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Invasive species and climate change: a framework for predicting species distribution when data are scarce

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Contents

Figures

Tables

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Executive summary

Invasive species pose a substantial risk to native biodiversity and agriculture and will continue to be a key management priority under rapid climate change. As distributions of species shift in response to changes in climate so will management priorities and investment. Species that currently pose a major management issue may cease to be, whereas others that pose little threat at present may become serious pests. To develop cost-effective invasive species management strategies into the future it is necessary to understand how species distributions are likely to change over time and space. For most species, however, few data are available on their current distributions, let alone predicted future distributions.

We demonstrate the benefits of Bayesian belief networks (BBNs) for predicting current and future distributions of invasive species when empirical data are lacking. Using the commercially valuable invasive species buffel grass (*Pennisetum ciliare* [syn.] *Cenchrus ciliaris*) as an example, we propose a framework by which expert knowledge and available empirical data can be used to build a BBN to predict species distribution under various climate scenarios.

BBNs are extremely flexible and can incorporate a range of diverse influential variables, such as soil quality and climate, management variables such as fire and grazing, landscape characteristics such as topography and aspect, and ecological processes such as plant competition. Our framework models the susceptibility and suitability of the Australian continent to buffel grass colonisation using three invasion requirements: the introduction of plant propagules to a site, the establishment of new plants at a site, and the persistence of established, reproducing populations at a site.

Our results highlight the potential for buffel grass management to become increasingly important in the southern part of the continent. In the north, conditions are predicted to become less suitable. The overall suitability of hummock grasslands to buffel grass is predicted to decline modestly, while the National Reserve System (NRS) within this biome is predicted to increase in suitability. Our modelling suggests that overall the risk of buffel grass colonisation, establishment and persistence within the NRS is likely to increase with climate change as a result of the high number of small reserves located in the central and southern portion of the continent.

Due to the value of buffel grass for pasture, attitudes towards its costs and benefits are polarised which hampers efforts to develop policy for its sustainable management. Our results suggest that climate change will not diminish the issue of how to manage this invasive species. Indeed, the need to develop sustainable management policy in response to predicted shifts in spatial distribution of invasive species and subsequent threats to national assets has never been greater. We find BBNs to be an effective and inexpensive tool to predict species spatial distributions where resources are limited.

1 Introduction

Invasion by exotic species has been identified as a significant threat to biodiversity under climate change (Mooney and Hobbs 2000; Thomas et al. 2004; Hellmann et al. 2008). Whether passengers or drivers of biodiversity change, invasive species can dominate, affecting ecosystem structure and function as well as distribution of native species (MacDougall and Turkington 2005). Under rapid climate change the distributions of some invasive species are likely to expand, while others may contract. The relative risk posed by particular invasive species is therefore likely to change. What is currently viewed as a serious invasive species management issue may cease to be in the future. Likewise, species that currently pose little threat may become problematic as a result of increasing habitat suitability with climate change (Walther et al. 2009).

Mitigation and adaptation strategies for dealing effectively with invasive species under climate change will depend on good predictions of the likely change in habitat suitability, its susceptibility to invasion under different climate scenarios, and the subsequent impacts given these shifts. The problem is that for many invasive species the necessary data required to build species distribution models are lacking. Often we must turn to expert knowledge to fill this information gap (Kuhnert et al. 2010; Martin et al. 2012). Acknowledging this gap, we develop a modelling framework that encapsulates the uncertainty around available empirical data and expert knowledge, and we use this information to make predictions about the future habitat suitability and susceptibility to invasion under climate change.

We illustrate the benefits of our framework by considering the distribution of buffel grass, *Pennisetum ciliare* (syn.) *Cenchrus ciliaris* across Australia. Buffel grass is one of many exotic grasses deliberately introduced for livestock production and soil conservation. Native to parts of Africa, Asia and the Middle East, buffel grass is now widely distributed across the United States, Mexico and Australia (van Devender et al. 1997; Tu 2002; Arriaga et al. 2004; Lawson et al. 2004). Buffel grass is among a suite of commercially valuable invasive species, highly valued as a pasture species but widely unpopular among those concerned with its threat to native biodiversity (Friedel et al. 2009, 2011). The management of such species is contentious and offers a compelling case study to examine the impact of climate predictions on its future colonisation success.

At present, there is considerable uncertainty about the relative influence of climate change on the degree of threat posed by buffel grass and how this threat will vary across different regions (Sutherst et al. 2007). Despite this uncertainty, there is considerable pressure for natural resource management agencies to make management recommendations, particularly where areas of high conservation and cultural value such as the National Reserve System (NRS) are at risk.

Bayesian belief networks (BBNs) are useful tools for modelling ecological predictions and assisting natural resource management decision-making (Marcot et al. 2001, 2006; Smith et al. 2007). BBNs are tools for examining probabilistic scenarios where the structure of the network is decided on formally by experts. BBNs are made up of a set of variables, represented as a network of independent and dependent nodes that are linked with probabilities (Marcot 2006). The nodes represent variables that affect some outcome of interest and the links represent how the variables are related, that is, interaction between the nodes (Marcot et al. 2001). Nodes are related in 'parent–child' ways, with 'child' nodes being dependant on 'parent' nodes. Where a node does not have a 'parent', it is considered independent. Underlying each dependent node is a conditional probability table (CPT) that specifies the probability of each state within a node conditional on the parent nodes (Marcot 2006). For example, imagine a node representing the probability of introduction P(Intro) of a plant propagule to a site. This probability is dependent on the distance (Dist) to the nearest population to facilitate dispersal. In mathematical notation, the probability of introduction P(Intro) is therefore conditional on distance (Dist) or P(Intro|Dist). Data feeding into these types of models are typically the result of expert judgement through an expert elicitation process, but can also be based on empirical or modelled data about the relationship of interest. In ecological research, the use of BBNs to represent ecological processes and aid in natural resource management decision-making is growing (e.g. Rumpff et al. 2011; Smith et al. 2012). Methods for eliciting and using expert knowledge to inform ecological models is also gaining prominence (Kuhnert et al. 2010; Martin et al. 2012). Expert elicitation represents a way of capturing knowledge and informing management and policy when empirical data are limited, but it presents a number of interesting challenges, namely, the collection of robust and accurate, unbiased information from one or more experts and quantifying the uncertainty around the elicited response. If collected carefully, taking into account the inherent biases induced from eliciting judgements, this information can be used in a BBN to examine a range of probabilistic scenarios.

Using a BBN we assess the relative threat of buffel grass colonisation across Australia and its greatest conservation asset, the NRS. Specifically we ask:

1. What is the current susceptibility and suitability of the Australian continent to buffel grass colonisation?
2. How will climate change influence suitability for buffel grass colonisation in the future?
3. What are the management implications of these projected changes?

1.1 Buffel grass colonisation in Australia

The capacity of buffel grass to produce high yields, resist drought and heavy grazing, and respond well after fire makes it highly valued by some graziers in arid landscapes (Tu 2002). However, these same traits, coupled with a capacity for establishment in disturbed areas (McIvor 2003), rapid growth, fast maturation, prolonged flowering/fruiting, prolific seed production and high seed dispersal (Franks 2002) also make it a successful coloniser of non-targeted areas. Buffel grass can form dense single-species stands, out-competing native plant species and threatening native animal species through displacement of native vegetation. Several studies have highlighted its negative impact on biodiversity within remnant vegetation, tropical forests and woodlands of Queensland (Fairfax and Fensham 2000; Franks 2002; Jackson 2005; Eyre et al. 2009) and in the arid landscapes of central Australia (Clarke et al. 2005; Smyth et al. 2009). Buffel grass can generate high fuel loads, and so alter fire regimes by carrying frequent and more intense fires. Positive feedback between fire and buffel grass increases the impact of buffel grass colonisation (Butler and Fairfax 2003). Buffel grass is widely spread across Australia’s rangelands (Australia’s Virtual Herbarium 2005) and has been identified as one of the key threats to rangeland biodiversity (Martin et al. 2006). Lawson et al. (2004), using CLIMEX (Sutherst and Maywald 1985) modelling, predicted buffel grass expansion over 60% of the Australian continent under current climatic conditions.

2 Model and methods

We model the susceptibility and suitability of the Australian landscape to buffel grass colonisation. The framework is based on three invasion requirements: the introduction of plant propagules to a site, the establishment of new plants at a site, and the persistence of established, reproducing (seed-producing) populations at a site (Smith et al. 2012; Table 1). The establishment and persistence nodes combine to influence the suitability to invasion and the introduction and suitability nodes combine to influence a site's susceptibility to invasion (Figure 1). Introduction, establishment and persistence are influenced by key environmental variables such as landscape properties (e.g. soil type, tree cover, fire frequency), climate properties (rainfall, temperature, soil moisture), and dispersal properties (distance to nearest infestation). The relationship between these key environmental variables and the invasion requirements are defined by experts and empirical data and are illustrated through an influence diagram that forms the basis of the BBN (Figure 1).

To illustrate the predictions of the model spatially we use GIS layers to represent the key environmental variables directly or as proxies (Appendix A, Table A1). For example, the current known distribution of buffel grass as mapped by the Australian Virtual Herbarium can be used to estimate the distance to an infestation (Figure 1).

Table 1 Definition of key BBN nodes and their states as shown in Figure 1, for susceptibility, suitability and invasion requirements

NODE	DEFINITION	STATE		
		LOW	MODERATE	HIGH
Susceptibility	Risk of being colonised by buffel grass within 10 years based on the risk of being introduced within a 10-year timeframe and suitability of the site	Low risk of being invaded by buffel grass within a 10-year timeframe	Moderate risk of being invaded by buffel grass within a 10-year timeframe	High risk of being invaded by buffel grass within a 10-year timeframe
Suitability	Ability of buffel grass to establish and persist	Can support isolated plants only	Can support scarce to moderate densities	Can support moderate to high buffel densities – extensive monocultures possible
Introduction	The arrival of seeds from known sources within a 10 year timeframe	No: none or <1% chance of introduction from dispersal or direct planting Yes: introduction via dispersal from plants within 100km or planted at the site		
Establishment	Frequency and density of seedling recruitment (assumes seeds available)	Recruitment absent or infrequent and in low densities	Recruitment in low densities most years or moderate densities every 5–10 years	Recruitment moderate every year or dense every 5–10 years
Persistence	Ability of established buffel grass to survive, grow and reproduce	Poor: Adults fail to survive or small proportion of adult plants survive, grow and reproduce Good: Most adult plants survive, grow and reproduce		

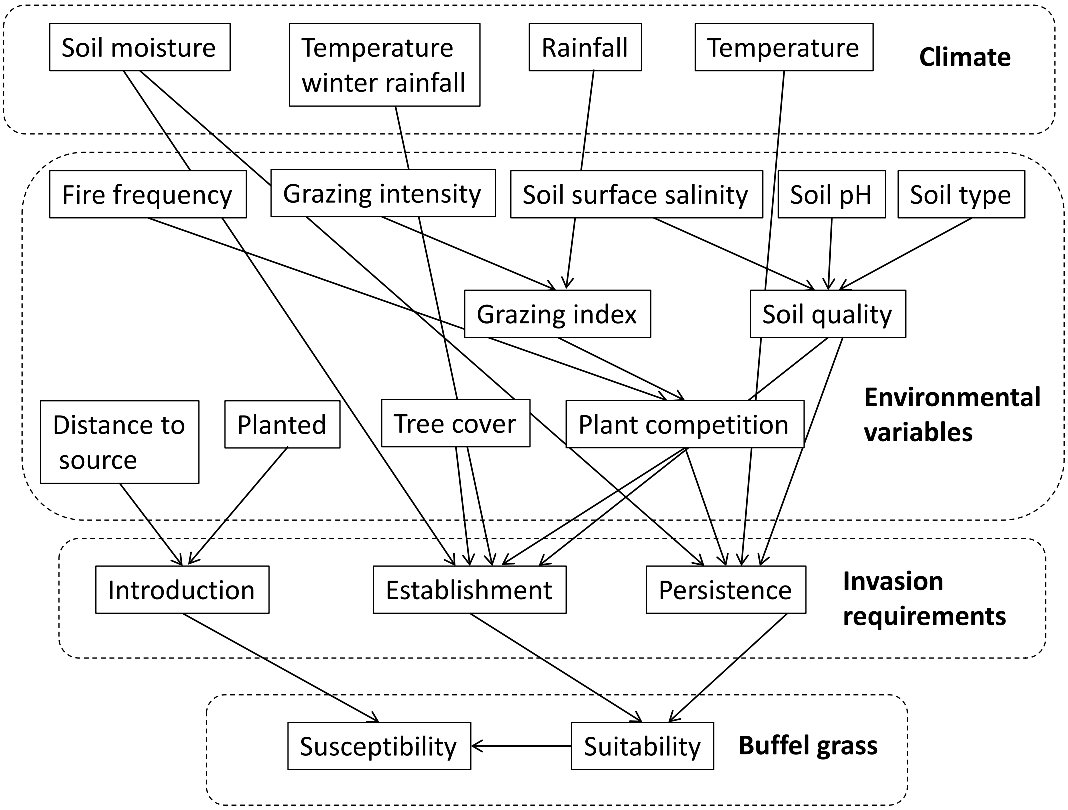

Figure 1 Influence diagram showing the key climate, environmental and invasion requirements driving landscape susceptibility and suitability to buffel grass colonisation

2.1 Eliciting expert knowledge

We captured the current understanding of buffel grass ecology, management and invasion through a review of the literature, expert workshop and follow-up discussion and elicitation with small groups and individual experts. After an initial review of existing empirical information, a two-day expert workshop was convened with experts in buffel grass ecology and management (see acknowledgements for list of experts). During this workshop, experts identified the key environmental variables that influence buffel grass invasion requirements – introduction, establishment and persistence – and the relationship between these variables (Table 1; Figure 1). Buffel grass ecology is known to vary considerably throughout Australia (Humphreys 1967). In this analysis we capture this variability through the experts' experience working on and managing buffel grass throughout the county. We also identified the GIS layers available for mapping the key environmental variables directly or indirectly. Using a combination of facilitated group discussion, small breakout groups, and feedback, we developed a set of feasible key environmental variables for consideration in the BBN (Figure 1).

During the workshop, the influence diagram was developed live using Netica (4.08), allowing experts to visualise the relationships between the nodes and facilitating easy updating and modifications as the workshop progressed. Over two days the structure of the BBN and initial states of the nodes were developed. The conditional probability tables (CPTs) for each dependent node were developed afterwards in consultation with small groups of experts. Probabilities were elicited via the following process: first, a facilitated group discussion was held about the combination of variables (i.e. nodes) in question; this discussion was then followed by an independent assessment of the probabilities by each expert; group discussion of each expert's response was then carried out; finally, each expert was invited to re-evaluate their respective response (if needed), based on the group discussion. The mean response from the group was then taken. This method of elicitation minimises biases associated with group elicitation while capturing the benefits of group judgement (Martin et al. 2012). For large CPTs, we used Cain's (2001) CPT calculator to generate the full CPT table from the elicited probabilities where the experts provided the key anchoring points. For example, to determine the anchoring points, the first set of probabilities elicited was such that the parent nodes were all in positive states and the second set such that the parent nodes were all in negative states. For all other sets, each parent node was switched from its positive to negative state. In our case, a positive state was one that facilitated buffel invasion and a negative state was one that impeded buffel invasion. For example, the dependent node ‘fire frequency’ with states (high, low), had two parent nodes ‘temperature’ with three states (too hot, just right, too cold) and ‘rainfall’ with three states (low, moderate, high). To establish the anchoring points when the parent nodes were in their positive states, we asked the experts: “What is the probability of ‘fire frequency’ being in the state ‘high’ when ‘temperature’ is ‘too hot’ and ‘rainfall’ is ‘too low’?” (Table A.1). Likewise for the negative state we asked: “What is the probability of ‘fire frequency’ being in the state ‘high’ when ‘temperature’ is ‘too cold’ and ‘rainfall’ is ‘too high’?” The full CPT was then interpolated from the elicited anchoring points using the CPT calculator.

2.2 Climate scenarios

Using outputs from the CSIRO Mk3.5 Global Circulation Model downloaded from OzClim (CSIRO 2012), three climate scenarios were examined. First, we modelled the predicted landscape susceptibility and landscape suitability of buffel grass across Australia based on current climate, centred on 1990 (recording range 1976–2005). Second, we examined the landscape suitability of buffel grass in 2070 (recording range 2065–2075) using a medium impact A1B emissions scenario, and a high impact A1FI emissions scenario (IPCC 2000). Monthly climate change grids were downloaded at 0.25° resolution for maximum temperature, minimum temperature, rainfall and evaporation, by specifying the above scenarios in OzClim. Spatial downscaling was carried out using the ANUCLIM software (Houlder et al. 2000), which incorporates three submodels: ESOCLIM, which outputs raw climate variable grids; BIOCLIM (Busby 1986), which outputs grids of bioclimatic parameters; and GROCLIM, which can output gridded indices from simple growth models. The beta release of ANUCLIM version 6.0 was used, which allows climate change grids to be applied over the historical 1990-centred climate surfaces. Software (Harwood and Williams 2009) was written to interpolate the raw 0.25° CSIRO grids to cover the whole Australian land mass, and relate evaporation change to the date range used in ANUCLIM 6 (Harwood and Williams 2009). Refer to Harwood and Williams (2009) for further details on generation of current climate and 2070 grids.

2.3 Connecting the BBN to GIS

All spatial layers (Table A1) were converted into a 25 km^2 national grid, generating a 146-row x 179-column matrix of grid cells totalling 26 134 cells. This spatial scale of modelling was deemed appropriate, given the precision of data we elicited from the experts on buffel grass ecology and current distribution. To read the GIS data into the BBN, we developed code which took as input a text file containing the GIS layers as a string of 26 134 values and fed it into Netica. Output from Netica was then converted back into a text file and then to a raster for projection using ArcGIS. Spatial analyst and R (version 2.9.2) were then used to calculate differences between the current and 2070 medium and 2070 high predictions.

2.4 Model sensitivity

The sensitivity of each of the three invasion requirements – introduction, establishment and persistence – to the environmental variables included in the BBN was tested using entropy reduction. Entropy reduction measures the degree to which findings at any node can influence the beliefs in another, given the findings currently entered in BBN network. The degree of entropy reduction I, is the expected difference in information H between variable Q with q states and findings variable F with f states (Marcot 2006) and is calculated as:

$$I = H(Q) - H(Q \mid F) = \sum_q \sum_f \frac{P(q, f)\log_2[P(q, f)]}{P(q)P(f)}$$

In general, entropy reduction calculates the degree to which variable Q influences the response variable F within the BBN. The greater the value of I, the greater the influence (Marcot 2006).

3 Results

3.1 Bayesian belief network

The BBN captured the key relationships between the invasion requirements and key environmental variables as defined by experts, literature and as dictated by available GIS layers. Introduction was defined as being influenced by the proximity of the site to source populations of buffel grass, ‘distance to source’, and whether or not buffel grass had been deliberately planted at a site (Figure 1, Table A1). Establishment was influenced by available soil moisture, temperature during winter rainfall, soil quality and competition from tree cover and plants, which is moderated by livestock grazing and rainfall. Warm season growing grasses (C_4) are linked to specialised Kranz leaf anatomy that particularly adapts grasses like buffel to hot climates. Where buffel grass grows well, the growing period coincides with summer rains. In regions where rainfall is highest in winter, conditions become suitable for buffel establishment when temperatures reach 16 °C or greater. We therefore used the BIOCLIM layer ‘mean temperature of wettest quarter’ to capture this feature. Soil quality was derived from three GIS layers: soil surface salinity, soil type and soil pH. Persistence was influenced by soil moisture, plant competition, temperature and soil quality.

3.2 Current climate

Under current climate conditions, the probability of high susceptibility reflects regions that are currently experiencing the highest colonisation pressure from buffel grass (Figure 2). In general, central Australia, central Queensland and pockets of Western Australia are predicted to experience the highest colonisation pressure. After the invasion requirement of introduction is removed, the model reveals regions that are predicted to have highest suitability (43–95%) for buffel grass (Figure 3). In other words, if buffel were to be introduced via dispersal or planting in the future, these areas are predicted to be most suitable for buffel colonisation. Highly suitable areas are found in the southern portion of the Northern Territory, and reach as far west as the Pilbara in Western Australia, east to the Brigalow Belt in Queensland, and south through north-western New South Wales.

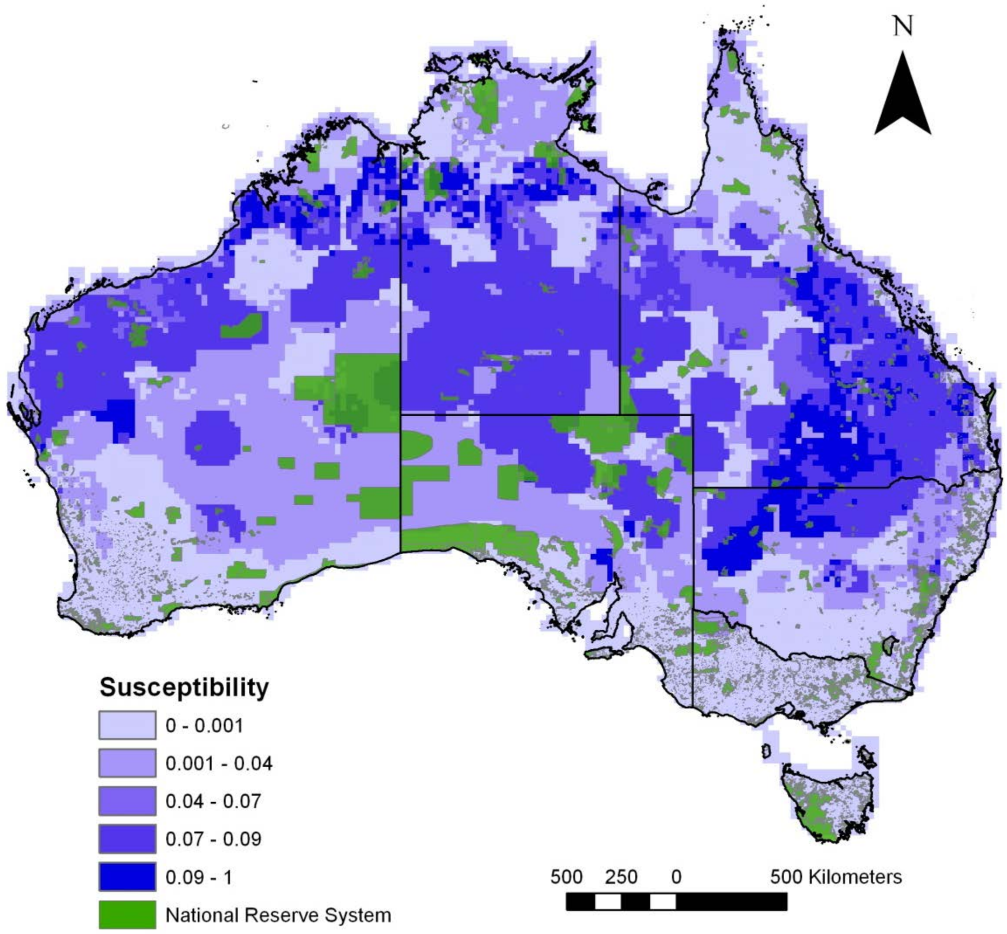

Figure 2 Probability of high susceptibility for buffel grass under current climate conditions. Locations of the NRS are shown in green

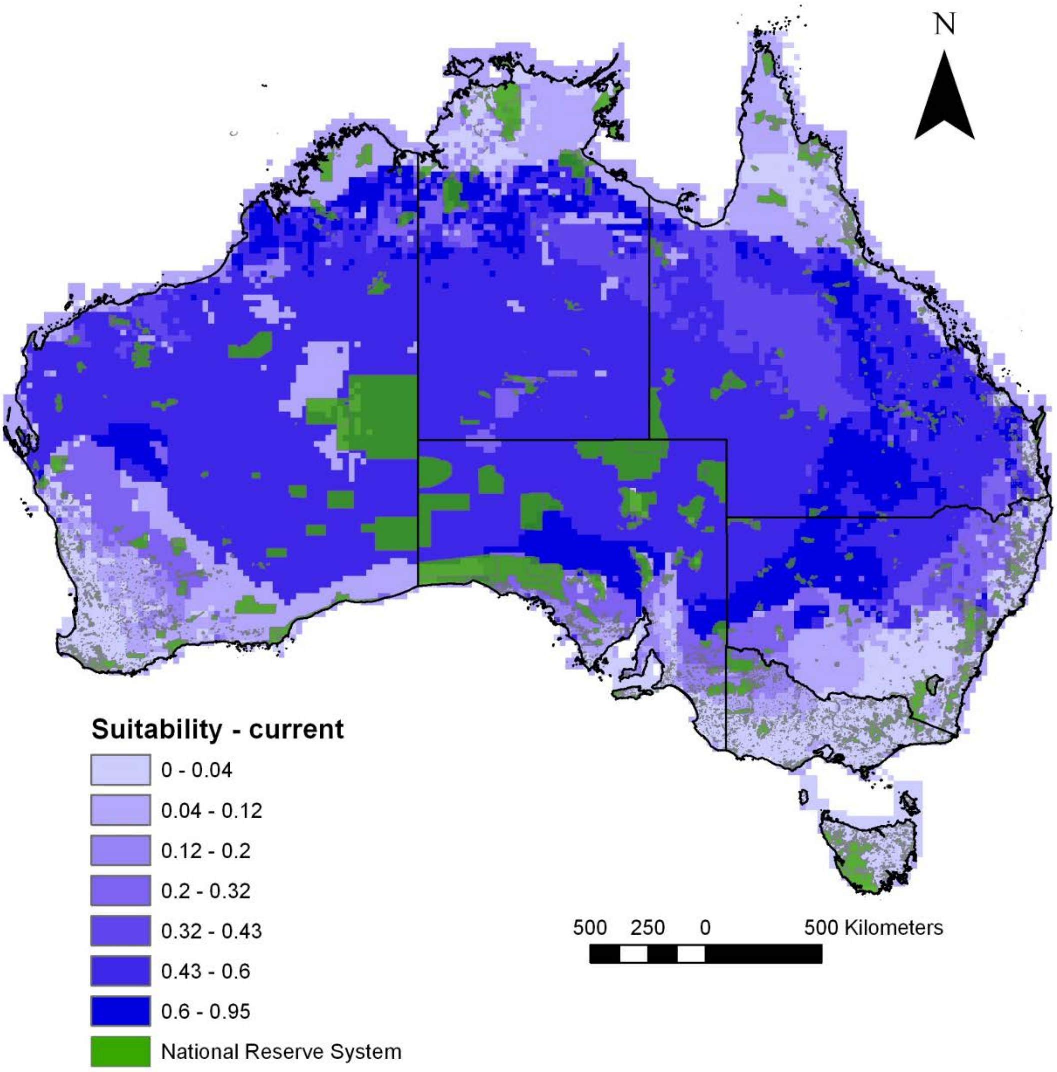

Figure 3 Probability of high suitability for buffel grass colonisation under current climate conditions

3.3 Future climate

3.3.1 2070 MEDIUM SCENARIO

Examining the suitability of the continent to buffel grass invasion under a 2070 medium climate scenario (Figure 4) shows that there is a shift in high suitability southwards and a decreasing suitability in the northern and north-western parts of the continent. Central Australia and Queensland remain buffel grass strongholds; however, southern parts of Western Australia and much of western New South Wales and South Australia become highly suitable.

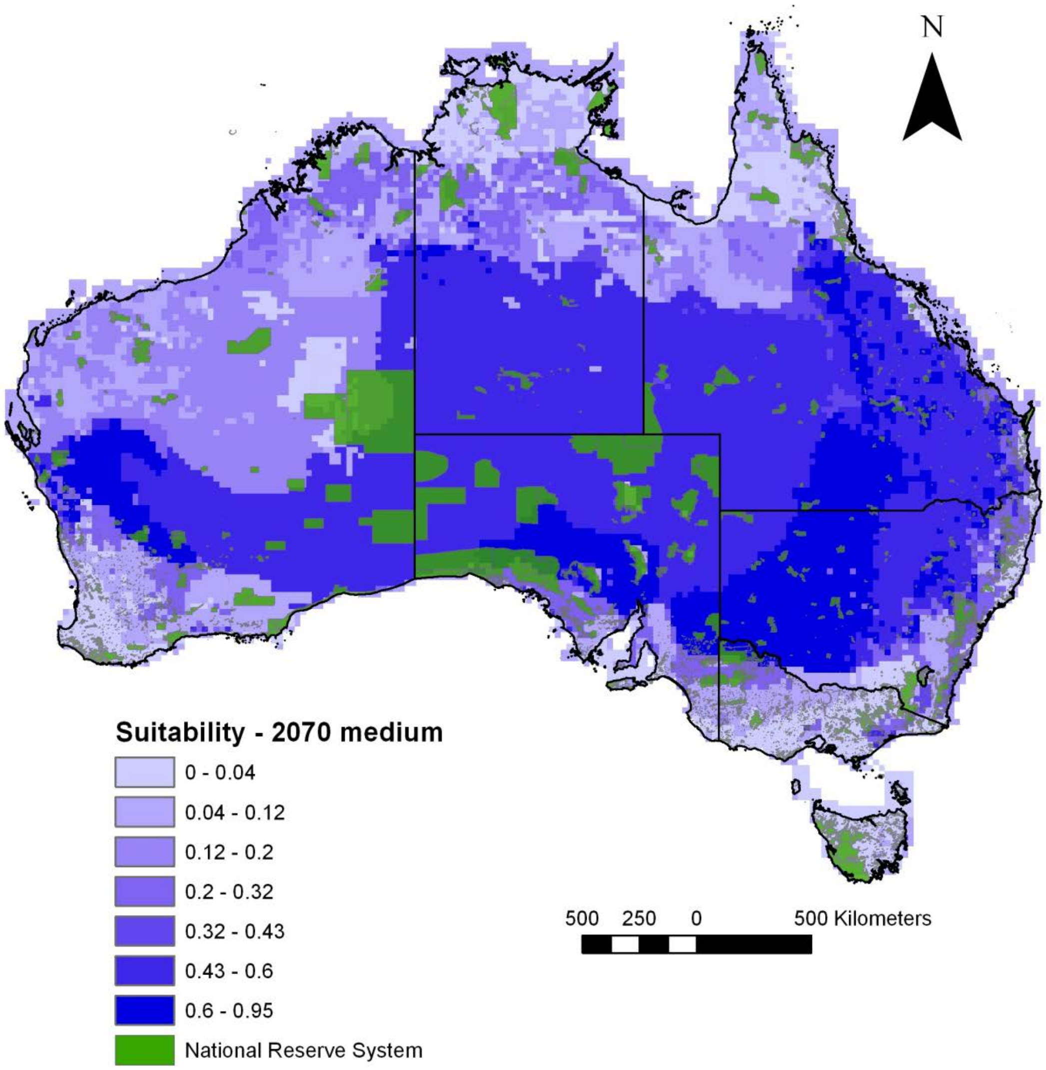

Figure 4 Probability of high suitability for buffel grass colonisation under 2070 medium climate scenario

3.3.2 2070 HIGH SCENARIO

Under the 2070 high scenario (Figure 5), the patterns observed in the 2070 medium scenario become more pronounced, with high suitability now predicted in pockets of south Western Australia, South Australia, Queensland and New South Wales. Interestingly, the suitability of central Australia declines for the first time below 43%.

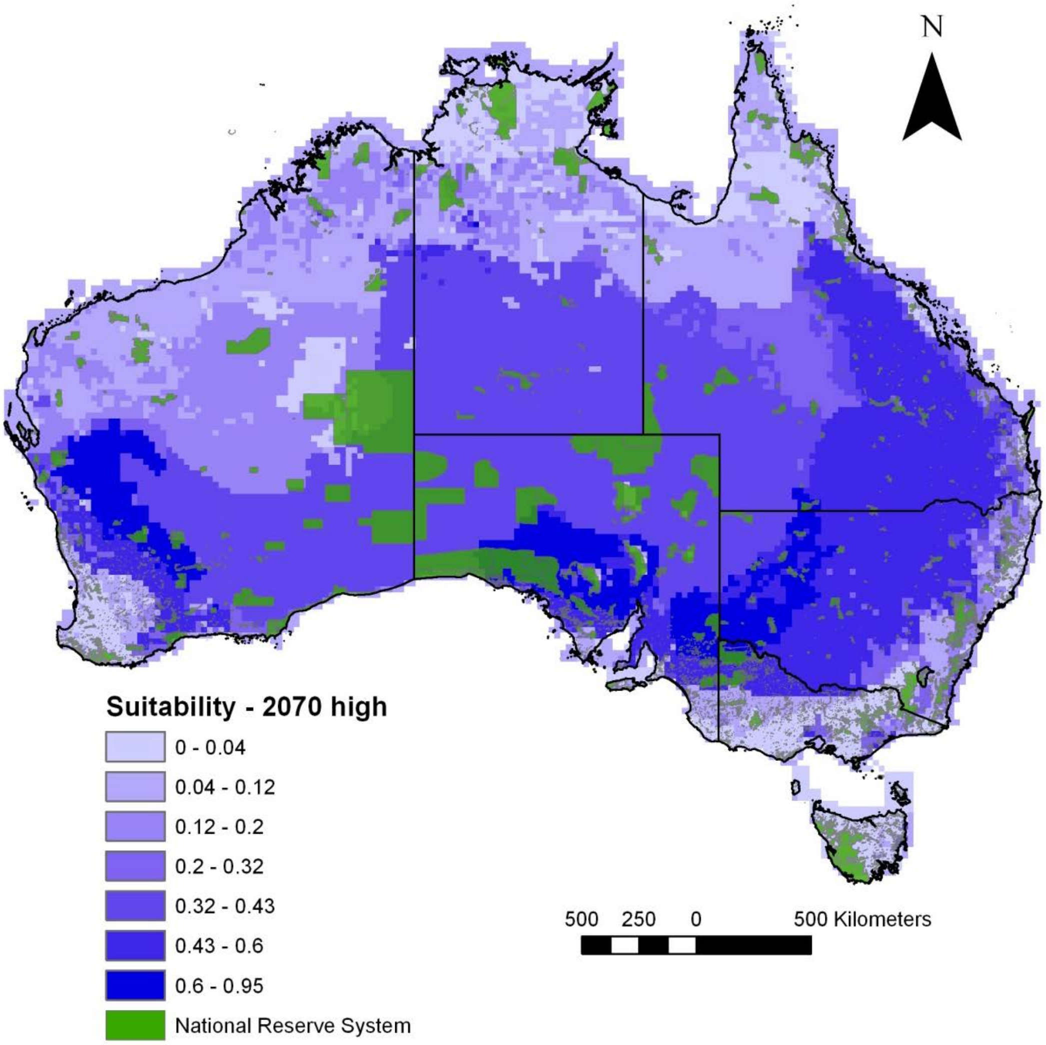

Figure 5 Probability of high suitability for buffel grass colonisation under 2070 high climate scenario

3.4 Impact of buffel grass across biomes and the NRS

We classified the predicted probability of high suitability into four classes corresponding to low (<20%), medium (20–39%), high (40–59%) and very high suitability (>60%) (Figures 6–8). The predicted suitability of four Australian biomes (temperate woodlands, south-eastern forests, hummock grasslands and tropical savannas, Figure 6), to buffel grass colonisation reveals a shift in suitability across the biomes under climate change. Temperate woodlands and south-eastern forests are predicted to become more suitable, whereas the suitability of hummock grasslands declines slightly and tropical savannas markedly.

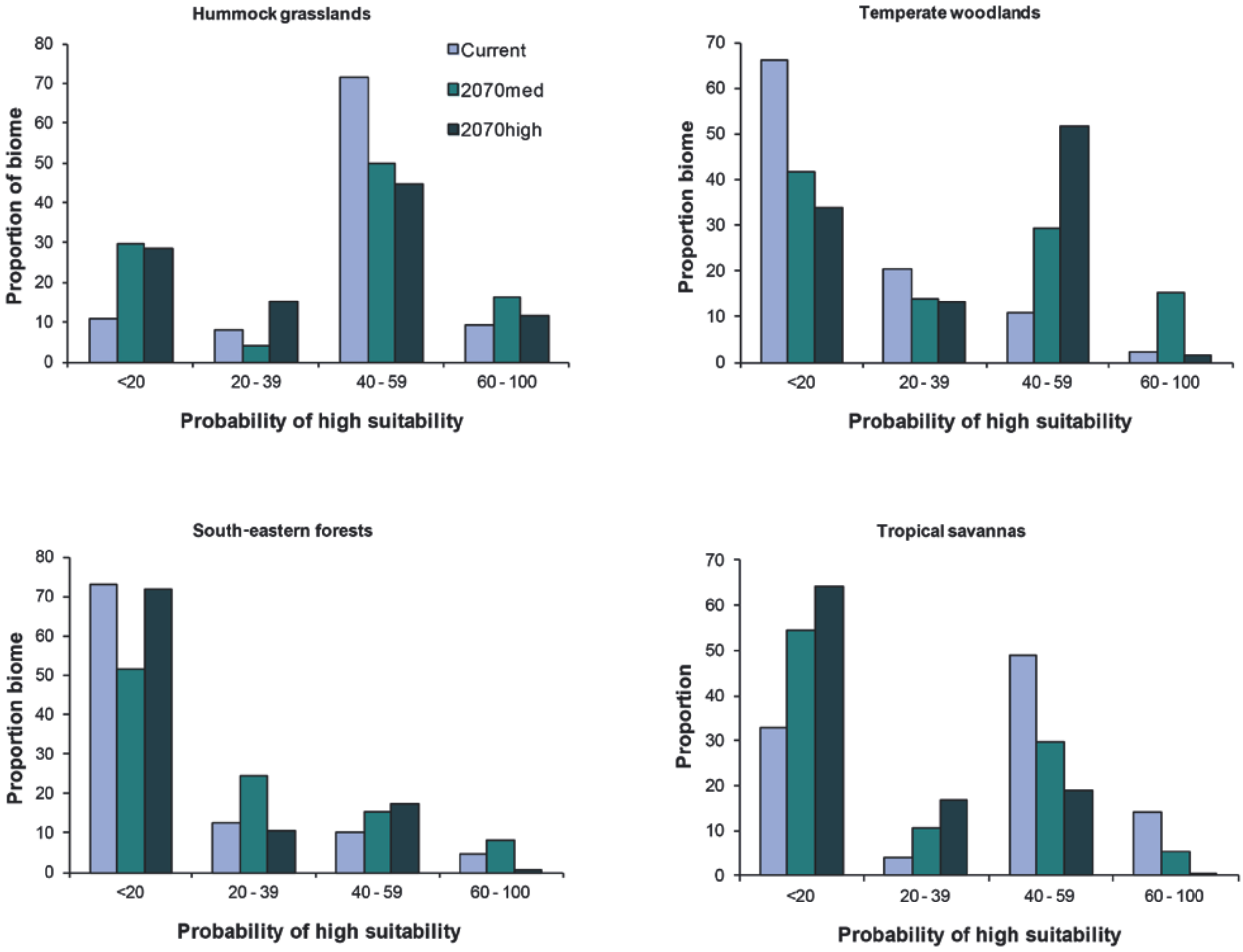

Figure 6 Proportion of each Australian biome predicted to be highly suitable to buffel grass colonisation under current, 2070 medium and 2070 high climate scenarios

We examined the impact of predicted buffel grass suitability across the NRS (Figure 7) and specifically within the NRS of each biome (Figure 8). Overall, the risk to the NRS is predicted to increase, with a greater proportion of the NRS predicted to be of high to very highly suitability in 2070 as compared to predictions under current climate conditions. The predicted high suitability of the NRS to buffel grass colonisation, within the four Australian biomes (Figure 8), reveals a dramatic shift in suitability across the relative biomes under climate change. The NRS areas within hummock grasslands, temperate woodlands and south-eastern forests are all predicted to become more suitable, with the greatest increases in hummock grasslands and temperate woodlands, whereas the NRS areas within tropical savannas are predicted to become less suitable.

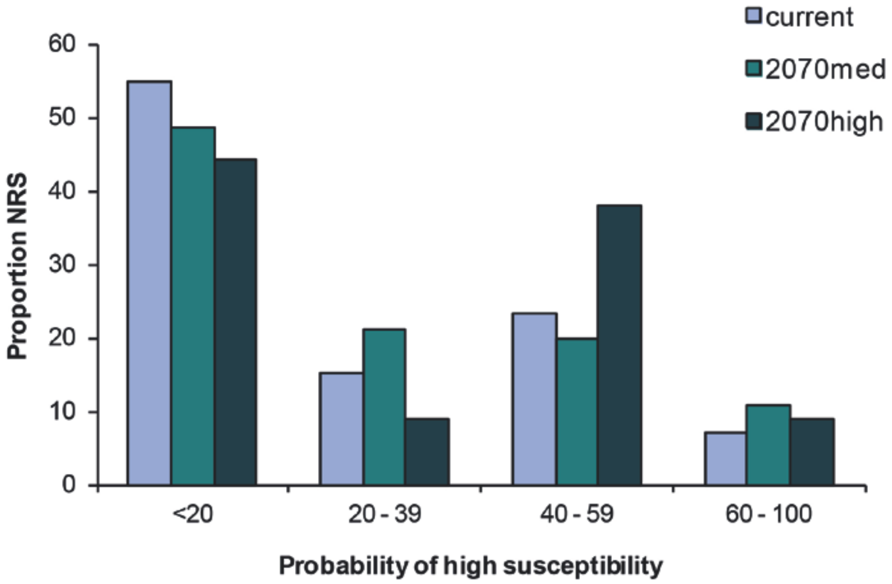

Figure 7 Proportion of the national reserve system predicted to be highly suitable to buffel grass colonisation under current, 2070 medium and 2070 high climate scenarios

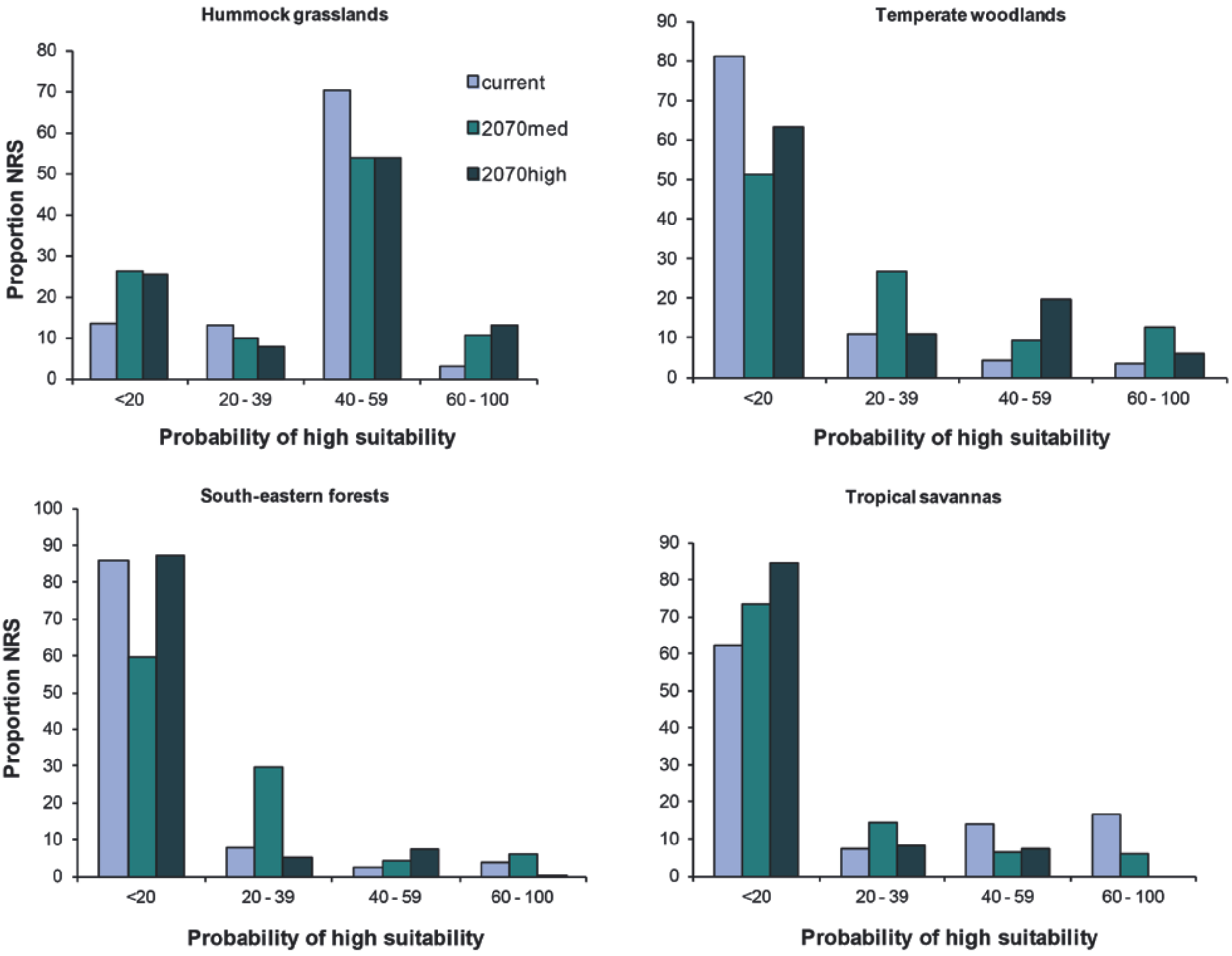

Figure 8 Proportion of NRS within each biome predicted to be highly suitable to buffel grass colonisation under current, 2070 medium and 2070 high climate scenarios

3.5 Change in buffel grass suitability

Subtracting the 2070 high suitability predictions from the predictions of high suitability under the current climate scenario reveals the regions that are likely to change the most with respect to buffel grass suitability (Figures 9 and 10) are revealed. Dark shades of brown show regions predicted to increase in suitability for buffel grass the most, whereas regions shaded dark blue reveal areas that are predicted to become less suitable for buffel grass. The 2070 medium scenario predicts a continent more suitable for buffel grass than the 2070 high scenario. This is largely driven by changes in soil moisture and timing of rainfall predicted with the 2070 high scenario. Having a C_4 photosynthetic pathway, buffel grass requires particular rainfall timing for establishment and persistence. The increase in winter temperatures predicted under the 2070 high scenario coinciding with sufficient rainfall will allow buffel grass to establish and grow, whereas previously insufficient rainfall during the warmer months prevented buffel establishment.

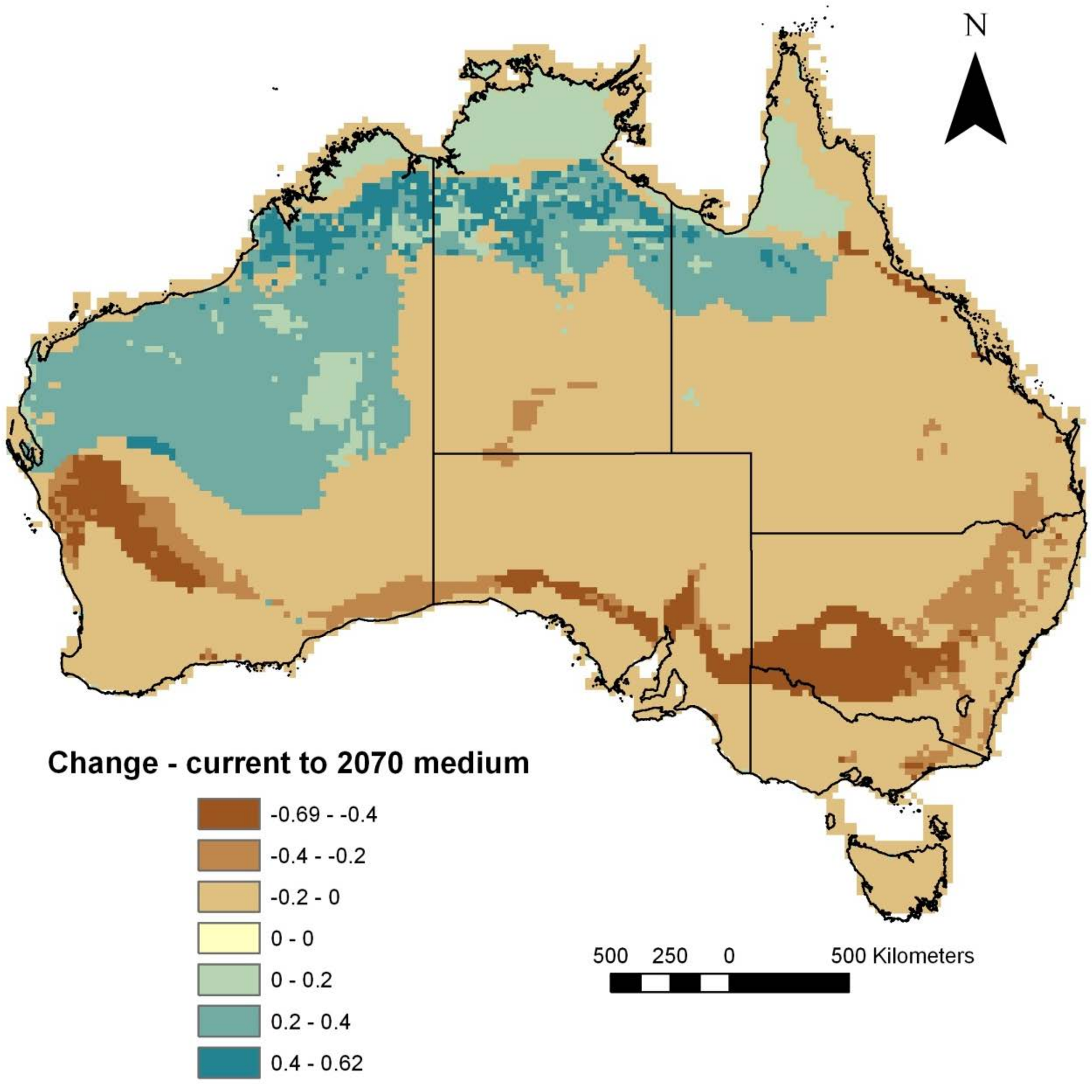

Figure 9 Change in predicted high suitability between current climate and 2070 medium climate scenario, where shades of brown reveal regions of increasing suitability and shades of blue decreasing suitability

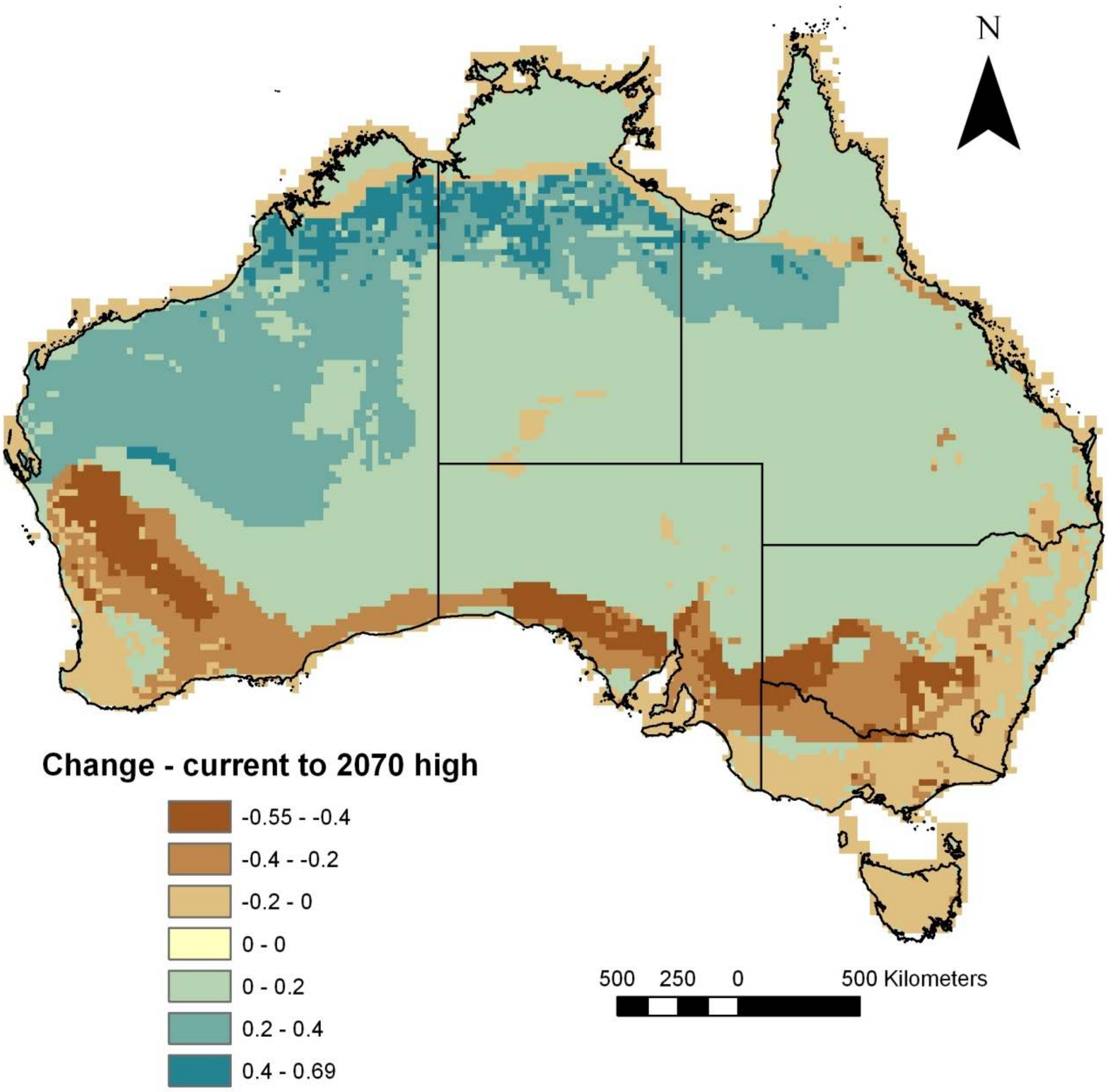

Figure 10 Change in predicted high suitability between current climate and 2070 high climate scenario, where shades of brown reveal regions of increasing suitability and shades of blue decreasing suitability

3.6 Hummock grasslands

Currently, a very large proportion of the hummock grasslands biome can be considered highly suitable to buffel grass invasion. This biome covers nearly half of the Australian continent and has a mean current suitability of 39% (±21 s.d) ranging from 1% to 77%. The majority of the biome (70%) currently falls within the high suitability range. The proportion of the biome falling within this suitability class decreases under both future climate scenarios (50% in 2070 medium, and 45% in 2070 high). However, under the 2070 medium future climate scenario, the mean buffel suitability across the biome increases to 46% (2070 medium), while under the 2070 high scenario there is only a marginal mean increase to 40%; the mean increase in the 2070 medium scenario is due to a higher proportion of very highly suitable habitat (>60% suitability) occurring across the biome (increasing from 9% to 16%). Of interest is that the maximum suitability actually decreases (to 62%) under the 2070 high scenario, while it remains unchanged (at 77%) in the medium scenario.

The largest changes in suitability across the biome are seen in the Pilbara, Gascoyne and Little Sandy and Gibson Desert areas, which all markedly decrease in suitability. Significant increases in suitability occur in western New South Wales and in South Australia.

The distribution of buffel suitability in the NRS within the hummock grasslands currently is generally in proportion to the distribution of buffel suitability across the biome, with the bulk of the NRS (70%) falling within the high suitability range. Under both future scenarios, the proportion of the NRS falling within this suitability class decreases (to approximately 53%), with consequent increases in the lowest (<20% suitability) class and in the highest (>60%) class.

3.7 Tropical savannas

The mean probability of suitability of the tropical savannas biome to buffel grass is currently 37% (±24 s.d) with a range of 1% to 94%. Under future climate scenarios, mean suitability across the biome decreases to 28% (2070 medium) and 23% (2070 high). The maximum values across the biome also decrease to 70% in the medium scenario and 56% in the high. The majority of the biome (49%) currently falls within the high suitability class. Under future climate scenarios there is a dramatic shift in the distribution of suitability, with marked decreases in the high suitability range and consequent increases in the low suitability range (<20%). In the 2070 high scenario, the proportion of the biome falling into the low suitability class doubles from current levels to 64%; the proportion of the biome occurring in the high suitability class more than halves to 19% (from 49%).

The decrease in buffel suitability across the biome is the result of a general southward shift in suitability across northern Australia. As a result the tropical savanna regions in Western Australia and the Northern Territory shift from currently medium-to-high suitability to low suitability in future scenarios. Under the 2070 medium scenario a large proportion of south-east Queensland in the Brigalow Belt bioregion remains highly suitable; however, this proportion decreases under the 2070 high scenario. In fact, under the 2070 high scenario, there is no longer any habitat in the tropical savanna biome considered very highly suitable (i.e. >60% suitability).

Currently, the majority of the NRS (62%) in the tropical savannas biome occurs within areas of low suitability. Under future scenarios this proportion increases further (to 73% in 2070 medium and 84% in 2070 high). There is also a decrease in the proportion of the NRS occurring in the very high suitability class from current levels (17%) to 6% (2070 medium) and 0% (2070 high).

3.8 Temperate woodlands

The mean probability of high suitability across the temperate woodlands biome is currently 14% (±18 s.d), ranging from 0% to 77%. Under future scenarios the mean increases to 31% (2070 medium) and 30% (2070 high). The majority of the biome (66%) currently falls within areas of low buffel suitability; in future scenarios the proportion of the biome in this suitability class falls to 42% (2070 medium) and 34% (2070 high). Marked future increases occur in the high suitability class with the proportion of the biome in this class increasing from 11% currently to 52% under the 2070 high scenario.

Across the biome, increases in suitability result from a general shift in higher levels of suitability towards the south and east of the biome, particularly in New South Wales. This shift also increases the suitability of areas of the biome in north-western Victoria.

The marked increase in mean suitability across the biome, and particularly the greater proportion of the biome occurring in the high suitability classes, is not as closely reflected in the distribution of buffel grass suitability in the NRS. The majority of the NRS remains in the low suitability class under future scenarios, although it does decrease in this class (from 81% currently to 51% in 2070 medium) and increase in the higher suitability class (from 4% currently to 20% in the 2070 high scenario).

3.9 South-eastern forests

The majority of the south-eastern forests biome covers areas of low buffel suitability both currently (73%) and under future scenarios (52% 2070 medium, 72% 2070 high). The 2070 medium scenario results in some increase in habitat suitability, particularly in the proportion of the biome shifting to medium suitability from currently low suitability; however, the 2070 high scenario results in only minor changes among the suitability classes compared to the current distribution.

These patterns are also reflected in the distribution of the NRS in the buffel suitability classes, that is, only minor changes between the current distribution and the 2070 high scenario distribution and an increase in the proportion of the NRS in the medium suitability class in the 2070 medium scenario.

3.10 Model sensitivity

The sensitivity of the three invasion requirements to the environmental variables reflects the expert opinions involved in constructing the conditional probability tables. For the invasion requirement 'introduction', whether or not buffel grass was planted at a site was the most important feature influencing this node (Figure 11). Soil quality, temperature of winter rainfall (temperature of wettest quarter) and tree cover were the most important variables influencing establishment. Soil quality was the key driver of persistence. The invasion requirements were least sensitive to fire frequency, high temperatures and grazing intensity. This may be due in part because grazing intensity was considered low across all of the rangelands (Bastin and ACRIS Management Committee 2008). Also, the influence of fire was driven through plant competition and, according to experts, buffel is tolerant to very high temperatures.

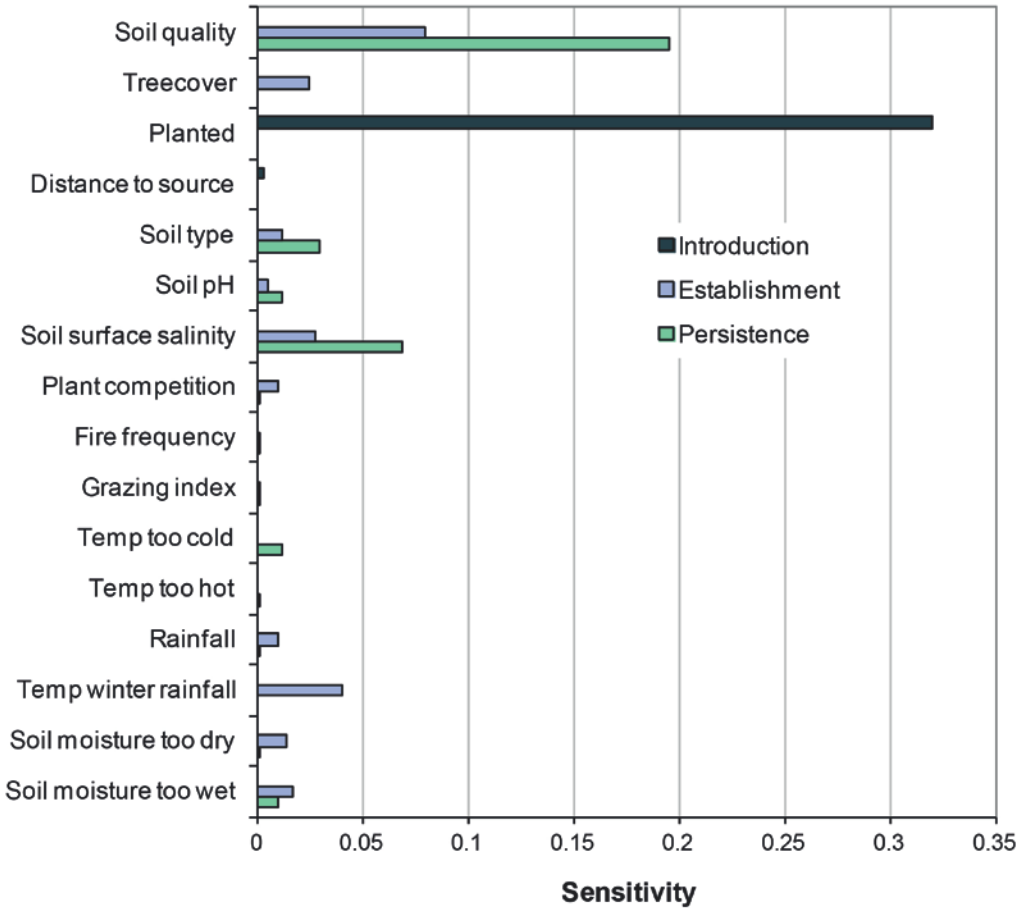

Figure 11 Sensitivity of each of the invasion requirements included in the BBN to key environmental variables

4 Discussion

The relative risk associated with invasive species is likely to change as climates shift. To best manage these threats an understanding of where changes in species spatial distribution are greatest is required. For most invasive species, we lack basic information on habitat suitability and current distributions. Our framework acknowledges this information gap and provides a method for generating species distributions under different climate scenarios when empirical data are lacking. Through the elicitation and use of expert knowledge within a BBN combined with available spatial data layers, we provide a set of predictions of the relative risk of the Australian continent and its NRS to colonisation by buffel grass, a species of commercial value and grave conservation concern.

Many modelling approaches have been proposed for predicting the distribution of invasive species (Venette et al. 2010). However, the benefits of using BBNs over common approaches such as CLIMEX (Sutherst and Maywald 1985) is their extreme flexibility in data-poor environments and ability to incorporate all influential variables, not only climate information. The use of BBNs with tools such as CLIMEX, where output from CLIMEX is fed into the BBN as a node representing a climate index, is a promising option. With the assistance of 15 experts we constructed a BBN that captured the key aspects of buffel grass ecology and spread. Experts agreed that the predictions provided by our buffel grass BBN are a substantial improvement on previous attempts using CLIMEX (Lawson et al. 2004).

Our results highlight the potential for buffel grass management to become increasingly important in the southern part of the continent, whereas in the north the threat of buffel grass is likely to lessen with climate change. While the overall suitability of hummock grasslands to buffel grass is predicted to decline modestly, the NRS within this biome is predicted to incur an increase in suitability. Our work suggests that overall the risk of buffel grass colonisation, establishment and persistence within the NRS is likely to increase with climate change. This is a consequence of the high number of NRSs located in the central and southern portion of the continent.

The negative impact of buffel grass colonisation on native biodiversity is now widely acknowledged (Fairfax and Fensham 2000; Franks 2002; Tu 2002; Clarke et al. 2005; Jackson 2005; Eyre et al. 2009; Smyth et al. 2009). However, the severity of impact varies depending on which environmental and biodiversity indicators are measured and the temporal and spatial scales that are investigated (Jackson 2005). Likewise, the economic benefits of buffel grass are also subject to variability depending on biophysical and climatic conditions. In particular, the value of buffel dominance within a pasture is subject to debate, where the lack of species diversity could increase pasture vulnerability to pests, diseases and unfavourable seasonal conditions.

For data-poor environments where inference is dependent on expert knowledge, we recommend BBNs as a cost-effective alternative to models that rely solely on empirical data or climate information. The development of cost-effective and efficient management strategies that account for trade-offs in production and biodiversity benefits will be a valuable contribution towards managing this dynamic threat in the future (Friedel et al. 2011).

Polarity of views on the costs and benefits of buffel grass have hampered efforts to develop policy for its sustainable management. However, perceptions of these costs and benefits may not be as polarised as popularly believed (Friedel et al. 2011). Our results suggest that climate change will not diminish the issue of how to manage invasive species such as buffel grass, but rather highlight the need to develop sustainable management policy in response to predicted shifts in spatial distribution of such species and subsequent threats to national assets.

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Appendix A Environmental variables

Apx Table A.1 Key environmental variables considered in the BBN and the GIS layer used

KEY ENVIRONMENTAL VARIABLE AND GIS LAYER USED	SOURCE OF DATA	VALUES USED IN BBN	DESCRIPTION OF MAP AND ASSUMPTIONS MADE WHEN SCALING UP TO 25 KM^2 GRID
Soil moisture			
Bioclim 1. mean moisture index of highest quarter 2. mean moisture index of the driest quarter	Bioclim layers generated for current climate and 2070 medium and high sensitivity scenarios	Moisture too wet >0.75 Soil moisture too dry = 0; Soil	Original data at 0.01 degree resolution. Resampled to 25 km grid via bilinear interpolation.
Temperature			
Bioclim 1. min temp for coldest period 2. max temp for warmest period	As above	Temperature too cold <2.5°C Temperature too hot >43°C	Original data at 0.01 degree resolution. Resampled to 25 km grid via bilinear interpolation.
Rainfall			
Bioclim mean annual rainfall	As above	Low <300 mm; Moderate 300–750; High >750	Original data at 0.01 degree resolution. Resampled to 25 km grid via bilinear interpolation.
Temperature winter rainfall			
Bioclim mean temperature of wettest quarter	As above	Suitable ≥16°C Unsuitable <16°C	Original data at 0.01 degree resolution. Resampled to 25 km grid via bilinear interpolation.
Grazing Intensity			
ACRIS, stocking rates DSE/km^2	livestock density (DSE/km^2) for rangeland IBRAs – 1992 to 2004 (Bastin and ACRIS Management Committee 2008)	Assumed equal probability of low, moderate and high grazing	Coverage only for rangelands.
Fire Frequency			
	Australia Fire Frequency, 1 km AVHRR maps for 1997–2008 covering the whole of Australia (Craig et al 2002).	High fire frequency calculated as an area burnt 3 times or greater during a 12-year period	Original data source at 1 km resolution. Resampled to 25 km grid using nearest neighbour assignment.
Tree cover			
NVIS – reclassified to suitable (vegetation with less than >70% tree cover) and unsuitable (more than 70% tree cover and water)	Australia – Present Major Vegetation Subgroups – NVIS Stage 1, Version 3.1 – Albers (Australian Government 2012)	Tree cover considered unsuitable when greater than 70%	Original data source at 1 km resolution. Reclassified to classes ‘suitable’ and ‘unsuitable’ based on major vegetation subgroup descriptions (ESCAVI 2003). Resampled to 25 km grid via nearest neighbour assignment.

KEY ENVIRONMENTAL VARIABLE AND GIS LAYER USED	SOURCE OF DATA	VALUES USED IN BBN	DESCRIPTION OF MAP AND ASSUMPTIONS MADE WHEN SCALING UP TO 25 KM^2 GRID
Distance to source			
Current distribution of buffel grass from Australian Virtual Herbarium	CHAH (2013)	Close <100 km Mid 100–500 km; Far >500 km	Point shapefile buffered at 500 km and 1000 km. Converted to raster 25 km grid.
Soil Surface Salinity			
Forecasted areas containing land of high hazard or risk of dryland salinity from 2000 to 2050	Australia Dryland Salinity Assessment Spatial Data (1:2,500,000) – NLWRA (2001)	Spatial coverage very poor – Assumed equal probability for results presented here	Original data at 1:2,500,000. Resampled to 25 km grid via nearest neighbour assignment. Current layer covers <10% of Australia, therefore did not use.
Soil pH			
	Soil ph for Australian Areas of Intensive Agriculture, NLWRA (2001)	Soil pH <5.0 considered strongly acidic and unsuitable	Original data at 0.001 degree resolution. Resampled to 25 km grid via bilinear interpolation.
Soil Type			
Northcote key	Atlas of Australian Soils Northcote et al. (1960–1968), ASRIS (2013)		Lawson et al. 2004 and expert knowledge from John McIvor. Original data source at 1:2,000,000 resolution. Resampled to 25 km grid via nearest neighbour assignment.

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