RESEARCH ARTICLE



Understanding misunderstandings in invasion science: why experts don't agree on common concepts and risk assessments

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Abstract

Understanding the diverging opinions of academic experts, stakeholders and the public is important for effective conservation management. This is especially so when a consensus is needed for action to minimize future risks but the knowledge upon which to base this action is uncertain or missing. How to manage non-native, invasive species (NIS) is an interesting case in point: the issue has long been controversial among stakeholders, but publicly visible, major disagreement among experts is recent.

To characterize the multitude of experts' understanding and valuation of non-native, NIS we performed structured qualitative interviews with 26 academic experts, 13 of whom were invasion biologists and 13 landscape experts. Within both groups, thinking varied widely, not only about basic concepts (e.g., non-native, invasive) but also about their valuation of effects of NIS. The divergent opinions among experts, regarding both the overall severity of the problem in Europe and its importance for ecosystem services, contrasted strongly with the apparent consensus that emerges from scientific synthesis articles and policy documents. We postulate that the observed heterogeneity of expert judgments is related to three major factors: (1) diverging conceptual understandings, (2) lack of empirical information and high scientific uncertainties due to complexities and contingencies of invasion processes, and (3) missing deliberation of values. Based on theory from science studies, we interpret the notion of an NIS as a boundary object, i.e., concepts that have a similar but not identical meaning to different groups of experts and stakeholders. This interpretative flexibility of a concept can facilitate interaction across diverse groups but bears the risk of introducing misunderstandings. An alternative to seeking consensus on exact definitions and risk assessments would be for invasive species experts to acknowledge uncertainties and engage transparently with stakeholders and the public in deliberations about conflicting opinions, taking the role of honest brokers of policy alternatives rather than of issue advocates.

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Keywords

Alien, biosecurity, concept, conservation, exotic, expertise, invasion, impact, management, native, nonnative, uncertainty, risk, stakeholder, valuation

Introduction

To judge from the biological conservation literature, there is a general consensus that invasions of non-native species per se pose major risks to biodiversity and ecosystem services (Mack et al. 2000, Millennium Ecosystem Assessment 2005, Mooney et al. 2005, Vilà et al. 2010, Simberloff et al. 2013). However, this view is increasingly being challenged by experts (Davis et al. 2011) and it is debated whether invasive species are a main driver of species extinctions (Gurevitch and Padilla 2004, Clavero and García-Berthou 2005). Because ecological as well as other environmental and human-driven processes interact in complex ways, it can be difficult to determine whether invasive species are indeed a driver of environmental change or merely a symptom of some other events (Didham et al. 2005, Kueffer et al. 2013). Furthermore, the positive values of non-native species for conservation are increasingly discussed in the literature (Ewel and Putz 2004, Kueffer and Daehler 2009, Kueffer et al. 2010, Goodenough 2011, Schlaepfer et al. 2011), triggering critical responses (e.g., Vitule et al. 2012, Richardson and Ricciardi 2013). Then again, native species are sometimes considered to be invasive (Valéry et al. 2009, Carey et al. 2012) in disagreement with standard definitions (Richardson et al. 2011). These conflicting perspectives on invasive organisms and their effects on ecosystems can impede conservation action. This is particularly true if policies build on preventative measures on the grounds that an early response is likely to be more effective than a later cure (Leung et al. 2002, Hulme 2009). Such types of conservation actions rely on a general consensus among experts and stakeholders on the potential future negative impacts of non-native, invasive species (NIS).

It is therefore important to understand how perceptions about the effects of biological invasions and the need for management are shaped among stakeholders (affected interest groups) and experts (a person with a high degree of knowledge of a subject that is acknowledged by society, which leads to the attribution of a special role to the person in certain decision-making situations, Mieg 2009).

There has been some work on how stakeholders and the general public perceive the risks and consequences of biological invasions, and the appropriate management options to be taken (Bardsley and Edwards-Jones 2006, Binimelis et al. 2007b, Bremner and Park 2007, Fischer and van der Wal 2007, Garcia-Llorente et al. 2008, Andreu et al. 2009, Selge and Fischer 2010, Rotherham and Lambert 2011, Selge et al. 2011, Young and Larson 2011, Gozlan et al. 2013, Kueffer 2013). These studies show that learning about scientific facts related to effects of NIS is just one factor determining attitudes and opinions. Attitudes of stakeholders can also be influenced by the social context (Bremner and Park 2007, Fischer and van der Wal 2007, GarciaLlorente et al. 2008), differences in value judgments (e.g., emotional connectedness towards a species or towards specific management methods, Fischer and van der Wal 2007), conflicts of interest (e.g., managers vs. visitors of public parks, Garcia-Llorente et al. 2008), and the various roles that humans play in promoting invasions (McNeely 2001, Selge and Fischer 2010, Rotherham and Lambert 2011, Selge et al. 2011). Importantly, these studies suggest that stakeholders often differ strongly from experts and among themselves in their attitudes to invasive species and their willingness to participate in management actions (Bardsley and Edwards-Jones 2006, Andreu et al. 2009).

Less is known about how individual experts or expert communities differ in their perception and assessment of invasion processes, but there are indications that opinions do vary (Young and Larson 2011) and may be influenced by factors other than scientific facts (Selge et al. 2011). Indeed, it can be expected that in situations where facts and values are highly uncertain, as in the case of biological invasions, expert assessment also becomes highly dynamic and uncertain (Funtowicz and Ravetz 1993), and the influence of intuitions, ideologies and values is more pronounced (Fischhoff et al. 1982, Slovic 1999). Therefore, it is crucial to understand better how and why experts differ in the understanding and valuation of invasive species and their effects on ecosystem services and biodiversity.

We mapped the understanding of basic concepts commonly used to describe and explain biological invasions, and the ways experts value the risks and effects of biological invasions. To do this, we conducted 26 structured, face-to-face expert interviews. We used a qualitative approach because we were interested in elucidating the interrelated arguments, values and attitudes regarding biological invasions that are difficult to uncover through other methodologies. The experts belonged to two, equally sized groups, one of 13 invasion biologists and the other of 13 landscape experts. Both groups have a professional interest in ecological change, including the spread of non-native species; however, while plant invasions are the main focus of the work of invasion biologists, they are only one issue among many others in the work of landscape experts. By including landscape experts, we control for the convergence of perceptions in a scientific discipline, in this case invasion biology, that may be driven by an intra-scientific need to focus research (paradigm, Kuhn 1962) or the societal expectation for a profession to speak with one voice and act according to certain standards (Mieg 2009).

The overall aims of this interdisciplinary study (the authors include three biologists / environmental scientists and a risk psychologist) were: (i) to document the variability of the general conceptual understanding and the assessment of biological invasions among invasive species experts, (ii) to identify those aspects where the diversity of understandings and assessments among experts is particularly high and which therefore might account for dissent among invasive species experts, (iii) to investigate whether the consensus among invasion biologists differs from that among other relevant experts, and (iv) to identify possible explanations for any dissent among experts. We found that not only the framing of basic concepts (e.g., non-native or invasive) but also experts' thinking about the relevance of these concepts as well as the valuation of effects of NIS varied widely.

Methods

We used a qualitative research approach, which is often used in the social sciences to gain a multidimensional understanding of why individuals see the world in a particular way, and to explore the range of different thoughts, feelings, and interpretations of meaning of individuals in respect to an issue (Given 2008).

Study participants

The study was based upon face-to-face interviews with 26 academic experts with contrasting expertise in the broad field of ecological change. Prior to the interviews, these experts were assigned to two equal groups, one with a research focus on plant invasions (invasion biologists, IB, 9 males) and one with a research focus on ecological change in the landscape in general with plant invasions as one among many possible drivers (landscape experts, LE, 9 males). Landscape experts formed a heterogeneous group, including experts from agricultural and environmental sciences, biology, and geography (Appendix II). To avoid contingent differences in the use of terms such as native versus non-native in particular geographic regions (e.g., USA vs. Europe), we focused on a well-contained group of European experts. In Europe biological invasions have become a major concern for research and management only in the last decades, but currently invasive species research is one of the most active research areas in ecology in particular due to two large European research programs: ALARM (Settele et al. 2005) and DAISIE (DAISIE 2009). Given that invasive species are a fresh and very prominent topic, Europe is an ideal study system for understanding the diversity and dynamics of expert thinking. All experts were German speaking and the interviews were conducted in German, and they were all affiliated with an academic institution in Switzerland or Southern Germany. The experts were chosen to represent the major research groups at universities as well as applied research institutions in the study area that are working on plant invasions in terrestrial ecosystems. Some study participants were recommended by other experts. With the exception of four young scientists (3 IB, 1 LE), at the time of the interviews all participants had a long-standing record of major contributions to the literature on the issue of biological invasions and/or ecological change.

Structure of the interview guideline

We performed structured face-to-face interviews including closed and open-ended questions. A strength of this method is that it allows for a direct elicitation of individual understandings and valuations without the bias of social interactions in group settings possibly hampering the expression of extreme views or the recognition of individual uncertainties or lack of knowledge. Our interview guideline (Appendix I) was compiled following a literature search and a review of the international scientific literature on biological invasions, and especially plant invasions. We limited ourselves to the perceptions of ecological change caused by plants because a) plant invasions are particularly intensively studied and have driven most of the theoretical debates in invasion science (especially also in Central Europe), b) plants significantly shape ecosystem processes, and c) the analysis as well as the full acknowledgement of the debate about animal rights inherently linked to the issue of biological invasions by animals would go beyond the scope of this investigation. We focused on concepts that are of particular importance both in the scientific literature on biological invasions and the sociopolitical deliberations about the issue (non-native, invasive, ecosystem services). To finalize the interview guideline, we ran two pilot interviews with a geographer and an environmental scientist, respectively.

The interview guideline consisted of three main parts: in the first part (Q1-Q10), participants were asked about their understanding of key concepts (native, non-native, invasive). The second part focused on the valuation of effects of non-native, invasive plants on ecosystem services (Q11-Q12) (sensu Millennium Ecosystem Assessment 2005). Experts were presented 12 cards that listed various ecosystem services: two provisioning services (Biodiversity, Food), four regulating services (Climate Regulation, Human Health, Pollination, Protection from Natural Hazards), two supporting services (Primary Production, Soil Formation), and four cultural services (Cultural Heritage, Landscape Aesthetics, Sense of Place, Recreation / Tourism). The study participants then had to assess whether non-native, invasive plants have a predominantly negative, neutral, or positive influence upon the twelve ecosystem services, resulting in twelve separate assessments per expert. Additionally, experts were asked to briefly motivate their decisions. Before participants valued the effects of non-native, invasive plant species on ecosystem services (Q10) they were informed about the definition of an invasive species by the Swiss Commission for Wild Plant Conservation and Swiss federal legislation SR 814.911. However participants were also told that they are free to stick to their own definitions. In the third part, we focused on the invasive species issue as a societal problem. We asked the experts why they considered biological invasions to be a problem (Q13-Q15), confronted them with the problem understanding of the Swiss government (Q16), explored some key dimensions of the problem understanding in more detail (Q17-Q19), asked about the availability of sufficient scientific evidence (Q20), and asked for an assessment of the scale of the problem (Q21-Q25). Answers to questions Q20-Q21 and Q23-Q25 were measured on 5-point Likert scales. Additionally the participants were asked to motivate their decisions shortly. The interviews ended with questions seeking information on participants' current research (Q26) and basic demographic data (Q28, Appendix II). Further, experts were asked if they want to make a concluding statement (Q27). Before the start of the interviews, participants were informed about the general direction of our study, i.e., to elicit the perception of ecological processes related to non-native plants (see interview guideline, Appendix I). At the start of the interviews, all experts provided verbal consent to audio record and transcribe their answers. Participants were ensured that after transcription, the data would be anonymized. All interviews were led by the first author.

Data analysis

All interviews, which mainly lasted for about one hour, were digitally audio recorded and transcribed verbatim in German. The interviews were performed between September and October 2009. In the case of the valuation of effects on ecosystem services (Q11), we were not only interested in the overall assessment (effect evaluated as positive, negative or neutral) by the experts but also in the types of arguments that they used to motivate their valuations. For this analysis, the authors identified different recurring arguments used by the study participants to motivate their valuations. A few questions (Q12, Q13–Q19) were omitted from the analysis because they yielded redundant data only. Questions Q20–Q21 and Q23–Q25 were closed questions, which allowed us to quickly gain information on specific attitudes experts held towards NIS and biological invasions in the societal context.

Results

Irrespective of the expert group (invasion biologists or landscape experts) we found diverging framings of key concepts related to biological invasions, varying valuations of effects of non-native, invasive plant species (NIS) on ecosystem services (ES), as well as differing understanding of, and attitudes towards biological invasions as a societal problem. We found a clear difference between the two expert groups for only a few questions, while within-group variation was generally high.

Understanding of key concepts

1. Non-native origin

Experts generally agreed that a non-native plant is a species that arrived in a certain geographic area through movement facilitated by humans. However, expert definitions differed in their temporal and spatial reference, and only some referred to environmental change or human perception. None of the experts mentioned any biological characteristics of a species, e.g., that a non-native species has different traits than a native species, as part of the definition of non-nativeness.

Landscape experts (LE) offered a greater diversity of definitions than invasion biologists (IB), and tended to discuss more explicitly their difficulties in defining a

non-native species. For instance, three LE emphasized that the choice of a spatial or temporal reference is a subjective decision:

[...] there is no absolute definition of what is native and non-native. [...] what is new, say 10 or 20 years, this I would classify as non-native. [LE8].

But also some IB argued that definitions are arbitrary:

The definition used is completely arbitrary [...] This means in fact transitions are fluid and [...] if one would comprehend the definition in a broader sense, almost every vascular plant is non-native in Switzerland because they re-migrated after the ice age. [IB8].

Temporal reference: Experts based their distinction between native and non-native species upon arrival time, using events in human history to define such temporal references. However, while invasion biologists mostly adhered to the same definition, land-scape experts varied widely in their temporal reference (Fig. 1). Most invasion biologists (IB) defined non-native species as those species introduced after the year 1500 AD (i.e., Columbus' discovery of the Americas), usually adding that this is the accepted or official definition in the literature. However, many of them perceived this definition as somewhat arbitrary. Only three landscape experts (LE) referred to the year 1500 A.D., and five LEs did not address the time question; the other five LE proposed dates ranging from some unspecified time in the past, to the Neolithic period, the industrial revolution, and the period of globalization (Fig. 1).

Spatial reference: In contrast to a temporal reference, most experts used unspecific spatial references (e.g., "moved to here" or "moved to where we are"). Only 5 IB and 2 LE specified a spatial reference, basing this upon either human or biogeographical considerations. Thus, some referred to a political unit (such as "not from Switzerland", "not from Europe") while others mentioned biogeographical features ("from another continent", "from a different biogeographic area", or "from an area separated by topographic features (such as mountains or oceans) that hinder dispersal"). The various spatial references varied so widely that, applied to an area such as Switzerland, they would define strongly differing sets of non-native species.

Environmental change: Some experts, both LE and IB, acknowledged that natural or anthropogenic environmental change can affect what is considered to be a nonnative species. Some went on to state explicitly that species dispersing to a new area in response to anthropogenic environmental change (esp. climate change) should also be considered non-native.

Human perception of the non-nativeness of a species: Some LE referred to human perception in their discussion of the definition of non-nativeness. One LE argued, for instance, that species present for a long-term are sometimes considered to be native by local inhabitants, while another LE specified that non-native species are those that arrived in an area over a period shorter than a human lifespan.



Figure 1. Contrasting conceptualizations of the non-native origin of a plant species in Central Europe. Invasion biologists mainly referred to the notions of archaeo- and neophytes and thus to the year 1500 A.D. to distinguish non-native from native species (blue boxes). Landscape experts referred to a wide range of different time frames, including no mentioning of any reference point in time (brown boxes).

2. Native species

To define a native species, most experts used similar considerations as for non-native species, but some experts used "presence since the last glacial period" as their criterion for a native species (3 IB / 2 LE). One invasion biologist pointed out that experts did not agree about whether to regard archaeophytes, i.e., species moved to Europe by humans before 1500 A.D. (Fig. 1) as native or as non-native. Thus, as for non-nativeness, nativeness of a species was mainly related to both its geographical distribution and to the period it was present in an area (Fig. 1); however, some experts also referred to biological characteristics, mentioning that native species are likely to be adapted to the local conditions (especially climate). Correspondingly, some experts mentioned that a native species evolved in a place, and others raised the possibility that a species can be native to a particular climate zone in mountains. Contrary to criteria used to define non-nativeness, only one LE discussed environmental change, and no-one considered the possibility that human perception might have a bearing upon a species' native status.

3. Invasive species

After clarifying the terms native and non-native, we asked our participants whether native and non-native plants differ in their behavior. Experts agreed that such biological differences are not inevitable (9 IB / 9 LE), though some regarded them as likely (3 IB / 7 LE). In this connection, the following characteristics of non-native plants were mentioned: i. novel interactions with or dominance of resident organisms due to a lack of coevolutionary history, ii. adaptation to fast or human-related dispersal, and iii. the possession of novel traits enabling species to occupy an empty niche. In general, however, experts explained that the question was "difficult to answer", due to "insufficient scientific information", or "high complexity", meaning that "evaluations must be done on a case-by-case basis". Ambiguity among experts became particularly obvious in how they related the non-nativeness and the invasiveness of species: some experts spontaneously valued the behavior of non-native plant species as problematic (4 IB / 5 LE), while others did not mention an invasive behavior at all.

We then explicitly asked our participants for a definition of a non-native, invasive plant species (NIS). Experts generally agreed that an NIS is one that spreads spontaneously and rapidly, and exerts a negative impact on native species, ecosystem processes, the economy, or human health. Two experts (1 IB / 1 LE) stated explicitly that the term invasive does not necessarily imply a negative impact. To them, range expansion alone was a sufficient condition for being an invasive plant species.

Valuations of effects on ecosystem services

Each expert was then asked to value the influence of NIS in Europe on twelve different ecosystem services (ES) as negative, neutral or positive, resulting in twelve separate assessments per expert. Eight of the ES can be regarded as provisioning, regulating, or supporting services, and four as cultural services. For every ES there were some negative, neutral, or positive assessments, and in general both IB and LE ranged widely in their assessment of the effects of NIS on ES (Fig. 2). In total, experts made more neutral valuations (56%) than negative (32%) or positive ones (12%). Our study participants perceived the strongest negative impacts of NIS on ES Biodiversity (56% negative valuations) and ES Cultural Heritage (54% negative valuations). Most favorable effects of NIS were attributed to ES Landscape Aesthetics with 33% positive valuations. On average, invasion biologists (IB) tended to assess the effects of NIS upon ecosystem services more negatively than landscape experts (LE), especially for ES Cultural Heritage, Sense of Place, Food, and Soil Formation (Fig. 3).

We were particularly interested in how experts reached their opinions concerning the influence of NIS on ES, and the arguments they used to substantiate them. We identified four issues characterizing various uncertainties that complicate the valuation process: 1. how to deal with a lack of empirical information; 2. how to deal with value judgments; 3. what to do when the same species has both positive and negative effects; and 4. how to treat the non-nativeness of a species in value judgments.



Figure 2. Number of positive, neutral, and negative assessments of the predominant effect of not further specified non-native, invasive plant species on 12 different ecosystem services for 12 invasion biologists (IB1-IB11, IB14, blue dots) and 12 landscape experts (LE1-LE12, brown dots). The perpendicular distance of the parallel lines to the respective corner corresponds to the number of positive, neutral, and negative assessments of a study participant (e.g., LE7: 3 neutral, 5 negative, and 4 positive assessments).

1. Decision making with limited information

Experts consistently mentioned a lack of empirical information about effects of NIS on ES. At best experts knew about documented effects of one to a few particular species. Information about effects caused by a broad range of different invasive species, however, was mostly missing. We identified five ways through which experts coped with this uncertainty: (i) concluding that there were no effects of NIS on ES, (ii) acknowledging the lack of empirical information, (iii) extrapolating from their knowledge about the effects of particular species, (iv) building on general knowledge about effects of NIS on certain ES, or (v) referring to the frequent overabundance of NIS, that is often stated as a specific characteristics of NIS in the literature, and deriving predictions about effects from this general pattern.



Figure 3. Average valuations of the effects of non-native, invasive plant species (NIS) on different ecosystem services (ES). On average, invasion biologists (blue dots) assessed NIS effects on ecosystem services (ES) more negatively than landscape experts (brown squares), particularly in the case of cultural ES (asterisks). The overall mean of the evaluations (black triangles) is most negative for ES Biodiversity and most positive with respect to ES Landscape Aesthetics.

Acknowledged lack of knowledge (*i*, *ii*): In almost a third (32%) of all assessments, experts could not recall any effects of NIS on ES. The experts drew one of two conclusions from this lack of knowledge: either that NIS have little or no effect compared with native species, or that important information was missing (either to them as an individual expert or more generally in the literature). Some experts suggested that more research on the subject is needed. But otherwise, with very few exceptions only, experts assessed neutrally in both cases.

Extrapolation from information about particular species (iii): Sometimes experts based their assessments on well-known effects associated with particular species, such as *Solidago* sp., *Ambrosia ambrosiifolia*, *Heracleum mantegazzianum*, *Reynoutria* sp. and *Impatiens glandulifera*. In particular, experts recalled the adverse impact on human health of *A. ambrosiifolia* and *H. mantegazzianum*, and the destabilizing effects of *Reynoutria* sp. on soil in general and particularly on stream banks. But experts also em-

phasized e.g., the attractiveness of flowers of *Solidago* species. Some experts concluded from these examples that other invasive species may have similar effects, while other experts emphasized that extrapolation is not possible.

Extrapolation from general knowledge about NIS (iv): In some cases experts felt confident to make general statements about NIS effects on ES. These statements were based on generalized knowledge about NIS without reference to particular species. For instance, an expert explained the negative impact of NIS on ES Biodiversity, arguing that "globally NIS were the second most important cause for a decrease of biodiversity" [IB5]. Such generalizations were common for statements about effects on ES Biodiversity: most experts were prepared to assume that NIS have a generally negative effect upon native biodiversity, though few explained the underlying mechanisms or cited empirical evidence. Most experts generalized at least once (9 IB / 10 LE).

Reference to overabundance (v): The only general characteristic of NIS that was explicitly mentioned to substantiate general claims about effects of NIS on ES was the fact that invasive species often form dense stands. For all ES except ES Human Health at least one expert recognized overabundance as a reason for negative impact. Overabundance was most frequently stressed in the context of ES Biodiversity, Pollination, and the cultural ES Cultural Heritage and Sense of Place. Overabundance of NIS always led to a negative valuation and was the basis for one third (34%) of all negative valuations.

2. Explicit consideration of values and value judgments

Valuation of an effect entails understanding how an NIS changes an ecosystem property, and then assessing whether this change is positive or negative. Experts rarely explicitly mentioned the second step, and the importance played by values. In particular, experts assumed that the preferred state of non-cultural ES (and associated cultural views or ethical values) was clear and uncontroversial, the only exceptions being for ES Pollination and Food (2 IB). In contrast, for assessments of NIS, influences on cultural ES, more often value judgments were made explicit. All experts except for three (1 IB / 2 LE) stated at least once either their own feelings or values towards NIS or their effects (9 IB / 9 LE), or they referred to feelings or values of particular stakeholder groups (e.g., tourists, agriculture, general public) (8 IB / 10 LE). Experts remarked for instance that because of positive experiences with a particular NIS their sense of place was "positively connected" to the presence of that species; on the other side, they spoke of "negative feelings" towards "change in a familiar landscape", or "getting irritated by monocultures", and "being distressed" by negative impacts of some NIS on recreation. Interestingly, however, explicit consideration of personal values or different stakeholder views was less prominent for ES Cultural Heritage.

Some experts acknowledged that valuation of stakeholders is rooted in cultural history. LE6 for instance considered NIS effects on ES Cultural Heritage as positive and explained:

It is positive because...the fact that plants were moved to particular places is part of our culture, whether we consider it positively or not. [LE6]

LE3 referred to the evolution of perceptions over time:

If one accepts that over time invasive plants [...] *become a cultural heritage, then it is not negative.* [LE3]

Similarly conifers that were extensively planted in Switzerland during the 19th century were recognized by one LE as a "kind of invasion at the time" [LE2] but were perceived today as enhancing landscape aesthetics. However, only few experts elaborated more generally on the value-laden nature of assessing effects on cultural ES.

3. Ambiguous valuations

All experts except 5 LE emphasized the difficulty of valuating effects in situations where a species has both positive and negative effects on different or even the same ES; or when different people value the same effects differently. LE3, for instance, argued that while invasive species might reduce biodiversity in the short term, they might lead to a higher, new biodiversity in the longer term. Or, LE11 valued the influence of NIS on ES Landscape Aesthetics neutrally and commented:

Related to landscape aesthetics it's a matter of taste - there are people who are enthusiastic about dense Solidago stands, but from the point of view of nature conservation it's rather negative. [LE1]

4. The role of non-nativeness in valuation of effects on ecosystem services

The non-nativeness of a species was used both in value judgments and to explain how the species might affect ecosystem services. It was not always evident whether the nonnativeness of a species was valued in itself or as a reason for expecting some negative impact. Non-nativeness was mentioned in the context of all ES, but was not considered equally important by all participants.

Particularly in the context of ES Cultural Heritage, experts described a sense of loss associated with the spread of NIS - for example, "loss of a landscape" they had been used to or "loss of identity" as the result of the presence of a non-native species; similarly, experts mentioned their feeling that the "new species did not belong" to their culture. Thus, some experts considered the presence of non-native species in itself as negative for cultural heritage:

Invasive, non-native plants have to be negative, because they are new and not native, and so not part of our heritage. [IB2]

Several experts implied that valuing the non-nativeness of a species depends on knowing which species are non-native and which ones are not. IB9 for instance argued that:

Most people do not have any idea of what is indigenous und what is non-indigenous. Hence they [invasive plant species] do not have any influence on the recreational factor at all. [IB9]

In other cases, the novelty of non-native species was positively valued – for example, when the species was seen as "an enrichment" of the preexisting flora or a "contribution to the aesthetic value" of a landscape.

Biological invasions as a societal problem

To reveal experts' evaluations of how serious they consider the problem of NIS in Central Europe to be, we asked a series of quantitative questions (Fig. 4). All participants recognized NIS as a problem in Central Europe, although most rated it as small to medium at present (Fig. 4A). Yet almost all experts expected problems related to NIS to increase in the future (Fig. 4B), emphasizing anthropogenic environmental change as a driver of future invasion threats. Especially IBs called for action against NIS through concrete management measures (Fig. 4C). Most participants of both expert groups agreed that our causal understanding of why some plants become a problem is inadequate (Fig. 4D), arguing, for example, that the complexity of ecosystem processes makes general assessments difficult or even impossible. Interestingly the two expert groups clearly diverged in their assessment on how the problem is recognized by a particular stakeholder group of their choice (Fig. 4E). In general, invasion biologists considered that the problem was underestimated by the public and in politics. Landscape experts tended to see the problem as overestimated, particularly due to anxiety and xenophobic feelings among the public.

Discussion

Our interviews with experts of plant invasions and/or ecological processes in the landscape indicate that their understanding of the phenomenon of non-native plant invasions is diverse and influenced by individual conceptualizations, beliefs, and values. While we expected a rather high diversity of perspectives in the heterogeneous group of landscape experts, we were surprised by the lack of consistency in the use of basic concepts amongst invasion biologists, since the research field is well defined, and its leaders have invested much effort in standardizing key concepts (e.g., Colautti and McIsaac 2004, Valéry et al. 2008, Colautti and Richardson 2009, Pyšek et al. 2009, Richardson et al. 2011). In fact, the diversity of perceptions within both experts groups was so large that for most issues we examined there was no clear difference between



Figure 4. Experts' responses to a set of closed questions regarding the invasive species issue as a societal problem (Appendix I, Q20–Q25). Blue boxes: invasion biologists, brown boxes: landscape experts.

the groups. Our study was restricted to German-speaking experts of Switzerland and Southern Germany, and an even higher diversity of expert opinions might be expected if we had included a broader geographical range. Studies from other regions indicate that many of the relevant dimensions of expert thinking that we identified for German-speaking Europe might also be relevant elsewhere (Selge et al. 2011, Young and Larson 2011). We suggest that the heterogeneity of expert judgments observed in our study is related to three major dimensions: (1) diverging understandings of basic concepts, (2) complexities and contingencies of biological invasions, and (3) valuation uncertainties with respect to the qualitative assessment of the effects of non-native, invasive plant species on ecosystems and their services.

Diverging understandings of basic concepts

Central to any understanding of a non-native, invasive species (NIS) are the definitions of non-native and invasive species. Many of our participants accepted, at least in part, conventional definitions widely used in the research field, though the interviews also revealed more diverse thinking. We screened the publications of the participating invasion biologists to check whether the results from the interviews were also reflected in the ways experts used definitions in their scientific publications. We found that authors generally reported a definition of a non-native and invasive species in the introduction or methods section of a publication, but in the rest of the text this definition was rarely strictly applied. For instance, authors might present a definition that distinguishes between non-native and invasive species, but then use the terms interchangeably in the text; or they might compare invasive non-native species with native species without specifying whether or not the native species are also invasive (fast spreading / having a negative impact). This tension between a shared definition and a much broader understanding of key notions is also more generally apparent in the biological invasion literature. Indeed, many of the difficulties in operationalizing definitions of non-native and invasive species that we uncovered in this study can be found scattered throughout the literature (Garrott et al. 1993, Shrader-Frechette 2001, Brown and Sax 2004, Sagoff 2005, Warren 2007, Davis 2009, Valéry et al. 2009, Rotherham and Lambert 2011, Young and Larson 2011, Webber and Scott 2012).

Given that the definitions of an NIS can be regarded as core elements of the paradigm of the research field (e.g., they are introduced in every textbook), it is surprising that we found such a high diversity of alternative understandings among experts. Even among invasion biologists only two thirds mentioned a common temporal reference for the definition of the non-nativeness of a species (1500 A.D., Fig. 1) and only half explicitly stated that non-native species are those moved through human-assisted dispersal. And landscape experts did not agree at all on a common temporal reference. There was also no agreement on other aspects necessary for a non-ambiguous definition of an NIS, such as where a species must come from to count as non-native, and some important aspects were not mentioned at all, in particular how to determine whether a species is fast spreading. This aspect, although basic to the definition of NIS, is difficult to operationalize and several different approaches are described in the literature (compare Richardson et al. 2000, Wilson et al. 2009, Sorte et al. 2010, Webber and Scott 2012). In fact, the different answers given by the experts lead to substantially different selections of non-native and invasive species. Experts also differed in their understanding of what a native species is, despite the extensive literature on this topic in Central Europe (Schroeder 1968, Webb 1985, Kasparek 2008). In summary, we found uncertainties related to at least eight conceptual dimensions that affect a common understanding of the key notions of a non-native species and an invasive species: (i) minimum and maximum residence time in a new area, (ii) source area, and (iii) dispersal pathway (through human agency or not) of a non-native species; (iv) What counts as human-assisted dispersal? (v) Must an invasive species be fast spreading and/ or have a recognized negative impact? How are (vi) fast spread and (vii) negative impact defined? And, (viii) should the term invasive be reserved for non-native species or also be used for native species?

In many cases, differences between experts' definitions reflected different ways of framing a socioecological problem. In particular, some experts understood invasions primarily as a biological phenomenon, while others approached it as a sociocultural phenomenon. According to the biological perspective, the non-native origin is important because species introduced into new areas often exhibit distinctive ecological behavior, with respect to both the source population and to the native flora where the species establishes. A non-native species may, for instance, behave differently from a native species because it is released from its natural enemies (Keane and Crawley 2002), or has novel traits that are not present in the native flora (Vitousek et al. 1987). In contrast, some landscape experts approached the subject with primarily a sociocultural perspective in mind. Thus, they placed emphasis upon the temporal dynamics of human perception of and cultural attachment to nature and biodiversity, or different important historical episodes such as the beginning of industrialization or globalization as the basis for separating native and non-native species (Fig. 1). Interestingly, ecological and sociocultural types of reasoning were often intermingled. For instance, while most invasion biologists indicated that they intended to gain an ecological understanding of why non-native species behave differently from native species, most of them nevertheless referred to a cultural criterion for separating non-native from native species, namely the year 1500 A.D. Thus, a cultural definition of the non-nativeness of a species is used in an ecological argument.

The notion of a non-native, invasive species as a boundary object

Several authors in the invasion literature have expressed confidence that the problem of conceptual pluralism in research on biological invasions can be overcome by defining key notions more precisely (Colautti and McIsaac 2004, Pysek et al. 2004, Valéry et al. 2008, Colautti and Richardson 2009, Pyšek et al. 2009, Richardson et al. 2011,

Webber and Scott 2012). However, experience in invasion biology and other fields of ecological research indicate that it is difficult to establish precise definitions that all experts can share (e.g., Shrader-Frechette 2001, Haila 2002, Sagoff 2005, Hodges 2008, Moore et al. 2009). The situation is further complicated by the fact that through anthropogenic environmental change, patterns and processes are changing so fast, with the consequence that concepts and research approaches must be continuously adapted (Kueffer 2013). In the case of complex and interdisciplinary problems, therefore, it may not always be possible to reach a consensus on definitions. There is probably no way to avoid a melting pot of diverse terms and perspectives characteristic of an increasingly inter- and transdisciplinary invasion science. It is clearly important for authors to define their key terms in a particular context, but even this may not help much; a better solution may be to classify alternative definitions of concepts that are valid for particular purposes (Hodges 2008).

It may even be that partially ambiguous terms can be beneficial for the research field by facilitating inter- and transdisciplinary dialogue. For this to occur, they must serve as boundary objects, meaning concepts that have a similar but not identical meaning to different expert groups (adapted from Star and Griesemer 1989). Thanks to this fluidity, these concepts can facilitate collaboration between different communities because they can be adapted to different specialized expert discourses without losing a shared core meaning. Indeed, our data shows that the term non-native, invasive species encompasses a range of different meanings that resonate with different research interests, an observation that is also reflected by the diversity of perspectives in the literature on invasive species (compare e.g., Davis 2009, Richardson 2011, Heger et al. 2013b, Fig. 5). For instance, biogeographers are interested in the role of geographic barriers in determining species distributions and richness patterns, and non-native species - defined as species that cross biogeographic barriers - resonate with their interests. Some evolutionary biologists and ecologists are interested in how species respond to novel abiotic and biotic conditions and, in turn, how species with novel characteristics can change ecological processes. For them, it is less important whether a species is from another biogeographic area, but it matters whether it introduces some form of ecological novelty to a system. Invasions offer a suitable system for population and community ecologists to study the processes of spread and colonization, but these do not necessarily differ between non-native and native species. Overabundance of some NIS is a feature that they share with some native winners of anthropogenic change, which can be unrelated to biogeographic origin or processes of spread (e.g., Fig. 1 of Rejmánek 2000). In turn, scientists from the social sciences and humanities are interested in, for instance, the cultural connotations of the terms invasive and non-native (and associated terms), and in human-nature relationships and how these influence the geographic distribution and human perception of species. In management, NIS are also addressed differently in contrasting realms, such as transnational biosecurity policies vs. the local management of natural areas. For biosecurity policies the non-native origin of species is central, while origin may be of lesser importance for local ecosystem management.



Figure 5. The notion of a non-native, invasive species (NIS) as a boundary object: different groups of experts use the same notion with a different specific meaning and purpose in different contexts. Thereby the notion of an NIS as an ill-defined concept can help to facilitate collaboration across these diverse experts group (see main text for further explanation).

Of course, the pluralistic usage of concepts also bears risks. For instance, the sometimes vigorous conflicts between social and natural scientists related to the invasive species issue (e.g., Simberloff 2003, Raffles 2011) may have arisen from a failure to recognize that they were using the same term to mean different things. Social scientists, accustomed to deliberations about the cultural connotations of terms like alien or nonnative, accuse invasion biologists of being xenophobic (which is a legitimate concern within the narrow boundaries of their specialized debates), though biologists use the term in a very different context and usually without any cultural connotations. It is therefore important to carefully reflect on the different contexts when using terms such as non-native (or alien, exotic, foreign, etc.) in science or policy.

Complexity and contingencies impede proactive action

Most participants stressed that risk assessments of biological invasions are made difficult by our lack of basic understanding of the important processes. In more than 50% of the assessments of effects of NIS on ecosystem services, experts decided for a neutral assessment, saying that potentially unknown effects or lack of knowledge prevented them reaching any other conclusion. They also often pointed to the complexity and contingencies of biological invasions, emphasizing that factors such as habitat context and anthropogenic disturbances interact, and that the dynamics and outcomes of invasions can change in time. In particular, they emphasized the difficulty of making general statements across many species and contexts, especially when considering the longer-term spatio-temporal dynamics of ecosystems. The only general characteristic regularly used by experts to legitimate their valuations of effects was the overabundance of an invasive species; while in almost all other cases they were forced to extrapolate effects from individual NIS to all invasions. Such extrapolation - from individual cases to invasions in general - is also widely used for predicting the potential effects of NIS in the literature (e.g., Pimentel et al. 2000).

We designed our interviews in a way that forced experts to make general statements to mimic their expert role in decision-making processes. Due to the emphasis of current invasion policy upon proactive action, in particular measures to prevent potentially problematic non-native species from being introduced (Leung et al. 2002, Hulme 2009), decisions often have to be taken for species that are not well known or only from other areas. Thus, there may be considerable uncertainty in determining whether or not a non-native species poses a risk (without in-between categories) across all habitats. Many experts in our interviews stated that such extrapolation from a few, often poorly known case examples is problematic, thus echoing a strong critique of invasive species management by philosophers of science (Shrader-Frechette 2001, Sagoff 2005). Alternative approaches to biosecurity that might circumvent this problem include adaptive management processes, participatory methods, or risk assessments that are specific to particular habitats or introduction pathways (e.g., Kueffer and Hirsch Hadorn 2008, Liu et al. 2011, Hulme 2012).

Valuation uncertainty influences risk perception and risk assessments

The process of risk assessment is also complicated by uncertainties related to the valuation of effects of NIS. In our study we found at least three different kinds of valuation uncertainties: (i) ambiguous endpoints for risk assessments, (ii) differing value systems or perceptions, (iii) the role in value judgments of controversial concepts such as non-nativeness.

A first valuation uncertainty – ambiguous endpoints of risk assessments – became obvious when our study participants stated that the same invasion can simultaneously lead to several outcomes - some positive, others negative. For instance, according to the experts *Solidago* species can provide an important food source for native pollinators and at the same time out-compete native plant species. About one quarter of all neutral assessments reflected such ambiguities.

Second, valuation options may vary among experts and stakeholders depending on their value system and perception. For example, in assessing the contribution of *Solidago* species for the landscape, some may value the yellow flowering in late summer positively, while others will negatively value the fact that the landscape differs from what they consider to be a natural landscape. Especially for cultural ecosystem services, experts emphasized that valuation depends on the affected stakeholders that are considered.

Third, specific to the invasive species debate is the use of the native vs. non-native species dichotomy (Fig. 1). Not surprisingly, the controversial perception of the importance of a species' origin for risk assessments added as a third factor to the hetero-

geneity of expert valuations. Most participants agreed in principle that invasive species should be judged according to their effects on native biodiversity and ecosystems, and not by their origin, i.e., their non-nativeness per se. Many experts therefore stressed the need to distinguish clearly between non-native and invasive species. This corresponds with the way lay people value invasive species, with detrimental impacts being more important than biogeographic origin (Fischer and van der Wal 2007, Selge and Fischer 2010). Nevertheless, invasion biologists are regularly criticized for condemning non-native species solely because of their foreign origin (Larson 2007, Davis et al. 2011). Indeed, despite their intention not to use non-nativeness as a value, many experts revealed an implicit bias against non-native species in their answers to interview questions. This was especially evident when valuing cultural ecosystem services such as Cultural Heritage, Sense of Place, or Landscape Aesthetics, with several experts treating the presence of non-native species negatively because of their non-nativeness. Whether and how non-nativeness is used to make value judgments adds to valuation uncertainty, especially because this criterion is often not explicitly mentioned.

The problems of multiple effects and multiple adequate values are widespread in environmental problem solving, and there is a broad literature on multi-criteria and participatory valuation and decision-making methodologies (Scholz and Tietje 2002). However, such methods have rarely been applied in the context of invasive species (Binimelis et al. 2007a). Indeed, established procedures such as risk screening systems or black lists (Pheloung et al. 1999) do not consider the possibility of the context-dependence of effects and conflicting valuation, and new approaches are only now being developed (Randall et al. 2008, Hulme 2009, Liu et al. 2011, Kumschick et al. 2012, Dahlstrom Davidson et al. 2013). Similarly, media communications rarely represent the diversity and uncertainty of valuation of NIS (Chew and Laubichler 2003, Larson 2005).

Speaking with one voice to the public: an outdated expectation from invasive species experts?

In our study, expert opinion diverged strongly in questions concerning the effects of non-native, invasive plant species (NIS) on individual ecosystem services (Fig. 2 and 3), and the assessment of the problem posed by these species in Europe (Fig. 4). This divergence of opinion revealed in interviews contrasts with the broad consensus on the risks and effects of biological invasions that experts claim in scientific synthesis articles and policy documents (Mack et al. 2000, Millennium Ecosystem Assessment 2005, DAISIE 2009, Hulme et al. 2009, Vilà et al. 2010). Indeed, the invasion biologists in our survey have all published articles concerning plant invasions in Central Europe in which they state that biological invasions lead to major biodiversity loss and/or economic costs. In most cases, however, these statements were of a general nature and supported by data from outside of Europe (citing e.g., Pimentel et al. 2000, Mooney et al. 2005).

One possible interpretation for this paradoxical situation is to consider the dual nature of an expert as on the one hand a person with a high degree of knowledge of a subject and on the other hand someone with a special role in certain decision-making situations attributed by society (Mieg 2009). Invasion biologists are faced with the difficult challenge of reconciling high uncertainties in internal expert deliberations (i.e., in their role in producing new knowledge) with their public role as experts, expected to speak with one voice to decision-makers and the public. This situation is even more complicating when a consensus is needed for action to minimize future risks but the knowledge upon which to base this action is uncertain or missing. Indeed, while disagreeing on the current severity of the problem, both invasion biologists and landscape expert tended to agree that the severity of the problem will increase and intervention is urgent (Fig. 4).

Nevertheless, recent examples of conflicting debates among invasive species experts played out in the media (Davis et al. 2011, Simberloff et al. 2011) suggest that such accord may not be possible in the future. It is questionable whether speaking with one voice is even desirable: in the context of climate change, Curry (2011) argues that pressure to achieve consensus may have led the Intergovernmental Panel on Climate Change (IPCC) to oversimplify some issues of high uncertainty, thereby hampering the formulation of appropriate policy decisions; and similar concerns have been raised in the context of biodiversity conservation (Turnhout et al. 2012). An alternative to seeking consensus would be for invasion biologists to acknowledge the uncertainties and to engage transparently with stakeholders and the public in deliberations about conflicting opinions (Larson et al. 2013) or diverging management priorities (Bayliss et al. 2013). Here invasion biologists should take the role of "honest brokers of policy alternatives", taking into account different prevalent values and policy preferences, rather than adopting the role of "issue advocates" (Pielke Jr. 2007, Sarewitz 2011).

Conclusions

Our results uncovered a high diversity of perspectives within and between two expert groups, invasion biologists and landscape experts, on how to frame and to value biological invasions. Such dissent is in strong contrast with the broad consensus that experts claim in scientific synthesis articles and policy documents (e.g., Millennium Ecosystem Assessment 2005).

We propose that dissent among experts arises for many reasons, and multifarious solutions are therefore needed to improve the situation. First, irreducible uncertainties and contingencies should be acknowledged and taken into account in invasive species research and risk assessments (Hulme 2012, Jeschke et al. 2012, Heger et al. 2013a, Kueffer et al. 2013, Larson et al. 2013). Second, rather than attempting to establish precise definitions for key concepts such as 'non-native' or 'invasive' that all experts can share, it may be better to recognize explicitly alternative definitions that are valid for particular purposes (Hodges 2008, Heger et al. 2013a, Heger et al. 2013b). It can be argued that many conflicts about invasive species between social and natural sciences have arisen from a failure to recognize that different disciplines may use the same term

to mean different things. Third, the process of risk assessment is complicated by uncertainties related to the valuation of effects of non-native invasive species. The problems of multiple effects and multiple adequate values are widespread in environmental problem solving, and there is a broad literature on multi-criteria and participatory valuation and decision-making methodologies. Such approaches should be applied in invasive species risk assessment, management, and communication. Lastly, invasion biologists have differing views of the appropriate role for experts in societal decision-making, and especially the degree to which they should advocate particular viewpoints (Young and Larson 2011). Our results indicate that invasion biologists, rather than claiming to represent a consensus when none exists, should engage transparently with stakeholders in deliberations about conflicting opinions and alternative concepts, thereby adopting the role of "honest brokers of policy alternatives" (Pielke Jr. 2007, Sarewitz 2011).

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Appendix I

Questionnaire. (doi: 10.3897/neobiota.20.6043.app1) File format: Microsoft Word Document (docx).

Explanation note: Interview guideline: perception / valuation of ecosystem change related non-native, invasive plants.

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Appendix II

Socio-demography of the study participants. (doi: 10.3897/neobiota.20.6043.app2) File format: Microsoft Word Document (docx).

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Forestry trial data can be used to evaluate climate-based species distribution models in predicting tree invasions

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Abstract

Climate is frequently used to predict the outcome of species introductions based on the results from species distribution models (SDMs). However, despite the widespread use of SDMs for pre- and post-border risk assessments, data that can be used to validate predictions is often not available until after an invasion has occurred. Here we explore the potential for using historical forestry trials to assess the performance of climate-based SDMs. SDMs were parameterized based on the native range distribution of 36 Australian acacias, and predictions were compared against both the results of 150 years of government forestry trials, and current invasive distribution in southern Africa using true skill statistic, sensitivity and specificity. Classification tree analysis was used to evaluate why some Australian acacias failed in trials while others were successful. Predicted suitability was significantly related to the invaded range (sensitivity = 0.87) and success in forestry trials (sensitivity = 0.80), but forestry trial failures were under-predicted (specificity = 0.35). Notably, for forestry trials, the success in trials was greater for species invasive somewhere in the world. SDM predictions also indicate a considerable invasion potential of eight species that are currently naturalized but not yet widespread. Forestry trial data clearly provides a useful additional source of data to validate and refine SDMs in the context of risk assessment. Our study identified the climatic factors required for successful invasion of acacias, and accentuates the importance of integration of status elsewhere for risk assessment.

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Keywords

Species distribution models, model evaluation, Australian acacias, classification tree, forestry, alien trees, invasions, Southern African Plant Invaders Atlas

Introduction

Predicting which species will escape from forestry plantations and become invasive remains a challenge in invasion biology (Daehler et al. 2004). Such prediction is an essential requirement for proactive management (Ficetola et al. 2007). Propagule pressure, residence time, species traits, environmental factors, interactions of introduced species with the native species, and historical factors have all been indicated as drivers of invasion success (Castro-Díez et al. 2011; Křivánek et al. 2006; Lockwood et al. 2009; Pyšek et al. 2009; Thuiller et al. 2006; Wilson et al. 2007), with invasions from silviculture as no exception (Castro-Díez et al. 2011; Gallagher et al. 2011). However, climate plays a fundamental role in determining species distributions (Gaston 2003), and the predictive success of invasive risk assessments is still largely a function of invasive siveness elsewhere and climate suitability (Hulme 2012).

Species distribution models (SDMs) have been widely used to predict invasions (Elith and Leathwick 2009; Pauchard et al. 2004; Peterson 2003; Zhu et al. 2007). An SDM is a mathematical description of the species distribution in environmental space that can be used to predict the distribution of species in geographic space (Peterson et al. 1999). The models combine species occurrence records and environmental variables (Peterson and Holt 2003) to create a climatic envelope model. The resulting model can be projected to any geographic space to identify regions that are suitable for species. The models can be based on native distribution records, introduced distribution records, or both (Steiner et al. 2008). SDMs can therefore be used to identify areas that are suitable for species even before introduction to predict which areas are likely to be invaded (Guisan and Zimmermann 2000). SDMs have considerable potential in risk assessment but they are seldom tested in predicting successful tree establishments but see Nuñez and Medley (2011).

The use of SDMs in management of invasive species can be considerably improved by independent datasets to validate SDM predictions (Allouche et al. 2006; Fielding and Bell 1997). Appropriate datasets should contain information on species that were repeatedly introduced in different localities with a clear indication of introduction outcome (i.e. success or failure). It is important that the records on introduction outcome explicitly indicate which factors influenced the outcome (e.g. climate or biotic). However, these ideal datasets are rarely available. Therefore, invaded range data have been used to evaluate SDM predictions (McGregor et al. 2012b; Nuñez and Medley 2011; Nel et al. 2004; Rouget et al. 2004; Wilson et al. 2007). However, such analyses are limited to established widespread invasive species, ignoring any failed introductions.

While alien trees and shrubs have been introduced in different parts of the world to fulfil a wide range of human needs (Richardson and Rejmánek 2011), historically forestry has been one of the most important pathways (Pyšek et al. 2009; 2011). Introduced forestry species contribute to the economies of many countries, but can also cause major problems as invaders of natural and semi-natural ecosystems (Essl et al. 2010, 2011; Richardson and Rejmánek 2011). Such introductions have often been well documented, for example government forestry trials throughout southern Africa were reviewed by (Poynton 1979a, b; 2009). The data from these trials provide historical information on intentional introductions and on their outcome, making it possible to explore factors influencing the success of introductions across different areas.

The aims of this study are to evaluate species distribution models using both forestry trial data and invaded range data, and to investigate why some trials succeeded while others failed. To do this, we narrowed the taxonomic range to a well studied group, Australian acacias. Australian acacias are a good model group to understand plant invasions because *Acacia* is a speciose genus that contains many introduced and invasive species (Richardson et al. 2011). They are also a good group for exploring SDMs because native ranges in Australia and introduced ranges in southern Africa are well known and documented (Van Wilgen et al. 2011). Around 80 Australian acacias have been introduced in southern Africa, 36 of which were included in forestry trials (Richardson et al. 2011; Poynton 2009, Table 1). Currently, sixteen *Acacia* species are confirmed as invasive and three species are reported to be naturalized, but it is not clear whether other species are also likely to invade or not (Richardson et al. 2010, 2011; Van Wilgen et al. 2011; Wilson et al. 2011).

First we used data on the outcome of forestry trials and data on invasive plant distributions to evaluate SDMs. We then assessed why some forestry trials succeeded but others failed. Lastly, we determine which introduced species have a large potentially suitable but not currently occupied range, i.e. which species have a high invasion debt (Essl et al. 2011).

Methods

Study species and datasets

Species distribution models for Australian acacias were calibrated using occurrence records from their native range (Australia) and then projected to southern Africa based on Richardson et al. (2011) approach. The models were evaluated using presence records from the invaded range in the Southern African Plant Invaders Atlas (SAPIA: Henderson 2007) and records of success and failure obtained from government forestry trials (Poynton 2009).

Species distribution modelling

Model calibration

Numerous approaches have been developed to model the potential distribution of invasive species with various degrees of success (Gallien et al. 2012; Peterson 2003).

Here we chose a simple SDM approach that was quick to implement. The models were originally developed for 838 Australian *Acacia* species (Richardson et al. 2011). The approach was slightly modified as our pilot study indicated that some of the species ranges were under-predicted when using the exact approach. Minimum and maximum values for each variable over the range of species occurrence were used to define the range of each species. We also decided to use four predictor variables instead of six as this gave more sensible predictions. The model that we produced is equivalent to the marginal range of BIOCLIM but uses only four predictor variables (Nix 1986).

We obtained a dataset of occurrence records for the selected species (Table 1) from the Australian Virtual Herbarium (accessed 29th June 2010) with only one occurrence record retained per 10 minute grid cell for each species to reduce spatial sampling bias. Richardson et al. (2011) reported that to clean data all names were checked against the native species list while hybrid, varieties, subspecific information and authorities were generally removed for simplicity and to make the list comparable. The four bioclimatic variables used to build the SDMs were annual mean temperature (Bio_1), maximum temperature of the warmest month (Bio_5), minimum temperature of coldest month (Bio_6), and annual precipitation (Bio_12) all obtained at a 10 minute spatial resolution from Worldclim [www.worldclim.com (Hijmans et al. 2005)].

For each species we calculated the minimum and maximum values extracted from occurrence records for each predictor variable. These values were used to identify the range of values that each species could tolerate. For each species, we reclassified each of the four predictor variable maps into a map consisting of presence (value = 1) or absence (value = 0), using the minimum and maximum values calculated for that species. We then multiplied these presence/absence maps to generate a final map indicating the potential distribution of that species. The analysis was conducted using the R statistical software (v. 2.11, R Development Core Team 2010). The models were projected to southern Africa to identify climatically suitable regions for each species.

Model evaluation

We evaluated the relationship between predicted distributions and actual distributions (forestry trials and SAPIA data) using several measures. Sensitivity is the proportion of observed presences predicted present and quantifies the omission error; specificity is the proportion of observed absences predicted absent and quantifies commission error (Fielding and Bell 1997). These measures range from 0 to 1 with 0 indicating no agreement between predicted and actual data and 1 indicating a perfect agreement. True skill statistic (TSS) includes omission and commission errors (Allouche et al. 2006; Fielding and Bell 1997), and ranges from -1 to +1, where +1 indicates perfect agreement and values of zero or less indicates a performance no better than random. We used TSS to evaluate SDMs because TSS has been shown to be insensitive to prevalence (Allouche et al. 2006).

Species	Total number of trials	Success	Number of records in SAPIA	QDGCs occupied in SA	Status in southern Africa
A. acuminata	13	3	0	0	Introduced
A. adunca	1	0	2	2	Naturalized
A. adsurgens	2	2	0	0	Introduced
A. aneura	4	3	0	0	Introduced
A. aulacorpa	4	2	0	0	Introduced
A. auriculiformis	3	2	0	0	Introduced
A. baileyana	5	4	184	101	Invasive
A. binervata	1	1	0	0	Introduced
A. cowleana	2	1	0	0	Introduced
A. crassicarpa	2	1	0	0	Introduced
A. cultriformis	7	3	1	1	Naturalized
A. cyclops	2	2	1282	172	Invasive
A. dealbata	13	12	1667	299	Invasive
A. decurrens	5	2	341	124	Invasive
A. elata	9	3	99	48	Invasive
A. falciformis	4	2	0	0	Introduced
A. fimbriata	1	1	1	1	Naturalized
A. holosericea	4	1	1	0	Introduced
A. implexa	0	0	3	3	Invasive
A. leptocarpa	2	2	0	0	Introduced
A. ligulata	1	1	0	0	Introduced
A. longifolia	5	4	446	97	Invasive
A. mangium	3	1	0	0	Introduced
A. mearnsii	13	10	4313	462	Invasive
A. melanoxylon	28	20	678	167	Invasive
A. paradoxa	1	1	4	2	Invasive
A. pendula	6	3	0	0	Introduced
A. podalyriifolia	3	2	159	78	Invasive
A. prominens	2	2	0	0	Introduced
A. pycnantha	9	8	182	38	Invasive
A. retinodes	2	2	0	0	Introduced
A. rubida	1	1	0	0	Introduced
A. saligna	8	5	1302	164	Invasive
A. schinoides	1	1	0	0	Introduced
A. stricta	0	0	6	6	Invasive
A. viscidula	1	1	1	1	Naturalized
Total	168	109	10672	1766	

Table 1. The number of government forestry trials, the number of successful trials; the number of records in SAPIA, the number of QDGCs occupied in South Africa, Lesotho and Swaziland; and status in southern Africa for the species explored in the study.

The role of forestry trials and invaded range data for SDMs evaluation

Government forestry trials

In southern Africa, forestry trials for Australian acacias were conducted at 67 stations from the 1820s to the 1960s for 36 species (Poynton 2009). Trial data include records on introduction date (that can be used to quantify the importance of residence time in explaining invasions), and the number of stations and the number of times that a species was trialled (that can be used to quantify the effect of propagule pressure). The forestry trials dataset covers ten countries (namely, Angola, Botswana, Lesotho, Malawi, Mozambique, Namibia, South Africa, Swaziland, Zambia, and Zimbabwe), i.e. most of southern Africa.

Of the 168 forestry trial records obtained from this dataset, 129 records had precise geographic location and trial outcome and could be used to evaluate the SDMs (see Table 1). While subspecific taxa can occupy different climatic niches (Thompson et al. 2011), for simplicity and as naming was not consistent or verifiable, all species that had varieties or subspecies were grouped together (e.g. plantings of *Acacia longifolia* subsp. *longifolia* and *Acacia longifolia* ssp. *sophorae* were considered jointly as *Acacia longifolia*). We also only analysed species with four or more trials. This gave 14 Australian acacias with which to evaluate SDMs and the relative importance of variables in explaining the outcome of the forestry trials. We quantified the accuracy of predictive power of SDMs for each species (n=14) found in forestry trials by calculating true skill statistic, sensitivity and specificity.

Southern African Plant Invaders Atlas (SAPIA)

This dataset contains records for over 700 naturalized and invasive species, with information on abundance, habitat preferences, time of introduction and distribution (Henderson 1998). Here we restricted our analyses to Lesotho, South Africa and Swaziland as the other regions are relatively poorly sampled and use the SAPIA version accessed April 2012. The accuracy of SDMs for each species (n=11) found in SAPIA was quantified by calculating sensitivity only as SAPIA is a presence only dataset.

Why did some forestry trials succeed while others failed?

A classification tree approach (Breiman et al. 1984) was used to identify which of several potential predictor variables could predict the outcome of forestry trials (Table 2). We considered the following variables: 1) indication of herbivory or other biotic factors (birds or hares eating seedlings as noted on the original trial record); 2) climatic suitability; 3) South African Biome; and 4) the invasive status of the species globally. The current invasive status in South Africa and global invasive status of each species
Variable	Coded	Criteria	Justification	Data sources	
Trial	0/1	0- failure (absence)		Pownton (2000)	
outcome	0/1	1-success (presence)		roynton (2009)	
Biotic	Y/N	Did species fail because seeds were eaten by animals and birds?	Biotic factors have been indicated to influence survival that can lead to naturalization (Nuñez and Medley 2011)	Poynton (2009)	
Climatic suitability	0/1	0-Climate not suitable 1-Climate suitable	Climatic suitability is widely used to predict outcome of introductions McGregor et al. (2012).	Species distribution models	
Climatic variables	Bio_1,bio_5, bio_6, bio_12	Annual Mean temperature, Maximum Temperature of the Warmest Month, Minimum Temperature of the Coldest Month & Annual precipitation	Did trials succeed because of precipitation and temperature ranges? Castro-Díez et al. (2011)	Hijmans et al. (2006)	
Biome	Names	South African biomes	Were trials successful because of the biomes they were introduced to? Rouget et al. (2004)	Mucina and Rutherford (2006)	
Status	Introduced, Natura- lized or invasive (sensu Richardson et al. 2000)	Invasiveness elsewhere according to Richardson et al. (2011)	Invasiveness elsewhere is one of the best predictors of the outcome of species introductions Hulme (2012)	Richardson et al. (2011)	

Table 2. Variables used to quantify why some forestry trials of *Acacia* species in southern Africa succeeded while others failed.

were obtained from Richardson et al. (2011). Climatic suitability was coded as either suitable or unsuitable as predicted by SDMs and biotic factors [e.g. whether seeds or seedlings were eaten by hares or birds as recorded in Poynton (2009)] were coded as either yes or no depending on trial outcome.

The classification tree was constructed by repeatedly splitting data, defined by a simple rule based on a single explanatory variable at each split. At each split, the data were partitioned into two exclusive groups, each of which was as homogeneous as possible (Breiman et al. 1984). An optimal tree was then determined by testing for misclassification error rates for the largest tree as well as for every smaller tree by tenfold cross-validation constructed in CART Pro Ex v. 6.0. The program builds a nested sequence of branches by recursively snipping off the less important splits in terms of explained deviance. The length of the tree was controlled by choosing the one-SE rule, which minimizes cross-validated error within one standard error of the minimum cost tree rule (Pyšek et al. 2009).

Which species that are not yet widespread have a large potential suitable range?

Occupancy of each species was calculated at the quarter degree grid cell (QDGC, 15 min. × 15 min.) level. The current distribution of Australian acacias in Lesotho, South

Africa, and Swaziland was based on the number of QDGCs occupied as recorded in both the SAPIA and the forestry trial databases. Species potential distribution was estimated based on climatic suitability and range size as the percentage of southern Africa (South Africa, Lesotho and Swaziland) predicted suitable by SDMs.

Results

Evaluation of SDMs using forestry trials and invaded range data

The SDMs successfully predicted the outcome (success or failure) for 81 of the 129 forestry trials (63%) (overall TSS = 0.15, Table 3), with a high percentage of true presences predicted as present (sensitivity = 0.80) but a rather low percentage of true absences predicted as absent (specificity = 0.35). However, there was a higher proportion of false absences than false presences (Table 3). SDM evaluation varied between species, with five species having low sensitivity values and ten with low specificity values (Table 3).

Observed invasive ranges of Australian acacias in southern Africa are generally correctly predicted as suitable based on the SDMs (sensitivity = 0.87). However, the predictions mismatched 461 (13%) invasive range records (i.e. 13% of the records indicate that species invaded areas that are climatically unsuitable; Table 4). Most of the invasive species have the potential to substantially increase their ranges because more than half of southern Africa is predicted to be suitable.

Acacia dealbata and A. mearnsii are provided as visual examples (Fig. 1).

Explaining success or failure of forestry trials

Using climatic suitability alone, 81 trials out of 129 (model accuracy = 0.63) were correctly predicted (Table 3), while 87 (model accuracy = 0.67) records were correctly predicted by the criterion "invasive elsewhere" (Fig. 2: Node 2 and 3). Based on the classification tree (Fig. 2), three variables (invasive elsewhere, annual mean temperature, and mean temperature of the coldest month) together accurately predicted 72% of the forestry trial records (i.e. 93 trials). The classification tree analysis correctly predicted forestry trial outcome significantly (sensitivity = 086, specificity = 0.36 and TSS = 0.22).

Determining species that have a high risk of becoming widespread invaders

The wetter parts of the region were identified as most suitable for the analysed suite of Australian acacias. SDMs predicted that thirteen species can be widespread with 20 % of southern Africa predicted to be suitable [*Acacia acuminata*, *A. adunca*, *A. aneura*,

Table 3. Measures used to evaluate models using government forestry trials dataset in southern Africa; a-number of cells for which presence was correctly predicted by the model; b- number of cells for which the species was not found but the model predicted presence; c, number of cells for which the species was found and the model predicted absence; d, number of cells for which absence was correctly predicted by the model. Sensitivity (proportion of actual presences predicted as such); specificity (proportion of actual absences predicted as such); TSS [true skill statistic (sensitivity + specificity-1].

Species	Number of trials	a	b	с	d	Sensitivity	Specificity	TSS
A. acuminata	13	1	5	1	6	0.50	0.54	0.04
A. aneura	4	1	1	2	0	0.33	0.00	-0.67
A. baileyana	5	4	1	0	0	1.00	0.00	0.00
A. cultriformis	5	0	2	1	2	0.00	0.50	-0.50
A. dealbata	13	11	0	1	1	0.91	1.00	0.91
A. decurrens	7	2	4	0	1	1.00	0.20	0.20
A. elata	9	2	4	2	1	0.50	0.20	-0.30
A. falciformis	4	2	2	0	0	1.00	0.00	0.00
A. longifolia	5	4	1	0	0	1.00	0.00	0.00
A. mearnsii	13	7	2	3	1	0.70	0.33	0.03
A. melanoxylon	28	20	8	0	0	1.00	0.00	0.00
A. pendula	6	1	1	2	2	0.33	0.67	0.00
A. pycnantha	9	7	1	1	0	0.88	0.00	-0.20
A. saligna	8	2	0	3	3	0.40	1.00	0.40
Overall	129	64	32	16	17	0.80	0.35	0.15

Table 4. Measures used to evaluate models using Southern African Plant Invaders Atlas; a-number of cells for which presence was correctly predicted by the model; c-number of cells for which the species was found but the model predicted absence.

Species	Number of records	a	с	Sensitivity
A. baileyana	86	82	4	0.95
A. cyclops	141	137	4	0.97
A. dealbata	717	707	10	0.99
A. decurrens	157	155	2	0.99
A. elata	20	17	3	0.85
A. longifolia	79	79	0	1.00
A. mearnsii	1916	1485	431	0.78
A. melanoxylon	163	163	0	1.00
A. podalyriifolia	56	51	5	0.91
A. pycnantha	83	82	1	0.99
A. saligna	53	52	1	0.98
Overall	3471	3010	461	0.87



Figure 1. Current distribution [from both forestry trials (noted as trial failure or success) and SAPIA] and potential distribution for: **a** *Acacia dealbata* and **b** *A. mearnsii* in Lesotho, South Africa, and Swaziland.



Figure 2. Classification tree analysis of the probability that a species will succeed (blue part of the bar) or fail (red) in southern African forestry trials based on various variables (see Table 2: trial data and variables used). Each node shows the number of successes and failures in each class, the total number of cases (N) and a graphical presentation of the percentage of success and failure cases (horizontal bar). For each node the splitting criterion is written in caps on top of the nodes. Status is similar to invasiveness elsewhere and the two environmental variables: Bio_1 is annual mean temperature and Bio_6 is minimum temperature of the coldest month.

A. cultriformis, A. falciformis, A. fimbriata, A. implexa, A. paradoxa, A. pendula, A. retinodes, A. rubida, A. stricta, and A. viscidula (Fig. 3)]. The remaining four species (A. mangium, A. prominens, A. schinoides and A. binervata), appear to have a potential of localized extensive spread (Fig. 3). All of these species have not yet reached the full extent of climatically suitable ranges (see Appendix – Fig. S1).



Figure 3. The relationship between potential and current distributions in Lesotho, South Africa, and Swaziland expressed as total number of QDGCs currently occupied from SAPIA and forestry trial successes (with a cut off of 20% of southern Africa QDGCs climatically suitable) for 17 species that are not yet widespread in southern Africa.

Discussion

In this study, we found that forestry trial data provided useful data for SDM evaluation as it contains information on species that were repeatedly introduced in different localities within southern Africa with a clear indication of trial outcome. Trials were successful in areas that are predicted as climatically suitable by SDMs (sensitivity = 0.80; Table 3). McGregor et al. (2012b) found that successful naturalization of pine species in plantations was linked to a good climate match between their native range and introduced ranges. The results emphasize the value of incorporating forestry data in to SDMs when predicting species distributions.

SDMs could not accurately predict the failures of species in trials (specificity = 0.35; Table 3) and this suggests that climatic suitability only provides a broad picture of where an introduced species might survive, but there are other factors that determine whether an introduced species will be successful like biotic interactions and evolutionary capacity to adapt (Blackburn et al. 2011; Nuñez and Medley 2011; Soberón and Peterson 2005). Factors such as seed predation, competition with local plants and herbivory can have strong effects on *Acacia* success in trials.

SDMs correctly identified invaded ranges of Australian acacias in southern Africa. SDMs correctly predict regions of introduction but not the total invaded ranges (e.g. *A. mearnsii*, Fig. 1). Similarly, previous studies indicated that SDMs calibrated on native range records were able to predict region of introduction, but not the total invaded range, indicating a possible niche shift (Beaumont et al. 2009; Broennimann et al. 2007). This suggests that species may alter climatic niches during the invasion process. However, there is an on-going debate in literature about the prevalence of niche shift (Peterson 2011). According to the SDMs predictions, even widespread species (e.g. *A. dealbata*) have not yet fully occupied all climatically suitable areas in southern Africa. So management actions should be focused on containment, with resources dedicated to detecting and removing outlying populations of such species.

In line with other studies, we found that the success of species after introduction in the new ranges was greater for species recorded as invasive elsewhere (McGregor et al. 2012a; Reichard and Hamilton 1997; Scott and Panetta 1993; Williamson and Fitter 1996). As such Australian acacias that succeeded in trials appear to be a non-random subset in the global pool: they tended to be species that are invasive elsewhere and are within climatic areas similar to their native ranges hence they are likely to invade large areas. Since Australian acacias that are known to be invasive elsewhere are already planted in southern Africa for forestry purposes (Richardson et al. 2011), their spread should be controlled.

Australian Acacia species that are not yet widespread are likely to spread to currently unoccupied climatically suitable ranges as SDMs predictions indicate that a large portion of Lesotho, South Africa and Swaziland is suitable for invasion by 13 of the 17 currently introduced or naturalized (Fig. 3). We believe this is a major invasion debt and not simply an over-prediction in the SDMs, because there is a strong correlation between extent of usage and invasive distributions for Australian acacias in South Africa (Wilson et al. 2011). The widespread invaders are those species that have been planted for forestry, dune stabilization or ornamental purposes. However, many other introduced species were only ever planted in forestry trials or arboreta. As such their currently restricted distribution is the result of low propagule pressure, but given opportunities and time, these species can and do spread (Kaplan et al. 2012; Zenni et al. 2009; Kaplan et al. in press). Species that have a large potential range and are invasive elsewhere (Fig. 3 and Supplementary material Fig. S1) should be prioritised for management, and where possible eradicated, e.g. Acacia implexa, A. paradoxa and A. stricta in South Africa (Kaplan et al. 2012; Zenni et al. 2009; Kaplan et al. in press). Commercial forestry is one of the major pathways to tree invasions and availability of introduction data can be useful for screening potential invaders when coupled to SDMs. SDMs provide useful information that can influence management decisions on early detection, prioritization, and more targeted research. SDMs also provide information for rapid assessment of potential distributions of alien species based on climate, even before introduction.

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Appendix



Figure S1. Current and potential distributions of sixteen species that are not widespread in southern Africa arranged on the basis of their suitable range size : **a** *Acacia paradoxa* **b** *A. implexa* **c** *A. cultriformis* **d** *A. falciformis* **e** *A. pendula* **f** *A. rubida* **g** *A. stricta* **h** *A. retinodes* **i** *A. fimbriata* **j** *A. aneura* **k** *A. viscidula* **I** *A. acuminata* **m** *A. adunca* **n** *A. binervata* **o** *A. schinoides* **p** *A. prominens* **q** *A. mangium.* The grey shading indicates areas that SDMs have identified as suitable by SDMs while the white shading indicates unsuitable areas.

RESEARCH ARTICLE



Condition and morphometric changes in tilapia (Oreochromis sp.) after an eradication attempt in Southern Louisiana

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Abstract

A hybrid form of tilapia was introduced into Port Sulphur, Louisiana and was subsequently managed by treatment with rotenone and stocking of native predatory fishes. Measurements of tilapia from before this management event were compared to measurements of tilapia in the two years after the treatment. Post-management tilapia were consistently deeper in body and had greater weight per unit length (condition) when compared to pre-management fish. Procrustes generalized least squares data supported this by consistently finding post-management tilapia to be consistently deeper in body and head shape than pre-management fish. Although this could indicate the effectiveness of stocking native predators, several other factors, including two cold winters, seasonal effects, and less competition, may have contributed to this result.

Keywords

Ivasive, tilapia, morphology, eradication, cichlid

Introduction

Previous work has shown that both natural and human impacts can change the morphology of populations. Grant and Grant (2002) and Witte et al. (2008) found that changes can occur as a fixed result over years, while Tollrian and Harvell's (1999) work found it could occur within a generation as phenotypic plasticity. Rapid morphological change has been observed as a response to predation in a variety of species, including plants, cladocerans (Stibor 1992), snails (Brönmark et al. 2011) and fishes (Brönmark and Miner 1992). Fish have shown repeatedly that they can alter their body change in response to predators. Brönmark and Miner (1992) suggested that Crucian Carp (Carassius carassius) could increase their body depth to prevent their consumption by Northern Pike (Esox lucius). Additional studies have shown that Western Mosquitofish, Gambusia affinis, can also change their morphology in response to predators. In contrast to the Crucian Carp, G. affinis have been shown to decrease their body depth, improving their biomechanical capacity for escape (Langerhans et al. 2004). In addition to predation, other factors can affect fish morphology as well, such as salinity (Collyer et al. 2005), water velocity (Imre et al. 2002) and stunting (Chizinski et al. 2010). A previous study examining tilapia found that invasive Oreochromis mossambicus exhibit a decrease in body depth when compared to their native populations (Firmat et al. 2012).

Tilapia, in particular the genus Oreochromis, have been introduced extensively and are listed as one of the 100 worse invasive species in the world (Lowe et al. 2000). Eradication and understanding of their invasive biology is an important concern to protect biodiversity and local fisheries. Although tilapia are a common invasive, no study has examined morphological changes in invasive tilapia after eradication efforts. In Port Sulphur, Louisiana there was an introduction of an unknown tilapia species into a seven-mile canal system. Over one million invasive tilapia were killed by rotenone treatment in the summer of 2009 in an eradication attempt monitored by Louisiana Department of Wildlife and Fisheries. No Largemouth Bass (Micropterus salmoides), gar (Lepisosteidae), or other species capable of eating an adult tilapia were collected after the rotenone treatment. One month after rotenone treatments, a variety of predatory fish were then stocked by LDWF and a monitoring program was put in place for the next several years. Ten tilapia were collected during the next two years and then they were not observed for two more years, from April 2011 until at least February of 2013 (Lorenz, unpublished data). The tilapia collected after rotenone treatment and predator stocking were noticeably unique in appearance, apparently with a deeper body.

Of note, Firmat et al. (2012) observed a strong effect of phylogenetic history on morphology, regardless of a variety of environmental conditions faced by multiple populations of invasive *O. mossambicus*. This would indicate the importance of founder effect as opposed to phenotypic plasticity. The unique aspect of this Louisiana population is the possibility of multiple founder events (the initial founding population and the founders that survived rotenone and/or other environmental effects).

Methods

Twenty pre-management tilapia were collected by the initial rotenone treatment (2009), and ten post-management tilapia were collected by electrofishing (2010). Electrofishing was performed in the identical location to where fish were sampled before rotenone, within 100 meters of where the canal passes under Highway 23, north of Port Sulphur, Louisiana (29°31'29.87"N, 89°44'49.89"W). Standard length (SL) of each fish was measured to the nearest 0.1 cm on a Wildco fish measuring board, and body mass (BM) was weighed to the nearest 0.1 g on a Ohaus Navigator portable scale. Body depth was also measured to the nearest 0.1cm and all specimens were photographed by a digital camera (Pentax K-10D).

Analysis of Covariance Models

Two different analysis of covariance (ANCOVA) tests were performed to compare fish pre and post management. Each measurement (standard length, body depth, and weight) was \log_{10} -transformed prior to analysis for allometric scaling. The predictor variables for both ANCOVAs were standard length and a factor designating whether each individual fish was pre or post management (hereafter referred to as year). The first ANCOVA weight as a response variable and the second used body depth as a response variable. The design of these tests was to see if year was a significant predictor for either response variable with standard length as a covariate (*a*=0.05). Each model initially included an interaction between year and standard length. If the interaction term was not statistically significant (at *a*=0.05), it was removed. The ANCOVAs were created using R statistical software package version 2.12.1 (R Core Team 2012).

Geometric Morphometrics

Standardized photographs of individuals were entered into TPSDig2 where 15 landmarks were placed on each individual to generate the *x* and *y* coordinates used for further analyses (Rohlf 2005). Landmarks were chosen in a fashion similar to Klingenberg et al. (2003), with additional measurements to indicate other possible morphological changes, such as eye size (Figure 1). Landmark files were imported into MorphoJ version 1.04a where partially generalized Procrustes coordinates were generated (Rohlf and Slice 1990, Rohlf and Marcus 1993, Klingenberg 2011).

The Procrustes coordinates were then used to generate principal components (PCs). A multivariate analysis of covariance (MANCOVA) design was then implemented with two covariates, and year as predictor variables. The response variable of this model was all PC components with an eigenvalue > 1 (PC1 – PC5), accounting for 82% of the variance. Previously, centroid size alone has been used as a covariate for similar MANCOVAs, but in this case it was also found to be correlated with standard



Figure 1. Description of the landmarks. I tip of snout at fold anterior to ethmoid/nasal bones, with mouth closed 2 anterior base of dorsal fin 3 base of the caudal fin at the level of the lateral line 4 anterior base of the anal fin 5 center of the eye 6 bottom of the eye 7 top of the eye 8 edge of the head directly above the center of the eye 9 posterior end of the dorsal fin base 10 base of the caudal fin, dorsal 11 base of the caudal fin, ventral 12 posterior end of the anal fin base 13 anterior end of the anal fin base 14 most posterior edge of operculum 15 corner of the mouth, where maxillary angle rests when the mouth is closed

length (Firmat et al. 2012). For our study, it was not highly correlated with standard length ($R^2 = 0.028$, p = 0.432), therefore both standard length and centroid size were used as covariates in our MANCOVA. All interactions were initially included in the model and any non-significant (*a*=0.05) terms were removed step-wise with higher order interactions being removed first.

A between groups PCA (bgPCA) was also performed. We modified the bgPCA section of the ordination program for R statistical software found in Zeldich et al. (2012) for this part. To remove the effects of centroid size and standard length, residuals from a multivariate regression were used (Shape ~ centroid size + standard length). The deformation along the first PC axis was plotted for each coordinate as this has been suggested as a preferred method for interpreting the change in shape data between groups (Mitteroecker and Bookstein 2011).

All analyses after generation of Procrustes coordinates were performed using R statistical software, unless otherwise noted (R Core Team 2012).

Results

Analysis of Covariance Models

An interaction between standard length and year was not found to be a significant predictor of weight (ANCOVA, d.f = 1, 26; F = 0.10; P = 0.760) or body depth (AN-



Figure 2. Relationship between log transformed standard length and log transformed weight as a scatter plot for fish from pre and post management (2009 and 2010, respectively). Two lines of best fit were created, one for each year group. The regression function for 2009 was y = -3.03x - 4.53, and was y = -3.12x - 4.57 for 2010, where y is \log_{10} transformed weight in grams and x is \log_{10} transformed standard length in mm.

COVA, d.f. = 1, 26; F = 0.06; P = 0.815), therefore it was excluded from the reduced model for both response variables. The covariate standard length was found to be significant for both the weight and the body depth ANCOVAs (ANCOVA; d.f. = 1, 27; F = 1041, P < 0.001; ANCOVA; d.f. = 1, 27; F = 539; P < 0.001; respectively). Weight was found to be significantly different between year groups (ANCOVA; d.f. = 1, 27; F = 109; P < 0.001). Body depth was also found to be significantly different between year groups (ANCOVA; d.f. = 1, 27; F = 67; P < 0.001). The relationship between both predictor variables and standard length were plotted as a scatter plot. Lines of best fit from a linear regression were fit to fish from 2009 and 2010. These plots show that both weight and body depth were higher for fish collected post management (2010) than pre management (2009; Figs 2 and 3).

Geometric Morphometrics

The step-wise model reduction of the MANCOVA indicated there were no significant interactions included in our model (all *P* values > 0.05). Using both centroid size and standard length as covariates, year bins were significantly different with respect to Procrustes coordinates (d.f = 5, 22; F = 8.9; P < 0.001; Table 1). These data suggests that variation between years is still apparent and it aligns along the first PC axis which



Figure 3. Relationship between log transformed standard length (x-axis) and log transformed body depth (y-axis) as a scatter plot for fish from pre and post management (2009 and 2010, respectively). Two lines of best fit were created, one for each year group. The regression function for 2009 was y = 1.11x - 0.61, and was y = 1.08x - 0.48 for 2010, where y is \log_{10} transformed body depth in mm and x is \log_{10} transformed standard length in mm.



Figure 4. Representative fish from 2009 and 2010.

Table 1. Table showing the results of the MANCOVA performed on shape for year bins.

Effect	df	Pillai	F	Р
Standard length	5, 22	0.73	11.9	< 0.001
Centroid size	5, 22	0.74	12.8	< 0.001
Year	5, 22	0.67	8.9	< 0.001

explains 35% of the total variation in shape among measured fish. Figure 4 shows representative fish from 2009 and 2010.

Figure 5 shows the deformation along PC1 of the bgPCA and illustrates marked differences between year categories. Procrustes coordinates near the anterior end of the



PC1

Figure 5. This figure shows the deformation along the first principal component (PC) of a between groups principal components analysis (bgPCA; between year groups). The principal components were calculated from the residuals of a multivariate regression (see Materials and Methods for more details). The solid line and points represents the mean shape of the Procrustes coordinates and the dashed line is the change along PC1 of the bgPCA. The arrows show the change for each coordinate.

fish are drawn in a posterior direction, while Procrustes coordinates at the anterior end of the dorsal and anal fins shift outward dorsoventrally and toward the anterior of the fish (Figure 5). This suggests the fish are becoming taller in body depth and shorter in overall length between year classes.

Discussion

Results from both ANCOVAs and all geometric morphometric analyses suggest that tilapia from each year bin were morphologically distinct. Post-management fish had higher bodies and were heavier per unit length than pre-management fish. The nature of our study, as well as other natural experiments, makes determining casual agents difficult if not impossible. However, the results presented here indicate that some underlying process(es) between the rotenone treatment in 2009 and 2010 caused significant changes in the morphology of tilapia from our study area.

Many possible reasons could explain this change in morphology. This apparent change in morphology could be an indicator of the success of the management plan stocking native predators. Past studies have shown that stocked predators can cause a change in the morphology of their prey (Brönmark and Miner 1992). Body depth increased in these tilapia in the same way that carp have shown increases in their body depth in response to predacious northern pike. It is important to consider other environmental conditions that occurred during this time, as well as other factors that are known to affect fish morphology besides predation.

After rotenone treatment there was a dramatic decrease in fish density and a clear decrease in tilapia abundance. While this is the desired effect of this method of management, it also reduces the level of competition in this habitat. Multiple tilapia could easily be caught with a blind throw of a cast net before the rotenone treatment (Lorenz pers. obs.). This sort of density can create stunting in fish, and stunting often has the opposite morphological effect of predators (Chivers et al. 2008). The higher bodied tilapia after the rotenone treatment may have acquired this morphology because of a release from such competition. Other studies on the effects of resource limitation have not been as conclusive, with different morphological changes observed in different species (Chizinski et al. 2010). The winters of 2009 and 2010 created water temperatures below 10 degrees Celsius in these canals, which is below the normally accepted lower thermal limit for this species (Green et al. 2012). The effect of temperature on morphology of fishes has been mostly unexplored, however one study did observe European sea bass (Dicentrarchus labrax) to be more slender at lower temperatures (Georgakopoulou et al. 2007). While this pattern would be opposite of our observations in this study, we felt it is important to acknowledge that temperature has been shown to affect fish morphology.

Breeding condition may also be a factor, as tilapia have been shown to have a change in body condition (and presumably morphology) depending on season (Hirpo 2012). Body condition changes were observed in Nile tilapia (*Oreochromis niloticus*), between the breeding and non-breeding seasons (Hirpo 2012). It is worth noting that the 2009 tilapia from this study were caught during the breeding season and the 2010 tilapia were caught out of the breeding season. It has also been shown that invasive species such as bluegill (*Lepomis macrochirus*) can produce different morphologies to feed on more pelagic or benthic prey (Yonekura et al. 2007). Such a large scale change in the Port Sulphur canal ecosystem driven by the rotenone treatment could have changed what food was available to the tilapia. But all stomach contents examined for both years appeared to contain only algae and detritus (Lorenz, unpublished data), leading us to believe this effect was minimal.

The relatively rapid response (possibly one generation) may indicate a stronger influence of either plasticity or a bottleneck effect as opposed to selection. There is a high probability of a founder event occurring in this closed and heavily monitored system. Founder effects are a part of invasive species biology, and this population likely had multiple founder effects (the original introduction and the dramatic decrease in individuals post-rotenone). However, a stochastic event such as the rotenone treatment was also a likely selective event on the phenotypes of the surviving fish. Morphology has been shown to change as a result of bottleneck events in fish (Shao et al. 2007), including with inbred cichlids (Winemiller and Taylor 1982). For invasive tilapia, the founder effect appeared more important than local selective forces in *O. mossambicus* (Firmat et al. 2012). The question of the relative importance of stochasticity, selection, and plasticity is still speculative at this point and requires further study.

Conclusion

Invasive species are a serious threat, in part because they can be phenotypically plastic (Davidson et al. 2011) and can induce morphological changes in native species (Phillips and Shine 2006). Examining these changes can indicate the adaptability and impact of invasive species. If these changes can also indicate the success or unintended impact of management practices, there is a tremendous potential benefit. Tilapia from Port Sulphur changed significantly in morphology between pre and post-management year groups, and this change may have occurred because of the predators intentionally introduced to control their population. Further experiments could eliminate other reasons for such a change in morphology and determine if the predators were the most likely cause for the morphological changes observed. Using predatory game fish for management of invasive species can be successful, as seen with the reduction of invasive alewife (*Alosa pseudoharengus*) by introduced Pacific salmon (*Oncorhynchus spp.*) in Lake Michigan (Fenichel et al. 2010). In addition to control of non-native species, there are additional benefits gained from these methods including the preservation of biodiversity and native fisheries.

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RESEARCH ARTICLE



The reproductive biology of Saccharum spontaneum L.: implications for management of this invasive weed in Panama

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Abstract

Saccharum spontaneum L. is an invasive grass that has spread extensively in disturbed areas throughout the Panama Canal watershed (PCW), where it has created a fire hazard and inhibited reforestation efforts. Currently physical removal of aboveground biomass is the primary means of controlling this weed, which is largely ineffective and does little to inhibit spread of the species. Little is known about reproduction of this species, although it is both rhizomatous and produces abundant seed. Here we report a series of studies looking at some of the basic reproductive mechanisms and strategies utilised by *S. spontaneum* to provide information to support development of better targeted management strategies.

We found that seed produced between September and November was germinable both in the lab and *in situ*. Genetic diversity of mature stands was assessed using microsatellite markers and found to be high, even at small scales. Studies of vegetative reproduction showed that buds on stems that had been dried for up to six weeks were still capable of sprouting. Separate experiments showed that stem fragments could sprout when left on the surface or buried shallowly and that larger pieces sprouted more readily than smaller pieces.

Collectively these results demonstrate that *S. spontaneum* in the PCW has the capability to produce many propagules that can successfully recruit and it is likely that seed dispersal drives the spread of the species. Timing of management actions to reduce flowering would significantly reduce the seed load into the environment and help to prevent spread to new sites. Similarly, where biomass is cut, cutting stems into smaller pieces will allow the stems to dry out and reduce the ability of buds to sprout. Additionally, attention should be paid to prevent accidental transport to new sites on machinery.

Keywords

Invasive species, seed germination, asexual reproduction, microsatellite

Introduction

Many of the "World's Worst Weeds" are perennial species with the ability to spread with both seeds and vegetative structures (Holm 1977) and perennial grasses are notorious invaders of both agricultural and natural areas (D'Antonio and Vitousek 1992). Of these, large-statured grasses are particularly difficult to manage due to their high biomass and rapid dominance both above- and belowground (Lambert et al. 2010). Grasses can produce copious amounts of seeds, which are often wind-dispersed and may remain dormant until conditions are right for germination (Donohue et al. 2010). In addition, many are rhizomatous and can spread vegetatively both to new sites and rapidly within a site once established (e.g. *Arundo donax* L., *Phragmites australis* (Cav.) Trin. ex Steud.; Boose and Holt 1999, Bart and Hartmann 2003). Stem fragments containing axillary buds may also play a role in dispersal to new sites (Boose and Holt 1999).

Saccharum spontaneum L. (wild sugarcane; Poaceae) is a polymorphic species believed to have evolved in India (Mukherjee 1957). It is a highly adaptable polyploid that grows in a wide range of habitats across southern Asia and east Africa to the Mediterranean, spanning the tropics to temperate regions from latitudes 8° S to 40° N (Daniels and Roach 1987; Tai and Miller 2001). Although it is both wind-pollinated and -dispersed, it also reproduces vegetatively, through clonal spread either from underground rhizomes or culm fragments. Because of S. spontaneum's potential to propagate via seeds and its propensity for aggressive rhizomatous spread, it is considered a weed, even in countries to which it is native such as India (Panje 1970, Yadav et al. 2007) and Thailand (Pichitkul 2009). It has also been introduced into other countries for use in sugarcane breeding programs (Bonnett et al. 2008) and is considered a noxious weed in many countries including the USA (USDA 2010). Research in India has shown that flowering in S. spontaneum is controlled by photoperiod, with vegetative growth occurring in the wet monsoon season, followed by a dormant phase during the dry season. In India, flowering is initiated at the end of the rainy season, with diurnal variations in humidity and temperature likely influencing both pollen and seed dispersal (Panje and Srinivisan 1959).

In the Republic of Panamá, *S. spontaneum* (Paja Canalera) has spread extensively in the Panama Canal Watershed (PCW) since the first herbarium specimen was collected in 1960 (MO1824369 J.E. Ebinger 490). It now dominates in abandoned agricultural lands and along human transportation corridors, such as roads and railroad tracks, encompassing over 3 percent of the watershed (ACP-ANAM 2006). It grows to an average height of 3-4 m in dense, impenetrable stands which impede growth of other plants and provide little useful habitat for wildlife. Efforts towards reforestation of the PCW are seriously hindered by this species, as it can inhibit germination, establishment, and growth of native tree species (Hammond 1999, Hooper et al. 2002, Jones et al. 2004) and increases the vulnerability of reforestation projects and nearby forests to devastating fires in the dry season (Saltonstall and Bonnett 2012).

Flowering of *S. spontaneum* across the landscape in Panama typically begins in August, midway through the rainy season which normally occurs from May through December. Inflorescences can be seen year-round, but are typically restricted to certain clones on a small scale during other times of the year (K. Saltonstall, pers. obs.). Flowering densities vary, averaging 4-5 stems/m² during the peak flowering season (Saltonstall and Bonnett 2012), and hundreds of seeds are produced by each inflorescence. However, the reproductive biology of *S. spontaneum* as an invasive species has not yet been studied. The relatively recent establishment and spread of *S. spontaneum* in Panama makes this an ideal environment to understand the relative contribution of sexual vs vegetative dispersal between and within sites.

The case for understanding the biology of invasive plants as a precursor to developing control strategies has been well made. Zamora et al. (1989) identified knowledge of the population dynamics and life cycle as key to finding the stage of development most vulnerable to control measures. In many cases the relative contributions of sexual and vegetative reproduction to invasive spread are largely unknown. Here we present a series of studies which evaluate reproductive and genetic factors that may contribute to the invasive success of *S. spontaneum* in Panama. The hypotheses that we tested were: 1) Seeds collected *in situ* are viable through the period of production, as tested under control conditions; 2) seeds can germinate *in situ*; 3) stands of mature plants are genetically diverse; 4) vegetative buds are able to produce plants under a range of conditions. We hope that a better understanding of these reproductive factors will assist in improving management strategies to prevent further spread throughout the country and beyond.

Methods

Study area

The Republic of Panamá is located at approximately 8–9° N latitude (Fig. 1), which is a latitude central to the native range of *S. spontaneum* (Mukherjee 1957). Day length varies only about one hour from its maximum at the June summer solstice to December and average daily temperatures range between 19°C and 35°C. During the rainy season months of May to December, rainfall averages around 240 mm per month, with rainfall occurring frequently (World Meteorological Organization 2010). All studies occurred during 2009, which was a year with typical rainfall patterns.

Germination ability

We collected seeds of *S. spontaneum* from 12 sites (Sites 1–12 Fig. 1; Appendix 1) in the PCW weekly between September and December. Each week three mature inflo-



Figure 1. Map of Panama showing the locations of 22 sites where *S. spontaneum* samples were collected. Seeds were collected weekly at Sites 1-12 for germination trials. Lines in the larger map indicate district boundaries. In the inset, the canal is shown between Panama City and Gamboa and major roads are indicated by grey lines.

rescences, from different plants within a few meters of each other, were sampled and assayed separately. Seeds that had disarticulated from the inflorescence but remained loosely attached were collected, and kept at room temperature until assayed within two days of harvest. When wet at the time of harvest due to rain, seeds were dried under ambient conditions prior to conducting germination assays.

One hundred seeds were taken at random from those collected from each inflorescence and germinated on moist paper towel in petri dishes (n=3 inflorescences per site per week). Seeds were germinated at 36°C as *Saccharum* seeds have a very high temperature optimum for germination of around 36°C (Skinner 1959, Singh 1988). Assays were conducted in the dark, as there is no evidence of a light requirement for the germination of *Saccharum* seeds (G. Bonnett, unpublished).

Germination was defined as root or radicle emergence visible to the naked eye. Seed germination was checked every three to four days and counted seedlings were removed from the plates. Total number of seeds germinated after two weeks is presented. For analysing the effect of date of collection on germination percentage we carried out a one-way ANOVA with date as a factor and log-transformed (log10(value+1)) germination data as the dependent variable (Sigmaplot 11, Systat Software Inc. San Jose, CA). Post –hoc comparisons of means were conducted using the Tukey method, for this and all subsequent analyses significance was tested at the 0.05 level.

In situ germination

To test if seeds would germinate *in situ*, vegetation was cleared and the soil surface raked on 16 September exposing areas of bare soil between two *S. spontaneum* stands (Site 6, Fig. 1, Appendix 1). The experiment comprised 10 replicates of three treatments, each in 60 by 120 cm plots. Treatment one, bare soil, was designed to observe any seedlings emerging from seeds deposited by wind. The second treatment comprised six mature inflorescences placed on each plot and covered with nylon flywire to prevent seeds from blowing away. Plots in treatment three were bare soil covered by nylon flywire, with no additional seeds added. One replicate of each treatment was randomly placed in each of 10 evenly spaced blocks. After 19 days we removed the mesh to allow continued growth of seedlings. The number of germinated *S. spontaneum* seedlings per plot was recorded one week after, and then every two weeks until nine weeks after the start of the experiment.

To test for differences in seedling numbers between treatments, we conducted a repeated measures analysis with time (within subject) and treatment (between subjects) as factors and the number of seedlings as the dependent variable (Sigmaplot 11). The number of seedlings was log-transformed (log10(value+1)) prior to analysis and post – hoc comparisons of means were conducted using the Holm-Sidak method (a variation of the Holm multi-comparison test using the Sidak correction (Sidak 1967)).

Genetic diversity of mature stands

To assess levels of genetic diversity within stands, plants were collected at 22 sites across central Panama, with a focus on the PCW but including the eastern- and westernmost edges of the invasion (Fig. 1, Appendix 1). Green leaves were harvested from individual culms spaced up to 10 m apart (n = 3 per site). To examine if the patterns we found at these sites were consistent across large stands, we also sampled parallel transects separated by 20 m at two independent stands in Soberania National Park within an area dominated by *S. spontaneum* (Sites 5 and 6, Fig. 1, Appendix 1; see Saltonstall and

Bonnett 2012 for a description of the stands). Five transects were laid out in Stand 1 and three in Stand 2 and samples collected every 10 m along the transects (n=26 for Stand 1, n=9 for Stand 2). All samples were kept frozen at -20°C until DNA was extracted using a CTAB extraction protocol (Doyle and Doyle 1987).

We assessed multilocus allele profiles using 12 microsatellite loci (msscir14, msscir17, msscir53, msscir58, SMC28, SMC221, SMC334, SMC336, SMC597, SMC1047, SMC1237, SMC1493; Brown et al. 2007; Pan 2006) targeting different regions of the genome. PCR amplifications were performed in 7 µL reaction volumes containing approximately 1 ng DNA, 0.056 U Amplitaq (Applied Biosystems, Inc., Carlsbad, CA), 1x reaction buffer (Applied Biosystems, Inc.), 3 mM MgCl₂, 200 uM dNTPS, 0.5 pmol of forward primer including an M13 tag, 2.5 pmol of reverse primer, 2 pmol of FAM, PET, VIC, or NED labelled M13 primer, and 1 mg mL⁻¹ BSA. All PCR reactions were conducted with 2 min of denaturation at 94°C, 35 cycles of denaturation at 94°C for 45 s, annealing at 56°C for 25 s, and 25 s of extension at 72°C, and a final extension period of 72°C for 5 min in a thermal cycler (Eppendorf Multimax, Eppendorf, Hamburg, Germany). Primers were not multiplexed due to the high ploidy level of the species, but PCR reactions with differing florescent tags were multiloaded for capillary electrophoresis on an ABI prism 3730 automated sequencer. Fragment sizes were analysed using GeneMapper 3.7 (Applied Biosystems Inc.) and individuals were scored for presence or absence of identified alleles for each locus. All scored alleles had consistent results over replicate amplifications. Due to polyploidy in this species, allele frequencies are unknown thus multilocus allele profiles are hereafter referred to as allele phenotypes. We compared all multilocus allele phenotypes found within and among sites to identify repeated allele phenotypes, which we assumed to result from asexual reproduction (e.g. clonal expansion).

Sprouting of vegetative propagules

Effect of drying: To assess the ability of buds to remain viable and sprout after different periods of drying, culms were collected from Site 4 (Fig. 1, Appendix 1) on 3 September. Culms, approximately 2 m tall, that had not flowered were cut at the base and randomly assigned to five treatments (drying durations) spread out on benches that were shielded from rainfall but otherwise open. Drying durations were 0 days (day of harvest), one, two, four, and six weeks. After drying, stem pieces with a node at either end were cut from the culms and ten were placed into each of five replicates and covered with commercial peat. Each replicate comprised two plastic seedling trays (53 cm by 26 cm). Plants were grown under an open structure with a transparent roof, watered daily, and the plants that sprouted recorded four weeks after planting. To assess changes in moisture content, plant material was harvested from the same site on 19 November. Fresh and dry weights of stem pieces cut from culms at the time of harvest and after one, two and four weeks were recorded. Dry mass was taken after drying the stem pieces to constant weight at 40°C.

Data from the different times of drying were compared by ANOVA and times of drying were compared with Tukey multiple comparison tests (Sigmaplot 11). The proportion of buds that sprouted was square root transformed, other data was not transformed prior to analysis.

Effects of propagule size and planting depths on sprouting

Fresh culms and rhizomes were collected at Site 6 (Fig. 1, Appendix 1) on July 3 and propagules were cut to the appropriate size and planted the same day. Both experiments were performed under a covered shelter, open on the sides. Unmodified soil representative of the area (Oxisol, collected in Rio Hato, Panama) was used and all pots were watered daily or as needed. All propagules were harvested on September 12 when the presence of a sprout above-ground, a sprout below-ground but not emerged, or the presence of roots was recorded.

Propagule size: Culm pieces with one node (and bud) were cut into either 2, 5, 10, or 20 cm lengths or two node (and bud) pieces ranging in length from 9.9 to 12.7 cm. Rhizomes were cut into pieces ranging from 15–40 mm in length, either with or without visible axillary buds. There were 10 replicates for each culm length (single and two node pieces) and 25 pieces of each rhizome type. Culm pieces shorter than 10 cm were planted individually in 10 cm diameter plastic nursery sacks while longer pieces were planted in 12 L pots. Rhizomes were planted individually in 10 cm sacks. All propagules were planted at a depth of 5 cm.

Planting depth: Individual propagules (5 cm single node stem pieces or single node rhizome pieces (ranging from 11–44 mm in length)) were planted at different depths in 10 cm nursery sacks. Planting depths were surface, 5 cm, 10 cm, and 20 cm for stem pieces, and surface, 10 cm, and 20 cm for rhizome pieces; there were ten replicates per planting depth. Time to sprouting was recorded for each propagule.

Our original intent was to analyse growth of sprouts using analysis of variance appropriate to the experimental design. However, because of the frequency of failure to sprout, and thus zero growth, we decided to analyse only the proportion sprouted either aboveor belowground, as the percentage of the 10 replicates that sprouted for each treatment.

To test if soil type influenced the results of this experiment, growth was also tested using commercial potting mix in nursery sacks. Single node stem pieces (5 cm) were planted at the surface or 2 cm depth, in either commercial potting mix or unmodified soil from Rio Hato, with six replicates per treatment. Presence of sprouting was recorded after four weeks.

We further distinguish between propagules that produced roots at the node but did not initiate other growth, propagules that sprouted but died before they reached the soil surface, and propagules that produced visible growth above the soil surface. Results were analysed using generalized linear models (Poisson GLM for propagule depth and Binomial GLM for propagule size and soil type) as implemented in R 2.13.1 (R Development Core Team 2010). The proportion of variance explained by each model (r²) was calculated from the null and residual variances.

Results

Sexual reproduction

Germination ability

The proportion of seeds germinating and the temporal patterns of germination varied greatly across the 12 sites (Appendix 2). The range of maximum germination percentages were 72%–30% (Appendix 2), with an average level of germination around 35% across sites until November (Fig. 2). Significantly fewer seeds germinated after 16 November (ANOVA, $F_{12,403}$ = 25.5, *P*<0.001, Fig. 2).

In situ germination

The numbers of seedlings germinating *in situ* showed a significant effect of treatment ($F_{2,18} = 21.6$, p<0.001), week ($F_{4,36} = 7.4$, p<0.001) and treatment by week interaction ($F_{8,72} = 29.9$, p<0.001), so the effect of treatment was dependent upon time. One week after the experiment was initiated, germination was evident in all plots (Fig. 3) and there were significant differences in the number of seedlings between each treatment, with the plots with added seeds having many more seedlings than the controls. The average numbers of seedlings in plots with added seeds decreased from week to week, while those in control plots increased over time. Within the flywire treatment, there was a significant increase in the number of seedlings between weeks 3 and 5, corresponding with the removal of the flywire, whereas the seeds added and bare soil control plots did not show significant changes after week 3. After nine weeks there were no significant differences in the numbers of seedlings remaining between any of the treatments.

Genetic diversity of mature stands

High levels of genetic diversity were found both within and across sites. A total of 227 alleles were observed across the twelve microsatellite loci, of which 215 were shared between sites. The average number of alleles per locus (A_o) was 18.4 and up to ten alleles per individual were found within a locus (range 1-10).

In the two stands sampled with transects, the majority of culms sampled were unique (Stand 1 at Site 5 = 89% and Stand 2 at Site 6 =65%) and all replicate allele phenotypes were found in adjacent plots. Similarly, in the 22 sites where only 3 samples were collected, 86% of them contained multiple allele phenotypes (19 of 22 sites). Fifty four multilocus allele profiles were found across the 22 sites, with three unique phenotypes sampled at each of 13 sites (Sites 3, 5, 6, 11, 13-16, and 18-22), two phenotypes at each of six sites (2, 4, 7, 9, 10, and 17), and a single phenotype at each of three sites (1, 8, and 12; Appendix 1). The same multilocus profile was not found at more than one site.



Figure 2. Weekly average germination percentage of *S. spontaneum* seeds from 12 sites. Error bars represent standard error of the mean. Dates of collection with different letters are significantly different.





Figure 3. Average numbers of *S. spontaneum* seedlings germinating each week per plot in the *in situ* germination experiment. "*Saccharum* added" plots had mature inflorescences placed in them and were initially covered with flywire, "flywire control" plots were initially covered with flywire but no seeds were added, and control plots were similar sized plots of bare soil. Error bars represent standard error of the mean (n=10). Weeks with different capital letters are significantly different from each other. Treatments with different small letters are significantly different within that week.

Table 1. Moisture content of stems and the proportion of buds that sprouted after various times of drying. Prior to testing for sprouting, buds were cut from culms immediately after harvesting (0) and 1-4 weeks of drying. Sprouting of buds was recorded after 4 weeks. Results are presented as the mean with the standard error in parenthesis. Values within a column with different letters are significantly different.

Time (weeks)	Moisture content (%)	Proportion of buds sprouting (%)
0	80.2 (1.08) ^a	70.9 (4.39) ^{ab}
1	76.7 (1.21) ^{ab}	84.0 (2.92) ^a
2	77.2 (0.68) ^{ab}	57.0 (6.63) ^{bc}
4	73.7 (0.74) ^b	45.0 (3.16)°
6	N.D.	38.8 (3.75)°

N.D. = not determined

Vegetative propagation

Effects of drying

There was a significant effect of time of drying of the culm on the proportion of buds that sprouted (ANOVA $F_{4,19} = 16.992$, P<0.001, Table 1), less than half of the buds sprouting after 4 weeks. However while significant over time, the reduction in moisture content was only 8% lower after 4 weeks of drying (ANOVA $F_{3,16} = 7.819$, P<0.01, Table 1).

Effects of propagule size

Increased size of stem fragments increased sprouting ability (p<0.01, $r^2 = 0.34$; Fig. 5). While roots were produced in the majority of fragments of 5, 10 and 20 cm lengths, no fragments of 2 cm, 5 cm, or 10 cm produced active sprouts from the node. One 20 cm (10%) and one 2-node fragment (10%) sprouted belowground but died before reaching the soil surface. Three (30%) 20 cm fragments and seven (70%) 2-node fragments sprouted aboveground. All 2-node fragments that grew sprouted at only one node, but had roots present at both nodes. No rhizome fragments, with or without buds, sprouted.

Effects of planting depth

There was a significant negative effect of planting depth on the ability of stem cuttings to sprout, with lower depths having an inhibitory effect on sprouting (p<0.05, $r^2 = 0.29$, Fig. 4). While 100% of stem cuttings laid at the soil surface sprouted, only 40% successfully grew aboveground from a depth of 5 cm and only 20% from 10 cm. Stems at a depth of 20 cm failed to grow aboveground, but 20% of propagules at this depth sprouted and died before reaching the soil surface. All rhizome pieces, at any depth, failed to sprout suggesting that single node pieces of *S. spontaneum* rhizomes may have low sprouting ability (data not shown). One rhizome piece, at 10 cm depth, produced



Figure 4. Proportion of buds sprouting from different depths of planting. Proportion of buds that produced visible growth above the soil surface (Above ground), that sprouted but died before they reached the soil surface (Below ground), or produced roots at the node (Roots), but did not initiate other growth as determined by depth of planting.



Figure 5. Proportion of buds sprouting from different sizes of culm piece planted. Proportion of buds that produced visible growth above the soil surface (above ground), that sprouted but died before they reached the soil surface (below ground), or produced roots at the node (roots), but did not initiate other growth as determined by size of culm piece.

roots but did not produce a sprout. Rhizome pieces laid at the soil surface dried out quickly, despite daily watering, and did not even produce roots.

Depth trials comparing commercial potting soil (PS) to the unmodified soil (US) used in the previous trial showed similar results, with 83.3% (PS) and 67.7% (US) of cuttings laid at the soil surface sprouting aboveground and 67.5% (PS) and 50.0% (US) sprouting when planted at a depth of 2 cm, respectively. No significant differences were seen between depths or soil types (p>0.05, $r^2 = 0.05$).

Discussion

The spread of *S. spontaneum* in the PCW has been rapid and dramatic, occurring largely in recent decades. Flowering across the landscape is extensive and our results suggest that seed dispersal clearly plays a major role in this spread. Seed germination rates were high when tested under optimal conditions, and we found seedlings readily establish *in situ*. Although we did not follow the fate of these seedlings to maturity, 79% of our samples collected in mature stands had unique allele phenotypes, with all replicated genotypes occurring in adjacent samples within a site. Such high genotypic diversity cannot result from vegetative spread and can only be the result of sexual reproduction. Our trials with vegetative propagules also showed that growth can occur from stem fragments, although they can be highly sensitive to the conditions under which they are grown.

Although we did not test viability directly, our germination trials indicate that on a landscape scale large numbers of germinable seeds are produced annually. Variability in germination within and between sites was high but seeds germinated from all sites, particularly those collected during the peak flowering months of September and October. Other invasive grasses, such as *Phragmites australis* and *Spartina alterniflora* in North America, have also been shown to have highly variable production of viable seeds across sites (Daehler and Strong 1994, Kettenring and Whigham 2009). Although the average viability of these other species is typically much lower than the rates we have observed (e.g. less than 20 % for *Phragmites australis* (Kettenring and Whigham 2009)), they are aggressive invaders in North American wetlands and seeds play an important role in their dispersal (Belzile et al. 2010; Daehler and Strong 1994; McCormick et al. 2010).

Seeds which germinated *in situ* showed high mortality in plots where they were added, but control plots which received seeds only through natural dispersal increased their numbers of seedlings from week to week. In the case of the bare soil control plots, seedling densities were ~27 seedlings/plot (37 seedlings/m²) by the end of the experiment, which is similar to densities counted in plots measured in a *S. spontaneum* stand which had burned earlier in the year (Saltonstall and Bonnett 2012). While we did not follow the fate of individual seedlings, it is likely that mortality occurred in the control plots as well and it was a constant rain of novel seeds landing and germinating
in the plots that kept their numbers increasing. The high mortality seen in the seedadded plots could be due to negative interactions on a seed-seed or seed-seedling basis, such as competitive or allelopathic effects which were compounded by the high densities of seeds and seedlings. Such effects have been shown in sugarcane (Sampietro et al. 2007) and several other species (Inderjit and Streibig 2001; Murray 1998) but not yet demonstrated for *S. spontaneum*. As the fate of the seedlings established in this experiment was not followed after the nine weeks of observations, additional research regarding the long-term survivorship of *S. spontaneum* seedlings is needed.

Genetic diversity across the landscape is high. We found high numbers of alleles both within individuals and between sites, and nearly all samples tested were genetically unique. This suggests that stands of *S. spontaneum* typically form from the coalescence of multiple individuals recruited from seeds rather than vegetative propagation of a single clone across a large area. Consequently, though we have not demonstrated recruitment of adult plants from seedlings, flowering is a life-history stage that needs to be targeted to effectively manage the spread of the species.

The effects of disconnection of stems and rhizomes on vegetative reproduction has been studied extensively in rhizomatous grasses, and disconnection from the parent plant has been shown to release buds from inhibition by other buds on the stem or rhizome. This response may be influenced by the length of the segment containing the buds as well as which the conditions to which propagules may be exposed to following disconnection from the parent plant (Kigel and Koller 1985, Boose and Holt 1999). Saccharum spontaneum appears to regenerate better from larger cuttings, with larger stem fragments having a greater chance of sprouting and reaching the soil surface. Dessication reduced sprouting ability to some extent but 39% of buds still sprouted after six weeks of drying. Similar results have been seen in experiments with other rhizomatous grasses, such as Agropyron repens (Turner 1968) and Pennisetum macrourum (Harradine 1980) where successful emergence and establishment decreased with planting depth and increased with size of the fragment. It is likely that larger segments are able to sustain buds in a dormant condition for longer periods of time and that once growing is initiated by the dominant bud, heterotrophic growth (e.g. underground) can be sustained for longer periods of time (Kigel and Koller 1985).

Ability of buds to sprout also appears to be strongly affected by planting depth. Planting stem cuttings at depths as shallow as 5 cm reduced the number of aboveground sprouts by 60%, and deeper plantings inhibited even the sprouting of fine roots from the nodes. The lack of growth in our initial studies prompted concerns about the soil that we used inhibiting growth in this experiment. Although the bags we used had drainage holes, the Oxisols used here have high clay content and waterlogging may have been an issue preventing growth of propagules. However, our secondary trials comparing growth in the Oxisol versus commercial potting mix showed similar results, with reduced growth when fragments were planted below the soil surface suggesting that the inhibition of growth could be a light response rather than an effect of the growth substrate.

Management of S. spontaneum

Management of *S. spontaneum* in Panama is restricted to controlling aboveground biomass, and generally involves physical cutting of mature biomass, and in some cases, chemical control where reforestation is a goal (Craven et al. 2009). Fire is also used during the dry season months to remove biomass. When cut, biomass is typically left on site to dry and degrade naturally. These activities occur year round, and regrowth of stands following biomass removal occurs frequently and rapidly (Saltonstall pers. Obs). Like many other weeds (Holm et al. 1977), the remaining buds and rhizome system thus presents the greatest barrier to control of established stands of *S. spontaneum*. However, little thought goes into the effect of these management efforts on seed production and further spread of the species.

Timing and method of control thus become important when considering management of this aggressive invader in Panama. While intermittent flowering of S. spontaneum occurs year round, the peak season of flowering is from August - October. Our studies have shown that seed germinability is highest in the months of September, October, and early November with a rapid decline in germinability in December. We suspect that germinability of seeds produced at other times of the year is also much lower. Timing of biomass removal can be important, with removal in June or July, prior to inflorescence emergence and seed development but late enough in the year that reproduction will not occur in the months of August – November, possibly being a method to reduce spread by seed. This may be particularly important in areas on the edges of the distribution where S. spontaneum does not yet dominate and spread can be minimized on a local scale. As herbicides are not commonly used in Panama except during the initial stages of reforestation projects, repeated cutting of stems throughout the year to deplete below-ground carbohydrate resources in rhizomes is another approach which may help to prevent flowering at optimal times of the year. However, as our studies have shown that cut stems are still capable of sprouting after six weeks of desiccation, cut biomass should also be handled to minimize sprouting and spread to new sites.

Better control of dry-season fires is also needed to help control spread of *S. spontaneum* by seed, as rapid regrowth following the onset of the rainy season typically leads to stems with mature infloresences developing in the peak months of seed production. Further, burned areas have higher densities of flowering stems and comparable seed germination rates as unburned areas (Saltonstall and Bonnett 2012) suggesting that the potential for spread to new sites is increased by fire.

As *S. spontaneum* in Central Panama is widespread and many thousands of seeds are produced by each plant, a strategy to control seed numbers will have to be co-ordinated over a large area to be truly effective. While the extent of seed dispersal has not been experimentally quantified, research conducted on Barro Colorado Island (BCI) in the Panama Canal, utilising 200 seed rain traps (Wright and Calderón 2006), provides some evidence. *Saccharum spontaneum* is found only in small, isolated patches on BCI, mostly within treefall gaps in the forest interior (S.J. Wright, personal communication). However, between 1990 and 2011 over 7500 *S. spontaneum* seeds were trapped (annual median 229); S.J. Wright unpublished data). These seeds were likely wind dispersed from mainland areas and would have travelled at least 2 km across the Canal from the nearest sources of *S. spontaneum* plants. Information regarding the longevity of *S. spontaneum* seed remaining in the seed bank is also lacking, but a concerted effort over several years to eliminate *S. spontaneum* seed from the seed bank will be required to stop spread by seed. The closely related invasive *Andropogon gayanus* has been shown to retain 1% of germination of seed after one year in burial experiments (Flores et al. 2005), suggesting that establishment of new plants could continue to occur for some time even if annual seed production is reduced across the landscape.

In conclusion we have presented evidence that the spread of *S. spontaneum* in Panama has been driven by seed production, but that vegetative propagules derived from stem fragments are also robust and can be the source of new plants. Seed production from *S. spontaneum* can be reduced through the timing of management actions to reduce biomass that prevents re-growth of flowering stems. However the mobility of the seed means that to be effective, such actions would have to be conducted over large areas. Once established, the persistence of individual stands through re-growth from buds lower on the stems and rhizomes will continue to impede control and eradication over large areas so further research to determine a weak point in the vegetative growth stage is needed.

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Appendix I

Locations, description and diversity of the sites used for the collection of *Saccharum spontaneum* seeds. (doi: 10.3897/neobiota.20.6163.app1) File format: Adobe PDF file (pdf).

Explanation note: The table gives the latitude and longitude, description and number of genotypes found among the 3 plants of *Saccharum spontaneum* tested from each of 22 Sites. Sites 1–12 were used to assess seed germinability through time.

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Appendix II

Germinability of *Saccharum spontaneum* seed through time from 12 sites. (doi: 10.3897/neobiota.20.6163.app2) File format: Adobe PDF file (pdf).

Explanation note: Proportion of seeds that germinated each week between September and December from samples taken at 12 sites. 100 seeds were germinated from each of three replicate samples and tested for germination in laboratory conditions. Results are presented as the mean and the error bar represents the standard error of the mean.

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