IDEA AND PERSPECTIVE

Predicting species distributions for conservation decisions

Antoine Guisan,[1,2,3,4]* Reid Tingley,[5] John B. Baumgartner,[5] Ilona Naujokaitis-Lewis,[6] Patricia R. Sutcliffe,[3] Ayesha I. T. Tulloch,[3] Tracey J. Regan,[5] Lluis Brotons,[7,8] Eve McDonald-Madden,[3,4] Chrystal Mantyka-Pringle,[4,9] Tara G. Martin,[3,4] Jonathan R. Rhodes,[9] Ramona Maggini,[3] Samantha A. Setterfield,[10] Jane Elith,[11] Mark W. Schwartz,[12] Brendan A. Wintle,[5] Olivier Broennimann,[1] Mike Austin,[13] Simon Ferrier,[13] Michael R. Kearney,[14] Hugh P. Possingham[3,15] and Yvonne M. Buckley[3,16]

Abstract

Species distribution models (SDMs) are increasingly proposed to support conservation decision making. However, evidence of SDMs supporting solutions for on-ground conservation problems is still scarce in the scientific literature. Here, we show that successful examples exist but are still largely hidden in the grey literature, and thus less accessible for analysis and learning. Furthermore, the decision framework within which SDMs are used is rarely made explicit. Using case studies from biological invasions, identification of critical habitats, reserve selection and translocation of endangered species, we propose that SDMs may be tailored to suit a range of decision-making contexts when used within a structured and transparent decision-making process. To construct appropriate SDMs to more effectively guide conservation actions, modellers need to better understand the decision process, and decision makers need to provide feedback to modellers regarding the actual use of SDMs to support conservation decisions. This could be facilitated by individuals or institutions playing the role of 'translators' between modellers and decision makers. We encourage species distribution modellers to get involved in real decision-making processes that will benefit from their technical input; this strategy has the potential to better bridge theory and practice, and contribute to improve both scientific knowledge and conservation outcomes.

Keywords

Biological invasions, conservation planning, critical habitats, environmental suitability, reserve selection, species distribution model, structured decision making, translocation.

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SETTING THE SCENE: SPECIES DISTRIBUTION MODELS FOR CONSERVATION APPLICATIONS

Species ranges are shifting, contracting, expanding and fragmenting in response to global environmental change (Chen *et al.* 2011). The emergence of global-scale bioinformatic databases has provided new opportunities to analyse species occurrence data in support of conservation efforts (Jetz *et al.* 2012) and has paved the way toward more systematic and evidence-based conservation approaches (Margules & Pressey 2000; Sutherland *et al.* 2004). However, records of observed species occurrence typically provide information on only a subset of sites occupied by a species (Rondinini *et al.* 2006). They do not provide information on sites that have not been surveyed,

or that may be colonised in the future following climate change (Hoegh-Guldberg *et al.* 2008) or biological invasions (Thuiller *et al.* 2005; Baxter & Possingham 2011; Giljohann *et al.* 2011). However, this information is important for making robust conservation management decisions and can be provided by predictions of species occurrences derived from environmental suitability models that combine biological records with spatial environmental data.

Species distribution models (SDMs; also commonly referred to as ecological niche models, ENMs, amongst other names; see Appendix S1) are currently the main tools used to derive spatially explicit predictions of environmental suitability for species (Guisan & Thuiller 2005; Elith & Leathwick 2009; Franklin 2010; Peterson *et al.* 2011). They typically achieve this through identification of statistical

[1]*Department of Ecology and Evolution, University of Lausanne, 1015, Lausanne, Switzerland*

[2]*Institute of Earth Surface Dynamics, University of Lausanne, 1015, Lausanne, Switzerland*

[3]*ARC Centre of Excellence for Environmental Decisions (CEED), School of Biological Sciences, The University of Queensland, St Lucia, Brisbane, Qld, 4072, Australia*

[4]*CSIRO Ecosystem Sciences, Ecosciences Precinct, Dutton Park, Brisbane, Qld, 4102, Australia*

[5]*ARC Centre of Excellence for Environmental Decisions (CEED), School of Botany, The University of Melbourne, Parkville, Vic, 3010, Australia*

[6]*Ecology & Evolutionary Biology, University of Toronto, Toronto, Canada*

[7]*Centre de Recerca Ecològica i Aplicacions Forestals (CREAF), Bellaterra, Spain*

[8]*Centre Tecnològic Forestal de Catalunya (CTFC - CEMFOR), Solsona, Spain*

[9]*ARC Centre of Excellence for Environmental Decisions (CEED), School of Geography, Planning and Environmental Management, The University of Queensland, St Lucia, Brisbane, Qld, 4072, Australia*

[10]*Research Institute for Environment and Livelihoods, Charles Darwin University, Darwin, NT, 0909, Australia*

[11]*School of Botany, The University of Melbourne, Parkville, Vic, 3010, Australia*

[12]*John Muir Institute of the Environment, University of California, Davis, 95616, USA*

[13]*CSIRO Ecosystem Sciences, GPO Box 1700, Canberra, ACT 2601, Australia*

[14]*Department of Zoology, The University of Melbourne, Parkville, Vic, 3010, Australia*

[15]*Imperial College London, Department of Life Sciences, Silwood Park, Ascot SL5 7PY, Berkshire, England, UK*

[16] *Present address: Zoology Department, School of Natural Sciences, Trinity College, Dublin 2, Ireland*

Correspondence: E-mail: antoine.guisan@unil.ch

relationships between species observations and environmental descriptors, although more mechanistic modelling approaches, and approaches involving expert opinion, also exist (Appendix S1). SDMs have the potential to play a critical role in supporting spatial conservation decision making (Margules & Pressey 2000; Addison et al. 2013; Appendix S2), but their applicability and relative utility across the breadth of conservation contexts remains unclear, as does the extent of their adoption in aid of conservation decision making.

The last decade has seen a surge in the development of SDMs (Fig. 1a, Appendix S3). However, despite large numbers of SDM-based studies published in the peer-reviewed literature, and widespread claims of applicability to conservation problems (Guisan & Thuiller 2005; Rodriguez et al. 2007; Cayuela et al. 2009; Elith & Leathwick 2009; Franklin 2010; Peterson et al. 2011), evidence of the practical utility of these models in real-world conservation management remains surprisingly sparse. An indicative assessment of keywords in ISI suggests that < 1% of published papers using SDMs are specifically targeted at conservation decisions (Fig. 1b, Appendix S3). A recent review of SDMs used in tropical regions (Cayuela et al. 2009) similarly concluded that < 5% of studies addressed conservation prioritisation. Furthermore, in the few published applications of SDMs to conservation decision making (e.g. Brown et al. 2000; Soberón et al. 2001; Ferrier et al. 2002; Leathwick et al. 2008), the importance of their contribution to the decision-making process and implementation of actions is often unclear (but see Pheloung et al. 1999). The bulk of the peer-reviewed literature
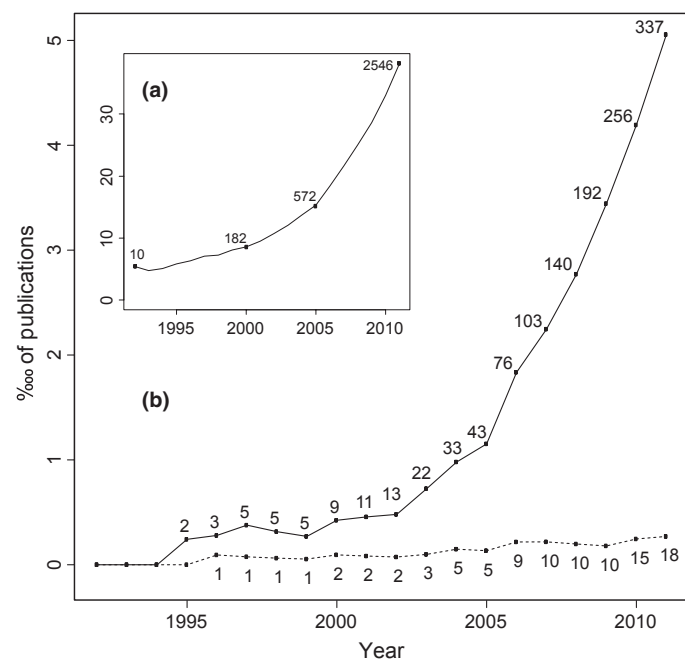
clearly lacks the perspective of practitioners and decision makers on how SDMs can contribute to solving environmental problems, despite SDM construction often being justified based on their potential utility for decision making. As a result, there are a wide variety of tools published, but little guidance on how SDMs – and other models (Addison et al. 2013) – could be used to support decision making in relation to clear conservation objectives (Possingham et al. 2001). More practice-oriented assessments of the use of models to support conservation are urgently needed.

Here, we investigate instances outside the peer-review literature where SDMs have been used to guide conservation decisions, how they were constructed when used, and how they could be used more effectively in the future. We do not propose a review of SDMs, or their use in conservation, nor do we undertake an exhaustive quantitative assessment of the grey literature, which is difficult to access in many countries. Rather, based on chosen examples in different countries (including developed and developing ones), we emphasise the importance of clearly articulating the decision context to determine where and how SDMs may be useful. We examine how closer consideration of the decision-making context and better collaboration with decision makers may encourage the development and use of SDMs for guiding decisions. Our primary focus is on statistical SDMs, as they are the most frequently and readily applied, although other approaches, such as mechanistic SDMs (Kearney & Porter 2009), may also provide input for conservation decision making.

FROM PROBLEMS TO DECISIONS: HOW CAN SDM CONTRIBUTE TO DECISION MAKING?

The potential of SDMs to guide conservation actions is best assessed by first considering the full decision-making process, a step rarely taken. Structured decision making (Gregory et al. 2012; Fig. 2) provides a rigorous framework for this process and is increasingly proposed to address environmental problems (Wintle et al. 2011; Addison et al. 2013). This approach is usually sequential (Possingham et al. 2001), with potential roles for SDMs at most stages of the decision process (Fig. 2, Table 1), as outlined below.

Identifying a problem

The need to make a conservation decision arises from the identification of a conservation problem (Fig. 2a). SDMs could play a role by highlighting likely shifts of suitable habitat for a species due to climate change (Araujo et al. 2011), or by identifying areas likely to be invaded by a pest species (Thuiller et al. 2005; Araujo et al. 2011), and therefore allow the identification of potential conflict areas if species may not be able to migrate across human-modified landscapes, or if the native communities at threat of being invaded shelter threatened species (e.g. Vicente et al. 2011).

Defining the objectives

Once a problem is identified, the definition of conservation objectives is usually the realm of decision makers and stakeholders. However, scientific input may be used to ensure objectives are realistic, given the current, or projected, state of the environment. SDMs may be used as a frame of reference for setting objectives retrospectively from the identified problem, or interactively by refining conservation objectives within an adaptive framework (Runge et al.
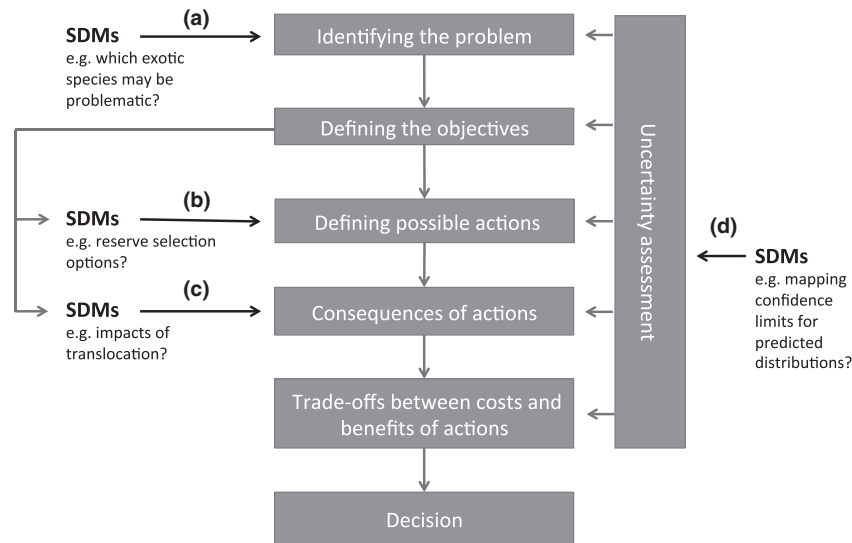

Figure 1 Cumulative trends over the last 20 years extracted from the Web of Science (WoS), showing the increasing number of peer-reviewed papers related to SDMs (keyword search). Curves are drawn as proportions (‰) of the cumulative number of papers published in the WoS category 'Ecology'. The cumulative number of papers for each year is indicated on the curves. (a) All SDM papers. (b) Only SDM papers in the four important conservation domains (biological invasions, critical habitat, reserve selection, translocation) discussed in the paper, without (solid line) or with (dashed line) the keyword 'decision'. For choice of keywords see Appendix S3.

Figure 2 A structured decision-making process (Gregory *et al.* 2012) with indication of potential entry points for the use of SDMs. See main text and Table 1 for details. The black arrows indicate where SDMs can contribute to steps in the decision-making process.

Table 1 Examples of ways to increase the utility of SDMs within four conservation domains and the structured decision analysis process (DAP). The first five rows correspond to specific DAP steps, whereas the final three rows describe general issues requiring consideration.

	Biological invasions	Critical habitat	Reserve selection	Translocation
Problem identification	A new invader is likely to impact particular habitats.	Particular habitat patches drive species' extinction vulnerabilities.	Inappropriate habitat protection leads to higher extinction vulnerabilities.	The rate of climate change may exceed species' capacity to respond.
Defining the objectives	Reduce harmful impacts by prevention or mitigation of invasion.	Provide adequate habitat protection for threatened species.	Provide adequate habitat protection for threatened species.	Increase persistence probabilities of climate vulnerable species.
Defining possible actions	When and where to carry out quarantine, surveillance, eradication, containment or local control.	Strengthen protection, acquire new reserves, foster migration, translocation.	Acquire reserves, private landowner incentives, restoration, reserve management.	Translocate species, manage dispersal corridors, passive migration management.
Consequences of actions	Estimating the extent to which potential impacts may be prevented or mitigated through actions.	Estimating extent of opportunity costs for other habitat uses, estimation of extinction risk.	Estimating which subset of at risk taxa may be conserved.	Selecting subset of at risk taxa for action, risk of creating invasion problem.
Trade-off analysis	Cost efficiency of surveillance and management vs. risk of adverse impacts.	Social and economic conflict over land use.	Social and economic conflict over land use.	Cost-benefit and potential conflicts of placing species in novel environments.
Decision that can be informed by SDM	Predicting areas of potential occupancy to target surveillance and management.	Determining most favourable habitats.	Model diversity at a landscape level to set priorities.	Identify target locations for managed relocation.
How SDM uncertainty influences decisions	Under-prediction may miss critical surveillance, over-prediction may waste management resources.	Distribution model error misidentifies optimal habitats leading to excess opportunity costs or species extinction.	Uncertain suitable environments may lead to suboptimal reserve selection.	Spatial scale constraints limit the specificity of targeting locations.
Key issues for integrating science and management	Biotic interactions may play a strong role in determining environmental suitability in novel habitats.	Careful integration of population persistence processes into management decision.	Project regional diversity hotspots under global change models.	Apply SDMs to assess future distributions for species targeted for dispersal assistance.

2011). For example, initial objectives may be set based on low quality data but through the course of subsequent conservation and research actions, better quality data may inform an SDM and lead to changes in the initial objectives. It is essential that the outcomes of any subsequent action (see the following two points) be evaluated against the objectives (Chauvenet *et al.* 2012).

Defining possible alternative actions

The definition of feasible actions (Fig. 2b) may be informed by SDMs. For example, when making decisions about where to translocate a threatened species (Chauvenet *et al.* 2012) or where to target control of an invasive species (Baxter & Possingham 2011),

SDMs may be used to identify candidate locations as alternative actions that may subsequently be evaluated in greater detail. Information about the costs of management actions, logistical constraints (e.g. distance) or conflicting conservation priorities (e.g. various land ownerships) for example will ultimately determine the feasibility of different actions, but the SDM provides a suite of options.

Evaluating the consequences of alternative actions

Species distribution models can be used to evaluate the implementation of alternative actions (Fig. 2c) in terms of predicting resultant changes to species' distributions, or to the quality of habitat. For example, use of SDMs has been proposed to assess alternative reserve designs and their role in conserving biodiversity under current and possible future climates (Hannah *et al.* 2007).

Assessing the trade-offs between benefits and costs of actions

This important step builds on the identified consequences of actions (Fig. 2). SDMs can be used to quantify benefits to be traded off against costs of actions, such as in prioritising competing wetland bird management options ranging from adding artificial habitat features to controlling disease outbreaks and changing pond inundation regimes (Sebastian-Gonzalez *et al.* 2011), or in optimising various control actions for invasive species across space (Giljohann *et al.* 2011).

Assessing and dealing with uncertainty

All conservation decisions are made in the presence of some uncertainty, and most involve the implicit or explicit specification of an acceptable level of risk (Fig. 2d). Assessment of risk includes estimation of the differential cost to biodiversity of errors associated with under-protection vs. over-protection (Schwartz 2012). In particular, the type (Barry & Elith 2006) and magnitude (Carvalho *et al.* 2011) of uncertainty that are acceptable need to be based on the needs of decision makers, and incorporated into the definition of the objectives (Richardson *et al.* 2009; Fig. 2a). SDMs enable the quantification of some types of uncertainties in the spatial predictions of environmental suitability (Barry & Elith 2006), and these can be explicitly incorporated in conservation prioritisation processes (Moilanen *et al.* 2006). However, some other types of uncertainties are not directly retrievable from SDMs (Appendix S1) but need to be recognised and where possible considered. When deciding whether to invest in reducing uncertainty, it is useful to consider whether the uncertainty is reducible (Barry & Elith 2006) and whether a reduction in uncertainty might lead to decisions that yield better management outcomes (Regan *et al.* 2005), a concept generally known as value of information (Runge *et al.* 2011).

EXAMPLES OF USING SDM FOR GUIDING CONSERVATION DECISIONS

Despite the numerous potential conservation applications proposed for SDMs, examples where SDMs have explicitly guided decisions relating to the management of natural resources are difficult to find in the scientific literature. We searched the grey literature (partially based on our own linkages with practitioners) and found various examples of the practical use of SDMs to guide decisions in different conservation domains, with differences in use intensity. We discuss four areas where SDMs have been used to guide management decisions: the use of climate-matching SDMs in some invasive species risk assessments (Managing biological invasions), the use of SDMs to guide the legal identification of critical habitats for threatened species (Identifying and protecting critical habitats), the use of SDMs in regional conservation planning (Reserve selection) and the use of SDMs for informing translocation of threatened or captive-bred populations (Translocation) (Table 1, Fig. 3).

Managing biological invasions

In some countries, SDMs are commonly used to guide decisions about invasive species management. For instance, Australia has implemented advanced detection, prevention and impact mitigation programmes that include SDMs. Pre-border weed risk assessment encourages the use of SDMs to aid decisions about whether to allow the import of new plant species (Pheloung *et al.* 1999; see *Defining possible actions*, Fig. 2b). Post-border weed risk assessments use maps of potential distributions, developed using SDMs, to assist in the identification of potentially widespread, high impact, invaders and to apportion control costs among potentially affected regions. SDMs are systematically used to contribute to the classification of species as weeds of national significance (NTA 2007). At the regional scale, such an approach recently contributed to the official listing of gamba grass (*Andropogon gayanus*) as a weed in the Northern Territory of Australia (NTA 2009; Fig. 3a). In Mexico, SDMs were used to predict the potential impact of the invasive cactus moth (*Cactoblastis cactorum*) on native cacti (*Opuntia* spp) to facilitate planning and mitigation of future impacts (Soberón *et al.* 2001).

Identifying and protecting critical habitats

Critical habitats are typically defined as habitats necessary for the persistence, or long-term recovery, of threatened species (Greenwald *et al.* 2012), and their identification is required by law in some countries (e.g. Canada, USA, Australia). SDMs are one tool for differentiating habitat quality at a range-wide scale, and can be combined with other sources of information, such as population dynamics, to define critical habitat (Heinrichs *et al.* 2010). In Canada, hybrid SDM-population dynamics models were used to determine critical habitat for the Ord's kangaroo rat (*Dipodomys ordii*; Heinrichs *et al.* 2010). In Catalonia (Spain), SDMs were used to identify critical habitats for four threatened bird species to guide land-use decisions in a farmland area affected by a large-scale irrigation plan. In the latter case, SDMs were first developed by scientists (Brotons *et al.* 2004), explained to practitioners (CTFC 2008) and finally influenced policy and were considered in a legal decree in the framework of the Natura 2000 network management plan (DMAH 2010; Fig. 3b; see Appendix S4). In Australia, the Victorian State Government developed SDMs for use in regulating vegetation-clearing applications (DEPI 2013).

Reserve selection

The delineation and establishment of protected areas often forms the cornerstone on which conservation plans are built (Margules & Pressey 2000). An early example of the use of SDMs in systematic conservation planning involved the development of SDMs for over
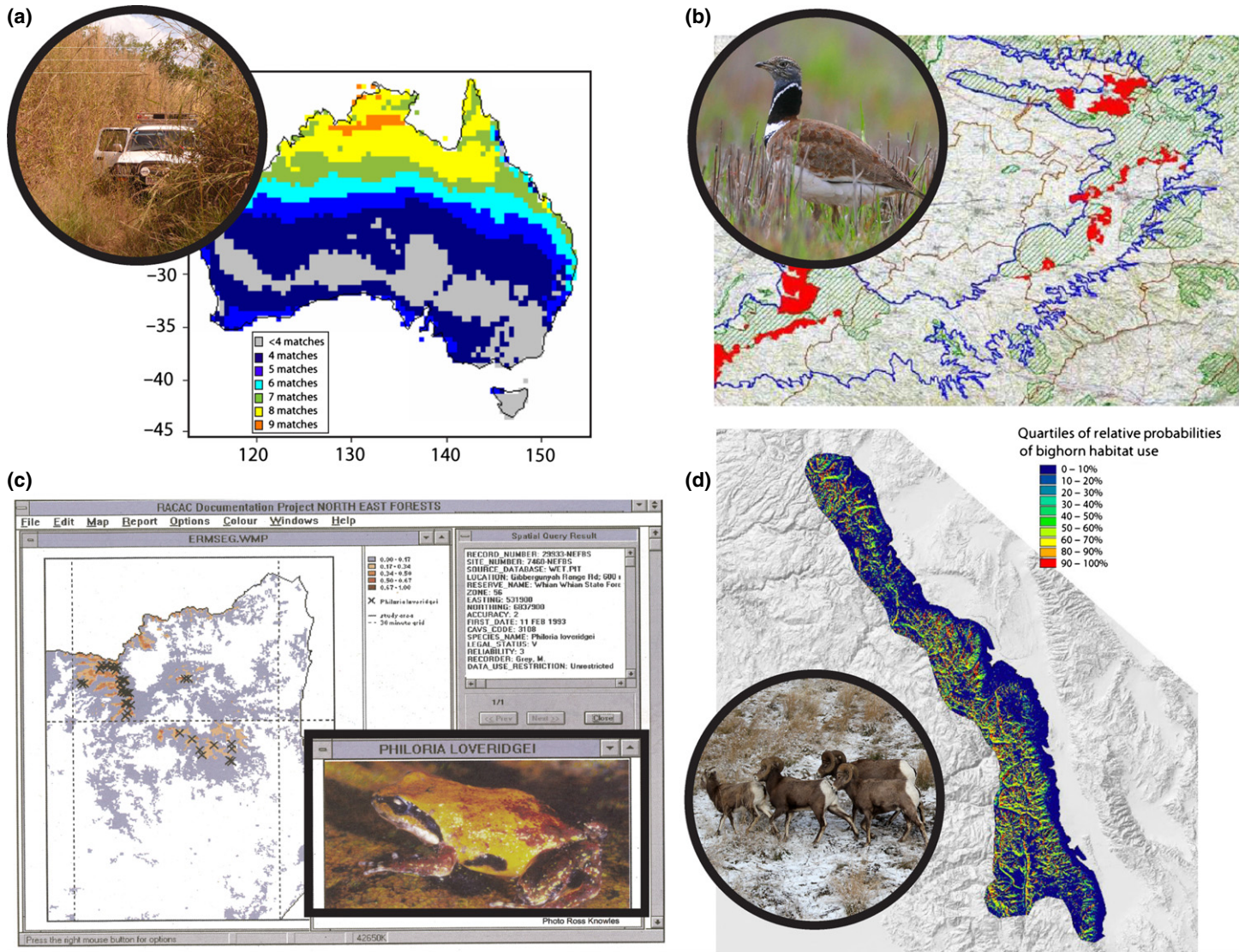
Figure 3 Four examples of maps used in conservation decision making based on SDMs. (a) Declaration of gamba grass (Andropogon gayanus, picture by Samantha Setterfield) as a weed using the weed risk assessment process in the Northern Territory of Australia (NTA 2009). (b) Identifying critical habitats (red) for three endangered bird species in Catalonia, Spain, as used in a legal decree (DMAH 2010) (picture of Tetrax tetra by Blake Matheson). (c) E-RMS tool windows and spatial query result for an endangered frog (Philoria loveridgei), as used in the conservation planning project for northeast New South Wales forests (Brown et al. 2000). (d) Identification of habitat use by the Bighorn sheep (Ovis canadensis sierra, picture by Lynette Schimming) in the Sierra Nevada, California, based on historical records only (NPS Seki 2011); SDM were not used to plan current translocation efforts but to predict the future distribution of potential translocation sites (Johnson et al. 2007).

2300 species of plants and animals throughout the northeast forests of New South Wales, Australia (results first presented in a report in 1994, cited in Brown et al. 2000; Ferrier et al. 2002). This region was the focus of a long-running conflict between the needs of commercial forest harvesting and the protection of exceptionally high biodiversity. The SDM outputs were integrated with data on other conservation and timber values in an environmental decision-support system by a team of negotiators representing all relevant government agencies and non-government stakeholders (see example in Fig. 3c). The aim was to identify areas of high conservation value for exclusion from logging, thereby resulting in major additions to the regional network of protected areas (Ferrier et al. 2002). This SDM application also provides an early demonstration of various approaches to evaluating and quantifying some sources of uncertainty in predictions (e.g. through expert ecological apprai-

sal, cross-validation, and independent field testing), and to communicating this uncertainty to decision makers (e.g. through mapping of confidence limits for predicted distributions). In another example in Madagascar, SDMs for large numbers of species in the main biodiversity groups (mammals, birds, reptiles, amphibians, freshwater fishes, invertebrates, plants) were developed by scientists and managers, and used to define priority areas for conservation (Kremen et al. 2008) using the Zonation software (Moilanen et al. 2009). These were then combined with other 'priority areas' using the Marxan software (Watts et al. 2009) and put on the map of 'potential sites for conservation'. Following a legal decree (Arrêté Interministériel n18633/2008/MEFT/MEM, renewed in 2013), no mining and forestry activities can be permitted in these priority areas for conservation as long as the decree remains in force (Appendix S5).

Translocation

The active transport of species by humans has been proposed as a measure to mitigate the threats species face under present or future conditions (Richardson *et al.* 2009; Chauvenet *et al.* 2012). SDMs can potentially inform the translocation decision process at three key stages. First, SDMs can identify suitable habitat under current and future climates to reveal whether habitat suitability is likely to decline in regions currently occupied by the species (Fig. 2a), thereby supporting the decision of whether translocation is necessary (Hoegh-Guldberg *et al.* 2008; Thomas 2011). Second, if translocation is deemed necessary, SDMs can identify potential recipient sites, which may be climate refugia within the current range, or sites that are projected to become newly suitable (Chauvenet *et al.* 2012; McLane & Aitken 2012; Fig. 2b). Third, SDMs can be used to identify which local species may be at risk of impact from the introduction of a translocated species through predicted overlapping distributions, in the same way as they are used to identify conflict areas between native and invasive species (Vicente *et al.* 2011; Fig. 2c). An example of the identification of suitable translocation sites in present and/or future climates exist for the bighorn sheep (*Ovis canadensis sierrae*) in the Sierra Nevada (Johnson *et al.* 2007; NPS Seki 2011; Fig. 3d). An SDM was used to identify suitable sites for reintroductions and translocation by avoiding areas of overlap with existing grazing stock allotments and areas of high predator densities.

These four groups of examples show that SDMs can be used to guide different decision-making steps in different conservation contexts (Table 1, Figure 2). Yet, the bulk of SDMs currently remains primarily developed for scientific purposes. However, as we show below, the way SDMs are built may vary depending on the requirements of the decision-making context, which are primarily influenced by the conservation objectives and the decisions to be made (often – but not necessarily – defined independently of the SDMs; e.g. select reserves to minimise biodiversity loss below some arbitrary threshold).

TOWARD A DECISION-MAKERS PERSPECTIVE: HOW CAN THE DECISION-MAKING CONTEXT GUIDE SDM DEVELOPMENT?

Many methodological choices are made when building and using an SDM (Guisan & Thuiller 2005; Elith & Leathwick 2009; Franklin 2010; Peterson *et al.* 2011), often with very general, research-oriented objectives in mind, such as answering macro-ecological questions, predicting range shifts under climate change (Keith *et al.* 2008; Carvalho *et al.* 2011; Fordham *et al.* 2012) or assessing the potential spread of invasive species (Thuiller *et al.* 2005). The use of SDMs is conditional on the availability of suitable data, skilled staff, modelling tools, funds and time. Many methodological factors, such as error in locational or temporal accuracy, or biased data, also potentially affect SDMs and their predictions (Kadmon *et al.* 2003; Cayuela *et al.* 2009; Appendix S1). Using an inappropriate modelling method or disregarding influential methodological factors can have consequences for the intended use of an SDM. The utility of an SDM for decision makers is therefore highly context sensitive. Below, we present examples that show why choices of various options for building/using an SDM may require more careful attention in a decision-making context where modelling methods should be determined by the nature of the conservation problem at hand and the decision to be made (Table 1).

Decision context

The example from the northeast forests of New South Wales (Brown *et al.* 2000; Ferrier *et al.* 2002) provides a rare documented case where all necessary conditions for building SDMs in a conservation context were met. Foresight by planners in the state environmental agency and funding by both commonwealth and state governments, along with data availability and sufficient lead-time for skilled staff to develop SDMs appropriate for the conservation objectives, made the use of SDMs in the decision-making process possible. The Madagascar case is another example where careful evaluation of the decision needs led to appropriate decisions for building SDMs, in this case by: ensuring species-environment temporal matching, using models above some validation threshold only, correcting for biogeographical overprediction and adding expert validation. In some cases, however, an SDM could be constructed for a species in the context of a conservation action to be taken, but the desired outputs (e.g. spatial predictions, ecological response curves) may not meet the criteria (e.g. spatial accuracy, level of certainty) necessary for its contribution to a final decision. Hence, early awareness of decision criteria increases the chance of developing SDMs that are useful for decision makers. This requires a close association between decision makers and SDM-developers from the onset of SDM development (McAlpine *et al.* 2010). Collaboration between decision makers and SDM-developers also offers opportunities for evaluation of other sources of ecological knowledge and data as a substitute for or complement to SDMs.

Time

Many threatened species have restricted distributions and specific habitat requirements, so decisions to protect critical habitat may need to be made with some urgency to avoid extinction (Martin & Maron 2012). This urgency often leads to protection of minimum amounts of habitat based on occurrence data alone. For example, the endangered Banff Springs snail (*Physella johnsoni*) is found in only five thermal springs, all of which are designated as critical habitat for this species (Lepitzki & Pacas 2010). In such cases, allocating time to collect more data and build accurate SDMs or more complex spatially explicit population models may not necessarily improve predictions but may delay the action of protection. However, deciding to build a simple SDM, or to not build one at all, may overlook some potentially critical habitats for the species (Heinrichs *et al.* 2010). There is thus a trade-off between allocating conservation resources to model construction or to immediate action with uncertain consequences (McDonald-Madden *et al.* 2008). For situations where time is less critical, more sophisticated SDMs might suggest new sites where a threatened species could be found, or areas that could be recolonised (Fig. 2b), as demonstrated in the cases of the Sierra Nevada bighorn sheep (*Ovis canadensis sierra*; NPS Seki 2011; see above) and the whitebark pine (*Pinus albicaulis*) in western North America (McLane & Aitken 2012).

Population dynamics

Modelled probabilities of occurrence from SDMs may not always correlate with the population processes necessary for species' persistence (Fordham *et al.* 2012). In such cases, it may be necessary to combine process-models such as population viability analyses with

SDMs to better evaluate the effects of management actions on long-term species' persistence (Keith *et al.* 2008; Wintle *et al.* 2011; Fordham *et al.* 2012). Such an approach was recently used to assess critical habitats for Ord's kangaroo rat in Alberta, Canada (Heinrichs *et al.* 2010) and revealed that 39% of habitat predicted as suitable for this species is unlikely to contribute to population viability. These habitats are therefore unlikely to support long-term species persistence and should not be given high conservation priority. This study highlights the importance of using, e.g. hybrid SDM-population models and/or the use of proximal environmental variables (Austin 2007) directly relevant to the species' demography (Eckhart *et al.* 2011) when predictions of species' persistence are the primary modelling output.

Type of error

Species distribution model predictions are susceptible to two types of errors (Franklin 2010): suitable habitat predicted as unsuitable (false negatives) and unsuitable habitat predicted as suitable (false positives). Both errors can be costly when using SDMs to support conservation decisions. For example, for biological invaders, false negatives are considered more serious than false positives at the pre-border stage, as underestimating the extent of a species' potential distribution could lead to an incorrect decision to allow import (Pheloung *et al.* 1999), which might subsequently lead to high impact and mitigation costs (Yokomizo *et al.* 2009). However, for established invaders, both types of errors can matter. False negatives may result in invaders being incorrectly labelled as harmless in a given area, leading to a failure to establish appropriate surveillance or containment measures. Alternatively, false positives can lead to wasted surveillance effort, or concentration of management effort in inappropriate areas (Baxter & Possingham 2011). Deciding how to balance both types of error will thus vary from one decision-making context to another, depending on the consequences of the errors in relation to the conservation objective. Errors can emanate from several sources (e.g. data, algorithm, parameterisation options), but one factor that has a direct effect on error rates is the choice of a threshold to classify continuous predictions of environmental suitability as either 'unsuitable' or 'suitable' (Franklin 2010). Several criteria exist that depend on the type of species data. For SDMs built with presence-only data, predictions of environmental suitability are not probabilities of occupancy but rather relative surrogates of occupancy, as the baseline probability of occupancy (i.e. prevalence) is typically unknown and cannot be used as the criterion. For presence–absence SDMs, the decision to set a certain threshold can be formally considered by explicitly accounting for the respective consequences of each type of error (omissions, commissions) when choosing a threshold, or by using different thresholds for different decisions (e.g. when to monitor, when to eradicate, when to change categorisation of threat; Field *et al.* 2004; Royle & Link 2006). A promising alternative is to base decisions on the continuous environmental suitability predictions derived from SDMs and incorporate the uncertainty directly, rather than categorising 'suitable' and 'unsuitable' habitat using specific thresholds (Moilanen *et al.* 2005). The important point is that decision makers need to specify the intent of SDM predictions so that modellers can understand the implications of the different types of errors. Ideally, this would be an iterative process involving modellers and decision makers, whereby methodological decisions such as model complexity and choice of threshold are continuously updated until decision-makers are satisfied with the balance of both types of errors.

Uncertainty

Given the large variability in output resulting from using different SDM techniques, data or environmental change scenarios (Appendix S1), it is important to quantify uncertainty in environmental suitability predictions used to make decisions (Moilanen *et al.* 2006; Carvalho *et al.* 2011). However, it is critical that conservation scientists specify which components of uncertainty are estimated (Barry & Elith 2006) and which are not. For example, using an ensemble of global climate models (GCMs) to project future distributions will provide a suite of projections from which means and variances of suitability can be calculated. This measure of uncertainty, however, can only capture the uncertainty derived from different projections of future climate and does not include uncertainty that derives from different model constructions, errors in the species data used to fit the model, in the estimation of current climate, or in the goodness-of-fit of the SDM. In addition, this uncertainty estimate assumes that the ensemble model captures the spectrum of potential future climates: an attribute that the current suite of GCMs is not designed to have (Schwartz 2012). New structured approaches for dealing with uncertainty associated with SDM outputs (Barry & Elith 2006; Appendix S1) exist in conservation decision support tools such as Marxan (Carvalho *et al.* 2011) and Zonation (Moilanen *et al.* 2006). These generally involve some form of assessment of the robustness of decisions to large errors in key data, models or assumptions (Regan *et al.* 2005; Wintle *et al.* 2011). For instance, info-gap decision theory has been used to identify reserve networks that achieve conservation targets with the highest robustness to uncertainty (Moilanen *et al.* 2006). Because much uncertainty about the predictions of SDMs is irreducible (Regan *et al.* 2005; Barry & Elith 2006), methods for explicitly dealing with this uncertainty in decision making will be critical for successful application.

WHY HAVE SUCCESSFUL EXAMPLES OF SDM SUPPORTING DECISION MAKING BEEN SO POORLY REPORTED?

We have found evidence that SDMs can help guide decisions (e.g. Brown *et al.* 2000; Soberón *et al.* 2001; NTA 2007; US Fish & Wildlife Service 2007; CTFC 2008; Cayuela *et al.* 2009; NTA 2009; DMAH 2010; Lepitzki & Pacas 2010; Environment Canada 2011; NPS Seki 2011), but most examples are hidden in the grey literature and only rarely reported in the peer-reviewed literature. Our keyword search (Fig 1 and Appendix S3) suggested that applications to decision problems are rare compared to the breadth of published SDM-based conservation papers. This suggests that reporting, to the scientific community, of successful use of SDMs to support decision making is sparse, and leaves open the question as to how many of these successful applications actually exist but remain largely hidden? A useful perspective in this regard would be to assess comprehensively how frequently and how effectively SDMs have been used in practice to support conservation decisions in a large number of countries.

Greater clarity in these issues is incumbent upon both scientists, who need to better explain the potential value of their models to managers, and managers, who need to feed the results of existing model applications back to scientists. This viewpoint considers the whole conservation decision-making framework and process as one

within which these two groups should have ideally been involved. A variety of decision-making systems exist. Here, we have outlined a decision process that entails defining a problem, defining objectives, identifying potential actions, describing consequences of those actions, assessing associated uncertainty and considering trade-offs among these consequences (Gregory *et al.* 2012; Schwartz *et al.* 2012; Addison *et al.* 2013; Fig. 2). Having a common, transparent framework that both decision makers and modellers can access is part of the solution to making better conservation decisions. However, considerable barriers remain which must be overcome. Broader inclusion of SDMs in decision-making processes seems limited by engagement impediments (see below). The published cases of SDMs developed for conservation purposes highlight the need for scientists to do a better job of engaging decision makers early in the development of SDMs but also conversely for decision makers to involve scientists early in the decision process. It is easy for scientists to become focused on developing and improving tools with relatively little attention to the information needs of decision makers. In turn, SDMs remain difficult for non-experts to use confidently, because there are many methodological options, high output variability and many nuances to consider for their targeted applications (Addison *et al.* 2013). Consequently, although scientists and decision makers often need similar information to solve their respective questions (e.g. spatially explicit distribution data), these communities can remain disconnected, with results from research left unread and unused by decision makers, and constraints faced by decision makers not known or not considered by researchers (Soberón 2004; Sutherland & Freckleton 2012).

There are also cultural differences between researchers and decision makers arising from differences in sources of funding, career aspirations, temporal contingencies to solve problems, or differences in the philosophy of the evaluation of the work done (i.e. economic vs. peer-reviewed; Laurance *et al.* 2012). This disparity results in researchers too rarely communicating with decision makers, and decision makers too often not inviting researchers (and especially modellers) to participate in the decision-making process (Cash *et al.* 2003; Soberón 2004; Addison *et al.* 2013). The lack of information exchange across the research/management boundary reflects a failure of researchers to answer real conservation management questions (Knight *et al.* 2008), and a failure of decision makers to capitalise on useful research outputs (Schmolke *et al.* 2010; Addison *et al.* 2013). This problem is exacerbated by the almost overwhelming peer-reviewed science literature, the bulk of which can be hard to access and/or not directly relevant to management needs (Haines *et al.* 2004; Sutherland *et al.* 2004; Pullin & Knight 2005; Knight *et al.* 2008), controversy surrounding terminology and modelling philosophy (Appendix S1) and by the often confidential communication streams that drive agency and organisational decisions (Cash *et al.* 2003; Schwartz *et al.* 2012). Finally, SDMs may be used, but their conservation application not reported, since practitioners often lack the time or incentive for publishing their findings in the scientific literature.

BRIDGING THE GAP BETWEEN MODELLERS AND DECISION MAKERS

Making SDMs more useful in decision making requires improved communication, appropriate translation of scientific and decision-context knowledge, mediation and timely collaboration between researchers and decision makers to ensure that SDMs are designed to meet the needs of, and constraints faced by decision makers (Cash *et al.* 2003; Addison *et al.* 2013). This could partly be achieved by making SDMs compliant with the *Open Standards for the Practice of Conservation* (Schwartz *et al.* 2012), an operationalised multi-criteria framework used to plan and prioritise conservation actions. In many instances, however, decision making does not proceed in a linear fashion (as in Fig. 2), or managers may object to the use of models (Addison *et al.* 2013), making it difficult for researchers to design the most appropriate SDMs. Therefore, the greater the transparency in the decision-making process (Gregory *et al.* 2012; Schwartz *et al.* 2012), the more likely researchers will be able to provide models and outputs that are actually useful in that process. In turn, the greater the transparency in the modelling tools, and their linkage to ecological theory (Appendix S1), the more likely managers will be able to use them (Schmolke *et al.* 2010). We have observed that SDM applications and their explicit conservation objectives, particularly in the grey literature, tend to be insufficiently documented and, therefore, are difficult to assess and reproduce, with some notable exceptions (e.g. the Madagascar case study in Appendix S5, Nature-Print in S7). Developing SDMs with a clear understanding of the decision problem at hand fosters the development of SDMs that deal appropriately with issues such as spatial scale, species considered, variables to include in the model, time frame for the study and the use of projections of environmental change (Schwartz 2012).

Developing more useful SDMs to assist conservation decisions is a necessary condition, but obviously not sufficient to have SDMs routinely used by decision makers. Communication, translation and mediation between scientists and decision makers are reported as necessary functions to better bridge the research/management gap in other fields (Cash *et al.* 2003), and reported as particularly critical in the case of SDMs (e.g. Schwartz *et al.* 2012; Addison *et al.* 2013). As suggested by Soberón (2004), these functions could be performed by intermediate institutions playing the role of 'translator' (or facilitators) between scientists and decision makers (Fig. 4), but the concept can also be expanded to individuals, groups or consortia (e.g. BI/FAO/IUCN/UNEP; see van Zonneveld *et al.* 2011; Appendix S6). These translators would synthesise, standardise and communicate the most recent scientific insights useful for solving identified problems to managers (Fig. 4), and mediate the different steps of a structured decision process (Fig. 2) to ensure that modellers and managers are jointly involved where needed. It is an important aim of our paper to promote this linkage. Such institutions already exist in some countries (see Table 1 in Soberón 2004; Appendix S6), but could be promoted in other countries and their role as translator institutions clarified and made more systematic. Such institutions could ensure that modellers are informed on precisely how SDMs are used in particular decision contexts so that their development can be adjusted and improved in future applications (Fig. 4). Such translators could also ensure that SDMs comply with the Open Standards for conservation discussed above (Schwartz *et al.* 2012). Institutions playing this translator role may stand alone as governmental or non-governmental bodies (e.g. CONABIO in Mexico or the Future Earth programme; Appendix S6), be nested within institutions with other primary functions (e.g. universities, government departments; e.g. Centre for Evidence-Based Conservation; Appendix S6), or be virtual web-based entities such as the recent Environmental Evidence initiative (Pullin & Knight 2005; Appendix S6). Individuals need to be trained, encouraged and
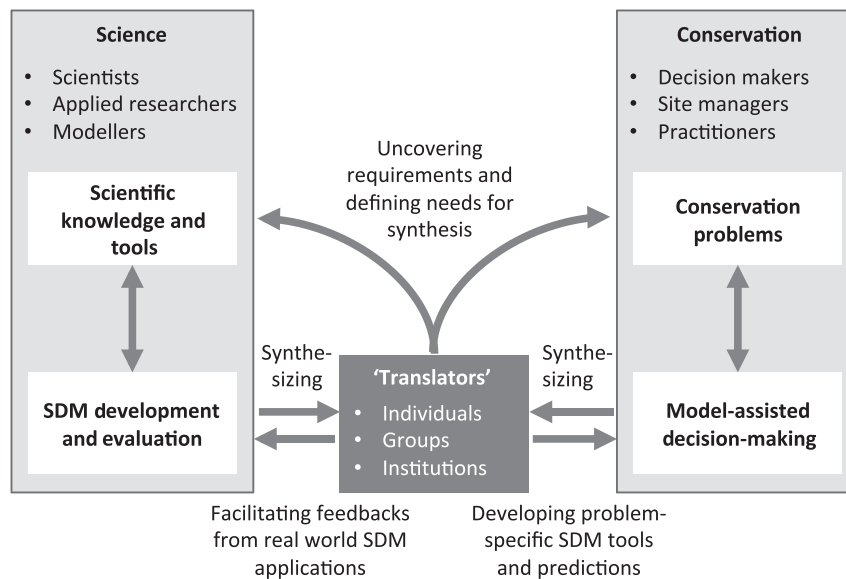
Figure 4 Proposed role of 'Translators' (being individuals, groups or institutions; Cash *et al.* 2003; Soberón 2004) as bridges between SDM development and conservation decision making. See Figure 2 for details of the steps of the structured decision-making process and where SDM can provide support.

rewarded for taking on 'translator' roles and engaging directly with modellers and decision makers.

Translators can provide a valuable service in promoting and supporting the development of appropriate tools for management. However, although an increasing number of online initiatives are making it easier for non-experts to directly access biodiversity data and build SDMs through user-friendly web interfaces (Graham *et al.* 2010; Jetz *et al.* 2012), these web tools only afford – in their current implementation – a limited ability to explore different data sets and model settings (Table 2; Appendix S7). They therefore currently cannot be considered sufficient alternatives to the direct involvement of professional modellers in a decision process, ideally mediated by translators. For example, key components of the model building process (e.g. use of a combination of techniques, evaluation of model fit and performance, uncertainty assessment, inspection of response curves) are currently not available in most of the popular applications (Table 2), although potentially crucial to support decision making. While we hope that options to refine biodiversity data sets and SDM settings become more widely available in the future (Jetz *et al.* 2012), we cannot advocate the use of overly simplified tools to support conservation decisions (e.g. the use of box-like envelopes may inflate areas identified as critical habitat requiring protection, and thus conservation cost). The increasing availability of these tools in the future will therefore make close collaboration between modellers and decision makers even more critical, as there is the potential for perverse conservation decisions to be made on the basis of poorly developed and understood models. What we need is not simpler implementations of SDMs, but a wider recognition that SDMs should be developed by experts with a clear conservation objective in mind and a clear knowledge of the decision process in which they take part. Translators, participatory or co-design principles (Appendix S6) may all be involved in achieving useful and appropriately used SDMs.

Better understanding of the decision process and its constraints would allow modellers to determine whether or not an SDM can be used, and if so, which type of SDM is best suited. It is usually not enough to read about a conservation problem, it is incumbent upon scientists to reach out to decision makers to understand their needs in making a decision, and it is incumbent upon decision makers to report to modellers how SDMs have been used to support decisions to enable iterative improvement of models. More visibility of partnerships between researchers and decision makers in the scientific literature will motivate the development of better-integrated SDM approaches that have a higher chance of being used to inform important conservation decisions. Finally, a better integration of SDM science and management would be beneficial to conservation decision making but would also advance our understanding of basic ecological processes.

THE OUTLOOK

This study was motivated by our observation that conserving biodiversity is important, that SDMs may contribute to this aim, but that more useful SDMs can be developed through practice-oriented case studies. Conservation science has made significant progress in developing an applied arm that helps managers make better decisions (Sutherland *et al.* 2004; Pullin & Knight 2005; Gregory *et al.* 2012; Schwartz *et al.* 2012; Sutherland & Freckleton 2012). At the same time, SDMs have benefitted from over two decades of development as a set of tools with many potential conservation applications (Guisan & Thuiller 2005; Rodriguez *et al.* 2007; Franklin 2010; Peterson *et al.* 2011), but have remained largely the purview of academic studies that inform other academic scientists. These tools are now sufficiently mature to take on a larger role in supporting conservation decisions. Yet, although successful SDM applications exist, they remain poorly reported in the scientific literature, suggesting the linkage between SDM science and practice is still weak. We identified three critical components likely to better bridge these two communities. First, SDM scientists need to better engage decision makers and understand the decision-making process, to better assess how and when SDMs could be used to guide conservation decisions. Second, SDMs must be designed to meet the spatial and tem-

Table 2 Examples of online SDM tools (web information acquired May 2013) for predicting the distributions of a large number of species. All examples allow users to upload occurrence data and fit models online, but with very little flexibility in model parameterisation and evaluation. See also Appendix S7.

Programme	Atlas of Living Australia (ALA)	LifeMapper (LM)	National Institute of Invasive Species Science (NIISS)	OpenModeller (OM) coupled with Global Biodiversity Information Facility (GBIF)
1. Name of supporting organisation(s)	Atlas of Living Australia, Canberra (Australian branch of GBIF)	Consortium of US Universities and University of Goias in Brasil	National Institute of Invasive Species Science (US consortium of govern. and non-govern. organisations)	Centro de Referência em Informação Ambiental (CRIA), Escola Politécnica da USP (Poli), and Instituto Nacional de Pesquisas Espaciais (INPE), Brasil
2. Can occurrence data be vetted for accuracy?	Yes	No	No	Yes
3. Predictors available	Climate, topography, land-use	Climate	Climate	Terrestrial – climate; Marine –climate, bathymetry and satellite data
4. Modelling techniques	MaxEnt, GDM	BIOCLIM, GARP*	Maxent, BRT	Envelope Score
5. Spatial coverage	Australia	Global	USA	Global
6. Temporal extent of predictor variables	Current	Current + Future (3 IPCC scenarios)	Current + Future (1 scenario/GCM)	Current
7. Uncertainty assessment?	No	No	Yes (SD across 3 runs)	No
8. Website link	http://www.ala.org.au/	http://lifemapper.org/	www.niiss.org	http://data.gbif.org/http://openmodeller.sourceforge.net/
9. Link to an official occurrence database	ALA	GBIF	NIISS	GBIF
10. Reference (if available)	–	Stockwell et al. 2006;	Graham et al. 2010;	Munoz et al. 2011

*ANN, Aquamaps, CSM, SVM and ED to be included in future versions.

poral needs of the conservation problems using transparent methods (e.g. Open Standards) that incorporate uncertainties and recognise model limitations, especially given potential legal consequences of decisions. Third, decision makers must in turn provide feedback to modellers about the success or failure of SDMs used to guide conservation decisions (i.e. practical limitations, key features of success). To achieve progress, we support the role of 'translators' (institutions, groups or individuals) to facilitate the link between modellers and decision makers. We strongly encourage species distribution modellers to get involved in real decision-making processes that will benefit from their technical input. This strategy has the potential to better bridge theory and practice, and to contribute to improve both scientific knowledge and conservation outcomes.

AUTHORSHIP

AG organised the three workshops and study design, with support from YMB and HPP. All co-authors attended at least one of the workshops and/or interacted by videoconference with the group. All authors helped outlining the manuscript and contributed substantially to its writing. RT and YMB led the invasive literature search with help from SAS, OB, JE, LB and AG. AITT, PRS and HPP led the reserve selection literature search, with help from LB, CMP, JRR, SF, JE, LB, INL and AG. JBB and TJR led the translocation literature search, with help from EMM, CMP, TGM, MRK and AG. INL and TGM led the critical habitat literature search, with help from RM, AITT, LB and AG. MWS and BAW contributed substantially to the bridge with practitioners section. MWS and YMB drafted Table 1. AG and OB prepared all figures.

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