

A little goes a long way when controlling invasive plants for biodiversity conservation

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Abstract Invasive species, particularly animals, are being eradicated from islands at ever more ambitious scales. In order to protect island biodiversity and the essential ecosystem functions that it provides, however, plant invasions should be given more management attention. While many advances have been made, plant eradication is inherently more difficult than animal eradication due to persistent seed banks, and eradication may not be possible for more extensive populations. While maintenance control has been successful, critics question the sustainability and priority of these efforts, and targets vary widely. Developing consistent and informed targets requires an understanding of how biodiversity varies with invader cover, yet little is known about this topic. Our research suggests that limited control efforts may be highly beneficial. We conducted a meta-analysis of 54 studies to investigate the effects of plant invasions on invertebrate diversity, incorporating invader cover and residence time as potential causal mechanisms. We also contrasted restored plots with otherwise native plots. We found that invertebrate species richness was 31% lower in exotic plots than in native plots, and that there is a threshold at around 70% invader cover after which the negative effects are significant across all studies. Furthermore, these negative effects tended to decrease with time, and invertebrate richness was even greater in restored plots. The implication is that by removing 30% or less of invasive plant cover and restoring natives, we can achieve many of our conservation goals. We argue that by maintaining invasive patches at or below 70% exotic cover at a site in the near term, we can buy time for both the islands' insect herbivores to adapt to use the invader, and for managers to continue improving plant eradication technologies. By retaining native diversity in this way, we can help to increase the resistance and resilience of these systems to global change and other stressors.

Keywords: invader management, invasive plants, invertebrates, island biodiversity, meta-analysis, threshold

INTRODUCTION

Islands support many organisms found nowhere else in the world, and contribute disproportionately to global biodiversity (Kier, et al., 2009). They also provide critical habitat for 45% of the IUCN-listed species (Keitt, et al., 2011). To protect this extraordinary biological diversity, invasive species are being eradicated from islands at ever more ambitious scales (Clout & Veitch, 2002; Burbidge, 2011), and eradication is increasingly promoted as an important direction for island conservation. This is promoting recovery of many rare and endangered species, and of biodiversity as a whole (e.g. Klinger, et al., 2002; Rauzon, et al., 2002). This retained biodiversity can increase the stability of a system (Hautier, et al., 2015), its resistance and resilience to global change (Mori, et al., 2013; Isbell, et al., 2015) and its resistance to further invasion (Tilman, 1999).

Island eradication and control efforts overwhelmingly target invasive vertebrates, as an analysis of previous Island Invasives conference proceedings reveals (Veitch & Clout, 2002; Veitch, et al. 2011; 87% and 97% of the papers, respectively). Yet plant invaders are also key factors in native biodiversity decline (Wilcove, et al., 1998; Gaertner, et al., 2009), with their impacts to disturbance regimes, nutrient cycling, and fluxes of materials and energy altering ecosystem structure and function (Mack & D'Antonio, 1998; Liao, et al., 2008; Ehrenfeld, 2010). Furthermore, invasive animal removals often result in the ecological release of invasive plants (e.g., Klinger, et al., 2002; Zavaleta, et al., 2001). In order to protect island biodiversity and the essential ecosystem functions that it provides, plant invasions should be given more management attention. Yet eradication, the widely preferred alternative to control (Clout & Veitch, 2002; Burbidge, 2011), is often problematic for invasive plants.

Plant eradication is inherently more difficult, and generally more expensive, than animal eradication due to persistent seed banks, although many advances have been

made. Under the right conditions, seeds can persist for several hundred years or more (Jha, 2005). On the Pacific Islands of French Polynesia, Hawaii, and New Caledonia, eradication of the invasive alien tree *Miconia calvescens* has not yet been completed despite more than 15 years of intensive control, due to a prolific and persistent seed bank (Meyer, et al., 2011). Similar issues have plagued an eradication programme for *Sagina procumbens* on Gough Island in the South Atlantic, despite an impressive array of innovative control techniques (Cooper, et al., 2011). Invasive plant eradication can be achieved, but it typically involves small populations, treated early in the invasion process, with a swift and strong response (Mack & Lonsdale, 2002; Rejmanek & Pitcairn, 2002).

Where eradication is not feasible, maintenance control may be implemented. Maintenance control is the "coordinated and consistent management of invasive plants in order to maintain the plant population at low levels" (University of Florida, 2018). This approach has been successful, but typically requires a large labour force, and critics question the sustainability and priority of these efforts (Simberloff, 2009). Furthermore, targets for native cover vary widely and invasive cover targets are typically highly stringent. For example, a survey of 21 California habitat restoration plans containing specified thresholds (gathered via a Google search) reveals native cover targets ranging from 15% to 90%, with an average target of 62% (n=20). Exotic cover targets, on the other hand, were never greater than 10% (n=7). It is also unclear how these targets were derived. Developing consistent and informed targets requires an understanding of how biodiversity varies with invader cover, however little is known about this topic.

An important link between plant communities and the greater food web is the invertebrate fauna. Invertebrates are a key component of biodiversity, comprising 97% of all animal species (Spelman, 2012) and playing key roles in nutrient recycling, pollination, seed dispersal, energy flow,

and structuring plant and animal communities (Gullan & Cranston, 2005). They also respond quickly, sensitively, and locally to environmental changes (Kremen, et al., 1993), and are thus excellent indicators of the consequences of plant invasions and other disturbances. Analysis of invertebrate responses to plant invasions can help delineate the drivers of biodiversity and community patterns, thus guiding the conservation and restoration of diverse native ecosystems (Lodge, 1993; McMahon, et al., 2006).

We conducted a meta-analysis to investigate the effects of plant invasions on invertebrate diversity (as a whole, including both native and non-native species), incorporating invader cover and residence time in the system as potential explanatory variables. We also contrasted the type of sites (restored or intact) used as the native comparison. A meta-analysis approach can be used to combine multiple studies and detect overall trends in biotic responses to environmental factors. Our research suggests that in control efforts, a little may go a long way.

METHODS

We compiled studies through both database queries and subsequent surveys of the references cited in compiled papers. We searched ISI Web of Science in November 2012, using the search string “Topic = (invasive OR exotic AND plant) AND Topic = (arthropod* OR insect* OR invertebrate*)”. From these searches, we assembled 106 published studies which compared insect, arthropod, or other invertebrate diversity in invaded versus native habitats. These studies were from both island and mainland environments and included dissertations. Studies included by richness and other diversity indices, which were analysed separately. We extracted the data directly from tables or from graphs using the programme Digitizeit v. 1.5 (Island Bormann, Braunschweig, Germany: <<http://www.digitizeit.de>>).

Fifty-four studies were eligible for testing using a meta-analysis approach (means, variances and sample sizes were reported) and are included in our meta-analysis (Appendix 1). These studies represent a variety of habitat types throughout the world, ranging from grassland to scrub to riparian. Fifty-two of these studies reported invertebrate richness, and fifteen studies reported values for diversity indices incorporating evenness, with 12 reporting results for the Shannon index, two for the Simpson’s index, and one for Fisher’s alpha. Insects were the focus of 26 studies, while 16 studies reported results for entire arthropod assemblages, and 12 studies described results for other invertebrate groups.

We extracted descriptor variables, where available, from each study, including latitude, time since establishment of the non-native plant at both the local (study site) and/or regional (hundreds of square kilometres) scale, invader cover, and whether or not the native-dominated site was restored habitat. Where time since establishment was not reported for a given study, we obtained this information from other sources where possible. In order to utilise the studies which reported cover classes or ranges rather than exact values (over half of them), we placed invader cover into six cover classes. We used natural breaks in the data to develop the following classes: <10%, 10–30%, 30–50%, 50–70%, 70–90%, and >90%. Cover was thus considered ‘absolute’ and not relative. Studies reporting that the invasive plant “formed a monoculture”, was “dense and continuous,” or “completely dominated the landscape” were conservatively classified into the 70–90% group. We found that model results were not changed by reclassifying these into either 50–70% or >90% cover.

We used the response ratio as an estimator of effect size; in this case, the natural log of the ratio

$(X_{\text{exotic}}/X_{\text{native}})$, where X represents the mean of either invertebrate species richness or diversity index (analysed separately) for a given study in either the ‘exotic’ or the ‘native’ locations. We chose the response ratio for several reasons: first, we were interested in the magnitude of the relative difference in invertebrate diversity between exotic and native vegetation; second, use of the logarithm ensures that deviations in these two variables are treated equally (Hedges, et al., 1999). Lastly, it allowed us to assess both the model and residual variation, giving an estimate of the importance of the variables analysed here.

We calculated a single effect size per study by averaging data collected over multiple years or seasons. When we compared invertebrate richness or diversity in one native area to those in multiple invaded areas or vice versa, we calculated separate effect sizes for each comparison. When studies included multiple levels of descriptor variables (e.g. two or more establishment times), we calculated an average effect size to determine the overall effect of invasion (vs. native plant communities) but calculated separate effect sizes for each level of the descriptor variables when analysing the effects of these descriptor variables on invertebrate richness or diversity.

We performed meta-analyses using the *metafor* (Viechtbauer, 2010) package for R 2.15.0, and used random effects models to calculate overall effect sizes for invertebrate richness and diversity (Viechtbauer, 2010; Gurevitch & Hedges, 1999). To estimate the variation in the effect size described by different categorical variables (cover, study scale, and type of control plot), we used mixed-effects models using the Q statistic. This analysis treats the variables as fixed but includes a random variance component to account for variability across the studies. In one case (invader cover), we also report results from a fixed-effects model, which restricts our inferences to the studies examined. For continuous descriptor variables (latitude, invader time since establishment) we used weighted generalised least squares regression to test their relationships with effect size.

After accounting for the variation attributable to descriptor variables, we estimated residual variation (τ^2) using a restricted maximum likelihood estimator (Viechtbauer, 2005). For studies which reported results for all descriptor variable groups (22), we used the Akaike information criterion (AIC) to determine the model that best fit the data.

RESULTS

Invertebrate species richness was 31% lower in exotic plots than in native plots (effect size = -0.37 ± 0.10 on a 0–1 scale; $Z = -5.48$, $p < 0.01$; Fig. 1). There was a high amount of variation in the studies using richness to indicate diversity, however ($Q = 111$, $p < 0.001$). Invertebrate diversity indices that incorporate evenness were less strongly affected than richness values, but still 14% lower in exotic plots (effect size = -0.15 ± 0.10 ; $Z = -3.42$, $p < 0.01$). Unlike the effect sizes for species richness, there was not much variation among studies using diversity indices ($Q = 13$, $p > 0.50$). The absolute value of latitude did not explain a significant amount of heterogeneity in effect sizes for species richness ($Q = 1.09$, $p = 0.30$), nor did study scale ($Q = 0.06$, $p = 0.97$).

Using just data from native plots that had not undergone habitat restoration, invaded plots had lower invertebrate richness compared to native plots (-0.35 ± 0.07 ; $Z = -5.02$, $p < 0.01$). There was a stronger effect when plots restored to native species were used for comparison (-0.61 ± 0.17 ; $Z = -1.73$, $p = 0.08$), although this was just a statistical trend, likely due to both low sample size ($n=11$) and high variability. When analysed together, effect sizes were

significantly more negative for the comparisons between invaded and restored sites than invaded vs. otherwise native sites ($Q = 5.1, p = 0.02$; Fig. 1), indicating that invertebrate diversity was even greater in restored plots than in native plots that did not undergo habitat restoration.

At the local scale, the negative effects of invasive plants on invertebrate richness were greatest at the shortest time since establishment and decreased with time, but this pattern relies on a few key data points and was only marginally significant ($Q = 3.0, p = 0.08$, Fig. 2). At the regional scale, time since invader establishment was not related to effect size ($Q = 0.40, p > 0.50$).

The impact of exotic plants on invertebrate species richness was highly variable below 70% invader cover, and only cover classes above 70% had confidence intervals that did not overlap zero (Fig. 1). When the cover classes below 70% were combined into a single category, the difference in effect sizes between exotic plant cover classes was marginal in a mixed-model analysis ($Q = 4.7, p = 0.09$), while the groups were very different when the data were fitted to a fixed effects model ($Q = 176, p < 0.0001$).

In all models except time since establishment, residual heterogeneity was significant ($p < 0.01$), indicating substantial amounts of variation in the effects that were not explained by the models. The effects of descriptor variables on effect sizes for diversity indices were not analysed, both because low sample sizes prevented it and because low residual heterogeneity obviated the need for it.

DISCUSSION

Our results showed a clear negative effect of plant invasions on invertebrate richness and diversity. This has important implications for the diversity and function of the system as a whole, since insects and other invertebrates perform so many important roles in an ecosystem – including food provisioning for higher trophic levels such as reptiles and amphibians, birds, and small mammals (Weisser & Siemann, 2004).

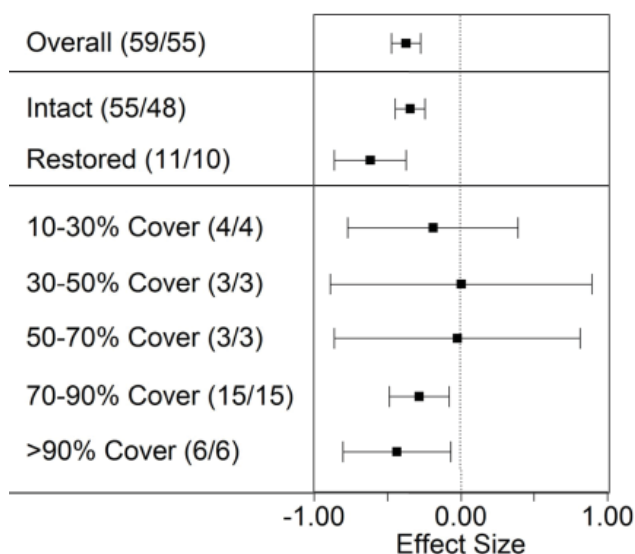


Fig. 1 Mean invertebrate richness effect sizes (\pm 95% confidence limits) across all studies (top panel), as well as between studies contrasting effect sizes where native plots represented restored or intact habitats (middle panel). The bottom panel shows mean richness effect sizes for exotic plant cover classes. Numbers in parentheses indicate the number of effect sizes and the total number of studies, respectively (some studies had more than one comparison).

Furthermore, the most consistent and significant negative effects of plant invaders on invertebrate richness occur when invasive plants comprise over 70% of cover. One likely reason for this threshold is a decline in the diversity of other plant species when an invader comes to dominate; for instance, Almeida-Neto, et al. (2011) found that only host plant richness explained the unimodal relationship they found between insect herbivore richness and invasive grass cover. Many previous studies have shown that insect and arthropod diversity is positively related to plant species richness, presumably owing to structural and food diversity as well as abiotic variables (e.g., temperature, moisture) (Price, et al., 2011).

The implication of these results is that, in general, with a moderate reduction of invasive plant cover and restoration of native plants to at least 30% cover, we can achieve meaningful progress towards the goal of biodiversity conservation. While some invasive plants will have impacts below this threshold (e.g. Knapp, 2014) this provides a general guideline in the absence of species-specific impact information. If a critical level of plant and invertebrate diversity can be maintained, then so can key ecosystem functions such as nutrient cycling and pollination (Gullan & Cranston, 2005).

Many will be legitimately concerned about indefinite “maintenance management” of plant invaders. Invasive plant management is challenging, and requires a long-term commitment (e.g. Mack & Lonsdale, 2002; Meyer, et al., 2011). However, holding that 70% line by removing invaders and, when needed, restoring at least 30% native plant cover will buy time, both: 1) to allow the islands’ insect herbivores to adjust to using the invader, and 2) for managers to continue improving plant control technologies and eradication strategies. We elaborate on these points below.

A novel plant species may be avoided by insect herbivores because it differs from native plants in characteristics such as nutritional quality, chemical composition, and architecture (Strong, et al., 1984; Kuhnle & Muller, 2009). Even a plant that can technically be eaten may be avoided because it is not recognised as a food source (Lankau, et al., 2004; Dudley, et al., 2012). The number of different herbivores using a novel plant tends to increase with the invader’s time since establishment, however (Kennedy & Southwood, 1984; Brandle, et al., 2008).

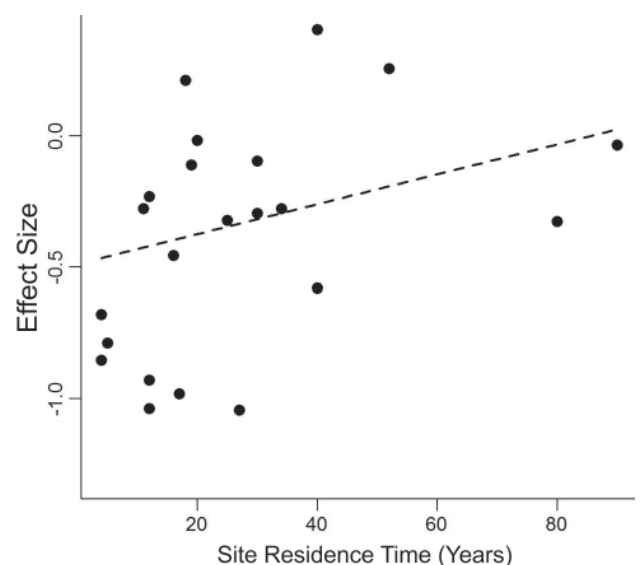


Fig. 2 Relationship between effect size for invertebrate richness and time since invader establishment at a site for the 22 studies for which these data were available. Dashes indicate line of best fit.

In our meta-analysis, where we consider the richness of invertebrates as a whole including multiple feeding guilds in addition to herbivores, we found a trend for invertebrate richness to increase with time since invader establishment (Fig. 2). This effect was only marginally significant – perhaps because it was driven by just a few key points, or perhaps because the effect of residence time is not as strong for invertebrates as a whole as it is for insect herbivores alone.

While these natural enemies are adapting to utilise invasive plant species over time, our control techniques are improving – allowing for both larger and more efficient, effective projects. For instance, a transition from ground to helicopter shooting enabled the eradication of goats on Western Australian islands (Burbidge & Morris, 2002), as did Judas goat technologies (Campbell & Donlan, 2005). Aerial surveys help with plant detection and eradication as well (Coulston, 2002; Knapp, et al., 2011), and treatment techniques have improved to avoid vectoring plant material (Coulston, 2002). Experimentation with techniques from hand-pulling to herbicide to heat and saltwater applications have improved the efficacy of invasive grass control efforts on Laysan Island (Flint & Rehkemper, 2002). Similarly, better herbicides and mapping systems have improved invasive plant control in New Zealand (Wotherspoon & Wotherspoon, 2002). Improvement in baiting technology has enabled the eradication of rats in multiple locations (Thomas & Taylor, 2002; Howald et al., 2007). Lastly, targeting multiple species at one time has proven to be both efficient and effective (Griffiths, 2011; Morrison, 2011).

It is heartening that our results showed restored plots containing even more invertebrate species than other native plots relative to invaded plots (although with greater variability). Flower visitors can be more diverse at restoration than reference sites, even after \leq one year (Waltz & Covington, 2004; Lomov, et al., 2010). This may be because early-colonising butterflies can be attracted to more open, sunny restored areas disturbed by earth moving, invasive plant removal, and outplanting (Magoba & Samways, 2010; Hanula & Horn, 2011a). Conversely, butterfly richness can decrease as percent plant cover rises (Florens, et al., 2010). Higher invertebrate richness in restored areas is likely also related to greater plant richness and cover (Hanula & Horn, 2011), perhaps due to elements of both early- and later-successional communities being present. In this case, richness would also decrease with time as succession occurs.

CONCLUSION

The theme of this conference is “Scaling Up to Meet the Challenge.” Invasive species eradication successes are being achieved at ever-increasing scales, but more attention should be paid to the significant threat of plant invasions. Although invasive plant control is challenging, our research suggests that reducing invader density to just 70% cover can have significant benefits for invertebrate biodiversity and thus ecosystem function. Furthermore, habitat restoration can give that diversity an extra boost. While the existence of seed banks dictates that this is a long-term proposition, we argue that, over time, insect herbivores will adapt to using the invader, while land managers develop ever-better control technologies. The biodiversity that is thus conserved will increase the resistance and resilience of these systems to further invasion and other stressors such as global climate change (Millennium Ecosystem Assessment, 2003; Haddad, et al., 2011), and allow us to truly achieve island conservation.

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Appendix 1 Studies used in the meta-analysis and their attributes. “Time?” indicates whether or not time since establishment was reported in the reference, and “Cov?” indicates whether or not cover of the invader was reported. “Control” indicates if the native comparison included restored habitat. “#Exotics” indicates the number of different exotic plant species that were included in the study. “Richn.” Indicates if the study evaluated invertebrate species richness, while “Div.” indicates if the study evaluated invertebrate diversity.

Reference	Location	Latitude	Native Habitat	Time?	Cov?	Control	#Exotics	Richn.	Div.
Ando, et al., 2010	Central Japan	35.07	Experimental forest field	X			1	X	
Bailey, et al., 2001	Arizona, USA	34.67	Riparian woodland	X			1	X	
Bartomeus, et al., 2008	Spain	42.32	Mediterranean shrubland	X	X		2	X	
Bassett, et al., 2012	New Zealand	35.02	Lake margin	X	X		1	X	
Bickel & Closs, 2009	New Zealand	45.03	Littoral	X		restored	1	X	X
Bock, et al., 1986	Arizona, USA	31.65	Semidesert grassland	X	X		1	X	
Brandle, et al., 2008	Germany	51	Multiple				1	X	
Burghardt, et al., 2009	Pennsylvania, USA	40.25	Suburban residences				1	X	
Cameron & Spencer, 2010	Texas, USA	29.53	Coastal prairie	X	X		1	X	X
Chey, et al., 1998	Sabah, Borneo	5.42	Tropical rainforest	X			5	X	
Christopher & Cameron, 2012	Ohio, USA	39.12	Hardwood forest		X		1		X
Cord, 2011	Texas, USA	27.49	Grassland	X	X		1	X	
de Groot, et al., 2007	Slovenia	46.05	Agricultural fields & ruderal areas		X		1	X	X
Durst, et al., 2008	Arizona, USA	33.65	Floodplain	X	X		1	X	X
Florens, et al., 2010	Mauritius	20.4	“Indigenous forest”			restored	1	X	
Gerber, et al., 2008	Switzerland, Germany, & France	47	Grassland, scrub	X			1	X	
Gossner & Ammer, 2006	Germany	48.18	Spruce forest	X	X		1		X
Gremmen, et al., 1998	Marion Island, SubAntarctic	46.83	“Drainage lines”	X	X		1	X	
Hagen, et al., 2010	Robinson Crusoe Island, Chile	33.63	Lower montane forest	X			1	X	
Hanula & Horn, 2011a	Georgia, USA	33.88	Riparian hardwood forest	X	X	restored	1	X	X
Hanula & Horn, 2011b	Georgia, USA	33.88	Riparian hardwood forest	X	X	restored	1	X	X
Harris, et al., 2004	New Zealand	41.2	Kanuka scrub		X		1	X	
Hartley, et al., 2010	Texas, USA	29.53	Tree plantations	X	1		1	X	
Harvey, et al., 2010	Australia	34	Coastal salt marsh		X		1	X	X
Herrera & Dudley, 2003	California, USA	38.23	Riparian forest	X	X		1	X	X
Hills, et al., 2008	Australia	33.82	Cave trees				2	X	
Holmquist, et al., 2011	California, USA	36.45	Desert spring	X			1	X	

Appendix 1 (Cont'd) Studies used in the meta-analysis and their attributes. "Time?" indicates whether or not time since establishment was reported in the reference, and "Cov?" indicates whether or not cover of the invader was reported. "Control" indicates if the native comparison included restored habitat. "#Exotics" indicates the number of different exotic plant species that were included in the study. "Richn." Indicates if the study evaluated invertebrate species richness, while "Div." indicates if the study evaluated invertebrate diversity.

Reference	Location	Latitude	Native Habitat	Time?	Cov?	Control	#Exotics	Richn.	Div.
Hugel, 2012	Rodrigues Island, SW Indian Ocean	19.72	Tropical forest			restored	1	X	
Kappes, et al., 2007	Germany	51.15	Floodplains		X		1	X	
Magoba & Samways, 2010	South Africa	23.02	Riparian		X	restored	1	X	
Magoba & Samways, 2012	South Africa	18.9	Fynbos scrub		X	restored	1	X	
Magura, et al., 2000	Hungary	48.47	Oak-hornbeam forest	X	X		1	X	X
Moron, et al., 2009	Poland	50.05	Wet meadow	X	X		1	X	
Osunkoya, et al., 2011	Australia	27.83	Eucalyptus & subtropical rainforest	X	X		1	X	X
Parr, et al., 2010	Australia	12.72	Mesic eucalyptus savanna	X	X		1	X	
Pinto, et al., 1997	Portugal	40.28	Riparian				2	X	
Pryke & Samways, 2009	South Africa	33.95	Southern afrotemperate forest, fynbos scrub			restored	1	X	
Robertson, et al., 2011	South Africa	25	Savanna, Sabie-crocodile thorn thicket	X	X		1	X	
Samways & Sharrat, 2010	South Africa	33.55	Riparian			restored	1	X	
Samways, et al., 2011	South Africa	33.3	Riparian, fynbos scrub				1	X	
Sax, 2002	California, USA	37.88	Oak woodland	X			1	X	
Schirmel, et al., 2011	Germany	54.53	Coastal dunes within heath	X	X		1	X	
Schoeman, 2008	South Africa	34.05	Fynbos scrub, renosterveld	X			1	X	
Simao, et al., 2010	Indiana, USA	39.22	Experimental	X			1	X	
St John, et al., 2006	Kansas, USA	39.1	Prairie	X			1	X	
Tallamy & Shropshire, 2009	Eastern USA	36.5 to 45	Multiple				1	X	
Talley, et al., 2012	California, USA	32.75	Riparian woodland				1	X	X
Theel, et al., 2008	Mississippi, USA	33	Aquatic				1	X	
Triet, et al., 2004	Vietnam	10.7	Seasonally inundated grassland	X	X		1	X	X
Ulyshen, et al., 2010	Georgia, USA	33.88	Floodplain forest	X		restored	1	X	
Webb, et al., 2000	Australia	35.4	Coastal foredunes	X	X		1	X	
White, et al., 2008	Australia	27.83	Pasture & grassland	X			1	X	
Wu, et al., 2009	China	31.52	Salt marsh	X	X		1	X	X
Zuefle, et al., 2008	Delaware, USA	39.7	Common garden				1	X	