

Addressing Uncertainty and Limited Data in Conservation Decision-Making

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Abstract

Biodiversity is declining worldwide at alarming rates, through a range of human-induced changes. At the same time, there are great uncertainties and biases in our understanding of biodiversity that limit our ability to detect changes. New approaches in estimating and managing uncertainty can inform assessments of the status of biodiversity, and identify what actions might be most beneficial. The thesis examines the applications of these methods in diverse contexts that are of importance to conservation and in which there is limited data available.

The potential for Value of Information method to contribute to the prioritisation of conservation action was explored (chapter 2). While its use is increasing, there are currently substantial gaps in its application. Probabilistic graphical models (Bayesian Networks) were built with different Machine Learning algorithms to predict the Red List status of plants, both in the Caatinga region in Brazil (chapter 3) and globally (chapter 4) and to assess why some tiger reserves contain higher tiger numbers than others (chapter 5). Red List status of plants could be predicted reliably by using the number of herbarium specimens of each plant species. The method was used to predict which plants might be threatened globally. The number of poached tigers was a good indicator for the number of tigers in a tiger reserve, but a lack of data at similar spatial scales across the tigers' range inhibits decision making.

Overall, the thesis suggests that we can: a) better predict which species are threatened and prioritise these species for future Red List assessments; b) standardise our research approaches using core outcomes; and c) make better decisions despite uncertainty. We need to make better use of these methods and the currently available data to prevent species from going extinct and to meet global targets aimed to halt the biodiversity crisis.

Collaborations

The following people made contributions to the thesis.

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All analyses were undertaken by Friederike Bolam, under the guidance of Gavin Stewart and Matthew Grainger. All text was written by Friederike Bolam. All draft chapters were read by Philip McGowan, Gavin Stewart and Matthew Grainger. Eimear Nic Lughadha at Royal Botanic Gardens, Kew, also read drafts of Chapter 1, 3 and 4.

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Chapter 1 Introduction

1.1 Background

Species are going extinct at such alarming rates that we may have entered a sixth mass extinction event, the first one caused by humans (Barnosky *et al.*, 2012; Ceballos *et al.*, 2015). 866 species are listed as Extinct on the IUCN Red List of species, and a further 69 species are listed as Extinct in the Wild (IUCN, 2018b). Species face extinction for a variety of reasons, but habitat loss is still the number one reported threat to species (Tilman *et al.*, 2017). Habitats are being lost due to conversion to agricultural lands, deforestation, and development for housing and transport, and is exacerbated by an increasing human population (Tilman *et al.*, 2017). There are also great uncertainties around how climate change will impact species in the future (Pacifiçi *et al.*, 2015). The extent of our knowledge on species and their threats varies across different taxonomic groups, and for different geographic areas (Yesson *et al.*, 2007; Boakes *et al.*, 2010; Beck *et al.*, 2014). In some cases there is also a mismatch between where most threatened species occur, and where most conservation funds are spent (Miller *et al.*, 2013; Waldron *et al.*, 2013), and the resources available for conservation are not enough to do what needs to be done to save species (McCarthy *et al.*, 2012). It is therefore crucial that resources are allocated efficiently for science, management and policy to have the biggest possible impact (Waldron *et al.*, 2013).

1.2 Global targets on preventing extinctions

To address the declines in species, there is a range of global targets to which most nations have committed. Most notable are the Aichi biodiversity targets and the Sustainable Development Goals, which are based on the Aichi targets. In Aichi target 12 preventing extinctions is mentioned specifically: "By 2020 the extinction of known threatened species has been prevented and their conservation status, particularly of those most in decline, has been improved and sustained" (Convention on Biological Diversity, 2014). This is mirrored in Sustainable Development Goal 15, target 15.5: "Take urgent and significant action to reduce the degradation of natural habitats, halt the loss of biodiversity and, by 2020, protect and prevent the extinction of threatened species"

(United Nations, 2015). The Sustainable Development Goals were signed by all 193 UN member states which are nearly all countries in the world, as well as Holy See, Palestine, Niue and the Cook Islands. To save all species and therefore to meet these targets, first of all we need to know which species are at risk of extinction and why. Then suitable conservation actions need to be identified and implemented. Progress towards Aichi targets was measured in 2014 using a range of indicators, all of which were showing declines in species, demonstrating that we need to increase efforts to save species (Convention on Biological Diversity, 2014; Tittensor *et al.*, 2014).

1.3 Uncertainty in conservation decision-making

Uncertainties are present in all stages of conservation decision-making for saving species. There are gaps in our knowledge about the actual number of species on earth, with recent disparate estimates of 5 million (Costello *et al.*, 2013) and 8.7 million (Mora *et al.*, 2011). Many new species are being described each year, for example over 2,000 new plants were described annually (Nic Lughadha *et al.*, 2016). Targeted conservation action to save species is only possible if we know that they exist in the first place. While our knowledge on which species are declining is increasing, this is not happening fast enough to meet the target of assessing a sample of 160,000 species by 2020, as set out in the Barometer of Life (Stuart *et al.*, 2010), with currently just over 90,000 assessments of extinction risk (IUCN, 2018b). We can only decide on targeted conservation if we know which species are in decline, but even then monitoring species does not always lead to conservation action (Lindenmayer *et al.*, 2013).

Knowledge of a species' conservation status and resulting conservation action can lead to improved conservation status of a species (Hoffmann *et al.*, 2011), but these can also fail for a variety of reasons.

The main drivers of the decline of a species may be unknown (Runge *et al.*, 2011) or difficult to address, such as climate change (Conroy *et al.*, 2011) or stopping poachers (Hoffmann *et al.*, 2010), or there may be uncertainty how best to address those drivers. Approaches such as structured decision making (Gregory *et al.*, 2012), adaptive management (Runge, 2011), and Value of Information analysis (Runge *et al.*, 2011) are designed to overcome some of these challenges in a systematic way. They do so by

analysing which conservation action is most likely to succeed given current knowledge, whether there is uncertainty around which is the best conservation action, and if research or monitoring would help determine the best conservation action (McDonald-Madden *et al.*, 2010).

1.4 Global data sources on species

1.4.1 The IUCN Red List of Species

There are a range of global data sources on species' extinction risk, traits and occurrences freely available. The IUCN Red List of Species is the most comprehensive assessment of extinction risk of species and is available online. It covers over 90,000 species globally as of 20 December 2017, from birds and mammals to orchids and fungi (IUCN, 2018b). Most assessment information is prepared by different specialist groups that are part of the Species Survival Commission, which have a taxonomic focus, by Red List authorities, which are often the same as the specialist groups, or by Red List partners such as Birdlife or Royal Botanic gardens, Kew (IUCN, 2018a).

The IUCN Red List assessments aim to be objective and applicable across taxonomic groups (Mace *et al.*, 2008). Extinction risk is assessed according to a range of criteria, including population size reduction, small population size, and geographic range of a species (IUCN, 2012b). There are different IUCN Red List categories that are then applied: Extinct, Extinct in the Wild, Critically Endangered, Endangered, Vulnerable, Near Threatened, Least Concern and Data Deficient (Table 1). The risk of extinction is highest for Critically Endangered species, followed by Endangered species, then Vulnerable species. Least Concern species are not threatened, and Near Threatened species may become threatened soon. Data Deficient covers species for which there is not enough knowledge to make a reasonable assessment, and the species could be in any category (IUCN Standards and Petitions Subcommittee, 2017), but Data Deficient is also applied to species with uncertain taxonomies for example (Butchart and Bird, 2010). IUCN Red List assessments are deemed outdated after ten years and should, ideally, be updated, so that changes in extinction risk of that species can be tracked. However, 17% of assessments are older than ten years (Rondinini *et al.*, 2014).

Table 1. Description of different Red List categories and corresponding threat status, adapted from IUCN (2012b).

Red List category	Threat status	Description
Extinct	Extinct	The last individual of the species has died, and extensive and appropriate surveys have not found evidence of further individuals.
Extinct in the Wild	Extinct	Individuals of the species remain in zoos, botanical gardens, or as naturalised populations outside their range. The last wild individual of the species has died, and extensive and appropriate surveys have not found evidence of further individuals.
Critically Endangered	Threatened	The species is facing an extremely high risk of extinction, as established through different criteria.
Endangered	Threatened	The species is facing a very high risk of extinction, as established through different criteria.
Vulnerable	Threatened	The species is facing a high risk of extinction, as established through different criteria.
Near Threatened	Non-threatened	The species has not been categorised as threatened, but it is likely that it will become threatened soon.
Least Concern	Non-threatened	The species has not been categorised as threatened and is not likely to become threatened.
Data Deficient	NA	There is not enough information to make an assessment. Data Deficient should only be applied when it can be assumed that a species could be in any of the above categories.

While the IUCN Red List currently covers over 90,000 species, it is not a random sample of species (IUCN, 2018b). Groups that are better studied or generate more public interest such as birds and mammals have been assessed completely, whilst bigger taxonomic groups such as insects have not seen the same degree of assessment (Butchart *et al.*, 2004; Butchart *et al.*, 2005). Equally, only about 5% of plants have been assessed on the IUCN Red List (Brummitt *et al.*, 2015). The only kingdom other than plants and animals to have had any assessments are fungi with only 33 assessments (IUCN, 2018b).

Information on species' IUCN Red List categories is freely available on the IUCN Red List website. The information from the assessments includes the habitats and countries species occur in, range maps, and in the case of threatened species, the threats species face and appropriate conservation actions (IUCN, 2018b). There are

packages specifically designed to download IUCN Red List data in the R statistical environment (R Core Team, 2017) such as *rredlist* (Chamberlain, 2017) or *letsR* (Vilela and Villalobos, 2015). Data can also be downloaded directly from the IUCN website (IUCN, 2018b).

1.4.2 *Tracking changes in species' extinction risk*

To be able to track changes in IUCN Red List assessments and therefore the conservation status of species, an extended coverage of IUCN Red List assessments has been proposed, known as the Barometer of Life (Stuart *et al.*, 2010). The 48,000 assessments in 2010 were to be increased to 160,000 by 2020, with the aim of having a sample that is more representative, and not biased towards vertebrates (Stuart *et al.*, 2010). Of the more than 90,000 assessments to date, more than 40,000 have been made in the past 7 years which is an impressive effort (IUCN, 2018b). If current rates of assessment continue, we might expect that by 2020, 108,000 species will have been assessed - still a shortfall of over 50,000 species.

To track changes in species' extinction risk over time and to rank relative extinction risk between taxonomic groups, the Red List Indices as well as the Sampled Red List Indices are used (Butchart *et al.*, 2004), for example to measure progress towards Aichi target 12 (Tittensor *et al.*, 2014). The Red List Index is used for completely assessed taxonomic groups, and is available for birds, mammals, amphibians and corals (IUCN, 2017). The Sampled Red List Index is used for taxonomic groups that are not completely assessed, so a random sample of species are assessed and reassessed. Sampled Red List Indices are available for freshwater crabs (Cumberlidge *et al.*, 2009), dragonflies and damselflies (Clausnitzer *et al.*, 2009), reptiles (Böhm *et al.*, 2013), crayfish (Richman *et al.*, 2015), and plants (Brummitt *et al.*, 2015).

1.4.3 *National Red Lists*

Apart from the IUCN Red List there are also National Red Lists to guide conservation action at national and regional levels. National Red Lists take into account the regional nature of assessments, unlike the IUCN Red List, and in some cases threat categories that differ from the IUCN Red List are used (Brito *et al.*, 2010). As of 21 December 2017 there were 148,921 National Red List assessments which used IUCN Red List categories

(National Red List, 2017). There are guidelines for applying IUCN Red List categories and criteria to the National Red Lists (IUCN, 2012a). Brito *et al.* (2010) found that most National Red List assessments and IUCN Red List assessments placed species into the same category, with differences for 16% of species that had been assessed on both lists in Brazil, China, Colombia and the Philippines. As such the National Red Lists can be a useful addition to the IUCN Red List for national and regional assessments.

1.4.4 *Other global data sources*

To accelerate estimates of extinction probability of species, modelling can be used to predict the extinction risk with different predictive variables, such as phylogeny (Davies *et al.*, 2011), occurrence records (Rivers *et al.*, 2011) or traits (Bland *et al.*, 2015). Some of these variables can be found in global datasets at species level. Most prominently, the Global Biodiversity Information facility (GBIF) holds a wide range of datasets of different species groups, all of which are freely available. GBIF was set up in 1999 (Redfearn, 1999) and holds nearly 100 million occurrence records for different species from bacteria to animals, and for a wide range of spatial scales from local surveys to global plant collections (Global Biodiversity Information Facility, 2017).

For plants, the use of herbaria to inform conservation assessments is important as herbaria globally hold approximately 350 million specimens, spanning 400 years (Thiers, 2017). Herbarium specimens are routinely used to estimate extent of occurrence or area of occupancy for plants which are used for IUCN Red List assessments, and historic specimens can help to show where declines have occurred (Willis *et al.*, 2003; Brummitt *et al.*, 2015). There is a database that holds information on herbarium records called Botanical Information and Ecology Network or BIEN (Botanical Information and Ecology Network, 2017), including an R package through which data can be downloaded (Maitner *et al.*, 2017). It includes both GBIF occurrence records as well as occurrence records from other datasets not currently included in GBIF.

1.4.5 *Challenges in using large-scale occurrence data*

Large-scale databases in ecology are usually made up of a plethora of surveys, museum records, and increasingly through citizen science projects such as ebird (Sullivan *et al.*, 2009). While databases like GBIF provide large amounts of data, the data are not

collected evenly across the globe, across time, or across taxa (Troudet *et al.*, 2017). When considering the proportion of species to occurrence records within classes, there are more bird, liliopsida and mammal records in GBIF than records of insects, arachnids and gastropods. There are biases in occurrence records of plants, both at taxonomic and geographic level (Meyer *et al.*, 2016). As an example from another kingdom, records of Galliformes are biased towards Western Europe and South East Asia, and are also biased towards non-threatened species (Boakes *et al.*, 2010). These biases can be a hindrance for analyses such as species distribution models, but can be overcome if some records are removed (Syfert *et al.*, 2013; Beck *et al.*, 2014). There can also be biases in records for sensitive species, for example those that are at risk of poaching (Jarnevich *et al.*, 2007).

If data from a range of sources are to be used in combination, it is crucial that taxonomic naming is consistent across datasets, and that there are no misspellings in the data. In a recent analysis of threat status of plants, 22,144 names could not be matched to accepted species names, showing how this is not a trivial issue (Bachman *et al.*, 2017). There is an increasing number of tools designed to overcome these problems, many of them implemented through the R statistical environment. For example, with the taxize package (Chamberlain and Szöcs, 2013) it is possible to check species names and their spelling as well as download taxonomic hierarchies of species. This ensures that large numbers of species names can be checked rapidly.

There are also issues of scale, and how to combine data that differ in their scales. This problem was first described in 1992 (Levin, 1992), with a more recent review from 2013 (Chave, 2013). Different spatial scales can have an effect on the patterns we observe (Chase and Knight, 2013), and there can be interactions between them too (Sullivan and Vierling, 2012). Often summarised data need to be used to combine data at different scales which means that information is lost in the process. There are statistical methods that are designed for dealing with different scales, for example hierarchical models (Wilson *et al.*, 2011).

Finally, making large-scale data available to other scientists is a challenge in itself (Hampton *et al.*, 2013). There are difficulties in sharing data due to the

heterogeneity of ecological data, a lack of incentives for sharing data (Reichman *et al.*, 2011), lack of training in managing data (Roche *et al.*, 2015) and a perceived loss of control over data (Enke *et al.*, 2012). To ensure more data are shared amongst ecologists, there is a need for platforms for data storing, as well as rewards for scientists who share their data, such as citations (Whitlock, 2011; Roche *et al.*, 2015).

1.5 From Red Lists to saving species

The IUCN Red List addresses the fundamental questions of what is threatened, to what extent, and why. How do we get from the assessments to saving species on the ground? The IUCN Red List assessments are used by governments to inform action plans to protect species and monitor their status, prioritise areas for conservation, as well as inform Environmental Impact Assessments (Azam *et al.*, 2016). They are also used by conservation NGOs to focus conservation efforts on species that are threatened with extinction, for example BirdLife International have undertaken conservation action for over 500 threatened bird species since 2008. They have also identified organisations which are in a position to implement conservation action to protect Critically Endangered bird species (BirdLife International, 2013). Further, the International Finance Corporation which supports projects in developing countries avoids investments that could negatively affect Critically Endangered or Endangered species (IFC, 2012).

Our increasing knowledge of the conservation status of species has led to a range of conservation actions such as protected areas, reintroductions or invasive species control (Hoffmann *et al.*, 2011). Due to these actions the conservation status of 24 mammal species has seen improvements (Hoffmann *et al.*, 2011), and the extinction of 16 bird species is likely to have been prevented (Butchart *et al.*, 2006). Not all species declines have been prevented however, and conservation action has been insufficient for 146 threatened mammal species and lacking completely for a further 18 (Hoffmann *et al.*, 2011). In many cases the main drivers of declines are not addressed, there is uncertainty about the effectiveness of conservation actions, or there remains uncertainty why a species is actually in decline, which hinders actions to save species (Hoffmann *et al.*, 2011; Rodrigues *et al.*, 2014).

1.6 Addressing uncertainty in conservation decision-making

As there is a pressing need to save species, we need to find ways to use available data whilst dealing with the uncertainties appropriately. In conservation, there can be uncertainty around the conservation status of a species, what is driving the numbers of threatened species, and which conservation actions are likely to yield the most benefits, for example. The following section will introduce two methods that can be used to deal with these uncertainties.

1.6.1 Bayesian Networks

Bayesian Networks (BNs) are probabilistic graphical models that can incorporate a wide range of data sources. They are useful for dealing with uncertainty because the probability distribution of variables can be displayed and the impact of changes in variables can be assessed transparently through scenario analysis. BNs can be used for predictive modelling, and predictions can be displayed alongside their associated probabilities, hence they are a useful tool for conservation decision making (Marcot *et al.*, 2006).

BNs can be constructed with input in the form of expert elicitation or with mixed data sources. The researcher assigns their structure through findings from the literature, or through experts (Landuyt *et al.*, 2013). These networks are called supervised networks (Scutari and Denis, 2014). Unsupervised networks (Scutari and Denis, 2014) can be machine-learned using a variety of algorithms allowing the construction of BNs based on data alone. This allows patterns from the data to determine the BN structure and the conditional dependencies rather than relying on that proposed by subject experts or the researcher. It is also possible to create semi-supervised models by combining prior knowledge of the system, for example through experts, with a Machine Learning algorithm. The network structure, as well as the conditional probability tables, can be learnt from the data separately. Machine Learning methods do not assume independence of predictor variables because dependencies are reflected in the model structure (Mayfield *et al.*, 2017). While arcs in a supervised network usually infer causal effects between variables, this is not necessarily the case for Machine Leant BNs, as

further assumptions need to be met for a BN to be a causal model and is therefore challenging (Nagarajan *et al.*, 2013).

Bayesian Networks

Conditional dependences between variables (called nodes in a BN) are demonstrated by arrows (called arcs) underpinned by conditional probability tables. For example, 40% of the habitats may be in good condition, and 60% of habitats may be in poor condition in a given area (Figure 1). If Habitat state is good, then 90% of those sites may see a high number in species, whereas this drops to 20% where habitat state is poor. Scenario analysis is possible by changing the states of nodes and updating the conditional probabilities of the other nodes. For example, if habitat state is set to 100% good, then species number would update to 90% high and 10% low.

Habitat state	
Good	40%
Poor	60%

↓

Species numbers	Habitat state	
	Good	Poor
High	90%	20%
Low	10%	80%

Figure 1. A simple Bayesian Network with conditional probability tables. The "Child" node (Species numbers) is conditionally dependent on the "Parent" node (Habitat State). The two are linked by a directional arc.

Data limitations in BN modelling can be dealt with in various ways. Missing data points of a variable can be imputed or elicited from experts. If that variable makes no difference in the overall outcome as shown by the BN, then collecting further data on this variable is unlikely to lead to any gains in conservation performance. Missing variables are more difficult to deal with, and in the absence of information are very difficult to model (Chung *et al.*, 2016). Expert elicitation could be used to find which variables may be important and missing, and include them in the network (Marcot, 2017). The effect of these variables could then be modelled to inform further research actions.

BNs are becoming more sophisticated, and the use of Gaussian BNs has removed the earlier requirement to work only with discrete data (Scutari and Denis,

2014). There are now various open source programmes and packages available for constructing BNs, such as GeNIe Modeler (Bayes Fusion LLC, 2017) or the bnlearn package in R (Scutari, 2010), not all of which have the ability to build or display Gaussian BNs however.

One of the key advantages of BNs is their transparency, especially when working with a range of stakeholders, policy makers and managers (Landuyt *et al.*, 2013). Unlike more traditional statistical models, BNs are easier to interpret because they are visual models. They can also be used directly as a decision support tool (Stewart *et al.*, 2013), for example for decision-analytic approaches, where each objective and each management action could be described within a node (Gregory *et al.*, 2012). This way trade-offs can be modelled either by updating the conditional probabilities of the outcome variables, or by updating the conditional probabilities of the management actions (Marcot, 2012). As it is possible to update the evidence within a BN, they are also useful for adaptive management (Landuyt *et al.*, 2013).

However, there are limitations in using BN models. BNs are deterministic, so every model run with the same initial conditions will lead to the same outputs; stochastic events are not included (Beissinger and Westphal, 1998). This limits the interpretation of the outputs, as there is no probability distribution of the outputs. Instead, the probabilities of the discrete states of a node are shown only. It is possible to model parameter uncertainty with other methods, such as Bayesian Hierarchical models, where full probability distributions of discrete node states can be estimated (Wikle, 2003). Further, BN arcs have to be directed and feedback loops within one network do not work, because this would make the creation of conditional probability tables impossible. This can limit the application of BNs. There are however emerging approaches for modelling temporal systems using Dynamic Bayesian Networks. In these, the outputs of one network are fed in as input for a second network (Uusitalo, 2007; Marcot and Penman, 2018), but this process is very complex (Aguilera *et al.*, 2011). While the use of continuous variables BN modelling is possible, it is still challenging (Aguilera *et al.*, 2011). Therefore, continuous variables are usually split into discrete variable states. The way in which variables are split can affect model performance

because relevant information may be lost in the process of discretisation (Uusitalo, 2007).

1.6.2 *BNs in ecology*

The use of Machine Learning algorithms for creating BNs in ecology and biodiversity conservation has been limited so far. They have been used for habitat suitability studies (Aguilera *et al.*, 2010; Milns *et al.*, 2010; Boets *et al.*, 2015), predicting locations of biomes, bioregions or vegetation types (Dlamini, 2011a; Dlamini, 2011b), predicting food webs and trophic relationships for fisheries (Trifonova *et al.*, 2014; Trifonova *et al.*, 2015), investigating species assemblages to inform monitoring (Pozsgai *et al.*, 2016) and predicting deforestation (Mayfield *et al.*, 2017). The use of BNs for conservation is underexplored, particularly with regard to networks that use data or a combination of data and expert elicitation (but see Amstrup *et al.* (2010) and Fortin *et al.* (2016)). As long as relevant data are available, Machine learnt BNs are quicker and cheaper to construct than those which rely solely on experts.

Major benefits of using BNs are the ability to use a wide variety of data sources to inform a single model, the transparency of the networks, the ability to include uncertainty and the possibilities of using BNs for decision analysis and adaptive management. In complex systems with missing data and uncertainty, such as conservation, BNs could help us to understand the system in question. For these reasons, the use of BNs could greatly enhance conservation decision making at national, regional and international level.

1.6.3 *Decision-making under uncertainty*

Decision-making in ecology or biodiversity conservation is usually accompanied by uncertainties in the effects of management actions and resulting outcomes. Different approaches have been proposed to deal with these uncertainties, and here I will focus on two fields that have received considerable attention; these are structured decision-making or decision analysis, and adaptive management.

Decision analysis follows a structured process of decision-making, which involves the identification of the decision context, the setting of objectives, the identification of management actions that can address those objectives, an evaluation of how each

management action would contribute to each objective, and the explicit consideration of trade-offs between management actions (Gregory et al. 2012). The identification of objectives is a key step of decision analysis, and will influence the further process. The evaluation of how management actions would contribute to objectives is usually done using predictive modelling, and may include not only changes to a population of a species of interest, but, depending on the objectives, also the social or economic impacts of such change (Runge, 2011). Uncertainty is considered during the evaluation of management actions, often through a Value of Information calculation, see section 1.6.4.

Adaptive management is considered to be a special case of decision analysis. It is a process in which learning is part of the decision process, because the optimal management action is unknown, and where decisions are repeated over time. The outcomes of one or more management actions are monitored to test whether the management action is effective, and then feed back into the next cycle of decision-making (Runge, 2011). Adaptive management can be active, where different management actions are tested simultaneously; or passive, where the management action that is considered to best address the objectives is implemented and outcomes are monitored (Williams, 2011). Learning is an objective for active adaptive management settings, but not for passive adaptive management. Which management actions to pursue, and whether adaptive management should be used at all, can be examined through a Value of Information analysis (McDonald-Madden *et al.*, 2010). Adaptive management can be difficult to implement, because of the difficulties in distinguishing between natural variation and the effects of management actions, and due to difficulties in establishing effective monitoring (Westgate *et al.*, 2013).

1.6.4 The Value of Information

Not all uncertainties affect management decisions, and quantifying when they do and when they do not can help decision makers (Runge *et al.*, 2011). A method rooted in decision analysis that helps to distinguish between when more data are needed and when to act is the Value of Information. Value of Information is routinely used in disciplines such as healthcare (Yokota and Thompson, 2004) and has been used in

ecology since 1991 (Sainsbury, 1991). The idea of the Value of Information approach is that research is only necessary when the changes detected by that research will result in a change in management action. For example, research may be necessary when there is uncertainty around why a species is declining, and hence which management action will lead to the most benefit (Runge *et al.*, 2011). It can also be used to decide which conservation action would be best under different budget levels (Maxwell *et al.*, 2015). There is scope to extend the use of Value of Information both for finding species-specific management actions, as well as for broader scale application in ecology. Value of Information now forms part of the IUCN's guidelines for species conservation planning as it can help to use resources for conservation wisely (IUCN – SSC Species Conservation Planning Sub-Committee, 2017).

1.7 Thesis aims

The overall aim of my thesis was to explore how uncertainty affects the different stages of preventing extinctions, from making conservation assessments right through to finding the best management actions to improve conservation status under uncertainty.

The individual aims of the thesis chapters are as follows:

- Evaluate the use of Value of Information in ecology
- Predict extinction risk of plant species in the Caatinga ecoregion in Brazil
- Predict extinction risk of plants assessed as Data Deficient globally
- Assess which variables are most influential in determining tiger numbers at different sites
- Assess when to reduce uncertainty and when to act, and whether Value of Information works for conservation

1.8 Thesis outline

In chapter 2 I explored the background to decision-making under uncertainty, what the Value of Information is, and how it can be calculated using a simple example. I undertook a systematic review of the use of the Value of Information in ecology and found 30 papers that have applied it to date. I summarised those papers according to their application, the management objectives, the uncertainties considered and how they were expressed, the predictive model used, the parameter of the net benefit and

the type of Value of Information calculation. I explored three of the papers in more detail, then discussed what has been achieved so far in using Value of Information in ecology, and where there were gaps.

In the next chapter I explored the extinction risk of plants in the Caatinga ecoregion in Brazil. I used Bayesian Network models to determine which variables were important in assigning Red List categories, using taxonomic information, habitat information, the number of site and occurrence records of each species, and the plant growth form. The best performing model was created with a Naïve Bayes classifier which predicted the threat status of 80% of assessed species correctly. I used the model to predict the extinction risk of 1,189 plants in the Caatinga, of which 68 were predicted to be threatened. A Value of Information calculation indicated that more Red List assessments are needed from the Caatinga.

Then I applied a similar methodology to predict extinction risk of Data Deficient plants globally. I merged IUCN Red List data with data from the TRY database of plant traits, imputed missing values, and predicted IUCN Red List category using Bayesian Network models. The best performing model was built using a hill-climbing algorithm with oversampled data which predicted 60.5% of threatened and 65.0% of non-threatened species correctly. The model predicted 53.8% of the 1,732 Data Deficient plants to be threatened or Extinct. A Value of Information calculation indicated that more work needs to be done in South America, both in terms of assessments and conservation action.

I then shifted the focus from predicting extinction risk of species to determining relevant information in conserving species, using the tiger *Panthera tigris* as a case study. I used information at the Tiger Conservation Landscape scale, including tiger numbers, habitat information, designations and poaching numbers, and built Bayesian Network models. The best performing model predicted tiger numbers correctly for 80% of Tiger Conservation Landscapes using a hill-climbing algorithm. Habitat loss had little influence on determining tiger numbers, but the amount of poaching did, indicating that preventing poaching is the best way to increase tiger numbers once again.

In the discussion I explore the current use of Vol in biodiversity conservation, what some of the difficulties are in applying it, and what lessons can be drawn from applying it to different settings. I then place the extinction risk predictions into the context of other literature in which extinction risk was predicted, and discuss the class imbalance problem of predicting categories when there is one majority category which drives predictions. Then I discuss what some of the difficulties are from Red Listing to deciding on conservation actions. I finish with recommendations for future work.

Chapter 2 Using the Value of Information to improve conservation decision making

Abstract

Conservation decisions are challenging, not only because they often involve difficult conflicts among outcomes that people value, but because our understanding of the natural world and our effects on it is fraught with uncertainty. Value of Information (Vol) methods provide an approach for understanding and managing uncertainty from the standpoint of the decision maker. These methods are commonly used in other fields (e.g. economics, public health) and are increasingly used in biodiversity conservation. This decision-analytical approach can identify the best management alternative to select where the effectiveness of interventions is uncertain, and can help to decide when to act and when to delay action until after further research. We review the use of Vol in the environmental domain, reflect on the need for greater uptake of Vol, particularly for strategic conservation planning, and suggest promising areas for new research. We also suggest common reporting standards as a means of increasing the leverage of this powerful tool.

The environmental science, ecology and biodiversity categories of the *Web of Knowledge* were searched using the terms 'Value of Information,' 'Expected Value of Perfect Information,' and the abbreviation 'EVPI.' *Google Scholar* was searched with the same terms, and additionally the terms decision and biology, biodiversity conservation, fish, or ecology. We identified 1225 papers from these searches. Included studies were limited to those that showed an application of Vol in biodiversity conservation rather than simply describing the method. All examples of use of Vol were summarised regarding the application of Vol, the management objectives, the uncertainties, the models used, how the objectives were measured, and the type of Vol.

While the use of Vol appears to be on the increase in biodiversity conservation, the reporting of results is highly variable, which can make it difficult to understand the decision context and which uncertainties were considered. Moreover, it was unclear if, and how, the papers informed management and policy interventions, which is why we suggest a range of reporting standards that would aid the use of Vol.

The use of Vol in conservation settings is at an early stage. There are opportunities for broader applications, not only for species-focussed management problems, but also for setting local or global research priorities for biodiversity conservation, making funding decisions, or designing or improving protected area networks and management. The long-term benefits of applying Vol methods to biodiversity conservation include a more structured and decision-focused allocation of resources to research.

2.1 Introduction

2.1.1 The changing landscape of biodiversity conservation

Our understanding of what constitutes biodiversity [the 'variety of life' (CBD Secretariat, 1992; Watson *et al.*, 1995)] has developed to encompass not only genes, species, and habitats or ecosystems but the variation within them and among all levels, and their inter-relationships. This has led over time to a desire for policy to go beyond the maintenance of species and protection of places. Whilst protecting species and habitats remain key and important conservation objectives, other objectives have emerged that reflect more fully such holistic definitions of biodiversity. These include maintaining genetic variability, evolutionary potential, food webs, ecological networks and the interactions within and among species, and ecosystem resilience and function (Mace, Norris & Fitter, 2012). A significant challenge is presented in both understanding the complex patterns and processes that these components of biodiversity represent and in shaping and implementing policies designed to ensure their maintenance. Amongst the most complex of globally agreed goals for biodiversity are those in the Convention on Biological Diversity's Strategic Plan for Biodiversity 2011–2020 and specifically their constituent Aichi Targets (Leadley *et al.*, 2014), and the environmental goals in the recently adopted Sustainable Development Goals.

There are many statutory initiatives to advance the conservation of biodiversity across the globe, but implementation and enforcement of these statutes has been hampered because of the potential regulatory burden they impose and potential for conflict with human activities such as economic development, recreation, and subsistence and sport hunting. As a result, a more nuanced view of biodiversity

conservation has emerged, one that recognises the choices and trade-offs implicit in decisions about environmental management.

The political complexity of decisions regarding biodiversity is exacerbated by the remaining uncertainties about the nature of biodiversity and its response to human interventions, to the extent that scientific uncertainty is sometimes used as a pawn during political debates and negotiations. There is a long way to go before the components of biodiversity are fully described, let alone their processes understood or the consequences of disrupting or even losing them are adequately predicted. In the meantime, policy and management decisions are still needed in the absence of such ecological knowledge and thus under substantial uncertainty. This leads to two important questions that are relevant for environmental managers: how should decisions about natural resource management be made in the face of uncertainty, and when is it valuable to reduce the uncertainty before committing to a course of action? The purpose of this review is to consider the literature concerning the second question, while placing it in the context of the first question.

2.1.2 Strengthening scientific input for management and policy

This changing landscape of biodiversity conservation has two important implications for the science that informs or underpins conservation policy. First, decisions about conservation policy are significantly enhanced when what is known about biodiversity is made available to decision makers in a form that they can understand and use (Pullin *et al.*, 2004). There is a significant body of thought and literature concerning how to achieve this, including making literature more available to decision makers, analysing management interventions and other relevant topics through systematic reviews (Pullin & Stewart, 2006; Sutherland *et al.*, 2017), and promoting research that bridges the 'knowing–doing' gap (Knight *et al.*, 2008). The diversity of these approaches reflects the large range of contexts in which information on biodiversity, in all its forms, is now sought to inform policy and decision making.

The second implication of the interplay between uncertainty and decisions about biodiversity is the need to identify which uncertainty is most valuable to reduce in order to improve the outcomes of policy or management decisions. The critical issue here is

determining which of the sources of uncertainty has the strongest influence on the choice of action. This requires an understanding of the decision context in which knowledge about biodiversity is being used. The question is not whether there is scientific uncertainty and how great it is, but rather, whether the scientific uncertainty impedes the choice of a management action. Here we examine the potential for a formal method called the 'Value of Information' (VoI) to address this question in support of conservation management and policy.

2.1.3 Decision making under uncertainty

Before turning to the topic of the VoI, we first introduce the background on decision making in the face of uncertainty. A summary of terms can be found in Table 1.

Table 2. Definitions of terms relating to decision making in conservation.

Term	Definition
<i>Decision analysis methodology</i>	
Decision analysis	A broad field that explores both how humans make decisions (descriptive decision analysis) and how they should make decisions (prescriptive or normative decision analysis). Importantly, normative decision analysis provides a framework for decision making that includes the context, the objectives, alternative actions, the consequences of the actions, the uncertainties involved and how learning can be implemented (Gregory <i>et al.</i> , 2012).
Decision context	What decision needs to be made and how? Who is the decision maker and what is their authority? What legal, policy, and scientific guidelines form the context for the decision? (Gregory <i>et al.</i> , 2012).
Objectives	The fundamental outcomes that the decision maker is pursuing in making the decision. Objectives need to encompass everything that should be achieved by the decision whilst being independent from each other. They can be used to build consensus amongst stakeholders (Gregory <i>et al.</i> , 2012).
Alternatives	Set of potential actions under consideration that could achieve the objectives. An alternative may encompass various tasks that will address all objectives, so different alternatives can be comparable. Alternatives need to be distinct from each other (Gregory <i>et al.</i> , 2012).
Consequences	The predicted outcomes of the different alternatives relative to the different objectives. Often the consequences show trade-offs between different alternatives (Gregory <i>et al.</i> , 2012).
Trade-offs	Competing consequences across objectives, such that improving the outcome associated with one objective requires giving up performance associated with another objective. The challenge to the decision maker is to evaluate consequences of the different

Term	Definition
	alternatives and make a decision on which alternative to implement (Gregory <i>et al.</i> , 2012).
<i>Uncertainty terms</i>	
Aleatory uncertainty	Uncertainty arising from inherent variability in random processes. Environmental, demographic, and catastrophic stochasticity are examples (Gregory <i>et al.</i> , 2012).
Epistemic uncertainty	Uncertainty arising from the limits of current human knowledge. Often linked to aspects of data, for example lack of data or imprecise measurements (Regan <i>et al.</i> , 2002).
Irreducible uncertainty	Uncertainty that cannot be resolved, for example environmental stochasticity (Conroy & Peterson, 2013).
Linguistic uncertainty	Uncertainty linked to language: vague or ambiguous terms, or terms that are context dependent (Regan <i>et al.</i> , 2002).
Parametric uncertainty	Special case of epistemic uncertainty: uncertainty about the values of the parameters in a model (Kujala <i>et al.</i> , 2013).
Reducible uncertainty	Uncertainty that can be resolved, if enough effort is exerted, for example epistemic or linguistic uncertainty (Conroy & Peterson, 2013).
Structural uncertainty	Special case of epistemic uncertainty: uncertainty around the systems model (Conroy & Peterson, 2013).

2.1.4 Decision analysis

The field of decision analysis aims to support decision makers by providing insights from a large array of disciplines, including decision theory, cognitive psychology, operations research, economics, and statistics. Based on the work of von Neumann & Morgenstern (1944) and harkening back to work of Nicolas Bernoulli in 1713, the field of decision theory recognises that all decisions have common elements, and searches for rational ways to structure decisions. Decision analysis aims to formalise the decision-making process by using a clear framework that incorporates all aspects that are relevant to making a decision, namely: the decision context (the authority of the decision maker and the environment in which the decision is being made); the objectives that are to be achieved by the decision and how they are measured; the different alternative actions that are under consideration to achieve the objectives; an analysis of the consequences of each action (the prediction of the consequences of each alternative in terms of the objectives is the central means by which scientific information is incorporated into a decision); and methods for navigating various types of trade-offs in choosing an action to implement (Gregory *et al.*, 2012; see Table 1). A

diverse set of analytical tools has been developed to aid decision makers, depending on the primary impediments to the decision, including multi-criteria decision analysis (Davies, Bryce & Redpath, 2013), risk analysis (Burgman, 2005), spatial optimisation (Moilanen, Wilson & Possingham, 2009), and Vol (Runge, Converse & Lyons, 2011).

Formal methods of decision analysis have been used extensively for decisions regarding natural resource management (Gregory et al., 2012), wildlife population management (Yokomizo, Coutts & Possingham, 2014), fisheries management (Peterson & Evans, 2003), and endangered species management (Gregory & Long, 2009), among other applications. In practice, decision analysis is often used in conjunction with collaborative and participatory facilitation methods, to allow negotiation and dispute resolution (Gregory et al., 2012).

2.1.5 Uncertainty

Our knowledge of the natural world is extensive, but incomplete. When scientists are asked to make predictions about the outcomes associated with alternative management actions, they should do so with an understanding of the uncertainties that underlie those predictions, where possible. Identifying types of uncertainties can be helpful in determining how to deal with them. It is useful to distinguish three types of uncertainty: linguistic, epistemic, and aleatory. Linguistic uncertainty is any type of uncertainty that is linked to language (vague or ambiguous terms, or terms that are context dependent for example; Regan, Colyvan & Burgman, 2002), and is often unresolved in conservation decision making (Kujala, Burgman & Moilanen, 2013). Sometimes disputes or confusion arise simply because different people ascribe a different definition to the same term. Epistemic uncertainty arises from limitations in our knowledge of the world and its workings and is often linked to aspects of available data, such as insufficient observations or imprecise measurements, which are often parameters in models used to forecast the effects of management actions. A special case of epistemic uncertainty is structural uncertainty, which refers to uncertainty in the structure of the systems model, or of model form, as opposed to model parameters (Morgan & Small, 1992; Conroy & Peterson, 2013). Both linguistic and epistemic uncertainty are, at least theoretically, reducible uncertainties, that is, with appropriate effort and study, we could resolve the

uncertainty (Conroy & Peterson, 2013). The third type of uncertainty, aleatory uncertainty, is irreducible, because it arises from sources that are not possible to know about in advance (Gregory *et al.*, 2012). For example, variation in the weather over the next ten years, and how it will affect a wildlife population relevant to a particular decision, is not something we can know in advance. We can describe its expected mean and variance, but we cannot know the specific temperature and precipitation patterns that will emerge. All three types of uncertainty can be relevant to a decision analysis but they often emerge at different stages of the process. For example, linguistic uncertainty often arises during problem framing or objective setting, whereas epistemic and aleatory uncertainty play a more important role during the prediction of the consequences of the alternative actions.

The first step to grappling with uncertainty in a decision context is simply to acknowledge that uncertainty exists and to identify the potential sources of uncertainty that could affect the prediction of the consequences of the alternative actions. The second step is to estimate the magnitude of the uncertainty. Statistical methods can be used to estimate the magnitude of uncertainty in empirical observations; in other cases, formal methods of expert elicitation (Martin *et al.*, 2012) can be used. Either way, uncertainty can be expressed as probability distributions associated with the state variables of interest (e.g. population abundance), the parameters of predictive models (e.g. survival or reproductive rates), the underlying alternative hypotheses about how the ecosystem responds to management (e.g. whether the population is limited by habitat or predation), and the efficacy of actions (e.g. fraction of a grassland burned by a prescribed fire). For analysis of empirical data, Bayesian statistical techniques are most useful, because the posterior distributions represent direct statements about the probabilities of values of the parameters in question. For analysis of expert judgment, various elicitation and aggregation methods are available to produce probabilistic summaries. Burgman (2005) discusses the range of methods available for estimating uncertainty in a risk-analysis context.

The third step in grappling with uncertainty is to propagate the uncertainty through the predictions of the consequences. If a model is being used to connect the

alternatives to the outcomes, then standard modelling techniques can be used to accomplish this; if not, then again, expert elicitation can be used. The fourth step is the most important – figuring out how to handle the uncertainty in the decision. There are essentially two different paths. Decisions can be made either without resolving uncertainty, or once some of the uncertainty has been resolved. For irreducible uncertainty, only the first choice is available. For reducible uncertainty, both choices are theoretically available, and the question is whether it is worth resolving the uncertainty first. Funders of research may also be interested in prioritisation where there are multiple sources of uncertainty to address. In some instances uncertainty may not be an important consideration, in others, however, uncertainty may play an important role. The next two sections describe the decision analytical tools for evaluating decisions in the face of uncertainty, and evaluating the value of reducing uncertainty.

2.1.6 Decisions in the face of uncertainty

Many decisions are made in the face of uncertainty, without an attempt to resolve the uncertainty before committing to action; analysis of such decisions is the focus of risk analysis (Burgman, 2005). The essence of such decisions is to choose the alternative action that best manages the risk associated with the uncertain outcomes in a manner that reflects the decision maker's risk tolerance. For a risk-neutral decision maker, the analysis involves calculating the expected outcome for each alternative, with the expectation (the weighted average) taken over all the uncertainty, and choosing the action with the best expected value. The decision maker, however, might not be risk neutral; for instance, they might be much more concerned about the risk of downside losses than the chance of upside gains. If the decision maker is not risk neutral, utility theory (von Neumann & Morgenstern, 1944) is used to express the decision maker's risk tolerance. Both the expected value (risk neutral) and expected utility approaches require a probabilistic expression of uncertainty. There are also approaches to risk analysis and management that do not require uncertainty to be described with probabilities, that instead seek actions that are relatively robust to uncertainty [for example, info-gap decision theory (Ben-Haim, 2006)]. So, there are methods for analysing decisions that

are made in the face of uncertainty. But what if there is an opportunity to reduce uncertainty before committing to action – is it worth doing so?

2.1.7 Prioritising research to reduce uncertainty about the things that matter: the Value of Information

From the standpoint of a decision maker, research and monitoring are expensive and time-consuming, and potentially take resources away from management interventions, but hold the promise of providing new information that can guide and improve future management actions. When is new information worth the cost? The Vol addresses this question by helping to focus research and monitoring efforts on uncertainty that impedes choice of an optimal action (Runge *et al.*, 2011). Vol can also be used to identify cases where monitoring or further learning would not improve the management actions (McDonald-Madden *et al.*, 2010).

As an example, if the threats to a declining species are unknown, there is uncertainty around the management action that would best address the decline. In some cases, research may lead to a better understanding of the causes of the decline so the decision maker can choose an appropriate management action. In other cases, research might not affect the choice of action, either because the decision maker cannot address some of the causes of the decline, or because the best action would not change even with more knowledge. The aim of Vol is to establish whether the removal of uncertainty by conducting research or undertaking monitoring would be beneficial. The ability to use Vol to prioritise and choose between different monitoring and research options is particularly useful, but to our knowledge has not become common practice among research-funding agencies or conservation organisations.

Vol was first described by Schlaifer & Raiffa (1961) and has since been used in a wide range of applied disciplines, notably health economics (Yokota & Thompson, 2004; Steuten *et al.*, 2013) and engineering (Zitrou, Bedford & Daneshkhah, 2013). Vol is calculated by determining whether the performance of objectives of a decision could be improved if uncertainty could be resolved before committing to a course of action.

There are several variants of Vol, all of which compare the expected benefit with new information to the expected benefit when the decision is made in the face of

uncertainty (Runge *et al.*, 2011). The expected value of perfect information (EVPI) calculates the improvement in performance if all uncertainty is fully resolved, and can be used to establish if research or monitoring is valuable to make effective management decisions. The expected value of partial perfect information (EVPXI or EVPPI) shows the relative value of resolving uncertainty about different hypotheses or different parameters, thus serving as a way to prioritise research questions (Yokomizo *et al.*, 2014). Finally, because reducing uncertainty to zero is likely to be impossible, the expected value of sample information (EVS) calculates the expected gain in performance from collecting imperfect information rather than for perfect information (Steuten *et al.*, 2013). The expected value of partial sample information (EVXSI) combines the concepts of EVPXI and EVS. Canessa *et al.* (2015) and Milner-Gulland & Shea (2017) advocate the use of Vol in ecology and also provide explanations and online documentation for ecologists on how it can be calculated (Canessa *et al.*, 2015) and in which contexts it would be useful for addressing uncertainty (Milner-Gulland & Shea, 2017).

2.2 Calculating the value of information

As the calculations can become complex, we provide here a simplified explanation of how to calculate Vol. A Vol analysis requires that the decision be formally structured (Gregory *et al.*, 2012). First, the decision maker's objectives must be articulated and appropriate performance metrics identified. This is often quite challenging, because it requires critical thought about the aims of management and how the outcomes can be measured. While managers may be able to identify costs of different interventions, estimating benefits for biodiversity conservation is usually more difficult, but there is a growing literature on this topic (Keeney, 2007; Runge & Walshe, 2014). Second, at least two alternative management actions need to be identified that could meet the objectives. Third, the consequences of the alternatives need to be estimated, specifically how effective each alternative will be in meeting the different objectives (Gregory *et al.*, 2012). This is where the evaluation of uncertainty begins. For each action, the uncertainty in achieving the objectives needs to be estimated. Often, this comes in the form of structural uncertainty: different hypotheses about how the system works that

result in different predictions of the outcomes associated with each action (see Case Study 3 in Section III.3c, for an example). Along with these predictions, the probability of the different hypotheses also needs to be estimated. This information (the objectives, the actions, the consequences, and the estimates of uncertainty) form the basis for a risk analysis, but they also provide the basis for the Vol analysis.

To demonstrate a Vol calculation by example, we consider three different areas that could be purchased, placed in protection, and managed for the benefit of an endangered species. The decision maker has the resources to purchase only one area, and would like to know which one will be of most benefit. The decision maker has indicated that the fundamental objective can be measured using the long-term population size of the endangered species.

There is uncertainty about the ultimate population size of the endangered species that could be supported in the three protected areas, so the population size has been estimated under five different hypotheses about what resource most limits the species, each of which is judged to be equally likely (Table 3). The expected population size across hypotheses is highest for area A with a mean of 1,000, so if we do no further research, area A would be the best option under current knowledge. That is, in the face of uncertainty, a risk-neutral decision maker would choose to acquire area A.

Table 3. Long-term population size resulting from choosing areas A, B or C to protect, and maximum long-term population size, as estimated under five different hypotheses, and their means.

Hypothesis	Area A	Area B	Area C	Maximum long-term population size
1	1,250	750	500	A - 1,250
2	1,000	1,250	450	B - 1,250
3	500	750	450	B - 750
4	750	500	800	C - 800
5	1,500	500	300	A - 1,500
<i>Mean</i>	<i>1,000</i>	<i>750</i>	<i>500</i>	<i>1,110</i>

For hypotheses 1 and 5, we estimate that area A has the highest long-term population size, so A is the optimal choice in 40% of the cases. For hypotheses 2 and 3, we estimate that area B would be best, while for hypothesis 4 area C would be best, so there is some uncertainty about the best area in which to invest, depending on which

hypothesis is correct. That is, the uncertainty matters to the decision maker. Now we can use Vol to decide whether to select area A now or invest in more research first.

The maximum long-term population size under each hypothesis arises if the decision maker can choose the best action associated with that hypothesis (A for hypothesis 1, B for hypotheses 2 and 3, C for hypothesis 4, and A for hypothesis 5). Taking the mean of the maximum long-term population sizes under each hypothesis, we can calculate the expected value of the maximum long-term population size, which is 1,110. Prior to undertaking research to resolve uncertainty about the true hypothesis, we do not know what we will find out, but we think it is equally likely it will be any one of the five hypotheses. The average of the performance of the best action for each hypothesis tells us the expected value of our decision if we can resolve uncertainty before we commit to action. In comparison, the highest long-term population size under current knowledge is the mean value of A, which is 1,000. The difference is the Vol – we could achieve an expected gain of 110 additional animals in the population if we had perfect knowledge. We assume here that one of the five hypotheses is correct and therefore one of the estimates for long-term population sizes of area A, B, and C under each hypothesis must be correct. The decision maker now knows that reducing uncertainty about the limiting factors would increase the expected outcome by 11% (110 more animals than the 1,000 expected by simply purchasing Area A). Several very difficult questions now arise. First, is research possible that can reduce the uncertainty and identify the limiting factor? This question requires careful consideration of research design. Second, how much would the research cost? A power analysis associated with the research design could help identify the amount of sampling necessary, which could help with estimation of the costs. Third, is the cost of the research worth the gain? Suppose the research would cost \$500,000; would the expected gain of 110 individuals of this endangered species be worth that investment? The decision maker needs to weigh this decision, taking into account such things as the importance of this species, the number of other populations that exist, and the other uses to which the funds could be put. This is not a trivial task, but the decision is greatly informed by the transparent analysis of uncertainty, the comparison with the expected outcome in the face of

uncertainty, and the estimate of the potential gain. It is now up to the decision maker to decide whether money should be spent on further research, or whether the decision should just be made to protect area A.

2.3 The use of VoI in biodiversity conservation

2.3.1 Methods

A literature search was undertaken to examine the extent to which the use of VoI in biodiversity conservation has been documented so far. Search criteria were established to identify papers that were written in English and were published in a peer-reviewed journal before the end of July 2017. The *Web of Science* was searched for papers containing the terms "value of information", "value of perfect information", or "EVPI" within the environmental science, ecology, and biodiversity conservation categories. To search for grey literature, *Google Scholar* was searched with the following terms: ("value of information" OR "value of perfect information" OR EVPI) AND (biology OR "biodiversity conservation" OR fish OR ecology) AND decision. The term fish was added to ensure that fishing and fisheries papers were included in the search results. Only the first 1,000 matches were examined, however this was deemed sufficient as none were relevant after entry 318. Not all articles found in this way applied VoI in biodiversity conservation, and articles whose research domains were, for example, medicine, meteorology, or economics were excluded. Studies that did not use VoI calculations and studies that advocated the use of VoI but showed no real-world application were also excluded: only studies that incorporated VoI calculations that were applied to biodiversity conservation were selected. We report our search using a PRISMA (Preferred Reporting Items for Systematic Reviews and Meta-Analyses; Liberati *et al.*, 2009) flow diagram. Citations of studies meeting the inclusion criteria were searched for further studies, then all studies were summarised with respect to: the application of VoI, management objectives, uncertainties considered and how they were expressed, the predictive modelling used, the performance metric used, and the type of VoI. Papers were further categorised according to the type of uncertainty (structural, parametric – empirical, or parametric – elicited), whether they had single or multiple objectives, whether uncertainty was expressed discretely or continuously, and what type of VoI was

used (EVPI, EVPXI, EVSI). We also plotted the number of papers we found and the overall citations over time.

Three papers were chosen as case studies, to illustrate in more detail the decision context, what data sources were used, how Vol was calculated, and whether it made a difference to the decision. They were chosen to represent a range of applications that show clearly how Vol was helpful.

2.3.2 Results

The searches returned 1225 unique references of which 30 met the inclusion criteria, or 2.5% of the total references (Figure 2). 901 references were excluded because their primary discipline was not biodiversity conservation. 294 were excluded due to no mention of Vol, no real-world application of Vol, or due to duplication of previously identified records.

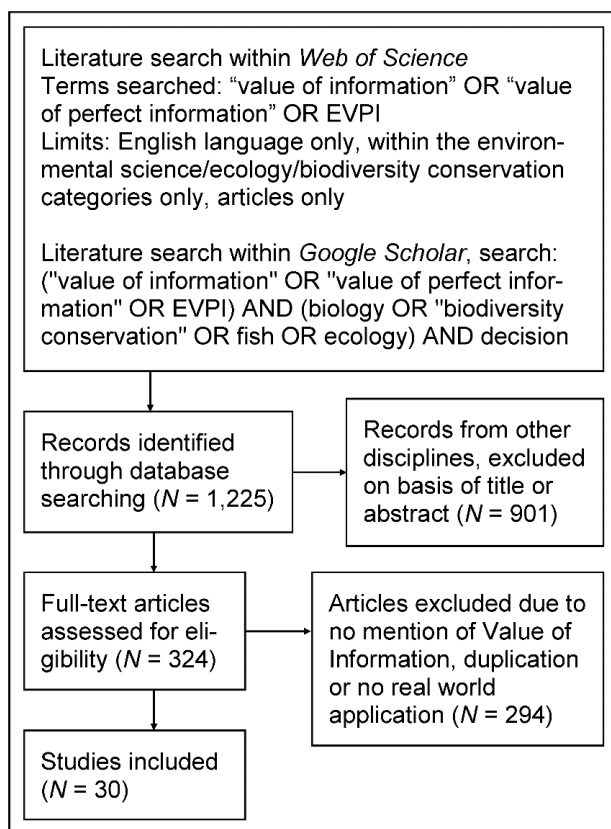


Figure 2. PRISMA flow diagram (Liberati et al., 2009) of results of literature search.

A range of relevant aspects of the included papers are summarised in Table 4. Single-species management problems were the focus of 18 (60%) of the papers. Of those, the disciplines within which Vol has been used included invasive species

management (eight papers: D'Evelyn *et al.*, 2008; Moore *et al.*, 2011; Sahlin *et al.*, 2011; Moore & Runge, 2012; Johnson *et al.*, 2014*b*, 2017; Williams & Johnson, 2015; Post van der Burg *et al.*, 2016) and protected species management (10 papers: Grantham *et al.*, 2009; Runge *et al.*, 2011; Tyre *et al.*, 2011; Williams, Eaton & Breininger, 2011; Smith *et al.*, 2012, 2013; Johnson *et al.*, 2014*a*; Canessa *et al.*, 2015; Maxwell *et al.*, 2015; Cohen *et al.*, 2016). Other papers focused on management of multiple species. Of those, fisheries were the subject of five papers (Sainsbury, 1991; Costello, Adams & Polasky, 1998; Kuikka *et al.*, 1999; Mäntyniemi *et al.*, 2009; Costello *et al.*, 2010) and the management of ecosystems was also the subject of five papers (Bouma, Kuik & Dekker, 2011; Convertino *et al.*, 2013; Runting, Wilson & Rhodes, 2013; Perhans, Haight & Gustafsson, 2014; Thorne *et al.*, 2015). The use of phylogenetic diversity for deciding which species to protect was used by one study (Hartmann & Andre, 2013) and the sustainable harvest of a species by another (Johnson, Kendall & Dubovsky, 2002).

While there was a range of different objectives considered, there were some common themes, including maximising populations or their growth rates, or having optimal populations (14 papers or 47%), maximising or maintaining harvests (seven papers or 23%) and minimising costs (seven papers or 23%). Many papers listed more than one objective, and further details of objectives that were specific to individual studies can be found in Table 4. The uncertainties considered are also listed (Table 4): six papers (20%) used expert elicitation for estimates of uncertainties, the others used various models.

Table 4. Summary of 30 papers identified by the literature search for inclusion in this study. EVPC, expected value of perfect choice (analogous to EVPI); EVPI, expected value of perfect information; EVPXI, expected value of partial perfect information; EVSI, expected value of sample information; Vol, Value of Information.

Paper	Paper summary	Vol application	Management objective(s)	Uncertainties considered	How was uncertainty expressed	Predictive model	Net benefit parameter	Vol type
<i>Invasive species papers</i>								
D'Evelyn <i>et al.</i> (2008)	To inform management of the invasive brown tree snake <i>Boiga irregularis</i> in the USA under uncertainty regarding population size	Establish social costs of invasive species management (control costs and damages) with and without learning about the true population size	Minimise costs of management Minimise damage to invasive species	Population size	Continuous – probability distribution for population size	Species population models	\$	Simulation comparison of expected value with and without learning
Johnson <i>et al.</i> (2014 <i>b</i>)	Establish management and monitoring options for pink-footed goose <i>Anser brachyrhynchus</i> in Western Europe under uncertainty regarding population dynamics to minimise negative	Choose most appropriate population model for pink-footed goose and whether information on survival or reproduction	Maintain viable goose populations Minimise losses on agricultural lands and of tundra habitat due to geese	Survival and reproductive rates of goose	Discrete – nine different population models considered	Annual life-cycle models	Objective value – relative measure of management performance	EVPI, EVPXI

Paper	Paper summary	Vol application	Management objective(s)	Uncertainties considered	How was uncertainty expressed	Predictive model	Net benefit parameter	Vol type
	effects on farmland and habitats	would be most beneficial	Allow goose hunting					
Johnson <i>et al.</i> (2017)	Control of invasive black and white tegu <i>Salvator merianae</i> in Florida, a newly introduced species that is increasing rapidly under uncertainty regarding population dynamics	Find best management action to control tegu abundance if uncertainty is resolved, and if uncertainty remains	Contain tegu population whilst minimising costs	Range of uncertainties of population ecology of tegu, and effectiveness of control	Continuous – population parameter elicited from experts, replicated to draw distributions, then included in models	Population matrix model, expert elicitation	Objective function value – combination of weighted management objectives	EVPI, EVPXI
Moore & Runge (2012)	Establish best management strategy for invasive grey sallow willow <i>Salix cinerea</i> in Australia despite uncertainty regarding some of its ecological traits and how they can be managed	Establish if further research would enhance management through improving dynamic models at different budget levels	Protect alpine bogs by removing willows Minimise resources used for willow removal	Frequency of fires, population dynamics of willow, effectiveness of management effort	Continuous – effects of actions elicited from experts, then incorporated in the model; discrete - different parameter values used	Expert elicitation, dynamic management model for different budgets	Budget – workdays allocated	EVPI, EVPXI

Paper	Paper summary	Vol application	Management objective(s)	Uncertainties considered	How was uncertainty expressed	Predictive model	Net benefit parameter	Vol type
Moore <i>et al.</i> (2011)	Establish which interventions are best for managing <i>Acacia paradoxa</i> , an invasive species occurring in South Africa, when its extent is unknown	Establish if more research needed before deciding whether eradication or containment is best for managing <i>Acacia paradoxa</i>	Minimise overall cost	Current extent of <i>Acacia paradoxa</i>	Continuous - probability distribution for the extent of infestation	Decision model	South African Rand	EVPI, EVPXI
Sahlin <i>et al.</i> (2011)	For cultivated introduced marine macroalgae in Europe, establish those that will become invasive and those that will not become invasive to avoid future costs of invasive species while not spending on non-invasive species	Evaluate which species of macroalgae are likely to become invasive so money can be spent on avoiding introductions of such species	Remove populations of species that will become invasive Do not remove populations of species that will not become invasive	Base rate of invasiveness	Continuous – different parameter values in pre-posterior Bayesian analysis	Screening model of species invasiveness	Cost ratio – relative loss of avoiding introduction of species that will not be invasive, and not avoiding introduction of species that will be invasive	EVSI (Bayesian pre-posterior analysis)
Post van der Burg	Find optimal management for two invasive species, leafy	Evaluate whether to prioritise one or both invasives	Maximise native	A whole range of uncertain	Continuous – probability distributions	State-and-	US\$ per year with less than	EVPI, EVPXI

Paper	Paper summary	Vol application	Management objective(s)	Uncertainties considered	How was uncertainty expressed	Predictive model	Net benefit parameter	Vol type
<i>et al.</i> (2016)	spurge <i>Euphorbia esula</i> and yellow toadflax <i>Linaria vulgaris</i> , on private and public lands under different budgets	and whether to focus on managing public lands directly or private land indirectly through incentives, under different budgets	species populations Minimise costs	values was modelled, see S3 at http://www.fwspubs.org/doi/suppl/10.3996/032015-JFWM-023	for species-specific spread and establishment parameters	transition model	50% infestation	
Williams & Johnson (2015)	Inform management of pink-footed goose <i>Anser brachyrhynchus</i> in Western Europe despite uncertainty regarding population dynamics over a 50-year time horizon. Establish which aspect of population dynamics would be most beneficial to understand. Data from Johnson <i>et al.</i> (2014 <i>b</i>).	Determine which management option would be best over a 50-year time horizon, looking at different population levels	Maximise sustainable harvest whilst keeping to the population goal	Nine models that differ in the survival and reproductive rates of geese	Discrete – nine different population models considered	Annual cycle models	Objective value – relative measure of management performance	EVPI, EVPXI
<i>Protected species papers</i>								

Paper	Paper summary	Vol application	Management objective(s)	Uncertainties considered	How was uncertainty expressed	Predictive model	Net benefit parameter	Vol type
Canessa <i>et al.</i> (2015)	Inform reintroduction strategy for the European pond terrapin <i>Emys orbicularis</i> under uncertainty about post-release effect on different age classes	Determine optimal age class at which to release captive terrapins into the wild under uncertainty of post-release effects in different age groups	Maximise survival of terrapins	Uncertainty if post-release effect on terrapins is stable, or increases or decreases with increasing age	Continuous – different parameter values in the model	Population model	Probability of survival of different age classes	EVPI, EVSI
Cohen <i>et al.</i> (2016)	Inform management of piping plovers <i>Charadrius melodus</i> at nest sites for improved nesting success and adult survival under different predation rates	Decide if and in which situations nest exclosures improve breeding success and whether this exceeds the effect on adult mortality	Maximise breeding success Minimise adult mortality	A whole range of uncertain population values was considered, see Materials and Methods in Cohen <i>et al.</i> (2016)	Continuous – means and confidence intervals identified through literature or expert elicitation	Mixed multinomial logistic exposure model, expert elicitation	Population growth rate in per cent	EVPI

Paper	Paper summary	Vol application	Management objective(s)	Uncertainties considered	How was uncertainty expressed	Predictive model	Net benefit parameter	Vol type
Grantham <i>et al.</i> (2009)	Decide on survey effort to maximise protection of members of the Proteaceae family in South Africa	Choice of six different survey durations or use of a habitat map alone under uncertainty regarding future habitat loss and protection	Maximise protection of Proteaceae	Rate of surveying by volunteers, rate of habitat loss, rate of establishment of newly protected areas	Discrete – habitat suitability of plots; continuous – varying mean rates of habitat loss, habitat protection and volunteer survey hours spent	Maximum entropy model for habitat suitability; minimum loss algorithm and maximum gain algorithm for designation of protected areas	Proteaceae retention rate at the end of 20-year simulation period	EVSI
Johnson <i>et al.</i> (2014a)	Inform management of a declining population of Northern bobwhite quail <i>Colinus virginianus</i> in the USA despite uncertainty regarding population	Choose which management option would be best and which potential reasons for a decline in Northern bobwhite quail	Maximise population growth rate and harvest of bobwhites Minimise costs	Cause of decline of bobwhites	Discrete – hypotheses elicited from experts, then ranked	Expert elicitation, population model	Objective value – calculated with weighted objectives	EVPI, EVPXI

Paper	Paper summary	Vol application	Management objective(s)	Uncertainties considered	How was uncertainty expressed	Predictive model	Net benefit parameter	Vol type
	limitations and how management options could address these	would be most beneficial to study further	Maximise feasibility of management					
Maxwell <i>et al.</i> (2015)	Inform management options for a declining koala <i>Phascolarctos cinereus</i> population in Australia despite uncertainty regarding survival and fecundity rates and how habitat affects different threats	Determine if more research is necessary to decide whether habitat restoration or preventing vehicle collisions or dog attacks would be most cost-effective	Maximise koala population growth rate	Survival and fecundity rates	Discrete – eight different structures of the population model; continuous – varying parameter values	Deterministic age-structured matrix population model	Relative benefit of actions at different monetary levels in AU\$	EVPI, EVPXI
Runge <i>et al.</i> (2011)	Establish which management interventions are best for whooping crane <i>Grus americana</i> conservation in the US whilst reasons for low reproduction are unknown	Distinguish between different hypotheses regarding reasons for low productivity as well as possible management actions	Provide suitable nest sites Maximise reproductive success Maximise survival during the	Cause for reproductive failure	Discrete – hypotheses elicited from experts	Expert elicitation	Multi-criteria scale – relative values of objectives	EVPI, EVSI

Paper	Paper summary	Vol application	Management objective(s)	Uncertainties considered	How was uncertainty expressed	Predictive model	Net benefit parameter	Vol type
			breeding season Maximise body condition prior to migration					
Smith <i>et al.</i> (2013)	Establish harvest rates in the US for Delaware Bay horseshoe crabs <i>Limulus polyphemus</i> with uncertainty regarding its link to red knot <i>Calidris canutus rufa</i> abundance	Determine best population model of red knot with and without uncertainty	Maintain crab harvest Ensure red knot recovery	Relationship between horseshoe crab spawning, red knot mass and red knot vital rates	Discrete – three different population models	Species-specific population models	Mean outcome of populations averaged over model weights	EVPI
Smith <i>et al.</i> (2012)	Find optimal management to combine extraction of shale gas with maintaining populations of brook trout <i>Salvelinus fontinalis</i> under	Determine level of gas extraction under uncertainty regarding effect of density of well pads on brook trout, and uncertainty	Extract shale gas while maintaining brook trout populations	Well pad density	Discrete – three predictive models; continuous – different well pad densities considered,	Urban-type, forestry-type and intermediate type impact models	Increase in gas extraction while maintaining brook trout populations	EVPI

Paper	Paper summary	Vol application	Management objective(s)	Uncertainties considered	How was uncertainty expressed	Predictive model	Net benefit parameter	Vol type
	different densities of well pads	around occupancy model			different model likelihood considered			
Tyre <i>et al.</i> (2011)	Inform stream management for bull trout <i>Salvelinus confluentus</i> conservation in north-western USA under uncertainty about migratory behaviour	Choose between four assumptions and a model of bull trout movement	Maintain current distribution Maintain stable/increase in abundance Restore/maintain habitat suitable for all life-history stages Conserve genetic diversity	Mechanisms that determine life-history strategy	Discrete – four different models	Patch network models	Probability of population persisting for 256 years (for demonstration of concept)	EVPI
Williams <i>et al.</i> (2011)	Establish optimal habitat management for the recovery of Florida scrub-jay <i>Aphelocoma</i>	Find the best option for habitat management under	Maintain stable scrub jay population	Rate of scrub regeneration, future burning	Discrete – multiple transition models	Habitat occupancy model	Smallest average loss in objectives	EVPI, EVPXI, EVSI

Paper	Paper summary	Vol application	Management objective(s)	Uncertainties considered	How was uncertainty expressed	Predictive model	Net benefit parameter	Vol type
	<i>coerulescens</i> despite uncertainty regarding the effect of different habitat management interventions	uncertainty of how vegetation will regenerate		rate after removal of combustibles				
<i>Ecosystems papers</i>								
Bouma <i>et al.</i> (2011)	Potential use of Earth Observation data for Great Barrier Reef protection, used to assess if non-targeted or targeted Water Action Plan would best address sediment discharge	Determine when Earth Observation data has most value: if sediment discharge is an equal issue from all catchments or if there are differences among catchments	Decrease sediment discharge into Great Barrier Reef	Difference in sediment discharge between catchments Cost of pollution abatement	Discrete – differing simulations in model, expert elicitation on data accuracy incorporated as prior belief	Four different simulations for cost minimisation model, expert elicitation	Million AU\$/year	EVPI
Convertino <i>et al.</i> (2013)	Find optimal interventions and monitoring plans for restoring water flow in the Florida Everglades to meet objectives	Distinguish between different monitoring efforts (low – medium – high)	Improve ecological conditions whilst minimising	Uncertainty around decisions on restoration alternatives	Discrete – three rainfall scenarios and two soil oxidation scenarios	Probabilistic decision network consisting of	Cost in \$, benefit is relative utility of management interventions	EVPI - Change in payoff of different monitoring plans

Paper	Paper summary	Vol application	Management objective(s)	Uncertainties considered	How was uncertainty expressed	Predictive model	Net benefit parameter	Vol type
	including biodiversity conservation and flood protection under uncertainty regarding future rainfall and soil oxidation		operational costs	and monitoring as well as climate change	were modelled	environmental, monitoring and decision sub-models		for one management plan
Perhans <i>et al.</i> (2014)	In areas to be clear-cut, find optimal method for selecting trees that are to be conserved with highest biodiversity value, using lichens as indicator species	Decide which method of selecting trees to retain will give most biodiversity benefit	Find trees that would give highest number of lichens Find trees that would give highest number of protected lichens Maximise probability that a protected species is represented	Relationship between different tree attributes and lichens present	Continuous – model averaging of model parameters	Generalised linear model	Swedish krona	EVPI

Paper	Paper summary	Vol application	Management objective(s)	Uncertainties considered	How was uncertainty expressed	Predictive model	Net benefit parameter	Vol type
Runting <i>et al.</i> (2013)	Find optimal allocation of resources for conservation areas under uncertainty around sea level rise in coastal South East Queensland	Find optimal allocation of budget towards either research or conservation of coastal areas at different budget levels	Maximise areas for conservation	Future sea-level rise, accuracy of elevation data, budget level	Discrete – different models, coarse/ fine resolution elevation data, different sea-level rise scenarios; continuous – different budget levels	Sea Level Affecting Marshes model or Inundation model	AUS\$	EVPXI
Thorne <i>et al.</i> (2015)	Find management options robust to different climate change scenarios in the San Francisco Bay area	Decide if and which uncertainty to reduce – storm or marsh resilience	Maximize marsh ecosystem integrity Maximize likelihood of recovery of California Ridgway's Rail (<i>Rallus</i>	Frequency and intensity of storms and tidal marsh resilience	Discrete – discrete states in network with conditional probabilities	Bayesian network	Relative utility of management under different assumptions on scale from 0 to 100	EVPI

Paper	Paper summary	Vol application	Management objective(s)	Uncertainties considered	How was uncertainty expressed	Predictive model	Net benefit parameter	Vol type
			<i>obsoletus</i> <i>obsoletus</i>) Maximize human benefits from tidal marshes					
<i>Fisheries papers:</i>								
Costello <i>et al.</i> (1998)	Find optimal harvest rates of Coho salmon <i>Oncorhynchus kisutch</i> under uncertainty around future El Niño events	Choose optimal harvest rate for coho salmon under uncertainty about future El Niño events and if uncertainty can be resolved	Maximize expected net present value of the Coho fishery	Future El Niño occurrences	Discrete; three different states for the annual El Niño phase	Bioeconomic model of Coho salmon fishery	US\$	EVPI, EVSI
Costello <i>et al.</i> (2010)	Design optimal Marine Protected Areas network for sheephead <i>Semicossyphus pulcher</i> , kelp bass <i>Paralabrax clathratus</i> and kelp rockfish	Choose location and extent of Marine Protected Areas	Maximise fishery profits whilst ensuring conservation of species	Dispersal of fish larvae	Discrete – 10 different dispersal kernels used	Stage-structured spatial model, ocean circulation model	Net profit of fishing – unitless	EVPI

Paper	Paper summary	Vol application	Management objective(s)	Uncertainties considered	How was uncertainty expressed	Predictive model	Net benefit parameter	Vol type
	<i>Sebastes atrovirens</i> to maximise fishery profits							
Kuikka <i>et al.</i> (1999)	Management of Baltic cod <i>Gadus morhua</i> fisheries in the Baltic Sea	Determine best mesh size for cod fishery	Minimise risk of spawning biomass going below critical levels Maximise yield	Growth rate of cod, recruitment of cod, critical spawning biomass	Discrete – three different models for recruitment	Bayesian influence diagram that combines three different recruitment models	Utility function reflecting both yield (kilotons) and risk of falling below critical spawning mass	EVPI
Mäntyniemi <i>et al.</i> (2009)	Management of North Sea herring <i>Clupea harengus</i> fisheries in the North Sea	Determine ideal fishing pressure under uncertainty around the stock–recruitment relationship	Maximise expected profits over 20-year period	Stock–recruitment relationship	Discrete – two stock–recruitment relationships considered	Bayesian probability model	Norwegian Krone	EVPI
Sainsbury (1991)	Management of a multi-species fishery in north-western Australia of genera	Find optimal management option for fishery by using trap or trawl catch and	Maximise value of fisheries	Effect of intra- and interspecific competition	Discrete – four different models; continuous –	Population growth models	Million AUS\$	EVPI

Paper	Paper summary	Vol application	Management objective(s)	Uncertainties considered	How was uncertainty expressed	Predictive model	Net benefit parameter	Vol type
	<i>Lethrinus, Lutjanus, Nemipterus, Saurida</i>	using adaptive management to incorporate learning into the management process		n as well as habitat on abundance of different fish species	different parameter values			
<i>Other topics</i>								
Hartman & Andre (2013)	A framework for the use of phylogenetic diversity to inform which species should be protected, and the associated costs and benefits	Distinguish when to use species richness as a measure of biodiversity, and when to use phylogenetic diversity as a better measure	Maximize phylogenetic diversity	Uncertainty in the underlying phylogenetic relationships among a set of species	Continuous – 10,000 samples of possible phylogenetic trees for a set of 20 species	Calculation of phylogenetic diversity, based on the edge lengths for the included species from a phylogenetic tree	Proportion of maximum phylogenetic diversity retained	EVPC

Paper	Paper summary	Vol application	Management objective(s)	Uncertainties considered	How was uncertainty expressed	Predictive model	Net benefit parameter	Vol type
Johnson <i>et al.</i> (2002)	Find optimal harvest strategy under uncertainty regarding population processes of mallards <i>Anas platyrhynchos</i>	Optimal harvest strategy if accurate population model was known compared to if uncertainty remained	Maximise long-term cumulative harvest	Density dependence and additive or compensatory mortality	Discrete – four population models and their probabilities	Age-structured population models	Harvested mallards/year, converted to \$	EVPI

The type of performance metric, that is, how the achievement of objectives by different management interventions was expressed, was conveyed in a wide variety of ways. Monetary values for costs and benefits were used by 12 papers (40%) (Sainsbury, 1991; Costello *et al.*, 1998, 2010; Johnson *et al.*, 2002; D'Evelyn *et al.*, 2008; Mäntyniemi *et al.*, 2009; Bouma *et al.*, 2011; Moore *et al.*, 2011; Moore & Runge, 2012; Runting *et al.*, 2013; Perhans *et al.*, 2014; Post van der Burg *et al.*, 2016). Two papers used monetary values for costs only, and relative benefits that can be achieved at those costs (Maxwell *et al.*, 2015; Convertino *et al.*, 2013). Another eight (27%) papers used a unitless value that reflected a weighted response across multiple objectives (Runge *et al.*, 2011; Smith *et al.*, 2013; Williams *et al.*, 2011; Johnson *et al.*, 2014*a,b*, 2017; Thorne *et al.*, 2015; Williams & Johnson, 2015). Other papers used a range of performance metrics, namely cost ratio (Sahlin *et al.*, 2011), probability of survival of different age classes (Canessa *et al.*, 2015), population growth rate in per cent (Cohen *et al.*, 2016), species retention rate at the end of a 20-year simulation period (Grantham *et al.*, 2009), increase in gas extraction while maintaining brook trout (*Salvelinus fontinalis*) populations (Smith *et al.*, 2012), probability of population persisting for 256 years (Tyre *et al.*, 2011), utility function reflecting both yield (kilotons) and risk of falling below critical spawning mass (Kuikka *et al.*, 1999), and proportion of maximum phylogenetic diversity retained (Hartmann & Andre, 2013).

Of the 30 papers found, 19 considered multiple objectives (63%), whereas 11 (37%) considered single objectives (Table 5). 17 papers (57%) were concerned with structural forms of uncertainty and 19 with parametric forms of uncertainty (63%) – six papers considered both forms of uncertainty (20%). While 27 papers used EVPI (90%), 10 used EVPXI (33%), all of which were published since 2011, and six used EVSI (20%). Twelve papers used more than one Vol calculation.

Table 5. Table summarising papers according to the uncertainties and objectives considered and depending on the type of Vol used. EVPI, expected value of perfect information; EVPXI, expected value of partial perfect information; EVSI, expected value of sample information.

	Uncertainty	EVPI	EVPXI	EVSI
Single Objective	Structural	Sainsbury (1991); Costello <i>et al.</i> (1998); Johnson <i>et al.</i> (2002); Mäntyniemi <i>et al.</i> (2009); Bouma <i>et al.</i> (2011); Williams <i>et al.</i> (2011); Maxwell <i>et al.</i> (2015)	Williams <i>et al.</i> (2011); Runting <i>et al.</i> (2013); Maxwell <i>et al.</i> (2015)	Costello <i>et al.</i> (1998); Grantham <i>et al.</i> (2009); Williams <i>et al.</i> (2011)
	Parametric	Sainsbury (1991); Bouma <i>et al.</i> (2011); Moore <i>et al.</i> (2011); Canessa <i>et al.</i> (2015); Maxwell <i>et al.</i> (2015)	Moore <i>et al.</i> (2011); Runting <i>et al.</i> (2013); Maxwell <i>et al.</i> (2015)	Grantham <i>et al.</i> (2009); Canessa <i>et al.</i> (2015)
Multiple Objectives	Structural	Kuikka <i>et al.</i> (1999); Costello <i>et al.</i> (2010); Tyre <i>et al.</i> (2011); Smith <i>et al.</i> (2012, 2013); Convertino <i>et al.</i> (2013); Johnson <i>et al.</i> (2014 <i>b</i>); Williams & Johnson (2015)	Johnson <i>et al.</i> (2014 <i>b</i>); Williams & Johnson (2015)	
	Parametric	D'Evelyn <i>et al.</i> (2008); Runge <i>et al.</i> (2011); Moore & Runge (2012); Smith <i>et al.</i> (2012); Hartmann & Andre (2013); Johnson <i>et al.</i> (2014 <i>a</i> , 2017); Perhans <i>et al.</i> (2014); Thorne <i>et al.</i> (2015); Cohen <i>et al.</i> (2016); Post van der Burg <i>et al.</i> (2016)	Moore & Runge (2012); Johnson <i>et al.</i> (2014 <i>a</i> , 2017); Post van der Burg <i>et al.</i> (2016)	Runge <i>et al.</i> (2011); Sahlin <i>et al.</i> (2011)

Use of Vol in the field of biodiversity conservation is a recent phenomenon. The number of papers has increased markedly since 2011, with eight papers published before 2011, and 22 papers published since the start of 2011 (Figure 3). The number of citations has increased steadily and was at 813 at the end of 2017, a mean of 27 citations per paper. Leadership in this arena comes primarily from the USA and Australia: the country of affiliation for first authors was USA for 18 of the papers (60%), Australia for seven (23.3%), and European countries for five (16.7%). 18 papers (60%) had at least one author who worked for the US Department of Interior.

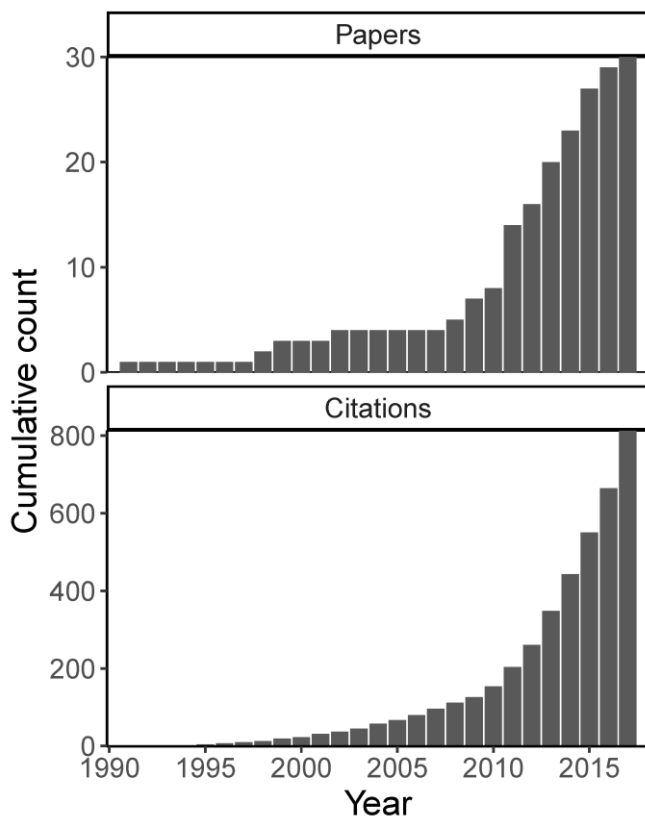


Figure 3. Cumulative number of applied Value of Information (Vol) papers in biodiversity conservation and their total citations over time. The citations are tallied until the end of 2017.

2.4 Case studies

All 30 examples found through the literature search undertook a Vol analysis that shed light on whether more information would be valuable to the decision maker, but they varied in the transparency of their presentation, the thoroughness of the uncertainty analysis, and the clarity of the usefulness to the decision maker. Rather than a detailed analysis of the strengths and shortcomings of all 30 cases, we present here three case studies that describe clearly how Vol was used and calculated, represent a range of applications of Vol, and document how Vol informed the decision-making process. These three case studies are exemplary applications of Vol, but each also has a few shortcomings; these shortcomings help identify fruitful areas for improved application. They are also amongst the Vol papers with the highest annual citations.

2.4.1 Case study 1

Costello *et al.* (2010) used Vol to find an optimal marine protected area network in California, under uncertainty around dispersal of larval fish. Their aim was to design an

optimal Marine Protected Areas network for sheephead *Semicossyphus pulcher*, kelp bass *Paralabrax clathratus*, and kelp rockfish *Sebastes atrovirens* to maximise fishery profits whilst ensuring the conservation of the three fish species. They investigated the trade-offs between maximising profits and maximising conservation by changing the weighting of the two objectives across the different scenarios. The authors considered 135 patches of 10 km². There was uncertainty around the dispersal of the fish larvae, which affects where the species will be, which is relevant both for fishing these species as well as for protecting them. They used ten different dispersal kernels, of which only eight may accurately represent the real dispersal of fish larvae. The other two were simplified kernels, included to see how incorrect assumptions might affect the outcomes. The management alternatives were based around these kernels: to choose the best possible spatial harvest either under uncertainty or with perfect information, or under the two incorrect dispersal kernels. A stage-structured spatial model as well as an ocean-circulation model were used, and EVPI was calculated.

To maximise profits from fishing, the two incorrect dispersal kernels led to the least profits, while imperfect information led to higher profits and perfect information to the highest profits, for all three species of fish. To maximise the conservation benefits, there was no difference in the value of all three fisheries between the different dispersal kernels. The area in marine protected areas increased with certainty, and was lowest for the two incorrect dispersal kernels. The Vol to maximise profits was 11%.

Two observations about this case study point towards challenges in the application of Vol methods. First, the analysis of uncertainty focused on one aspect of the fish model, the larval dispersal kernels, and did not consider uncertainty in other aspects of the model, such as in the other fish population parameters or in assumptions about the fidelity with which optimal designs are implemented in practice. How comprehensive does the expression of uncertainty need to be? To some extent, the practice of modelling involves judgments about which uncertainties will matter and so which should be explored; these are essentially informal Vol evaluations. There is no guidance yet about how modellers should navigate this question. Second, to generate alternative larval dispersal kernels, Costello *et al.* (2010) used alternative realisations

from a stochastic ocean circulation model, but then acknowledge that they assumed those represented fixed dispersal kernels for the purpose of developing an optimal protected area design. Does their set of eight alternative kernels represent the full range of uncertainty for this aspect of their model? Would an alternative ocean circulation model have added to the range of dispersal kernels? We believe this is a valuable open research question – is there a way to evaluate whether a candidate set of models captures the relevant degree of uncertainty for the decision problem at hand?

2.4.2 Case study 2

Maxwell *et al.* (2015) used Vol to determine the value of more research in choosing the best management intervention for a declining koala *Phascolarctos cinereus* population in Australia. Their objective was to maximise the growth rate of the koala population. Three actions were suggested that could address threats to koalas, and the authors investigated how much should be invested in each action under different budget levels: preventing vehicle collisions by building fences and bridges; preventing dog attacks by building enclosures for dogs; and preventing spread of disease by buying land for conversion to koala habitat, which was also considered to reduce the other two threats. There was uncertainty about how habitat cover affected koala mortality, as well as about the survival and fecundity rates of koalas. These uncertainties were described using eight population models. The optimal strategy (how much of a given budget should be spent on each action) was calculated for various budget levels. EVPI and EVPXI were calculated by determining which uncertainties to reduce under different budget levels to achieve a certain population growth rate, which was then converted into a financial Vol.

The authors found that preventing vehicle collisions was the most cost-effective action at low budget levels but that larger budgets allowed more to be spent on habitat restoration instead, due to the disparity in costs of the different actions. The Vol differed between different budget levels; at budgets below AUS\$45 million it was best to resolve the uncertainty around survival and fecundity, whereas at budgets above \$45 million it was best to resolve uncertainty around habitat cover. Maxwell *et al.* (2015) made a valuable methodological contribution: even though the management objective was not

stated in monetary terms (the objective was to maximise the population growth rate of koalas), the Vol could be converted to a financial value by comparing budget levels that could achieve the same expected population growth rate with and without resolving uncertainty. Interestingly, the Vol was never more than 1.7% of the budget.

Maxwell *et al.* (2015) analysed both structural and parametric uncertainty in a combined analysis, serving as a good example for how others can include both types of uncertainty in a Vol analysis. They found that parametric uncertainty explained around 97% of the EVPI, with structural uncertainty contributing very little, but is this a general result? There has not yet been a comprehensive study to look at how structural and parametric uncertainty contribute to EVPI and whether there are any general patterns that can be inferred.

2.4.3 Case study 3

A study using expert elicitation was undertaken by Runge *et al.* (2011) who studied the management of a reintroduced whooping crane *Grus americana* population in the USA. At the time of the study, the population was failing to reproduce and so the aim was to enhance the current population under uncertainty around the reasons for low reproductive success. They formulated four objectives to contribute to a self-sustaining population of whooping cranes: provide suitable nest sites; maximise reproduction; maximise survival during the summer months; and improve body condition when the birds leave for their winter quarters. Because quantitative data were not available to evaluate the effectiveness of all proposed actions, they used an expert elicitation process to articulate competing hypotheses for reproductive failure, develop alternative management action, and evaluate the management actions under each hypothesis. Eight hypotheses to explain the pattern of reproductive failure were developed, ranging from nutrient limitation to harassment by black flies. Seven alternative management actions were developed, using the competing hypotheses as motivation. Using formal methods of expert judgment, the experts were then asked to estimate how well each action would address each of the four different objectives, under each hypothesis.

Three variants of Vol (EVPI, EVPXI and EVSI) were calculated with the information provided by the expert panel. Under uncertainty, the best action was meadow

restoration, which was thought to address all four objectives best. For three of the four objectives, the Vol was nearly 0, because the best action was the same under most of the hypotheses. But for one objective (maximising the fledging rate), the best action depended on the underlying hypothesis for reproductive failure, thus the Vol was substantial (25.7%). Calculation of the expected value of partial information (EVPXI) revealed that the most important hypotheses to resolve were how parasitic flies and human disturbance affected whooping cranes. In part as a result of this analysis, a controlled experimental study of the effect of parasitic flies on reproduction was undertaken, lending strong support to this hypothesis; in response, management agencies have refocused reintroduction efforts to areas with lower parasitic fly densities.

This study reveals one difficult challenge in estimating uncertainty. The authors considered eight hypotheses against seven alternatives and four objectives, thus, each expert had to estimate 224 values. A panel of experts was used, but uncertainty across experts was not analysed, nor were the experts asked to estimate their internal uncertainty, in part because the sheer magnitude of the elicitation task was already exhausting for the experts. Thus, differences across objectives and hypotheses were evaluated, but differences across and within experts were ignored. In this setting, expert judgement was needed, because empirical data could not inform the full set of questions being asked. But there are not yet methods in the expert judgment literature for eliciting large patterned matrices of responses, while properly estimating within- and among-expert uncertainty and minimising expert fatigue.

2.5 Discussion

Natural resource managers have to make decisions despite uncertainty on issues such as rapid species declines, increasing numbers of invasive species, or changes in ecosystems due to land-use change. In many cases, there is an urgency to take action even though the science behind these, and other pressing issues, is generally not fully understood (Tittensor *et al.*, 2014). Vol is a method for evaluating this uncertainty, yet its potential remains relatively unexplored, with only 30 papers so far using it in biodiversity conservation.

The pursuit of a Vol analysis requires a structured approach to decision analysis, which has rewards in its own right (Gregory *et al.*, 2012; Possingham, 2001). Applied biodiversity conservation is about decisions, and the field of decision analysis provides a rich set of tools for helping decision makers navigate the complexities in natural resource-management settings. The consistent use of these methods is emerging in a few conservation organisations around the world, supported by a rapidly expanding literature.

The specific benefit of a Vol analysis is to ascertain whether uncertainty surrounding the effects of management actions should be reduced or not. It is valuable to note that the answer to this question is context specific. There are examples from our review where using Vol showed that uncertainty should be reduced first (Costello *et al.*, 2010; Bouma *et al.*, 2011; Runting *et al.*, 2013), and other examples where it makes little difference to the overall outcomes whether uncertainty is reduced or not (Johnson *et al.*, 2014*a,b*; Maxwell *et al.*, 2015). There are two endeavours where the resolution of uncertainty takes a central role: research design and adaptive management. There is potential to extend the application of Vol to prioritising research topics through the use of EVPXI. This could be used by conservation NGOs or funding agencies to prioritise which projects to fund, or by policy makers to help set national or international conservation and research priorities. Vol can also be used to decide when adaptive management is warranted, as it shows whether resolution of uncertainty will improve the expected outcomes associated with management decisions and, if so, which elements of uncertainty contribute most to that improvement.

Attention to Vol methods in the conservation literature is recent. The first suggestion for using Vol in biodiversity conservation was made by Walters (1986), followed by the earliest paper included in our review (Sainsbury, 1991). Seven more papers on Vol were published in the next 20 years. A turning point appears to have occurred in 2011: 22 of the 30 papers we found were published since then. Because the introduction of Vol methods into the biodiversity conservation literature is fairly recent, the coverage of topics to which it has been applied is incomplete. Most of the papers we reviewed focus on EVPI, while the use of EVPXI has increased since 2011. Only six of

the 30 papers used EVSI, so its use remains poorly explored. Uncertainty was dealt with in a range of ways: either by using different model structures, by using the same model but with different parameters, or by eliciting uncertainties from experts. A wide range of predictive models has been used for Vol analysis, with many papers using population models, but there is the potential to explore its use with other modelling structures, such as machine-learning methods like Random Forests or Neural Networks.

Our review revealed that although many scientists are talking about Vol methods (hundreds of papers), their use in applied settings is more limited (30 papers) – why is the uptake of Vol so slow? Using Vol in a structured decision-making context is advocated by many in ecology and biodiversity conservation, for example, at the US Department of the Interior (Williams, Szaro & Shapiro, 2009), and recently by the IUCN in their guidelines for species conservation planning (IUCN – SSC Species Conservation Planning Sub-Committee, 2017). It does not appear, however, that these calls have yet resulted in the systematic use of Vol in conservation decision making, with the 30 cases presented herein encompassing the bulk of the applications. The methods are novel enough that applications warrant publication in the peer-reviewed literature. While there is not a mechanism to systematically search the grey literature, during our search we only came across two or three indications of unpublished Vol analyses by conservation decision makers. We have not undertaken an institutional analysis to identify the impediments to faster uptake of these methods, but we suspect that the methods are simply at an early stage of adoption. Widespread introduction to the concept of Vol in the conservation field only occurred in 2011 and conservation agencies are only now deliberately building capacity in decision analysis. The study of organisational change, especially adoption of decision-analysis methods, suggests that it typically takes 15–25 years to achieve widespread adoption of new practices (Spetzler, Winter & Meyer, 2016).

Standardised reporting of Vol analyses might help in the communication and adoption of the methods. The calls for using Vol (Williams *et al.*, 2009; IUCN, 2017) ensure there is a clear framework within which Vol can be applied. It also means that reporting standards for Vol analyses can be developed readily (Table 6). These

standards include a description of the full decision context, whether a real or hypothetical decision is considered, what the uncertainties are, which type of Vol was used, how the objectives were measured, and the time horizon. As Vol is implemented more widely, these reporting standards can increase the transparency of the Vol calculation. Most of the items we suggest in the reporting standards were listed in the papers we found and have been summarised in Table 6, but for some papers stating the reporting standards explicitly would aid in making the papers easier to understand. Rarely was the decision maker named however, and no paper stated whether the research would be used to inform management.

Table 6. Suggested reporting standards for the use of Value of Information (Vol) in biodiversity conservation. Adapted from PrOACT (Hammond et al., 2015). See also Section 1.3. EVPI, expected value of perfect information; EVPXI, expected value of partial perfect information; EVSI, expected value of sample information.

Reporting standard	Description
Problem	What is the problem or the decision to be made? Is it a real-world decision to be made?
Objectives	What objectives are considered to ensure delivery of the decision?
Alternatives	Which alternative actions are proposed to meet objectives?
Consequences	What are the consequences of different alternatives? How have they been estimated?
Trade-offs	What are the trade-offs of the alternative actions?
Uncertainty	What are the key uncertainties? Are they structural or parametric? Are they discrete or continuous? How have they been dealt with?
Type of Vol	EVPI, EVPXI or EVSI
Performance metric	The performance metric needs to be stated and fully explained. Ideally this would have a financial value too, to make the analysis more useful for managers, and to enable synthesising of different studies in the future.
Decision makers	State whether the research is undertaken on behalf of a decision maker and whether they are planning on implementing the findings.
Time horizon	State time horizon. If the Vol shows that more research is necessary, and therefore there is a need for adaptive management, a timeframe should be given when the information will be re-assessed. State how long intervention implementation will take.

Our review of the extant literature applying Vol methods suggests a number of fruitful areas for future research and development. First, Tables 4 and 5 reveal a number of gaps in application (e.g. no examples of using EVSI in ecosystem management settings); the continued expansion of Vol methods into all types of conservation decisions, with all system model types, could provide greater guidance for other decision makers. Second, there is a need for guidance about which uncertainties to include in a Vol analysis. That is, how should scientists and decision makers work together to identify the sources of uncertainty to examine, and what are the consequences of leaving out important sources? Third, there are not yet methods for evaluating whether the range of values or range of alternative models used to capture uncertainty adequately does so. Put another way, does uncertainty about the uncertainty matter? Can the usefulness of a Vol analysis be undermined if uncertainty is inadequately captured? This question is perhaps most applicable when uncertainty is expressed as a discrete set of alternative models or parameter sets. Fourth, perhaps to help in developing the guidance for the previous two items, is it possible to identify what types of uncertainty contribute most to EVPI? Is there an important difference between structural and parametric uncertainty? Are there other properties of sources of uncertainty that are associated with greater EVPI? Fifth, there is a need for new methods of expert judgment that are designed to elicit patterned matrices of values, with expression of uncertainty, without exhausting the cognitive resources of experts. For example, a decision setting that involves four possible actions and five alternative models of system response (representing uncertainty) requires elicitation of 20 values, but these values should not be viewed as independent – there are presumably relationships across rows and columns that are part of the expert knowledge. Sixth, and finally, there is a curious pattern in many of the examples we reviewed – EVPI can often be smaller than one might expect. Is this a common occurrence across conservation applications, and if so, why? Is it because the intuitive expectations of a high Vol are biased, or is it because the analysis of uncertainty is too narrow?

Decisions regarding biodiversity conservation, especially in the face of climate and land-use change, are often impeded by uncertainty. Risk-analysis methods can help

managers make decisions in the face of uncertainty, and Vol methods can help them decide whether to gather more information before committing to action. The increased use of Vol since 2011 is a positive sign, and its wider implementation will be beneficial for making robust decisions in an uncertain future. To support expanded implementation, there are a number of open research questions regarding how best to conduct Vol analyses.

2.6 Conclusions

- (1) Formal methods of decision analysis provide tools for making rational conservation decisions in the face of uncertainty, whether those decisions concern management of imperilled species, control of invasive species, establishment and management of protected areas, setting of harvest quotas, or any other of the classes of decisions faced by natural resource-management agencies.
- (2) Vol methods allow decision makers to understand the value of resolving uncertainty, and thus provide a way: to evaluate whether more information is needed before taking action; to set a research agenda by ranking the influence of different sources of uncertainty; and to motivate and guide the development of adaptive management.
- (3) The increasing use of Vol in biodiversity conservation since 2011 indicates that there are efforts to tie the analysis of uncertainty more explicitly to decision-making contexts. The variety of Vol methods have been explored fairly thoroughly in conservation settings, but there are few examples of the expected value of sample information (EVSI).
- (4) While Vol has been extensively promoted as a tool to inform management, it is much less common that it has been implemented for managing conservation issues. For Vol to make a difference, it needs to be used by managers, policy makers and funders, not just scientists. The use of decision analysis and formal Vol could do much to reduce the incoherence of information flow from scientists to practitioners. We postulate that this is a critical missing piece required to bridge the knowing–doing gap.
- (5) Common reporting standards to document the use of Vol could be a valuable way to share insights and motivate further application of these methods.

Chapter 3 Predicting extinction risk and using Value of Information to prioritise conservation assessments in the Caatinga Domain in Brazil

Abstract

To accelerate measurable progress on species conservation, we need to have knowledge regarding species' conservation status. While the number of species assessed on the Red List is increasing, the vast majority of species have not been assessed. We used Bayesian Network algorithms to predict extinction risk of plants in the Caatinga Phytogeographical Domain, a species-rich area of Brazil, identified factors determining threat status, and calculated the Value of Information of the predictions in order to prioritise future actions. We used information from a catalogue of vascular plants of the Caatinga, IUCN Red List data, and Brazilian National Red List data. We built Bayesian Networks to predict extinction risk using three different algorithms, and predicted both Red List category and threat status (combining Red List categories into 'threatened' and 'not threatened'). The best-performing algorithm was Naïve Bayes which predicted the threat status of 81.8% of non-threatened and 63.0% of threatened species correctly. The most important predictors of threat status were the genus, the number of occurrence records, and the growth form of a species, and in which habitats they occur. We predicted threat status and IUCN Red List category for 1,002 species not assessed on Red Lists, of which 81 species were predicted to be threatened. Value of Information analysis indicated that Begoniaceae was the family with highest extinction risk, but there was substantial uncertainty around this. We can predict extinction risk using Bayesian Networks in data-poor situations with high accuracy, adding to the computational methods used so far. Value of Information could be used in the future to identify species groups that are at high risk, and decide whether to assess more species or to undertake conservation action.

3.1 Introduction

3.1.1 *Need for quick assessments to meet global targets*

Humans are impacting the world's biodiversity, mainly by changing and destroying natural habitat through agriculture, logging and development (Maxwell *et al.*, 2016). These impacts are likely to be amplified in the future because of the increasing human population, consumption patterns, land use changes from natural to managed areas (Tilman *et al.*, 2017) and changes in the world's climate (Pacifi *et al.*, 2015). Because of these actions, species are going extinct at rates comparable to those of the five previous mass extinction events (Ceballos *et al.*, 2015). Several global targets aim to halt species extinctions, for example the Convention on Biological Diversity's Aichi Target 12, or Target 15.5 of the Sustainable Development Goals, Life on Land (Convention on Biological Diversity, 2016), to which most countries have committed. If we are to take active measures to prevent species from going extinct, we first need to know which species are at risk of extinction, where and why.

The IUCN Red List of threatened species is the most comprehensive assessment of extinction risk globally. Some well-studied groups such as birds have been comprehensively assessed for the IUCN Red List (IUCN, 2017). In the case of land plants (Embryophyta) however, an estimated 403,911 species had been described by 2016 (Nic Lughadha *et al.*, 2016) but only 25,323 or 6.3% have been assessed on the global IUCN Red List (IUCN, 2018b). A considerable number of plant species are discovered each year, and between 2007 and 2015, a mean of 2,137 new plants were described annually (Nic Lughadha *et al.*, 2016). Around 1,500 plants assessments are added to the IUCN Red List each year (Brummitt *et al.*, 2015). In other words, current rates of assessment are not keeping up with descriptions of new species. Development of rapid, replicable and reliable methods for assessing species level of threat on the IUCN Red List are therefore imperative.

3.1.2 *Predicting extinction risk*

For species lacking IUCN Red List assessments, it is possible to model which species are threatened. Examples include studies on mammals (Davidson *et al.*, 2012; Di Marco *et al.*, 2014; Bland *et al.*, 2015; Jetz and Freckleton, 2015), birds (Machado *et al.*, 2013),

amphibians (Howard and Bickford, 2014), fish (Dulvy *et al.*, 2014; Comeros-Raynal *et al.*, 2016), and also plants (Leão *et al.*, 2014; Darrah *et al.*, 2017). Most of these studies model species extinction risk of species from particular taxonomic groups, for example species in a single animal order, except for the two papers on plants which predicted the extinction risk of species from two different orders (Darrah *et al.*, 2017) and for Angiosperms as a whole in the Atlantic Forest (Leão *et al.*, 2014). Predictor variables in these studies included, amongst others, information about phylogeny, taxonomy, range size, habitat, life history, and threats.

Many of the studies modelling extinction risk do so using Random Forest models (Davidson *et al.*, 2012; Di Marco *et al.*, 2014; Howard and Bickford, 2014; Comeros-Raynal *et al.*, 2016; Darrah *et al.*, 2017) or other Machine Learning tools such as Neural Networks, Support Vector Machines or the K-Nearest Neighbour algorithm (Bland *et al.*, 2015). Often the models used to predict extinction risk struggle to predict which of the species are threatened (for example, Machado *et al.* (2013) or Comeros-Raynal *et al.* (2016)), as there is usually a much smaller number of threatened species than non-threatened species. This issue, known as the class imbalance problem (Johnson *et al.*, 2012), is not unique to biodiversity conservation but widely discussed in the machine learning literature (Guo *et al.*, 2008; Galar *et al.*, 2012; Nanni *et al.*, 2015).

Bayesian networks are graphical models in which variables (called nodes) are linked through conditional probabilities. The network structure can be built by hand, using expert knowledge, or through Machine Learning using different algorithms. Machine Learning implementations of Bayesian networks have shown promise for problems such as classifying deforested areas (Mayfield *et al.*, 2017) or different types of vegetation (Dlamini, 2011b), and can be useful for classification of groups with small sample sizes (Mayfield *et al.*, 2017). Until now, machine learnt Bayesian Networks have not been used for predicting extinction risk (but see Newton 2010), though their potential is promising. Updating probabilities of node states through scenario analysis can reveal changes in the probability distribution of other nodes, providing novel insights into the impact of system perturbation.

3.1.3 Value of Information

Value of Information is a method rooted in decision science and is a way of assessing the consequences of acquiring new information for decision-making, as opposed to making decisions with current information. The premise is that new information is only worth collecting if it is likely to change the course of management actions, so Value of Information calculations are based on modelling what the new information might be, and how it would impact on decision-making. For example, the impact of different management actions on a declining species may be modelled when there are varying theories around the causes of decline, to assess whether investigating the cause of decline would be informative for management (Runge *et al.*, 2011). Value of Information has been applied in biodiversity conservation at species level for managing both endangered and invasive species, at ecosystem level, and for fisheries, but it has not been applied in the context of prioritising IUCN Red List assessments.

3.1.4 The Caatinga

The Caatinga is a semi-arid phytogeographical domain in South America, located in north-eastern Brazil (Figure 4). Although located in the tropics, it has low rainfall with erratic patterns of precipitation and dry seasons that can last from six to eleven months (Nimer, 1972). In the past, conservation efforts of the Brazilian government were focussed on other natural areas of Brazil such as rainforests, leaving the semiarid Caatinga understudied and unjustly declared to be an area of low importance for biodiversity conservation (Banda *et al.*, 2016). In recent years, efforts have been made to study the Caatinga vegetation and its threats more closely (Leal *et al.*, 2005), revealing a considerable number of species (Moro *et al.*, 2014; Zappi *et al.*, 2015) and endemic genera (de Queiroz *et al.*, 2017).

A catalogue of plants summarises the current state of knowledge about plant communities in the Caatinga Domain (Moro *et al.*, 2014), showing that more than 1,700 plant species have been recorded and well over 2,500 are expected to occur there. It also reveals some biases in data collection, with most vegetation surveys focussing on woody species, excluding the species-rich herb assemblages also found there. By far the most common habitat type, the crystalline Caatinga (Figure 4), has seen a relatively

small number of surveys and it is likely that many species have not been recorded yet. The second most common habitat type is sedimentary Caatinga. Other habitat types include inselbergs, riverine forests, arboreal Caatinga and the Chapada Diamantina mountains, a very complex biogeographical area within the Caatinga Domain (Moro *et al.*, 2016).

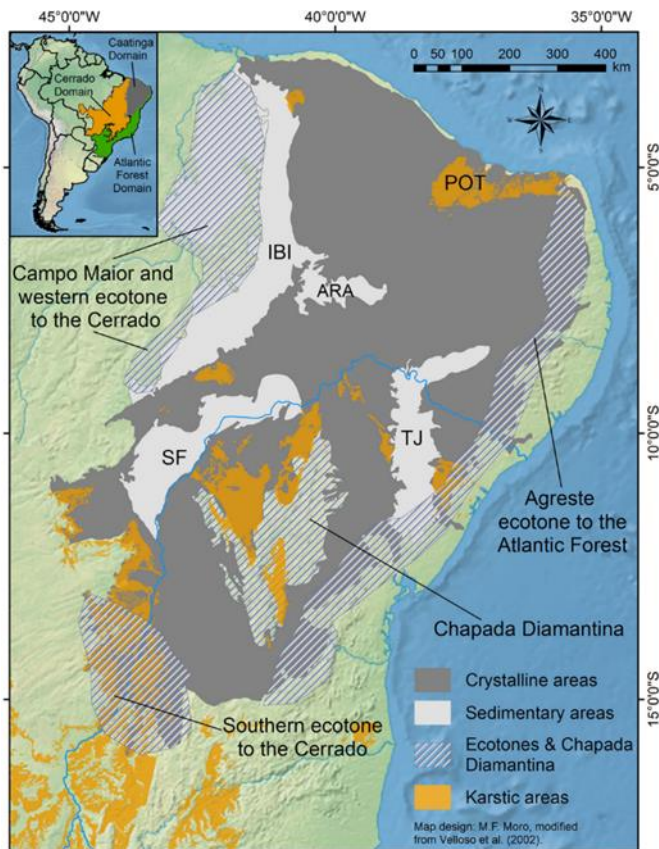


Figure 4. The location of the Caatinga ecoregion in South America, and the different habitat types within. Map reproduced from Moro *et al.* (2016). Sedimentary areas: TJ - Tucano-Jatobá sedimentary Basin, IBI - Ibiapaba sedimentary basin, ARA - Araripe sedimentary basin, SF - São Francisco Continental Dunes, POT - Potiguar sedimentary basin. Reprinted by permission from Springer Customer Service Centre GmbH, Springer Nature, *The Botanical Review* ('A Phytogeographical Metaanalysis of the Semiarid Caatinga Domain in Brazil' by M.F. Moro, E.N. Lughadha, F.S. de Araújo and F.R Martins, Copyright 2016).

Our choice of Caatinga as the model system for this study is based on data availability, timeliness and potential impact. Caatinga is the only phytogeographical domain with its entire extent confined within Brazilian national boundaries. Because of this, assessments of Caatinga endemic plants (Brazil Flora Group 2015; de Queiroz *et al.* 2017) for the Brazilian Red List of threatened species (Martinelli & Moraes, 2013, not yet incorporated in the global IUCN Red List), are equivalent to global assessments,

doubling the data available for our analysis. Furthermore, Caatinga is a highly threatened domain in Brazil, with only 53% of native vegetation cover remaining, much of which is degraded by selective logging, invasive species and road effects (Leal et al. 2005; Castelletti et al. 2003), such that 63% of Caatinga is now composed of anthropogenic ecosystems (Cardoso da Silva & Barbosa, 2017). Although threatened, Caatinga has received low legal protection. Only 1.2% is encompassed in fully protected nature reserves with a further 6.3% in “sustainable use nature reserves” that afford a lower level of protection (Brazil, 2015). Economic and political factors have impeded realisation of the Brazilian federal government’s aspiration to extend protected area coverage of Caatinga to 17% (Brazil, 2015) and delayed initiation of an approved and funded programme to complete extinction risk assessments of more Caatinga plant species (Gustavo Martinelli, pers. comm.). Such assessments represent important evidence for recognition of Important Plant Areas and/or Key Biodiversity Areas (Darbyshire et al. 2017), helping ensure that future extensions to protected area coverage contribute to the goal of achieving ecological representativeness (Brazil, 2015). Thus, the Caatinga Domain provides an interesting and timely model to evaluate modelled estimates of extinction risk, insights from Value of Information and their potential to inform future resource allocation in a species-rich but data-poor system.

3.1.5 Aim and objectives

Our aim was to predict the extinction risk of plant species that have not been assessed on the Red List and evaluate whether further assessments are likely to be important in guiding conservation action. As a study model we focussed on the Caatinga Phytogeographical Domain in north-eastern Brazil. We wanted to predict both threat status and IUCN Red List category, and to identify those variables that were most important for classifying a plant species as threatened or non-threatened. We also calculated how well each model correctly predicted the status of species already assessed on the Red List, with a view to predicting the conservation status of species not currently assessed for the Red List. Finally, we calculated the Value of Information for each plant family included, to identify families with species at highest risk of extinction and to quantify uncertainty surrounding their extinction risk.

3.2 Methods

3.2.1 Data preparation

We used a subset of the catalogue of plants that occur in the Caatinga ecoregion (Moro *et al.*, 2014) which lists 1,586 species (Moro *et al.*, 2016). This subset excluded exotic species, surveys from degraded sites and studies with fewer than 20 species. The Caatinga catalogue listed all species recorded in vegetation surveys in the Caatinga, their growth form, their taxonomy, at which sites they were observed and the habitat of each site. The habitat type Agreste is a subgroup of the crystalline Caatinga (Moro *et al.*, 2016) so these were merged into one habitat type. Campo Maior is a sedimentary habitat type and a subgroup of the sedimentary Caatinga (Moro *et al.*, 2016) so they were also merged. We excluded 92 species only recorded in transitional habitats between sedimentary and crystalline as they may not be typical of either habitat (Moro *et al.*, 2016). We calculated the number of study sites from which each of the remaining 1494 species in our dataset was reported.

We sourced Red List assessments from the IUCN Red List (IUCN, 2018b), by downloading all assessments of plants in Brazil, and from the National Red List of threatened species for Brazil (Martinelli and Moraes, 2013; National Red List, 2017). Since Brazilian Red Listing activities in recent years have focused on endemic species and applied IUCN Red List Categories and Criteria: version 3.1 (IUCN, 2012b), these assessments are comparable to global assessments. Both sources used the following Red List categories: Extinct (EX), Critically Endangered (CR), Endangered (EN), Vulnerable (VU), Near Threatened (NT), Least Concern (LC) and Data Deficient (DD). Species that have not yet been assessed are classed as Not Evaluated (NE). Apart from the Red List category of each species, both datasets contained information on species' taxonomy, date of assessment, and version of the criteria used. The IUCN Red List also specified the particular criteria used for assessment for threatened species.

The spelling of species names in the Caatinga Database (Moro *et al.*, 2016), in the IUCN Red List dataset and in the Brazilian National Red List dataset were all checked using the "taxize" package in R to ensure consistency between lists (Chamberlain and Szöcs, 2013). Taxize uses the Global Names Resolver (Global Names Resolver, 2017) and

finds the best match for each species name. We then merged the IUCN and Brazilian National Red List datasets. Red List data were then merged with our Caatinga dataset according to the species names.

Of the 1,494 species included in our analysis, 93 or 5.9% had been assessed for the IUCN Red List and another 153 had been assessed for the Brazilian National Red List. Just 23 species had assessments published in both sources. Of those 23 species on both lists, 11 had the same Red List category and six were in adjacent Red List categories on the national and IUCN Red Lists (see appendix S1). All species that appeared on both lists, but with different Red List categories, were in a higher threat category on the IUCN Red List, compared to the national Red List. To avoid underestimation of extinction risk, for those species with differing national and IUCN Red List assessments we used IUCN Red List assessments as the reference. In addition to the 93 IUCN Red List assessments we therefore used 130 assessments from the Brazilian National Red List (Martinelli and Moraes, 2013; National Red List, 2017).

We downloaded occurrence data for all species in the Caatinga Database using the BIEN package in R. The BIEN 3+ dataset contains occurrence records from a wide range of herbaria globally. Many of these are harvested from databases such as GBIF (Botanical Information and Ecology Network, 2017; Maitner *et al.*, 2017). We removed duplicate records from the BIEN dataset by first removing records with the same record number and species name, and then removing records of the same species that were recorded at the same latitude, longitude and on the same date.

3.2.2 Model building

We used Bayesian Network models for analysis. Bayesian Networks are models based on Bayes theorem. Variables in discrete (or categorical) form are required to build Bayesian Networks and assess their performance in GeNIe Modeler (Bayes Fusion LLC, 2017). Any continuous variables are split into discrete categories or states, such as low and high. The number of categories that a continuous variable is assigned can affect model performance, so we used a range of discrete groups to find which performed best and used this discretisation in the final model. Number of sites with occurrence of each species (from the Caatinga catalogue) and number of records of each species

(from BIEN 3+) were the only continuous variables and were split into different groups by splitting the data into either two, four, six, eight, 10, 12 or 14 equal bins. The number of bins was increased until model performance dropped. We also built a custom discretisation that kept site numbers in four bins, but split smaller numbers of occurrence records into more groups (see appendix S2), following Rivers *et al.* (2011).

The different states of a variable are assigned a probability in the Bayesian Network, and all probabilities of one variable combined sum to one. A variable that has ingoing arrows is called a child node, and has different probabilities for the different states of the parent node. For example, if the state of the parent node is low, the child node may have a 60% probability to be low and 40% to be high. If the state of the parent node is high, the child node may have a 20% probability to be low and 80% to be high.

The structure of the Bayesian Networks can be built using expert knowledge (as in Newton, 2010), or with data using Machine Learning algorithms. Our networks were learnt from the data using three different Machine Learning algorithms: a Naïve Bayes classifier, a tree-augmented Naïve Bayes classifier, and a hill-climbing algorithm, all in the bnlearn package in R (Scutari, 2010). In bnlearn, the model structure is built first, then the conditional probabilities are calculated separately. Naïve Bayes has a fixed model structure where the variable to be predicted is at its centre, and all other variables have ingoing arrows from the variable to be predicted (Nagarajan *et al.*, 2013). In our case the variable to be predicted was threat status or Red List category (Figure 5). Naïve Bayes assumes independence of predictor variables, and although this assumption is rarely met, it often outperforms other algorithms (Zhang, 2004). There are various theories as to why, including the distribution of the node states (Zhang, 2004), or that independence does not have to be assumed in many instances (Domingos and Pazzani, 1997).

To test whether incorporating hierarchical relationships between some variables would improve model performance, we also built models using a tree-augmented Naïve Bayes classifier, which can take into account relationships between variables other than the variable to be predicted.

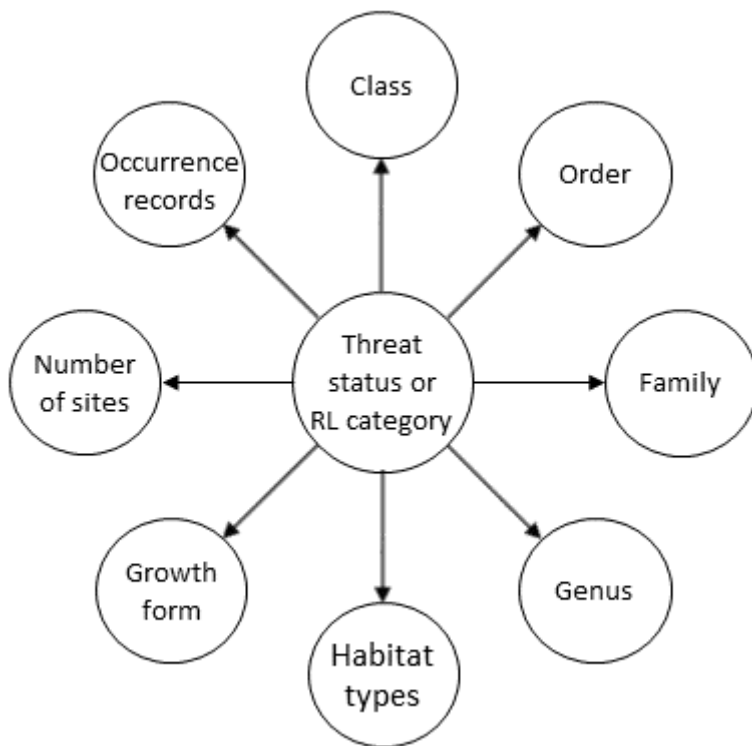


Figure 5. Naïve Bayes model structure for the Caatinga ecoregion.

Hill-climbing, our third approach, is a score-based algorithm. The network is built by adding one arrow at a time at random, then a score penalising unnecessary complexity such as Akaike’s Information Criterion (AIC) or Bayesian Information Criterion (BIC) is calculated for the network. Here we used BIC. A second arrow is added, and BIC is calculated again. If the score improves, the arrow stays; if not, it is removed. In this way all possible options are explored until the final network cannot be improved further (Nagarajan *et al.*, 2013). For the hill-climbing algorithm, predictor variables do not need to be independent as they can be incorporated into the model structure (Mayfield *et al.*, 2017).

Reducing the number of groups that are to be predicted can improve model performance, especially when some groups contain very few observations (Guo *et al.*, 2008). Therefore, as well as building models predicting five Red List categories, we also built models predicting just two status groups: threatened and not threatened. Following earlier authors (Rivers *et al.*, 2011; Bland *et al.*, 2015), species categorised as Critically Endangered, Endangered or Vulnerable were treated collectively as threatened, while those categorised as Near Threatened or Least Concern were treated collectively as non-threatened species.

3.2.3 Model and variable selection

The three algorithms, with eight discretisations each, and predicting either Red List category or threat status resulted in 48 models in total. To identify the best-performing model we used 10-fold cross-validation in GeNIe Modeler (Bayes Fusion LLC, 2017). This method splits data into 10 groups of equal numbers of observations (Marcot, 2012). Nine of the groups are used to recalculate the conditional probabilities whilst maintaining the model structure, to predict the state of the outcome variable for the tenth group. This process is repeated for each group, so that every Red List category or threat status of assessed species in the Caatinga is predicted once. The variable to be predicted was either Red List category or threat status. The overall percentage of correct predictions, called accuracy, was calculated and plotted (Allouche *et al.*, 2006). We also calculated the sensitivity, which is the percentage of correctly predicted threatened species of all threatened species, and the specificity, which is the percentage of correctly predicted non-threatened species of all non-threatened species (Allouche *et al.*, 2006). The accuracy can be driven by the specificity when most species are non-threatened, which was the case here. We also calculated the True Skill Statistic (Allouche *et al.*, 2006), which is the sensitivity plus the specificity less 1. This value ranges from 1 to -1 and balances the numbers of threatened and non-threatened species, so it was used for model selection. Where the True Skill Statistic is above 0, the model performs better than if all species were predicted to be Least Concern, or non-threatened.

We ran scenario analysis, also called influence analysis (Marcot, 2012), in GeNIe Modeler (Bayes Fusion LLC, 2017) by changing the state of threat status to 100% non-threatened, then to 100% threatened, and plotted those variables that changed by more than 10%.

The best-performing models predicting Red List category and the best model predicting threat status were used to predict extinction risk of plants not yet assessed. As these models contained the taxonomic ranks genus, family and order, predictions could only be made for species in genera from which at least one species had already been assessed. In this way 413 species from 95 genera were evaluated (see appendix S3). We then rebuilt the models excluding genus and predicted the threat status and

Red List category for species from genera lacking any assessments, but belonging to a family from which at least one species had been assessed. In this way we predicted the status for an additional 589 species in 47 families. As model performance decreased substantially once genus and family were removed, the threat status and Red List category for other species were not predicted.

3.2.4 Value of Information calculation

To find the families whose species are most at risk of extinction in Caatinga, and quantify uncertainty around which family was most at risk of extinction, the risk of extinction was calculated for each family in the following way. The probability of extinction, or severity, varies for each IUCN Red List category, as defined by IUCN (IUCN, 2012b). Extinct has a value of 1, Critically Endangered has a value of 0.5, Endangered has a value of 0.2 and Vulnerable has a value of 0.1. Near Threatened and Least Concern have a value of 0, because there is no immediate risk of extinction. The best-performing model predicting category not only predicts which category a species is most likely to be in, but also provides a probability of the species being assigned to each category. The probability of the predicted category for each species was multiplied by the probability of extinction (or severity). The concept of risk is defined as the severity multiplied by the probability (Chen *et al.*, 2013), so we will call this value the risk value. For example, if a species was predicted to be Critically Endangered, and the model gave this prediction a probability of 0.8, then the risk value was $0.5 \times 0.8 = 0.4$. Because both values (the probability of extinction and the probability of the predicted category) can only be between 0 and 1, the risk value could also only be between 0 and 1. The higher the risk value, the more likely it is that a species will go extinct. If a species was Near Threatened or Least Concern however, it would always have Risk Value 0.

The risk value was calculated for all species not previously assessed on Red Lists. Risk values were then summed for each plant family in the Caatinga under each Red List category and divided by the number of species in that family, thus giving three mean values per family, for Critically Endangered, Endangered and Vulnerable. These mean values were summed for each family to give an overall expected value for each family. The family with the highest overall expected value was the one with the greatest risk

that species are going extinct. In other words, in the absence of more conservation-relevant information about Caatinga plant species, e.g. socioeconomic or cultural value of the species, this family is one on which conservation effort should be focussed. The value for this family is the expected value of imperfect information. The highest values for each Red List category were also summed, from different families, to represent perfect information. The difference between this value of perfect information, and the value of the family with the highest value, was the Value of Information.

3.3 Results

3.3.1 Data summaries

Species from the Caatinga Database were recorded in 74 different sites (Moro *et al.*, 2016). For some species there were no occurrence records from the BIEN 3+ database, whereas the maximum number of occurrence records was 4,847 for one species. Most species were recorded from the Sedimentary Caatinga with 784 species, followed by Inselbergs (642) and Crystalline Caatinga (491), with some species being recorded from more than one habitat type. Woody species were more numerous (779) than non-woody species (679), reflecting documented bias in botanical surveys in the region towards woody species (Moro *et al.*, 2014).

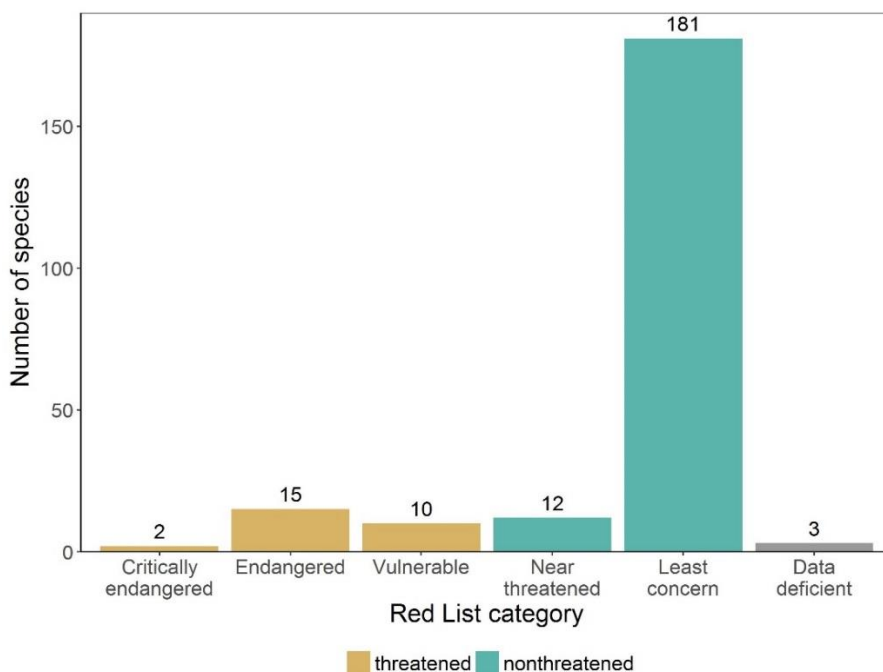


Figure 6. Count of species from the Caatinga in each Red List category that have been assessed on the IUCN Red List and/or the Brazilian National Red List.

Of the 223 species recorded in our Caatinga database which had been previously assessed on the IUCN Red List or the Brazilian National Red List, 193 (86.6%) were categorised as Least Concern or Near Threatened, and three (1.4%) were deemed as Data Deficient (Figure 6). Just 27 (12.1%) were categorised as Vulnerable, Endangered or Critically Endangered.

3.3.2 Modelling extinction risk

We built 48 different models and selected for further use the ones that best predicted Red List category or threat status of previously assessed species, judging relative performance by the True Skill Statistic, which is measured between 1 (best model performance) and -1 (worst model performance), see appendix S4. Threat status was better predicted than Red List category. Threat status of assessed species was best predicted by a model using discretisation into 12 groups and Naïve Bayes to build the model structure, with a True Skill Statistic of 0.45 (Figure 7). The Red List category of assessed species was best predicted by a model using discretisation into four groups and Tree-Augmented Naïve Bayes to build the model structure, with a True Skill Statistic of 0.15. Overall, specificity, or the percentage of correctly classified non-threatened species, was greater than sensitivity (the percentage of correctly classified threatened species). There were differences in performance between the algorithms. Naïve Bayes generally showed greater sensitivity, while the hill-climbing algorithm showed greater specificity. Differences between discretisations were greatest for sensitivity.

To find variables which contributed most to a species' threat status, we changed the threat status in the best model, using 12 groups and a Naïve Bayes classifier, to 100% non-threatened first, then to 100% threatened. Number of occurrence records, growth form and habitat type showed greatest differences. For species previously assessed on Red Lists that were non-threatened, the median number of occurrence records was 167, compared with 16 for threatened species (Figure 8). Least Concern species had a median of 177 occurrence records, and Critically Endangered species had a median of 30.5 occurrences. 187 assessed species had 15 or more occurrence records.

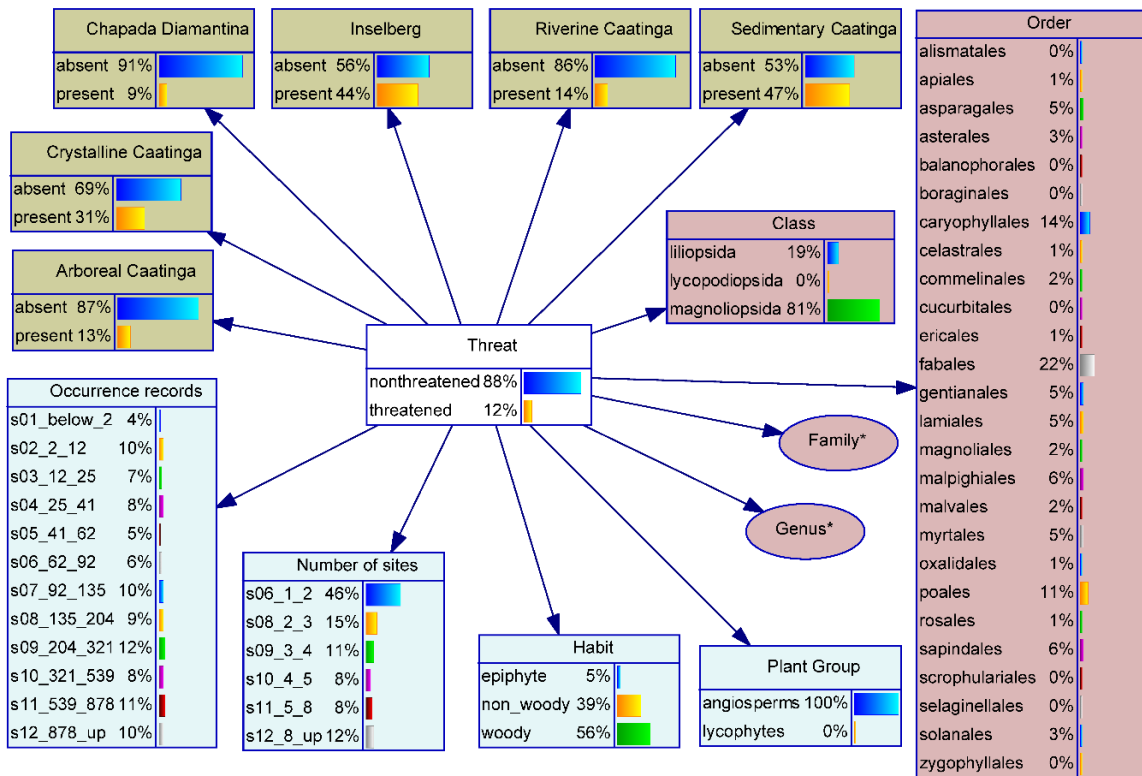


Figure 7. The best performing Bayesian Network predicting threat status with all variables and the probabilities of each state of each variable, built using 12 groups and with a Naïve Bayes classifier. Family and genus not shown due to the high number of states, but included in the model when processed on our computer.

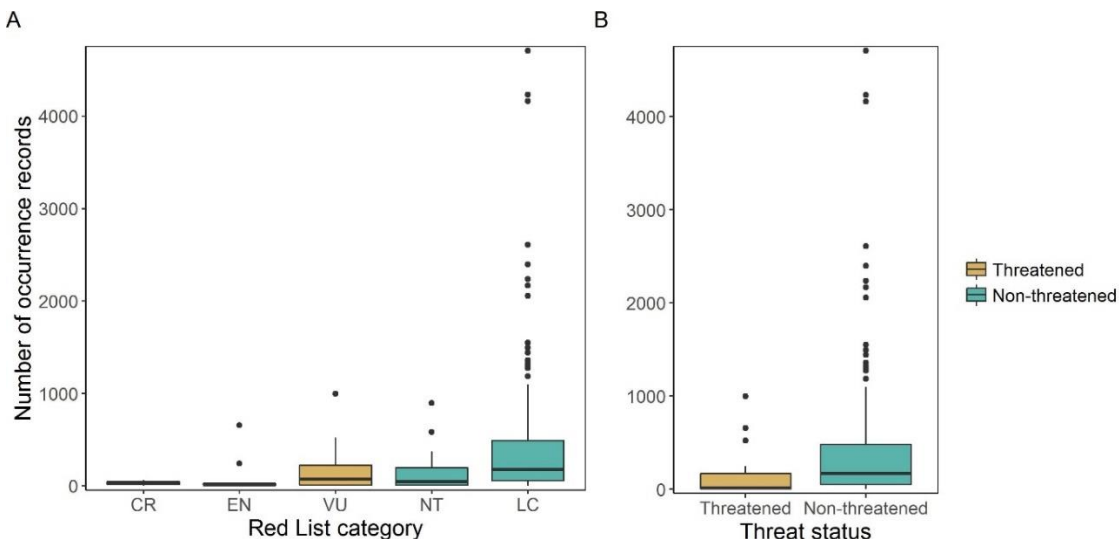


Figure 8. Number of occurrence records in BIEN database for species assessed on Red Lists and recorded in the Caatinga Database. We show the number of records of assessed species for different IUCN Red List categories (A) or threat status (B). Colour denotes threat status. IUCN Red List categories: CR – Critically Endangered; EN – Endangered, VU – Vulnerable; NT – Near Threatened; LC – Least Concern.

Among assessed species, trees were in the majority for both non-threatened and threatened species (Figure 9 A and B). Strikingly, there were no Data Deficient trees,

suggesting that trees are better studied than herbs in the Caatinga. Habitat type also differed with threat status: there were relatively more threatened species from the arboreal Caatinga, and fewer from the sedimentary Caatinga (Figure 9 C).

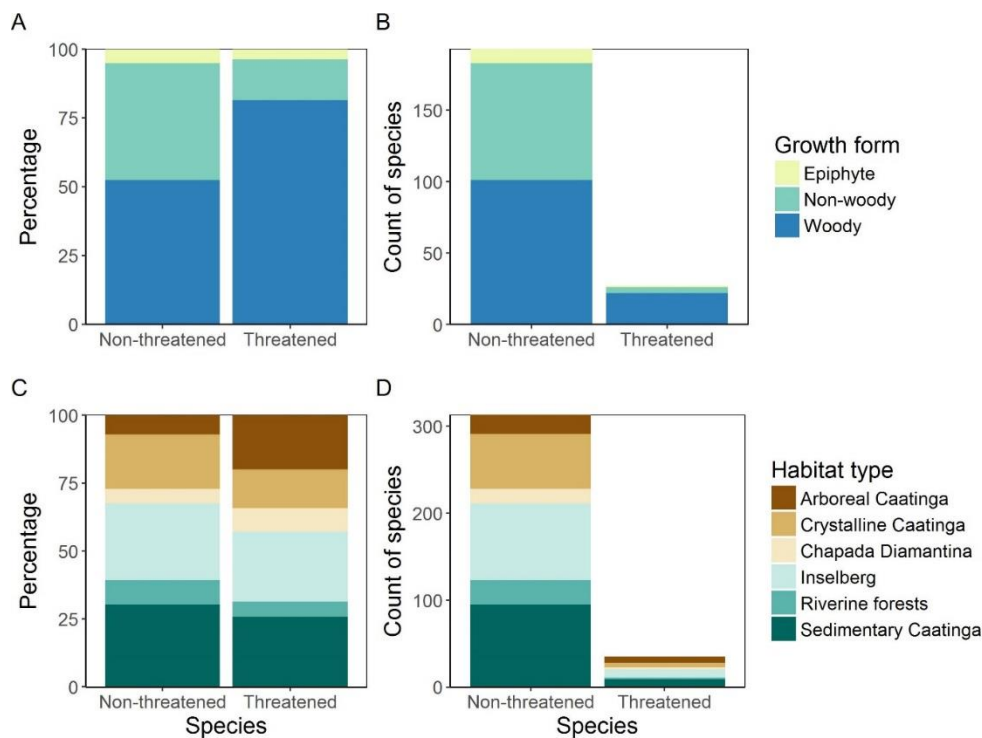


Figure 9. Breakdown of completely assessed species by threat status combined with: growth form (A and B) and habitat type (C and D). Data are presented both as percentages (A and C) and as counts (B and D). A and B show each assessed species once, for a total of 27 threatened and 193 non-threatened species. C and D also show all assessed species, but each species may occur in more than one habitat. Thus species \times habitat combinations total 35 for threatened species and 313 for non-threatened species.

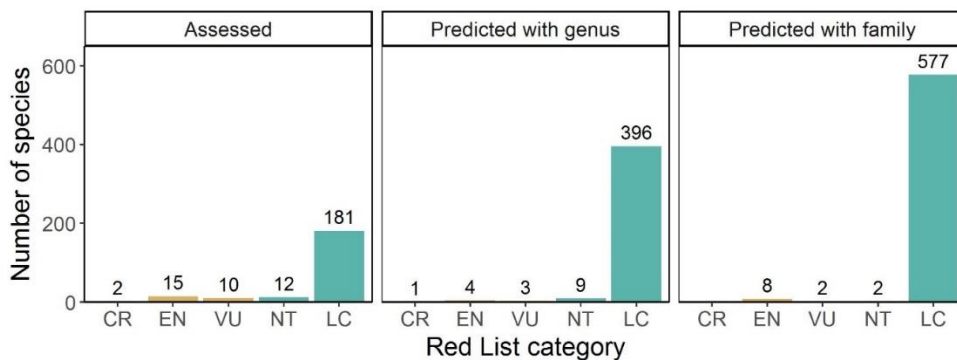
3.3.3 Predicting threat status of unassessed species

The models were then used to predict Red List category or threat status. Another two models were built that excluded genus as a predictor, for use with species from a genus lacking Red List assessments, but in whose families some species had been assessed. For threat status, the True Skill Statistic dropped from 0.45 to 0.39 (accuracy: 84%, specificity: 88%, sensitivity: 52%). For Red List category, the True Skill Statistic dropped from 0.15 to 0.11 (accuracy: 81%, specificity: 89%, sensitivity: 22%).

Of the 1,002 unassessed species for which predictions could be made, extinction risk category predictions assigned 18 species to one of the threatened categories (Critically Endangered, Endangered or Vulnerable), while 11 were predicted to be Near

Threatened, and 973 were predicted to be Least Concern. In contrast, the model simply predicting whether species were threatened or non-threatened predicted 78 species to be threatened and 924 to be non-threatened. Of the assessed species, 12.3% are threatened. In our predictions for unassessed species where Red List category was predicted, 1.8% were predicted to be threatened, and where threat status was predicted, it was 7.8%. In total, 81 species were predicted to be Critically Endangered, Endangered, Vulnerable, or threatened. Just one species was predicted to be Critically Endangered (*Begonia lealii*). Of the 78 species that were predicted to be threatened, 13 were also predicted to be either Critically Endangered, Endangered or Vulnerable (see appendix S5). Of the 1,002 species where threat status and Red List category were predicted, those predictions matched for 93% of species – species that were predicted to be both threatened and Critically Endangered, Endangered or Vulnerable, and species that were predicted to be both non-threatened and Near Threatened or Least Concern.

A



B

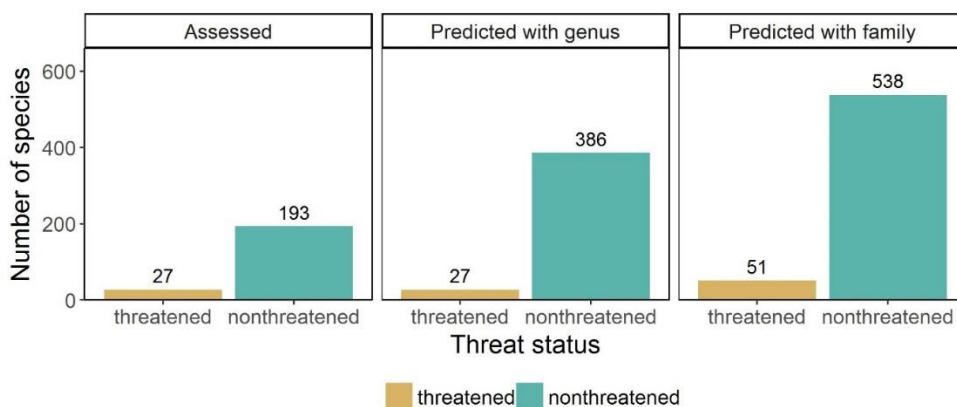


Figure 10. Red List category (a) and threat status (B) of species already assessed on the Red List and of predicted species. Predictions from models which either included the taxonomic ranks of genus, family and order, or only family and order.

For each species where no Red List assessments were available (NE Category of IUCN), the model gave probabilities of that species being in each Red List category, and for each threat status. These probabilities were plotted, both for Red List categories and for threat status (Figure 11). Most unassessed species that were predicted to be Least Concern or non-threatened had high probabilities to be in that category/status. In total, two species had probabilities below 50% for their predicted Red List category, which were both predicted to be Least Concern. The categories between Critically Endangered and Least Concern had lower median probabilities. Probabilities below 75% were attributed to the predicted threat status of 67 species, of which 26 were predicted to be threatened, and 41 were predicted to be non-threatened. The median probability for threatened species was lower than for non-threatened species. Some of the predictions did not match, so that species predicted to be threatened were also predicted to be near threatened or Least Concern, or vice versa. For these species where predictions did not match, the probabilities were lower with 85%, compared to species where the predictions did match with 98%.

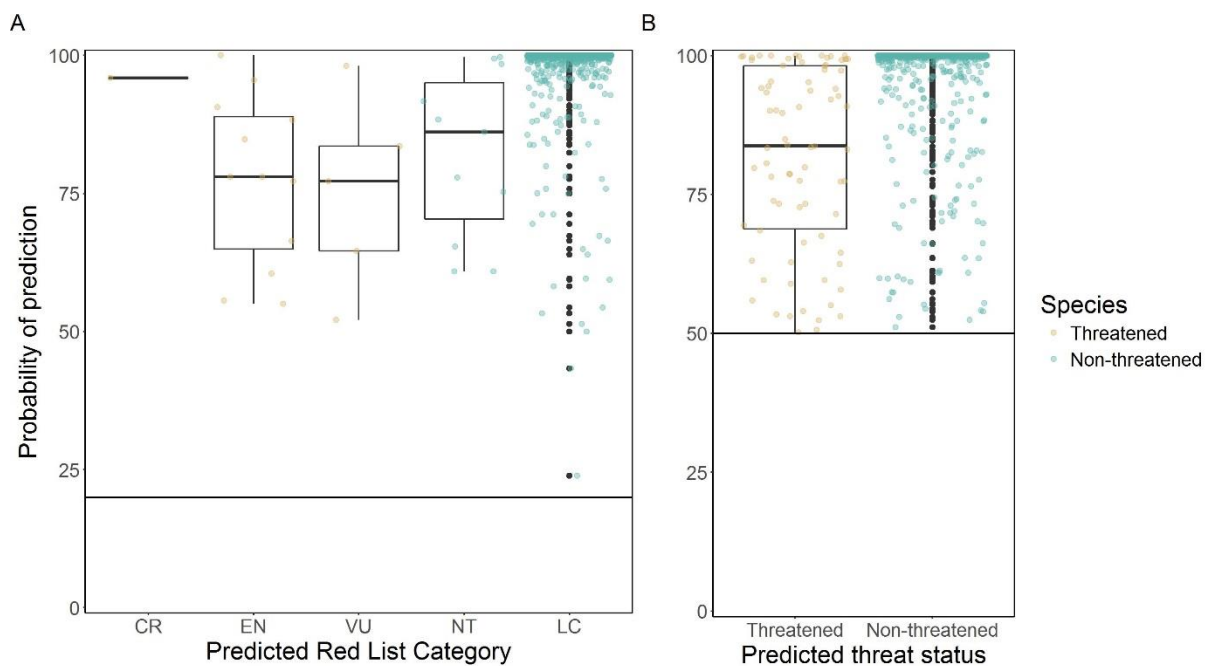


Figure 11. Probability of 1,002 unassessed species to be in the predicted Red List categories (A) and threat status (B). Each species is placed at random as a dot over the boxplot. The probability had to be at least 20% for the Red List category (A), and 50% for the threat status (B), shown by the horizontal lines. Colour denotes threat status. IUCN Red List categories: CR – Critically Endangered; EN – Endangered, VU – Vulnerable; NT – Near Threatened; LC – Least Concern.

Since the models were based on a relatively small set of species, we checked the percentage of assessed and predicted species within each genus (see appendix S6). For genera in which at least one species had been assessed, the mean number of assessed species per genus was 1.6, while the mean number of unassessed species predicted in each genus was 4.5 – or in other words, two species predicted the threat status of five species on average. The 27 species predicted as threatened by our best performing model were concentrated in 11 genera, all of which contained at least one species already assessed as threatened. In seven genera all assessed species were threatened, and of those seven genera, two had all species predicted to be threatened, namely *Apuleia* and *Pilocarpus*.

3.3.4 Value of Information

We calculated the Value of Information for each family with species for which Red List categories were predicted. The family with the highest expected value was Begoniaceae with a value of 0.179 (Table 7). Begoniaceae also had the highest value for Critically Endangered species with 0.179. For Endangered species, Meliaceae had the highest value with 0.120. For Vulnerable species, Moraceae had the highest value with 0.108. The Vol was the sum of the highest values for the each Red List categories, which was 0.341 – an increase of 90.5% compared to Begoniaceae. While Vol was expressed as a unitless value here, the possible increase in performance if uncertainty was resolved was large. As uncertainty was large, further assessments may show that in fact families other than Begoniaceae contain more threatened species, and should be the focus of future conservation action. This result suggests that further extinction risk assessments are highly likely to change the course of conservation action in the Caatinga domain.

Table 7. Risk values for different Red List categories for different plant families in the Caatinga. Bold red values are the highest values for a particular Red List category. The expected value is the sum of values for each family. The highest expected value under uncertainty is also highlighted in bold and red. No values were zero, but many were below 0.0005.

Family	Critically Endangered	Endangered	Vulnerable	Expected Value	Number of species
Begoniaceae	0.179	< 0.0005	< 0.0005	0.179	3
Meliaceae	0.007	0.060	0.054	0.120	2

Family	Critically Endangered	Endangered	Vulnerable	Expected Value	Number of species
Moraceae	< 0.0005	0.108	< 0.0005	0.108	6
Rutaceae	< 0.0005	0.053	< 0.0005	0.053	10
Solanaceae	< 0.0005	0.029	< 0.0005	0.029	20
Celastraceae	< 0.0005	< 0.0005	0.021	0.021	6
Rhamnaceae	0.007	0.005	0.002	0.015	9
Bignoniaceae	< 0.0005	0.011	0.002	0.013	36
Myrtaceae	< 0.0005	< 0.0005	0.009	0.009	28
Erythroxylaceae	< 0.0005	0.008	< 0.0005	0.008	20
Malpighiaceae	< 0.0005	0.007	< 0.0005	0.007	29
Apocynaceae	< 0.0005	0.007	< 0.0005	0.007	33
Fabaceae	0.001	0.001	0.001	0.003	208
Loganiaceae	0.001	0.001	< 0.0005	0.001	2

3.4 Discussion

To prioritise which species should be assessed for the Red List, it is possible to model factors correlated with species already assessed and apply this information to predict the threat status of species not yet assessed. We have predicted both threat status and Red List category for 1,002 Not Evaluated species in the Caatinga, 81 (8%) of which are predicted to be threatened. The Naïve Bayes classifier worked well for predicting threat status, and important predictors were the genus, number of occurrence records and growth form of species and the habitat types they occur in. If we are to focus conservation action on a certain family in the Caatinga, based only on current Red List evidence, it should be Begoniaceae, but it is likely that further research will lead to greater benefits.

The strongest predictors for Red List category and threat status for species assessed as threatened were the genus to which a species belongs and the number of occurrence records available for that species in the BIEN database. Species with more occurrence records were predicted to be less threatened overall which is consistent with other studies (Nic Lughadha *et al.*, 2005). It is possible to calculate extent of occurrence or area of occupancy accurately enough to predict extinction risk for species represented by at least 15 specimens (Rivers *et al.*, 2011), which is the case for 1,223 species from the Caatinga. There are now tools available to facilitate calculating extent

of occurrence or area of occupancy accurately such as GeoCAT (Bachman *et al.*, 2011) or the rCAT package (Moat and Bachman, 2017), which can help with Red List assessments.

It has been suggested that Naïve Bayes is one of the most efficient classifiers (Zhang, 2004), performing well for smaller datasets with up to 1,000 observations (Domingos and Pazzani, 1997) and this seems to be true for predicting threat status for plants in the Caatinga. Random Forest approaches have been used multiple times for predicting extinction risk, achieving varying levels of sensitivity (percentage of correctly predicted threatened species) which differed between studies predicting threat status and Red List category. Sensitivities ranged from 88.0%, N = 148 (Darrah *et al.*, 2017) to 55.6%, N = 54 (Machado *et al.*, 2013) in studies predicting threat status. Studies predicting Red List category achieved sensitivities from 58.1%, N = 4,402 (Howard and Bickford, 2014) to 0%, N = 40 (but including only one threatened species) (Comeros-Raynal *et al.*, 2016). Our models using the Naïve Bayes classifier had a sensitivity of 63.0% when threat status was predicted, while the tree-augmented Naïve Bayes classifier had a sensitivity of 29.6% when Red List category was predicted. Our results suggest that Bayesian Networks can be a valuable tool for predicting extinction risk when there is class imbalance in the data as is almost always the case for extinction risk data. They also show a clear trade-off between predicting with high levels of accuracy whether or not species are threatened (using just the two classes threatened and non-threatened) as opposed to predicting assignment to the more informative five Red List categories but with much lower accuracy.

The genus of a species was important in determining the predicted threat status in our model. This could be due to phylogenetic autocorrelation between threats to species, suggesting that when a species is threatened in a phytogeographical domain, phylogenetically correlated species have a higher chance of being also threatened. There is some evidence that more closely related plant species that are of young, fast evolving lineages may be at increased risk of extinction (Davies *et al.*, 2011), but most evidence is to the contrary, with phylogenetic signal in extinction risk absent (Daru *et al.*, 2013; Cardillo and Skeels, 2016) or not detectable in the species at greatest risk of

extinction (Yessoufou *et al.*, 2012). It is also possible that our model is overfitted, and predicts threat status mainly based on genus.

For the Caatinga, 15.8% of woody species and 13.1% of non-woody species have been assessed on the IUCN or Brazilian National Red List. It is thought that many more non-woody species are yet to be reported and described. Moro *et al.* (2016) estimated a total of 1,098 non-woody plants and 938 woody plants in Caatinga vegetation, which would decrease the percentages assessed to 13.1% for woody plants and 8.1% for non-woody plants. There also appear to be biases in assessment effort in different habitats, with 30.5% of assessed species from the crystalline Caatinga, the most common habitat type, but 47.1% from the sedimentary Caatinga and 44.4% from inselbergs, suggesting that the crystalline Caatinga is underrepresented in the assessments. Therefore, more non-woody species in the crystalline Caatinga should be assessed, ideally in genera or families which have not yet had any assessments.

To assess the Value of Information, the full decision context is usually required, which includes setting objectives, identifying possible actions, modelling the outcomes of the actions on objectives, and considering trade-offs (Gregory *et al.*, 2012). Objectives could be to prevent extinctions, avoid declines for a certain number of threatened species, or move all threatened species back to non-threatened categories. This could be measured by counting the number of extinctions or calculating a Red List index for Caatinga (Bubb *et al.*, 2009). Here we have calculated the Vol in a more theoretical setting without specifying the full decision context, but as an example of how the method could be applied to prioritising whether more species should be assessed on the Red List or whether conservation action should be taken immediately. Our Vol calculation would therefore also rely on the knowledge of threats and possible conservation action to mitigate the threats. While Begoniaceae had the highest risk value under uncertainty, there is great potential that by resolving uncertainty a higher value can be achieved. Begoniaceae was also the only family in which a species was predicted to be Critically Endangered, which is likely to drive the Value of Information calculations. Red Listing of plants is often done by region or by taxonomy such as

family, so our method could be used to prioritise different groups of species, not just taxonomically, but also geographically or trait based.

One question that remains to be answered is how well the model predictions match the actual threat status of those species which have not been assessed yet. The only way to answer it is to assess the species whose threat status was predicted by our model. The type of analysis we present could be used as a way of prioritising which species should be assessed next, either by using the outcomes from the Vol calculations, or by assessing those species next which our models predicted to be threatened, or by assessing those with the greatest uncertainties in the predicted threat status. Brazil is leading the way in meeting the targets of the Global Strategy for Plant Conservation (Convention on Biological Diversity, 2018), and aspired to have 50% of plants assessed on the Brazilian National Red List by 2020, though the economic downturn has magnified this challenge (Martins *et al.*, 2017). New assessments and more information on Caatinga vegetation can lead to opportunities to further improve our model. We have shown that extinction risk can be predicted for a range of taxonomic ranks for one geographic area, even when there is little information available about the species. The genus of a species and occurrence records were important predictors, and it would be useful to test whether they are important predictors for other taxonomic groups too, especially the genus. Bayesian Networks performed well for predicting extinction risk, and are likely to be a useful method when sample sizes are low. The Value of Information can be calculated for predictions of extinction risk and this knowledge can help to prioritise which species to assess on Red Lists or when to focus on conservation actions instead. This is crucial if we are to prevent species from going extinct.

Chapter 4 Predicting Extinction Risk of Data Deficient Plants

Abstract

To take targeted action to save species globally, we need to know first of all which species are at risk of extinction. While there are just over 400,000 described plant species, only 6% have been assessed according to their extinction risk. Predicting extinction risk of species can help to identify groups of species that are at increased risk of extinction.

I used publicly available information on plants that have been assessed on the IUCN Red List of species, as well as trait information from the TRY database. I built Bayesian Network models with Machine Learning algorithms to explore what drives extinction risk in plants and to predict what IUCN Red List category plants have that have so far been assigned the Data Deficient category. There were 1,732 Data Deficient species, of which 932 were predicted to be extinct or threatened. Value of Information analysis showed that South America has a high percentage of species predicted to be threatened and should be the focus region for plant assessments.

My work confirms results from other taxonomic groups that Data Deficient species are more likely to be threatened than a random sample of species. Using models to predict extinction risk is a cost-effective way of getting estimates of extinction risk and can help to inform future conservation action.

4.1 Introduction

Plants offer an enormous number of benefits to humans: we eat them (Dempewolf *et al.*, 2014), we use them to build and heat our homes, they store carbon and therefore combat climate change (Isbell *et al.*, 2015), they provide climate regulation and flood mitigation (Duarte *et al.*, 2013), they are the basis for many medicines we use (Khazir *et al.*, 2014). Because plants are important, one of the objectives of the Global Strategy for Plant Conservation is to conserve plant diversity by 2020, and more specifically, one of the targets aspires to assess “[...] the conservation status of all known plant species, as far as possible, to guide conservation action”. There are an estimated 403,911 described land plants as of 2016 (Nic Lughadha *et al.*, 2016), of which 24,230 species (6%) have

been assessed on the IUCN Red List as of 18 December 2017 (IUCN, 2017). These assessed species are not a random sample however, because plants that scientists consider likely to be threatened are more likely to be assessed (Brummitt *et al.*, 2015). This means that overall threat status of plants is thought to be overestimated. To provide an overall assessment of threat status of plants, the Sampled Red List Index was developed which is an assessment of a random sample of plants (Brummitt *et al.*, 2015). Between 972 and 1,026 species in the groups monocotyledons, legumes, gymnosperms and pteridophytes were assessed to give a representative sample of different major plant groups. 21.4% of plants on the Sampled Red List Index were estimated to be threatened (classed as Critically Endangered, Endangered or Vulnerable) compared to over 50% of species already assessed on the IUCN Red List. A recent study gathered data on the conservation status of plants from many different data sources, and found 37,543 plants to be threatened of 111,824 accepted plant names (Bachman *et al.*, 2017).

Data Deficient species accounted for 15.8% of over 90,000 plant and animal species assessed on the IUCN Red List as of 18 December 2017 (IUCN, 2017). The Sampled Red List Index considered 5.1% of the plants they assessed to be Data Deficient (Brummitt *et al.*, 2015). Previous research has predicted the IUCN Red List categories of Data Deficient mammals (Bland *et al.*, 2015; Jetz and Freckleton, 2015) and amphibians (Howard and Bickford, 2014). While the Data Deficient category should only be applied when a species could truly be in any of the IUCN Red List categories (Butchart and Bird, 2010), the predictive approaches estimated more Data Deficient species to be threatened than would be expected if it were a random sample of species (Howard and Bickford, 2014; Bland *et al.*, 2015; Jetz and Freckleton, 2015). This could mean that Data Deficient species might need urgent reassessments where possible to estimate the true extinction risk of the species.

Different methods have been used so far for predicting extinction risk of species at different taxonomic levels, for example random forest models for bulbous monocotyledons (Darrah *et al.* 2017) and amphibians (Howard and Bickford, 2014), and linear models for mammals (Jetz and Freckleton, 2015). One paper compared seven different methods for predicting extinction risk of mammals, namely classification trees,

random forest, boosted trees, k nearest neighbour, support vector machines, neural networks, and decision stumps, of which neural networks performed best (Bland et al. 2015). All of the studies have focussed on predicting Red List category or threat status for one class or family, some with geographic restrictions as well. None have predicted Red List category or threat status for more than one class.

No papers so far have used machine learnt Bayesian Networks for modelling extinction risk, even though some Bayesian Network algorithms predict well, especially for classifications with class imbalance (Mayfield et al., 2017). Investigating the use of Bayesian Networks for predicting extinction risk would therefore add to the growing body of literature on this topic.

4.1.1 Aim and objectives

The aim was to predict the IUCN Red List category of plants that have been classed as Data Deficient with models not previously used for predicting Red List category. To do so I needed to identify whether any trait, taxonomic or occurrence information was correlated with IUCN Red List categories of plants that have been assessed already. Then using the best-performing model I looked to extend the model to predict IUCN Red List category for the Data Deficient plants. I also investigated a method of prioritising species for assessment. Finally, I tested whether the model predicted similar IUCN Red List categories for plants that were assessed more than 10 years ago, and therefore are due for a reassessment (Rondinini *et al.*, 2014).

4.2 Methods

4.2.1 Data sources

A variety of data sources were used. First, assessments of all plant species assessed on the IUCN Red List so far were downloaded. This was a total of 23,078 plants and included taxonomic information on each species (genus, family, order, class and phylum) and the IUCN Red List category (IUCN, 2017). The IUCN uses the following categories: Extinct, Extinct in the Wild, Critically Endangered, Endangered, Vulnerable, Near Threatened, Least Concern and Data Deficient (see Chapter 1 for definitions of the categories). The habitats and countries each species occurs in were downloaded using the letsR package in R (Vilela and Villalobos, 2015). This information was used to

calculate the number of habitats a species occurred in as well as the number of countries. Countries were then classified into regions and continents to get an overview of where the assessed plants occurred, based on the geographic regions as defined by the United Nations (United Nations Statistics Division, 2011).

Species trait information was downloaded from the TRY database (Kattge *et al.*, 2011). A total of 66,044 records were available. The dataset contained trait information such as woodiness, leaf type, plant growth form, photosynthetic pathway, leaf compoundness, and number of leaflets. Not all of the traits were recorded for all species, and where variables were missing for more than 90% of species these variables were excluded from the analysis.

For the species in the IUCN dataset, digital occurrence records were downloaded with the BIEN package in R (Botanical Information and Ecology Network, 2017; Maitner *et al.*, 2017). Duplicates were removed by first removing records with the same species name and the same catalogue number, then by removing records with the same species name, latitude, longitude and date of collection. I then calculated the total number of occurrence records per species.

The datasets were then merged into one big dataset containing all species information. There were differences in nomenclature, for example the family name *Fabaceae* in the TRY dataset was *Leguminosae* in the IUCN dataset, which was the biggest family group in both datasets. The taxonomy for all species was therefore standardised using the taxize package in R (Chamberlain and Szöcs, 2013) to ensure consistent use of names throughout. Following standardization 3479 species were represented by both IUCN Red List data and TRY data.

The final dataset contained the following variables: class, order, family, genus, 17 different habitats, the number of habitats in which a species occurred, phylogenetic group, plant growth form, whether the species was a succulent, climber, parasitic, aquatic, epiphyte, crop, or palmoid, further the leaf type, leaf phenology, the photosynthetic pathway, the woodiness, leaf compoundness, the number of occurrence records, the continent and the region. If a species occurred in more than one region, it was listed in the dataset more than once too.

4.2.2 Data preparation

As some trait values were missing for many species in the Red List dataset, I imputed those values from the TRY dataset, by imputing the values that were most common in each genus, following earlier authors (Bland *et al.*, 2015). For example if plant growth form for some species within a genus was unknown, and most of the species in that genus were trees, then tree was imputed where plant growth form was missing.

Data were analysed using Bayesian Network models (see chapter 1 and 3 for background on Bayesian Networks). The Bayesian Network software GeNIe Modeler (Bayes Fusion LLC, 2017) requires variables in categorical form, so the variables habitat number, and occurrence records were discretised into four categories and country number was discretised into five categories (Table 8). The aim was for the categories to have a similar number of counts which was not always possible. For example, most species only occurred within one habitat, so that was by far the biggest group for habitat number, and could not be split into further groups. Occurrence records on the other hand were discretised according to the ability to estimate range sizes from the number of records, which is important for conservation assessments (Rivers *et al.*, 2011). Areas cannot be estimated with one or two records. Three to five records give variable range estimates, whereas six to 14 records give fairly accurate estimates. With 15 records range sizes can be estimated with high accuracy (Rivers *et al.*, 2011).

Table 8. Three continuous variables and how they were discretised in the model.

Variable	State	Groups of different states	Count of observation
Habitat number	Low	1	20,528
	Medium	2	7,152
	High	3	2,900
	Very high	> 3	1,586
Country number	Very low	1	16,550
	Low	2	3,218
	Medium	3 – 5	2,801
	High	6 – 30	5,101
	Very high	> 30	4,496
Occurrence records	Low	1 – 2	2,136
	Medium	3 – 5	1,778
	High	6 – 15	3,953
	Very high	> 15	24,299

Classifying data into different categories can be difficult if the number of observations in each group is not even. This was the case for the IUCN Red List data of plants, where the largest number of species was classed as Least Concern (34%), and relatively few species were in each of the other categories. The smallest category, Extinct, accounted for 1% of species. The ROSE (Random Over-Sampling Examples) package in R (Lunardon *et al.*, 2014) uses over- and/or undersampling to balance the number of observations in each category. Oversampling of the less common categories was used to even out the dataset with the aim of building a more robust model, a method commonly used in Machine Learning (Guo *et al.*, 2008; Galar *et al.*, 2012; Nanni *et al.*, 2015). Species in categories that were less often applied were duplicated until there was an even number of species from all categories. Oversampling was chosen to preserve as many of the genera in the model as possible, but oversampling can lead to overfitting of the data (Galar *et al.*, 2012). Some species were removed for model building to decrease the number of genera, to be able to load the networks into GeNIe Modeler (Bayes Fusion LLC, 2017). The IUCN Red List categories of these removed species were predicted to check for overfitting.

The variable genus contained so many categories (genera) that networks could not be loaded into the GeNIe Modeler software for Bayesian Networks (Bayes Fusion LLC, 2017), therefore observations in the data were reduced to reduce the number of categories. Those genera containing the smallest number of species were removed first to remove as few observations as possible (1,846 removed in the original dataset – 6.2% of the original data, 3,321 removed in the oversampled dataset – 3.6% of the oversampled data). Based on earlier analyses in Chapter 3 genus was thought to be a key variable so this reduction was considered preferable to removing the variable genus from both datasets.

4.2.3 Model building

Bayesian Networks were used for analysis, building separate models with the normal and the oversampled dataset. A hill-climbing algorithm and a Naïve Bayes classifier were applied to both datasets in the bnlearn package (Scutari, 2010), see chapter 3 for details on hill-climbing and Naïve Bayes. All four models were evaluated using 10-fold

cross validation implemented in GeNIe Modeler (Bayes Fusion LLC, 2017). This validation method keeps the same model structure for each iteration, but recalculates the conditional probabilities. 90% of the data were used to predict the other 10%. This was repeated nine times so each IUCN Red List category of a species was predicted once.

Four measures of predictive performance were plotted for model selection. Accuracy is the percentage of all correct predictions for all IUCN Red List categories. Sensitivity, specificity and true skill statistic are measures using true and false positives, and true and false negatives (Allouche *et al.*, 2006). As two groups were necessary to calculate these, the data were split into threatened and Extinct species, (i.e. Extinct, Critically Endangered, Endangered, and Vulnerable species), and non-threatened species (i.e. Near Threatened and Least Concern species) for the calculations. Sensitivity was the number of assessed threatened species that were predicted to be in the correct IUCN Red List category, divided by the number of all species that were predicted to be threatened (Allouche *et al.*, 2006). Specificity was the number of assessed non-threatened species that were predicted to be in the correct IUCN Red List category, divided by the number of all species that were predicted to be non-threatened (Allouche *et al.*, 2006). The true skill statistic combined the two by adding the sensitivity to the specificity minus one (Allouche *et al.*, 2006). It gives a value that reflects both sensitivity and specificity equally, without giving more weight to the larger group, in this case non-threatened species. The true skill statistic value was used for model selection.

The model with the best predictive performance was used to determine whether any of the variables had different conditional probabilities between the threatened and non-threatened categories (Marcot, 2012). To do so, first I changed the probabilities of IUCN Red List category to 25% each for Extinct, Critically Endangered, Endangered and Vulnerable species, and then by changing them to 50% each for Near Threatened and Least Concern species. The resulting changes in the probabilities of other variables were noted and for those where changes were more than 10%, the distribution of their states was plotted from the original data, indicating those variables that contributed more to threat status than others. The percentage of false and correct predictions of IUCN Red List categories was plotted over time to see whether there were differences between

current records (less than ten years old) compared to records in need of re-assessment (more than ten years old).

4.2.4 Predictions

The best performing model was used to predict IUCN Red List categories of Data Deficient plants. First, I predicted the IUCN Red List category using the *bnlearn* package in R (Scutari, 2010). Then I used 10-fold cross validation for all species that were assessed on the IUCN Red List, including the Data Deficient ones for which I predicted the IUCN Red List category (Bayes Fusion LLC, 2017). 10-fold cross validation gave the probability for each species to be in each of the six IUCN Red List categories, and the sum of these probabilities is always one. The category with the highest probability was plotted against the probability of that species to be in that category for all Data Deficient species.

The original model was used for predicting the IUCN Red List categories for those Data Deficient species that were in a genus in which at least one species had an IUCN Red List assessment, as in Chapter 3. Then I rebuilt the model without genus as a variable, and predicted categories of those Data Deficient species which were in a family from which at least one species had an IUCN Red List assessment. Then I rebuilt the model without genus and family as variables, and predicted IUCN Red List categories for those Data Deficient species which were in an order from which at least one species had an IUCN Red List assessment. The number of predicted threatened plants globally was mapped by country, and the percentage of assessed and predicted threatened plants globally was also mapped by country.

4.2.5 Value of Information (Vol)

To find a way to prioritise which assessments of Data Deficient species should be undertaken first, Vol was calculated for different regions in the world, as a means of finding where to focus sampling (for a detailed description of Vol, see chapter 2).

The Vol was calculated as described in chapter 3, but for geographic areas rather than for families. The probability of extinction was multiplied with the probability of each Data Deficient species being in the predicted categories, which gave the risk value, or an estimate of the risk of extinction. The risk values of each Data Deficient species

were first summed for each IUCN Red List category, and then for all species within each region. The regions were assigned to countries according to UN classification (United Nations Statistics Division, 2011). The region with the highest summed risk value was the one with highest levels of threat. Perfect information was calculated by summing the risk values, for the regions that had the highest risk value for each of the IUCN Red List categories that are considered threatened categories. The Vol was the difference between the latter value and the value of the region with the highest level of threat.

4.3 Results

The model using a hill-climbing algorithm and the oversampled dataset (incorporating imputed and oversampled data) had the highest true skill statistic with 0.256 so this model was used for assessing variable importance and for undertaking predictions (Figure 12, Figure 13). Both models that used oversampled data had a higher sensitivity (they predicted threatened species better), and both models that used the original data had a higher specificity (they predicted non-threatened species better). The hill-climbing algorithm and the original data produced a model with marginally higher accuracy than the others (0.615). As a model built with oversampled data had the highest true skill statistic, I checked for overfitting. Predicting IUCN Red List category of species from the unseen data lead to a true skill statistic of 0.18, a decrease of 3.8%.

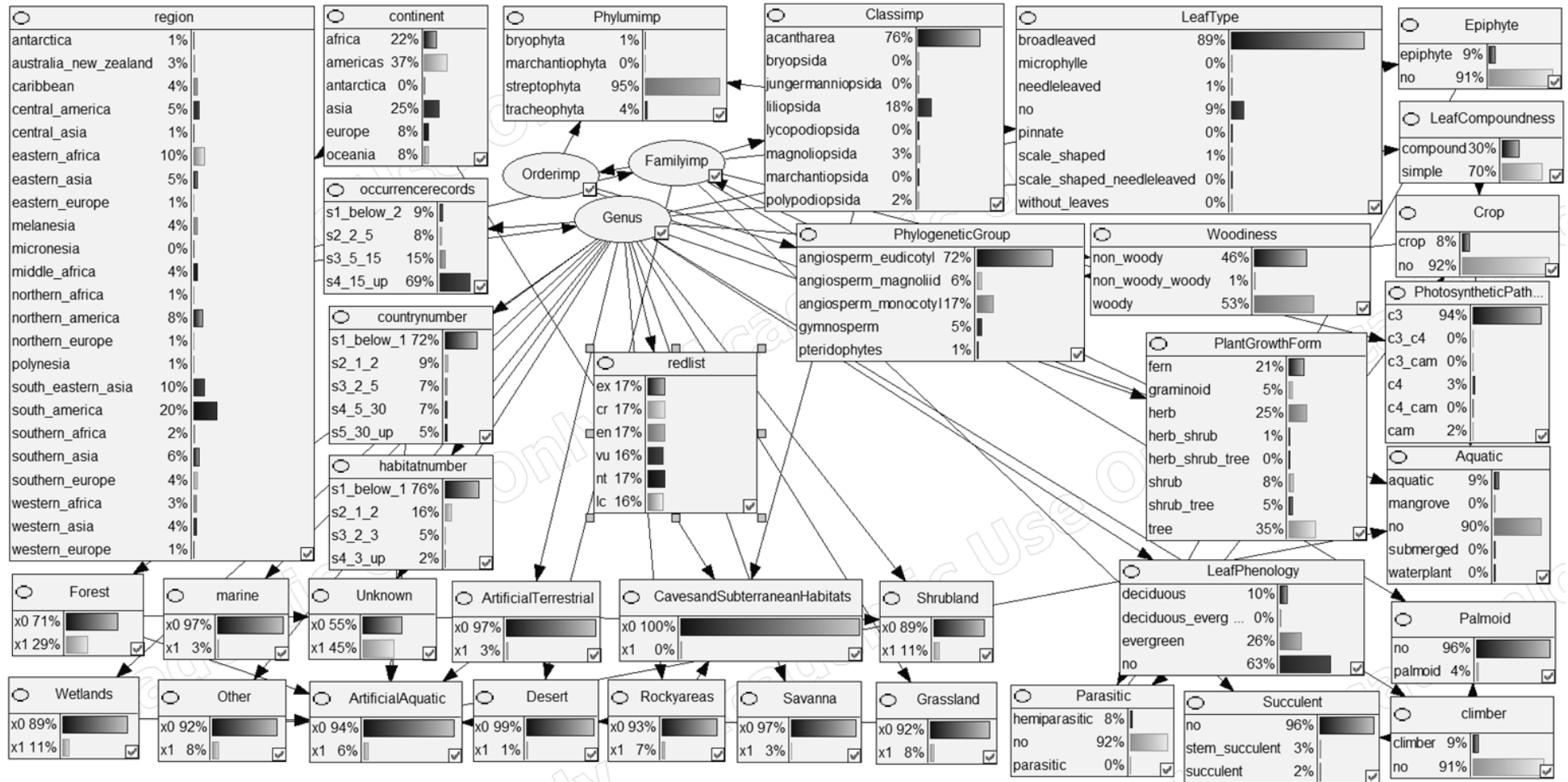


Figure 12. Best performing Bayesian Network, built using a hill-climbing algorithm and oversampled data. Variables are shown as nodes in the network, and probabilities of each state are also shown. Order, family and genus not shown due to the high number of states, but included in the model when processed.

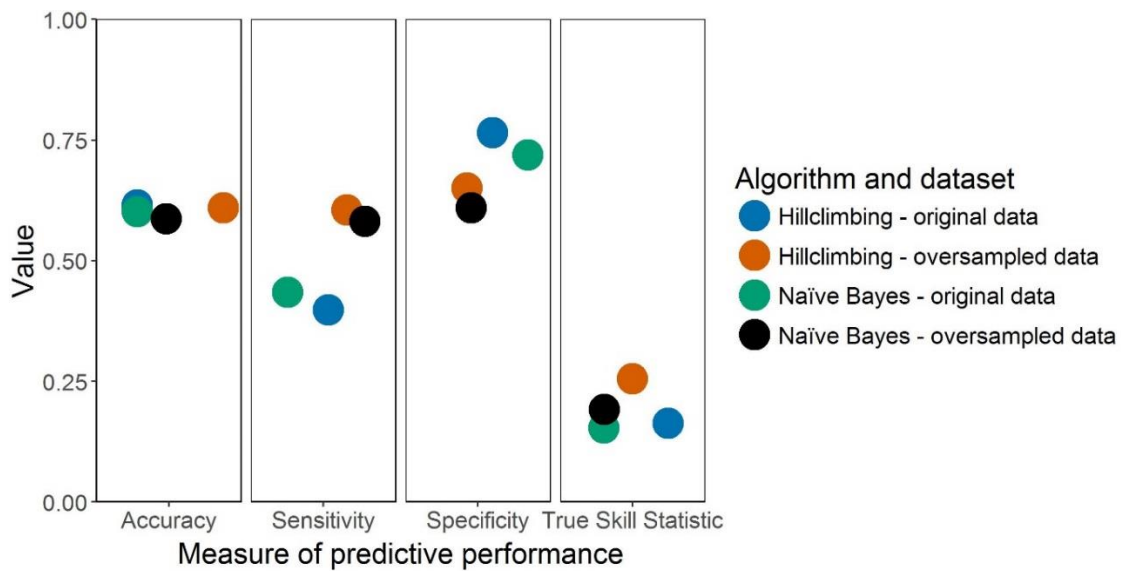


Figure 13. Performance of different algorithms and datasets for four different measures of model performance. The values for accuracy, sensitivity and specificity are measured between 0 (worst) and 1 (best). The value for the True Skill Statistic is measured between -1 (worst) and 1 (best).

Most plant species that have been assessed on the IUCN Red List so far were Least Concern, followed by Vulnerable, Endangered, and Critically Endangered (Figure 14). There were 150 Extinct species and 1,801 Data Deficient species.

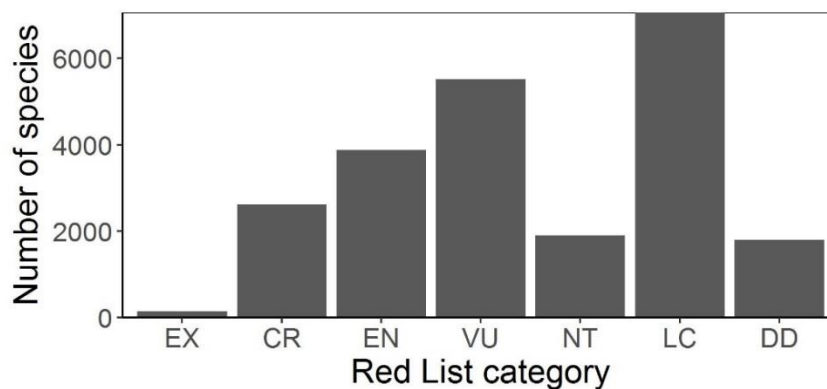


Figure 14. Count of different categories of all plant species assessed on the IUCN Red List. Red List Categories are: EX – Extinct, CR – Critically Endangered, EN – Endangered, VU – Vulnerable, NT – Near Threatened, LC – Least Concern, DD – Data Deficient.

4.3.1 Variable importance

Magnoliids had the highest percentage of threatened species apart from bryophytes, for which there was only one assessment (Figure 15). Monocotyledons were relatively less threatened, and pteridophytes had the highest percentage of Data Deficient species. 70.1% of assessed species were Eudicotyledons.

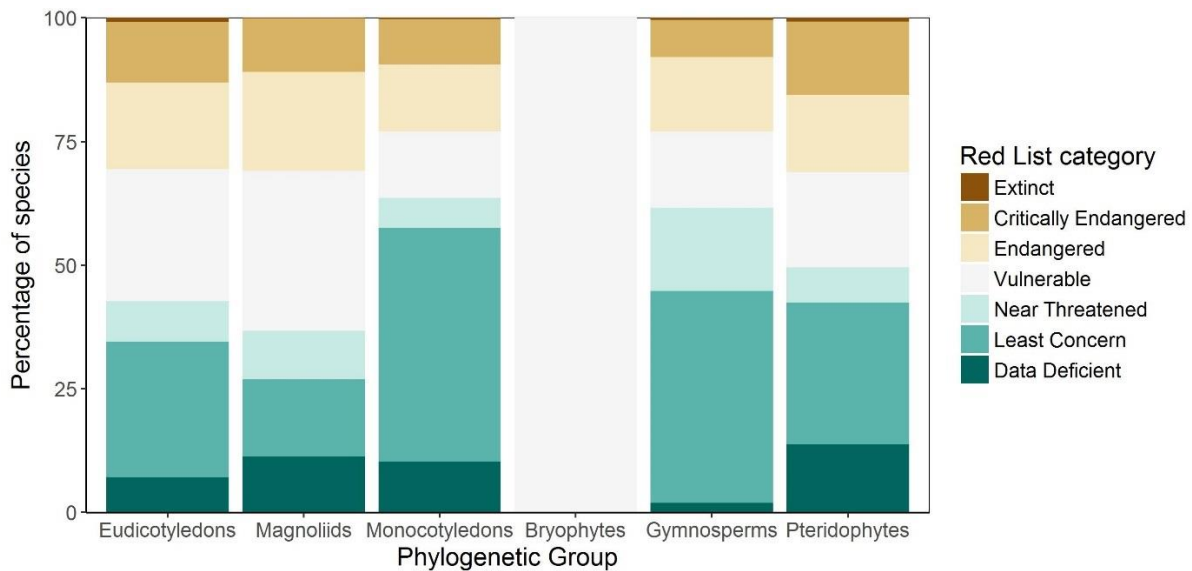


Figure 15. Percentage of IUCN Red List categories of assessed species with different phylogenetic groups.

Among assessed species, woody species appeared to be more threatened than non-woody species with more than 50% threatened species (Figure 16). Most of the species were either woody (48%) or non-woody (51%), with only 1% being reported as both woody and non-woody.

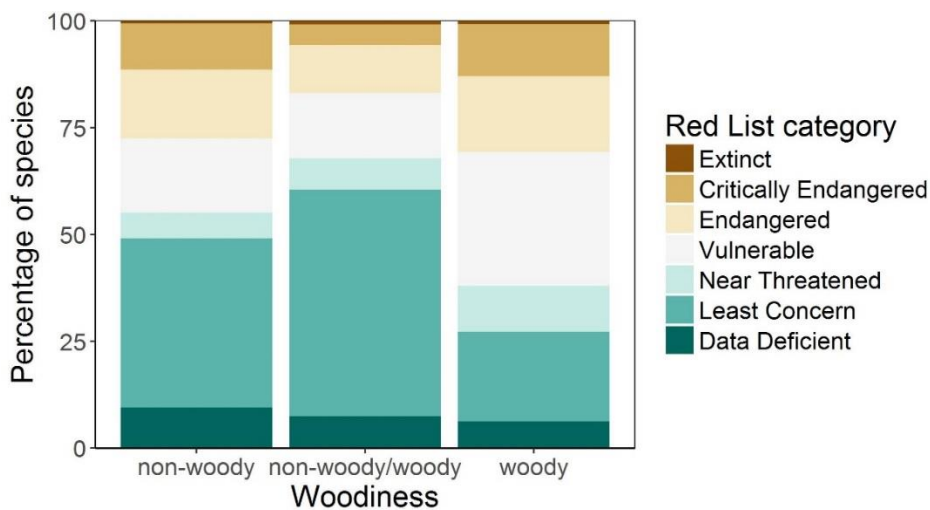


Figure 16. Percentage of IUCN Red List categories of assessed species with woodiness.

The percentage of threatened species was highest in the Americas, followed by Africa and Asia (Figure 17). Only two species were assessed in Antarctica, both of which were Least Concern. Europe had the highest percentage of Data Deficient species.

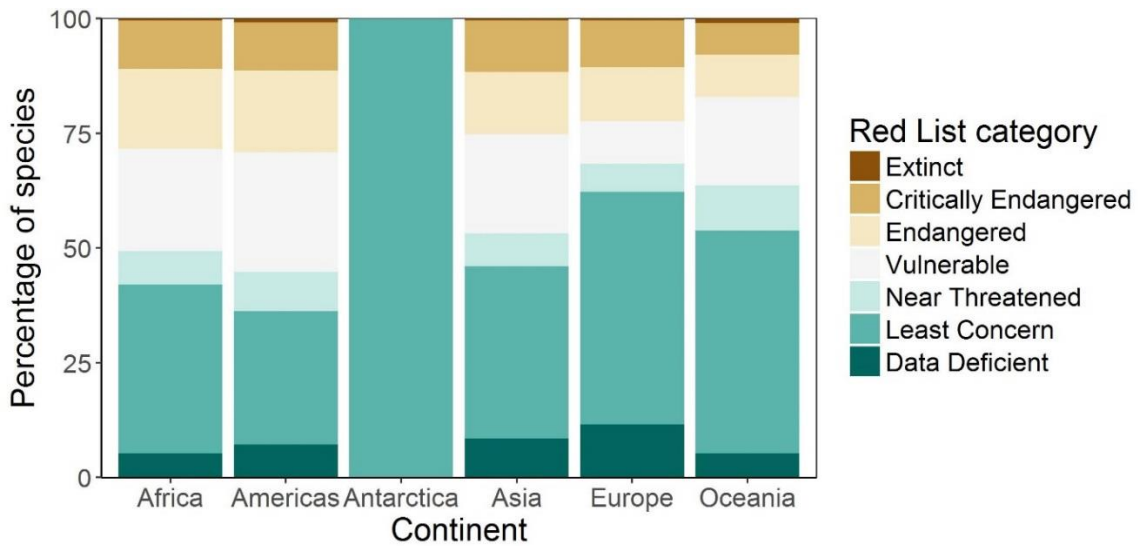


Figure 17. Percentage of Red List categories of assessed species in different continents.

The median number of countries of occurrence for species from all IUCN Red List categories was one (Figure 18). 72.8% of all species and 85.5% of assessed threatened species were endemics. Least Concern was the only category with species that occurred in more than 42 countries. The median number of habitats that species from each IUCN Red List category occurred in was one for all categories. Least Concern species occurred in more habitats than the other species.

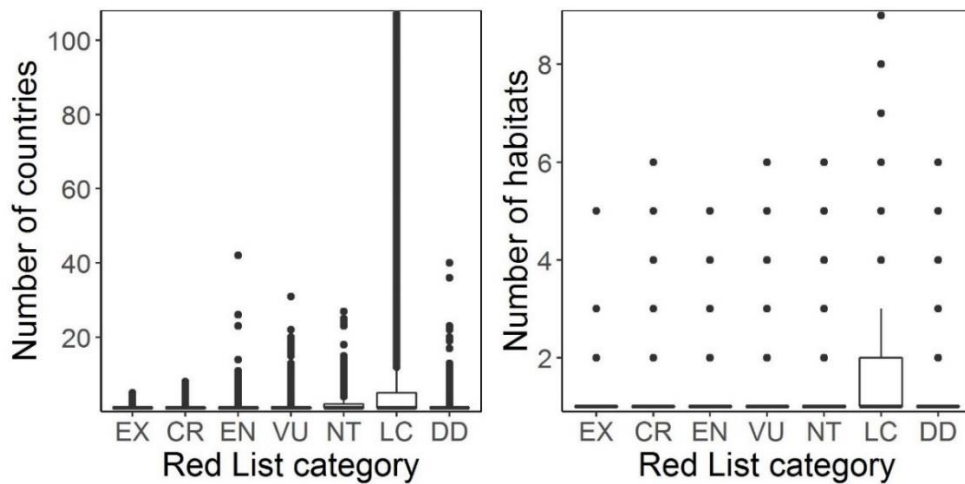


Figure 18. Number of countries comprising the native distribution of assessed plants (left) and number of habitats that plants occur in (right) for different Red List categories.

As the level of threat of species increased, the median number of occurrence records decreased (Figure 19). The median number of occurrence records was highest in species that were Least Concern with 55 records.

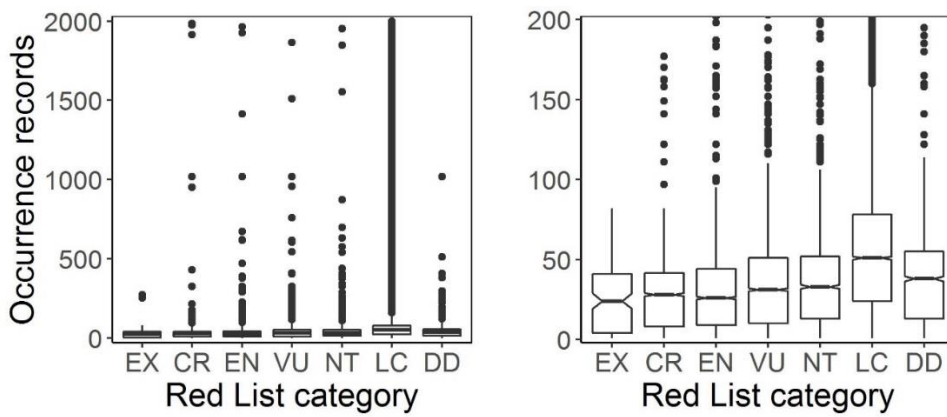


Figure 19. Number of occurrence records of plants for different IUCN Red List categories. Left shows all data, right shows species with up to 200 occurrence records.

There was no trend in the percentage of correct and false predictions over time (Figure 20). Predictions were best for 2006 with 58.7% correct predictions, and worst for 2009 with 31.0% correct predictions. The mean of correct predictions before 2008 was 45.0%, and 47.1% since 2008. Since 2011, more than 1,000 species were assessed each year, except for 2017. Data were downloaded from the IUCN on 22 September 2017 however so numbers are incomplete (IUCN, 2017).

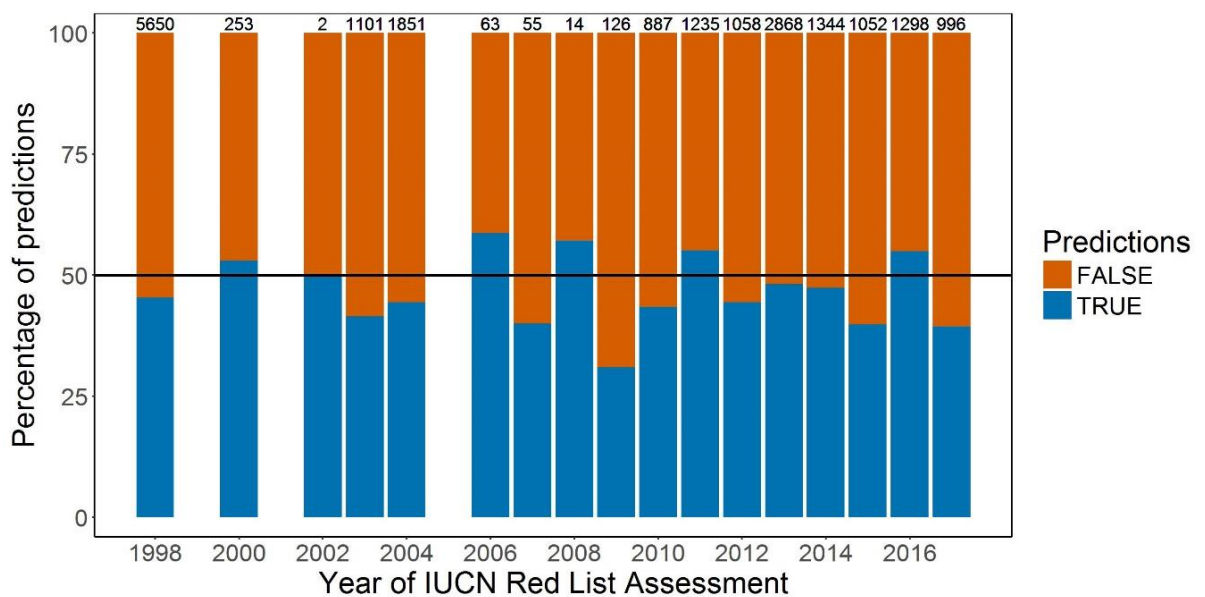


Figure 20. Percentage of true and false model predictions of IUCN Red List categories over time. Number of assessments within each year shown at the top.

4.3.2 Model predictions

Three models were used for predictions: one that included all variables, one that excluded genus, and one that excluded genus and family. The true skill statistic was 0.10, both for the model excluding genus and for the model excluding genus and family. This

was slightly below the true skill statistic for the model including all variables with 0.256, a change of 7.8%. Of the 1,732 Data Deficient species, 117 were predicted to be Extinct, 293 were predicted to be Critically Endangered, and 302 were predicted to be Endangered (Figure 21). 53.8% of Data Deficient species were predicted to be Extinct or threatened, compared to 53.1% of assessed species that were Extinct or threatened.

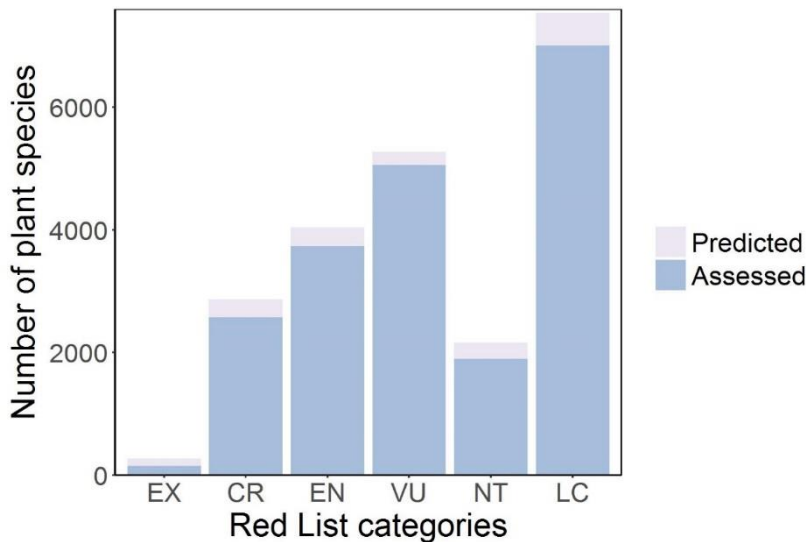


Figure 21. Number of plants in each IUCN Red List category, for assessed and predicted species. IUCN Red List Categories are: EX – Extinct, CR – Critically Endangered, EN – Endangered, VU – Vulnerable, NT – Near Threatened, LC – Least Concern.

When I predicted the IUCN Red List category of a Data Deficient species, I got a probability of the species being in each of the IUCN Red List categories. The predicted IUCN Red List category of Data Deficient species was therefore plotted against the probability of the Data Deficient species to be in the predicted IUCN Red List category (Figure 22). Of the species with probabilities at or above 50%, 72 were predicted to be Extinct, 144 were predicted to be Critically Endangered, and 70 were predicted to be Endangered. Overall, 46.8% of species had categories that were predicted with probabilities at or above 50%. The median probability values were highest for Extinct (56.2%) and Least Concern (55.4%) species, and lower for the categories in between them. Endangered had the lowest median probability with 37.0%.

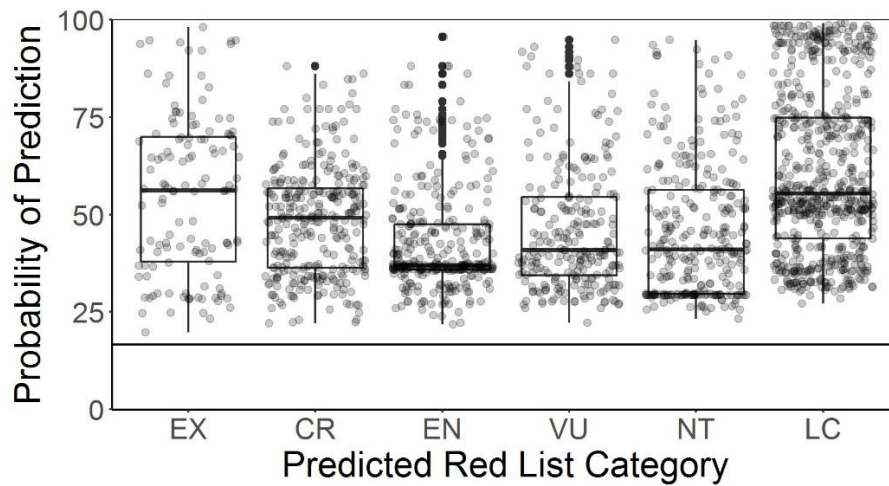


Figure 22. Probabilities of Data Deficient species to be in their predicted IUCN Red List categories. If the probability for each IUCN Red List category was the same, it would be 16.667% as there are six categories – this is represented by the horizontal line. This was the lowest possible probability value. Each species is represented by a light grey circle over the boxplot – darker circles are overlapping species. IUCN Red List Categories are: EX – Extinct, CR – Critically Endangered, EN – Endangered, VU – Vulnerable, NT – Near Threatened, LC – Least Concern.

The number of plants currently assessed as Data Deficient but predicted to be threatened were mapped by country (Figure 23). Half of the countries have four or fewer species that are currently listed as Data Deficient but were predicted to be threatened. Ecuador has the highest number of predicted threatened species with 133, followed by Indonesia with 55, and China with 48.

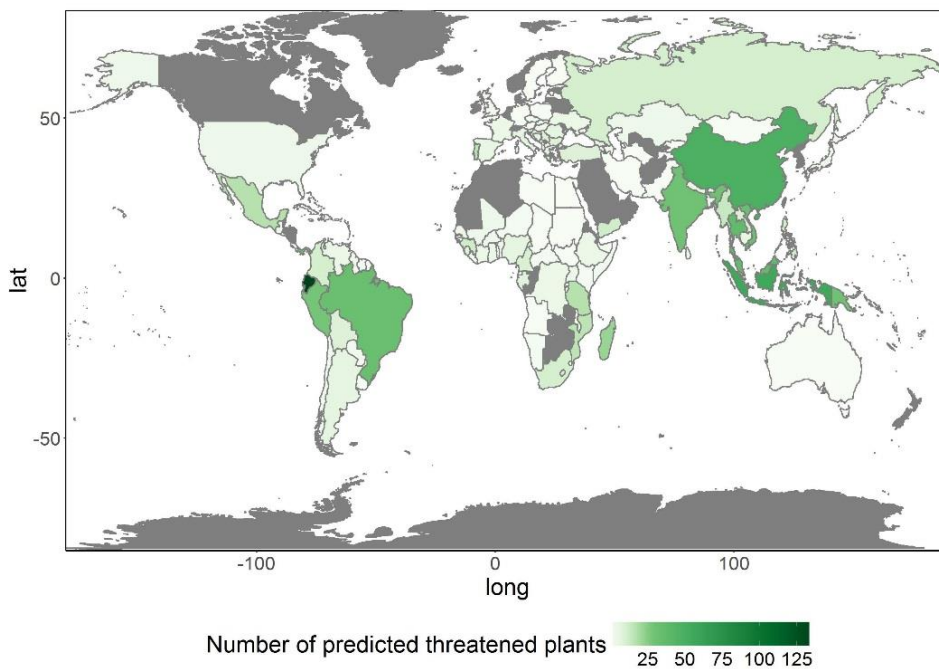


Figure 23. Number of predicted threatened plants per country. Threatened are those plants classed as Critically Endangered, Endangered or Vulnerable.

The percentage of threatened species, both assessed on the IUCN Red List and predicted by us, was mapped by country (Figure 24). For half of the countries the percentage of threatened species was 12.7% or lower. Ecuador had the highest percentage of threatened species with 70.4%, followed by New Caledonia (62.6%), Madagascar (57.8%), Cameroon (56.2%) and Jamaica (51.2%).

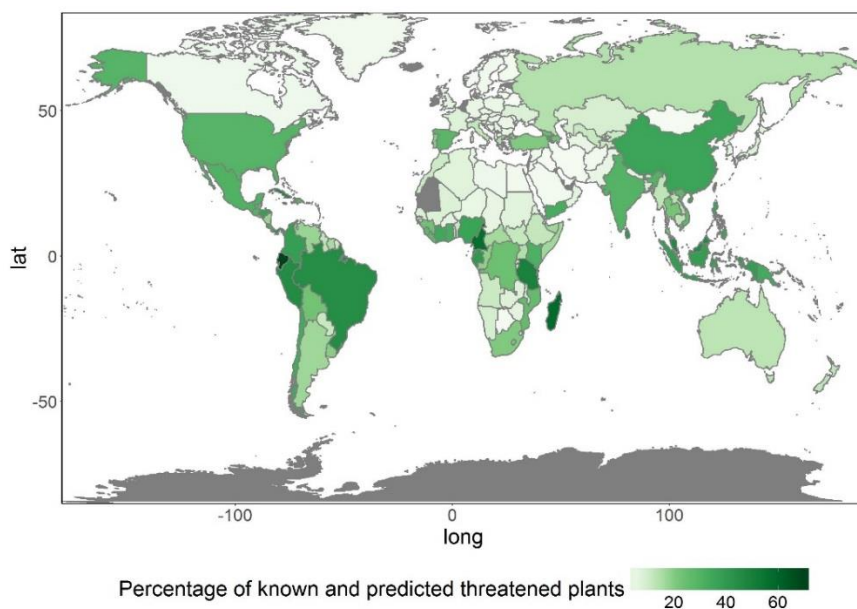


Figure 24. Percentage of known and predicted threatened plants per country. Threatened are those classed as Critically Endangered, Endangered or Vulnerable.

4.3.3 Value of Information

The Vol was calculated for each region and each IUCN Red List category (Table 9). The highest risk of extinction value under uncertainty for any region was for South America with 72.00. South America also had the highest risk values for each individual Red List category. The sum of these four values was 72.00 which is equivalent to perfect knowledge of extinction risk. The Vol was the difference between the value for perfect information (72.00) and the value for imperfect information (72.00), which was 0 in this case. This means that assessments could happen in South America without resolving uncertainty first around which area to sample.

Table 9. Risk values of different IUCN Red List categories in different regions of the world. Bold red values are the highest values for a particular IUCN Red List category.

The highest expected value is also highlighted in bold and red, which is the same as the expected value under uncertainty.

Region	Extinct	Critically Endangered	Endangered	Vulnerable	Expected value
Antarctica	1.75	1.31	0.37	0.13	3.56
Australia and New Zealand	0.79	0.98	0.37	0.08	2.21
Caribbean	0.55	3.06	1.57	0.57	5.74
Central America	3.05	9.84	5.43	2.40	20.72
Central Asia	3.71	2.95	0.79	0.36	7.81
Eastern Africa	5.73	11.23	5.03	2.05	24.04
Eastern Asia	6.30	11.29	7.36	1.65	26.60
Eastern Europe	6.92	5.80	2.48	0.94	16.13
Melanesia	1.05	5.30	2.00	1.05	9.40
Micronesia	0.56	0.04	0.05	0.01	0.66
Middle Africa	3.48	4.28	1.63	0.92	10.32
Northern Africa	0.20	1.35	0.30	0.09	1.95
Northern America	0.06	0.90	0.50	0.14	1.60
Northern Europe	0.09	7.66	1.95	0.41	10.10
Polynesia	1.41	4.38	1.23	0.98	8.00
South America	12.77	35.40	15.24	8.59	72.00
South-Eastern Asia	9.29	18.70	9.83	4.54	42.37
Southern Africa	1.23	2.97	1.13	0.50	5.83
Southern Asia	5.79	5.65	2.48	0.91	14.83
Southern Europe	12.22	12.86	5.41	1.40	31.88
Western Africa	2.55	2.85	1.64	0.84	7.89
Western Asia	6.60	9.33	2.99	1.36	20.28
Western Europe	1.09	1.83	1.13	0.29	4.33

4.4 Discussion

It was possible to predict the IUCN Red List category of Data Deficient species with a sensitivity of 60.5% and a specificity of 65.0%. IUCN Red List category was mainly determined by the number of occurrence records and countries for each species, the phylogenetic group, the woodiness and the continent where species occurred. Species that were assessed on the IUCN Red List more than 10 years ago were predicted with a similar accuracy to species assessed more recently. Of the 1,732 Data Deficient species, 117 were predicted to be extinct and 815 were predicted to be threatened. If a regional focus for assessing Data Deficient species is a priority, then South America would be the region to focus efforts on first.

Least Concern species appear to have greater numbers of occurrence records and native distributions that extend to more countries than species that are assessed as threatened, consistent with earlier studies (Rivers *et al.*, 2011). 60% of all plant species are estimated to be endemics (Bachman *et al.*, 2017), compared to 72.8% on the IUCN Red List. The responsibility for saving endemic species that are threatened lies within that country (Rodrigues and Gaston, 2002; Schuldt and Assmann, 2010). It may be possible to calculate extent of occurrence (EOO) and area of occupancy (AOO) with high accuracy for 71.7% of the Data Deficient species, because they have 15 or more occurrence records (Rivers *et al.*, 2011). This would help inform IUCN Red List assessments because EOO and AOO are often used as part of assessing criterion B, and there are tools available to estimate both EOO and AOO with occurrence data such as GeoCAT (Bachman *et al.*, 2011) or the rCAT package (Moat and Bachman, 2017).

Considering habits of species already assessed it seems that woody species are more threatened than other species, as are magnoliids. The species assessed were not from a random sample however, and so it is possible that IUCN Red List category is overestimated in both groups. This may affect the predictions for the Data Deficient species too.

53.8% of Data Deficient species are predicted to be threatened compared to 53.1% in whole IUCN Red List, but 21.4% in the Sampled Red List Index. Our analysis is based on the whole IUCN Red List, which overestimates extinction risk (Brummitt *et al.*, 2015), so it is possible that extinction risk in these Data Deficient species is also overestimated. Other research however has also shown elevated extinction risk of Data Deficient species both in mammals (Bland *et al.*, 2015; Jetz and Freckleton, 2015) and amphibians (Howard and Bickford, 2014). This suggests that Data Deficient species overall are more likely to be threatened and should therefore not be neglected in species conservation.

The predictive capabilities of the model are similar for newer and older IUCN Red List assessments. The IUCN categories changed in 2001 (IUCN, 2012b), and no assessments took place in that year. There was no change in the percentage of correct and false predictions in the years before 2001 compared to assessments after 2001.

IUCN Red List assessments should be repeated every 10 years, but 17% of assessments are older (Rondinini *et al.*, 2014). Around \$400,000 is spent annually by the IUCN on reassessments (Rondinini *et al.*, 2014), so using predictive models could help to prioritise which species to reassess first, by using those where model predictions were incorrect.

While it appears that many of the Data Deficient species in Ecuador and South East Asia are threatened, this is also where most of the Data Deficient species occur. When comparing the percentage of threatened plants per country to the assessments made by Brummitt *et al.* (2015), the overall global pattern of threat is similar, except that the percentages of threatened species estimated by us are much higher than those estimated by Brummitt *et al.* (2015). This might be due to overestimates of extinction risk on the IUCN Red List compared to the Sampled Red List Index. Differences include South Africa, Mexico and Australia, which were estimated to have a higher percentage of threatened species by Brummitt *et al.* (2015), but Australia and South Africa have comparably low numbers of Data Deficient species. Ecuador and Cameroon were estimated to have a higher percentage of threatened species by us compared to Brummitt *et al.* (2015).

Combining IUCN Red List categories into two threat statuses – threatened or non-threatened – can improve the accuracy of models. Darrah *et al.* (2017) for example have predicted extinction risk of bulbous monocotyledons, and their models predicted 88% of threatened species and 93% of non-threatened species correctly. In comparison, the Bayesian Network models used here predicted 60.5% of threatened species and 65% of non-threatened species correctly which is considerable lower. However, Darrah *et al.* (2017) predicted extinction risk for species from two orders within one class, whereas I predicted extinction risk of species from seven classes within three phyla. While reducing the number of categories improves model performance, the problem with this approach is that species that are predicted to be Critically Endangered cannot be distinguished from those that are Vulnerable for example, so prioritising plants with a very high risk of extinction would not be possible. Using threatened versus non-threatened categories only, as opposed to IUCN Red List categories, may also be too

coarse to detect whether the model predicts newer assessments better than older assessments.

Vol can help to decide when more research is necessary, and when to act to save a species (Runge *et al.*, 2011), or in this case, make an IUCN Red List assessment. As an example, I calculated the Vol for different regions, but this could be similarly done for different countries, taxonomic groups, or habitats. The calculations suggest that South America would be a good place to start making more assessments. Brummitt *et al.* (2015) found that on the Sampled Red List Index, more threatened plants occurred in the Neotropics, which include all of the South American region considered here.

Decision makers could also make use of the probabilities of Data Deficient species to be in a certain category. For example, species with a high probability of being threatened or extinct may be prioritised for IUCN Red List assessments. If suitable conservation actions for such species are known (which may be unlikely), they may not even be assessed but conservation action may be taken straight away. Alternatively, those species may be prioritised for IUCN Red List assessment where uncertainty from the predictions is very high, for example species that are predicted to be in a certain category with a probability of less than 50%.

It is possible to predict extinction risk of species using taxonomic, trait and occurrence information, even at a global level and with high uncertainties. Data Deficient species may be more threatened than the application of the category implies, and where possible those species should be reassessed to find their true threat status. With more and more global datasets on species' traits and occurrence information, we can use these predictions to help inform global targets like the Global Strategy for Plant Conservation, whilst being cautious about the uncertainties at various levels in the data.

Chapter 5 Predicting numbers of tigers *Panthera tigris* using publicly available data

Abstract

Conservation managers and policy makers often have to make time-sensitive decisions about species without all of the necessary information. For example, information that is available for analysis is rarely collected in a standardised manner or is inaccessible. It is important therefore to analyse existing information whilst accounting for uncertainty arising from the way that data have been collected and made available. I examined this issue in the tiger, analysing publicly available data on a standard set of variables (including habitat data, site designations, tiger numbers and poaching levels) and gathered at the same spatial scale (Tiger Conservation Landscapes) across the species' range to assess what determines tiger numbers. I built Bayesian Networks for analysis as they are well suited to dealing with uncertainty. I tested a range of algorithms to create models and used the best performing model to determine the most important variables. Higher tiger numbers were correlated with source sites, World Heritage Sites and number of poached tigers. This indicates the value of successful management, but could mean that successfully managed sites are specifically targeted by poachers. Habitat loss appeared to have little effect on tiger numbers. The model predicted tiger numbers correctly for 91% of TCLs. Even for a species of high conservation interest, relevant data at the same scales are not always available for decision making which can hamper efforts to save the species.

5.1 Introduction

Conservation decision making is beset by inadequate information and high uncertainty. The complexity of the ecological and social contexts within which decisions are made is increasingly understood. It is evident that in most cases we will never have all of the information needed to eliminate uncertainty about outcomes (Regan *et al.*, 2005). Not only are there great uncertainties, but often data are collected across different temporal or spatial scales, making it difficult to analyse such data. These problems of scale are not new (Levin, 1992), but they still exist today (Chave, 2013). Choosing appropriate spatial

scales is important for effective decision making in conservation so different interventions can be compared (Guerrero *et al.*, 2013), especially for wide-ranging species (Wheatley and Johnson, 2009).

5.1.1 Tigers

Tigers used to occur from the Russian Far East all the way across Asia into Turkey and South into Java (Sanderson *et al.*, 2006). The decline in the global tiger population is both well established (Dinerstein *et al.*, 2007; Goodrich *et al.*, 2015) and the subject of considerable attention from both civil society and governments (see Joshi *et al.* 2016). Despite a wealth of research establishing the tiger's ecological requirements and the pressures on populations, uncertainty around the overall population remains. Tigers are listed as Endangered on the IUCN Red List of Threatened Species (Goodrich *et al.*, 2015), and three of the six subspecies, namely the South China tiger, the Sumatran tiger and the Malayan tiger, have been classed as Critically Endangered (IUCN, 2017).

Recent changes in tiger numbers are thought to be driven by poaching (Wikramanayake *et al.*, 2011). Tigers themselves are poached due to international demand for tiger parts, and tiger prey are poached for local consumption or local trade (Dinerstein *et al.*, 2007; Walston *et al.*, 2010; Wikramanayake *et al.*, 2011). Tigers also kill humans and livestock, which leads to human-tiger conflict (Goodrich, 2010). This conflict is exacerbated by the continued expansion of the human footprint into tiger landscapes and the expansion of the domestic livestock herd across the tiger's range (Nyhus and Tilson, 2010). Habitat loss also affects tiger numbers, especially in South East Asia, where habitat is being converted at faster rates than elsewhere in the tiger range. Previous rapid habitat loss elsewhere has slowed (Joshi *et al.*, 2016). Some areas are also at risk of fragmentation due to the development of new infrastructure (Wikramanayake *et al.*, 2011).

India was the first country to tackle the tiger decline by protecting all tigers through the Wildlife Act of 1972, and by declaring a number of protected areas for tiger conservation under 'Project Tiger'. Across their range, tigers were first safeguarded in protected areas until the notion of Tiger Conservation Units emphasised that tigers can only be fully conserved in expansive landscapes as tigers range over large areas

(Sanderson *et al.*, 2006). This work then developed into what are now called Tiger Conservation Landscapes (TCLs) that overlap some (but not all) Tiger Conservation Units (Sanderson *et al.*, 2006). More recently, core sections of some TCLs have been considered tiger source sites and therefore central to solving the tiger 'crisis'. These sites have tiger populations big enough to populate adjacent areas (Walston *et al.*, 2010).

There is considerable interest and funding for conserving tigers, as demonstrated by the Tiger Summit in St. Petersburg in 2010. This was the first global summit held to save a single species, where the World Bank pledged \$100 million to tiger conservation (Global Tiger Initiative, 2010). Tigers are relatively well studied too: a search of *Panthera tigris* in the Web of Science returned 319 entries since 2013 (15/11/2017). At the same time, there are differing views about whether the efforts of tiger conservation should be focused primarily on protected areas (Walston *et al.*, 2010) or whether wider landscape approaches should simultaneously be addressed (Wikramanayake *et al.*, 2011), whether tiger numbers are increasing (WWF, 2016) or not (Karanth *et al.*, 2016), and whether there are six extant subspecies (Luo *et al.*, 2004) or two (Wilting *et al.*, 2015), and why tigers appear to be doing better in India and Nepal for example, compared to some areas in South East Asia (IUCN, 2017). Furthermore, it appears that no evidence syntheses or meta-analyses have been undertaken to collate findings and inform which conservation actions are likely to be most effective.

5.1.2 Aims

We sought to determine which variables were most strongly associated with tiger numbers in different contexts whilst accounting for the considerable uncertainty inherent in the available evidence. We identified TCLs as our unit for analysis since data on habitat across the tigers' current range were available for them, and the Global Tiger Initiative (2011) identified TCLs as appropriate units for conserving tigers.

5.2 Methods

There was a lack of literature on the whole tiger range, with many papers discussing case studies only. Tiger management usually takes place at a reserve or site-scale rather than at the whole TCL scale. Many papers reported their findings at site scale with site specific objectives and data gathering approaches. There was also a lack of studies that

compared across different sites. Additionally, it is likely that most information on tiger numbers is held by the range of countries and conservation NGOs that manage tiger reserves which is not always publicly available. Since habitat information was available for all TCLs, we based our analysis on this scale and worked from there finding other information that may be relevant for tiger conservation.

5.2.1 Data sources

We searched for publicly available data on tigers in Google Scholar and Web of Science, using the search term “tiger conservation landscapes” which was our unit of analysis. The searches resulted in a total of 159 papers (14/08/2017). Of those, 155 were concerned with one or a few tiger conservation landscapes only, or did not study tigers at all. The use of the other four is outlined below. All data used are shown in appendix S8.

A key report was identified: “Setting priorities for the conservation and recovery of wild tigers: 2005–2015”, written by a range of conservation NGOs, that used the notion of TCLs across the tiger’s range (Sanderson *et al.*, 2006). The location of each TCL was specified together with total area, habitat area suitable for tigers and how many tigers it could support, area of the largest habitat patch suitable for tigers, whether the TCL had a designated Ramsar site, World Heritage Site or a United Nations Educational, Scientific and Cultural Organisation Man and Biosphere reserve (MAB) within it, and whether other large megafauna, namely Asian elephants *Elephas maximus*, Indian rhinoceros *Rhinoceros unicornis*, Sumatran rhinoceros *Dicerorhinus sumatrensis*, Javan rhinoceros *Rhinoceros sondaicus* or orang-utans *Pongo pygmaeus*, were present, all contained in Sanderson *et al.* (2006). Habitat area and potential tiger numbers that the habitat could support were updated using recent estimates of forest loss by Joshi *et al.* (2016). The percentage of the total TCL that was a protected area was included (Forrest *et al.*, 2011), and whether the TCL was considered a source site, a potential source site, or was not considered a source site (Walston *et al.*, 2010).

We then extended the search to include information on tiger numbers and poaching. We mapped seized tiger parts to the different TCLs (<http://wildlifetracker.org/?db=tigers>, last accessed 14/08/2017), which were first

listed in a report by Verheij *et al.* (2010). We split the seizures into two groups – either tiger parts found within a TCL, or within 50km of a TCL.

Tiger numbers are usually reported by country, but for our analysis estimates of tiger numbers in each TCL were needed. As these were not given in the original TCL assessment, we used estimates that had been cited in the IUCN Red List entry for tigers (Wibisono *et al.*, 2009; Lynam, 2010; Jhala *et al.*, 2011; D'Arcy *et al.*, 2012; O'Kelly *et al.*, 2012; Sunarto *et al.*, 2013; Dhakal *et al.*, 2014; Goodrich *et al.*, 2015; Duangchantrasiri *et al.*, 2016). We also used data from Walston *et al.* (2010) who listed tiger source sites and the corresponding tiger numbers, and matched these to the TCLs. If we were not able to find estimates for tiger numbers within a TCL, this landscape was then classed as having “low” tiger numbers – see also section 2.5 on data discretisation below. We have included data in the supplementary material.

Parts of some of the TCLs were considered separately as tiger source sites (Walston *et al.*, 2010), which listed current spending for protection and monitoring, as well as an assessment of tiger numbers within the source site only. All source sites were used to plot the spending in each tiger source site per tiger. For Indonesia only the total spending for all TCLs combined was reported, so the cost per tiger nationally was used.

5.2.2 Data preparation

Tiger densities are directly linked to prey densities, and as prey densities vary across bioregions naturally, so do the carrying capacities of tigers (Sanderson *et al.*, 2006). The bioregions were used as defined in the TCL assessment of 2005 (Sanderson *et al.*, 2006): the Indian subcontinent bioregion which included most of India as well as Bangladesh, Bhutan and Nepal; the Indochinese bioregion which included some of the most easterly parts of India as well as Cambodia, Laos, Myanmar, Thailand and Vietnam; the Russian Far East bioregion which included Russia and northern China, and the South East Asian bioregion which included Indonesia and Malaysia. These bioregions were roughly equivalent with the tigers' remaining subspecies as defined by Luo *et al.* (2004) – the Bengal tiger in the Indian subcontinent, the Amur tiger in the Russian Far East, the Northern Indochinese tiger in Indochina and both the Malayan and Sumatran tigers occurring in the South East Asian bioregion. The South China tiger subspecies is likely to

be Extinct in the Wild as it has not been seen since the 1970s (Goodrich *et al.*, 2015). A more recent analysis found only two subspecies however (Wilting *et al.*, 2015). We calculated the percentage of carrying capacities achieved in different TCLs by dividing the number of tigers by the potential number of tigers in each TCL (Sanderson *et al.*, 2006).

Using Bayesian Networks (BNs) on a mixture of discrete and continuous variables is computationally difficult so we split continuous variables into groups of equal counts. We used five different discretisations where possible: we split continuous variables into groups of two, four, six, eight or ten equal counts. We built models with the different discretisations, and used the best-performing model for analysis.

The only exception to this method of discretisation was tiger numbers, where viable population sizes were used for discretisation, based on the assumption that a viable population needs a minimum of 25 female tigers, and better still 50 or more, and an assumed sex ratio of two females per male tiger (Smith and McDougal, 1991; Miquelle *et al.*, 2015). We used two different discretisations for tigers: two or three groups (Table 10).

Table 10. Groups of tigers used in models.

Number of groups	Low tiger numbers	Medium tiger numbers	High tiger numbers
2	0 – 37 tigers	NA	More than 37 tigers
3	0 – 37 tigers	38 – 74 tigers	More than 74 tigers

If no estimates of tiger numbers for a TCL could be found, it was assumed that tiger numbers were low, as otherwise by definition a site within the TCL would have been listed as a tiger source site in Walston *et al.* (2010) with information regarding the population size. We used all possible combinations of continuous discretisations with both tiger discretisations, then chose the model with the best model fit.

5.2.3 Machine-Learnt BNs

BNs are probabilistic models in which variables are linked through arrows, called arcs, and whose relationships are described through conditional probability tables (Nagarajan *et al.*, 2013; Scutari and Denis, 2014). BN model structures can be expert elicited or built using Machine Learning algorithms. We used one classifier and two

Machine Learning algorithms: the Naïve Bayes classifier, the hill-climbing algorithm, both implemented in the bnlearn package in R (Scutari, 2010) and the greedy thick thinning algorithm, implemented in GeNIe Modeler (Bayes Fusion LLC, 2017) to devise the structure of our network.

Naïve Bayes uses a fixed model structure in which the variable to be predicted (in our case tiger numbers) is the centre of the network, and points to all other variables in the network (Nagarajan *et al.*, 2013). Both the hill-climbing and the greedy thick thinning algorithms are score-based, which means that goodness-of-fit statistics are used to find the best network structure (Scutari and Denis, 2014). A network starts with no arcs between variables. Then one arc is added to the network, and this network is given a score. Then a second arc is added to the network, which is again given a score. If the second score is higher than the first, both arcs stay. If the score of the first network is higher, then the second arc is removed. This is repeated until the score increases no further (Nagarajan *et al.*, 2013). The hill-climbing algorithm (Nagarajan *et al.*, 2013) adds, removes and reverses arcs until all possible options are exhausted. The greedy thick thinning algorithm (Cheng *et al.*, 1997) adds one arc, then the next, until all possible arcs are exhausted. It then removes one arc at a time, until all possible arcs are exhausted.

We checked model fit with 10-fold cross-validation for tiger numbers in GeNIe Modeler (Bayes Fusion LLC, 2017). Observations, in our case TCLs, were randomly divided into equal parts and the conditional probabilities were recalculated using nine of these parts, called the training set. The data that were not used to build the model were then predicted, called the test set (Marcot, 2012; Nagarajan *et al.*, 2013). In our case tiger numbers of the test set were predicted, and could be compared with the real tiger numbers in a particular TCL. The number of correct predictions can be expressed as a percentage, called the accuracy.

5.2.4 Scenario and sensitivity analysis

Scenario analysis was used to examine which variables in the model were key and therefore warrant further investigation (Marcot, 2012; Stewart *et al.*, 2013), first by setting tiger numbers in the BN to 100% high, and then setting them to 100% low. This is also known as one-way sensitivity analysis, and can lead to changes in the states of other

variables in the network. We recorded the variables with changes of more than 10% between the states, and plotted them from the raw data.

There was considerable uncertainty around some of the variables in the model. We therefore varied these in the model to test whether changing them would lead to different model outputs. As tiger numbers of some TCLs were unknown, we varied the categories of these TCLs in the final model to half low and half high. Similarly, the numbers of seized tigers were not collected systematically, so we varied the four categories with one at 70% and the other three at 10% each, and repeated this three times. None of these sensitivity analyses had a substantive impact on model outputs.

5.3 Results

5.3.1 Realised tiger numbers against habitat capacity

We calculated carrying capacities of TCLs by dividing the actual tiger numbers by the potential tiger numbers listed in Sanderson *et al.* (2006). Of 76 TCLs, 21 (27.6%) achieved at least half of their carrying capacity (Figure 25). Of these, five (6.6%) have carrying capacities above 100%, possibly because potential tiger numbers in Sanderson *et al.* (2006) were incorrect for those sites, particularly in the Sundarbans. While the percentages are variable in the Indian subcontinent, the Russian Far East and South East Asia, the highest achieved carrying capacity in Indo-China was 2.2%.

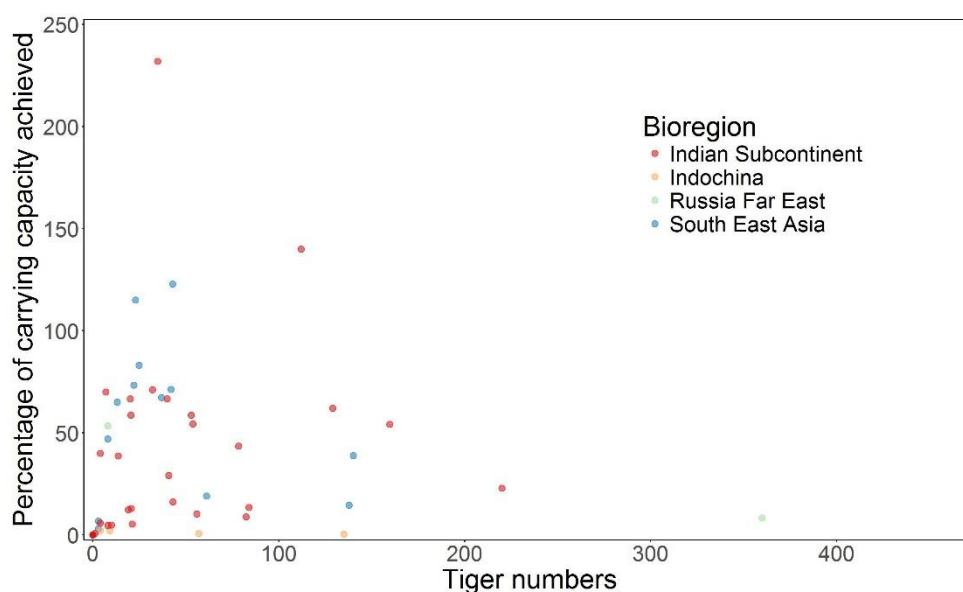


Figure 25. Tiger numbers and carrying capacity achieved at different TCLs, by bioregion. One outlier removed, Sundarbans with 470 tigers and 1880% carrying capacity.

5.3.2 Spending at source sites

Costs of conservation per tiger were calculated to examine whether differences in tiger numbers across bioregions were linked to differences in funding. The spending per tiger in each individual tiger source site ranged from \$5,640 to \$220,200 (Figure 26). The costs per tiger were very variable for sites with low densities, for example the lowest cost per tiger was \$5640 at a site with 1.5 tigers per 100km², and the second highest was \$101,200 at a similar density of 1.8 tigers per km². Most of the source sites were in the Indian subcontinent (21), with seven in South East Asia, six in the Russian Far East and three in Indochina. The Indian subcontinent had the sites with the highest densities and associated lowest costs. Of all sites, 18 had low tiger numbers and did not have minimum viable population sizes (Smith and McDougal, 1991; Miquelle *et al.*, 2015). Tiger densities varied from 0.1 tigers per 100km² to 22 tigers per 100km².

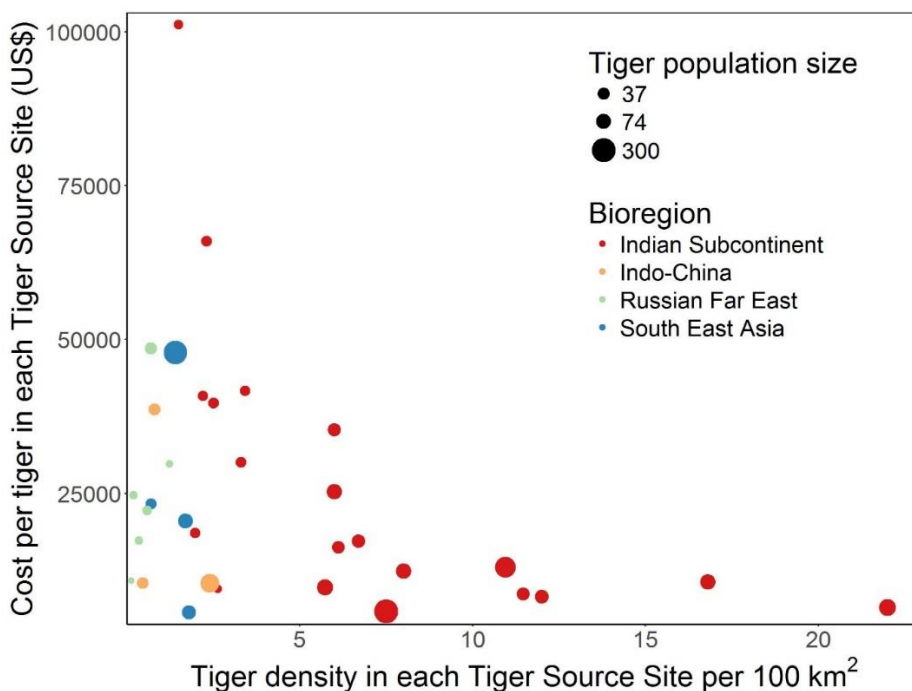


Figure 26. Tiger density per 100km² and spending per tiger in each Tiger Source Site in US\$. Bioregions in which Tiger Source Site is located is shown as well as tiger population size. One outlier was removed, the Indian part of the Sundarbans source site, with spending of \$220,000 per tiger, a tiger density of 0.84 and a tiger population of 22. Two sites are overlapping, with a cost of \$25,300 per tiger, a density of 6 tigers/100km² and populations of 35 and 78, both located in the Indian subcontinent.

5.3.3 BN analysis

We created BNs with five different discretisations for continuous variables, two different discretisations for tiger numbers, two different algorithms and one classifier. We

checked accuracy to find the best model fit (Figure 27). The model that used two groups for tiger numbers, eight groups for the other variables and was built with a greedy thick thinning algorithm performed best, see appendix S7. It predicted tiger numbers as either low or high correctly in 91% of cases. The models that used two groups of tiger numbers predicted these better than those that used three groups.

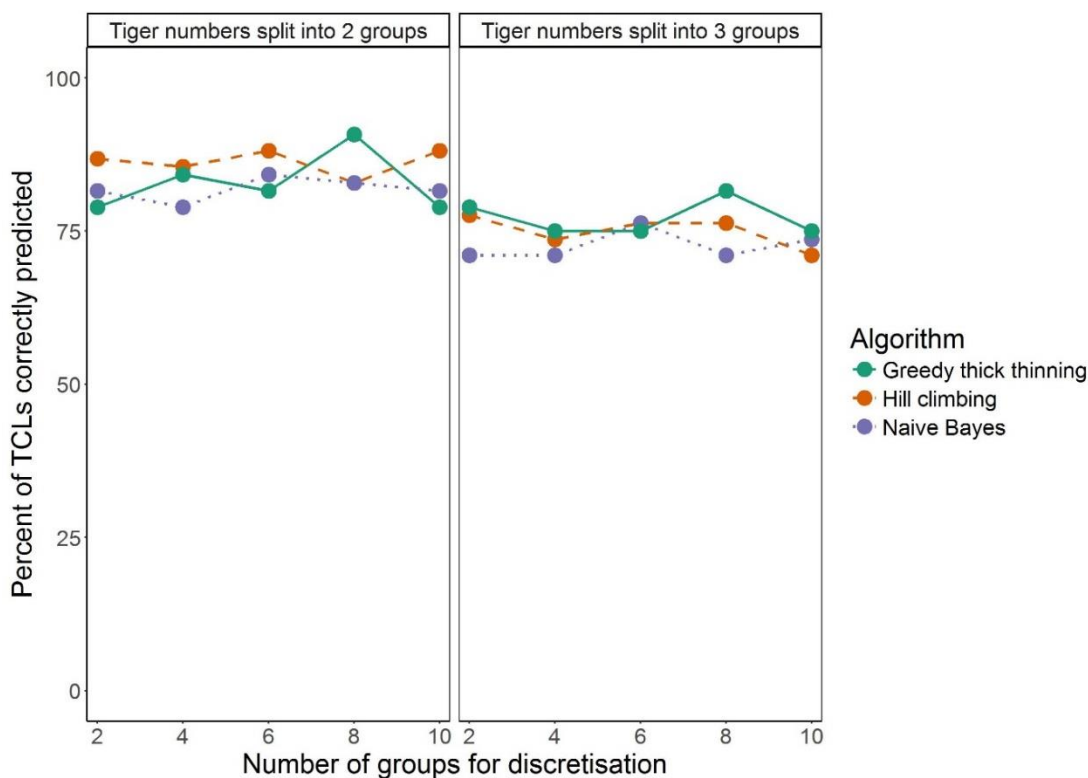


Figure 27. Accuracy of predictions of different discretisations and algorithms.

We used the best performing BN to run scenario analyses providing probabilistic predictions of variable states by changing tiger numbers to 100% low (worst case) or 100% high (best case). Changing tiger numbers in the BN led to changes in the states of the other variables. Four variables had individual states which changed by more than 10% - the numbers of seized tigers either within the TCL or within 50km and whether the TCL was a source site, or a World Heritage site. Habitat loss was very similar between the two scenarios, with no state changing more than 2%. Equally, bioregion changed little between scenarios, with no bioregion changing by more than 4%.

The number of seized tigers, both within the TCL and within 50km, increased with higher tiger numbers in the TCL (Figure 28). Tigers seized in TCLs were highest in the Indian subcontinent. Fewer tigers were seized in South East Asia and the Russian Far East compared to the Indian subcontinent and Indochina within 50km of a TCL.

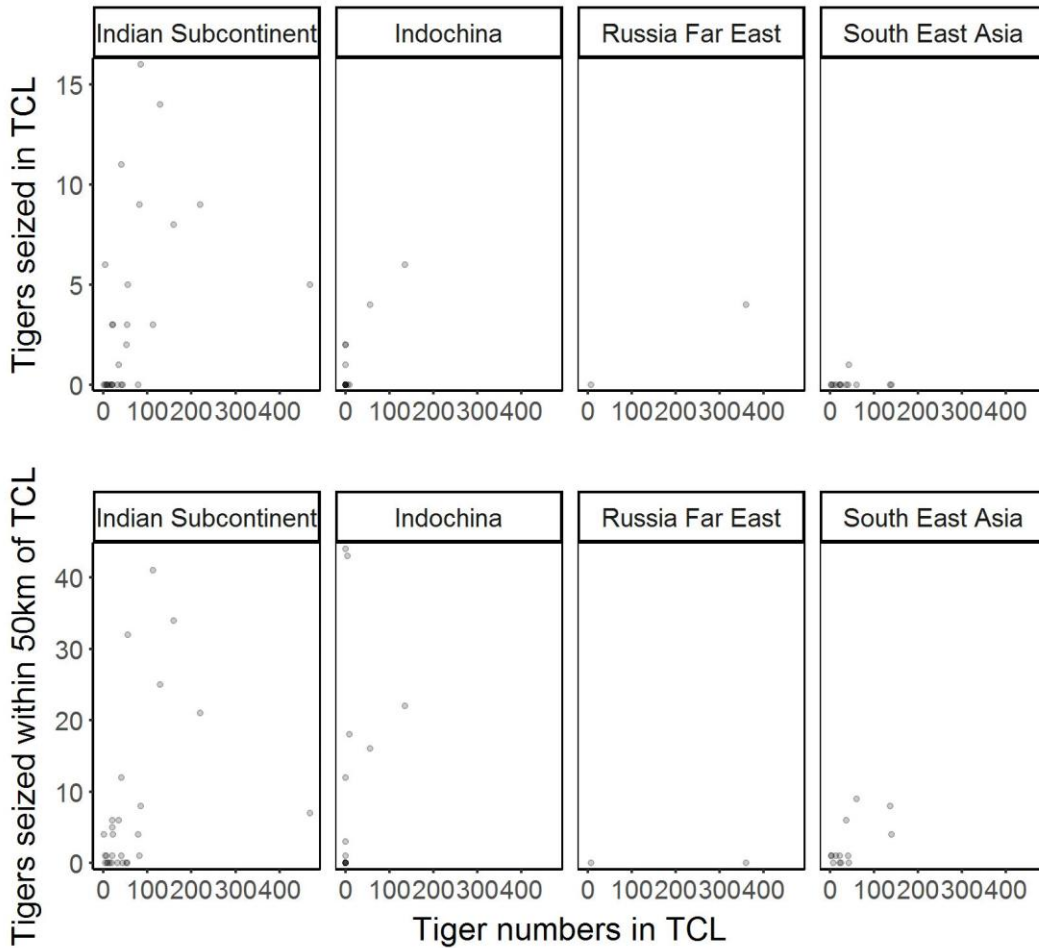


Figure 28. Tiger numbers in TCL, by tiger numbers seized within TCLs (top) and outside of a TCL but within 50km (bottom). All four bioregions shown.

By definition, tiger source sites were those that had large enough tiger populations to populate other areas. Source sites had higher tiger numbers than sites that were not source sites (Figure 29). Similarly, TCLs that were well protected and contained high tiger numbers were more likely to be World Heritage sites.

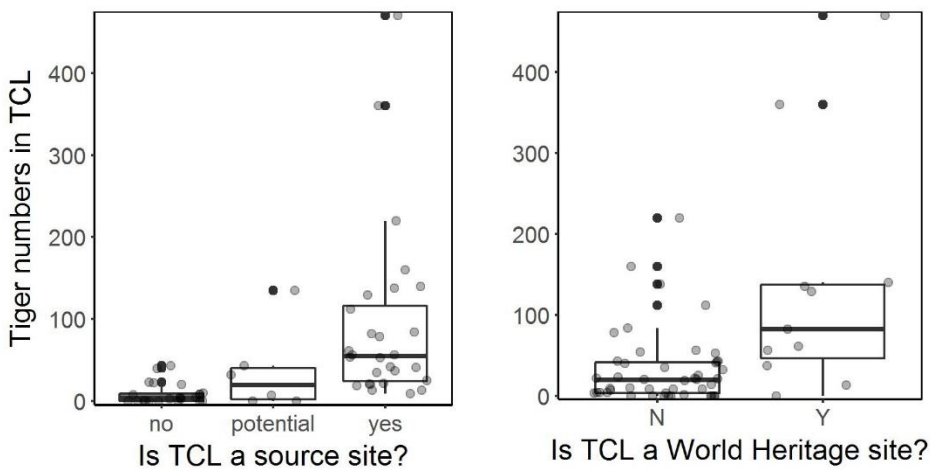


Figure 29. Source sites (left) and World Heritage Sites (right), by tiger numbers in TCL. All four bioregions shown. Each circle represents one TCL.

Habitat loss on the other hand appeared to have little effect on tiger numbers (Figure 30). Larger TCLs experienced higher habitat loss, and may therefore still be able to support the number of tigers found in them since tigers were not at carrying capacity in most of the TCLs. Habitat loss was lowest in TCLs in the Indian subcontinent, but variable in the other bioregions.

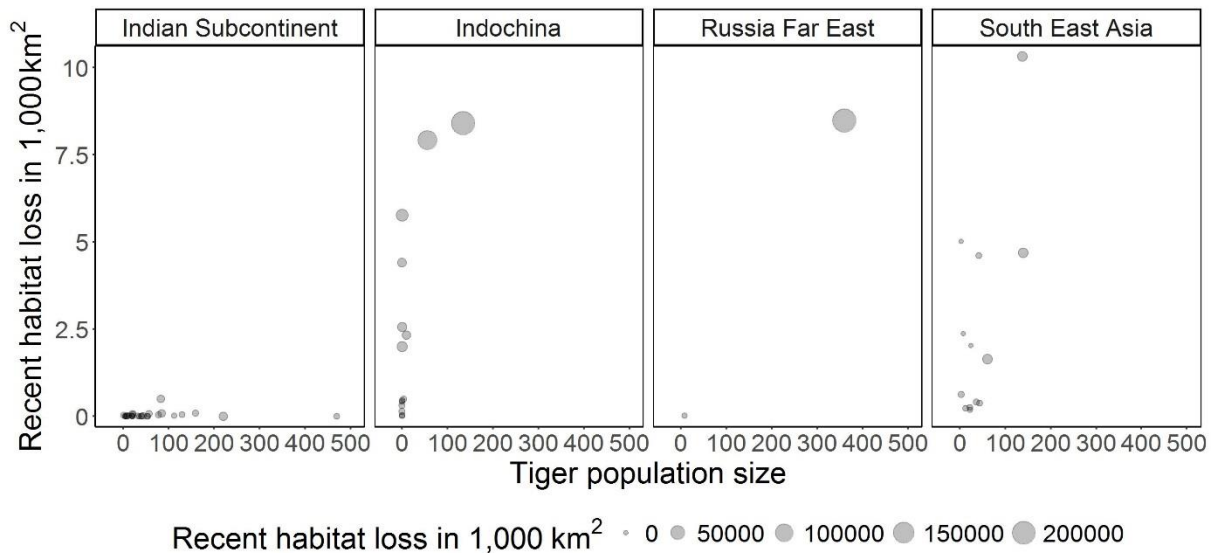


Figure 30. Habitat area and habitat loss in different TCLs, split by bioregion. Size of point reflects the tiger population in the TCL.

5.4 Discussion

Despite the huge amount of literature on tigers, and the pressing need to conserve what is left of the global tiger population if we are to save it from extinction, there is still uncertainty around how best to pursue tiger conservation. Tiger numbers in many of the 76 different TCLs are not near or at carrying capacity, and are particularly low in the Indochinese bioregion. The better protected a site is, the more tigers seem to be able to survive. TCLs that support more tigers have seen more tiger seizures too. Habitat loss on the other hand does not appear to have clear links to tiger numbers.

We investigated first of all whether there were big differences between bioregions in terms of tiger numbers, but both the numbers of tigers and the carrying capacities differ within bioregions. This is partly linked to different natural tiger densities (Sanderson *et al.*, 2006), as indicated by one Russian TCL with high tiger numbers but low carrying capacity. There also appears to be little effect of spending on tiger numbers, but cost per tiger declined with increasing tiger densities. Tiger populations

with high densities in the Indian subcontinent were cheap to protect per tiger as they are often smaller and the threats to them appear to be easier to mitigate. Tiger populations with lower densities had very variable costs per tiger. While our analysis does not reflect all of the funding going to tiger conservation, it appears indicative and would benefit from more accurate information on costs.

Both TCLs that contain source sites and those that are World Heritage sites have higher tiger numbers. Source sites do make a difference to tigers. Not surprisingly the model showed that the best protected and managed places are where most tigers are, indicating the importance of effective protection and management. It is possible that World Heritage Sites may see more tourism than other sites and may, therefore, be less subject to poaching, or receive higher levels of scrutiny and management may be more effective. This is likely since most of these sites are also source sites.

Scenario analysis showed that the number of seized tigers, both within the TCL and within 50km of it, are higher at those TCLs that have higher tiger numbers. More tigers may attract more poachers, which may lead to higher numbers of seizures. It is also possible that sites with higher tiger numbers see more enforcement, and seized tigers are more likely to be recovered in them than in sites with low rates of enforcement (and therefore low numbers of tigers).

The amount of habitat loss appears to have had little effect on tiger numbers. The five TCLs with highest habitat loss are well below their carrying capacities - 14.6% is the highest percentage of achieved carrying capacity of these five. While our analysis does not account for habitat fragmentation, these results suggest that stopping poachers is the crucial part for tiger conservation, while habitat protection can only lead to more tigers in combination with better law enforcement.

There are clear differences in the number of tigers between bioregions but these differences stay the same in the scenario analysis. This indicates that even if substantial efforts were made to protect tigers outside the Indian subcontinent, it would be difficult to increase tiger numbers to levels comparable with the Indian subcontinent. Increasing numbers in Indochina, however, looks to be more feasible from the analysis than in the South East Asian bioregion or the Russian Far East due to the large difference between

actual and potential tiger numbers. Both poaching pressure and habitat loss appear more pronounced in Indochina compared with the other bioregions. Further research is needed to find out what exactly is affecting this bioregion so badly that carrying capacities are not above 2.2%. There is not one bioregion in which all tiger populations are at or near carrying capacity, but it is not clear why some countries, most notably India, are doing better at protecting tigers than others.

To our knowledge no range-wide evidence synthesis of what appears to work in tiger conservation, and why, has been published. We have provided a starting point in analysing in a standard way what is known about tigers and the threats they face across their range. One of the biggest problems we faced in our analysis was bringing together data sources from the very large range of tiger studies that are usually reported either at site, TCL or country scale. The extent of this challenge is shown by the extensive description in the Methods section of this process and the work needed to make the available data suitable for standardised and repeatable analysis. There are examples from other fields of science where outcomes are used, agreed in advance, to ensure that the same variables are measured, such as the COMET initiative for clinical trials (COMET Initiative, 2017). The outcomes are agreed for different health conditions, with the aim of reporting the outcomes from clinical trials. Core outcome measures have been used in 227 studies between 1981 and 2014 in 29 different areas of health research (Gorst *et al.*, 2016). Guidelines on choosing and reporting of core outcome measures in health research are available (Kirkham *et al.*, 2016) and could be adapted for ecological research, for example by including information about the phylogeny, spatial and temporal scales. This would help with conducting systematic reviews and meta-analyses (Kirkham *et al.*, 2016). Gargon *et al.* (2014) suggest that core outcome measures are usually chosen by a range of stakeholders, and in ecology this could comprise scientists, site managers and the local population.

There are already standards to improve the effectiveness of tiger management with the Conservation Assured Tiger Standards (Conservation Assured, 2017). They could form a basis of core outcome measures that should be reported in tiger studies, and would likely include information regarding the spatial scale of the study, tiger and

prey populations, poaching levels of both tigers and prey, habitat loss, different management interventions used alongside their costs as well as metrics relating to the local human population. This is crucial to make scientifically robust comparisons across the tigers' range. The Global Tiger Recovery Program 2010 – 2022 states that innovative science, regular monitoring of tigers and their prey, and adaptive management are integral to saving tigers (Global Tiger Initiative, 2011), and is well placed to find a set of sensible core outcome measures to ensure tigers will not go extinct and to support the global goal to double the number of wild tigers.

Chapter 6 Discussion

6.1 Major findings

The aim of my thesis was to consider how to deal with uncertainty in different stages of the decision-making process in conservation, from Red Listing to taking action to save species. Value of Information (VoI) offers a way of quantifying the level of uncertainty, indicating where it is high and identifying areas of research where it is especially important to minimise uncertainty. I have explored the use of VoI in biodiversity conservation and found 30 papers to date that use the method in a variety of settings. There is uncertainty regarding which species are threatened that is impeding the conservation of those species. I therefore predicted extinction risk of plants in the Caatinga ecoregion in Brazil, and predicted 68 species to be threatened in addition to the 27 threatened species that have been assessed already. There is also uncertainty about the risk levels of Data Deficient species globally, so I predicted extinction risk for 1,732 Data Deficient plants worldwide. I predicted 815 to be threatened, and 117 to be Extinct. I also explored uncertainty in what drives the number of tigers in different Tiger Conservation Landscapes, the only spatial scale where there are data on a range of variables throughout the species' range. There is only limited data on Tiger Conservation Landscapes, but the available data suggest that poaching is the determining factor in the number of tigers in each landscape, and habitat loss and conservation management spending per site are not. To explore whether the use of VoI could be extended to other topics in conservation, I used VoI as a way of prioritising which plant species to assess on the Red List first. There was not enough information on tiger conservation actions at the right spatial scales to use VoI however, suggesting that we can extend the use of VoI in some but not all cases. The general discussion below considers the implications of these findings in the wider contexts of science-policy interaction and conservation decision-making.

6.2 VoI in biodiversity conservation

VoI is a method that can be used to distinguish when to act and when to do more research first. It is not a new method, but still relatively uncommon in ecology and biodiversity conservation with only 30 papers to date (chapter 2), though both use and

advocacy is on the increase. The examples I found span a range of management issues, mainly concerning threatened or invasive species. There are also examples of management at a landscape scale. Most of the Vol papers were written by research groups based in the USA or Australia, so there is scope for more application of the method in other regions of the world.

It is unclear to what extent Vol has actually informed management in any of the papers I found. Vol can only make a difference if the results inform management, and it is mentioned in a technical guide from the US Department of Interior (Williams *et al.*, 2009), and recent guidelines for species conservation planning by the IUCN (IUCN – SSC Species Conservation Planning Sub-Committee, 2017). There are many Vol papers from US universities and institutions, and it remains to be seen whether the IUCN guidelines will lead to more Vol papers or implementations designed to save species.

6.2.1 *Measuring net benefits*

In health economics, Vol has been advocated since 1999 (Claxton, 1999) with 59 applied uses of Vol analysis (Tuffaha *et al.*, 2014). There it is used to decide between different treatments for a condition, or to determine whether more research is necessary before a treatment is implemented to improve human health. In the UK, the benefits are estimated as quality-adjusted life years, combining life time and quality of life of a person, which are given a monetary value (Briggs *et al.*, 2006). Quality-adjusted life years are used with cost estimates of different interventions and their effectiveness to calculate the net benefits of different interventions and the Vol. In the 30 biodiversity conservation papers I found, Vol was measured in a variety of ways, from monetary net benefits (Costello *et al.*, 1998) as in health economics to unitless values (Runge *et al.*, 2011) and probabilities of populations persisting (Tyre *et al.*, 2011). Because there is not only one measure of net benefit like in health economics, it is more difficult to compare Vol studies in biodiversity conservation.

Even though the use of Vol is on the increase, the studies I found are almost all focused on single-species management, and undertaken for a particular site. Having to estimate costs and benefits might impede the application of Vol more broadly, as accurate values might be difficult to obtain. For cost data in conservation, many studies

do not detail assumptions, ignore heterogeneity in the data, and use proxies (Armstrong, 2014). Estimates of benefits might equally be difficult to obtain, such as ecosystem service evaluations of human wellbeing (Wegner and Pascual, 2011). These estimates are even more difficult to obtain if considered for larger spatial scales with greater uncertainties, or for more complex conservation problems that go beyond individual species or sites (Keith *et al.*, 2011), and thus inhibiting the use of Vol more broadly.

To facilitate the use of more uniform net benefits, I suggest some ways forward. Costs of interventions can be compared by calculating the benefit that could be achieved through different interventions at different budget levels, without having to put a value on a species or individual (Maxwell *et al.*, 2015). Methods like willingness-to-pay can be used to estimate what a species' value is, though estimates can incorporate a big range of values (Richardson and Loomis, 2009). It would also be possible to divide the annual conservation expenditure for a species by the number of individuals of the species. If a standardised monetary net benefit was used in Vol studies, it would not only be possible to compare species-specific actions, but also actions for different species. For example, we could answer questions such as should we undertake action to save species X, or would we gain more by undertaking action to save species Y. Clearly, achieving this would be difficult, but if we do not have such values, the question remains how we can make rational decisions about alternative actions with finite resources (Bottrill *et al.*, 2008).

6.2.2 Lessons from applying Vol to different settings

There are no papers that use Vol to prioritise for which species groups to do more Red List assessments, or when to undertake conservation action directly, as I have done in Chapters 3 and 4. Both chapters are quite theoretical in nature and the full decision context is not considered. My analyses could be extended however, and objectives could include stopping extinctions or further declines of threatened species.

Management actions could be to undertake further Red List assessments, or to undertake conservation action straight away. Predicting extinction risk and calculating the Vol could help to inform these decisions, using costs of Red Listing and costs of

management. Grouping species into sensible units for management, for example by habitat and location, would help this process, as it is unlikely that species groups such as families can be managed over a large range.

To use Vol, we need a measure of uncertainty around the values we are interested in – be it through predictive models or through expert elicitation. In my Vol calculations, three values contributed to the overall expected value of a group (family or region): the probability of extinction of a category, the uncertainty around species to be in that category, and the number of species that were predicted to be in that category. In both chapters 3 and 4 the groups with most species that were predicted to be Critically Endangered had the highest expected value– the family Bignoniaceae in chapter 3 and South America in chapter 4. As Critically Endangered species have an extinction probability of 0.5, higher than the other categories apart from Extinct, these were driving the overall expected value, and the uncertainties had little effect.

For Tiger Conservation Landscapes (TCLs) it would be possible to use tiger numbers as a basis for a Vol analysis. If there was information available on management costs of interventions and their effectiveness for the different TCLs then the costs could be multiplied with the effectiveness and the tiger numbers. However, this information is not publicly available for all TCLs, and unless conservation NGOs such as WWF hold such information calculating a Vol to inform their funding decisions is not possible. Using core common outcomes would be a way of facilitating Vol calculations, as long as the relevant information is included in the outcomes to be reported.

Decision analysis and adaptive management are important tools that can help ensure that our knowledge then leads to addressing threats to species, and Vol is embedded within them. Difficulties in applying these decision-making tools will therefore also impact on the use of Vol. Criticisms have highlighted that these methods may not include views of diverse stakeholders or non-scientific knowledge (McLain and Lee, 1996), and are impeded by institutional barriers and the difficulties in modelling complex ecological systems (Keith *et al.*, 2011). These problems could partly be addressed by ensuring all relevant stakeholders are considered and setting up the analysis well from the start, as is intended in structured decision-making (Gregory *et al.*,

2012). Approaches such as agent-based models could help to model socio-ecological systems (Rounsevell *et al.*, 2012), and mixed models could help to model patterns of biodiversity by including underlying processes (Brown *et al.*, 2014). Such approaches could help to better predict the effects of different actions on management objectives and so improve both the use of adaptive management and decision analysis, as well as consequently the application of Vol.

6.3 Predicting extinction risk

6.3.1 Contribution to estimates of extinction risk of plants

The first step in saving species has to be the knowledge of which species are threatened, and why they are threatened. While the Red List already contains over 90,000 species (IUCN, 2018b), and Red List Indices and Sampled Red List Indices help us track real change of species' threat status over time (Butchart *et al.*, 2004), none of them tell us what the conservation status of the vast majority of species is, which is crucial to meet global targets to prevent species' extinctions. One way of estimating which species are at risk of extinction is to predict species' threat status. These predictions could be used in different ways, for example to prioritise which species to assess next, or to focus on certain areas as they contain more species at risk.

Of 403,911 described plants (Nic Lughadha *et al.*, 2016), 24,230 species or 6.0% have been assessed on the IUCN Red List (IUCN, 2018b). I have predicted the extinction risk for 1,189 species in the Caatinga, and for 1,732 Data Deficient plants globally. This adds up to a total of 27,151 assessed plant species or 6.7%, and my predictions led to an increase of 0.7%. While 53.8% of Data Deficient species globally were predicted to be threatened or Extinct, only 5.7% of species were predicted to be threatened in the Caatinga. In comparison, the Sampled Red List Index estimated 21.4% of plants to be threatened. The data containing all species on the Red List is likely to overestimate extinction probability, as threatened species are more likely to have been assessed. It is possible that the species assessed so far in the Caatinga are also not a representative sample of threat status mainly because few of them were from the main Caatinga habitat types. Alternatively, plant species in the Caatinga may face fewer threats compared to other areas, and so have a lower probability of extinction.

I confirmed that the number of occurrence records can be valuable for estimating extinction risk of plants, both in the Caatinga and for assessed species globally, as was shown by Rivers *et al.* (2011) for endemic species from the Leguminosae and Orchidaceae families that are endemic to Madagascar. I also showed that taxonomy can be an important predictor for threat status as it was the most important variable for predicting threat status in the Caatinga, similar to findings from Davies *et al.* (2011). However, taxonomy was of less importance when I predicted Red List categories of Data Deficient species globally, which was also found by previous authors (Daru *et al.*, 2013; Cardillo and Skeels, 2016). Drivers for extinction risk might be more uniform in the Caatinga, and might affect closely related species in a similar way. Threats might differ geographically however, and so it is possible that closely related species in different areas globally face different threats, and therefore have different extinction probabilities.

6.3.2 Bayesian Networks and Machine Learning for predicting extinction risk

Bayesian Networks are visual models that use conditional probabilities between nodes. They are useful for combining quantitative and qualitative data, for working with stakeholders as they are visual, and for modelling trade-offs. They are increasingly used for model building with data and various Machine Learning algorithms, but have so far not been used for predicting extinction risk with Machine Learning algorithms. Newton (2010) used a Bayesian Network for predicting extinction risk, but built it as a decision-support tool and not based on data and Machine Learning. Bayesian Networks have also been used with Vol in biodiversity conservation, but again the network structure was constructed by the authors, not by algorithms (Thorne *et al.*, 2015).

There are some examples of studies predicting extinction risks of different taxonomic groups using Machine Learning methods such as decision trees (Sullivan *et al.*, 2006; Leao *et al.*, 2014) or Random Forests (Davidson *et al.*, 2012; Machado *et al.*, 2013; Di Marco *et al.*, 2014; Howard and Bickford, 2014; Pearson *et al.*, 2014; Comeros-Raynal *et al.*, 2016; Darrah *et al.*, 2017), see Table 11. There are examples of studies predicting extinction risk of other groups such as mammals, birds, amphibians and plants, and here I have compared them to the predictions I made in chapters 3 and 4. All the papers listed predicted Red List category or threat status for one class or family,

some with geographic restrictions as well. In comparison, I predicted Red List categories and threat status for plants from three different classes within one phylum in the Caatinga, and from seven different classes within three phyla for Data Deficient plants globally.

I have reported specificity (percentage of correctly classified non-threatened species) and sensitivity (percentage of correctly classified threatened species) from the papers that predicted extinction risk (Table 11). The model predicting Red List category for Data Deficient plants globally performed better in terms of sensitivity than the models from the other papers that predicted Red List category and the Bayesian Network I built for chapter 3, but performed worst in terms of specificity. Some of the papers with high sensitivity had low specificity and vice versa (Machado *et al.*, 2013; Howard and Bickford, 2014; Comeros-Raynal *et al.*, 2016), so there might be a trade-off between predicting threatened species and predicting non-threatened species correctly.

Table 11. Selection of papers that use Machine Learning methods to classify species according to their threat category, and which reported number of species correctly classified. Listed are species groups, type of model, whether Red List category or threat status was predicted, the accuracy of the model (overall correct predictions), the sensitivity (percentage of correctly classified threatened species) and the specificity (percentage of correctly classified non-threatened species).

Paper	Species group	Model	Type of prediction	Accuracy	Sensitivity	Specificity
Comeros-Raynal <i>et al.</i> (2016)	Sea breams and porgies	Random Forest	Red List category	90% (n = 40)	0%	92.3%
Darrah <i>et al.</i> (2017)	Bulbous monocotyledons	Random Forest	Threat status	91.0% (n = 148)	88.0%	93.0%
Davidson <i>et al.</i> (2012)	Marine mammals	Random Forest	Threat status	91.2% (n = 116)	80.0%	97.9%
Di Marco <i>et al.</i> (2014)	African Mammals	Random Forest	Threat status	92.7% (n = 1,044)	80.3%	96.4%
Howard and Bickford (2014)	Amphibians globally	Random Forest	Red List category	73.2% (n = 4,402)	58.1%	83.8%
Machado <i>et al.</i> (2013)	Sea birds in Brazil	Decision trees	Threat status	94.4% (n = 54)	77%	97.8%

Paper	Species group	Model	Type of prediction	Accuracy	Sensitivity	Specificity
Machado <i>et al.</i> (2013)	Sea birds in Brazil	Random Forest	Threat status	90.7% (n = 54)	55.6%	97.8%
Chapter 3	Plants in the Caatinga	BN – Naïve Bayes	Threat status	84.8% (n = 223)	82.9%	85.0%
Chapter 3	Plants in the Caatinga	BN – Naïve Bayes	Red List category	77.0% (n = 223)	57.1%	79.2%
Chapter 4	Plants globally	BN – Hill climbing	Red List category	61.0% (n = 1,732)	60.5%	65.0%

6.3.3 The class imbalance problem

Problems of class imbalance are well-known in Machine Learning (Guo *et al.*, 2008; Galar *et al.*, 2012; Nanni *et al.*, 2015). When the number of observations within one class far outweigh the number of observations of the other class(es), Machine Learning algorithms and classifiers often struggle to correctly classify the minority classes, and instead most or all observations are predicted to be in the majority class. This is also the case for Red List data, where the number of non-threatened species usually far outweighs the number of threatened species, for example threatened plants comprise 21.4% of plant species (Brummitt *et al.*, 2015). This can lead to most species being predicted to be non-threatened, even when they are in fact threatened, which is of little use for conservation purposes.

I have identified three methods to overcome the class imbalance problem. The most common one is to reduce the numbers of groups, by splitting data into two groups: threatened or non-threatened. Most of the papers in Table 11 predicted threat status, i.e. threatened or not, as opposed to Red List category, which generally leads to a higher overall accuracy compared to predicting Red List category.

The second method is to use a Naïve Bayes classifier as I did in chapter 3. It worked well for estimating threat status, and only one study predicted more threatened species correctly (Darrah *et al.*, 2017). Because Naïve Bayes is less sensitive to unbalanced groups for classification, it could be used more regularly for Red List predictions. If splitting the data into two groups only is not an option however, Naïve Bayes does not perform that well as I showed in chapter 4.

The third method I explored to address class imbalance is oversampling, commonly used in Machine Learning. Data can be over- and/or undersampled, by resampling observations from minority classes (oversampling), by removing observations from majority classes, or by combining the two methods. Over- and undersampling can be undertaken in R with the ROSE package (Lunardon *et al.*, 2014). In ecology over- and undersampling have been used for species distribution modelling (Evans and Cushman, 2009; Freeman *et al.*, 2012; Johnson *et al.*, 2012), tree species classification (Piiroinen *et al.*, 2017) and classifying habitat condition (Fox *et al.*, 2017), but not for predicting extinction risk. Oversampling can lead to overfitted models (Galar *et al.*, 2012), but I found no evidence of overfitting in the model used for predictions in chapter 4.

6.4 From Red Listing to saving species

Listing species on the Red List is an important first step in ensuring we know which species might need protection. The next step is to ensure we address the threats species face where possible. In many cases, there may be uncertainty around what the threats to a species or population are, or how best to address them. This is reflected in the Vol literature, for example by Runge *et al.* (2011), Williams *et al.* (2011), Johnson *et al.* (2014a) and Maxwell *et al.* (2015), all examples where Vol was used to decide which conservation action to use for a threatened species, or whether to do more research first.

Despite all our knowledge on tigers, I could not calculate a Vol, whereas for the very limited information on plants this was possible. While predicting extinction risk and assessing conservation actions for a species are very different endeavours, there was also a fundamental difference between them in terms of data availability. The Red List information is standardised, available for a range of species, and with published probabilities of extinction relating to each Red List category. All of the information is freely available online, and there are open data science tools to make workflows reproducible (Lowndes *et al.*, 2017). Other information at species level can be incorporated, as I did in chapter 4. The initial set-up of a tiger conservation database in 2006 was to be made available online, with updated annual survey results to track tiger

numbers over space and time (Sanderson *et al.*, 2006). To my knowledge this has not happened, and no annual survey results are available for Tiger Conservation Landscapes. While there are reasons not to have such a database made public because of poachers (Oksanen and Kumpula, 2013), it would be an invaluable tool for conservation NGOs, governments of tiger range countries and scientists. To make tiger conservation evidence based and efficient, priority should be given to having such a database realised.

For tigers, my work suggests that poaching is the main threat. Habitat loss is often mentioned as the other main threat (Goodrich *et al.*, 2015), but this is not supported by the models I built. Many Tiger Conservation Landscapes have very low tiger numbers, very few of them are at carrying capacity, and in some countries tigers have gone extinct fairly recently. All of this indicates that there is a lot of empty tiger habitat, and unless source populations are protected from poaching so they can expand into these areas, protecting those empty habitats will have no effect on the overall tiger numbers. Protecting those areas is of value for tiger conservation only if there is reasonable certainty that tigers will expand into those areas once again. In terms of management this indicates that stopping poaching should be the priority in all Tiger Conservation Landscapes.

Tigers are only one example of a threatened species, and arguably receive more conservation attention than most other species, with a global summit held to save them in 2010 and \$100 million towards their conservation (Global Tiger Initiative, 2010). Most species will never see this level of attention and funding. To ensure that resources for species conservation lead to increasing numbers of those species, a systematic approach is needed. If the reasons for a species decline are not known, we can use a Vol approach to decide whether to do research, or whether there is one conservation action that might address different hypotheses about the decline, as demonstrated by Runge *et al.* (2011). If there are various actions that would address the decline of a species, we need to decide which one is most effective, whilst bearing the cost of interventions in mind, as demonstrated by Maxwell *et al.* (2015). That could mean to implement adaptive management and monitor how well several actions work, or to

implement one action that was identified as meeting the objectives (McDonald-Madden *et al.*, 2010).

6.5 Recommendations for future work

There is clearly more work to be done on assessing extinction risk and the drivers of extinction so that we can save more species and ensure that the Convention on Biological Diversity's Aichi targets as well as Sustainable Development Goal 15 are met. More specifically, occurrence records from databases such as GBIF could be used to calculate extent of occurrence and area of occupancy using tools such as GeoCAT (Bachman *et al.*, 2011) or rCAT (Moat and Bachman, 2017) which are important for determining Red List status of plants. Incorporating this information into models to predict extinction risk could improve model performance, which means that we could predict extinction risk quite accurately without having to do full assessments. This would be particularly useful for plants, as many of their assessments are based on extent of occurrence. However, as occurrence records are not random samples, subsampling might be necessary to minimise spatial bias in the model outputs (Beck *et al.*, 2014).

To ensure we can predict Red List categories and threat status well, there is scope to explore more techniques for dealing with class imbalance. Over- and undersampling is one of these techniques, but there are others such as algorithms that can deal with imbalanced data, and a combination of different sampling and algorithms which is known as cost-sensitive learning (Galar *et al.*, 2012). These methods could help to better predict species at risk of extinction.

Bayesian hierarchical models are another method that could enhance our abilities to deal with bias and uncertainty in the data. If there are known biases then the real distributions could be incorporated as prior information into a Bayesian hierarchical model. For example, through the Sampled Red List Index for plants we know the distribution of Red List categories amongst plants, so that when we model extinction risk, we could incorporate this as a prior when our data are biased towards threatened species. All of these suggestions rely on ecologists with advanced statistical knowledge, data manipulation and programming skills in programmes such as R (R Core Team,

2017). Using open, reproducible workflows would ensure that work can be updated easily and for working on these issues as teams (Lowndes *et al.*, 2017).

6.6 Conclusion

To ensure species are not going extinct, it is crucial that we use available evidence in the best possible way. As more and more data are freely available online, we can incorporate this information into our models to explore which species are at risk and what the main drivers of extinction risk are. The range of modelling tools that ecologists use is increasing and becoming more sophisticated, meaning we can better predict extinction risk and model management actions to save species. Incorporating the available information and model outputs into decision making is important so that management addresses the most pressing threats efficiently. Decision analysis and adaptive management are tools to enable this, and Value of Information forms part of these methods. Uncertainty is an important factor in all stages of decision making, and ecologists are increasingly advocating and applying methods to ensure that uncertainties are dealt with appropriately. While there are big shortfalls in conservation spending, using these methods will ensure that the funding we do have is spent as effectively as possible. We have many tools to make rational decisions about what to research, when to act, and what actions to choose for different situations. It is up to us to use them to save as many species as we can.

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Supplementary material

S1. 23 species that were assessed both on the IUCN Red List and on the Brazilian National Red Lists, and the categories in which they were classified. Dark shading denotes coinciding categories. Categories: CR – Critically Endangered, DD – Data Deficient, EN – Endangered, LC – Least Concern, NT – Near threatened, VU – Vulnerable

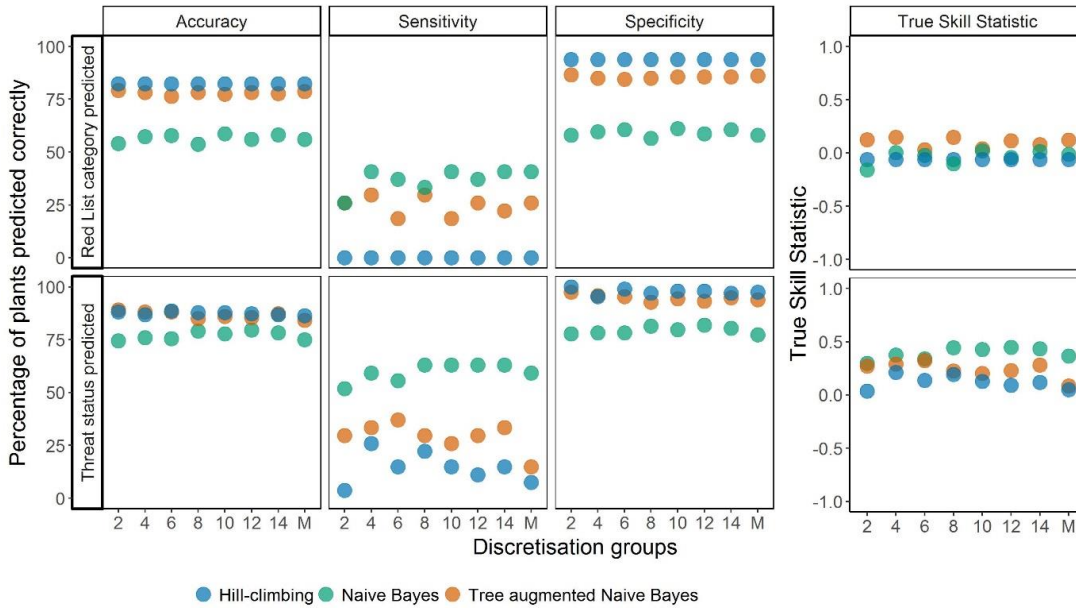
		IUCN Red List				
		CR	EN	VU	NT	LC
National Red List	VU	0	2	2	0	0
	NT	1	2	0	0	0
	LC	0	0	2	4	9
	DD	0	0	0	0	1

S2. Groups for custom discretisation for occurrence records from BIEN 3+.

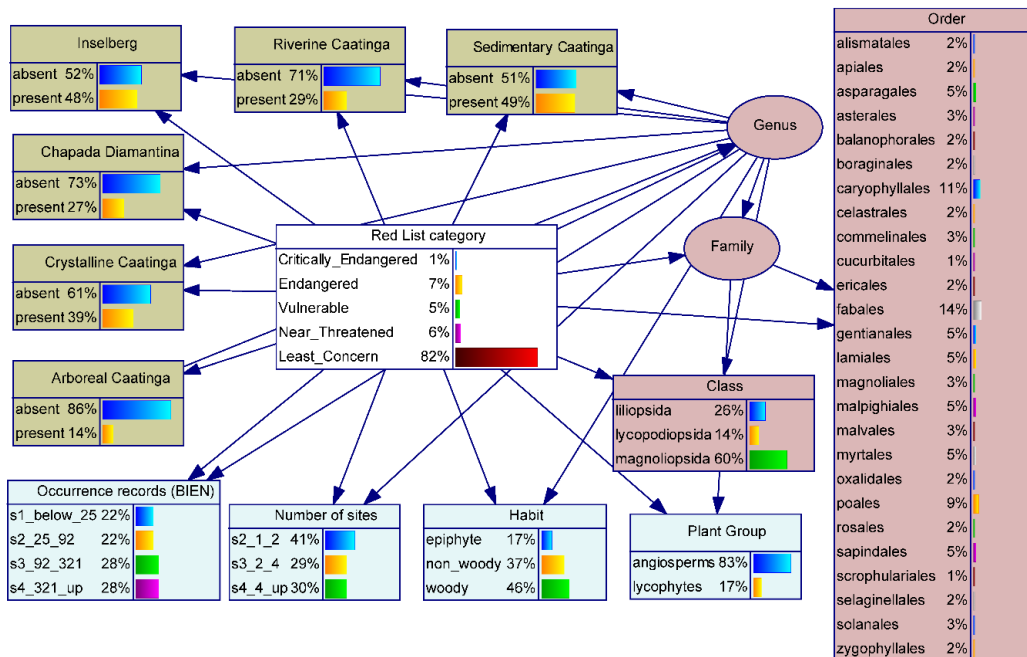
Group	Occurrence records	Number assessed species	Number unassessed species
1	0 – 2	10	118
2	3 – 9	17	71
3	10 – 14	7	50
4	15 – 50	35	258
5	51 – 100	24	190
6	101 – 500	79	371
7	501 – 1000	33	138
8	> 1000	18	77

S3. Taxonomic ranks in which some but not all species had Red List assessments, and number of species to be predicted with the inclusion of the taxonomic rank.

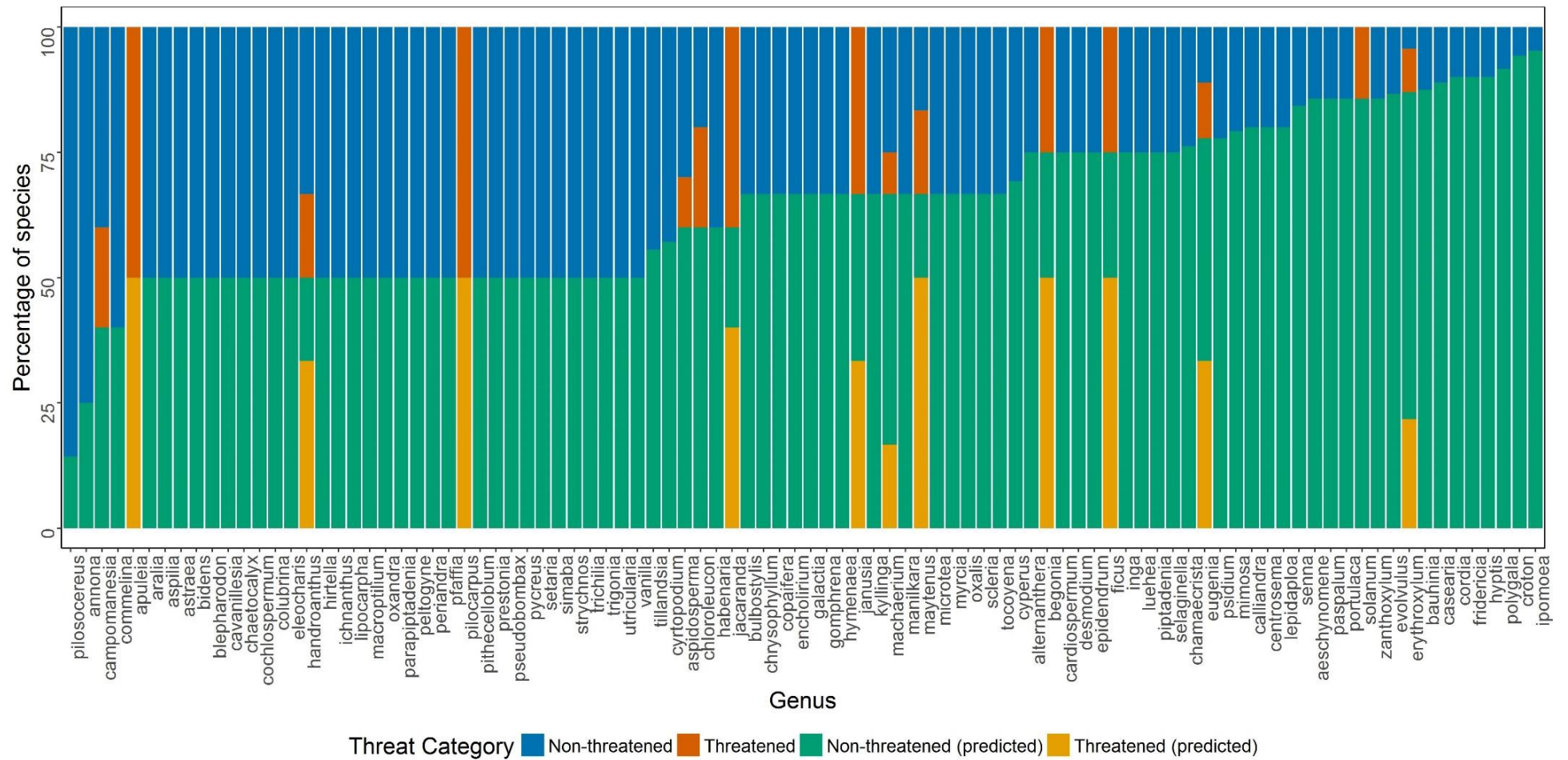
Taxonomic rank	Number of groups in which at least one species was assessed	Species to be predicted
Genus	95 genera	413
Family	47 families	589
Sum		1,002



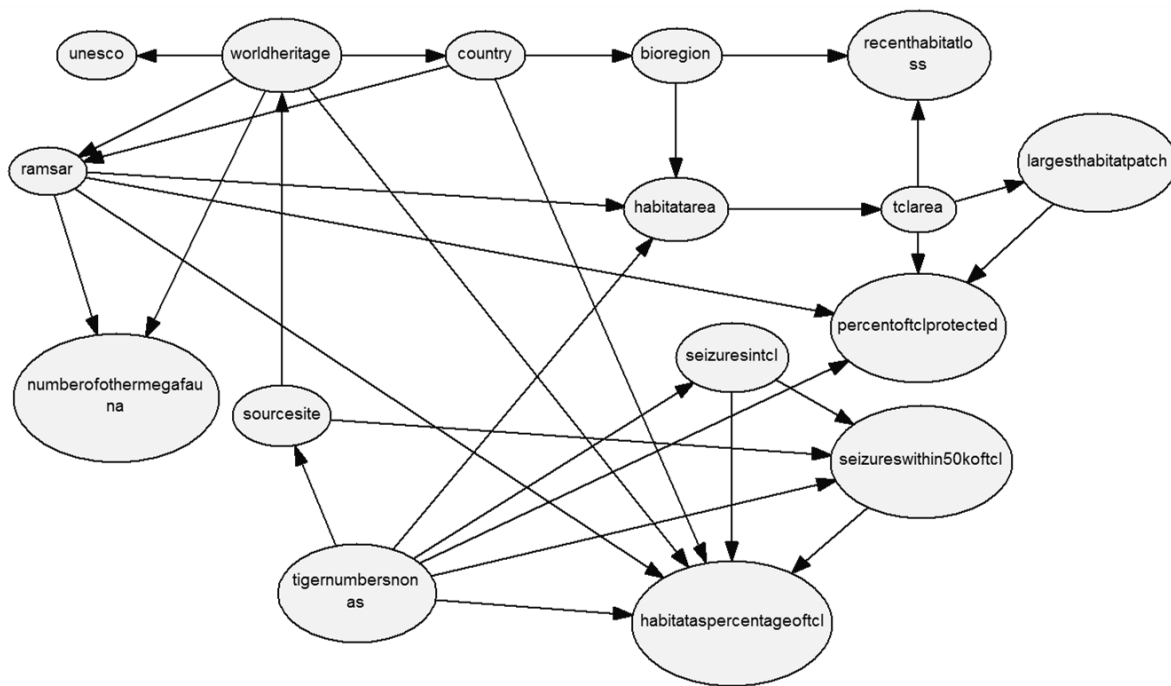
S4. Model performance of 48 different models, built using a hill-climbing algorithm, a Naïve Bayes classifier, or a Tree-Augmented Naïve Bayes classifier. Models predicted Red List category or threat status, and used different numbers of discretisations (2, 4, 6, 8, 10, 12 or 14 groups – see S2, or manually customised groups). Metrics shown for assessed species are the accuracy (percentage of correctly classified species), sensitivity (percentage of correctly classified threatened species), specificity (percentage of correctly classified non-threatened species), and True Skill Statistic (sensitivity + specificity -1).



S5. The best performing Bayesian Network predicting Red List category with all variables and the probabilities of each state of each variable, built using 4 groups and with a tree-augmented Naïve Bayes classifier. Family and genus not shown due to the high number of states, but included in the model when processed on our computer.



S6. Percentage of species in each genus that are assessed as non-threatened or threatened, and predicted to be non-threatened or threatened. All genera in which at least one species has been assessed and one species has been predicted on the Red List are shown.



S7. Final Bayesian Network structure. Network was created for two tiger group discretisations, eight discretisations for other continuous variables, and with a greedy thick thinning algorithm.

S8. Data for tiger BNs.

TCL Name	Source site	Main country	Tiger numbers	Source for tiger numbers	Potential tiger numbers	TCL Area	Habitat area	Largest habitat patch	World Heritage Site	Other megafauna species
Heilongjiang	no	China	8	Goodrich et al. (2015)	15	1315	697	660	N	0
Bukit Rimbang Baling	no	Indonesia	3	Sunarto and Zulfahmi (2013)	45	4395	1680	1563	N	0
Tesso Nilo Landscape	no	Indonesia	8	Sunarto and Zulfahmi (2013)	17	2332	-1240	525	N	0
Salak-Phra	no	Thailand		Lynam (2010)	10	647	377	379	N	0
Bi Dup-Nui Ba	no	Vietnam	0	Lynam (2010)	55	1660	775	792	N	0
Kon Ka Kinh	no	Vietnam	0	Lynam (2010)	90	6389	819	796	N	0
Xe Bang Nouan	no	Laos	0	Lynam (2010)	30	657	428	427	N	0
Royal Bardia South	no	Nepal			35	499	199	83	N	0
Panna East	no	India	4	Jhala et al. (2011)	70	1390	613	178	N	0
Panna West	no	India	4	Jhala et al. (2011)	10	539	171	103	N	0
Indravati	no	India			2755	44238	24275	1576	N	0
Sunabeda-Udanti	no	India	1	Jhala et al. (2011)	160	2287	1427	603	N	0
Painganga	no	India			10	442	162	148	N	0
Nagarjunasagar South	no	India	40	Jhala et al. (2011)	60	1699	832	337	N	0
Nagarjunasagar North	no	India	20	Jhala et al. (2011)	30	915	406	217	N	0

TCL Name	Source site	Main country	Tiger numbers	Source for tiger numbers	Potential tiger numbers	TCL Area	Habitat area	Largest habitat patch	World Heritage Site	Other megafauna species
Valley	no	India			5	321	-15	188	N	0
Chandoli	no	India			35	1682	915	433	N	0
South	no	India			5	344	177	177	N	0
Purna	no	India			20	1002	560	560	N	0
North	no	India			30	406	250	249	N	0
Shoolpaneswar	no	India			30	511	259	180	N	0
Nam Ha	potential	Laos	0	Lynam (2010)	35	3217	1469	1268	N	0
Pachmarhi Satpura - Bori	potential	India	43	Jhala et al. (2011)	265	4924	2396	299	N	0
Dandeli North	potential	India	7	Jhala et al. (2011)	10	517	291	177	N	0
Radhanagari	potential	India			120	2945	1662	708	N	0
Sundarbans	yes	Bangladesh	470	Goodrich et al. (2015), Jhala et al. (2011)	25	5304	1194	334	Y	0
Bandhavgarh - Panpatha	yes	India	53.76	Walston et al. (2010)	99	2020	905	249	N	0
Kanha - Phen	yes	India	84	Walston et al. (2010)	625	10598	5523	690	N	0
Melghat	yes	India	52.796	Walston et al. (2010)	90	2398	1277	503	N	0
Pench	yes	India	40.811	Walston et al. (2010)	140	2918	1269	205	N	0

TCL Name	Source site	Main country	Tiger numbers	Source for tiger numbers	Potential tiger numbers	TCL Area	Habitat area	Largest habitat patch	World Heritage Site	Other megafauna species
Andhari - Tadoba	yes	India	20.625	Walston et al. (2010)	160	3680	1411	331	N	0
Russian Far East - China	yes	Russia	360	Goodrich et al. (2015)	4325	269983	208095	183237	Y	0
Kuala Kampar-Kerumutan	no	Indonesia	3	Sunarto and Zulfahmi (2013)	99	9835	-117	2447	N	1
Berbak	no	Indonesia	22	D'Arcy et al. (2012)	30	2543	1347	1286	N	2
Rimbo Panti-Batang Gadis East	no	Indonesia	43	Wibisono et al. (2009)	35	2890	1338	1116	N	1
Rimbo Panti-Batang Gadis West	no	Indonesia	23	Wibisono et al. (2009)	20	1486	712	843	N	1
Sibologa	no	Indonesia			14	1292	812	654	N	1
Krau	no	Malaysia			10	1248	261	469	N	1
Khlong Saeng	no	Thailand		Lynam (2010)	65	4816	1559	1545	N	1
Phun Miang - Phu Thong	no	Thailand		Lynam (2010)	945	16273	12359	12934	N	1
Phu Khieo	no	Thailand		Lynam (2010)	260	5760	3614	2315	N	2
Khao Yai	no	Thailand		Lynam (2010)	125	2253	1701	1668	N	1
Cardamoms	no	Cambodia	0	O'Kelly et al. (2012)	1065	26345	12319	11470	N	1

TCL Name	Source site	Main country	Tiger numbers	Source for tiger numbers	Potential tiger numbers	TCL Area	Habitat area	Largest habitat patch	World Heritage Site	Other megafauna species
Cambodian Northern Plains	no	Cambodia	0	O'Kelly et al. (2012)	981	26835	11788	8526	N	1
Chu Mom Ray	no	Vietnam	0	Lynam (2010)	70	1787	579	885	N	1
Hin Nam Ho	no	Laos	0	Lynam (2010)	35	2727	1581	1236	Y	1
Northern-Central Annamites	no	Laos	0	Lynam (2010)	685	28826	17157	11191	N	1
Yamuna	no	India		Jhala et al. (2011)	15	322	120	82	N	1
Satkosia-Gorge	no	India	8	Jhala et al. (2011)	170	2699	1509	643	N	1
Palamau	no	India	10	Jhala et al. (2011)	205	3209	1849	727	N	1
Thap Lan - Pang Sida	no	Thailand		Lynam (2010)	214	4445	2970	2778	N	1
Cat Tien	no	Vietnam	4	Lynam (2010)	185	3359	2087	2567	N	1
Southern-Central Annamites	potential	Cambodia	0	O'Kelly et al. (2012)	2622	61252	31756	30063	N	1
Northern Forest Complex - Namdapha - Royal Manas	potential	Myanmar	135	Goodrich et al. (2015) (numbers for Myanmar and Bhutan)	35498	237820	204615	196851	Y	2
Dandeli South - Anshi	potential	India	32	Jhala et al. (2011)	45	2316	1257	411	N	1
Bukit Barisan Selatan South	yes	Indonesia	13	Walston et al. (2010), divided by percentage	20	2107	881	962	Y	2

TCL Name	Source site	Main country	Tiger numbers	Source for tiger numbers	Potential tiger numbers	TCL Area	Habitat area	Largest habitat patch	World Heritage Site	Other megafauna species
Bukit Balai Rejang - Selatan	yes	Indonesia	37	Walston et al. (2010), divided by percentage	55	3884	2270	2665	Y	2
Kerinci Seblat	yes	Indonesia	140	Walston et al. (2010)	360	28162	14971	10928	Y	2
Bukit Tigapuluh Landscape	yes	Indonesia	42	Walston et al. (2010)	59	7106	810	5213	N	1
Endau Rompin	yes	Malaysia	24.906	Walston et al. (2010)	30	6505	-472	629	N	2
Taman Negara - Belum	yes	Malaysia	137.659	Walston et al. (2010)	941	49181	16412	12908	N	2
Nam Et Phou Loey	yes	Laos	9	Lynam (2010)	419	17866	9634	6958	N	1
Kaziranga - Garampani	yes	India	82.32	Walston et al. (2010)	931	7514	5108	4648	Y	1
Royal Chitwan	yes	Nepal	129	Dhakal et al. (2014), Jhala et al. (2011)	208	4055	1216	560	Y	2
Royal Bardia	yes	Nepal	56	Dhakal et al. (2014), Jhala et al. (2011)	544	6777	3206	740	N	1
Royal Suklaphanta	yes	Nepal	112	Dhakal et al. (2014), Jhala et al. (2011)	80	1144	452	300	N	1

TCL Name	Source site	Main country	Tiger numbers	Source for tiger numbers	Potential tiger numbers	TCL Area	Habitat area	Largest habitat patch	World Heritage Site	Other megafauna species
Corbett - Sonanadi	yes	India	159.62	Walston et al. (2010)	295	5996	1677	251	N	1
Rajaji	yes	India	20.5	Walston et al. (2010)	35	1044	299	172	N	1
Simlipal	yes	India	19	Walston et al. (2010)	155	2412	1384	739	N	1
Shendurney	yes	India	13.545	Walston et al. (2010)	35	603	326	257	N	1
Periyar - Megamala	yes	India	21.275	Walston et al. (2010)	405	5978	3605	1567	N	1
Anamalai-Parambikulam	yes	India	78.24	Walston et al. (2010)	180	3071	1582	831	N	1
Biligiri Range	yes	India	34.8	Walston et al. (2010)	15	278	136	136	N	1
Leuser Ecosystem	yes	Indonesia	61.14343	Walston et al. (2010)	320	22319	14370	7817	Y	3
Tenasserims	yes	Thailand	56	Duangchantrasiri et al. (2016)	9127	162726	120324	113993	Y	2
Western Ghats - Bandipur - Khudrenukh - Bhadra	yes	India	219.9264	Walston et al. (2010)	965	18973	8677	831	N	1

