: Invasion by *Heracleum mantegazzianum* in different habitats in the Czech-Republic. *Journal of Vegetation Science* 6, 711–18.

Pyšek, P., Richardson, D.M., Rejmánek, M., Webster, G.L., Williamson, M. and **Kirschner, J.** 2004: Alien plants in checklists and floras: towards better communication between taxonomists and ecologists. *Taxon* 53, 131–43.

Rejmánek, M. 1989: Invasibility of plant communities. In Drake, J.A., Mooney, H.A., Di Castri, F., Groves, R.H., Kruger, F.J., Rejmánek, M. and Williamson, M., editors, *Biological invasion: a global perspective,* Chichester: Wiley, 369–88.

Rejmánek, M. and **Randall, J.M.** 1994: Invasive alien plants in California: 1993 summary and comparison with other areas in North America. *Madroño* 41, 161–77.

Richardson, D.M. and **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, 161–77.

Richardson, D.M., Holmes, P.M., Esler, K.J., Galatowitsch, S.M., Stromberg, J.C., Kirkman, S.P., Pyšek, P. and **Hobbs, R.J.** 2007: Riparian vegetation: degradation, alien plant invasions, and restoration prospects. *Diversity and Distributions* 13, 126–39.

Richardson, D.M., MacDonald, I.A.W. and **Forsyth, G.G.** 1989: Reductions in plant species richness under stands of alien trees and shrubs in the fynbos Biome. *South African Forestry Journal* 149, 1–8.

Richardson, D.M., Macdonald, I.A.W., Holmes, P.M. and **Cowling, R.M.** 1992: Plant and animal invasions. In Cowling, R.M., editor, *The ecology of fynbos: nutrients, fire and diversity,* Cape Town: Oxford University Press.

Richardson, D.M., Pyšek, P., Rejmánek, M., Barbour, M.G., Panetta, F.D. and **West, C.J.** 2000: Naturalization and invasion of alien plants: concepts and definitions. *Diversity and Distributions* 6, 93–107.

Ridenour, W.M. and **Callaway, R.M.** 2001: The relative importance of allelopathy in interference: the effects of an invasive weed on a native bunchgrass. *Oecologia* 126, 444–50.

Rosenzweig, M.L. 2001: The four questions: what does the introduction of exotic species do to diversity? *Evolutionary Ecology Research* 3, 361–67.

Rossiter-Rachor, N.A., Setterfield, S.A., Douglas, M.M., Hutley, L.B. and **Cook, G.D.** 2008: *Andropogon gayanus* (Gamba grass) invasion increases fire-mediated nitrogen losses in the tropical savannas of northern Australia. *Ecosystems* 11, 77–88.

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. *Biological Conservation* 112, 63–85.

Sala, O.E., Chapin, F.S., Armesto, J.J., Berlow, E., Bloomfield, J., Dirzo, R., Huber-Sanwald, E., Huenneke, L.F., Jackson, R.B., Kinzig, A., Leemans, R., Lodge, D.M., Mooney, H.A., Oesterheld, M., Poff, N.L., Sykes, M.T., Walker, B.H., Walker, M. and **Wall, D.H.** 2000: Biodiversity – global biodiversity scenarios for the year 2100. *Science* 287, 1770–74.

Sans, F.X., Garcia-Serrano, H. and **Afan, I.** 2004: Life-history traits of alien and native *Senecio* species in the Mediterranean region. *Acta Oecologica –International Journal of Ecology* 26, 167–78.

Sax, D.F. 2002: Native and naturalized plant diversity are positively correlated in scrub communities of California and Chile. *Diversity and Distributions* 8, 193–210.

Sax, D.F. and **Gaines, S.D.** 2008: Species invasions and extinction: the future of native biodiversity on islands. *Proceedings of the National Academy of Sciences of the United States of America* 105, 11,490–97.

Sax, D.F., Gaines, S.D. and **Brown, J.H.** 2002: Species invasions exceed extinctions on islands worldwide: a comparative study of plants and birds. *American Naturalist* 160, 766–83.

Seabloom, E.W., Harpole, W.S., Reichman, O.J. and **Tilman, D.** 2003: Invasion, competitive dominance, and resource use by exotic and native California grassland species. *Proceedings of the National Academy of Sciences of the United States of America* 100, 13,384–89.

Seabloom, E.W., Williams, J.W., Slayback, D., Stoms, D.M., Viers, J.H. and **Dobson, A.P.** 2006: Human impacts, plant invasion, and imperiled, plant species in California. *Ecological Applications* 16, 1338–50.

Seastedt, T.R. and **Suding, K.N.** 2007: Biotic constraints on the invasion of diffuse knapweed (*Centaurea diffusa*) in North American grasslands. *Oecologia* 151, 626–36.

Shea, K. and **Chesson, P.** 2002: Community ecology theory as a framework for biological invasions. *Trends in Ecology and Evolution* 17, 170–76.

Smith, M.L. and **Glass, G.V.** 1977: Meta-analysis of psychotherapy outcome studies. *American Psychologist* 32, 752–60.

Smith, S.A. and **Shurin, J.B.** 2006: Room for one more? Evidence of invasibility and saturation in ecological communities. In Cadotte, M.W., MacMahon, S.M. and Fukami, T., editors, *Conceptual ecology and invasion biology: reciprocal*, Dordrecht: Springer, 423–47.

Specht, R.L. and **Specht, A.** 1989: Species richness of sclerophyll (heathy) plant-communities in Australia – the influence of overstory cover. *Australian Journal of Botany* 37, 337–50.

Stylinski, C.D. and **Allen, E.B.** 1999: Lack of native species recovery following severe exotic disturbance in southern Californian shrublands. *Journal of Applied Ecology* 36, 544–54.

Tilman, D., May, R.M., Lehman, C.L. and **Nowak, M.A.** 1994: Habitat destruction and the extinction debt. *Nature* 371, 65–66.

Traveset, A. and **Richardson, D.M.** 2006: Biological invasions as disruptors of plant reproductive mutualisms. *Trends in Ecology and Evolution* 21, 208–16.

Turner, P.J., Scott, J.K. and **Spafford, H.** 2008: The ecological barriers to the recovery of bridal creeper (*Asparagus asparagoides* (L.) Druce) infested sites: impacts on vegetation and the potential increase in other exotic species. *Austral Ecology* 33, 713–22.

Underwood, E.C., Viers, J.H., Klausmeyer, K.R., Cox, R.L. and **Shaw, M.R.** 2009: Threats and biodiversity in the Mediterranean biome. *Diversity and Distributions* 15, 188–97.

Vanderhoeven, S., Dassonville, N. and **Meerts, P.** 2005: Increased topsoil mineral nutrient concentrations under exotic invasive plants in Belgium. *Plant and Soil* 275, 169–79.

van Wilgen, B.W. and **Richardson, D.M.** 1985: The effects of alien shrub invasions on vegetation structure and fire behaviour in South African fynbos shrublands: a simulation study. *Journal of Applied Ecology* 22, 955–66.

Vilà, M., Pino, J. and **Font, X.** 2007: Regional assessment of plant invasions across different habitat types. *Journal of Vegetation Science* 18, 35–42.

Vilà, M., Tessier, M., Suehs, C.M., Brundu, G., Carta, L., Galanidis, A., Lambdon, P., Manca, M., Médail, F., Moragues, E., Traveset, A., Troumbis, A.Y. and **Hulme, P.E.** 2006: Local and regional assessments of the impacts of plant invaders on vegetation structure and soil properties of Mediterranean islands. *Journal of Biogeography* 33, 853–61.

Vlok, J.H.J. 1988: Alpha-diversity of lowland fynbos herbs at various levels of infestation by alien annuals. *South African Journal of Botany* 54, 623–27.

Vlok, J.H.J. and **Yeaton, R.I.** 2000: Competitive interactions between overstorey proteas and sprouting understorey species in South African mountain fynbos. *Diversity and Distributions* 6, 273–81.

Vosse, S., Esler, K.J., Richardson, D.M. and **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, 432–44.

Wearne, L.J. and **Morgan, J.W.** 2006: Shrub invasion into subalpine vegetation: implications for restoration of the native ecosystem. *Plant Ecology* 183, 361–76.

Wilcove, D.S., Rothstein, D., Jason, D., Phillips, A. and **Losos, E.** 1998: Quantifying threats to imperiled species in the United States. *BioScience* 48, 607–15.

Witkowski, E.T.F. 1991: Effects of invasive alien *Acacias* on nutrient cycling in the coastal lowlands of the Cape Fynbos. *Journal of Applied Ecology* 28, 1–15.

Yelenik, S.G., Stock, W.D. and **Richardson, D.M.** 2004: Ecosystem level impacts of invasive *Acacia saligna* in the South African fynbos. *Restoration Ecology* 12, 44–51.

Yurkonis, K.A. and **Meiners, S.J.** 2004: Invasion impacts local species turnover in a successional system. *Ecology Letters* 7, 764–69.