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EDITOR'S PERSPECTIVE

Beyond control: wider implications for the management of biological invasions

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Summary

1. Government departments, environmental managers and conservationists are all facing escalating pressure to address and resolve a diversity of invasive alien species (IAS) problems. Yet much research to date is primarily concerned with quantifying the scale of the problem rather than delivering robust solutions and has not adequately addressed all stages of the invasion process, and only a few studies embrace the ecosystem approach.
2. Three successive steps, prevention, eradication and control, form the cornerstones of recommended best practices aimed at managing IAS. The goal of such actions is the restoration of ecosystems to preserve or re-establish native biodiversity and functions.
3. Prevention is widely promoted as being a more environmentally desirable strategy than actions undertaken after IAS establishment, yet is hindered by the difficulty in separating invasive from non-invasive alien species. Furthermore, the high number of candidate IAS, the investment required in taxonomic support and inspection capacity, and the expense of individual risk assessments may act against the net benefits of prevention. More rewarding avenues may be found by pursuing neural networks to predict the potential composition of pest assemblages in different regions and/or model introduction pathways to identify likely invasion hubs.
4. Rapid response should be consequent on early detection but, when IAS are rare, detection rates are compromised by low occurrence and limited power to discern significant changes in abundance. Power could be increased by developing composite indicators that track trends in a suite of IAS with similar life histories, shared pathways and/or habitat preferences.
5. The assessment of management options will benefit from an ecosystem perspective that considers the manipulation of native competitors, consumers and mutualists, and reviews existing management practices as well as mitigates other environmental pressures. The ease with which an IAS can be targeted should not only address the direct management effects on population dynamics but also indirect effects on community diversity and structure. Where the goal is to safeguard native biodiversity, such activities should take into account the need to re-establish native species and/or restore ecosystem function in the previously affected area.
6. *Synthesis and applications*. A comprehensive approach to IAS management should include consideration of the: (i) expected impacts; (ii) technical options available; (iii) ease with which the species can be targeted; (iv) risks associated with management; (v) likelihood of success; and (vi) extent of public concern and stakeholder interest. For each of these issues, in addition to targeting an individual species, the management of biological invasions must also incorporate an appreciation of other environmental pressures, the importance of landscape structure, and the role of existing management activities and restoration efforts.

Key-words: alien, dispersal, ecosystem approach, eradication, exotic, invasive, landscape, pest, prevention, weed

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Introduction

The introduction and transfer of invasive alien species (IAS) among continents, regions and nations has often had significant impacts on the recipient aquatic and terrestrial ecosystems. As evidence of the scale of the problem mounts, policymakers and stakeholders are increasingly being made aware of the threats posed by biological invasions to human health, economic output, ecosystem services and biodiversity (Millennium Ecosystem Assessment 2005). The issue is enshrined within the Convention on Biological Diversity (CBD) in which 'each Contracting Party shall, as far as possible and appropriate, prevent the introduction of, control or eradicate those alien species which threaten ecosystems, habitats or species' (Secretariat to the Convention on Biological Diversity 2001). As a result, government departments, non-governmental organizations (NGO), extension services, environmental managers and conservationists are all facing escalating pressure to address and resolve a diversity of IAS problems. As awareness of the consequences of biological invasions has increased, so ecological journals have seen an order of magnitude rise in the number of scientific publications on this topic (Puth & Post 2005). Yet the extent to which invasion research informs invasive species management remains unclear. This special profile issue of *Journal of Applied Ecology* brings together ten papers that encompass a range of perspectives at the interface between invasion and environmental management, including the optimization of prevention and control strategies, assessments of impacts, unintended negative consequences of restoration efforts and the conflicts that may arise in IAS management. These papers provide an opportunity to synthesize existing knowledge on the applied aspects of invasion ecology, largely drawn from four decades of publications in the *Journal of Applied Ecology*, that illustrate IAS management issues in terrestrial, freshwater and marine ecosystems from across the globe. The synthesis emphasizes that the application of ecological knowledge to manage (rather than describe) biological invasions probably represents one of the most powerful valedictions for the current investment of public funds in ecological research.

What are the management options available to tackle biological invasions? The CBD proposes three successive steps in IAS management: prevention, eradication and, if neither of the other steps is possible, control (Secretariat to the Convention on Biological Diversity 2001). The ultimate goal of such actions should be the conservation or restoration of ecosystems to preserve or re-establish native biodiversity and functions. These successive steps form the cornerstones of recommended best prevention and management practices aimed at targeting IAS (Wittenberg & Cock 2001). Management responses mirror the sequential stages in the invasion process: introduction, establishment, spread and impact (Fig. 1). Prioritization of actions undertaken earlier in the sequence is recommended as this should prove the most cost-effective strategy. There is therefore a clear connection between increased understanding of the invasion process and the transfer of this knowledge to support effective management strategies. However, at least three factors currently limit the linkages between pure and applied invasion ecology. First, although sustainable answers are being found, much research to date is primarily concerned with quantifying the scale and scope of the problems rather than delivering robust solutions (Hulme 2003). Secondly, even where research is applied it has not adequately addressed all stages of the invasion process, in particular initial dispersal (Puth & Post 2005), and this limits the scope of management, particularly related to rapid response. Thirdly, most studies focus on individual species' perspectives and only a minority embrace the ecosystem approach that integrates interactions between IAS and other species, ecosystem processes, landscape structure and anthropogenic inputs (including existing management practices).

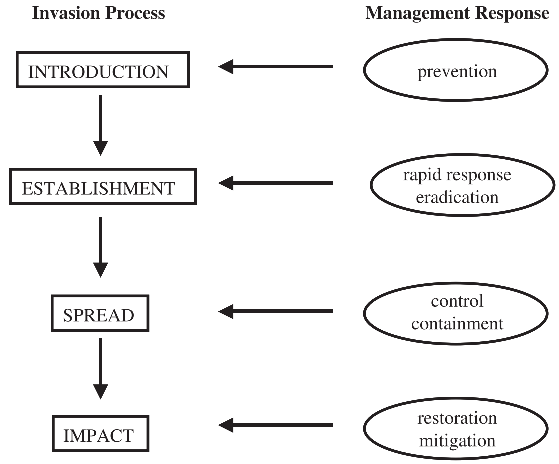

Fig. 1. Relationships between the core aspect of biological invasions and the targeting of management actions. There are clear parallels between the detailed understanding of the biological invasion process and the development of intervention strategies.

Prevention: when is it better than a cure?

Border controls and quarantine measures are often the first opportunity to respond to IAS incursions. The prevention of IAS introductions into and also within a region is widely promoted as being a far more cost-effective and environmentally desirable strategy than actions undertaken after IAS establishment (Leung *et al.* 2002). The approach to prevention is primarily one of risk assessment and requires information about the hazard (e.g. what particular IAS pose a threat) and its likelihood (e.g. probability of entry and establishment). Considerable effort has been expended in attempts to identify the characteristics that separate invasive from non-invasive alien species. However, the lack of success in both characterizing invasive species and predicting which will have negative impacts highlights the individual and unpredictable nature of invasions (Manchester &

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Bullock 2000; Hulme 2003). Another approach has been to use climate-matching algorithms to predict the likelihood and extent of IAS establishment in a new region, using knowledge of the environmental constraints in its native range (Kriticos *et al*. 2003). Where species distribution data are available in the native range and/or other invaded ranges, these tools can provide efficient first-step screening (Thuiller *et al*. 2005). However, numerous distribution-modelling techniques exist, for example classification trees, neural networks, genetic algorithms, etc. and model performance varies with the taxon, geographical region and environmental drivers assessed (Segurado & Araújo 2004). Thus caution must be applied when interpreting predictions based on climate matching alone (Hulme 2003).

An alternative to individual species approaches is to model entire IAS assemblages under the assumption that these are likely to be non-random species groupings that contain hidden predictive information. Under this assumption, Worner & Gevrey (2006) employed a self-organizing map (SOM), an artificial neural network algorithm, to analyse 844 insect pest species recorded in more than 459 geographical regions world-wide. The SOM analysis allowed each species to be ranked in terms of its risk of invasion in each area based on the strength of its association with the assemblage that was characteristic for each geographical region. Such information can undoubtedly assist with the identification and prioritization of species that have the potential to pose an invasive threat in regions where they are not normally found. By grouping countries with similar pest assemblages, the SOM may help quarantine officers identify countries for which trade and transport links require greater scrutiny. The approach can also inform response actions when pests are intercepted. For example, in 2002 the melon thrip *Thrips palmi* attracted attention as a possible invasive species to New Zealand and significant resources were invested in assessing the risk of establishment, yet the SOM analysis indicated that this species was not strongly associated with the New Zealand assemblage and, to date, it has not established in the country (Worner & Gevrey 2006). The advantage of this approach is that it integrates species and biogeographical information in a single analysis, uses widely available data on species presence–absence rather than less-accessible climate and species trait information, and can be used at regional (Céréghino *et al*. 2005) and global scales.

Independently of how well matched a species is to the recipient environment, invasion will not occur if IAS fail to be intentionally or unintentionally introduced into a region. By definition, humans are the primary vectors of IAS introductions and addressing the pathways of entry is a key step in early detection measures and risk analysis. The IAS traits underpinning invasion success may have as much to do with the pathway of entry as to species demography. Vascular plants may be introduced through a variety of mechanisms but the most common are as soil contaminants and garden discards. Species associated with soil contaminants depend essentially on soil movement, and are often small and fast-growing species that produce numerous, small, persistent seeds. In contrast, garden discards tend to be tall, spreading perennials with transient seed banks, attributes that are almost the exact opposite of the soil-borne group (Hodkinson & Thompson 1997). Attempting to discern a single suite of traits that can explain the risk posed by both groups is therefore often futile (Lloret *et al*. 2005). Under such circumstances it may prove more efficient to manage the pathway than the individual species. One approach is to consider invasion pathways as networks between IAS sources and their eventual destinations, connected to one another by human dispersal vectors, and to use knowledge of these links to target management actions. Surveys of boat movements from lakes invaded by an alien spiny waterflea *Bythotrephes longimanus* to other lakes in Ontario, Canada, were used to parameterize network models describing the cumulative number of invaded and non-invaded destinations (Muirhead & Macisaac 2005). These networks indicated that only a small proportion of sources function as hubs and that management efforts targeted to remove developing hubs from the invasion network, rather than equal effort applied to outward-bound boat traffic from all sources, may reduce the predicted rate of new invasions.

Traditional risk assessment methods applied in the screening of commercial imports are valuable when intercepting known IAS pests of agriculture or vectors of disease, as well as in cases where deliberate species introductions are proposed (e.g. biocontrol agents). However, for unintentional introductions of IAS that may harm semi-natural ecosystems the challenge is much greater, given the significantly higher number of taxa that would require screening and the additional uncertainty of probable impacts. Although often promoted as the most cost-effective option (Wittenberg & Cock 2001; Leung *et al*. 2002), the potentially high number of candidate IAS, the investment required in taxonomic support and inspection capacity, the expense of individual IAS risk assessments, as well as the cost of false positives (Smith, Lonsdale & Fortune 1999), may act against the net benefits of preventative IAS screening. The need to build and support an appropriate institutional capacity to deal with preventative measures may be a major limit to IAS management in developing countries. These issues have led to considerable debate regarding the value of generating IAS 'blacklists' because such lists can become too broad, and thus unwieldy, require regular revision and can give a false sense of security when introducing unlisted species (Wittenberg & Cock 2001). Whitelists of acceptable species need to be stringent but are often too short to be useful, leaving most species on intermediate 'greylists' for which further research is recommended, and thus this listing provides little management value. In this context, species-centred approaches may require revision, and modelling either the network of species assemblages or their pathways of introduction will prove a valuable way forward.

Nevertheless, even where the tools are appropriate and available, implementation of prevention measures requires action through voluntary codes of practice.

Early detection and rapid response

No matter how effective the existing prevention or screening approaches, there will always be the chance that one or more IAS will slip through to become established. Once established, even if impacts have not been quantified, the precautionary principle encourages action to be taken to eradicate potentially harmful IAS as soon as they are detected (Wittenberg & Cock 2001). In principle this should be straightforward but, in practice, for all but economic pests and vectors of disease, rapid response is often surprisingly sluggish. The limitation partly reflects the constraints identified with knowing which species to target and the problems of blacklisting, but an additional issue is the difficulty of detecting rare events.

Rapid response should be consequent on early detection of the first occurrence of a harmful IAS within a region and/or a marked change in their abundance or distribution. A key problem is that when IAS are rare, detection rates are compromised by low occurrence and limited power to discern significant changes in abundance. Thus vigilance is often focused at the sites of likely entry (e.g. ports and airports), where the probability of interception is expected to be highest. The intensity and efficacy of inspection at sources of entry tends to be variable. In many cases sampling protocols are rarely implemented in a consistent and statistically designed manner, data underestimate incursions because only the IAS occurrence rather than number of individuals is recorded, negative results are not usually reported, and only data on 'reportable' IAS are collated (NRC 2002). The situation is partly a result of limited funding but also reflects the terms of reference that were developed to serve plant and animal health control rather than protection of the natural environment. Nevertheless, an assessment of inspection protocols and the scope to extend them to cover a wider range of IAS threats would help provide guidance for future interception strategies at ports of entry.

Improvements in remote sensing, such as hyperspectral imagery at 2-m spatial resolution, may play an important role in large-scale surveys of relatively visible, recognizable and immobile IAS, for example clonal patch-forming plants (Lass *et al*. 2005). Aerial photography can even be used to detect individuals as well as the population structure of certain plants (Mullerova *et al*. 2005). Yet for cryptic, small, scattered or highly mobile species, remote sensing may have limitations and the only option is ground-based field surveys. Guidance does exist regarding the design, sample size and frequency of surveys aiming to estimate the occurrence of species established in the wider environment (Mackenzie & Royle 2005). As a general rule, the optimum strategy for rare species is to conduct fewer surveys at more sites. Unfortunately, even well-established monitoring schemes sample too few sites to have sufficient power to determine the significance of changes in distribution and abundance of rare species (Van Strien *et al*. 1997). Stratified sampling designs targeting specific habitats may be more efficient but become less feasible when IAS are habitat generalists or if a fixed survey design is adopted to detect a wide range of IAS. It is likely, however, that increasing the power of surveys to detect rare IAS incursions, or establishing new monitoring programmes where none previously existed, will require additional funding, and this cost is rarely considered when promoting early detection strategies. The mobilization of volunteers and 'citizen science' initiatives may provide a less costly approach but savings would need to be balanced against biases in reporting, misidentification and variable survey effort (Lepczyk 2005). While volunteer surveys may usefully contribute to more systematic monitoring programmes, they cannot replace them. In addition, citizen science may be better mobilized to address specific IAS rather than as a watchdog for all new incursions. Rather than respond to rare incursions, action could be mobilized at a higher abundance threshold, where the power of detection is increased and existing survey schemes might prove valuable. As the power of detection (number of detected incursions) increases so would the subsequent cost of eradication. However, a larger species distribution data set would strengthen the likelihood of correctly predicting occurrence in unsampled sites and inform response strategies (Engler, Guisan & Rechsteiner 2004). Balancing these conflicting aspects should be at the core of any rapid response strategy and would determine its viability. An alternative approach to improve the power of IAS surveys might be to use composite indicators rather than individual species (Maxwell & Jennings 2005). Power could be increased by developing a composite indicator that tracks trends in the relative abundance of a suite of IAS with similar life histories, shared pathways and/or habitat preferences. The indicator would help provide guidance on the probable trend in rare IAS abundance and enable informed decisions to be made regarding action. An index based on IAS pathway similarities might highlight changes in the frequency or scale of specific commercial or recreational activities, for example live marine species trade. Furthermore, the occurrence of one IAS may be indicative of incursions by other species in the same or similar sites, and thus composite indices may help target follow-up surveys. The response might target the entire guild of species forming the composite index, selected species or another attribute of the index, for instance the common pathway. Clearly, defining criteria and species weighting for such a composite index would require detailed consideration but may hold more promise than single-species surveys when individual IAS are too rare to be reliably surveyed.

Once early detection occurs, resources need to be mobilized to eradicate the IAS incursion. In the case of the invasive marine alga *Caulerpa taxifolia* field containment and eradication treatments were implemented only 17 days after discovery in the coastal waters of California in 2000 (Anderson 2005). In contrast, the species was discovered in the Mediterranean Sea in 1984, warnings were first sounded in 1989 and over the next decade it had colonized more than 100 km^2 of benthos (Meinesz 1999). These two contrasting scenarios illustrate the importance of prior experience, rapid confirmation of species identity and risk, as well as a consensus among stakeholders to follow a particular management strategy. Furthermore, an effective response system requires: (i) a sound scientific basis upon which to plan actions, (ii) the tools and protocols with which to respond and (iii) the capacity as well as resources to achieve its goals. Thus, while there are several examples of effective rapid response actions (Myers *et al*. 2000), it is uncommon to find all three components supported in IAS initiatives. While applied ecologists may only be able to influence the third component of response indirectly, there is plenty of scope to strengthen the science underpinning response strategies, techniques and tools.

Eradication, containment and control: opportunities or constraints?

The relatively short history of attempts to eradicate or control IAS encompasses impressive successes, dismal failures and considerable controversy (Myers *et al*. 2000). Eradication involves removal of the whole IAS population from a specific area. The larger the area invaded, the harder the task, and thus most examples of successful eradications are from islands or as part of a rapid response when IAS are found in a limited area (Myers *et al*. 2000; Courchamp, Chapuis & Pascal 2003). Containment should limit IAS spread either from an invaded region or alternatively exclude species from an uninvaded area. This strategy works best with species that spread slowly via short-distance movements or for which effective barriers can be established. Unfortunately, most IAS spread relatively fast, involving long-distance dispersal movements, and even the most impressive barriers, such as the 1700-km 'rabbit-proof' fence in Australia, often fail to exclude IAS. The success of both eradication and containment strategies rests on the ability to detect new incursions either at the margin of existing IAS ranges or in new regions, and thus faces the sampling problems identified for rapid responses. Control should aim to bring about the long-term reduction in IAS population size towards an acceptable level. While innumerable IAS control programmes exist, it is not clear what determines the acceptable level (Wittenberg & Cock 2001). Ideally, this should be based on reduced impact but often it reflects available resources.

The three management approaches are not mutually exclusive and it is possible to envisage a co-ordinated programme of IAS control within a region, containment at the edge of its range and eradication of outlying populations. Alternatively, containment may act as a holding response during which decisions are made regarding the costs and benefits of eradication, control or no management. However, it is also tempting to see eradication, containment and control as three successive steps down the slippery slope towards management failure: if an IAS cannot be eradicated, it should at least be contained, if not contained at least controlled, and if not controlled then managers must learn to adapt to or mitigate any harmful impacts. To avoid this scenario, future management strategies require a wider perspective that not only includes species management but also incorporates the implications of ecosystem processes, external environmental drivers, the landscape and the impact of existing management activities on IAS.

Managing the species: maximizing the benefits of bullets, burning and biocontrol

A diversity of tools exists that can be applied to manage IAS: poisons, pesticides, herbicides, snares, traps, culling, burning, cutting, mowing, biocontrol, etc., but they all generally come down to the same basic principle of removing (usually killing) the target organism. While chemical vendors and gunsmiths undoubtedly have their own recommendations, ecological advice to managers often arises from the results of model simulations. The key facts required from models are under what circumstances, at what cost and over what time scale a particular management technique will succeed. For example, the forecast mean time to cull the UK ruddy duck *Oxyura jamaicensis* population of approximately 6000 wintering birds by 97% was between 3 and 5 years, with 14 or 15 control officers reducing the population by between 65% and 70% per year (Smith, Henderson & Robertson 2005). Similarly, annually spraying 15% of the populations of the alien riparian weeds Himalayan balsam *Impatiens glandulifera* and giant hogweed *Heracleum mantegazzianum* could, assuming 100% herbicide treatment efficiency, eradicate the former from a catchment in 20 years but never succeed in the case of the latter species (Wadsworth *et al*. 2000).

The aim of classical biological control is generally not to eradicate the target species but to reduce IAS populations sufficiently over a large enough area that they no longer pose a significant problem. For weed biocontrol, models usually identify the level of damage necessary to reduce plant recruitment down to an acceptable level (Rees & Paynter 1997; Sheppard *et al*. 2002; Buckley, Briese & Rees 2003; Jongejans, Sheppard & Shea 2006; Shea, Sheppard & Woodburn 2006). These studies reveal that the impact of biocontrol agents often needs to be high to have a significant effect on the target population, and success can be habitat-dependent, providing scope for IAS refuges and hence less-effective control. Such constraints limit the value of biocontrol and, on average, only one-third of attempts are fully successful. This unfortunate statistic has spurred the

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development of integrated management, where several complimentary measures are applied. The range of management options can be daunting (herbicide, cutting, burning, etc.) and decisions may be assisted by models that not only identify what treatments to apply, but also in what combination and when (Buckley *et al*. 2004; Shea, Sheppard & Woodburn 2006).

The relatively high failure rate in biocontrol may result from an insufficient understanding of the role of natural enemies in plant population regulation, particularly the extent to which individual level impacts can be scaled-up to population responses and the relative importance of density-dependence in population regulation (Halpern & Underwood 2006). These authors highlight that, to be successful, models of biocontrol impacts on plants should examine the plant population dynamics in the presence and absence of natural enemies and identify whether: (i) the transitions that contribute most to plant population regulation change in the presence of herbivores; (ii) herbivores affect the strength of density dependence in a plant population; and (iii) herbivores change a plant population's equilibrium density. These issues are neither empirically or theoretically easy to answer and require both the development of relatively complex models and experimental rather than observational field studies. However, given that biocontrol may be one of the few options available for large-scale IAS control and the regulatory hurdles biocontrol must overcome before a deliberate release, any approach that can improve performance should be welcomed.

Strategic models that identify the optimum manner in which to deploy limited resources available for management can often generate valuable rules of thumb. One of the earliest such rules of thumb emphasized the importance of targeting small, isolated 'satellites' rather than a larger core IAS population because many satellites will contribute proportionally more to population expansion in a homogeneous environment (Moody & Mack 1988). In contrast to this population dynamic perspective, metapopulation approaches highlight that core populations should be targeted where they act as significant sources for the establishment of new satellites (Wadsworth *et al*. 2000; Hulme 2003). These two different perspectives were parameterized for cordgrass *Spartina alterniflora* invading intertidal mudflats (Taylor & Hastings 2004). For this system, the most effective strategy was to remove a large fraction of the invaded area every year, starting with the main core invasion, but it was also the most risky strategy as it would be dependent upon significant resources being made available. When annual resources are lower, control is only possible if priority is given to the management of satellites. A similar set of issues arises in biocontrol with regard to whether a few large releases of natural enemies are more effective than several small releases. Using a stochastic dynamic programming approach, Shea & Possingham (2000) propose that, when there are few well-established sites of invasion, making a few large releases of natural enemies is the optimal strategy. As the number of invaded sites increases, so the optimum strategy changes from a mixed strategy (a variety of release sizes) to many small releases as the probability of establishment of biocontrol agents from smaller inocula increases.

Managing the environmental drivers: should managers be perturbed by disturbance?

Although targeting management efforts against the specific IAS makes sense, in many cases invaders are opportunists that take advantage of environmental mismanagement and degradation. Under such circumstances, efforts to manage IAS may be repeatedly frustrated while the underlying environmental problems remain unresolved. A central tenet in invasion ecology is that ecosystem disturbance facilitates the establishment and spread of IAS (Hobbs & Huenneke 1992). There is no single, universal definition of disturbance adopted in ecology, although one of the most widely cited is 'any relatively discrete event in time that disrupts ecosystem, community or population structure and changes resource, substrate availability, or the physical environment' (Pickett & White 1989). Such a broad definition raises several difficulties. First, biological invasions could themselves be classed as a disturbance, and this results in a certain amount of circularity in one of the central tenets in the field. Secondly, the complexity of the underlying processes that occur under the umbrella term 'disturbance' suggests that, unless explicitly defined, statements such as 'increased disturbance facilitates invasion' do not further our ecological understanding significantly. For instance, suburban development (disturbance) increased the incursion of IAS into Atlantic white cedar *Chamaecyparis thyoides* wetlands in the New Jersey Pinelands (Ehrenfeld & Schneider 1991). Yet the actual mechanism of invasion could be through alterations of surface and groundwater chemistry, changes in the level of the water table, creation of new habitat or physical damage arising from construction associated with suburbanization. But which of these drivers is the primary cause of the invasion?

Enrichment by nitrate from run-off is thought to contribute to the increasing colonization and dominance of IAS in wetlands because the growth of these species responds to a greater extent to nutrient addition than co-occurring natives, and as a result the latter are displaced (Green & Galatowitsch 2002; Rickey & Anderson 2004). Both reduced water-level fluctuations (Van Geest *et al*. 2005) and increased physical damage, such as construction, heavy-vehicle activity and soil excavation (Stylinski & Allen 1999), can on their own lead to IAS dominance. As well as destroying or transforming ecosystems, construction can also create new habitats that, by changing 'substrate availability, or the physical environment', can be viewed as disturbance. The increasing transformation of coastlines via the construction of breakwaters, jetties, seawalls, floating pontoons and pier pilings has created novel hard substrata habitats in coastal ecosystems. Such artificial structures can provide suitable habitats for marine IAS and function as corridors for their expansion (Bulleri & Airoldi 2005). A further complication is that certain types of 'disturbance', particularly soil perturbation, may be important for native species and it may be difficult to develop management strategies that preserve the diversity of disturbance-dependent natives while still excluding IAS (Kotanen 1997). These examples illustrate the opportunistic nature of many IAS and highlight why the precise components of disturbance need to be dissected apart in order to understand the drivers of invasion as well as identify the appropriate options available for mitigation.

A good example of this approach is provided by Stokes & Cunningham (2006) in their study of willows *Salix* spp. invading riparian ecosystems in south-east Australia. Riparian environments are frequently invaded by non-native plants and this is often attributed to the frequent disturbance arising from variable river flows. Stokes & Cunningham (2006) examined two facets of disturbance: the magnitude of the difference in a river's peak and mean flow, and the river's sinuosity that determines the deposition of sediment. Both the flow-based and sinuosity measures significantly influenced the abundance of willows but in opposite ways. Willow abundance was negatively associated with dynamic flows but positively associated with higher channel sinuosity. Thus a simple statement based on the role of disturbance *per se* is inappropriate in this case. Furthermore, the role of 'disturbance' on willow abundance differed considerably between sexual and asexual recruits, being less significant in the former.

Although biological invasions may be assisted by the construction of roads, residential areas, industrial units, sea defences, dams, etc., IAS impacts are likely to form but one component of much greater ecosystem alteration and thus mitigative actions may not target invaders specifically. Although environmental impact assessment (EIA) may provide a mechanism for implementing sustainable development, such assessments often lack scientific rigour and rarely predict or evaluate probable future impacts such as biological invasions (Treweek 1996). Furthermore, EIA is not a requirement in many developing countries. Even in developed nations, a challenge will be to adapt current legislation and EIA procedures to incorporate the potential consequences of development on both IAS abundance and their subsequent impact on ecosystems.

Managing the ecosystem: competition, mutualism and predation

The impacts of IAS remain, for most species, poorly understood, but what is known indicates a considerable diversity of ecosystem-wide interactions (Levine *et al.* 2003). In South Africa, invasion of fynbos by *Acacia saligna* trees reduces native plant species richness, cover and frequency (Holmes & Cowling 1997), increases nitrogen levels in the normally nutrient-poor soils (Witkowski 1991), the different distribution of tree biomass alters the fuel loads, thus changing subsequent fire regimes (Van Wilgen & Richardson 1985), and the final coup-de-grace (that led to a concerted eradication campaign) is the marked reduction in rainfall run-off, which was predicted to result in significant losses in the water supply to the city of Cape Town (Le Maitre *et al.* 1996). This example, while perhaps not representative of the scale of impacts of most IAS, does illustrate that these species do become integrated within the ecosystems they have invaded and impacts must be viewed in this context. In the case of alien *Acacia* the interactions with other ecosystem processes were clearly negative and removal led to slow but progressive natural restoration of fynbos (Holmes & Cowling 1997), but IAS removal under other circumstances can sometimes lead to undesired (and unexpected) indirect effects (Zavaleta, Hobbs & Mooney 2001). Such indirect ecosystem effects are rarely discernible from correlative assessments of invaded vs. uninvaded sites and often only become apparent following removal. Removing the invasive Himalayan balsam from riparian habitats resulted in an increase in plant species richness, but the most responsive species were other aliens (Hulme & Bremner 2006). Although introduced red foxes *Vulpes vulpes* are thought to have had a significant impact on the populations of endemic bush rats *Rattus fuscipes* in Australia, the rat population did not respond to intensive fox culls, highlighting that fox predation operated as a compensatory rather than additive source of mortality (Banks 1999). In contrast, removal of rabbits *Oryctolagus cuniculus* from Sonoran desert islands led to changes in plant species composition that were expected from a knowledge of grazing preferences, and thus confirmed strong top-down control of the vegetation by introduced alien herbivores (Donlan, Tershy & Col 2002). More complex consequences of interventions are illustrated by saltcedar *Tamarix ramosissima* removal from streams in western USA, which led to increased algal densities and higher abundances of both native and alien herbivores but lower numbers of alien crayfish *Procambarus clarkii*, as a result of reduced litter inputs (Kennedy, Finlay & Hobbie 2005).

As an alternative to species removal, adding native species can lessen the impact of invasions. Species additions not only help restore native species lost from the ecosystem but can also increase the number of competitors, and these may act to reduce IAS population size, recruitment and spread (Bakker & Wilson 2004). An additional mechanism to encourage increased suppression of IAS by native species is through restoring soil nutrient balance. Soils may be exposed to increased levels of anthropogenic nutrient (especially N) input either from agricultural run-off (Rickey & Anderson 2004) or atmospheric deposition (Brooks 2003), and this may encourage IAS establishment by altering the competitive balance with native species. To restore soils markedly affected by N inputs, carbon enrichment, often through the addition of sawdust, wood chips, activated-carbon or sucrose, can significantly lower N availability and result in native species suppressing IAS (Perry, Galatowitsch & Rosen 2004). Not surprisingly, combining seed addition and carbon supplementation is more effective than either treatment on its own (Prober *et al*. 2005). The potential complexity of the interaction between IAS and the recipient ecosystem is illustrated by the study undertaken by Kulmatiski, Beard & Stark (2006). The study examined the distribution of native and exotic plants in abandoned agricultural lands and neighbouring fields that had never been cultivated. By removing plant neighbours, sowing seed (both native and alien), disturbing the soil and applying fungicide, the authors hoped to tease apart the ecosystem processes underpinning the higher abundance of IAS on abandoned agricultural land. Alien species performed better in communities dominated by aliens (abandoned agricultural fields) while natives performed best where they themselves dominated. These patterns did not appear to correlate with differences in soil nutrient availability in the two habitats. While both alien and native species benefited from neighbour removal, only native cover responded to seed additions and only aliens responded to soil disturbance. Fungicide application did not influence native abundance but did reduce alien abundance in abandoned agricultural fields. The authors concluded that abandoned agricultural soils maintain a small but highly beneficial mycorrhizal fungal community that enables alien plants to exploit labile nutrient pools and maintain fast growth rates. This fungal community is missing from non-agricultural soils and, in the absence of soil disturbance, alien species are outcompeted by natives. The implications are that management techniques that target the soil fungal community may be the most appropriate means to deal with IAS in this system and restore the balance in favour of native plant species.

Managing mutualists such as mycorrhiza that are fairly specific to IAS success is more straightforward than cases where mutualists are generalists and provide services to both native and alien species. This appears to be the case in the diffuse mutualism between plants and their frugivores. Buckley *et al*. (2006) reviewed the role of frugivore–plant interactions in facilitating biological invasions. The review highlights a number of areas where management conflicts might arise, such as when native frugivores assist IAS spread as well as the dispersal of native species, or alien dispersers assist the movements and recruitment of native plants. Additionally, although alien fruit may be highly preferred and replace native species in frugivore diets, alien plants may be crucial in supporting threatened frugivore populations. While not an exhaustive description of conflicts between mutualists and the management of IAS, such tensions are probably representative of many plant–animal interactions such as frugivory and pollination. The increasing importation of non-native commercially reared subspecies of bumble bee *Bombus terrestris* to facilitate the pollination of crops has the potential to endanger native bumble bee species through competitive displacement and/or hybridization (Ings, War & Chittka 2006). The non-native species not only exhibit higher reproductive success but their superior foraging ability and large colony size may lead to competitive displacement of natives. Ings *et al*. (2006) recommend a precautionary approach involving rearing of local provenances and appropriate regulation of the use of commercially reared bumble bees. Mutualistic interactions with IAS remain poorly documented and are not well understood, and as a result management strategies have yet to address such conflicts.

Managing the landscape: time for joined-up thinking about corridors

The natural landscape in much of the world has become increasingly fragmented as a consequence of the construction of roads and residential and industrial areas, as well as changes in land use brought about by agriculture. The potential negative consequences of fragmentation are widely acknowledged to the extent that wildlife corridors and stepping-stones have become recognized as potential ways of reducing fragmentation effects (Donald & Evans 2006). Corridors are now commonly used in conservation practice and, while they may help connect populations of species with poor dispersal ability, they may also facilitate the spread of highly dispersive organisms such as IAS. Increasing evidence indicates the propensity of IAS to spread along linear features of the landscape such as roadsides, rivers, forest trails and hedgerows, and that these features may promote longer dispersal events (Bryce, Johnson & Macdonald 2002; Mullerova *et al*. 2005; Wangen & Webster 2006). In contrast to IAS studies, the evidence regarding the value of corridors to native biodiversity is mixed and poses a dilemma for conservation ecologists (Donald & Evans 2006). As the connectivity of IAS populations increases, attempts to eradicate problem species locally become increasingly difficult and often result in a second-best strategy of long-term commitments to local control (Wadsworth *et al*. 2000; Watola *et al*. 2003). Furthermore, connected landscapes will impede attempts to contain IAS within a single region. An alternative to the establishment of corridors is to manage the surrounding habitat matrix to 'soften' the landscape by restoring parcels of land, especially less productive agricultural areas. Such a strategy may reduce the risks of biological invasion because habitats with more biodiverse matrices are potentially less prone to invasion and thus act as a filter, constraining invasive species while allowing the spread of native species (Donald & Evans 2006). Knowledge of IAS performance in different habitats and how this influences the rate of spread can help design appropriate landscape-softening strategies. Pines *Pinus nigra* are an invasive problem in New Zealand but spatiotemporal models of their spread highlight how the rate of invasion is contingent on the landscape matrix (Buckley *et al*. 2005). Abandoned grasslands facilitated a rate of spread approximately 40% higher than shrublands, but if grasslands were grazed this difference could disappear and even be reversed if grazing intensity was sufficiently high. Obviously the multifaceted nature of conservation targets would need to balance the advantages in limiting invasion against the value of the proposed land use to biodiversity, but the pine example does highlight the role of landscape management in containing spread.

Managing the management: damned if you do, damned if you don't

While land managers and conservationist may be frustrated by the complexity of external drivers influencing IAS spread and impact, they have greater opportunity to influence their own existing management actions. Livestock grazing is increasingly recognized as a 'disturbance' that when poorly managed can lead to IAS establishment, either through over-exploitation of palatable native plants rather than unpalatable IAS or opening up the vegetation to new colonists (McClaran & Anable 1992; Jansen & Robertson 2001; McIntyre, Heard & Martin 2003; Todd 2006). Cessation of grazing is rarely an option for economic reasons and also because IAS may persist and even continue to spread for decades in the absence of livestock (McClaran & Anable 1992; Jansen & Robertson 2001). In addition, grazing may be an important management tool in limiting IAS abundance (Hansen & Wilson 2006). In general, where the IAS is highly palatable, such as an introduced pasture grass, appropriately timed grazing may reduce population expansion, whereas for unpalatable species grazing may facilitate further establishment. The likelihood is that, in many rangelands, IAS covering the full range of palatabilities occur and an optimum grazing regime may not be possible without additional management interventions. It is therefore essential that any change in stocking rates be assessed in the light of the IAS assemblage rather than any individual species in particular.

Fire is a natural phenomenon that plays a key role in the dynamics of many ecosystems, and is frequently used (and abused) as a tool in the management of grasslands to improve forage yields, in heathlands to increase habitat heterogeneity and in forests either to clear woody debris or as prescribed fires to improve stand structure (Freckleton 2004). Fire can also be an important component of integrated weed management (Buckley *et al*. 2004). However, fire may facilitate the spread of IAS by opening up the vegetation for colonization, removing potentially competitive native species and increasing resource availability. Prescribed burning is a key tool used in prairie and savanna restoration, yet the timing and frequency of burning may have different consequences for native and alien species. Only annual summer burning is effective at reducing the population growth rate of spotted knapweed *Centaurea maculosa* in the prairies of Michigan, yet spring burning is favoured for the restoration of native grasses (Emery & Gross 2005). Burning of slash (woody debris) piles resulting from the harvest of fuel wood is a common management technique designed to reduce fire risk and increase establishment of understorey vegetation in many semi-arid woodlands. Examination of understorey vegetation in pinyon–juniper woodland in northern Arizona 5 years after harvest revealed that, compared with unburned controls, burned areas had significantly fewer understorey plant species but a four-fold higher IAS abundance (Haskins & Gehring 2004). These authors concluded that burning slash piles can result in plant communities that are persistently dominated by IAS, and management approaches that utilize fuel wood harvest alone or that incorporate seeding of native plants may achieve better results. Forest restoration treatments have been developed to move stand density and structure towards historical conditions and entail thinning of the canopy and/or burning. Dodson & Fiedler (2006) assessed the implications of different restoration treatments on the distribution and abundance of IAS in ponderosa pine forests of western Montana. Their results highlight that IAS responded significantly to restoration treatments, particularly when both thinning and burning were combined. Less intense treatments may therefore be preferable to avoid IAS incursions. Where more intense treatments are required to meet management objectives, specific strategies, such as seeding of native species, limiting grazing before and after treatment, and harvesting over a protective winter snowpack, may be necessary to limit invasion.

Reclamation of degraded lands is probably one of the toughest challenges land managers face. Soil conditions are usually nutrient poor or even toxic and suffer a high risk of erosion, with the result that establishing native vegetation cover is often a struggle. Perversely, IAS can succeed in such environments, often further confounding restoration efforts, as in the case of cogon grass *Imperata cylindrica* in sand-mined areas of Australia (Cummings *et al*. 2005). This characteristic of IAS has led to misguided efforts to use such species to minimize short-term soil erosion and accelerate long-term recovery. While IAS can certainly help achieve the short-term goals, evidence from reclaimed coal surface mines in Virginia reveals that such species may persist for more than 30 years and have probably slowed rather than hastened land recovery (Holl 2002). A common approach to deal with nutrient and/or toxic soils is through the application of organic and/or inorganic fertilizer. Serpentine substrates are formed from the natural breakdown of ultramafic rocks and are nutrient poor as well as containing potentially high levels of phytotoxic heavy metals. When these substrates are exposed as a result of construction activities, restoration of the (often endemic) flora is a significant problem. Soil nutrient amendment combined with sowing native species may provide a solution. O'Dell & Claassen (2006) experimentally assessed the potential of this treatment and found that revegetating serpentine substrates with native, serpentine-tolerant plant species could be achieved with a combination of organic and inorganic fertilizer. Yet such management comes at a risk because soil amendment could encourage the spread of IAS into the native plant community, potentially leading to habitat degradation. Managers therefore need to be aware of the wider ecosystem implications of their actions and, in this particular case, should be prepared to apply control methods to prevent the establishment of IAS into the revegetated community.

Freshwater ecosystems world-wide are under threat because of increasing demands for water, and in many cases the changes brought about by human activities have significantly altered ecological function (Giller 2005). The mitigation of these impacts has a focus on re-establishing river flow dynamics and connectivity of the river system. Yet even these laudable aims of river restoration may facilitate IAS impacts. In New Zealand the introduction of alien brown trout *Salmo trutta* has led to the extirpation of the native roundhead galaxias *Galaxias anomalus* wherever the species co-occur. Leprieur *et al*. (2006) analysed the environmental correlates of the distribution of these two species within a single river catchment. Using a supervised artificial neural network, they identified that, while the trout was relatively widespread, the galaxias were found in only one-quarter of the sites. The few sites where the native fish occurred could be distinguished from those with trout but, contrary to common perceptions, they were the sites most heavily influenced by human activities (especially water abstraction). Although these sites are not optimal for the native fish, they provide refuges from trout because the galaxias are better able to survive low flows and high water temperatures by burrowing into the riverbed. Leprieur *et al*. (2006) are keen to point out they do not recommend extracting more water from the catchment because in the long term this will be to the detriment of native fish species, but the example illustrates that restoration of natural river hydrology may not necessarily bring the desired benefits for all native species unless IAS are also managed as part of the restoration process.

Managing biological invasions: more than an invasive species approach

A comprehensive approach to IAS management should include a thorough assessment of six key considerations: (i) the expected impacts on the environment and economy; (ii) the technical options available to management; (iii) the ease with which the species can be targeted; (iv) the risks associated with the management options; (v) the likelihood of success in eradication, containment or control; and (vi) the extent of public concern and stakeholder interest. For each of these issues, the foregoing illustrates that, in addition to targeting an individual species, the management of biological invasions must also incorporate an appreciation of other environmental pressures, the importance of landscape structure and the role of existing management activities and restoration efforts

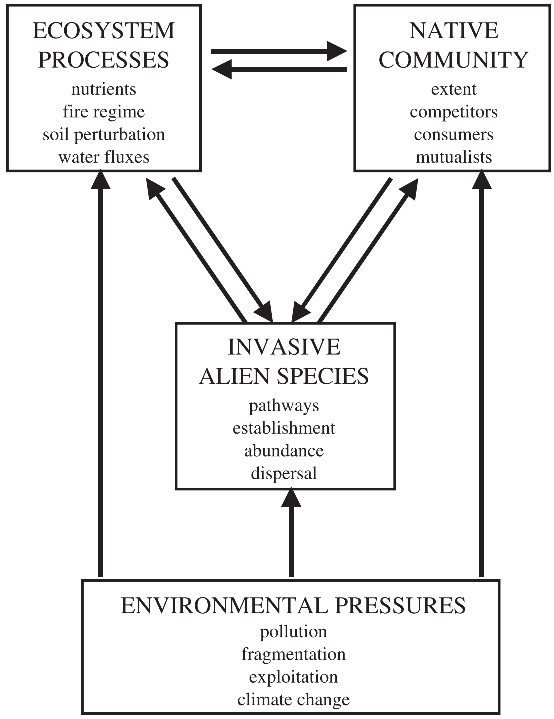

Fig. 2. The key linkages among the different components requiring consideration before any attempt to manage invasive species is undertaken. Targeting aspects of individual invasive species' ecology (pathways, establishment, etc.) may not yield sustainable management outcomes if the roles of environmental pressures (pollution, fragmentation, etc.), ecosystem processes (nutrient cycles, fire, etc.) and native community (consumers, mutualists, etc.) are not adequately addressed.

(Fig. 2). As invasions may be as much a symptom of environmental degradation as a cause, species removal studies rather than correlative surveys may provide a clearer perspective on ecosystem impacts. Detailed quantitative assessments may allow the direct impact of IAS to be discerned from other environmental pressures acting on biodiversity, and help prioritize management efforts towards the most significant (Thomson 2005). Although a wealth of information exists relating to the formulation, effectiveness and recommended application procedure for numerous herbicides and pesticides (Tomlin 2003), the assessment of the technical options for management will benefit from an ecosystem perspective that considers the manipulation of native competitors, consumers and mutualists, and reviews existing management practices as well as mitigates other environmental pressures. Similarly, the ease with which a species can be targeted should not only address the direct effects on the (meta)population dynamics of the species but also indirect effects on community diversity and structure (Rice *et al*. 1997). Such risks associated with management are often unexpected, especially where the result of species removal includes trophic cascades or competitor release. Where the ultimate goal of eradication, containment or control is to safeguard native biodiversity, such activities should take into account the need to re-establish native species and/or restore ecosystem function in the previously affected area. These countermeasures will not only accelerate ecosystem recovery but may also prevent subsequent re-invasion. The final aspect of management, which is arguably the most important but most often overlooked, is the role of public perception and stakeholder interest. Several well-intentioned eradication programmes have been frustrated by a lack of public buy-in, particularly on the grounds of animal welfare, as illustrated by the case of grey squirrels *Sciurus carolinensis* in northern Italy. Disputes are likely where IAS provide benefits as well as costs. Conflicts arise between the use of fast-growing alien trees in tropical agroforestry and the subsequent invasion of these species into natural ecosystems. Even conservation goals may diverge where IAS provide habitat or resources for one group of native species while reducing the diversity or populations of others. It does not require the skills of a social scientist to understand that such conflicts are often exacerbated by a lack of quantitative evidence of environmental impact. Indeed, conclusive data would be required in support of all the other five key considerations prior to addressing public perceptions. In summary, while improved management of invasions is often the ultimate goal of applied research, it is rare to find it as an actual proximate outcome. This unfortunate situation is partly the result of the scale of the task and the limited resources available. However, sustainable management requires consideration of more than a reduction in the density of the target IAS, specifically a long-term perspective that encompasses the wider ecosystem, its response and subsequent recovery. This special profile illustrates how such a perspective can be applied to prevention, rapid response, eradication and control of IAS, and thus can provide a sound basis for more holistic management of the entire invasion process rather than exclusively the invasive species.

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