Invasion debt—quantifying future biological invasions

Mathieu Rouget[a1], Mark P. Robertson[b], John R.U. Wilson[c,d], Cang Hui[e,f], , Franz Essl[g], Jorge L. Renteria[d,h], David M. Richardson[c]

[a] Centre for Invasion Biology, School of Agriculture, Earth and Environmental Sciences, University of KwaZulu-Natal, Private Bag X1, Scottsville 3209, South Africa

[b] Centre for Invasion Biology, Department of Zoology and Entomology, University of Pretoria, Private Bag X1, Pretoria 0002, South Africa

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

[d] Invasive Species Programme, South African National Biodiversity Institute, Kirstenbosch Research Centre, Claremont 7735, South Africa

[e] Centre for Invasion Biology, Department of Mathematical Sciences, Stellenbosch University, Private Bag X1, Matieland 7602, South Africa

[f] Mathematical and Physical Biosciences, African Institute for Mathematical Sciences, Muizenberg 7945, South Africa

[g] Division of Conservation Biology, Vegetation and Landscape Ecology, University of Vienna, Rennweg 14, 1030 Vienna, Austria

[h] School of Agriculture, Earth and Environmental Sciences, University of KwaZulu-Natal, Private Bag X1, Scottsville 3209, South Africa

[1] Corresponding Author: M Rouget, School of Agriculture, Earth and Environmental Sciences, University of KwaZulu-Natal, Private Bag X01, Scottsville 3209, South Africa, Tel: +27 33 260 6028, Fax: +27 33 260 6094, rouget@ukzn.ac.za,

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ABSTRACT

Aim: We develop a framework for quantifying invasions based on lagged trends in invasions ("invasion debt") with the aim of identifying appropriate metrics to quantify delayed responses at different invasion stages — from introduction to when environmental impacts occur.

Location: Worldwide; detailed case-study in South Africa

Methods: We define four components of invasion debt: the number of species not yet introduced but likely to be introduced in the future given current levels of introduction / propagule pressure; the establishment of introduced species; the potential increase in area invaded by established species (including invasive species); and the potential increase in impacts. We demonstrate the approach in terms of number of species for 21 known invasive Australian *Acacia* species globally, and estimate three components of invasion debt for 58 *Acacia* species already introduced to South Africa by quantifying key invasion factors (environmental suitability, species invasion status, residence time, propagule pressure, spread rate and impacts).

Results: Current global patterns of invasive species richness reflect historical trends of introduction—most acacia species that will become invasive in southern Africa have already invaded, but there is a substantial establishment debt in South and North America. In South Africa, the likely consequence of invasion debt over the next 20 years was estimated at: four additional species becoming invasive with an average increase of 1075 km^2 invaded area per invasive species. We estimate that this would require over US$ 500 million to clear.

Main conclusions: Our results indicate that invasion debt is a valuable metric for reporting on the threats attributable to biological invasions, that invasion debt must be factored into strategic plans for managing global change, and, as with other studies, they highlight the

value of proactive management. Given the uncertainty associated with biological invasions, further work is required to quantify the different components of invasion debt.

Keywords: *Acacia*, biological invasions**,** climatic suitability, global change, invasive species, lag phase, risk assessment, tree invasions

INTRODUCTION

The economic and environmental impacts of alien species have increased rapidly in extent and severity over the past few decades (Pimentel *et al.*, 2001; Butchart *et al.*, 2010). How to quantify and report on this increasing biodiversity threat is a matter of debate (Pereira *et al.*, 2013). Quantifying the potential future extent and impact of biological invasions is challenging for several reasons, including: a) the pattern and extent of alien species are generally poorly documented (McGeoch *et al.*, 2010), resulting in an underestimate of the extent of the invasion problem caused by the subset of species causing negative environmental or socio-economic impacts; b) biological invasions and their impacts often occur long after species were initially introduced to a region (Kowarik, 1995; Essl *et al.*, 2012); and c) patterns of biological invasions result from complex interactions of climatic, land-cover, economic, ecological, and demographic variables (Pyšek *et al.*, 2010; Essl *et al.*, 2011; Richardson & Pyšek, 2012).

Scientists and policy-makers have developed a wide range of pre-border invasive species risk assessments to predict which species will become invasive if introduced (Kumschick & Richardson, 2013). Although risk assessment protocols are widely applied, their overall usefulness in reducing problems with biological invasions has been questioned—more comprehensive assessments are certainly needed to improve their effectiveness (Hulme, 2012; Leung *et al.*, 2012). A complementary approach for dealing with biological invasions focusses on post-entry, adaptive management of introduced taxa (Groves, 2006; Hulme, 2012; Wilson *et al*. 2013). This approach targets species at an early stage of the invasion process in order to improve management effectiveness. However, robust conceptual frameworks to guide such interventions are lacking. In this paper we: 1) disentangle the components of lagged invasions which pertain to different invasion stages; 2) clarify key aspects and mechanisms; 3) suggest appropriate metrics to quantify delayed responses at different invasion stages; and 4) provide an application of the concept using invasions of Australian *Acacia* species.

INVASION DEBTS AT DIFFERENT INVASION STAGES: FUNDAMENTALS AND KEY ASPECTS

The term "invasion debt" has been used to describe the time-delayed invasion of species already introduced to a region (Seabloom *et al.*, 2006; Essl *et al.*, 2011). Given the time-lag between the introduction and the invasion phases in the introduction-naturalization-invasion process, many species which will become invasive in given regions have already been introduced, but have yet to reach their full invasion potential (Gassó *et al.*, 2010). Biological invasions are hard to predict because of the large number of factors influencing the different stages of the invasion continuum. Even if we assume that current drivers of biological invasions (e.g. trade patterns, propagule pressure, environmental change) will remain the same, new species will be introduced and some of the species already introduced will progress along the invasion continuum to become invasive. The concept of invasion debt is thus similar to that of extinction debt originally used by Tilman *et al*. (1994) to describe the time-delayed extinction of species that occur in remnant patches of natural habitat following habitat destruction. A cessation in habitat destruction will not protect species threatened by past habitat lost; similarly, new introductions are in many cases inevitable (e.g. through the

Suez Canal; Galil *et al.*, 2015); and even effective pre-border control will not prevent escalating impacts from species that have already been introduced (Seabloom *et al.*, 2006; Essl *et al.*, 2011). Although invasion debt has been recognized as a major problem, it remains to be operationally defined and few attempts have been made to quantify it. Here, we propose that an initial estimate of invasion debt for a region or a taxon can be quantified using a few reliable and widely available predictors of biological invasions.

The species in an area or country can be conceptualized as consisting of three pools of species: the native pool, the introduced pool, and, nested within the introduced pool, the invasive pool—with an additional pool of species from around the world that are not yet present in the region but that could potentially be introduced (Fig. 1). An alien species will become invasive if it is able to overcome a series of biotic and abiotic barriers that mediate introduction, survival, reproduction, dispersal and interactions with the local environment and biota (Blackburn *et al.*, 2011). We define invasive species as introduced species with individuals dispersing, surviving and reproducing at multiple sites across a greater or lesser spectrum of habitats and extent of occurrence (sensu Blackburn *et al.*, 2011). Invasion debt can be conceptualized as a consequence of the time lag existing across all invasion stages, from introduction to when the invader is sufficiently abundant and widespread to cause impacts. We therefore define invasion debt as the additional amount of invasion that could take place in the future in a given region. Invasion debt can be divided into four components, related to the invasion process and the various stages an introduced species has to go through (Blackburn *et al.* 2011). These are: 1) the additional number of species that could become introduced (introduction debt); 2) the additional number of species that could become established (establishment debt), 3) the additional area that could be invaded (spread debt); and 4) the additional environmental and socio-economic impact that could result from these invaders (impact debt) (Fig. 1).

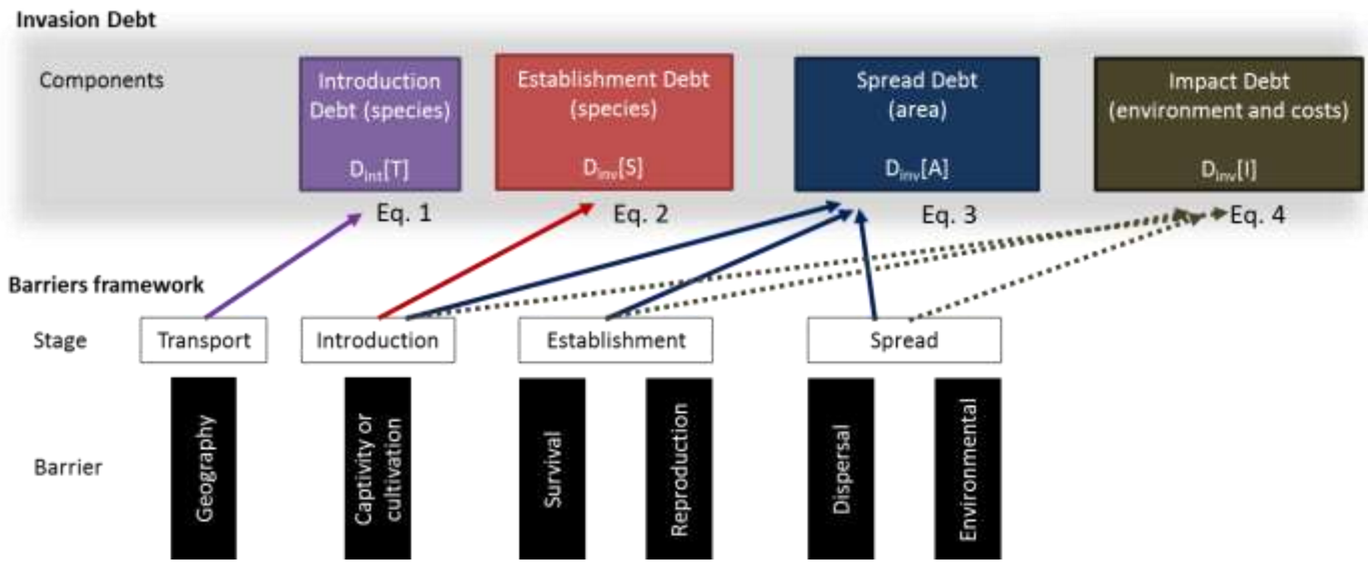

Figure 1: Conceptual framework for quantifying invasion debt in terms of number of species, potential area invaded and impact, aligned with the invasion framework of Blackburn *et al*. (2011). Complete formulae are listed in Box 1. Note that invasions can decrease, representing an invasion failure, contraction of invaded areas or mitigation of impacts associated with invasions.

Invasion debt therefore considers major dimensions of invasion biology (namely introduction dynamics, species invasiveness, habitat invasibility, and global change outcomes) and allows for their quantification using a series of simple metrics (Fig. 1, Table 1). The concept (and associated metrics) of invasion debt builds on existing invasion theory and approaches. It differs from other approaches in providing a comprehensive series of metrics along the introduction-naturalization-invasion continuum under one concept. Components of invasion debt (as proposed here) have been previously calculated for single taxa (e.g. *Acacia paradoxa*; Moore *et al.*, 2011) or for one or two components only (e.g. establishment debt for Cactaceae; Novoa *et al.*, 2015). To our knowledge, the concept of invasion debt has not been quantified for a large group of taxa across all stages of the introduction-naturalization-invasion continuum. Throughout the paper we illustrate ways to quantify three of the four components of invasion debt for *Acacia* species globally and, in more detail, for South

Africa. For the purpose of illustrating the concept, we assume that the current drivers of biological invasions will not change. Under a "Business As Usual" scenario, no major changes in the factors responsible for invasion are expected. However, at all stages, there is some level of uncertainty and over time, invasion debt can increase or decrease given changes in the factors influencing each stage.

Integrating individual invasion debt components and appropriate metrics

Here we describe each component of invasion debt in more detail and propose appropriate metrics to quantify each (see Box 1).

We define **introduction debt** as the additional number of species that will be introduced to a given area or country over a given period. Many of these introductions will fail, others will never establish, and a small fraction will establish and a subset of these will become invasive (e.g. Williamson and Fitter, 1996). Introduction debt can be quantified as a function of the probability of a non-introduced species (part of the global species pool) to be introduced to the focal area during a specific period (e.g. 20 years). This probability will vary between species and over time. Although not considered here, changes in invasion drivers will result in introduction probability varying over time (e.g. new pathways or change in species trade patterns; Seebens *et al.*, 2015), but obviously the longer the period under consideration the greater the probability of a given species being introduced. The consequence of any introduction can then be calculated as the increase in invasion debt (Fig. 1, Table 1, Box 1).

Box 1: Formulation of Invasion Debt

We here derive equations for quantifying invasion debt in terms of the number of species to become introduced (Introduction Debt, D_{int}), the number of species to become established

(Establishment Debt, $D_{\mathrm{inv(S)}}$), the potential area invaded (Spread Debt, $D_{\mathrm{inv(A)}}$) and the potential impact (Impact Debt, $D_{\mathrm{inv(I)}}$) as functions of time (T). Let p_j be the probability of a non-introduced species j (part of the global species pool (S) to be introduced to the focal area during a specific year. The introduction debt (Fig. 1) from now (year 0) to the future (year T) can be written as:

Eq. (1) $$D_{\mathrm{int}}[T] = \sum_{j \in S} \sum_{t=0}^{T-1} (1 - p_j)^t \cdot p_j .$$

Let S_I be the current introduced species pool, S_{NI} the current non-invasive introduced species pool, S_{IN} the current invasive species pool; we have $S_I = S_{NI} + S_{IN}$. The pool of introduced species at year T will be, $S_I(T) = S_I + D_{\mathrm{int}}[T]$. Note that we separate introduction debt from the following formulation of invasion debt (Fig. 1).

The establishment debt (species-based invasion debt, Fig. 1) from now (year 0) to year T due to current non-invasive introduced species (i.e. excluding those from introduction debt) is:

Eq. (2) $$D_{inv(S)}[T] = \sum_{j \in S_{NI}} \phi_j \cdot \alpha_j ,$$

where α_j is the establishment probability of introduced species j ($\alpha_j = 1$ if $A_j > \varepsilon$ and $\alpha_j = 0$ otherwise, where A_j is the climatically suitable area size and ε the minimum occupancy for growth and spread); ϕ_j is an compound probability of invasion, including factors of propagule pressure, residence time and species characteristics, and can be further specified pending on data availability.

The spread debt (area-based invasion debt, Fig. 1) from now to year T is:

Eq. (3) $$D_{ins(A)}[T] = D_{inv(A1)}[T] + D_{inv(A2)}[T] ,$$

The first term on the right is the debt from current invasive species, and the second term is the debt from non-invasive introduced species. The above formula can be further specified based on relevant scenarios. For instance, let r_j be the exponential rate of range expansion for species j, a_j be the current occupied area size by introduced species j, ε the minimum occupancy for initiating spread, and let T_{0j} and T_j be the residence time and time lag before spread of species j; we can have the area-based invasive debt for this specific case as follows,

$$D_{ins(A)}[T] = \sum_{j\in S_{IN}} \max\{A_j - a_j e^{r_j T}, 0\} + \sum_{j\in S_{NI}} \phi_j \cdot \alpha_j \cdot \max\{A_j - \varepsilon \cdot e^{r_j(T_{0j} - T_j + T)}, 0\}.$$

The impact debt (impact-based invasion debt, Fig. 1) from now to year T can be estimated as the following,

Eq. (4) $$D_{inv(I)}[T] = D_{inv(I1)}[T] + D_{inv(I2)}[T].$$

The first term on the right $D_{inv(I1)}$ indicates the impact-based invasion debt for current invaded area, and the second term $D_{inv(I2)}$ indicates the impact-based invasion debt for future invaded area. As above, these two terms can be further specified for relevant scenarios. For instance, let $I_j(t)$ be the annual impact of species j per unit area after t year since first arrival, $a_{t,j}$ the area that has been occupied by species j for t years ($a_j = \sum_{t=1}^{T_{0j}} a_{t,j}$). We have the following impact-based invasion debt for current invaded area:

$$D_{inv(I1)}[T] = \sum_{j\in S_{IN}} \sum_{t=0}^{T} \sum_{t'=1}^{T_{0j}} a_{t',j} \cdot I_j(t'+t).$$

The impact-based invasion debt for future invaded area is:

$$D_{inv(I2)}[T] = \sum_{j\in S_{IN}} \sum_{t=0}^{T} \sum_{t'=1}^{t} a_j (e^{r_j(t'+1)} - e^{r_j t'}) I_j(t+t') + \sum_{j\in S_{NI}} \sum_{t=0}^{\max\{T_{0j}+T-T_j, 0\}} \sum_{t'=1}^{t} \alpha_j \varepsilon (e^{r_j(t'+1)} - e^{r_j t'}) I_j(t+t')$$

where the first term on the right is the impact due to future range expansion of current invasive species, and the second term is the future impact of currently non-invasive introduced species. More realistic formulae can be developed following the above procedure and framework in Figure 1.

Table 1. The concept of invasion debt provides an important link between invasion science and management and policy

Component	Purpose	Management implications	Formulation (see Box 1)	Example
Introduction debt	Identification of likely new introductions	Development of pre-border biosecurity Prioritization of species for risk assessment Comparison between different pathways for regions or taxonomic groups	D_{int}	Not assessed here
Establishment debt (species-based)	Identification of likely new invasions	Development of post-border biosecurity Pro-active measures to prevent spread of potential invasive species	$D_{\text{inv(S)}}$	Figure 2
Spread debt (area-based)	Identification of additional areas likely to be invaded	Identification of priority areas for control Identification of areas where spread-reduction methods are required Spatial planning of the management of biological invasions	$D_{\text{inv(A)}}$	Figure 3
Impact debt (impact-based)	Identification of likely impacts and their associated costs	Determine returns on investment should be spent on control Prioritize current management activities	$D_{\text{inv(I)}}$	Table 2

Table 2. Invasion debt for Australian *Acacia* species in South Africa. The various components of invasion debt were calculated based on species attributes, current and potential distribution, spread rate and environmental impacts (see Box 1 for complete formulae)

Parameter	Current status	Debt (over 20-year time-horizon)
[a] Cost of *Acacia* clearing from 1998 to 2008 by the Working for Water programme (this represents an underestimate of the real impacts).		
Number of introduced species	66 species	Not estimated here
Number of invasive species	14 species	4 species
Area invaded	244,835 km^2	62,260 km^2
Impact	US$ 83.1 M[a]	US$ 593.6 M

Establishment debt is a species-based component and represents the difference in species richness between the current invasive pool and some estimated future invasive pool [formulated here specifically for species originating from the introduced (but not invasive) species pool, Fig. 1, but in practice it can also include new introductions that subsequently become invasive]. Since the time between introduction and naturalization can be several decades for some taxa (Caley *et al.*, 2008; Larkin, 2012), a large number of future invasive species have already been introduced and are progressing at different rates along the introduction-naturalization-invasion continuum (Richardson & Pyšek, 2012), amounting to a substantial invasion debt.

Many factors influence the establishment debt. Key factors include: 1) the number of introduced species (the more introduced species, the more likely some will become established); 2) the environmental suitability for each species to establish a viable population (species will be more likely to become established and invasive where the environmental conditions match its native environment); 3) species attributes (some traits are related to species establishment and invasiveness); 4) the length of time a species is present in an area (residence time and invasion rate are usually positively correlated; Wilson *et al*. 2007); and 5) propagule pressure (species introduced in large numbers and at repeated times have a greater probability of invasion). Establishment debt can be either quantified as the sum of the combined probability across all factors mentioned above for all introduced species, or as the number of species which are likely to establish (Box 1 Eqn. 1). The concept of establishment debt, resulting in an increase in the number of naturalized species, can be extended to an increase in area and impact of invasive species (see below).

Spread debt: there is often a substantial delay between a species first being recorded as invasive and spreading to many suitable sites, with species occupying the full available distribution at a broad-scale often only after several centuries (Wilson *et al.*, 2007; Williamson *et al.*, 2009), again amounting to a substantial debt. Area-based invasion debt, termed spread debt, is expressed as the additional area that invasive species will likely occupy in the focal region over a given time period (Fig. 1). Spread debt takes into account both already invasive species and introduced species which will become invasive and spread over time. It is determined by 1) the probability that a species will become invasive (see above); 2) the environmental suitability of a region for each species; 3) the rate of spread (both natural and human-mediated) of that species; and 4) propagule pressure (Box 1).

Impact-based invasion debt is an estimate of the additional impact (i.e. deleterious effects on native biota (Blackburn *et al.* 2014) or socio-economy (Binimelis *et al.*, 2007)) that current and future invasive species will have in the focal region over a given time period. Impacts of biological invasions include both negative environmental effects (e.g. decrease in population of native biota) and socio-economic costs (e.g. loss of grazing land). While in some cases impact is directly proportional to area affected, impacts can increase with time, often in a non-linear fashion (Kumschick *et al.*, 2015). While this is harder to quantify than the species- and area-based measures, it is an essential component to inform decision-making on the management of biological invasions. Impacts can be modelled in various ways but will most likely include parameters such as the area invaded, the characteristics of the invaded area (e.g. high-biodiversity areas versus anthropogenic habitats), changes in ecosystem functioning, and the economic costs of managing the invasive species. A direct measure, and one more easily quantified, is to estimate the management costs that an invasion will occur, although the costs for a response often do not correlate to the impact caused. Impact-based invasion debt will be typically expressed as the financial cost of invasive species in newly invaded areas, though could be modified to include other internationally standardized metrics (e.g. Blackburn *et al.*, 2014).

Clearly, the invasion debt could increase or decrease in a focal region in particular due to management or global change factors. For example, successful pre-introduction measures (e.g. border quarantine procedures) will reduce the likelihood of new introductions, eradication efforts will reduce establishment debt, while climate change can increase or decrease the potentially suitable area and so the spread debt (Thuiller *et al*. 2007). Our proposed framework (Fig. 1) can be used to measure both increases and decreases in invasion debt.

MEASURING INVASION DEBT AT DIFFERENT INVASION STAGES:

We demonstrate the concept of invasion debt using global and regional (within South Africa) introductions/invasions of Australian *Acacia* species as the model system. Although we illustrate the concept using plants, it can also be applied to animals.

Establishment debt of Australian acacias worldwide

Australian *Acacia* species have been proposed as a model group for studying the multiple dimensions of woody plant invasions (Richardson *et al.*, 2011; Kueffer *et al.*, 2013). Unlike some groups of woody plants (e.g. *Pinus*; Richardson, 2006) no species traits or life-history syndromes in Australian acacias clearly separate invasive from non-invasive taxa (Gibson *et al.*, 2011). Measures of propagule pressure and human usage and climatic suitability most strongly determine whether an invasion will occur in this group (Castro-Díez *et al.*, 2011; Wilson *et al.*, 2011). Despite the numerous studies on invasive *Acacia* species, basic data are still lacking to develop comprehensive models of invasion debt (see for example Leung *et al.*, 2012 for a comprehensive framework on risk assessment). For example, we do not know the invasion status of introduced acacias for many countries. Our case study of *Acacia* invasion debt is therefore based on a few reliable and widely available factors and is presented here to illustrate the concept and utility of invasion debt. More complex quantification of invasion debt can be developed in the future as more data and better modelling tools become available.

Globally, we could only calculate establishment debt (the additional number of invasive species) across thirteen regions of the world as data were lacking to calculate the other components. Our measure of establishment debt was calculated based on the following factors: potential range, propagule pressure, and invasion status (introduced or invasive) in the various regions (see Box 1, Eq. 1).

The invasion status of the species was determined using two datasets. We used the data on known invasive acacias across thirteen regions of the world (Richardson *et al.*, 2011; Rejmánek & Richardson, 2013) to list invasive species per region. We scrutinised the GBIF database (www.gbif.org, accessed June 2011) to list additional species which have been introduced per region (but not yet listed as invasive according to Richardson *et al.*, 2011).

Forecasting the suitable range of alien species is riddled with uncertainty. Various approaches have been suggested to model potential species distribution. For alien species, presence-absence models are likely to be unreliable as alien species are often not in equilibrium with the environment, and absences in a given location might simply reflect the spread dynamics of the species (i.e. the species has not reached this location) and not its habitat suitability. Given the uncertainty associated with species distribution modelling of alien species (e.g. Webber *et al.,* 2011 for *A. cyclops* and *A. pycnantha*), we used several presence-only models as potential indicators of the suitable range of introduced species and combined models considered acceptable (see below). Ensemble modelling has recently been developed and is considered as a robust technique to predict species distributions, addressing several limitations of previous modelling techniques (Araújo and New, 2007, Thuiller *et al.*, 2009). This allowed us to estimate the additional range of each introduced species per region.

Three presence-only models were selected (Bioclim, Mahalanobis Distance and Domain; Tsoar *et al.,* 2009) which identified climatic niches for each acacia species. All models used the following six bioclimatic variables: maximum temperature in warmest month, minimum temperature in coldest month, precipitation in wettest quarter, precipitation in driest quarter, precipitation in warmest quarter and precipitation in coldest quarter. The predictor variables were obtained from the WorldClim database (Hijmans *et al.*, 2005) at 10-minute spatial resolution. Models were calibrated and evaluated based on distribution records of *Acacia* species in Australia only (native range) from the Australian Virtual Herbarium using a 80/20 split for calibration and evaluation. GBIF records were considered unreliable to estimate the location of invasive records (not cultivated or managed) outside Australia. We standardised all records to 10 min (thus removing duplicates within 10’ cells) and developed three models per species (with a minimum of 50 records). To evaluate model performance, we used the area under the receiver operating characteristic curve (AUC). A set of pseudo-absences equal to the number of presences for each species was generated by randomly selecting points within a 50-km buffer area around species occurrences in the native range. Pseudo-absences were only used for model evaluation and not for model calibration. The mean AUC for each of the three model types was calculated by randomly selecting training records five times (k-fold = 5) for each model run. Only models with a mean AUC ≥ 0.70 were selected for further analysis; other models were discarded. This resulted in between 1 to 3 models for 21 of the species, with only *A. holosericea* and *A. salicina* having no models with an AUC ≥ 0.70. All models were converted to binary presence/absence suitability maps using a threshold to maximise species prevalence. For species with more than one model, all areas identified by at least one model were considered to be suitable. We then calculated the number of cells and proportion of the country predicted to be suitable for each species. To assign the probability of establishment (α_j in Box 1) based on habitat suitability, we used a threshold (ε) of 10 cells, or 10% of the country, whichever was smaller. This threshold was slightly arbitrary but for most cases (86%), habitat suitability was either below 5 or above 15 cells. We assigned a probability of $\alpha_j = 1$ if the potential distribution in the country exceeded the threshold (otherwise $\alpha_j = 0$).

In addition to habitat suitability, we used information on propagule pressure and the invasion status of the species to calculate the invasion probability of each species. In other words, species with large suitable habitat, high propagule pressure, and that are known to be invasive elsewhere (Rejmánek & Richardson, 2013) were assigned a high probability of invasion. We estimated propagule pressure according to species use in each region. Propagule pressure was considered higher for species used in large-scale forestry, erosion control and agro-forestry and lower for other uses (see Donaldson *et al.*, 2014a). We assigned a probability (p_1) of 1 for species with high propagule pressure, and 0.5 for others. For species characteristics, we assigned a probability (p_2) of 1 for species known to be invasive elsewhere and 0.5 for others. For each species, the compound probability of invasion (ϕ_j) was calculated as the product of the individual probability for each factor ($\phi_j = p_1 \times p_2$), and the invasion probability of an introduced species as $\alpha_j \times \phi_j$ (as in Eq. (2)). The establishment debt of a region was calculated as the sum of probabilities for all introduced non-invasive species in the region.

Further improvement is needed to derive invasion probability based on the factors mentioned above. Here, due to data limitations, a relatively simple approach was used to quantify invasion debt globally. The generic equations of invasion debt, proposed in Box 1, however allow for more complex approaches to be developed.

Quantifying *Acacia* establishment, spread and impact debt in South Africa

We were able to quantify three components of invasion debt (establishment, spread and impacts) for South Africa as Australian acacia invasions have been particularly well studied in this country (van Wilgen *et al*., 2014). To estimate the establishment debt, we used a similar approach as for the global establishment debt. For the purpose of quantifying the current distribution of invasive species in South Africa we used the Southern African Plant Invaders Atlas (SAPIA, accessed June 2011, Henderson, 1998), forestry trial records (Poynton, 2009) and herbarium searches. As most of the data in SAPIA were recorded at 15-minute spatial resolution we produced models (using the same approach as described above) for all 66 Australian *Acacia* species recorded in South Africa using climatic predictor variable grids that were resampled to 15-minute spatial resolution for South Africa. We calibrated and validated the three presence-only models based on the distribution records in Australia (as for the global debt) and in South Africa (introduced range) for species with more than 20 records. Models were only considered acceptable if AUC >= 0.7. This resulted in models for 58 of the

66 species. We calculated the number of cells that were predicted to be climatically suitable for each of the 58 species introduced to South Africa and applied a threshold of 10 cells. We assigned a probability of $\alpha_j = 1$ if the potential distribution in the country exceeded the threshold (otherwise $\alpha_j = 0$). In addition to habitat suitability, the probability of invasion was also determined by the species invasion status (i.e. whether the species is invasive elsewhere in the world), propagule pressure and residence time. We used the same probability values as above (see Table S1) for the criteria related to species invasion status (p_1) and propagule pressure (p_2). For residence time, we assigned a probability (p_3) of 1 for species introduced before 1877 (mean introduction date for invasive acacias in South Africa), and 0.5 otherwise. For each species, the compound probability of invasion (ϕ_j) was calculated as the product of the individual probability for each factor ($\phi_j = p_1 \times p_2 \times p_3$), and the invasion probability of an introduced species as $\alpha_j \times \phi_j$ (as in Eq. (2)). The establishment debt of South Africa was calculated as the sum of probabilities for all introduced species in South Africa.

To estimate spread debt, we used the following criteria: 1) probability of invasion (see above); 2) suitable area a species could occupy; and 3) spread rate. For each species, we calculated the additional area of natural habitats that a species could potentially invade (based on 2009 land cover; source: South African National Biodiversity Institute). We subtracted the area known to be occupied (obtained from SAPIA, GBIF and forestry trials (Motloung *et al.*, 2014)) from the area predicted to be suitable by the habitat suitability model (we only considered natural habitats). This represents the total area the species could occupy (based on 15-min cells) without considering its density. Invasion debt was plotted for each species against its status in South Africa (introduced, established or invasive). For each species, the spread debt was calculated by multiplying the probability of invasion by the unoccupied suitable area. This calculation of spread debt excludes relaxation time and is a simplification of the invasion debt concept.

We also estimated spread debt over a 20-year horizon as this is a period long enough to provide a long-term perspective needed in IAS management decisions, and short enough that it is still in the temporal scope of IAS management planning (e.g. the Working for Water programme). The annual rate for increase of spatial extent of invasive *Acacia* species in South Africa has been estimated at 10% (van Wilgen *et al.*, 2012); no information was available to differentiate spread rate among invasive *Acacia* species. As the spread rate of species that are currently introduced but not yet invasive is not known, we used a simple exponential model based on a 10% annual increase for all species. We assumed that the species would only spread within its climatically suitable area (as defined above). Although both the current and potential distribution of species was recorded at a resolution of 15-min grid cells, we could not assume that species occupy the full extent of each grid cell. We therefore assumed a species density of 1% per 15-min grid cell (a conservative estimate).

To estimate the impact-based invasion debt over a 20-year horizon, we used the following criteria: 1) spread debt over 20 years (as above); and 2) impact costs. Although the environmental impacts of invasive *Acacia* have been quantified in South Africa with regards to water use, lost grazing potential and biodiversity loss (De Wit *et al.*, 2001; van Wilgen *et al.*, 2008), these impacts are context-specific (i.e. they vary according to the area invaded). As we cannot predict with sufficient accuracy where the species are likely to invade in order to estimate the environmental costs, we used the cost of clearing invasive species as a proxy for impacts. Management costs in South Africa have been well quantified in the national Working for Water programme. Clearing methods and costs are similar for all invasive *Acacia* species in South Africa and we used a value of US$9535 per invaded km^2 as an estimate of the cost of clearing invasive *Acacia* (based on Working for Water costs). We calculated the total cost of clearing invasive *Acacia* after 20 years of spread (i.e. once-off clearing cost after 20 years of spread). A similar approach was used to quantify the impacts and eradication costs of *Acacia paradoxa* in South Africa (Moore *et al.*, 2011). Given the uncertainties associated with quantifying impact-based invasion debt, our estimates should be interpreted with caution but demonstrate the potential of using the concept of invasion debt to estimate future impacts.

RESULTS

Establishment debt varies across 13 regions of the world, with several regions facing a considerable increase in the number of invasive Australian *Acacia* species (Fig. 2). For example, 5 out of the 7 introduced acacia species in South America are predicted to become established based on habitat suitability, species invasion status in other regions and propagule pressure.

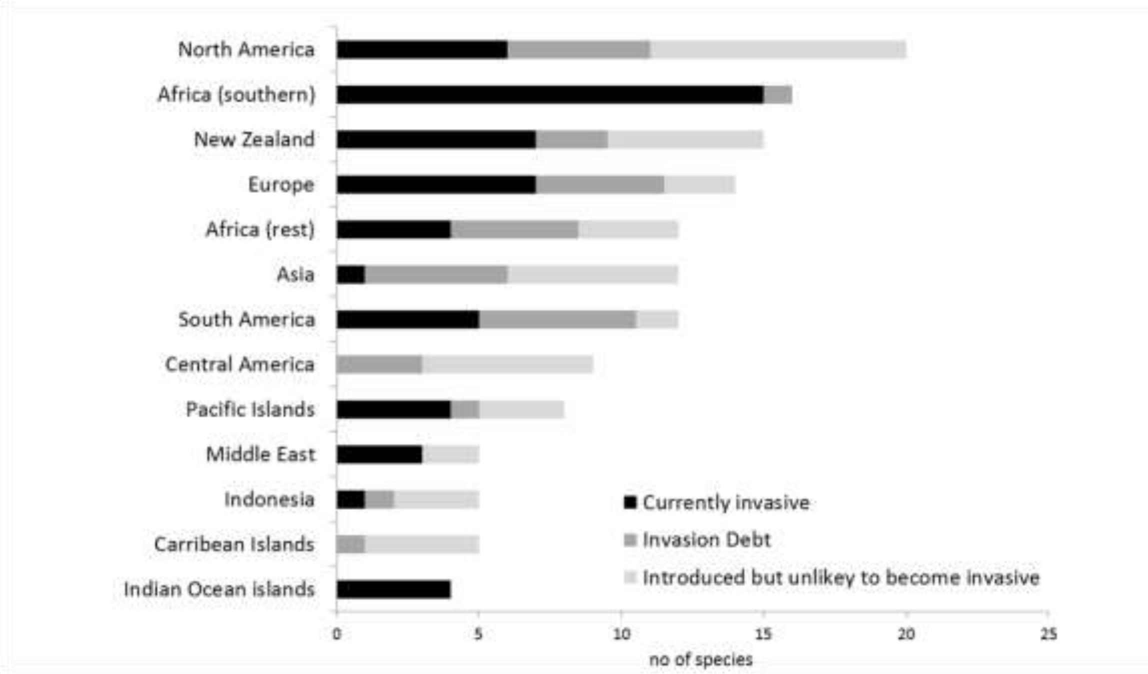

Figure 2: Species-based invasion debt for 13 regions of the world based on 21 Australian *Acacia* species known to be invasive. Invasion debt represents the additional number of future invasive species originating from the introduced species pool.

In South Africa, 14 acacia species are already invasive and an additional four species (one currently established, and three currently introduced) could become established out of the 45 modelled species that are currently not invasive. Many species have a very low probability of establishment with 17 unlikely to become established.

The spread debt was estimated to almost double the current extent of acacia invasion with a median increase value of 2,330 km^2 per species (unlimited time window, Fig. 3). Five introduced species (*A. acinacea, A. aneura*, *A. decora, A. pendula* and *A. verticillata*) have a considerable spread debt (Fig. 3). *Acacia elata* and *A. paradoxa*, two species that are currently invasive have the highest invasion debt (Fig. 3). *Acacia paradoxa* is currently invasive only at one locality in the country (Zenni *et al.*, 2009), whereas *A. elata* is invasive at many localities but occupies only 4.5% of its potential range in the country (Donaldson *et al*., 2014b). Similarly, populations of *A. implexa* in South Africa currently comprise around 30 000 individuals spread over about 600 ha in three geographically distinct populations, all in the Western Cape province, but the species has a large potential range in the country (Kaplan *et al*., 2012).

Over a 20-year period, the spread debt ranged between 0 for species unlikely to spread any further (n=18) to over 10,000 km^2 for *A. dealbata* and *A. mearnsii*. Given the estimated cost associated with managing *Acacia* invasions, this translates into economic impacts of up to US$ 174 million (in current value) per species based on control costs of 9535US$ per km^2. If left unmanaged, the clearing cost of the invasion debt of Australian acacias in South Africa over the next 20 years will exceed US$ 500 million.

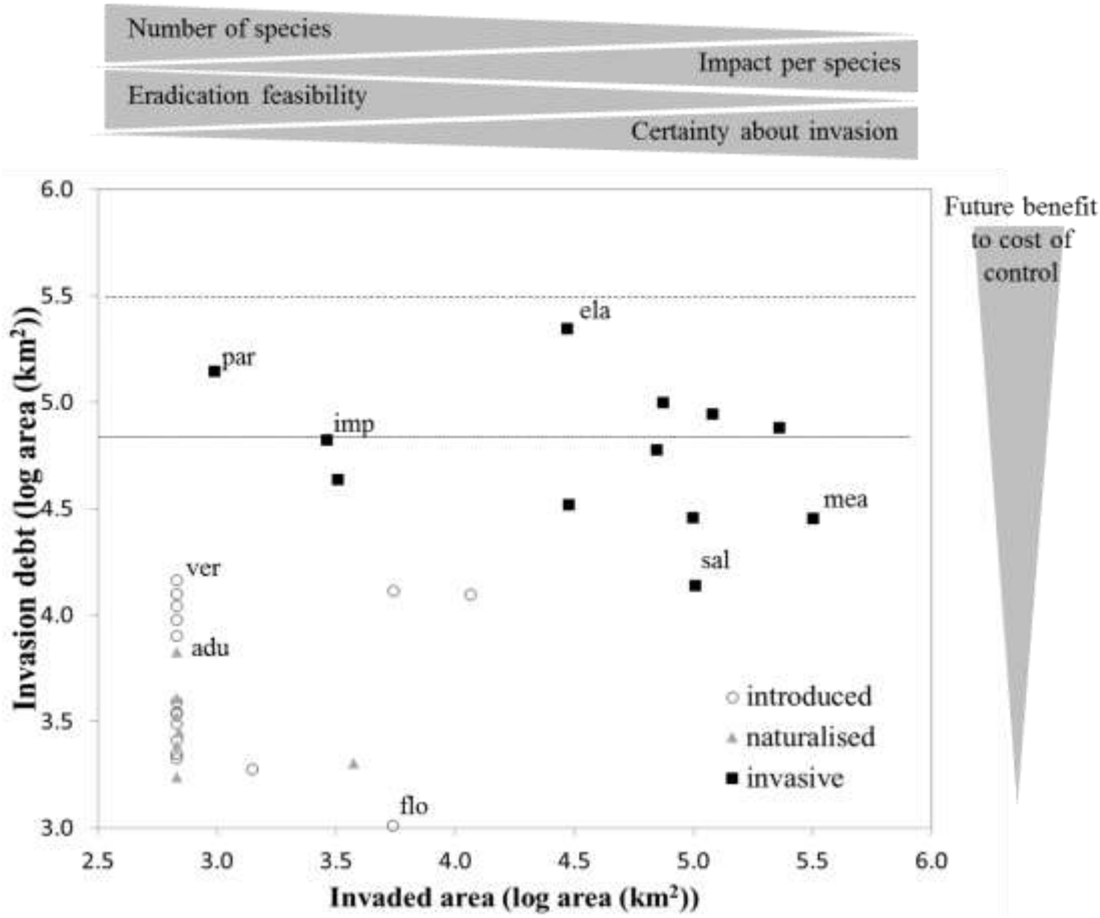

Figure 3: Area-based invasion debt (spread debt) for Australian *Acacia* species that are introduced, established or invasive to South Africa plotted against the area that they currently occupy (at 15-minute spatial resolution). The top line across the figure indicates the area occupied by most widespread invasive species (ca. 318 000 km²) currently in South Africa (area ca. 1.2 000 000 km²), while the lower line indicates the median area (ca. 72 000 km²) of all currently invasive acacia species in South Africa. Species names: adu – *A. adunca;* ela - *A. elata;* flo – *A. floribunda;* imp - *A. implexa*; *mea* - *A. mearnsii*; par - *A. paradoxa*; sal - *A. saligna*; ver - *A. verticillata.*

DISCUSSION

We have shown that predicting future invasion is riddled with uncertainty but that the concept of invasion debt provides a simple, practical approach for quantifying the extent of impending invasions that is easily translatable into policy documents. Separating the invasion debt into components corresponding to invasion phases allows one to estimate the contribution of the different invasion stages to the debt. The approach presented here allows for the consideration of species already introduced to a focal region (not explicitly included in previous frameworks) and species not yet present, but likely to become introduced given current levels of propagule pressure and habitat suitability. Using three key metrics (species, area and costs) to represent its four components, this approach could inform policy and management and places the emphasis on pro-active management. In contrast, previous measures for biological invasions (e.g. McGeoch *et al.*, 2010) provide an indication of current status, but not of future threat. Van Wilgen *et al*. (2011) proposed an approach for formulating management options for different species based on their current distribution, commercial value vs. impacts and other considerations. The quantification of invasion debt provides an additional layer for informing such strategic planning.

Introduced species sometimes remain as small populations for extended periods (often many decades) before suddenly expanding and becoming seriously invasive (Groves, 2006). The challenge is to act early and target those species with small populations but large potential impacts: those with large invasion debt (species at the top left of Fig. 3). The future benefit of controlling species with a large invasion debt (top of y-axis, Fig. 3) is high relative to the cost of control. The eradication feasibility of species however decreases as the areas that they occupy increases (Fig 3. x-axis). Species such as *A. paradoxa*, for example, should be prioritized for eradication in South Africa as it has a very large invasion debt. Moore *et al*. (2011) demonstrated that eradicating *A. paradoxa* would be cost-effective based on a detailed study of various management options (eradication, containment or take no action). Species such as *A. saligna* have a lower spread debt in South Africa because they have already invaded much of their potential range and are no longer viable candidate for eradication, but the likely increase in impacts over the short-term will be very high if there is no control.

Our ability to predict and manage future invasions is however limited by the lack of basic knowledge on introduced species and robust invasion models. Despite comprehensive risk assessment tools being developed (see Leung *et al.*, 2012), we found that modelling species habitat suitability and spread lack consistency. Furthermore, most countries lacked information on the distribution and status of introduced *Acacia* species, although they are a relatively-well studied group. There is an urgent need to collect basic distribution data on introduced species in a systematic manner to inform the management of tomorrow's new invasive species. One of the main challenges for the practical implementation of introduction debt and invasion debt will be to develop consistent measures to describe uncertainty.

We argue that invasion debt is a useful concept for disentangling and quantifying the scale of future invasions, for prioritizing control based on a long-term perspective, for raising awareness of invasion problems, and for comparing threats between countries and taxa. Quantifying invasion debt will however require robust estimates of invasion risk, spread and associated impacts.

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