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Invasive plants as drivers of regime shifts: identifying high-priority invaders that alter feedback relationships

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ABSTRACT

Aim A major challenge for invasion ecology is to identify high-impact invaders to guide prioritization of management interventions. We argue that species with the potential to cause regime shifts (altered states of ecosystem structure and function that are difficult or impossible to reverse) should be prioritized. These are species that modify ecosystems in ways that enhance their own persistence and suppress that of native species through reinforcing feedback processes.

Methods Using both systems analysis and meta-analysis approaches, we synthesized changes to ecosystems caused by 173 invasive plant species. For the systems analysis, we examined published studies of impacts of invasive plants to determine which presented evidence consistent with a reinforcement of feedback processes. For the meta-analysis, we calculated the effect size ratio between standardized changes in recipient ecosystem and in the status of introduced species as an indication of a reinforcing feedback in particular species-environment combinations. The systems analysis approach allowed us to conceptualize regime shifts in invader-dominated landscapes and to estimate the likelihood of such changes occurring. The meta-analysis allowed us to quantitatively verify the conceptual model and the key invader-context feedbacks and to detect the strength and direction of feedbacks.

Results Most reinforcing feedbacks involve impacts on soil-nutrient cycling by shrub and tree invaders in forests and herbaceous invaders in wetlands. Feedbacks resulting in regime shifts were most likely related to processes associated with seed banks, fire and nutrient cycling. Results were used to derive a key for identifying high-impact invaders.

Main conclusions Identifying combinations of plant life-forms and ecosystems most likely to result in regime shifts is a robust approach for predicting high-impact invasions and therefore for prioritizing management interventions. The meta-analysis revealed the need for more quantitative studies, including manipulative experiments, on ecosystem feedbacks.

Keywords
Alternative ecosystem states, biological invasions, exotic species, high-impact invaders, invader effects, invasive species, thresholds, tipping point.

INTRODUCTION

The magnitude of biological invasions is increasing world-wide: more species are invading, and the area affected by invasions and the types and overall extent and complexity of impacts are increasing (Pyšek & Richardson, 2010). Limited resources mean that not all invasions can be managed; there is increasing pressure on managers to apply objective and defendable protocols for deciding which invaders require priority treatment (Hulme *et al.*, 2013). Impacts are too often assumed rather than proven and quantified, and valuable resources may be spent on invasive species that have little or no impact (Hejda & Pyšek, 2006;

Meffin *et al.*, 2010). Some invasions generate only community-level changes, whereas others can fundamentally alter the structure and functioning of ecosystems (Levine *et al.*, 2003; Vilà *et al.*, 2011; Hui *et al.*, 2013), with major consequences for native biodiversity and ecosystem processes that underpin key ecosystem services (Pejchar & Mooney, 2009). To improve management efficacy, there is a critical need to distinguish species that have the potential for causing major ecosystem impacts from those with more limited impact (Hulme *et al.*, 2013).

We propose that species that have the potential to cause regime shifts – that is, to fundamentally restructure and transform ecosystems – should be considered the most high-impact species and be prioritized for management intervention. Regime shifts are large, often abrupt, changes in ecosystem structure and function associated with a reorganization of the internal feedback mechanisms, such as plant–soil feedbacks (Scheffer *et al.*, 2001, 2012; Rietkerk *et al.*, 2004). Regime shifts either occur due to a change in the balance between existing feedbacks in the system or the introduction of new feedbacks to the system (Bennett *et al.*, 2005) (Fig. 1). Because different sets of dominant feedbacks are associated with different regimes and as these feedbacks are often self-reinforcing, regime shifts are often hysteretic or 'sticky': once the system is in a particular regime, it tends to remain there even if the exogenous drivers that caused the shift are reduced or removed (Scheffer *et al.*, 2001). Regime-shift phenomena have been studied in many types of ecosystems, including freshwater lakes, coral reefs, semi-arid systems and savannas, and may be triggered by many factors, including pollution, overharvesting or biological invasions (Scheffer *et al.*, 2001). They are of substantial concern to ecosystem managers as they frequently have large impacts on ecosystem services and human well-being, often occur unexpectedly, and are difficult or impossible to reverse (MA, 2005) (further details on the theoretical background of regime shifts is given in Appendix S1 in Supporting Information).

Although the concept of feedback mechanisms has been explored in plant invasion ecology, especially for grass–fire feedbacks (Rossiter *et al.*, 2003; Brooks *et al.*, 2004) and plant–soil feedbacks (van der Putten *et al.*, 2013; Suding *et al.*, 2013), a comprehensive overview and synthesis of potential reinforcing feedback mechanisms that could drive shifts to invader-dominated landscapes is lacking. Numerous frameworks/concepts for conceptualizing, describing or quantifying impacts of alien plant invasions have been proposed. Vitousek (1990) argued that invaders will have large effects on ecosystem processes if they differ from the native species in important traits such those involved in resource acquisition, those that influence resource efficiency, or that alter disturbance regimes. Similarly, Chapin *et al.* (1996) proposed distinguishing between discrete-trait invaders (those that add one or more new functions to the ecosystem) and continuous-trait invaders (those that differ only quantitatively from native species). Parker *et al.* (1999) proposed quantifying impacts using the equation impact = range × abundance × per capita effect to

(a) Low-impact invader
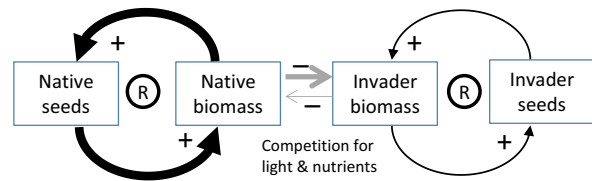
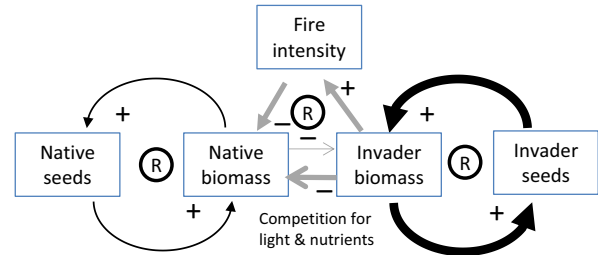**(b) Post regime shift for a high-impact invader**

Figure 1 Simplified conceptual diagram illustrating the change in dominant system feedbacks that may accompany a regime shift driven by a high-impact invader. The thickness of the curved arrows indicates the relative amount of energy and resources in the ecosystem that are entrained in the competing feedback loops. The grey arrows connecting the different loops indicate the size of the negative effect of the invader on the native species and vice versa. R indicates a reinforcing feedback. a) Feedback configuration of an ecosystem for a low-impact invader. The negative effects of the dominant native species (through competition) control population numbers of the invader. b) Feedback configuration of an ecosystem after a regime shift driven by a high-impact invader has occurred. The invader introduces a new reinforcing feedback (fire intensity) that destabilizes the ecosystem and shifts it to a regime where the invasive species has dominant influence.

distinguish between invaders with minor as opposed to large impacts. So, although invader impacts and underlying mechanisms have been investigated and described extensively, potential changes in feedback mechanisms or shifts to alternate states have not been described in detail (but see early attempts by Suding *et al.* (2004) and Chapin *et al.* (2011) and an elucidation of the closely related concept of novel ecosystems by Richardson & Gaertner (2013)). Here, we attempt to provide such a synthesis, and use it to develop a framework for identifying high-priority invaders.

Knowing whether a given species has the potential to alter feedbacks in ways that could lead to an ecological regime shift is not a trivial task. The impacts of invasives are strongly context-dependent and can have substantially different outcomes depending on the type of invader and the invaded habitat (Pyšek *et al.*, 2012). Improving our understanding of the conditions under which particular regime shifts occur, and identifying ecological thresholds that could lead to regime shifts, are urgent research priorities (Carpenter *et al.*, 2009; Reid *et al.*, 2010). Although not yet applied to invasive species, one approach is to provide 'early warning' of approaching thresholds, based on changes in the

statistical behaviour of a system such as increasing variance or autocorrelation (Scheffer *et al.*, 2012). However, this approach does not in itself give insight into the underlying drivers or processes leading to a regime shift. A complementary approach is to use systems analysis tools to analyse the feedback structure of a system based on knowledge about ecosystem drivers, processes and impacts, to understand whether a particular ecosystem may be susceptible to specific regime shifts (Scheffer, 2009; Biggs *et al.*, 2012).

In this paper, we apply such a systems analysis approach combined with a meta-analysis of the literature to propose a framework for identifying potential high-impact invaders. Drawing on systems theory, we argue that species that have the potential to cause regime shifts are those that modify ecosystems in ways that enhance their own abundance and persistence and suppress that of native species through the introduction or modification of reinforcing (positive) feedback processes that could eventually lead to invader-dominated landscapes. To determine which species may trigger such reinforcing feedback processes, we systematically reviewed the literature on invasive plant species that have been documented to cause significant ecosystem impacts and synthesize the different reinforcing feedback mechanisms implicated in each of these invasions. We also conducted a meta-analysis where we took the presence of amplified ecosystem effects – when the response effect size of the characteristic change in recipient ecosystems (e.g. the standardized change in soil nutrients) is greater than the cause effect size of status change in the invasive species (e.g. the standardized change in the invader's biomass), namely the effect size ratio (ESR) is greater than one – as an indication that there was a high probability that the species could trigger or change one or more reinforcing feedback processes (Scheffer, 2009). We then identified combinations of ecosystem types, plant growth forms and invader effects most clearly associated with amplified ecosystem effects and possible changes to reinforcing feedback processes that could lead to regime shifts. These analyses were used to derive a framework for flagging potential high-impact invaders that may fundamentally restructure and transform ecosystems, as well as potential indicators for monitoring whether specific ecosystems are undergoing regime shifts due to biological invasions.

METHODS

To identify alien plant invaders that potentially bring about ecological regime shifts, we used existing databases (e.g. DAISIE, IPANE and IUCN), review articles (e.g. Parker *et al.*, 1999; Levine *et al.*, 2003 and Vilà *et al.*, 2011) and a search of the literature to compile a list of 173 plant invaders that have been described as having effects on native ecosystems (for full lists of databases and literature used see Appendix S2). For our literature search, we used the respective species name AND (plant invader OR exotic plant OR alien plant OR plant invasion*) AND (impact* OR effect*) AND (community structure* OR diversity* OR ecosystem

process* OR competition*) AND (feedback OR regime shift OR alternative ecosystem state). According to Hulme *et al.* (2013) robust quantitative assessments of ecological impacts have been undertaken for fewer than 200 alien plant taxa. Pyšek *et al.* (2008) showed that invasive species with the greatest impact are best studied, and we consider our list of 173 species to be a representative sample of invasive plant species that cause major impacts.

We grouped the species into 12 categories of impact, distinguishing between impacts at the species level (e.g. competitive effects of invasive species on native species), impacts at the community level (e.g. changes in plant community composition and/or structure) and impacts at the ecosystem level (e.g. changes in soil properties or fire regimes). Our extensive review of the literature (443 publications; details in Appendix S2) allowed us to synthesize the types of impacts that have been documented for these species.

We used a combined approach of a systems analysis based on the literature study and a quantitative meta-analysis based on ESR estimated from data in published studies. The systems analysis allows us to build conceptual models by synthesizing key reinforcing feedbacks that may underlie regime shifts in invader-dominated landscapes and to estimate the likelihood of the type of invader and the specific context in which such changes occur. To quantitatively verify the conceptual model and the key invader-context feedbacks and to detect the strength and direction of feedbacks (i.e. whether response was negative (e.g. decreases of species richness) or positive (e.g. increases in soil nutrients), we conducted a meta-analysis on the ESR between standardized changes in recipient ecosystem and in the status of introduced species.

Synthesis of reinforcing feedbacks

In the systems analysis of the dataset, we identified studies that described or measured reinforcing feedback processes that enhanced the abundance and persistence of the invader. We distinguished between studies that described feedbacks without explicitly measuring them and studies that measured feedbacks using experimentation. Mutualistic relationships related to plant–soil biota interactions were included in the 'alteration of soil biota structure and function' feedback mechanism. This covered most studies focusing on mutualism as a feedback process. Feedback mechanisms involving other mutualistic relationships were excluded as we could only find two studies that examined interactions between invasive plants and invasive animals (Kourtev *et al.*, 1998; Barthell *et al.*, 2001). We also included studies where we felt feedbacks were implicated (based on the description, in cases where feedbacks were not explicitly mentioned; see Appendix S3).

To identify the combinations of growth form, ecosystem type and invader impact with high probabilities of causing changes in ecosystem feedbacks, we divided the number of studies on each of these parameters that have described feedback changes by the total number of studies that have

investigated ecosystem impacts. Based on the recorded feedbacks, we identified five generic types of reinforcing feedback processes and conceptualized a simple systems diagram to describe each main type (Fig. 2). For each species, we also reviewed whether their impacts on invaded ecosystems have been explicitly described as resulting in an ecosystem change that could be interpreted as ecological regime shift. All species in our dataset that were recorded as causing regime shifts were associated with one or more of the reinforcing feedback processes we had identified.

Meta-analysis

In the meta-analysis, we included only studies that quantified changes of invader biomass, abundance, cover and/or growth rate in ways that allowed us to calculate the cause effect size. The underlying assumption is that any invasion-based regime shift would be associated with an increase in invader biomass, which can also be measured in terms of abundance, cover or growth rate. We included as response variables all parameters of the native ecosystem that had been affected by the invasion (the full list of response variables appears in Appendix S4), from which the response effect size was estimated. The underlying assumption is that an increase in invader biomass that leads to an amplified response in the recipient ecosystem can be indicative of the presence of one or more reinforcing feedback processes in relation to that particular response variable.

For each combination of ecosystem type, growth form and impact, we calculated the ESR between the response effect size and the cause effect size. We took an amplified response (ESR > 1) to indicate a positive feedback, whereas a dampened response (ESR < 1) indicated a negative feedback. To calculate ESR, we recorded three types of data, depending on how it was reported in the literature: (1) means (μ), standard deviations (SD) and sample sizes (n) from studies with both cause and response variables (X and Y, respectively) at different stages; (2) correlation coefficient (r) or regression coefficient (b) with known standard deviations of the cause and response variables (SD_X and SD_Y); (3) statistics from an F-ratio or t-test (F or t).

For type (1) data, we first used the standardized mean difference for calculating effect size, $d = (\mu_1 - \mu_2)/SD_p$, where μ_1 and μ_2 are means of a focal variable, and SD_p the pooled standard deviation and equals the square root of $((n_1 - 1)SD_1^2 + (n_2 - 1)SD_2^2)/(n_1 + n_2 - 2)$. We then calculated the effect size ratio as $ESR = d_R/d_C$, where d_R and d_C are the effect sizes of the response and cause variable, respectively. For type (2) and (3) data, we first calculated the correlation coefficient based on the regression coefficient ($r = b \cdot SD_X/SD_Y$), F-ratio statistics ($r = F^{1/2}/(n-2 + F)^{1/2}$) or t-test statistics ($r = t/(n-2 + t^2)^{1/2}$), and then estimated the ESR using a z-transformation, $ESR = \ln((1-r)/(1 + r))/2$ (Borenstein *et al.*, 2011). All calculations were made using the *metafor* package (Viechtbauer, 2010) in R (R Core Development Team, 2006).

As the minimum ESR is -1.94 and the distribution is quite skewed, we transformed the effect size ratio as Ln (ESR+2) in the subsequent analysis. First, we ran a one-tail t-test for each invader–ecosystem combination of scenario to examine whether their ESR is significantly greater than positive one or less than negative one – that is, whether the native ecosystem response is positive (e.g. increasing soil nutrients) or negative (e.g. reducing native species richness). We then conducted a permutation test with 5000 runs and a two-tail t-test to examine whether the observed mean of transformed ESR is different from the mean expected from the random permutation. Based on this analysis, we examined the consistency between the conceptual model developed using the qualitative systems approach and the meta-analysis of ESR, highlighting those invader–ecosystem combinations of invader growth form, ecosystem type and invader impact that are most strongly associated with particular reinforcing feedback loops and hence the potential to cause regime shifts.

Figure 2 Causal loop diagram of five main feedback mechanisms [R1: seed-biomass (native); R2: seed-biomass (invasive); R3: fire feedback; R4, 5 and 6: soil-nutrient litter and soil biota feedback]. For the sake of clarity, only the most common direction in which the feedback operates is shown – feedbacks can also operate in the opposite direction (e.g. fire may be enhanced or suppressed).

RESULTS

Synthesis of reinforcing feedbacks

Of the 443 studies on effects of alien plant invasion involving 173 species in our dataset, only 75 described (or measured) ecosystem-level changes involving the establishment of or changes in reinforcing feedback mechanisms (see Appendix S3). In 52 of the 75 studies, the authors measured the feedback processes using experimentation; in seven studies, the feedback was described but not quantified; and in 16 studies, we inferred that the ecosystem changes involved changes in ecosystem feedbacks although such feedbacks were not explicitly described by the authors. Based on the feedbacks recorded for each species, we identified five generic types of reinforcing feedback processes that drive alien plant invasions: changes in (1) seed bank composition; (2) fire regime; (3) soil nutrients; (4) litter quantity and/or quality; and (5) soil biota structure and function. These feedbacks all lead to accumulation of invader biomass and increase the competitive ability of the invader. Through these feedbacks, the invader out-competes the native species for resources (light, nutrients and water), or changes the soil environment in ways that suppress the germination of native seedlings. Over time, this positive feedback results in a decrease in native species biomass and the native seed bank, and a further reduction in the germination of native seedlings (Fig. 1).

Seed bank composition feedback (R1&2)

Many invaders produce high numbers of seeds and can hence rapidly accumulate biomass, thus establishing a reinforcing feedback loop that promotes their own abundance (R2). For example, Australian *Acacia* species in South African fynbos produce large numbers of long-lived, hard-coated seeds that can remain dormant in the soil for many years, and seed banks in excess of 40,000 per m^2 have been recorded (Holmes *et al.*, 1987). During initial invasion, native fynbos seed banks remain relatively unaffected (R1), but with increasing invader density, especially after fire, *Acacia* species quickly outgrow the fynbos to form tall, dense stands that exclude the shorter native species.

Fire feedback (R3)

Changes in fire frequency and intensity are one of the most dramatic ways in which invasive plants alter ecosystems (D'Antonio *et al.*, 2000; Brooks *et al.*, 2004). Invasive grasses can lead to increased fire frequencies and altered fire intensities, changing habitats previously dominated by woody plants into grassland, reducing the recruitment of native species and enhancing that of the invasive grass species (Rossiter *et al.*, 2003; Rossiter-Rachor *et al.*, 2008). Invasive fire-prone woody plants can have similar effects by increasing fire intensities or altering fire continuity, for example in the case of *Chromolaena odorata* that can transform low-intensity surface-fires in to high-intensity canopy-fires (Te Beest *et al.*, 2012). Occasionally, fire-sensitive plants can successfully invade fire-prone landscapes, inhibiting fire in the landscape (Stevens & Beckage, 2009).

Nitrogen fixation feedback (R4)

Some invasive plants can accumulate nitrogen through nitrogen fixation and/or through increased biomass and net primary production leading to production of litter with higher decomposition rates than that produced by native species (Ehrenfeld, 2003). Increased nitrogen levels create reinforcing feedback loops that promote further proliferation of the invader and other weedy species (e.g. Vinton & Goergen, 2006), and suppress recruitment of native plants (e.g. Marchante *et al.*, 2008). Prominent examples of nitrogen increase in nutrient-poor habitats are South African fynbos invaded by Australian *Acacia* species (Yelenik *et al.*, 2004; Le Maître *et al.*, 2011), invasion of young volcanic soils in Hawaii by Fire tree (*Morella faya*) (Vitousek *et al.*, 1987) and Black locust (*Robinia pseudoacacia*) invasions into pine-oak ecosystems in north-eastern North America (Malcolm *et al.*, 2008).

Litter feedback (R5)

High litter volumes generated by some invasive species can inhibit native species growth while promoting the growth of the invader. Over time the accumulation of a litter layer can influence both nutrient and light availability and change the competitive relationship between native and invasive species. An increased litter layer can also negatively impact native plant species establishment and growth through reduced light availability and/or by creating a physical barrier (e.g. Farrer & Goldberg, 2009). For example, reed canary grass (*Phalaris arundinaceae*) can induce litter-feedbacks in its new habitat causing an ecosystem change (potential regime shift) to a high litter invader-dominated ecosystem state (Eppinga *et al.*, 2011; Eppinga & Molofsky, 2013).

Soil biotic processes feedback (R6)

Feedback loops initiated by a change of microbial processes are of growing interest (e.g. Reinhart & Callaway, 2006; Vogelsang & Bever, 2009). Invasive plants can release secondary compounds as exudates from their roots into the soil and thus alter the composition and function of the soil community (Wolfe & Klironomos, 2005). Altered soil communities can in turn facilitate the growth of the invader, establishing a reinforcing feedback loop (Wolfe *et al.*, 2008; Te Beest *et al.*, 2009; Felker-Quinn *et al.*, 2011). Inhibition of mycorrhizal fungi by invasive species can also be triggered by increased soil-nutrient levels; thus, invasive species can indirectly inhibit mycorrhizal fungi by increasing nutrient levels (Sanon *et al.*, 2009). In this case, reduced competition from native

species in combination with higher nutrient levels promotes proliferation of the invader.

A synthesis of the different reinforcing feedbacks associated with the 52 species (in 75 studies) for which feedback processes have been recorded reveals that the soil-nutrient feedback loop (recorded for 21 species in 23 studies) was the most commonly recorded feedback and was most common in forest ecosystems and grasslands. Other frequently described feedback loops were fire, mainly in shrublands (14 species in 15 studies), and soil biota mainly in greenhouse studies (19 species in 27 studies). Litter (8 species in 10 studies) and seed production (10 species in 10 studies) were the least frequently recorded feedbacks in a variety of different ecosystems. Across the 52 species with recorded feedback processes, 35 species were associated with only one reinforcing feedback process, 14 with two feedbacks, and only three species with three feedbacks (see Appendix S3).

Type of invader and specific conditions that trigger feedback changes

The following combinations of invader attributes have a high likelihood of being associated with a species that establishes or changes feedback loops in a way that could lead to regime shifts: tree invaders in dune lands, which have the capacity to lead to changes in soil-nutrient cycling and alter the soil seed bank compositions; tree invaders in shrublands, which change fire regimes and affect soil-nutrient cycling and tree invaders in forests, which lead to changes in litter quality, quantity and decomposition or soil-nutrient cycling or affect soil microbial communities; grass invaders in grasslands, which are known to lead to changes in fire regimes, soil-nutrient cycling and to changes in soil microbial communities and grass invaders in forests which change fire regimes and soil-nutrient cycling; and herbaceous species in grasslands and forests, which alter soil-nutrient cycling and affect the structure and functioning of soil microbial communities and herbaceous species in wetlands and forests, which change soil-nutrient cycling and lead to changes in litter quality, quantity and decomposition; and shrub species in forests, which change soil-nutrient cycling. Growth-form-ecosystem-impact combinations that have been identified as having no probability (0%) causing changes in ecosystem feedbacks are for all growth-form-ecosystem combinations 'changes in plant community composition and structure', 'effects on faunal communities', 'changes in hydrology' and 'allelopathy' (Fig. 3).

For the meta-analysis, we identified 461 cases from 64 studies that met our criteria (see Appendix S4). We then identified 215 cases with only causes specified or only responses specified, 177 cases with both the causes and responses specified, 69 cases with the effects recorded as either regression coefficient from linear models with known standard deviation of the causes and responses or F-ratio/t-test statistics. Overall, we calculated the ESRs for 246 cases.

Growth forms recorded for the 461 cases of the meta-analysis included tree invaders, shrubs, grasses and herbaceous
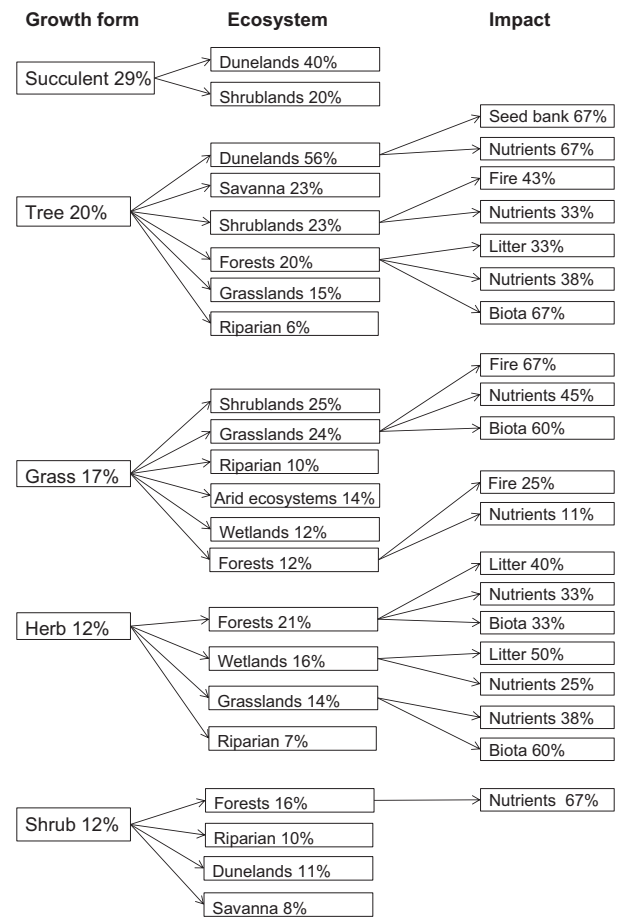

Figure 3 Probabilities of feedback changes in different growth-form-ecosystem-impact combinations. Effects are changes in soil-nutrient cycling (nutrients), alterations in structure and functioning of soil microbial communities (biota), alterations of soil seed banks (seed bank), changes in fire regimes (fire) and changes in litter quantity, quality or decomposition rates (litter). The listed probabilities are based on the number of studies that have investigated ecosystem feedbacks, compared with the full set of studies which investigated ecosystem impacts. Growth form-ecosystem-impact combinations that have been identified as having no probability (0%) of causing changes in ecosystem feedbacks were not included in the figure. These are for all growth-form-ecosystem combinations 'changes in plant community composition and structure', 'effects on faunal communities', 'changes in hydrology' and 'allelopathy'. Variables with sample size ≤ 3 were not included.

species which were studied in forests, grasslands, wetlands and riparian ecosystems. Invader effects included in the meta-analysis were changes in soil-nutrient cycling (nutrient), alterations of soil seed banks (seed bank), changes in litter quantity, quality or decomposition rates (litter), alterations in structure and functioning of soil microbial communities (biota), changes in fire regimes (fire), changes in native plant species composition (plantcomp) and effects on faunal communities (faunacomp) (see Appendix S4).

Results of the meta-analysis show that the following combinations of invader attributes have a high likelihood of

being associated with a species that leads to amplified ecosystem effects (ESR is not significantly different from one, indicating a positive feedback): grass invaders in forests that change fire regimes and alterations in soil-nutrient cycling; grass invaders in grasslands that have the capacity to lead to changes in soil microbial communities, litter quantity and decomposition rates and alterations in native plant community composition and soil seed banks; grass invaders in riparian ecosystems that trigger changes in plant community composition; grass invaders in wetlands that lead to changes in soil-nutrient cycling; herbaceous species in grasslands that lead to alterations in soil microbial communities; and herbaceous species in wetlands that change plant and animal community composition, soil-nutrient cycling and litter quantity and decomposition rates; shrub invaders in forests that change soil-nutrient cycling and plant community composition; and tree invaders in forests that affect native plant community composition and soil-nutrient

cycling and trigger changes in litter quantity and decomposition (Table 1). The following combinations showed an amplified response of the native ecosystem (indicating a positive feedback) in a negative direction: grass invaders in forests that lead to changes in fire regimes and soil-nutrient cycling; grass invaders in grasslands that alter soil seed banks and grass invaders in riparian ecosystems that trigger changes in plant community composition; herbaceous species in wetlands that lead to changes in faunal communities; and shrub and tree invaders in forests that change soil-nutrient cycling and plant species composition (Table 1).

Combinations that have been identified as leading to dampened ecosystem response (ESR is significantly different from one indicating a negative feedback) are grass invasion in forests that lead to changes in plant species composition; herbaceous species in agricultural lands and wetlands changing plant species compositions; and tree invaders in

Table 1 Summary of meta-analysis results (for details see table B in Appendix S4). The effect size ratio (ESR) between the response effect size and the cause effect size of 461 cases from 64 studies was calculated to identify growth-form-ecosystem-impact combinations with a high probability of initiating changes in ecosystem feedbacks and to show the direction of change (Direction) – that is, whether response was negative (e.g. decrease in species richness) or positive (e.g. increase in soil nutrients).

Species-ecosystem-impact combination	n	Direction	μ (ln|ESR|)	SD (ln|ESR|)	P (|ESR| < 1)	P ($\mu = \mu_p$)
grassforestsfire	7	−	−1.651	0.950	0.063	0.340
grassforestsnutrients	6	−	−1.260	0.838	0.092	0.800
grassforestsplantcomp	9	−	−2.054	1.068	0.043	0.053
grassgrasslandsbiota	17	+	−2.233	2.123	0.154	0.002
grassgrasslandslitter	19	+	−1.339	0.832	0.062	0.470
grassgrasslandsplantcomp	25	+	−0.248	1.030	0.406	0.004
grassgrasslandsseed	9	−	−0.241	0.522	0.328	0.094
grassriparianplantcomp	4	−	−2.793	2.869	0.193	0.035
grassshrublandsfaunacomp	1	−	0.496	0.000	NA	0.305
grasswetlandsnutrients	7	+	0.339	1.380	0.407	0.013
herbagricultureplantcomp	2	−	−1.120	0.146	0.008	0.976
herbgrasslandsbiota	3	+	−0.484	1.108	0.346	0.503
herbwetlandsbiota	1	+	−1.110	0.000	NA	0.995
herbwetlandsfaunacomp	3	−	−1.377	0.927	0.117	0.744
herbwetlandslitter	9	−	−1.435	0.810	0.055	0.510
herbwetlandsnutrients	11	+	−0.282	0.687	0.345	0.080
herbwetlandsplantcomp	9	−	−0.035	0.709	0.481	0.042
shrubagricultureplantcomp	1	−	−0.972	0.000	NA	0.947
shrubforestsnutrients	5	−	−0.547	0.565	0.189	0.416
shrubforestsplantcomp	4	−	−0.554	1.167	0.330	0.483
shrubshrublandsfaunacomp	1	+	0.172	0.000	NA	0.421
treeforestslitter	2	+	−1.692	3.154	0.323	0.574
treeforestsnutrients	39	−	−1.352	2.204	0.272	0.259
treeforestsplantcomp	7	−	−1.197	1.325	0.198	0.858
treegrasslandsfire	1	−	0.191	0.000	NA	0.405
treeriparianplantcomp	2	+	−0.845	0.059	0.002	0.818
treewetlandsplantcomp	2	−	−0.086	0.011	0.008	0.352

'n' indicates the number of cases for each combination, μ (ln\|ESR\|) is the mean of the logarithmic of the absolute ESR followed by standard deviation. P(\|ESR\| < 1) is the P value for the one-tail t-test against ln(1) (= 0) on whether the absolute ESR is less than 1. P < 0.05 means significantly less than 1, that is, dampened feedbacks. P > 0.05 means the species-ecosystem combination could indicate an amplified feedback. NA stands for n = 1. P ($\mu = \mu_p$) is the P value for the two-tail t-test on whether the mean of the logarithmic of absolute ESR is different from expected from the permutation test with 5000 runs.

riparian ecosystems and wetlands that lead to alterations in plant community composition (Table 1).

Feedbacks associated with regime shifts

Our review on ecosystem changes that could be interpreted as ecological regime shifts revealed that of the 75 species that have been identified as causing changes in ecosystem feedbacks, 20 species have been described as initiating ecosystem changes that can be interpreted as regime shifts (Table 2). For the 20 species that have been documented to cause regime shifts, the most commonly recorded feedback processes associated with invasion were the nutrient feedback (nine species), seed production feedback (8) and the fire feedback (6). The soil biota feedback was recorded for four species and the litter feedback for three species. Half of the species (11) were associated with only one feedback mechanism, while eight were associated with two feedback mechanisms, and only one species with three feedback mechanisms (see Appendix S3). Based on a comparison of the feedbacks associated with the 20 species that have been documented to cause regime shifts and the 55 species that have not, we found that the presence of the seed feedback has a 80% probability of being associated with a regime shift, the fire feedback and the nutrient feedback a 43% probability, the litter feedback a 38% probability and the biota feedback a 21% probability of being associated with a regime shift (see Fig. A in Appendix S3).

DISCUSSION

We have proposed an approach for identifying high-impact plant invaders that should be prioritized for management. The approach focuses on identifying species that pose a high risk of introducing or modifying ecosystem feedbacks in ways that may lead to regime shifts – fundamental changes of ecosystem structure and feedbacks, with long-lasting effects on native biodiversity and ecosystem services. We summarize our findings in an operational framework based on a descriptive analysis of the literature and a meta-analysis of selected studies (Fig. 4). This can be used to prioritize management interventions and could be integrated into widely used screening tools.

Table 2 Species for which regime shifts have been recorded in the literature. Two aquatic species not listed in Appendix S3 (*Pistia stratiotes* and *Salvinia molesta*) are included here because they have been mentioned explicitly in the literature as causing regime shifts (Scheffer *et al.*, 2001). References are given in Appendix S3.

Species	Growth form	Pre-invasion regime	Post-invasion regime
Acacia cyclops	Tree	Diverse shrubland (fynbos)	Tree monocultures
Acacia longifolia	Tree	Diverse shrubland (fynbos)	Tree monocultures
Acacia saligna	Tree	Diverse shrubland (fynbos)	Tree monocultures
Ageratina adenophora	Herbaceous perennial	Diverse understorey native forests	Forest with monospecific understorey
Agropyron cristatum	Grass	Sagebrush	Grasslands
Andropogon gayanus	Grass	Savanna	Grasslands (reduced tree cover)
Carpobrotus edulis	Succulent	Diverse shrubland (maritime chaparral)	Succulent- and shrub-dominated vegetation
Cenchrus ciliaris	Grass	Woodlands	Grasslands
Chromolaena odorata	Shrub	Savanna/grassland	Thicket
Chrysanthemoides monilifera	Shrub	Dunelands	Shrublands monocultures
Cinchona pubescens	Tree	Tree-less vegetation communities (Miconia and Fern-Sedge Zone)	Vegetation community dominated quinine tree
Fallopia japonica	Herbaceous perennial	Diverse understorey native forests	Forest with monospecific understorey
Heracleum mantegazzianum	Herbaceous perennial	Riparian, grassland, forest edges, disturbed sites	Monocultures
Lantana camara	Shrub	Savanna/grassland	Thicket
Melaleuca quinquenervia	Tree	Grasslands	Forests
Mesembryanthemum crystallinum	Succulent	Grassland	Monocultures
Morella faya	Tree	Diverse forests with understorey	Monospecific forests with no understorey
Phalaris arundinacea	Grass	Wetlands with low litter	Wetlands with high litter
Pinus radiata	Tree	Shrublands	Forests
Pistia stratiotes	Aquatic	Open waterbodies	Floating plant dominance
Salvinia molesta	Aquatic	Open waterbodies	Floating plant dominance
Schinus terebinthifolius	Tree	Fire-dependent pine savanna ecosystem	*Schinus terebinthifolius* dominated forest
Spartina alternifolia	Grass	Unvegetated mudflats	Meadow-like monocultures

That the systems analysis and the quantitative meta-analysis approach give slightly different results can be ascribed to the lack of quantitative studies on feedback changes due to biological invasions. Although some feedback changes, especially plant–soil feedbacks, have been investigated quantitatively, others, notably those relating to altered fire regimes, have so far been presented mainly as descriptive studies. There is clearly a need for quantitative studies on tree invasions in shrublands.

Despite such differences, the combined results clearly indicate that grass invaders in forest that change fire regimes, grass, shrub and tree invaders in forests and herbaceous species in wetlands that influence soil-nutrient cycling and litter quantity and decomposition rates and grass invaders and herbaceous species in grasslands that lead to alterations in soil microbial communities as well as tree invaders in forests that lead to changes in litter quantity and decomposition rates are likely to significantly affect ecosystem feedbacks and should therefore be prioritized for management (Fig. 4).

Although plant–soil feedbacks have been investigated comprehensively for particular invasive species in some ecosystems (e.g. Ehrenfeld, 2003; van der Putten et al.,

2013), this is the first time that the effects have been related to combinations of plant growth forms and ecosystems, thereby providing the means for objective management prioritization.

The main difference in the results of our two approaches is that the ecosystem effect 'changes in plant community composition' has not been a focus in the results of the descriptive analysis but features in the results of the meta-analysis, although more often as dampened response (i.e. suggesting a negative feedback) than as amplified response (i.e. suggesting a positive feedback). The prevalence of plant community composition as invader effect shows that plant invasions can indeed have significant impacts on native species richness (Gaertner et al., 2009). This result should, however, be interpreted with caution as it could simply mean that plant community composition is easier to measure quantitatively than, for example, changes in the fire regime. This would also explain why 'changes in fire regime' is only included once in the results of the meta-analysis as an ecosystem effect potentially leading to feedback changes, despite the fact that it features prominently in the descriptive study and has been shown to be one of the most dramatic ways in which invasive plants alter ecosystems (D'Antonio et al., 2000; Brooks et al., 2004). The high prevalence of the ecosystem effect 'changes in plant community composition' in the meta-analysis might be indicative of changes in other underlying ecosystem processes and might therefore act as an 'early warning' of approaching thresholds, similar to changes in the patchiness of vegetation in semi-arid rangelands (Rietkerk et al., 2004) or the statistical behaviour of a system such as increasing variance (Scheffer et al., 2012).

As more data and information become available, our approach can be iteratively refined and strengthened. Our study raises the question of what data should be collected when we study plant invasions. Once important feedback mechanisms are identified or proposed, it is critical to develop experimental tests to measure both the strength of the feedback and the response of the ecosystem. Without such data, studies of plant invasions will continue to be largely descriptive rather than prescriptive.

Determining the importance of feedback mechanisms requires some a priori knowledge of the factors that can drive ecosystem change. However, in many cases, this is unknown by ecologists or land managers. What is missing is a way of integrating this knowledge into a synthetic understanding of these feedback effects on ecosystems. One important but underused tool in invasion biology is the use of simple theoretical models to guide experimental studies (Eppinga et al., 2011). Such models allow us to determine when the proposed feedback mechanisms are large enough to cause critical transitions; follow-up experimental work can focus on determining whether a feedback mechanism of sufficient magnitude is likely to be achieved under different environmental conditions (see Eppinga & Molofsky, 2013 for an example). Even without such a modelling framework, we can assume that there is a relationship between the probability of a species causing a

Systems-analysis

	wetlands	riparian	grasslands	shrublands	forests
tree				N,F	**N,B,L**
shrub					**N**
grass			**B**,N,F		**N,F**
herb	**N,L**		**B**,N		N,B,L

Meta-analysis

	wetlands	riparian	grasslands	shrublands	forests
tree				*	**N**,P,**L**
shrub					**N**,P
grass	N	P	**B**,L,P,S		**N,F**
herb	**N,L**,A,R		**B**		

Figure 4 Key for identifying high-impact plant invaders that should be prioritized for management based on assessments, using both systems analysis and meta-analysis approaches, of 443 studies dealing with impacts of invasive species on ecosystems. Only growth forms and ecosystems that were been identified in both approaches are presented. Effects on the native ecosystem are: 'N' – changes in soil-nutrient cycling; 'B'– alterations in structure and functioning of soil microbial communities; 'S' – alterations of soil seed banks; 'F' – changes in fire regimes; 'L' – changes in litter quantity, quality or decomposition rates; and 'P' – changes in plant community composition.

change to one or more reinforcing feedback processes and the probability of a regime shift. Despite the substantive lack of studies on regime-shift phenomena related to invasive plants, we found that 20 of 75 of the species have been described as initiating ecosystem changes that can be interpreted as regime shifts. It is not always possible to determine whether an invasion has caused a regime shift until its impact becomes very difficult to manage or reverse. However, we suspect that if more studies were conducted focusing specifically on regime shifts, we will gain better understanding of the underlying processes.

Our study has highlighted the dearth of studies of plant invasions that have investigated and synthesized feedback mechanisms underlying alternative ecosystem states. We hope that this will stimulate further research in this area which is crucial for justifying and prioritizing effective and defendable management interventions. Knowing whether and in which context an invader has the capacity to cause regime shifts is important for determining whether management interventions are justified, feasible and desirable. Some invaders might affect certain ecosystem processes without ever establishing feedback loops that could transform ecosystems. Control of these species will be comparatively easy as, in most cases, the ecosystem should be able to 'self-repair' – to recover unaided once the invader has been removed (Gaertner *et al.*, 2012). However, invasions that push ecosystems beyond structural and functional thresholds will create multiple barriers to restoration. In such cases, restoration will require major management input or may even be futile (Richardson & Gaertner, 2013). The results of our study can further be used to identify species about which little may be known, but which may be at high risk of causing changes in feedback loops and hence causing regime shifts. It is important to acknowledge that the impacts of invasive species are strongly context-dependent and can have substantially different outcomes, depending on the type of invader and the invaded habitat. We therefore identified species-ecosystem combinations most likely to result in changes in feedback mechanisms and hence in regime shifts. By identifying these species-ecosystem combinations, we offer a tool for defining the risk of impact that can easily be integrated into widely used screening tools. For example, the widely used Australian Weed Risk Assessment (WRA) system asks only general questions to determine whether the taxon under assessment is known to, or has the potential to alter the composition, structure, or normal processes or function of a natural ecosystem (Gordon *et al.*, 2010; Kumschick & Richardson, 2013). Our results provide insights for more focused questions to improve the accuracy of such assessments.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Theoretical background on regime shifts.

Appendix S2 Dataset used for the analysis of studies on 173 plant invaders that have effects on native ecosystems.

Appendix S3 Descriptive analysis.

Appendix S4 Summary of meta-analysis results.

BIOSKETCH

Mirijam Gaertner's research at the Centre for Invasion Biology (http://academic.sun.ac.za/cib/) focuses on the effects of plant invasion on vegetation communities and ecosystems, and on ecosystem restoration.

Author contributions: M.G., R.B., M.T.B. and D.M.R. conceived the study. M.G. collected and analysed data, wrote the first draft and coordinated revisions. R.B. provided insights on regime shift concepts and contributed to the data analysis. M.T.B. assisted with data collection and contributed to the study design. C.H assisted with data capture and the meta-analysis and was involved in the study design. All authors contributed to writing.

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