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I am submitting herewith a dissertation written by Matthew Charles Fitzpatrick entitled "Biological Invasions, Global Climate Change and Species Distribution Models: An Investigation of Species-Climate Relationships Across Space and Time." I have examined the final electronic copy of this dissertation for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Doctor of Philosophy, with a major in Ecology and Evolutionary Biology.

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(Original signatures are on file with official student records.)

BIOLOGICAL INVASIONS, GLOBAL CLIMATE CHANGE AND SPECIES DISTRIBUTION MODELS

AN INVESTIGATION OF SPECIES-CLIMATE RELATIONSHIPS ACROSS SPACE AND TIME

A Dissertation
Presented for the
Doctor of Philosophy
Degree
The University of Tennessee, Knoxville

Matthew Charles Fitzpatrick
May 2008

DEDICATION

to Heather, who willed it,
and to Gwenyth, who reminds me of what's important…

…and to C.N.O., who I never met.

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ABSTRACT

Species distribution models are increasingly being applied to questions in ecology, biogeography and evolution, and in particular to the problem of predicting the potential spread of invasive species and the potential impacts of climatic change on biodiversity. However, despite their broad application, several conceptual limitations still preclude the use of species distribution models in many theoretical and practical applications. Chief among these is the assumption that climate alone determines the geographic ranges of species, as opposed to biotic interactions and dispersal limitations, and that such species-climate relationships remain largely unchanged across space and time. In this context, I explore the degree to which climate constrains the distributions of species and how such relationships change during biological invasions and under climate change. I first examine whether species-climate relationships are conserved during the invasion of the red imported fire ant (*Solenopsis invicta*) and find evidence, in contrast to model assumptions, that invasive species can undergo rapid niche shifts during invasive spread and that this result is robust to variable selection. Next, I explore the degree to which migration constraints may limit the ability of *Banksia* (Proteaceae) species endemic to southwestern Australia to respond to climate change. I find that migration constraints may not represent a major factor in determining future patterns of biodiversity in this region as ranges of most species were projected to collapse rather than shift and that this result was consistent across different scenarios of future climate. Finally, I investigate the relative importance of dispersal limitation (as implied by seed dispersal mode) and contemporary climate in determining of patterns of biodiversity for 2543 species of plants in southwestern Australia. In contrast to the predicted relationship, I find that the distributions of dispersal-limited species were less constrained by dispersal and more constrained by climate than the distributions of ostensibly more vagile species. Taken together, these studies suggest, in strong contrast with model assumptions, that species climate-relationships can change, sometimes rapidly, under environmental change such that future patterns of biodiversity and biological invasions may not be readily predictable from current distributions of species.

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Chapter One

General Background & Overview

During the last decade, the field of ecology has witnessed an explosion of interest in the application of models that predict the potential geographic ranges of species by combining observations on the distributions of species and environmental predictor variables (Fig 1.1). Such models, commonly called bioclimatic, ecological niche, or species distribution models (Guisan and Thuiller 2005) have now been applied to a range of questions in biogeography (e.g., Anderson *et al.* 2002; Martinez-Meyer *et al.* 2004), conservation biology (e.g., Ferrier *et al.* 2002; Araújo *et al.* 2004) and evolution (e.g., Graham *et al.* 2004; Knouft *et al.* 2006; Yesson and Culham 2006) and their use in forecasting biological invasions (Peterson 2003; Peterson *et al.* 2004; Thuiller *et al.* 2005b) and the potential impacts of climatic change on biodiversity (Peterson *et al.* 2002a; Thomas *et al.* 2004; Thuiller *et al.* 2005a) is now commonplace.

Despite the great potential of species distribution models to address both theoretical and applied questions, important conceptual ambiguities remain that reduce the applicability and confidence of model results (Davis *et al.* 1998; Lawton 2000; Hulme 2003; Pearson and Dawson 2003; Hampe 2004; Guisan and Thuiller 2005; Araújo and Rahbek 2006; Araújo and Guisan 2006; Heikkinen *et al.* 2006). Among several issues, two prominent themes emerge. The first issue relates to the relative importance of environmental versus biotic factors in determining current range limits. Species distribution models assume that abiotic factors alone (typically with a focus on climate) constrain the distributions of species (Pearson and Dawson 2003; Guisan and Thuiller 2005). Although many studies have demonstrated that the limits of the geographic ranges of species often coincide with certain climatic conditions (e.g., minimum temperature, Root 1988), it is readily apparent that both biotic interactions and dispersal processes also influence the distributions of species (Gaston 2003).

Given that species distribution models are discussed and applied in the context of niche theory, the distinction between abiotic versus biotic controls on distribution is often framed in the distinction between realized and fundamental niches. The fundamental niche represents the complete set of environmental conditions under which a species can maintain a positive net growth rate, whereas the realized niche is the subset of those conditions within the fundamental niche that the species actually occupies owing to biotic interactions, dispersal limitation, resource availability, disturbance, etc (Hutchinson 1957). The prevailing wisdom is that because geographic ranges of species reflect the influence of both abiotic and biotic factors, observed distributions represent the realized niche of species (but see Soberon and Peterson 2005; Soberon 2007). Thus, models developed from observed distributions may capture only a subset of the environmental conditions the species can tolerate. Any change in biotic interactions or dispersal rates may alter the realized niche and will affect the validity of predictions of distributions of species. Changes in the realized niche seem likely for example when a species is

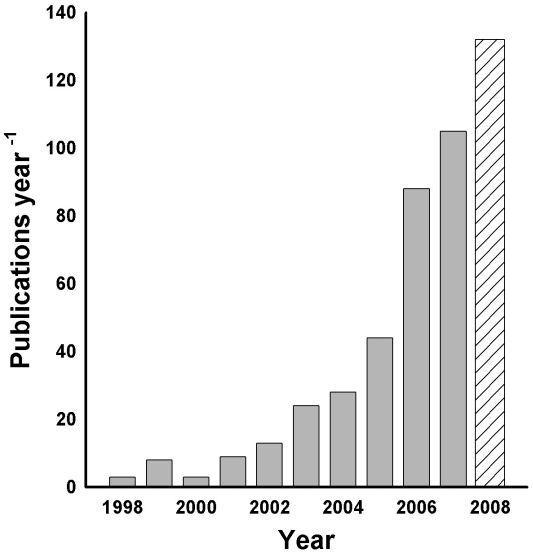

Figure 1.1: Number of citations per year found using the search terms "species distribution model*" OR "bioclim* model*" OR "ecological niche model*" OR "bioclim* envel*" on Web of Science. The hatched bar is the projected number of publications for 2008 based on publications in January 2008.

introduced to a new biogeographical setting and leaves behind natural enemies, or under climate change when interactions strengths will invariably change. Nonetheless, even if one did model the fundamental niche, this too can change owing to evolutionary processes (Ackerly 2003; Davis *et al.* 2005; Dietz and Edwards 2006).

Whereas the first issue concerns the degree to which realized and fundamental niches of a species are congruent under current environments and the degree to which the distribution of species reflect this relationship (Pulliam 2000), the second major conceptual issue facing the application of species distribution models relates to the propensity for species-climate relationships to change under future environments. The extrapolation of models to forecast biological invasions and the potential responses of species to climatic change relies uncritically on the assumption that species-climate relationships remain stable across space and time despite shifting biotic interactions, opportunities for dispersal, and genetic adaptation. When a model is developed from the observed distribution and that model is projected to a new set of environmental conditions, the model identifies where the species is likely to exist as long as the combinations of biotic and abiotic constraints on the modeled distribution of the species remain unchanged and the species does not evolve. Further, such projections do not distinguish between habitats that are suitable and that which the species can colonize by dispersal.

The propensity for changes in species-climate relationships ensures that no matter how good model fit is under one set of conditions, there is no guarantee that the model will exhibit a similar level of performance in a new environment. Whether species-climate relationships are stable or not, often discussed in terms of ‘niche conservatism’

(Wiens and Graham 2005), and at which spatial and temporal they remain unchanged is debated (Pearman *et al.* in press) and sometimes ignored (Peterson and Nakazawa 2008). However, evidence is mounting that niches can and do change and sometimes rapidly (Broennimann *et al.* 2007; Fitzpatrick *et al.* 2007).

Despite the growing application of species distribution models, they remain poorly integrated with ecological concepts and their underlying assumptions – though widely acknowledged as problematic – remain largely untested. My goal in this dissertation is to provide direct tests of the ecological concepts upon which models are based in the context of projecting biological invasions and the potential impacts of climatic change on biodiversity. I focus on two broad questions: (1) are species-climate relationships stable across space and time? and (2) What is the role of dispersal in determining present and future distributions of species? In Chapter 2, I focus on the issue of niche conservatism in the context of biological invasions. Using a novel approach (Fitzpatrick and Weltzin 2005) and the invasion of the red imported fire ant (*Solenopsis invicta*) as a model system, I find evidence that *S. invicta* underwent a rapid niche shift upon its invasion of North America. I conclude that species may spread into environments unlike those characterizing their native range and that the full geographic extent of some biological invasions may be largely unpredictable based on native distributions. This chapter is published in *Global Ecology & Biogeography*. In Chapter 3, prompted by a rebuttal (Peterson and Nakazawa 2008) of my findings in Chapter 2, I further explore issues concerning the stability of species-climate relationships and the invasion of the fire ant, but this time in the context of the environmental variables used to forecast biological invasions. Using a different dataset and new statistical test, I again find evidence for a rapid niche shift. This chapter is in press at *Global Ecology & Biogeography*.

In Chapters 4 and 5, I move from ants in the western hemisphere and the topic of biological invasions to climatic change and plants in the hyper-diverse heath lands of southwestern Australia. Here I investigate the role of dispersal in determining present and future distributions of species. In Chapter 4, I ask how the potential impacts of climatic change are related to assumptions regarding the ability of *Banksia* (Proteaceae) species to migrate and whether projected impacts interact with assumptions regarding how climate is projected to change in the future. I find that changes in precipitation regimes are primarily what drive changes in the distributions of *Banksia*. Because the ranges of many species are projected to collapse rather than shift regardless of the scenario of climatic change considered, assumptions regarding migration rates had little influence on projected impacts. This chapter is in press at *Global Change Biology*.

In Chapter 5, I assess the relative importance of climate and dispersal ability (in terms of seed dispersal mode) in determining the current geographic distributions of plant species in southwestern Australia. I test the prediction that the distributions of species with adaptations for short-distance dispersal of seeds (by ants or no mechanism) will be more constrained by dispersal than species adapted for long distance dispersal of seeds (by vertebrates or wind). In support of my findings in chapter 4, I find that current distributions of species are tightly coupled to precipitation regimes. However, in contrast to my prediction, I find that the distributions of dispersal-limited species appear less constrained by dispersal and more constrained by climate than the distributions of

ostensibly more vagile species. I argue that this unexpected finding appears to be linked, albeit loosely, to the role of short-distance dispersal in facilitating habitat specialization and therefore smaller geographic ranges. This chapter is to be submitted to *Ecography*.

Chapter Two

The biogeography of prediction error: why does the introduced range of the fire ant over-predict its native range?[1]

[1] A slightly modified version of this chapter was published as: Fitzpatrick MC, Weltzin JF, Sanders NJ, Dunn RR (2007) The biogeography of prediction error: Why does the introduced range of the fire ant over-predict its native range? *Global Ecology and Biogeography* 16:24-33. My use of "we" in this chapter refers to my co-authors and myself. My primary contributions to this paper include: 1) development of idea and hypotheses; 2) collection and preparation of inputs to the GARP algorithm; 3) modeling; 4) data analysis; and 5) most of the writing.

ABSTRACT

The use of species distribution models (SDMs) to predict the potential spatial extent of biological invasions is a rapidly developing area of ecology. However, most studies investigating the ability of SDMs to predict invasions typically take a confirmatory approach and ignore discrepancies between where models predict invasive species to occur and the known occupied invaded distribution and instead focus on regions where native distributions correctly predict invaded ranges. Using the Genetic Algorithm for Rule-set Prediction (GARP), we investigated the ecological significance of prediction errors using reciprocal comparisons between the predicted invaded and native range of the red imported fire ant (Solenopsis invicta) (hereafter called the fire ant). We questioned whether fire ants occupy similar environments in their native and introduced range, how environments that fire ants occupy in their introduced range changed through time relative to their native range, and where fire ant propagules are likely to have originated. We found that native range occurrences under-predicted the invasive potential of fire ants, whereas occurrence data from the invaded distribution over-predicted the southern boundary of the native range. Secondly, models suggest that introduced fire ants first established in environments similar to those in their native range, but subsequently invaded harsher environments. Time-series data suggest that fire ant propagules originated near the southern limit of their native range. Taken together, our findings suggest that fire ants from a peripheral native population established in an environment similar to their native environment, and then ultimately expanded into environments in which they are not found in their native range. In the context of predicting biological invasion using SDMs, we argue that reciprocal comparisons between predicted native and invaded ranges may facilitate a better understanding of the biogeography of invasive and native species and of the role of SDMs in predicting future distributions.

INTRODUCTION

Invasive species threaten global biodiversity, but also represent unparalleled opportunities to explore ecological factors that limit the distribution of species, and how and why those distributions change across space and time. In many ways this opportunity has not been fully realized, particularly in the context of species distribution models (SDMs). SDMs (also termed bioclimatic envelopes or ecological niche models) are often used to predict the potential spread of invasive species by first relating the observed distribution of a species to environmental conditions in its native range and then projecting these relationships in space to predict the potential distribution of the species in an unoccupied region (e.g., Welk *et al.* 2002). Most studies investigating this approach have focused on the prediction successes, i.e. regions where the native range correctly predicts the invaded range, and then consider regions in which ranges are predicted to expand (e.g., Peterson and Vieglais 2001; Peterson *et al.* 2003; Peterson 2003). However, all SDM predictions have errors, which have largely been ignored. Some such errors may represent inadequacies in the algorithm or data used to perform modeling, and may hold little biological meaning (Fielding and Bell 1997). Alternatively, and of greater potential interest to ecologists, errors may reflect genuine ecological differences between native and invaded ranges if they result from biological processes not included in models, such as interactions among species, dispersal, history, resource heterogeneity and evolution of environmental tolerances (Beerling *et al.* 1995; Fielding and Bell 1997; Peterson and Holt 2003; Fitzpatrick and Weltzin 2005; Holt *et al.* 2005; Wiens and Graham 2005).

Here we use a new method, reciprocal distribution modeling (RDM), to investigate the biological meaning and significance of prediction errors in modeling the distribution of invasive species (Fitzpatrick and Weltzin 2005). RDMs are conceptually similar to SDMs, in that they assess the ability of the native range to predict the invaded range. However, RDMs also use distributional data from the invaded range to predict the native range, and evaluate the degree and spatial location of prediction errors. The spatial patterning of prediction errors relative to observed ranges can suggest non-climatic control of distributions. For example, Beerling *et al.* (1995) used models developed from the introduced European range of *Fallopia japonica* to predict its native Asian distribution. They found that the invaded range over-predicted the native range, and suggested that dispersal limitations and interspecific interactions explained the discrepancies between the observed and predicted native distribution.

In this study, we assess spatial and temporal patterns of prediction errors relative to the native and invaded distributions of the red imported fire ant (*Solenopsis invicta* Buren) (hereafter referred to as the fire ant), a noxious invader to the southeastern United States (US) of America (Tschinkel 1993). Specifically, we use RDM and the Genetic Algorithm for Rule-set Prediction (GARP) (Stockwell and Noble 1992; Stockwell and Peters 1999) to address three questions. (1) Do fire ants occupy the same environments in their native and invaded range? (2) How did environments that characterized the occurrence of fire ants in the US change through time relative to the native range? (3) Can RDM be used to determine the likely origin of fire ant propagules from South America? We conclude that reciprocal comparisons between actual and predicted native

and invaded distributions facilitate development of explanatory and mechanistic biological hypotheses for the factors that mediate species distributions.

METHODS

Modeling approach

SDMs are empirical models that relate the observed distribution of a species and environmental data to predict the potential distribution of the species (reviewed by Guisan and Zimmermann 2000; Guisan and Thuiller 2005). Once developed from the native distribution, SDMs can be applied to another region to identify areas prone to invasion there (Peterson 2003).

RDMs rely on this same basic approach, but differ in that they use models developed concurrently from separate and independent occurrence data sets, one from the native range and one from the invaded range, and then make reciprocal predictions of native and invaded ranges based on these models (Fitzpatrick and Weltzin 2005). The RDM approach proceeds in four distinct steps. First, we model the native distribution based on native range occurrences. Secondly, we apply native range models to the invaded range and compare the predicted invaded range to the observed invaded range. Thirdly, we model the invaded distribution based on invaded range occurrences. Finally, we apply invaded range models to the native range and compare the predicted native distribution to the observed native distribution. This process produces four predicted distributions: two of the native range and two of the invaded range, from which the degree and spatial locations of prediction errors are noted relative to observed and predicted native and invaded ranges. Model quality is assessed during the first and third steps, as described below.

Study species

We chose the fire ant as a model system because its present native and invaded distributions are relatively well known, its record of introduction and subsequent spread are well documented, and its life history is at least somewhat known in both its native and invaded range. The native range of the fire ant encompasses southern Brazil, Paraguay, Uruguay, Bolivia and north-eastern Argentina (Buren *et al.* 1974; Pitts 2002). Fire ants established in the US near Mobile, Alabama, in the 1930s (Callcott and Collins 1996), and have since spread throughout the southeastern US and into Texas, New Mexico and California, and as far north as Maryland and Delaware. Fire ants have also recently invaded several Caribbean islands (Davis *et al.* 2001).

Model inputs

Native and introduced distribution data sets consisted of presence data only. We collected 74 native range occurrences of fire ants within South America from primary literature (Allen *et al.* 1974; Buren *et al.* 1974; Pitts 2002). For invaded range occurrence data, we used latitude – longitude center points of only those US counties under 'entire county quarantine' by the US Department of Agriculture, Animal and Plant Health Inspection Service (APHIS 2004), which constituted 741 counties in 2004. We obtained

year of first infestation for these 741 quarantined counties from the National Agricultural Pest Information System (Table 2.1; APHIS 2004). Because we used centers of counties instead of actual locations of populations, we wanted to ensure to the greatest degree possible that our models did not include what may be temporary, or isolated, populations. Thus, by including full-quarantine counties in the US only, we excluded Caribbean islands and counties where fire ants have invaded, but may not be firmly established, such as locations in the western US (where counties tend to be large and environmentally heterogeneous). Further, developing models using full-quarantine counties only allowed us to demonstrate how the use of occurrence data from an invading population impacts upon the predictions of RDMs and to avoid potential biases of including absences that may result from active colonization rather than from environmental suitability. Environmental data consisted of 12 WorldClim data sets (Hijmans *et al.* 2004) at 10-minute resolution, including elevation and 11 bioclimatic variables that summarize temperature and precipitation aspects of climate – variables typically used to model distributions of species and to predict the potential geographic extend of biological invasions (Table 2.2).

Reciprocal distribution modeling

We modeled distributions using the Genetic Algorithm for Rule-set Prediction (GARP) (Stockwell and Noble 1992; Stockwell and Peters 1999). Applications of GARP to prediction of the potential distributions of invasive species have been described elsewhere (e.g., Peterson *et al.* 2002b; Peterson 2003). In short, GARP uses an iterative process, and several individual modeling algorithms (e.g., logistic regression, bioclimatic rules), to develop, modify and test models describing the relationship between the presence of the species and environmental conditions. The occurrence dataset is divided by GARP based on user specification into training and test data (e.g., 50/50 or 70/30). GARP uses the training data and one of the individual algorithms to develop a rule predicting the distribution of the species. The rule is then modified and re-assessed for predictive accuracy using the test data. The change in predictive accuracy between iterations is used to determine whether the rule is incorporated into the model.

Table 2.1: Occurrence datasets used to develop reciprocal distribution models of fire ants.

Dataset	Time period	New occurrences	Total occurrences	Training / test data proportion
Native Range	--	--	74	70 / 30
Invaded range t_1	1930-1952	30	30	70 / 30
Invaded range t_2	1930-1959	173	203	50 / 50
Invaded range t_3	1930-1966	172	375	50 / 50
Invaded range t_4	1930-1979	184	559	50 / 50
Invaded range t_5	1930-2004	182	741	50 / 50

Table 2.2: Environmental variables (including units and abbreviations used in Figure 2.3) used to develop predictions of potential distributions of fire ants and factor loadings from a Principal Components Analysis (PCA) of environmental conditions associated with presence of fire ants.

			Factor loadings		
Variable	Units	Abbreviation	PC-1	PC-2	PC-3
Elevation	m	ELEV	0.005	0.031	0.915
Mean annual temperature	^{o}C	MAT	-0.907	0.3	-0.219
Mean diurnal temperature range	^{o}C	MDTR	0.529	0.265	0.535
Isothermality	--	ISO	-0.9	-0.075	0.333
Temperature seasonality (σ*100)	--	TSEAS	0.978	0.084	-0.111
Maximum temperature of warmest month	^{o}C	MXTWM	0.091	0.833	-0.359
Minimum temperature of coldest month	^{o}C	MTCM	-0.973	0.077	-0.153
Temperature annual range	^{o}C	TAR	0.964	0.193	0.031
Annual precipitation	mm	APR	-0.233	-0.907	-0.033
Precipitation of wettest month	mm	PWM	-0.71	-0.537	0.023
Precipitation of driest month	mm	PDM	0.509	-0.801	-0.148
Precipitation seasonality	--	PSEAS	-0.742	0.527	0.189

The final model, a set of rules describing the distribution of the species, is selected after either 1000 iterations or when predictive accuracy converges between iterations. We selected GARP to develop models because the algorithm is well-established in the literature as a method to successfully predict distributions using presence-only data sets, and its predictions are considered more robust than similar approaches (Peterson and Cohoon 1999; Stockwell and Peterson 2002).

Native range modeling

We randomly assigned the 74 native range occurrences into 50/50 splits of extrinsic training and test data. To ensure that division of the data did not influence model quality, we repeated the randomization process 10 times. The 10 resulting training data sets contained a random sample of half of the 74 original occurrences. Within GARP, we specified that these training data be divided 70/30 into intrinsic training and test data. We produced 100 models from each of the 10 training data sets, for a total of 1000 models. Because model development is stochastic, and resultant models vary in quality, we used a procedure described by Anderson *et al.* (2003) to select the best subset of models. From the 1000 models, we retained either all models with zero omission errors (i.e. false negatives) based on intrinsic test data, or, if there were less than 200 models with omission errors of zero, we selected the 200 models with lowest omission error rates. Using this subset, we calculated the median area predicted as present and selected 100 models closest to this median area. We then summed this best subset of 100 models to

produce a final composite prediction ranging from zero (no models predict the presence of fire ants) to 100 (all models predict the presence of fire ants).

We evaluated models by comparing the proportional area predicted as occupied by fire ants against the number of extrinsic test points that would be occupied if fire ants were distributed randomly (χ^2 statistic) (Peterson and Shaw 2003). Native range models were projected onto the invaded range and summed to produce a composite prediction of the potential invaded distribution of the fire ant relative to its known invaded range.

Invaded range modeling

We assigned the 741 invaded range occurrences to one of five groups based on year of first infestation in the US (Table 2.1). The first group (t_1) encompassed the first 20 years of fire ant invasion (i.e. 1930–1952) and included 30 US counties, a minimum number of locations required for robust predictions in GARP (Stockwell and Peterson 2002). We divided the remaining occurrences such that each successive group contained an equal number of newly invaded counties.

To ensure that our use of county centre points (as opposed to actual occurrences) in the invaded range did not influence model quality, we also constructed models using random points in each county. Models based on random points did not differ qualitatively from models based on centre points; thus, we used centre points for all subsequent analyses.

To develop invaded range models from the five invaded range data sets, we employed a procedure similar to that used for native range models, with two modifications. First, the initial time series data set was too small to divide into extrinsic training and test data, so we used all 30 points for model development in GARP and did not evaluate these models using χ^2 tests. Secondly, the remaining four data sets were sufficiently large, so we specified GARP to divide training data sets into 50/50 (instead of 70/30) splits of intrinsic training and test data (Table 2.1). Otherwise, random partitioning of data sets, development and selection of best models, and model evaluation followed procedures described above. Invaded range models were projected onto South America and summed to produce a composite prediction of the native range of the fire ant relative to its known native range.

Environmental correlates with fire ant distributions

We used principal components analysis (PCA) on the correlation matrix (using NCSS; Hintze 2001) to analyze patterns of fire ant distribution in relation to environmental data (listed in Table 2.2) for each occurrence point. The PCA model included occurrence points from invaded range time period t_1 (30 points), invaded range time periods $t_2 - t_5$ pooled (711 points total), and the current native range (74 points).

RESULTS

Models based on native range occurrences

All 100 best native range models performed better than random expectation (χ^2 test, d.f. = 1, $P < 0.001$). Predicted distributions coincided with the extent of the native

range in South America on the southern, western and northern boundaries, but extended considerably beyond the eastern boundary (Fig. 2.1a). Conversely, projections of native range models onto the invaded range in North America greatly under-predicted the actual extent of invasion (Fig. 2.1b). According to these models, peninsular Florida and the Pacific Northwest in the US, the Gulf Coast and Yucatan Peninsula in Mexico, and the Caribbean are most susceptible to invasion. Several models (< 25) also identified a narrow band of suitable environments along the Gulf Coast of the US, including where fire ants first established in southern Alabama.

Models based on invaded range occurrences

All the best invaded range models performed better than random expectation (χ^2 test, d.f. = 1, $P < 0.001$). Predicted distributions of the invaded range based on all 741 invaded counties overlapped the actual extent of invasion (Fig. 2.1c). Models predicted several areas beyond the extent of the current invaded range to be prone to invasion by fire ants as well, in particular the central valley of California, the Pacific North-west, and north of the current northern limit of the invaded range in the south-eastern US. Over-prediction in these regions overlaps many US counties where fire ants have invaded, but that are not currently quarantined (APHIS 2004). These findings are qualitatively similar to other attempts to predict fire ant distributions in North America, using both statistical (Sutherst and Maywald 2005) and simulation (Killion and Grant 1995; Korzukhin *et al.* 2001) models. Invaded range models, when projected onto South America, predicted a distribution that overlapped only the southern half of the native range and extended several degrees of latitude (c. 1000 km) beyond the southernmost limit of the native range in Argentina (Fig. 2.1d).

When superimposed, predicted distributions of the native range developed using the five temporal data sets comprised of invaded US counties (Table 2.1; Fig. 2.2a) produced a bull's eye pattern (Fig. 2.2b). Models based on the first 30 invaded counties in the US predicted a limited and patchy distribution near the southernmost region of the native range. Each successive prediction (based on the temporally expanding distribution of fire ants in North America) grows radially from its predecessor, ultimately spreading equally north and south of the southern limit of the native range.

Comparison of predicted distributions

Native and invaded range occurrence data did not predict similar distributions in either North or South America. In South America, predicted distributions from native and invaded range models overlapped in the southern half of the native range only and did not overlap in the northern half of the native range or regions in Argentina south of the native range (Fig. 2.1a, d). In North America, prediction distributions from both data sets overlapped in peninsular Florida, along the coast of the Gulf of Mexico, the Pacific Northwest, although they differed across large portions of the south-eastern and western US and the Caribbean (Fig. 2.1b, c).

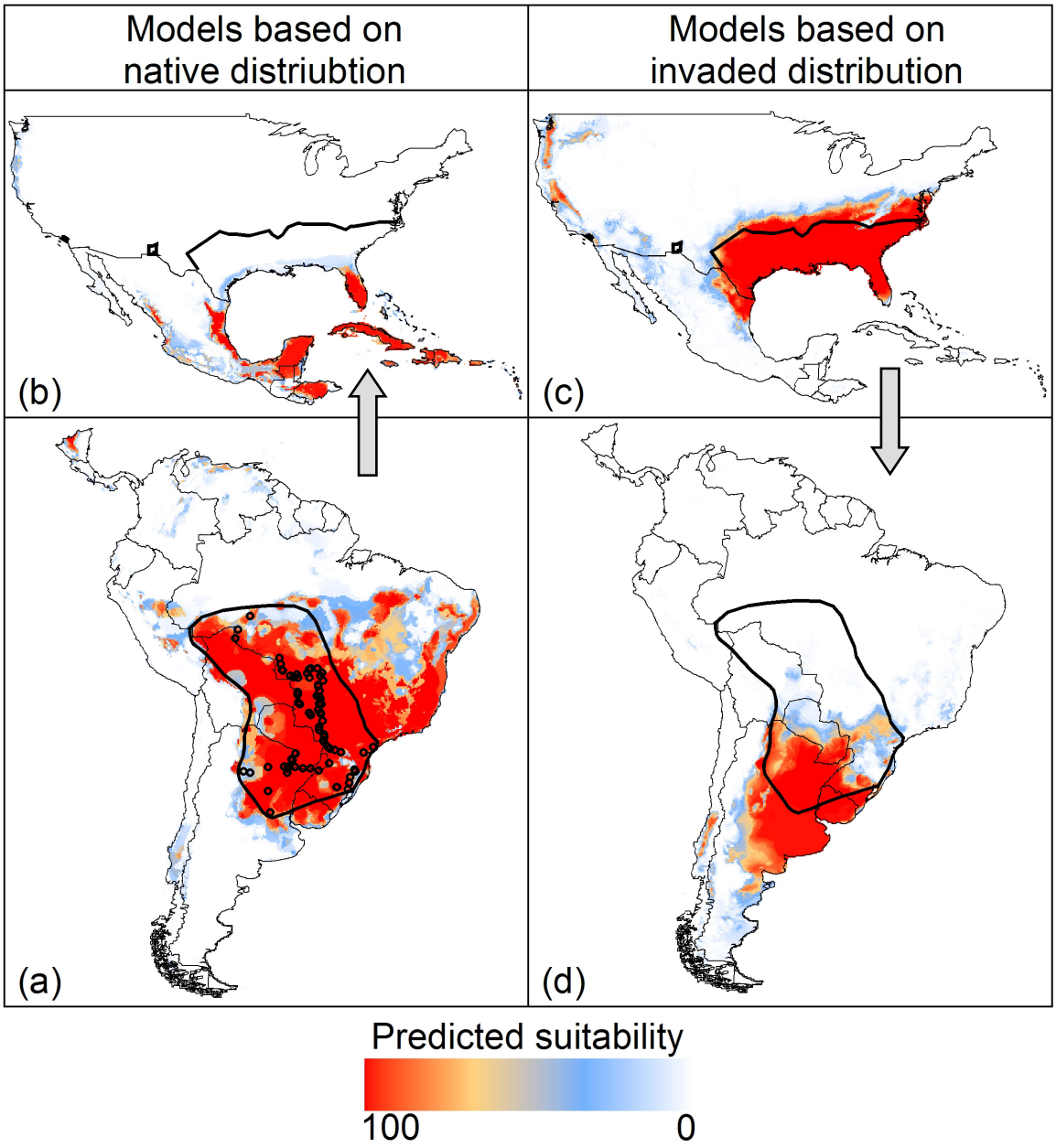

Figure 2.1: Potential distributions of the red imported fire ant. Native range models represent (a) the potential native, and (b) invaded distributions of the fire ant based on 74 known occurrences in South America (a, open circles). Invaded range models represent (c) the potential invaded and (d) native range of the fire ant based on the centre points of 741 US counties (c, points not shown). Shading corresponds to the number of models out of 100 that predict presence of fire ants. Bold, solid lines indicate the approximate extent of the native (a, d) and invaded (b, c) range of the fire ant.

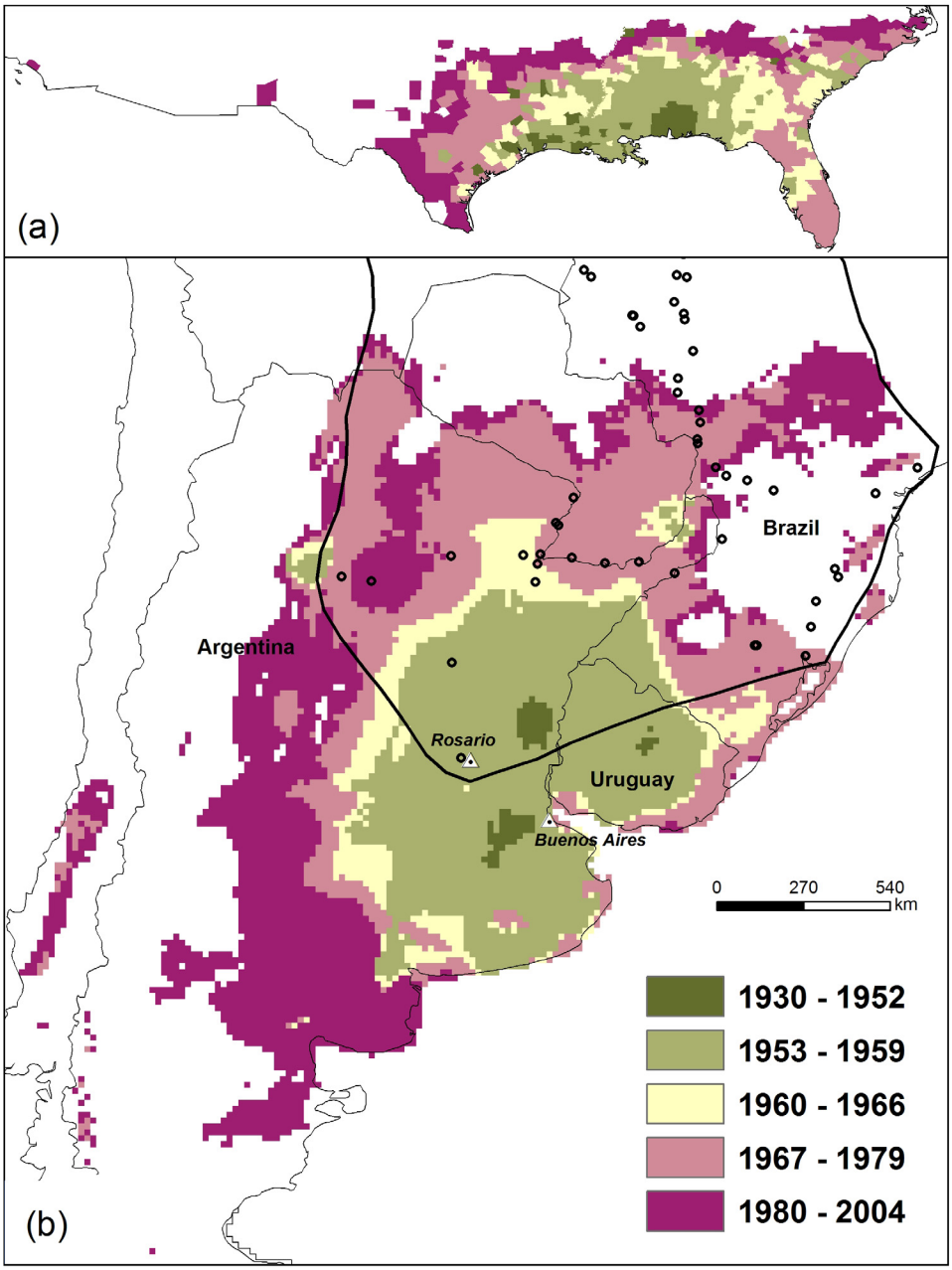

Figure 2.2: (a) Actual US counties invaded by fire ants, showing initial establishment in counties radiating from southern Alabama. (b) Predicted distributions of the fire ant in South America based on models from these time series data, relative to known occurrences (open circles) and the extent of the native range (bold line). Triangles indicate the port cities of Rosario and Buenos Aires, Argentina. Shading represents areas predicted by a majority (> 50) of the 100 best models.

Environmental correlates with fire ant distributions

The first three principle components accounted for 88.2% of the total variation in the data. The first principle component (PC-1, 51.5%) was related to aspects of temperature, whereas PC-2 (24.5%) was related to precipitation and maximum temperature of the warmest month. PC-3 (12.6%) was mainly related to elevation.

DISCUSSION

We report three novel findings related to the spatial patterning of prediction errors that would be largely indiscernible without reciprocal comparisons of predicted native and invaded distributions. First, fire ants occupy environments in their invaded range that they do not occupy in their native range. The environments that fire ants occupy in North America, but not in South America, tend to be colder and drier (Fig. 2.3) and characteristic of environments adjacent to, and south of, the southern border of their native range (Fig. 2.1). Second, comparisons of predicted distributions through time suggest that fire ants initially invaded environments in North America that were similar to those found within their native range, and subsequently spread into harsher environments outside their native range (Fig. 2.2). Finally, the extreme southern extent of the native range is most environmentally similar to US counties in which fire ants initially established, suggesting the southern region of the native range is a potential source of invading propagules. This result corroborates a similar prediction made by Mescher *et al.* (2003) based on genetic analyses. Together, our findings suggest a model in which fire ants from a peripheral native population established in an environment similar to their native environment, and then over time expanded into environments in which they are not found in their native range. We discuss these results below both in terms of their ecological interpretation and their broader implications for predicting future distributions using SDMs.

Native vs. invaded range environments

Fire ants in the US occupy colder, drier and more seasonal environments than in their native range (Fig. 2.3). Differences between the environments fire ants occupy in their native and invaded ranges are apparent as prediction errors in reciprocal comparisons (Figs 2.1 and 2.2b). Two broad hypotheses may explain these disparities between predicted and observed distributions of fire ants in the US. First, factors governing the southern boundary of the native range of the fire ant may not be present, or may not be limiting, in the invaded range. Secondly, and not mutually exclusive of the first hypothesis, environmental tolerances of the fire ant may have changed post-invasion. In particular, a hypothesis that accounts for both of these possibilities is that genetic changes subsequent to introduction and release from natural enemies resulted in changes in the social structure of fire ants, which in turn promote their invasive success by allowing fire ants to form dense, ecologically destructive colonies (Tschinkel 1998; Tsutsui and Suarez 2003).

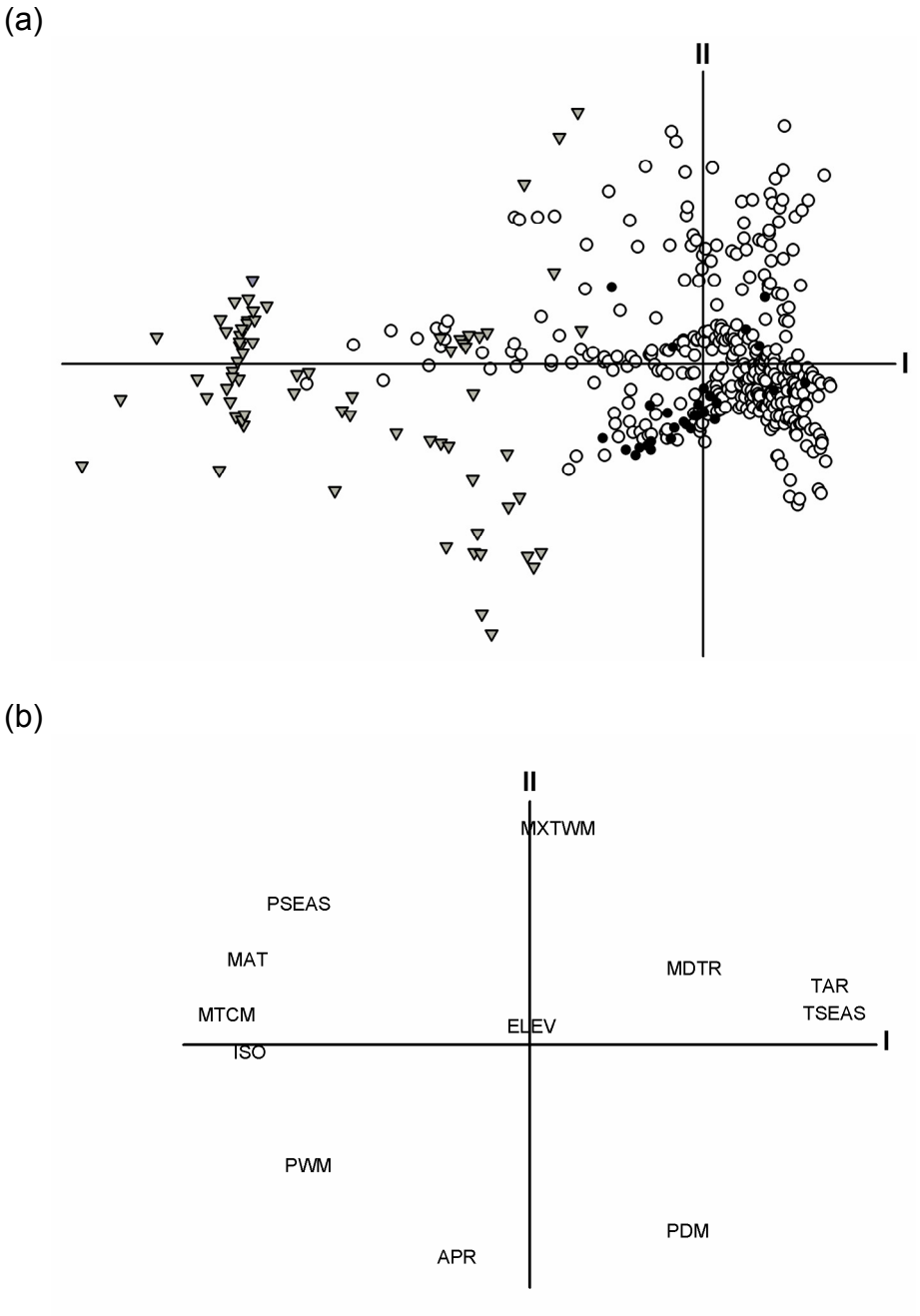

Figure 2.3: (a) PCA ordination of environmental variables associated with presence of fire ants in their native South American range (triangles) and their invaded US range (circles). Closed circles represent the first 30 counties in which fire ants became established in the US between 1930 and 1952. Open circles represent US counties in which fire ants became established between 1953 and 2004; one-half of the open circles were excluded at random to reduce excessive detail. (b) Contribution of environmental variables to the distribution of points along each axis. Abbreviations of environmental variables and factor loadings for each principle component are in Table 2.2.

To our knowledge, no studies have explicitly investigated factors that limit the distribution of fire ants in both their native and invaded ranges. However, several lines of evidence suggest North and South American populations of fire ants demonstrate different life histories and experience different biotic environments, including (in North America): (1) higher rates of dispersal (Mescher et al. 2003), (2) greater population densities, possibly resulting from enemy release (Porter et al. 1997), (3) changes in social structure such that fire ants in the US form dense, polygynous colonies of unrelated queens free from density-limiting effects of territorial defense (Morel et al. 1990; Porter and Savignano 1990), (4) absence of infection by Wolbachia, a bacterium that can reduce the fitness of its hosts (Shoemaker et al. 2000), and (5) reduced competition stemming from anthropogenic disturbance and chemical eradication programs that ultimately benefit fire ants while adversely affecting native North American ant species (Tschinkel 1993; Zettler et al. 2004).

Release from natural enemies is one of the most commonly invoked explanations for the proliferation of invasive populations (Colautti *et al.* 2004), and the success of introduced fire ants has been attributed to enemy release (Porter *et al.* 1997). Such release could allow fire ants to invade regions in which the combined mortality due to environmental and biotic factors would be too high to persist in the native range. Reduced biotic stresses stemming from the loss of natural enemies, coupled with increased dispersal rates (which could rescue peripheral populations), could reduce constraints on the distribution of introduced fire ants such that they can occupy a different set of environments in North America than those characteristic of their native range in South America.

Reduction of biotic stresses could also facilitate the initial establishment of propagules in non-optimal environments in North America. Less than 25% of distribution models based on native occurrences predicted fire ants to be present in the Mobile basin (Fig. 2.1b). In contrast, all models predicted fire ants to be present in peninsular Florida. However, fire ants did not occupy these potentially more favorable environments in Florida until later stages of the invasion (Fig. 2.2a). This suggests that if broad-scale environmental conditions alone controlled the establishment of fire ants in the US, and ignoring other factors potentially important to initial establishment, namely propagule pressure, then Florida was probably more susceptible than was Alabama as the primary point of initial establishment.

The expansion of invasive fire ants into environments in which they do not occur in their native range could result from changes in biotic interactions, but it could also be due to the evolution of life-history traits that facilitate persistence in novel environments. Rapid evolution of introduced species is widely reported (see Cox 2004), and evolutionary changes in environmental tolerances of introduced fire ants could easily explain differences between environments occupied in the native and invaded range. Consistent with this hypothesis, and with our prediction that fire ants may have established in marginal environments, Holt *et al.* (2005) theorized that evolution of environmental tolerances is most likely if species are introduced into novel environments just outside their optimum environment.

Although there is no published evidence of evolution of environmental tolerances of fire ants per se, there is evidence of genetic changes subsequent to introduction

coupled with changes in social structure that have influenced the success of fire ants as an invasive species (reviewed in Tsutsui and Suarez 2003). Native and invasive fire ant colonies possess two social forms: colonies are either monogynous and contain a single queen, or colonies are polygynous and contain multiple queens. The polygynous colonies were not reported in the US until 20 years after the monogyne form was first detected, possibly stemming from multiple introductions (Tsutsui and Suarez 2003). The appearance of the polygyne form in the US is significant because, unlike monogynous colonies, workers from polygynous colonies display reduced aggression towards individuals from other colonies (Morel *et al.* 1990). Invasive polygynous colonies, free from density-limiting effects of territorial defense, attain greater densities of both workers and nest mounds than monogyne populations (Porter and Savignano 1990). The ecological destructiveness of polygynous colonies and their ability to displace native ant species and previous invaders (including monogynous colonies) are correspondingly greater (Porter and Savignano 1990). Thus, polygyny may allow fire ants to invade harsher environments by reducing both biotic resistance and extinction risk through increased abundance.

Hybridization could also facilitate persistence in novel environments. In the US, the fire ant hybridizes with another pest ant species, *Solenopsis richteri*, the black imported fire ant (Shoemaker *et al.* 1996). Hybridization might lead to introgression of genes favoring range expansion into colder and drier environments. In South America, the native range of *S. richteri* overlaps the southern portion of the native range of *S. invicta* and extends southward into colder and drier environments in Argentina (Pitts 2002; Ross and Shoemaker 2005), but hybridization does not appear to occur in the native range (Ross and Shoemaker 2005). Finally, an additional genetic/evolutionary hypothesis is that, in the native range, local adaptation to conditions at the edge of the range (where the invasive propagules appear to have originated, see below) are not possible because of gene flow with the centre of the range where less extreme conditions predominate.

Source of founding propagules

Based on reciprocal comparisons we identify the extreme southern extent of the native range as being most environmentally similar to counties in the US initially invaded by fire ants (darkest shading in Fig. 2.2b). If greater environmental similarity between source and recipient locations increases the likelihood of successful establishment, then the southern portion of the native range is the most likely source of invading propagules.

Several other lines of evidence also support the suggestion that the southern portion of the native range represents the source of propagules. First, preliminary genetic analyses of native and invasive fire ant populations also suggest that the most likely source of individuals founding the US population is the southern half of the native range, and north-eastern Argentina in particular (Mescher *et al.* 2003). Secondly, Ahrens *et al.* (2005) reported a sharp genetic discontinuity in the native distribution of fire ants along the border between Argentina and Brazil. In this region, a 2500 km-long geographical barrier to gene flow (the Mesopotamia wetlands) divides the distribution of fire ants into two evolutionary independent groups, one in the south-western portion of the range and the other in the north-eastern portion (Ahrens *et al.* 2005). Environments characteristic of

the counties first invaded by fire ants occur primarily to the west of this division. Finally, historical patterns of commerce provide circumstantial evidence that propagules are likely to have originated from the southern portion of the native range. When fire ants were first discovered in the US, the port in Mobile, Alabama, was receiving cargo from eastern South America (Buhs 2004). Ships originating in South America often used soil as ballast, which was unloaded in Mobile when American goods were loaded for transport back to South America (Buhs 2004). Rosario and Buenos Aires, two massive port cities in Argentina, occur within 150 km of the regions identified by models as most environmentally similar to the areas where fire ants first established in the US (Fig. 2.2b). Taken together, these findings suggest that populations of fire ants west of the Mesopotamia wetlands in north-eastern Argentina, near the port cities of Rosario and Buenos Aires, are the most likely source of fire ants introduced to the US. Evolutionary biologists searching for the founding populations of fire ants should focus their attention on this region.

Caveats

As stated above, prediction errors can result from both a failure to account for biotic processes (the interesting errors) and/or from inadequacies in the algorithm or data (the problematic errors). Of potentially greatest concern to the use of RDMs, in terms of inadequacies in the algorithm or data, are incomplete distribution data. Apparent prediction errors (e.g., over-prediction of the native range) could represent environments where the species is present but has yet to be detected. Incomplete distribution data, however, seem an unlikely explanation for the prediction errors observed in our analysis because *S. invicta* apparently has yet to be collected south of Rosario, Argentina, despite surveys in this region (Pitts 2002; Ross and Shoemaker 2005). Instead, other species of fire ants occur south of Rosario, such as *S. richteri* (Pitts 2002; Ross and Shoemaker 2005).

Of secondary concern to the application of RDMs is that many invasive species may still be expanding their distribution, in which case the introduced range may be more immediately constrained by dispersal and time than by environmental factors (Welk 2004). However, invasive species often spread rapidly. Therefore, although an introduced species may be actively spreading in some parts of its range, its distribution may be limited by environmental tolerances in other areas, or the species may have already colonized novel environments. If this were the case, the expectation would be for RDMs to over-predict portions of the introduced range that are suitable, but not yet invaded, and under-predict environments in the native range that are not currently invaded in the introduced range. This is precisely the pattern observed in this study. This analysis suggests the introduced range of the fire ant could expand to include tropical Mexico and the Caribbean (as over-predicted by models), which have environments similar to the northern-most portion of the native range (as under-predicted by models). Consistent with this prediction, fire ants recently invaded several Caribbean islands (Davis *et al.* 2001). However, the southward expansion of fire ants into Mexico may be biologically hindered given the gradient of increasing ant diversity with latitude (Kaspari *et al.* 2003).

Implications for predicting future distributions

The projection of SDMs in space or time, either to predict biological invasions or the impacts of climate change on biodiversity, assumes: (1) climatic tolerances of the species are the primary determinants of its current distribution (as opposed to ecological factors, notably biotic interactions and dispersal limitation); and (2) climatic tolerances of the species are conserved such that the species will occupy similar environments in new biogeographical settings. Debate concerning the validity of this latter assumption, often referred to as 'niche conservatism' (reviewed in Wiens and Graham 2005), has transpired in the recent literature. Our results suggest that novel biotic interactions and evolutionary change may invalidate the assumption of niche conservatism. That said, our models successfully predicted the initial stages of the invasion of fire ants into the US. Thus, although SDMs may predict regions where invaders are most likely to establish, they may be ineffective at predicting subsequent spread in some cases. Given the increasing application of SDMs, and their potential to (mis)inform conservation, it is important to investigate further the precepts of this approach and to integrate ecological principles more fully with SDMs. Our study demonstrates that reciprocal comparisons of the native and invaded ranges of invasive species can serve as powerful tests of the underlying assumptions of SDMs, and of niche conservatism in particular. We suggest that more studies incorporating reciprocal comparisons, and a greater focus on prediction errors, are required and should include additional modeling techniques, more invasive species and different regions of the globe. Such studies may lead to a better understanding of biological invasions, niche conservatism and the role of SDMs in predicting future distributions (Fitzpatrick and Weltzin 2005; Wiens and Graham 2005).

CONCLUSIONS

Our analysis allowed us to make four conclusions about the distribution of fire ants. First, we identified environments occupied in the invaded range but not in the native range. Secondly, we identified how the environmental conditions occupied by fire ants in their invaded range have changed (non-randomly) through time relative to their native range. Thirdly, we identified a potential origin of source propagules. Finally, we identified regions of the invaded range into which fire ants may spread based on environmental tolerances. Although these four findings could ultimately be best further informed by field studies, they were detected using available occurrence data sets only. We propose that these types of analyses can be performed – and that consequent biogeographical hypotheses can be developed – for other species for which we know the native and invaded ranges well. Rather than focusing on prediction successes, we argue that reciprocal comparisons between predicted native and invaded ranges, coupled with careful scrutiny of prediction errors, will facilitate a better understanding of the biogeography of invasive and native species than was previously possible.

Chapter Three

Datasets matter, but so do evolution and ecology.[1]

[1] At the time of this writing, a slightly modified version of this chapter was in press as: Fitzpatrick MC, Dunn RR, Sanders NJ, (in press) Datasets matter, but so do evolution and ecology: A response to Peterson and Nakazawa. *Global Ecology and Biogeography*. My use of "we" in this chapter refers to my co-authors and myself. My primary contributions to this paper include: 1) development of ideas; 2) collection and preparation of inputs to models; 3) modeling; 4) data analysis; and 5) most of the writing.

INTRODUCTION

In a recent paper, Peterson and Nakazawa (2008), hereafter PN, contest key findings in our study (Fitzpatrick *et al.* 2007) that suggests that *Solenopsis invicta* (hereafter fire ant) underwent a niche shift upon its invasion of North America. Using niche-based models, we proposed that the fire ant established in environments similar to those found in its native range but subsequently spread into environments unlike those found within its native range – a pattern strikingly similar to that suggested by Broennimann *et al.* (2007) for Spotted Knapweed (*Centaurea maculosa*). PN counter that our findings are simply an artifact of the environmental variables we used to model the fire ant's distributions and suggest instead that selection of alternative variables can produce a more correct prediction of the fire ant's invasion. PN conclude that the biological explanations offered in Fitzpatrick *et al.* (2007) for the non-predictivity between the fire ant's native and invaded distributions, namely enemy release, genetic founder effects, and hybridization, are not necessary. Here we respond to PN's criticisms.

We disagree with the contentions outlined in PN on the grounds that the authors (1) subjectively consider what represents a "correct" prediction of the fire ant's niche, (2) do not discuss the potential for niches to be conserved along some environmental axes but not others and, most significantly, (3) do not adequately represent our original analyses in Fitzpatrick *et al.* (2007) by not testing the ability of the fire ant's invaded distribution to predict its native range using their alternative datasets. We demonstrate using the procedures outlined in Fitzpatrick *et al.* (2007) and the set of environmental variables in PN that represents a subset of the variables used in Fitzpatrick *et al.* (2007) that the results from our original study stand.

Issue 1: Subjective consideration of what constitutes a "correct" prediction

PN state that, owing to small sample sizes, their "test" of model predictions was qualitative. The failure of models to "anticipate the full northward extent of the species' invasion was taken as an indication of poor generalization" (emphasis ours). We do not take issue with such a qualitative and subjective 'test' of model quality per se. But, if PN apply such a test to predictions of the invaded range, they must also apply the same "test" to distributions predicted for the native range. PN seem satisfied with predictions of the fire ant's invaded distribution in North America as long as models anticipate at least a portion of the northern limit of the fire ant's invasion (not the full northern limit or the western limit) – no matter how low model agreement or how poorly models predict other portions of the fire ant's distributions (e.g., over-prediction of the fire ant's native range). In contrast, they dismiss models that fail their test of a "correct" prediction, but that replicate the fire ant's native distribution in South America (upon which the models were based), including models that correctly predict the southern limit of the native range, which is roughly analogous to the north limit of the introduced range.

Our differences in interpretation originate, at least in part, from an essential difference between the goal of Fitzpatrick *et al.* (2007) and that of PN. Fitzpatrick *et al.* (2007) attempted to test for and offer hypotheses that might explain a niche shift, while PN attempt to replicate a well documented invasion by selecting variables that generally predict the fire ant's invaded distribution, regardless of model performance elsewhere.

Therefore, PN consider the fire ant's niche to be modelled "correctly" when the prediction meets their criteria in the invaded range, even if models fail to predict the native range. We consider the fire ant's niche to be modelled "correctly" when models predict all extents of both the native and invaded ranges, because if the niche of a species is conserved, then a single model should in principle predict both the native and the invaded range (Wiens and Graham 2005). Such a gestalt evaluation, in tandem with comparisons in bioclimatic space (rather than geographic space alone, e.g., using principal components analysis), is more likely to identify instances of niche shifts (or lack thereof) rather than a focus on particular characteristics of the predicted invaded distribution alone.

On these grounds, we take particular issue with PN's claim that four of the environmental datasets used in their paper could correctly predict the fire ant's potential to invade North America – even when considering their definition of a "correct" prediction. These four datasets include data from: (1) the Intergovernmental Panel on Climate Change (IPCC), (2) the Center for Climate Research at the University of Delaware (CCR), (3) monthly surface reflectance values drawn from the normalized difference vegetation index (NDVI), and (4) a subset of the data layers from the WordClim dataset ('reduced WC2', see Peterson and Nakazawa (2008) for full descriptions of these data and citations). Of these four, only the 'reduced WC2' dataset comes close to correctly predicting both the invaded and native range using native range occurrence data (but see Issue 3 below). Both IPCC and CCR do a poor job at predicting the fire ant's invasive potential in North America. There are absences in the predicted distributions where fire ants are known to be present and regions with thin coverage (i.e., low model agreement). The IPCC dataset predicts, also with low model agreement, that fire ants could invade areas north of the Arctic Circle. To consider these models as correct predictions of the fire ant's invasive potential is misleading. NDVI does anticipate the full northward extent of the fire ant's invasion. However, NDVI also over-predicts the native range (including its southern extent), suggesting that NDVI does not limit the fire ant's native distribution. This notion is strengthened by the fact that NDVI also predicts coastal Maine and regions of Canada north of Minnesota to be susceptible to invasion by fire ants. Because fire ant physiology has been intensively studied, we know that these northern regions are not suitable areas fire ants have yet to colonize. Such over-prediction is to be expected when remotely-sensed data are used as surrogates for climate variables because distant regions may exhibit similar spectral signatures even if they have substantially different climates.

Issue 2: The potential for niches to be conserved along some environmental axes but not others

Given the amount of baggage that comes with the niche concept and its relationship to niche-based models, it is debatable whether differentiating between fundamental and realized niches is useful (Guisan and Thuiller 2005; Araújo and Guisan 2006; Soberon 2007). However, in a general sense, distinguishing between fundamental and realized niches is a simple way to clarify the primary issue with projecting biological invasions using observed distributions of species in their native range. Further, distinguishing between fundamental and realized niches is useful when discussing niche

conservatism because niche shifts can result from a change in the realized niche only (e.g., relaxation of biotic constraints on distribution with no change in climatic tolerances), or also from a change in both the realized and fundamental niche (Pearman *et al.* in press).

Niche-based models are applied and often discussed in the context of Hutchinson's niche concept. As defined by Hutchinson (1957), the fundamental niche represents the complete set of environmental conditions under which a species can persist, whereas the realized niche is the subset of those conditions within the fundamental niche that the species actually occupies. Because observed distributions of species reflect multiple determinants, including climatic tolerances, biotic interactions, and dispersal limitation, niche-based models developed using observed distributions will predict the geographic equivalent of the realized niche. When such a model is projected, the model identifies where the species is likely to invade as long as the combinations of biotic and abiotic constraints on the native distribution of the species remain unchanged and the species does not evolve. As has been widely theorized and empirically validated, changes to both realized and fundamental niches are possible during an invasion given the potential for release from biotic and other non-climatic constraints on distribution and adaptation (see Pearman *et al.* in press for a recent review of these topics as well as a comprehensive list of examples of both niche shifts and niche conservatism drawn from many taxa).

A larger issue is the fact that there is no standard measure of what constitutes a niche shift. How much a species' niche has to change for it no longer to be conserved is an open question. It is unlikely that any introduced species invades a new territory without experiencing some degree of niche shift, since it is highly unlikely that identical combinations of environmental conditions exist in both the native and introduced ranges – especially when considering more than a few environmental variables. Whether such niche shifts result from species realizing more of their fundamental niche or from founder effects or subsequent evolution that lead to change in both the realized and fundamental niche is irrelevant to our argument as niche-based models cannot distinguish these possibilities. Nonetheless, decades of evolutionary and ecological theory and a large body of empirical evidence documenting that invasive species can experience rapid evolution as well release from biotic constraints on distribution suggest that niche shifts should be commonplace when species are introduced to new biogeographical settings.

In this vein, PN do not explore as a possible explanation for the ability of their models with fewer variables to better replicate the fire ant's invasion that niches may shift along some environmental axes while being conserved along others. There is little reason to think that a species' niche will shift along all environmental axes simultaneously. It is entirely plausible, and we would argue much more likely, for a species' niche to shift along one axis or a few axes such that they may tolerate, say, different moisture conditions, while conserving their tolerance of minimum temperature. Such a scenario may explain why the 'reduced WC2' dataset predicts more of the fire ant's invaded distribution than variables used in our original analysis. The fire ant's niche may have shifted along an environmental axis represented by variables in the 'full WC2' dataset, but which is not represented in the 'reduced WC2' dataset. Further, given that dimensionality is reduced as environmental variables are removed from consideration,

models will tend to produce a broader predicted niche (and distribution) because the number of possible constraints on the niche is correspondingly reduced as well. In any event, as we outline in Issue 3, our analysis using the 'reduced WC2' dataset does not eliminate the necessity for biological explanations for the non-transferability of models between the fire ant's ranges as claimed by PN.

Issue 3: Incomplete replication of our original analysis

Despite the availability of data describing the fire ant's invaded distribution, PN employed only native distribution data in their analysis (and used slightly different native distribution data than the data used in our original analysis). We performed an analysis identical to that described in Fitzpatrick *et al.* (2007) using PN's 'reduced WC2' dataset and the original Desktop GARP algorithm within the Open Modeller framework. We focus on the 'reduced WC2' dataset because it represents a subset of the original variables used in Fitzpatrick *et al.* (2007). In addition, we used the 'ade4' package in R 2.6.0 to test for niche conservatism by comparing the positions of native and invaded range distribution data in the climatic space resulting from a principle components analysis on the 'reduced WC2' dataset. We weighted occurrences to ensure that both the invaded range (741 points) and the native range (74 points) had equal representation. The significance of the difference between the fire ant's native and invaded niches (i.e., the two clusters of points in PCA space) was assessed using a between-class analysis (see Broennimann *et al.* (2007) for a relevant application) and by performing a Monte-Carlo test (99 permutations) on the resulting between-class inertia percentage.

Our analysis using the 'reduced WC2' dataset confirmed our original findings. When examined in 'reduced WC2' climatic space, the invaded niche of the fire ant is significantly different than its native niche (between class inertia: 40.0%; $P < 0.01$), mainly along an axis associated with temperature (Fig. 3.1). This finding suggests that the fire ant has invaded colder temperatures than those characterizing its native distribution. This niche shift was revealed in geographic space when models developed using the 'reduced WC2' dataset were projected (Fig. 3.2, right panel). Models developed using native range occurrences failed to predict the full northward extent of the fire ant's invasion (even when we considered model agreement as low as 25%, black shading Fig. 3.2(b), right panel), whereas models developed using invaded range occurrences also over-predicted the southern limit of the native range (Fig. 3.2(d), right panel). These projections are nearly identical to those obtained in our original analysis (Fig. 3.2, left panel).

We continue to argue that these "prediction errors" are biologically interesting and a more biologically-rigorous model confirms our notion. Morrison *et al.* (2004) used a mechanistic, physiological model based on colony growth rates in North America (Korzukhin *et al.* 2001) to predict the potential global extent of the fire ant's distribution. In accordance with our analysis, predictions from the colony-growth model also suggest that the fire ant's native distribution could extend further south than its currently recognized boundary in South America (Morrison *et al.* 2004). The most parsimonious explanation, supported by both niche-based and physiological models, is that the fire ant's niche was not conserved upon its invasion of North America. Whether this apparent niche-shift represents a change in the fire ant's realized or fundamental niche remains

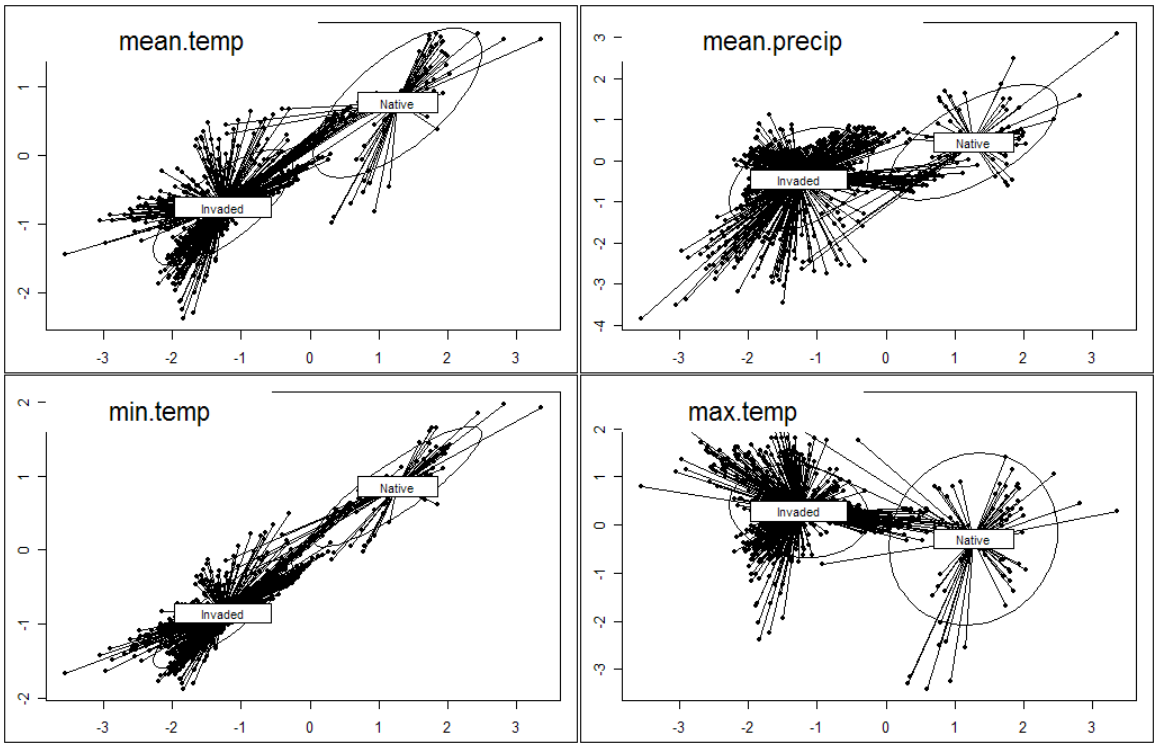

Figure 3.1: Illustration of the niche shift of *Solenopsis invicta* in the bioclimatic space of the reduced WorldClim dataset (reduced WC2). The position of occurrences from the native and invaded ranges along the principal climatic gradients derived from Principle Components Analysis (PCA) is indicated with black dots. Climatic predictors are: mean.temp = annual mean temperature, mean.precip = annual sum of precipitation, min.temp = minimumtemperature of the coldest month, and max.temp = maximum temperature of the warmest month.

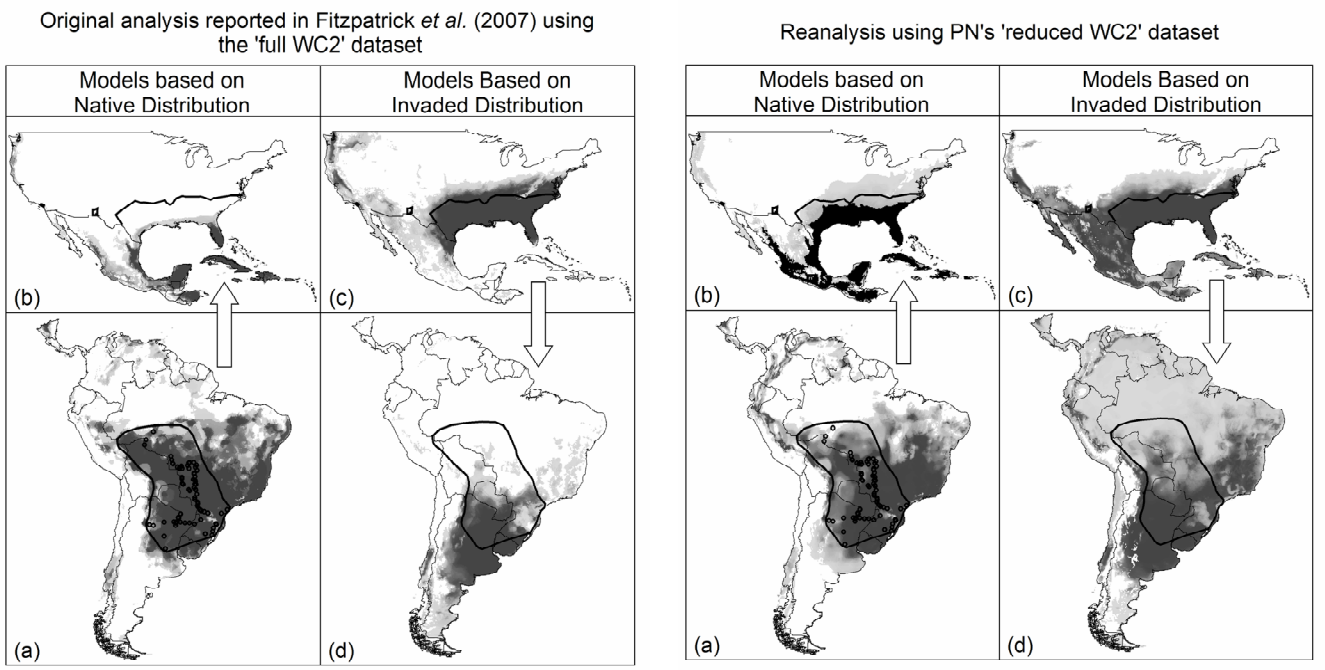

Figure 3.2: Potential distributions of *Solenopsis invicta* developed using niche-based models and two environmental datasets. The left panel is the original as published in Fitzpatrick *et al.* (2007) and contended by Peterson and Nakazawa (2008). The right panel replicates our original analysis using the reduced WorldClim dataset (reduced WC2) of Peterson and Nakazawa (2008). In both panels, native range models represent the potential (a) native and potential (b) invaded distributions of the fire ant based on 74 known occurrences in South America (a, open circles). Invaded range models represent the potential (c) invaded and potential (d) native range of the fire ant based on the center points of 741 US counties (c, points not shown). Bold, solid lines indicate the approximate extent of the native (a, d) and invaded (b, c) range of the fire ant. Darker shading represents greater model agreement. Black shading in the right panel (b) represents areas where model agreement is at least 25%. As in the original analysis at left, the 'reduced WC2' dataset under-predicts the invaded range (b, right panel) and over-predicts the native range (d, right panel).

unclear, because, to our knowledge, no such physiological model has been developed for fire ant populations in South America.

There is little reason to believe that predicted distributions based on species distribution models will ever match observed distributions perfectly. Certainly some prediction errors will prove to be uninteresting and related to data quality or statistical inaccuracies. Therefore, it is important to point out such potential sources of uncertainty in both our original analysis and that presented here. For example, the environmental conditions fire ants experience on the ground are likely to differ vastly in some regions from those characterized by temporally- and spatially-generalized climate data – especially in regions such as the desert southwest of the United States where fire ants persist mainly where irrigation is prevalent. This fact alone could account for some modelling discrepancies and highlights the caution required when using niche-based models to test hypotheses regarding species-climate relationships (Araújo *et al.* 2005). Further, there is now a consensus among researchers that projections can vary widely with the statistical technique used to model geographic distributions and therefore a range of modeling techniques and ensemble forecasting (Araújo and New 2007) ideally should be used to reduce and quantify such model-based uncertainty. In both the analysis here and our original analysis, we used only one algorithm, GARP. An investigation of the ability of other statistical approaches to predict the invasion of the fire ant (and other invasive species) is warranted. In fact the well-studied fire ant could serve as an excellent test of the ability of different techniques to project invasions. Finally, in keeping with our interest in replicating our original analysis, we did not validate our findings using all of PN's datasets, namely IPCC, CCR, or NDVI.

Nonetheless, we view certain model errors as biologically interesting and necessitating biological explanations – since it is biological processes that species distribution models notoriously ignore. Niches can change owing to drift, enemy release, selection, hybridization and simply as a consequence of genetic founder effects during invasion. Some or all of these factors could result in niche shifts that are potentially detectable at the broad spatial scales at which niche-based models are commonly applied. Understanding the prevalence of and mechanisms behind such shifts is of theoretical and applied interest and may facilitate improvements in our ability to anticipate both biological invasions and the potential impacts of climate change on biodiversity. We agree that the role of environmental datasets in these issues merits careful investigation. However, by implying that model errors are simply the result of variable selection and do not warrant biological explanations, PN may have inadvertently exposed niche modelling studies to yet another criticism.

Chapter Four

Climate change, plant migration, and range collapse in a global biodiversity hotspot: The Banksia *(Proteaceae) of Western Australia.*[1]

[1] At the time of this writing, a slightly modified version of this chapter was in press as: Fitzpatrick MC, Gove AD, Sanders NJ, Dunn RR (in press) Climate change, plant migration, and range collapse in a global biodiversity hotspot: The *Banksia* (Proteaceae) of Western Australia. *Global Change Biology*. My use of "we" in this chapter refers to my co-authors and myself. My primary contributions to this paper include: 1) development of idea and hypotheses; 2) collection and preparation of inputs to models; 3) modeling; 4) data analysis; and 5) most of the writing.

ABSTRACT

Climate change has already altered global patterns of biodiversity by modifying the geographic distributions of species. Forecasts based on bioclimatic envelop modeling of distributions of species suggests greater impacts can be expected in the future, but such projections are contingent on assumptions regarding future climate and migration rates of species. Here, we present a first assessment of the potential impact of climate change on a global biodiversity hotspot in southwestern Western Australia. Across three representative scenarios of future climate change, we simulated migration of 100 *Banksia* (Proteaceae) species at a rate of 5 km decade^{-1} and compared projected impacts to those under the commonly applied, but acknowledged as inadequate, assumptions of 'full-' and 'no-migration'. Across all climate × migration scenarios, 66% of species were projected to decline, whereas only 6% were projected to expand or remain stable. Between 5 and 25% of species were projected to suffer range losses of 100% by 2080, depending mainly on climate scenario. Species losses were driven primarily by changes in current precipitation regimes, with the greatest losses of species projected to occur in a transition zone between wet coastal areas and interior arid regions and which is projected to become more arid in the future. Because the ranges of most species tended to collapse in all climate scenarios, we found that climate change impacts to flora of southwestern Western Australia may be large, even under optimistic assumptions regarding migration abilities. Taken together, our results suggest that the future of biodiversity in southwestern Western Australia may lie largely in the degree to which this hotspot experiences increased drought and in the ability of species to tolerate such decreases in precipitation. More broadly, our study is among a growing number of theoretical studies suggesting the impacts of future climate change on global biodiversity may be considerable.

INTRODUCTION

Recent climate change has altered global patterns of biodiversity by modifying the geographic distributions of species (Hughes 2000; Walther *et al.* 2002 *et al.* 2002; Parmesan and Yohe 2003; Root *et al.* 2003). Projections based on bioclimatic modeling of distributions of species suggest extinction rates may increase dramatically in response to future climate change, with potentially drastic implications for biodiversity (Peterson *et al.* 2002a; Thomas *et al.* 2004; Thuiller *et al.* 2005a). However, projections derived from species distribution models are sensitive to many widely-acknowledged uncertainties (Pearson and Dawson 2003; Guisan and Thuiller 2005; Heikkinen *et al.* 2006), including assumptions regarding migration rates of species (Pearson 2006; Botkin *et al.* 2007; Midgley *et al.* 2007) and the magnitude and pattern of future climate change (Thuiller 2004).

To account for uncertainties inherent in projecting distributions of species under climate change using species distribution models, studies often incorporate multiple future climate scenarios (e.g., Thuiller *et al.* 2005a; Araújo *et al.* 2006) or different assumptions regarding migration rate (e.g., Williams *et al.* 2005; Midgley *et al.* 2006). However, these factors have largely been considered in isolation. Further, the most common approach to incorporating multiple migration rates in climate change impact assessments has been to bracket the range of potential responses and assume either that species cannot migrate ('no-migration') and only lose range as climate changes or that species have no constraints on migration ('full-migration') and can colonize all areas that become suitable in the future. The projected impacts of climate change often differ strongly between these contrasting 'full-' and 'no-migration' assumptions (e.g., Thomas *et al.* 2004; Thuiller *et al.* 2005a).

Certainly the dispersal ability of most species falls between the unlikely extremes of full- and no-migration and varies as a function of their life histories. Thus, recent studies have attempted to reduce uncertainties related to migration limitations by assigning an estimated migration rate according to the dispersal syndrome of the modeled species. For example, Williams *et al.* (2005) and Midgley *et al.* (2006) used a "time-slice" method and assigned an average migration rate per unit time to Proteaceae species based on seed morphology. Under the time-slice model, species with ant-dispersed seeds could move a maximum 1 km decade^{-1}, whereas wind-dispersed species could move a maximum of 4 km decade^{-1} (Williams *et al.* 2005; Midgley *et al.* 2006). When information regarding dispersal syndromes of species is lacking, an alternative approach may be to approximate migration rates using those inferred for migration of species during the Holocene (Broennimann *et al.* 2006). These time-slice approaches, though admittedly simplistic, compromise model complexity for generality and are therefore amenable to multi-species climate change impact assessments.

Although the relative importance of migration rates of species and the manner in which climate change is projected to alter distributions of species is likely to vary in a complex, species-specific manner, in general migration rates should be most important in regions where large range shifts relative to the migration ability of species are projected. In contrast, migration rates should have little influence on projected impacts if ranges of species contract because under such a scenario no new areas become suitable for

colonization. In short, assumptions regarding migration rates should be important to projected future patterns of biodiversity mainly in regions where the persistence of species is contingent on their ability to migrate to new, favorable areas.

Among the world's ecosystems, Mediterranean-type ecosystems (i.e., shrublands characterized by summer drought and winter rainfall, Cowling *et al.* 1996) are some of the most biologically diverse (Cowling *et al.* 1996) and most sensitive to multiple drivers of global change (Sala *et al.* 2000). All five regions of the earth containing Mediterranean-type ecosystems are designated biodiversity hotspots (Myers *et al.* 2000), highlighting both their importance to global biodiversity conservation and the degree to which they are currently threatened. Because Mediterranean-type ecosystems may be especially sensitive to climate change (Fischlin *et al.* 2007), it is crucial to consider the potential effects of future climate change on these regions.

Southwestern Western Australia is a Mediterranean-type ecosystem and global biodiversity hotspot that contains more than 8500 species, 62% of which are endemic (Cowling and Lamont 1998; Beard *et al.* 2000). The biodiversity of the region is at potentially large risk from climate change and migration constraints due to the concentration of species at the cool, wet end of a hot, dry continent. However, despite the importance of southwestern Western Australia to global biodiversity and the potential threat posed by climate change, the consequences of climate change for biodiversity in this region have been poorly considered. Because future climate scenarios for Western Australia differ markedly in their projections, this region represents an ideal location to consider whether climate change scenario or assumptions regarding migration rate represent greater sources of uncertainty for projections of potential climate change impacts.

Here we present a first assessment of the potential impact of climate change in southwestern Western Australia. We focus on 100 wind-dispersed *Banksia* (Proteaceae) species endemic to the region to assess how three assumptions regarding migration rate influence projections of future distributions of species across multiple scenarios of future climate and how such assumptions alter projected future patterns of biodiversity in this region of high diversity and endemicity. We address three key questions: (1) To what extent do the potential impacts of climate change depend on migration rate? and (2) Are assumptions regarding future climate or migration rate greater sources of uncertainty in projected impacts? Finally, (3) do climate scenarios and migration rate interact, such that the importance of migration is conditional on climate scenario?

METHODS

Why study migration in the Banksia *of Western Australia?*

Proteaceae species are an obvious, important and representative component of most southwestern Western Australian habitats. Among the seventeen currently recognized genera within Proteaceae, we selected *Banksia* as the focus of our study because the genus is relatively well-studied, known to contain both widespread and narrowly distributed species (Lamont and Connell 1996), and forms a critical part of southwestern Western Australian food webs as copious producers of nectar and pollen (Saffer 2004). Therefore impacts to these species may have cascading ecological effects.

Further, diversity patterns of *Banksia* are representative of diversity patterns of plants in general in southwestern Western Australia (Fitzpatrick *et al. unpublished data*) and therefore impacts to *Banksia* species may be broadly indicative of impacts to plant species generally. Finally, *Banksia* includes species in which dispersal distances and gene flow patterns have been relatively well-resolved (He *et al.* 2004). Because dispersal traits are fixed within *Banksia* (Cowling and Lamont 1998), species in this genus have similar seed morphologies and dispersal characteristics (Hammill *et al.* 1998). It is therefore reasonable to assign the same estimated migration rate to all *Banksia* species (see *Incorporating migration* below). Finally, to ensure that models captured the full realized niche of species under study (rather than arbitrary limits such as political borders), we focus on those species of the genus *Banksia* (including *Dryandra*) considered endemic to Western Australia. We include species of the genus *Dryandra* as *Banksia* was recently found to be paraphyletic with respect to *Dryandra* (Mast *et al.* 2005) and a new taxonomic arrangement transferring *Dryandra* to *Banksia* has been initiated (Mast and Thiele 2007). Here forth, we use the term *Banksia* to describe both *Banksia* and *Dryandra* species.

Distribution data

Georeferenced, presence-only distribution data for 105 *Banksia* species were obtained from the Western Australia Herbarium (PERTH, data provided May 2005). The database covers all of Western Australia and includes nearly 650,000 vouchered plant specimens for over 10,000 vascular plant species.

Environmental data

Environmental data included seven layers characterizing climate and seven layers describing soil properties. We represented current climate (averaging period 1961-1990) using temperature, precipitation, and evaporation datasets provided by the Australian Bureau of Meteorology (http://www.bom.gov.au/) at a resolution of 0.025^{o} (approximately 2.5 km × 2.5 km in Australia). From these datasets, we developed the following seven variables: mean annual temperature, minimum temperature of the coldest month, maximum temperature of the warmest month, annual, winter (June, July August) and summer (December, January, February) precipitation, and an index of growing season length in months that incorporates precipitation and evaporation and estimates the amount of precipitation necessary to start and maintain plant growth above the wilting point (Prescott and Thomas 1949). The seven soil variables included soil texture (i.e., percent clay, silt and sand content), total plant-available nitrogen and phosphorus, saturated hydraulic conductivity, and plant-available water capacity (Australian Natural Resources Data Library, http://data.brs.gov.au/; accessed September 2006). These variables are considered critical to the physiological function (and thus the distribution) of plants generally (Woodward 1987) and of plants in Western Australia in particular (Hopper and Maslin 1978; Hnatiuk and Maslin 1988; Beard 1990; Groom and Lamont 1996; Keighery 1996; Lamont and Connell 1996; Cowling and Lamont 1998; B. Lamont, *pers. comm*.).

Future climate scenarios

Future climate projections were developed for each decade between 2000 and 2080 by perturbing baseline climate with anomalies extracted from OzClim 2.0.1, a database of fine-resolution future climate simulations available in five-year intervals for Australia (for details see http://www.cmar.csiro.au/ozclim). To explore a range of uncertainty in projections of future climate, we selected three combinations of general circulation model, socio-economic emission scenarios developed by the IPCC (IPCC 2001), and climate sensitivity from the many possible combinations within OzClim that approximate the least-severe, intermediate-severity, and most-severe scenarios of future climate change for Western Australia in terms of increase in mean annual temperature and decrease in mean annual rainfall. These included: (1) CGCM1 (Canadian Centre for Climate Modelling and Analysis Coupled Global Climate Model) scaled using the B1 emission scenario and low climate sensitivity (hereafter low-severity), (2) CSIRO2 (Australia's Commonwealth Scientific and Industrial Research Organization Atmospheric Research Mark 2 Climate Model) scaled using the A1B emission scenario and mid climate sensitivity (hereafter mid-severity), and (3) HadCM3 (Hadley Centre for Climate Prediction and Research Coupled Climate Model) scaled using the A1F emission scenario and high climate sensitivity (hereafter high-severity). See Table 4.1 for additional details regarding emission scenarios and climate models. Given the spatial scale of our analyses, we assumed soil properties would remain constant under future climate. Also, because of a paucity of adequate data, we did not consider landcover change in our analysis, which is likely to intensify impacts due to climate change (Travis 2003).

Table 4.1: Description of future climate scenarios to which distributions of species were projected using MAXENT models. Atmospheric CO_2 refers to global CO_2 concentrations by 2080. Anomalies refer to the projected mean change in the mean annual value across southwestern Western Australia by 2080.

	Low-severity	Mid-severity	High-severity
Global climate model	CGCM1	CSIRO2	HadCM3
IPCC emission scenario	B1	A1B	A1F
Climate sensitivity	low	mid	high
Atmospheric CO_2 (ppm)	520	615	815
Temperature anomaly (^oC)	1.3	1.9	4.2
Precipitation anomaly (%)	-5	-12	-40

Species distribution modeling

We related environmental conditions to species occurrence data using MAXENT 2.3.3 (Phillips *et al.* 2006). MAXENT is a recent implementation of a statistical approach called maximum entropy that characterizes probability distributions from incomplete information (Phillips *et al.* 2006). In the context of modeling distributions of species using maximum entropy, the assumptions are that (1) occurrence data represent an incomplete sample of an empirical probability distribution, that (2) this unknown distribution can be most appropriately estimated as the distribution with maximum entropy (i.e., the probability distribution that is most uniform) subject to constraints imposed by environmental variables and that (3) this distribution of maximum entropy approximates the potential geographic distribution of the species (see Phillips *et al.* (2006) for more details). MAXENT has been found to be a promising and robust approach for modeling species distributions under both current (Elith *et al.* 2006; Hernandez *et al.* 2006) and future environments (Hijmans and Graham 2006).

Many methods exist to model distributions of species and the statistical approach used is often an important source of uncertainty (Pearson *et al.* 2006). We selected MAXENT because it has several characteristics that make it particularly suitable for our study. These include a deterministic algorithm, the ability to use presence-only distribution data, and the option to automatically batch process using command line scripts – a critical characteristic given our need to construct models for three climate scenarios per species and to then project each of these models to nine time periods in the future. A potential problem with projecting species distribution models to future environments is that projections may require that models be extrapolated to conditions beyond those used to train the model (i.e., non-analog climates). For example, a drawback of maximum entropy is that when projecting to future environments the exponential model of MAXENT can produce very large predicted values for environmental conditions outside the range observed under present conditions (Phillips *et al.* 2006). However, a beta version of MAXENT that addresses this issue by automatically setting the upper and lower bounds of environmental variables (i.e., "clamping") to those observed under present conditions was made available to us by S. Phillips during the preparation of this chapter. This version of MAXENT confirmed that clamping of environmental variables did not appreciably alter the projected distributions of species under future climate.

To avoid potential problems relating to small sample sizes, we developed models only for species that had at least 20 spatially unique distribution records (Stockwell and Peterson 2002). Five species did not meet this criterion and were not considered for further analysis, leaving 100 species. We used the default values for the convergence threshold (10^{-5}) and maximum number of iterations (1000) suggested by Phillips *et al.* (2006). Setting of regularization values, which address problems of over-fitting, and selection of 'features' (environmental variables and/or functions derived from combinations of such variables), were performed automatically by the program per the default rules dependent on the number of distribution records and features used in model construction.

We retained 30% of the distribution records at random for model evaluation using area under the curve (AUC) of the receiver operating characteristic (ROC) plot of sensitivity versus (1-specificity) and pseudo-absences rather than observed absences (Phillips *et al.* 2006). For models found to have good predictive performance (test AUC >80%), we projected the model from present (1990) to each of nine decades between 2000 and 2080. Before performing migration simulations (described below), we converted the relative suitability values (0-100) from MAXENT to presence/absence (1/0) using the threshold that maximized sensitivity plus specificity under current climate.

The models developed here by MAXENT all exhibited excellent predictive ability with a mean AUC of 0.98 ($0.94 < AUC < 0.99$) as measured against test data. Thus, we excluded none of the 100 species from modeling and can reliably project our models to future environments, subject to the assumptions that the identified species-climate relationships remain unchanged under increased CO_2 and shifting interactions among species.

Incorporating migration

We calculated potential range shifts between each decade and under each of the three climate scenarios by assigning to species three different migration rates: full-migration (unlimited km decade^{-1}), simulated-migration (5 km decade^{-1}) and no-migration (0 km decade^{-1}). The full-migration scenario is a "best-case" assumption that makes no distinction between areas that become environmentally suitable from those that can be colonized and simply assumes species can colonize all locations that become suitable. In contrast, the no-migration scenario, or "worst-case" scenario, assumes species cannot migrate at all and only lose range as climate changes. For simulated-migration we used a methodology similar to that described by Midgley *et al.* (2006). In short, we simulated migration in decadal time steps using an adjacent spread algorithm whereby species migrate from locations that are climatically suitable at t_1 (e.g., 2000) to locations that become climatically suitable at t_2 (e.g., 2010) and are within 5 km (2 grid cells or pixels in this analysis). We repeated the time-slice migration process between each decade, with one migration event per interval to account for lags in responses to climate change and to mimic the roughly decadal fires that represent the only colonization opportunities for many fire adapted *Banksia* species of southwestern Western Australia.

We consciously use the term migration as distinct from "dispersal." As we consider it here, dispersal is a measure of individual movements across the landscape. Migration, in turn, is the net movement of a species across the landscape as a consequence of individuals dispersing. Migration of plant species is a function of population growth, dispersal, establishment, and landscape structure, including the availability of suitable habitat (Neilson *et al.* 2005; Midgley *et al.* 2007; Thuiller *et al.* in press). However, dispersal itself, and long-distance dispersal in particular, are considered the most important factors in determining migration rate (Higgins and Richardson 1999). For this analysis, species were assigned an estimated migration rate of 5 km decade^{-1}. In one of the most detailed studies of plant dispersal and gene flow patterns in Western Australia, He *et al.* (2004) found that between 3 and 7% of seed dispersal events for one *Banksia* species, *Banksia hookeriana*, appeared to have originated approximately 2 km away, which could be considered long-distance dispersal. In addition, Emu (*Dromaius*

novaehollandiae) faeces have been found to contain viable *Banksia* seeds and the combination of long-distance movements by emus with long gut retention times (Calvino-Cancela *et al.* 2006) means that dispersal by emus or other non-standard means might yield occasional dispersal events much longer than 2 km. However, because most *Banksia* species are highly serotinous and seeds do not remain viable in the soil for longer than one year (Enright *et al.* 1996), size and frequency of bush fires ultimately set colonization potential by limiting germination opportunities and rare long-distance dispersal events. In contrast to the importance of long-distance dispersal, Hammill *et al.* (1998) found that, despite differences in seed mass and size, three *Banksia* species exhibited similar seed dispersal distances both in the field and in a wind tunnel experiment and that post-fire patterns of seedling regeneration were predominately determined by short-distance wind dispersal events on the order of 0 to 40 m. We have no reason to believe that the dispersal abilities of the four *Banksia* species considered in the above studies are in any way anomalous for the group. Thus, we used an estimated migration rate of 5 km decade^{-1}, or 500 m year^{-1}, to place emphasis on rare long-distance dispersal events, which have been repeatedly invoked to explain rapid migration rates of plant species during the Holocene (Clark 1998; Higgins and Richardson 1999; Cain *et al.* 2000; Clark *et al.* 2003; but see McLachlan *et al.* 2005). Nonetheless, we experimented with many migration rates, but for reasons that will become clear in the results, such additional scenarios did not prove to be informative.

Quantifying risk and impacts

After projecting future distributions of species, we sought to also assess the risk of extinction and impacts to ecosystem functioning. To quantify potential threats from climate change, we assumed that range size is negatively correlated with risk of extinction (Gaston 2003) and that changes in species composition (i.e., change in species richness) will result in impacts to ecosystems functioning. To evaluate species extinction risks, we assigned species to threat categories using criteria loosely analogous to those employed by the International Union for Conservation of Nature and Natural Resources (IUCN) to determine the current conservation status of species (IUCN 2001). Because at present there is no standard for assigning species to climate change threat categories using such criteria (Akçakaya *et al.* 2006), we simply calculated the projected percentage change in range area by 2080 and grouped species into six risk classes using the following thresholds: Extinct (projected range loss equal to 100%), >80% range loss, >50% range loss, >30% range loss, >0% range loss, and gain (<0%). To investigate the rate at which ranges changed in area between decades, we calculated a measure of the proportional change in range size as $[(R_{t2} / R_{t1}) -1]$, where R represent the range size of the species in number of pixels. By this formulation, loss of range would yield a negative rate of change in range size. To evaluate the percent change in species richness in 2080, we divided the change in species richness in each pixel in 2080 by current species richness in each pixel.

Range shift correlates

We performed regression tree analysis (Breiman *et al.* 1984) to infer which environmental factors were associated with species declines. For each climate scenario,

we fit the number of species lost by pixel in 2080 (species richness in 2080 – present species richness) to a model that included both present environmental conditions and climate anomalies (climate in 2080 – present climate) as predictors. We considered both present and future conditions because as noted by Araújo *et al.* 2006, the manner in which anomalies drive changes in distributions of species may vary depending on where they presently occur in environmental space. Regression trees were built using the RPART library (Breiman *et al.* 1984; Therneau and Atkinson 1997) in R 2.4.1 (R Development Core Team 2006) with tenfold cross-validation and an ANOVA splitting rule.

RESULTS

Our models projected that many, if not most, of Western Australia's endemic *Banksia* species may be threatened by climate change (Fig 4.1). This general conclusion was consistent across climate scenarios and three assumptions regarding migration rate. By 2080, 85% of *Banksia* species are projected to have reduced ranges across at least seven of the nine possible climate × migration scenarios, with 66% of species consistently projected to decline across all nine scenarios (Appendix A). In contrast, only 6% of species were consistently projected to exhibit expanded or stable ranges across nine climate × migration scenarios. Twenty-four species were projected to suffer range losses of 100% by 2080 in at least one of the climate × migration scenarios and five were projected to suffer range losses of 100% in all nine scenarios. The proportion of species projected to become at risk depended more on the climate scenario than on migration rate (Fig 4.1). Additionally, we tested whether these outcomes were phylogenetically independent (as opposed to clustered in particular regions of the phylogeny) and found that the risk of extinction was distributed randomly across clades (J. Fordyce, *unpublished data*).

Across all climate scenarios and beginning in year 2000, species on average were projected to decrease in range size, a trend that continued until 2080. The most notable difference across climate scenarios was the degree to which species were impacted and the role of migration in mediating such impacts (Fig 4.2). Differences in projected impacts between migration rates were related to the degree to which favored species experienced range expansions rather than to migration limiting range shifts (e.g., Fig 4.2c).

The severity of projected impacts and the importance of migration rate in mediating such impacts followed the same trend as the severity of climate change scenario. The least-severe impacts occurred under the low-severity (B1) climate scenario, which also had the most consistent projections across migration assumptions. In contrast, the high-severity (A1F) climate scenario exhibited the highest extinction rates on the order of 20% and the fewest species with expanding ranges (Fig 4.1, Table 4.2). Projected outcomes under the high-severity (A1F) climate scenario were also most influenced by migration rate (Fig 4.2c), but mainly because full-migration allowed two species to expand their ranges by more than thirteen-fold and three species to expand their ranges by more than eight-fold. Such unrealistic gains were eliminated when

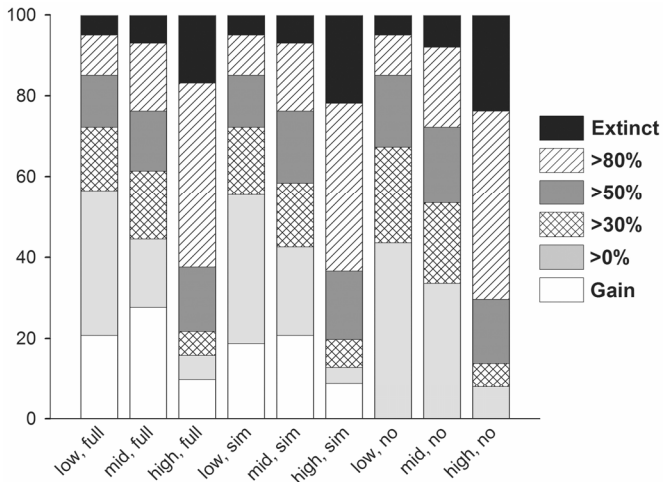

Figure 4.1: Proportion of 100 Western Australian endemic *Banksia* (Proteaceae) species classified into range loss categories under three future climate scenarios: low- (B1), mid- (A1B) and high-severity (A1F), and three assumptions regarding migration rate: full-, simulated- (5 km decade^{-1}) and no-migration. Percentages in legend refer to the amount of range loss projected to occur by 2080. Species are considered extinct when projected to suffer range losses equal to 100%.

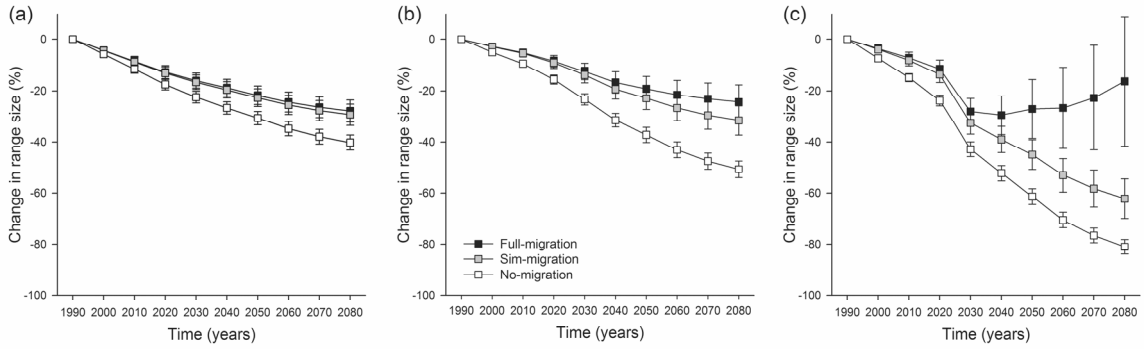

Figure 4.2: Mean change in range size through time for 100 Western Australian endemic *Banksia* (Proteaceae) species under (a) low- (B1), (b) mid- (A1B) and (c) high-severity (A1F) climate change scenarios. Shading within climate scenarios refers to different assumptions regarding migration rate: full-migration (black), simulated-migration of 5 km decade^{-1} (grey) and no-migration (hollow). Error bars represent standard errors.

Table 4.2: Projected impacts of climate change by 2080 in terms of changes in range size and numbers of species with ranges projected to expand or contract across three climate and three migration scenarios. 'Sim' refers to simulated-migration of 5 km decade^{-1}. Numbers in brackets are standard errors of means. Italicized numbers represent species whose ranges contract to extinction (projected range loss equal to 100%).

	Low-severity (B1)			Mid-severity (A1B)			High-severity (A1F)		
	Full	Sim	No	Full	Sim	No	Full	Sim	No
Change in Range Size (%, n = 100)	-27.9 (4.4)	-29.4 (4.2)	-40.3 (2.9)	-24.3 (6.6)	-31.6 (5.7)	-50.8 (3.3)	-16.3 (25.3)	-62.2 (7.6)	-81.0 (2.8)
Range Expansion (no. of species)	21	19	--	28	21	--	10	9	--
Range Contraction (no. of species)	80	82	100	73	80	96	91	92	97
Extinctions (no. of species)	*5*	*5*	*5*	*7*	*7*	*8*	*17*	*22*	*24*

migration rate was limiting. The mid-severity (A1B) climate scenario resulted in the fewest species projected to decline and the most projected to expand (Table 4.2), but in terms of projected impacts and the influence of migration rate in mediating such impacts, this scenario was intermediate to the results of low- (B1) and high-severity (A1F) climate scenarios (Fig 4.2b). Under both the low- (B1) and mid-severity (A1B) climate scenarios, simulated-migration was more similar to full- than no-migration, whereas simulated-migration was more similar to no-migration under the high-severity (A1F) climate scenario.

Rates of change in range size differed across climate scenarios, but were generally not influenced by migration rate (Fig 4.3, negative rates indicating range loss on average). Further, across all climate scenarios, the rate at which ranges changed in area was not constant through time. Under the low- (B1) and mid-severity (A1B) climate scenarios, rates of range loss were generally less than 10% and 20% respectively, but the rate of range loss slowed in later decades, beginning in 2030 under the low-severity (B1) climate scenario and 2070 under mid-severity (A1B) climate scenario (Figs. 4.3a,b). In contrast, rates of change in range size under the high-severity (A1F) climate scenario, which had the highest rates of range loss, tended to accelerate with time, beginning at 10% early in the century and increasing to nearly 40% by 2070 (Fig 4.3c).

Projected range losses equal to 100% (extinction) began in 2030 in all nine climate × migration scenarios, but the cumulative percent of species projected to suffer extinction differed between scenarios and diverged rapidly by 2050 (Fig 4.4). Under the low-severity (B1) climate scenario and across the three migration rates, the cumulative percent of species projected to go extinct reached a maximum of nearly 5% by 2050, after which time no additional species were projected to go extinct. In contrast, the cumulative percent of species projected to go extinct sustained a rapid increase after 2050 under the high-severity (A1F) climate scenario and differed between migration rates. The mid-severity (A1B) climate scenario exhibited the lowest cumulative percent of species projected to go extinct, until 2080 when projected extinctions surpassed those under the low-severity (B1) climate scenario.

Impacts on patterns of species richness

The most striking differences in changes in patterns of species richness across climate scenarios and migration rates related to increases in species richness. Coastal regions and the desert interior were projected to gain species when migration rate did not limit range expansions, with the most substantial gains (in terms of area) projected for the desert interior under the high-severity (A1F) climate scenario and full-migration (Fig 4.5, blue shading). In contrast, patterns of decline in species richness were geographically widespread and generally similar across climate scenarios (Fig 4.5, red shading) and mainly differed in magnitude rather than geographical arrangement.

Range shift correlates

For ease of interpretation, we report range-shift correlates only for species losses under simulated-migration. Regression tree analyses suggested that, regardless of climate

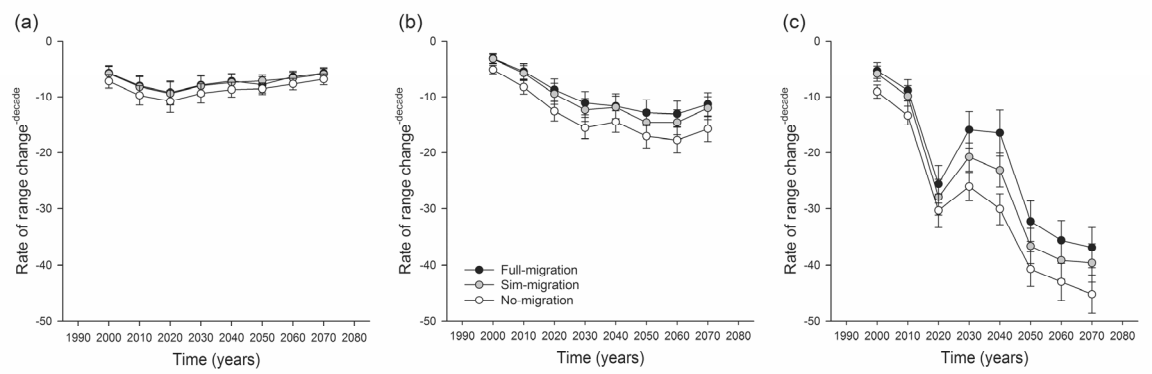

Figure 4.3: Mean rate of change in range size through time for 100 Western Australian endemic *Banksia* (Proteaceae) species under (a) low- (B1), (b) mid- (A1B) and (c) high-severity (A1F) climate change scenarios. Shading within climate scenarios refers to different assumptions regarding migration rate: full-migration (black), simulated-migration of 5 km decade^{-1} (grey) and no-migration (hollow). Error bars represent standard errors.

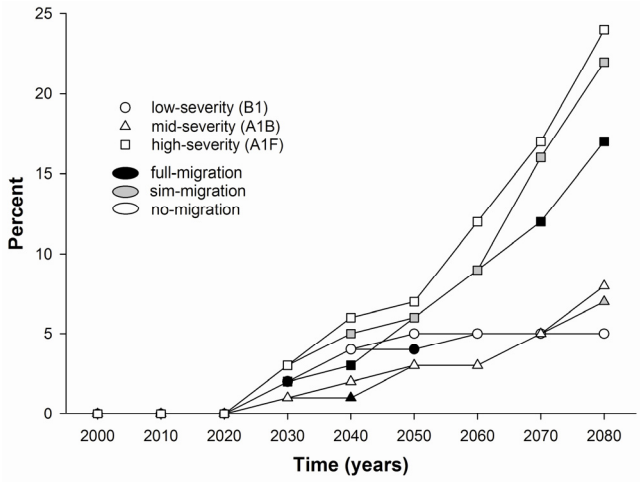

Figure 4.4: Cumulative percentage of 100 Western Australian endemic *Banksia* (Proteaceae) species projected to suffer range losses equal to 100% through time under (circles) low- (B1), (triangles) mid- (A1B) and (squares) high-severity (A1F) climate change scenarios. Shading within climate scenarios refers to different assumptions regarding migration rate: full-migration (black), simulated-migration of 5 km decade^{-1} (grey) and no-migration (hollow).

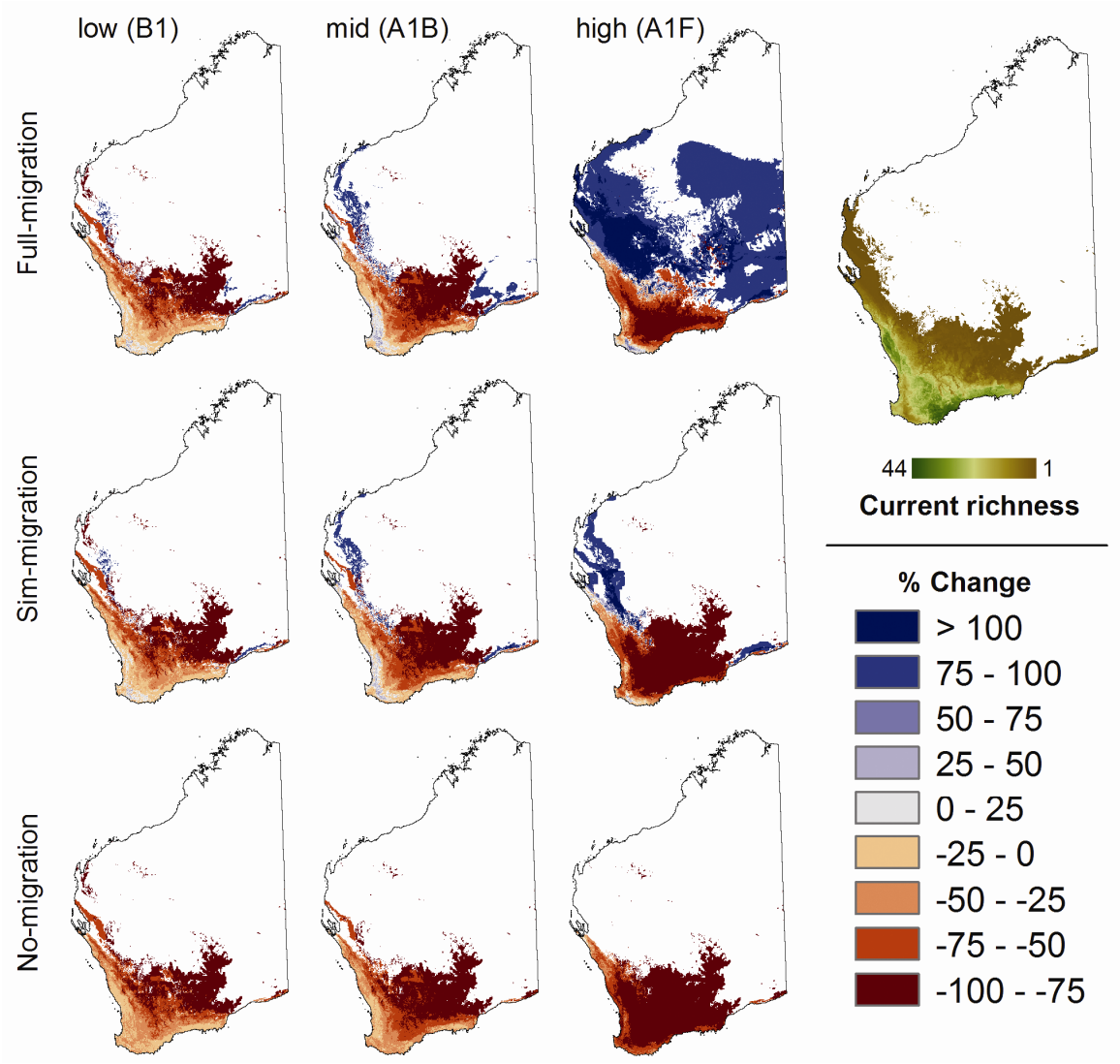

Figure 4.5: Projected percent change in Western Australian endemic *Banksia* (Proteaceae) species richness by 2080 versus predicted current richness (inset, upper right) under three scenarios of future climate (columns, increasing severity from left to right) and across three assumptions regarding migration rate (rows, increasing migration limitation from top to bottom). Simulated-migration refers to a rate of 5 km decade^{-1}. Color scale indicates the percent increase (blues) or decrease (reds) in species richness.

scenario, cumulative species losses by 2080 (left branches, Fig 4.6) were driven primarily by changes in current precipitation regimes. The number of nodes in the trees declined from low- (Fig 4.6a) to high-severity (Fig 4.6c), suggesting the strength of the relationship between precipitation variables and species losses increased as the severity of climate change increased. The greatest losses of species tended to occur in a transitional zone of intermediate precipitation and a growing season length of at least five months between wet coastal areas and arid interior regions and which is projected to become more arid in the future. Soil factors did not enter into any of the regression trees suggesting the availability of suitable soil conditions did not hinder range expansions at the spatial scale considered here.

DISCUSSION

We found that projected impacts of climatic change on *Banksia* species in Western Australia were similar across climate scenarios and differed mainly in the degree rather than in the kind of impact. Differences in migration rates did not appreciably alter projected outcomes within climate scenarios, but the importance of migration rate increased as severity of climate change increased.

Why might migration rates not be important? Migration rate could have little influence on projections for two main reasons: either (1) ranges do not change appreciably such that species simply do not need to track climate changes or (2) ranges of most species tend to contract, an outcome even full-migration cannot prevent. Our results suggest that for Western Australian *Banksia* species, migration rates had a minor influence on projected outcomes because ranges of species tended to contract rather than expand into new regions. This finding was consistent across the climate scenarios. Because changes in distributions of species under simulated-migration were generally more similar to those under full-migration, range shifts that did occur were generally small (i.e., around 5 km decade^{-1}).

Because range contraction may be a common response of many of Western Australia's endemic *Banksia* species to climate change, migration rates of species may represent a relatively unimportant factor in determining future patterns of diversity in this region and taxon. Our approach represents a compromise between the detail and mechanism of single species dispersal models (e.g., Clark *et al.* 1998) and the near total lack of mechanism of the multi-species, time-slice method used here and elsewhere. However, because ranges of most species contracted, different (i.e., more informed) assumptions regarding dispersal or migration rates or more complex dispersal models that explicitly simulate population growth and rare, long-distance events would have provided additional insight for only those few species projected to gain new range. In sum, improved (or even perfect) estimates of migration rates would not significantly alter our results or our interpretation. Thus, a simple time-slice migration model can provide useful insights into dynamics of potential range change of *Banksia* in Western Australia.

The patterns of range contraction projected by our models are also important in the context of conservation planning in southwestern Western Australia. Because migration may not be an option for many of the plant species considered here, conservation efforts focused on dispersal corridors, though potentially beneficial to some other taxa, may offer little benefit to many *Banksia* species. Instead, conservation efforts

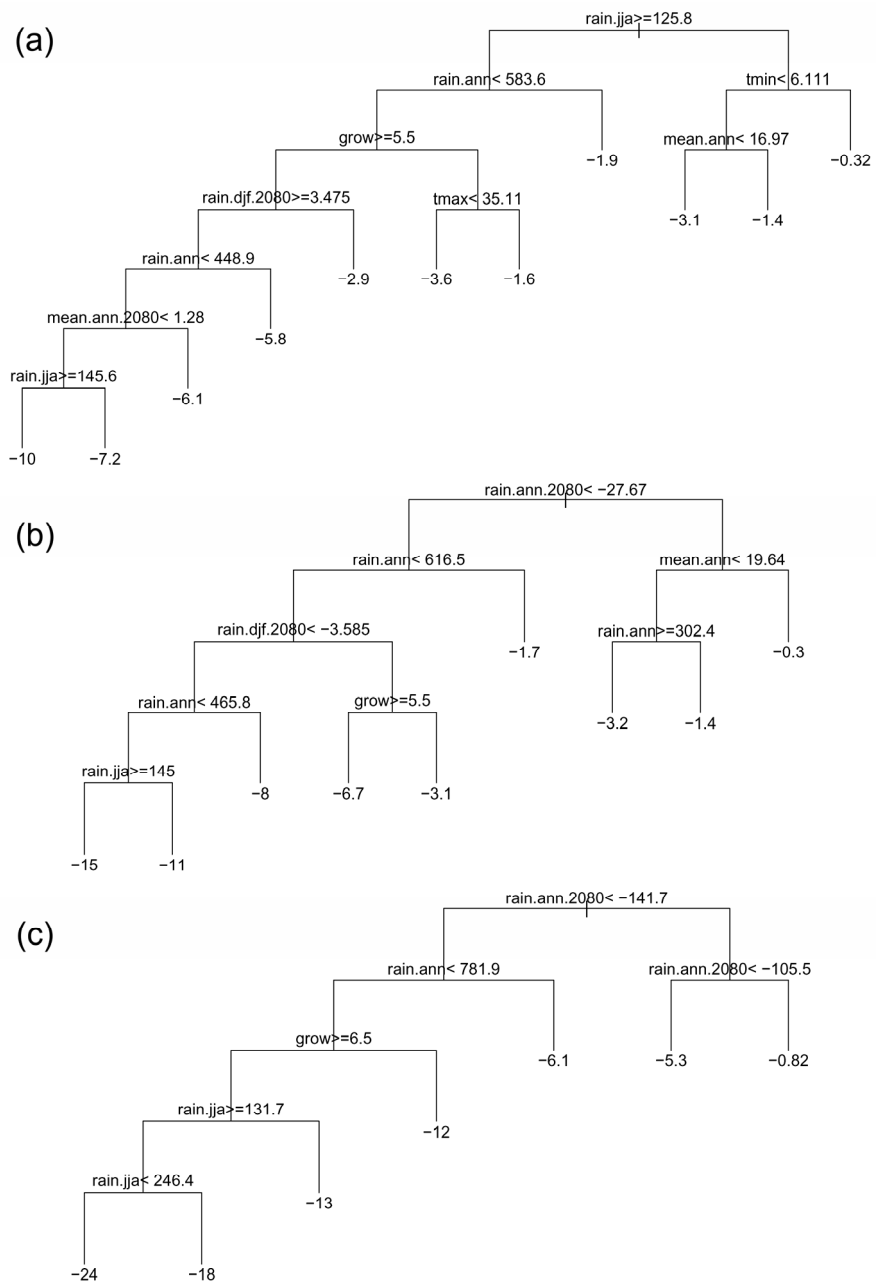

Figure 4.6: Regression trees for range losses for 100 Western Australian endemic *Banksia* (Proteaceae) species by 2080 under (a) low- (B1), (b) mid- (A1B) and (c) high-severity (A1F) climate change scenarios and a migration rate of 5 km decade^{-1}. Abbreviations are as follows (postfix 2080 refers to climate anomalies): grow (growing season length), mean.ann (mean annual temperature), rain.ann (mean annual precipitation), rain.djf (summer precipitation), rain.jja (winter precipitation), tmax (maximum temperature of the warmest month), tmin (minimum temperature of the coldest month).

might more appropriately be directed towards preserving areas where species are projected to persist (e.g., coastal areas). This assertion is further strengthened by our finding that the rate at which species lost range tended to decline with time in both the low- (B1) and mid-severity (A1B) climate scenarios. Midgley *et al.* (2006) interpreted a similar result in their analyses as suggesting species may first lose sensitive, marginal areas of their range and contract to core areas more resilient to climate change. If this is the case, then conservation would be most effective if core areas of ranges of species are identified and protected. However, under the high-severity (A1F) climate-scenario, species lost range more rapidly as time progressed, suggesting that even core areas of ranges of species may eventually become vulnerable under severe climate change. Under such a scenario, one viable, though controversial, option would be to establish populations in other regions of the world that become climatically suitable in the future (McLachlan *et al.* 2007).

Are the *Banksias* of Western Australia a special case? We argue that the answer to this question is both yes and no. Our results are general among regions to the extent that in regions where ranges of species are projected to contract or remain stable, migration dynamics will be of relatively little importance. However, Western Australia may be a special case in that the southwest, where most of the biodiversity of the region is concentrated and where our models predict current richness of *Banksia* species to be greatest (Fig. 4, inset), is confined to the cool, wet end of a hot, dry continent – a situation loosely comparable to isolated alpine habitats found on mountain peaks. In contrast to the high richness of *Banksia* in southwestern Western Australia, the predicted current richness for *Banksia* is zero in the central arid region. This finding is consistent with the observed pattern of species richness in *Banksia*, which is strongly linked to precipitation gradients (Lamont and Connell 1996). Thus, Western Australia may be a special case in that ranges tended to collapse rather than shift because as drought increased and the central arid region expanded, few opportunities for colonization emerged.

Within southwestern Western Australia, we suspect that *Banksia* species are representative of many groups of plants, at least in terms of patterns of species richness. The predicted pattern of current *Banksia* species richness not only matches nearly identically that documented by Lamont and Connell (1996), it is also is correlated with the pattern of plant species richness overall in southwestern Western Australia ($r = 0.77$, Fitzpatrick *et al. unpublished data*). Because the pattern of richness of *Banksia* tends to match that of most other plant taxa, unless other aspects of *Banksia* distribution (range size, for one) are very different than for other plant taxa, we suspect our results generalize. To make the point, if the same proportion of southwestern Western Australia's flora overall is committed to extinction as projected for *Banksias*, we can extrapolate that by 2080 between 5 to 20% (i.e., 225 to 900 of southwestern Western Australia's approximately 4500 endemic plant species) may be at risk of range declines severe enough to threaten their persistence. However, we stress that given the many uncertainties inherent in the modeling approach applied here, projected impacts should be interpreted with full consideration of the limitations involved and as a first approximation of potential risk rather than a definitive forecast of extinction rates. Nonetheless, we suggest that climate change impacts to southwestern Western Australia's flora may be

large under even relatively moderate climate change scenarios and optimistic assumptions regarding migration abilities of species.

Limitations & assumptions of models

When projecting models in either space or time, species distribution models are subject to many uncertainties beyond those addressed in this paper (see Guisan and Thuiller 2005 and Heikkinen *et al.* 2006 for reviews), such as failure to consider factors other than climate in shaping distributions of species, notably biotic interactions. In this study, a few unaddressed sources of uncertainty likely include the use of presence-only distribution data rather than presence-absence data, effects of CO_2 fertilization on plant performance, whether distributions of species are at equilibrium with their current environment due to biotic factors or otherwise (Svenning and Skov 2004; Araújo and Pearson 2005; Svenning and Skov 2007a), the potential for species to adapt *in situ* to new climatic conditions, and the role of current and future land use patterns in shaping distributions of species (Broennimann *et al.* 2006; Thuiller *et al.* 2006). Failure to include these factors could results in spurious species-climate relationships and model error when such relationships are extrapolated to new biogeographical settings (Fitzpatrick *et al.* 2007).

In particular, we may overestimate declines if (1) species are able to adapt *in situ* to new climatic conditions, (2) the coarse scale of our analysis hides potential micro-refuges, or (3) species are able persist outside of conditions in which they have been observed (Lamont and Connell 1996). For example, CO_2 fertilization and potential changes to water use efficiency of plants (Drake *et al.* 1997), and the interaction of these factors with soil water content via vegetation, may allow species to tolerate conditions more arid than those in which they presently occur, thereby buffering the impacts of decreases in precipitation. However, increases in atmospheric CO_2 concentrations may provide limited benefit to Mediterranean-type ecosystems (Fischlin *et al.* 2007). We also assume time lags in responses to climate change are relatively short and thus species are immediately at risk even though they may persist for several decades.

We may have underestimated impacts because we did not quantify potential impacts of land degradation. For example, over 40% of land in southwestern Western Australia currently is under agriculture. Therefore actual current ranges are likely smaller than those predicted here and areas for future range will be correspondingly smaller as well, especially if future biodiversity hotspots for *Banksia* coincide to a great extent with the only areas in southwestern Western Australia where wheat and other important Australian crops will be able to be grown. In addition to directly reducing the amount of available habitat, both agriculture and urbanization may exacerbate the impacts of drought by exploiting already limited water resources. Finally, *Banksia* species are susceptible to the plant pathogen *Phytophthora cinnamomi* (Tynan *et al.* 1998), and it is unclear how the spread and impacts of *P. cinnamomi* may be exacerbated under climate change (Harvell *et al.* 2002).

Projected impacts also can be sensitive to the statistical approach used to model distributions of species (Pearson *et al.* 2006) and therefore a range of modeling techniques and ensemble forecasting (Araújo and New 2007) ideally should be used to reduce and quantify such model-based uncertainty. However, given that our focus was on

the interaction of migration rate and climate scenario, we modeled distributions of *Banksia* using only one technique, maximum entropy. Although maximum entropy tends to provide a good compromise to ensemble forecasting (Araújo and New 2007) and has been shown to be among the better performing techniques for modeling *current* distributions of species (Elith *et al.* 2006), it is an open question whether maximum entropy, or any other technique for that matter, will exhibit similarly predictive performance when projecting *future* distributions of species under climate change.

CONCLUSIONS

Given the uncertainties inherent in our analysis, what conclusions can we draw? First, our results suggest that future climate scenario generally and the severity of future drought in particular might be most important factors in determining future patterns of *Banksia* diversity in Western Australia. Second, migration may not be a viable option for most species to avoid reduction in range size or extinction, even at the high rates simulated here. Because the diversity patterns for *Banksia* closely match those for plant species overall and because migration rate was relatively unimportant, we suspect these conclusions generalize to the southwestern Western Australian flora as a whole. Taken together, our results suggest that the future of Western Australia's endemic species in the genus *Banksia,* and the future of plant biodiversity in southwestern Western Australia generally*,* may rest largely in the degree to which this region experiences increased drought in coming decades and in the ability of species to tolerate such decreases in precipitation. Thus, future experimental research in the region should investigate the ability of species to persist in conditions outside of those in which they presently occur.

Chapter Five

Seed dispersal, range equilibrium, and patterns of species similarity in the diverse flora of southwestern Australia.[1]

[1] At the time of this writing, a slightly modified version of this chapter was in prep for *Ecography* as: Fitzpatrick MC, Ferrier S, Sanders NJ, Gove AD, Dunn RR (in prep) Seed dispersal, range equilibrium, and patterns of species similarity in the diverse flora of southwestern Australia. My use of "we" in this chapter refers to my co-authors and myself. My primary contributions to this paper include: 1) development of ideas; 2) collection and preparation of inputs to models; 3) modeling; 4) data analysis; and 5) most of the writing.

ABSTRACT

We assessed the relative importance of dispersal ability (in terms of seed dispersal mode) and climate in determining the current geographic distributions of plant species in a global biodiversity hotspot in southwestern Australia. Using a new statistical framework, Generalized Dissimilarity Modeling, we examined differences in patterns of spatial turnover in species composition to infer the degree to which they fill their potential ranges. We found that turnover in species composition is most strongly linked to a gradient in winter precipitation and that patterns of turnover differed starkly at an ecotone along this gradient. In contrast to the prediction that the distributions of species with adaptations for short-distance dispersal of seeds (by ants or no mechanism) will be more constrained by dispersal than species adapted for long distance dispersal of seeds (by vertebrates or wind), we found that the distributions of dispersal-limited species appear less constrained by dispersal and more constrained by climate than the distributions of ostensibly more vagile species. The mechanisms behind these patterns are not readily apparent, but we argue that they can be reconciled by invoking the ecological and evolutionary implications of dispersal ability, spatial structure of the environment and the propensity for long-distance dispersal events by non-standard means.

"The concrete highway was edged with a mat of tangled, broken, dry grass, and the grass heads were heavy with oat beards to catch on a dog's coat, and foxtails to tangle in a horse's fetlocks, and clover burrs to fasten in sheep's wool; sleeping life waiting to be spread and dispersed, every seed armed with an appliance of dispersal, balls of tiny thorns, and all waiting for animals and for the wind, for a man's trouser cuff or the hem of a woman's skirt, all passive but armed with appliances of activity, still, but each possessed of the anlage of movement."

--John Steinbeck, Grapes of Wrath.

INTRODUCTION

Geographic ranges of species are influenced by many factors and processes that operate on a variety of spatial and temporal scales (Gaston 2003). However, given the increasing need to predict the potential responses of species to climatic change, understanding the relative importance of dispersal limitation and contemporary climate as determinants of patterns of biodiversity has received increasing attention of late (Svenning and Skov 2004; Araújo and Pearson 2005; Svenning and Skov 2005; Graham *et al.* 2006; Svenning and Skov 2007a; Svenning and Skov 2007b; Araújo *et al.* in press). In this study, we examine differences in patterns of spatial turnover in species composition (i.e., beta diversity) to distinguish the relative roles of dispersal limitation and climate in determining the current distributions of groups of plant species in a global biodiversity hotspot.

Dispersal limitation and range equilibrium

The influence of dispersal limitation on broad-scale patterns of biodiversity is most often considered in the distinction between realized versus potential ranges. The potential range is the area that would be occupied if species were not limited by dispersal, whereas the realized range is the portion of the potential range that species actually occupy (Gaston 2003). The ratio between realized and potential ranges, termed 'range filling' (Svenning and Skov 2004), is a measure of the influence of dispersal limitation and historical effects on distribution. Species with low ratios are considered dispersal-limited, relatively slow to recover from historic changes in the environment and thus in disequilibrium with current climate. In contrast, those species with range-filling ratios near or equal to one are said to be at equilibrium with contemporary climate, less dispersal limited, and potentially more able to respond rapidly to climatic change.

Species turnover and range equilibrium

Range filling ratios can be difficult to quantify because they rely on accurate estimates of realized and potential ranges. However, in a seminal paper on the analysis and interpretation of spatial patterns in species composition, Nekola and White (1999) proposed that dispersal limitation will also manifest itself in patterns of beta diversity because groups of species with different dispersal abilities will vary in the rate at which they turnover along environmental gradients. Differences in equilibrium among groups of species can be investigating by determining how well changes in current environmental

conditions explain change in species composition. For example, Araújo and Pearson (2005) argued that an examination of patterns of spatial covariation between change in species composition and change in the environment (Ferrier *et al.* 2002) can infer differences in equilibrium among groups of species because if species are at equilibrium, then turnover in species composition will be accompanied only by corresponding change in the environment (e.g., at an ecotone). Under these circumstances spatial covariation between change in species composition and change in the environment will be high. Conversely, if species are dispersal limited and not at equilibrium, then changes in biota will occur despite change in the environment and therefore change in environmental conditions will not fully explain change in species composition. In other words, to the extent that dispersal ability mediates the ability of species to attain their equilibrium distributions, *the limits of distributions of dispersal-limited species should tend to be more random with respect to environmental transitions than the distributions of species which attain equilibrium*. Thus, strong climate-biota covariation suggests a relatively high degree of equilibrium, whereas weak climate-biota covariation suggests species do not tend to occupy all climatically suitable locations because of ecological factors such as dispersal limitation or biotic interactions. Weak spatial covariation could also indicate that the environmental variables do not adequately represent the determinants of range limits, but this possibility can be minimized by selecting environmental factors that are believed to be related to the environmental tolerances of the species under analysis.

Nekola and White (1999) also proposed that in addition to being a function of dispersal processes in space, changes in species composition will also be a function of the niche characteristics of species. Because of dispersal limitation, geographically separated sites will show low species similarity even if they share similar environmental conditions (Hubbell 2001). However, environmental conditions are spatially autocorrelated, so proximate sites will always be more similar in environmental conditions than distant sites. Therefore turnover will also be related to the niche characteristics of species, and in particular niche breadth. Species with broad niches will turnover less rapidly than those with narrow niches over a fixed amount of environmental distance. Thus, any attempt to understand relationships between turnover in species composition and range equilibrium must take into account the niche characteristics of species in addition to dispersal ability.

Dispersal ability and range equilibrium

All else being equal, vagile species should occupy a larger proportion of their potential range and thus be closer to equilibrium than poorly-dispersing species. Within plants, the greatest differences in the degree to which species attain equilibrium are expected between species with adaptations for dispersal of seeds by wind or vertebrates (and hence long distance dispersal) and those species with adaptations for short distance dispersal of seeds, such as passive-dispersal or dispersal by ants. In the same habitat, wind-dispersed species can disperse several kilometers (He *et al.* 2004), whereas ant-dispersed species (Gomez and Espadaler 1998; Gove *et al.* 2007; but see Whitney 2005) and passively-dispersed species may disperse no more than a few meters.

Why study range equilibrium?

The degree to which species are at equilibrium with contemporary climate and how this relates to dispersal ability has important implications for our ability to understand and forecast responses of species to climatic change. Species distribution models assume that species have attained their full potential ranges, are not dispersal limited, and hence are at equilibrium with climate (Pearson and Dawson 2003; Araújo and Pearson 2005; Guisan and Thuiller 2005). However, recent studies have suggested that dispersal constraints can prevent species from reaching their potential ranges (Schurr *et al.* 2007), perhaps for as long as millennia following broad-scale disturbance such as glaciation (Svenning and Skov 2004; Araújo and Pearson 2005; Svenning and Skov 2007b). Although the assumption of range equilibrium is key to the validity of projections of species distribution models made in space or time (e.g., to forecast biological invasions or the responses of species to climatic change), and despite the fact that ample empirical evidence demonstrates distributions of species can be influenced by dispersal, few studies have examined whether species are at equilibrium and whether this varies with dispersal ability or other traits (but see Leathwick 1998; Araújo and Pearson 2005). In short, species that can not attain equilibrium under current climate because of dispersal limitation are those for which projected changes in distribution are least certain and which may also be least likely to keep pace with future changes in climate.

Here we implement a relatively new statistical framework, generalized dissimilarity modeling (GDM, Ferrier *et al.* 2002; Ferrier *et al.* 2007) to investigate range equilibrium across many species. GDM is a nonlinear extension of Mantel correlation analysis (Manly 1998) that models compositional dissimilarity (i.e., turnover or beta diversity) between all possible pairs of locations as a function of environmental and geographic separation. For 2543 species of vascular plants in southwestern Australia, a global biodiversity hotspot (Myers *et al.* 2000), we use GDM to test the prediction that ant- and passively-dispersed plants, both of which have dispersal kernels characterized by a preponderance of short distances (Cain *et al.* 1998; Gomez and Espadaler 1998), are relatively more distant from equilibrium than ostensibly more-vagile wind- and vertebrate-dispersed plants (Willson 1993; He *et al.* 2004). Unlike previous studies that have considered range equilibrium on taxa in regions that have experienced recent glaciation, such as northern Europe, southwestern Australia is characterized by long-term climatic stability (Hopper and Gioia 2004) and a very steep gradient in winter precipitation (Fig. 5.1). Further, obvious adaptations for long-distance dispersal (Johnson and Briggs 1975) and short-distance dispersal (Berg 1975) are common in the flora and each have evolved multiple times (Beattie 1985; Dunn *et al.* in press). Finally, given the extreme climate changes projected for southwestern Australia (IOCI 2005) and the corresponding projected impacts on the flora (Fitzpatrick *et al.* in press), relationships between seed dispersal mode and distributions of species may help understand the impacts of climate change on this biodiversity hotspot. In sum, this region provides a contrast to similar studies and an opportunity to test whether the signal of dispersal limitation remains apparent in patterns of range equilibrium over very long periods of climatic stability. We conclude with a consideration of our findings in the context of modeling the potential responses of species under climatic change using species distributions models.

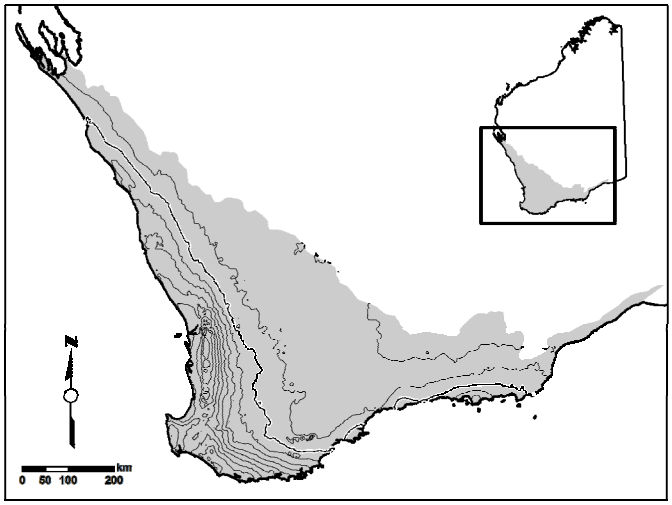

Figure 5.1: Map showing the extent of the study area (gray shading) in southwestern Australia and the gradient of winter precipitation (black contours). Contour lines indicate a change of 50 mm of precipitation. The contours increase from a minimum of 100 mm of rainfall in the east to 600 mm in the west along the coast. The highlighted, dotted line indicates the location of the 180 mm ecotone.

METHODS

In order to investigate range equilibrium, our analysis proceeded in two steps. First, we examined spatial covariation between changes in species composition and environmental change as a function of seed dispersal mode using generalized dissimilarity modeling (GDM, Ferrier *et al.* 2002; Ferrier *et al.* 2007). Second, because spatial variation in species composition is also a function of both dispersal processes and the niche requirements of species (Nekola and White 1999), and the interactions of those requirements with the distribution of environmental conditions in space (Steinitz *et al.* 2006), we also investigated the niche characteristics of species along the primary environmental gradient influencing turnover in species composition. After introducing our statistical model, we describe data inputs into the model.

Modelling patterns of turnover in community composition

We assessed differences in range equilibrium by investigating patterns of climate-biota covariation. This was accomplished by modelling patterns of turnover in species composition in relation to environmental gradients using Generalized Dissimilarity Modelling (GDM, Ferrier *et al.* 2002; Ferrier *et al.* 2007, software available from: http://www.biomaps.net.au/gdm/) in R 2.6.0 (R Development Core Team 2006). GDM models spatial turnover in community composition (i.e. "compositional dissimilarity", quantified with a Bray-Curtis measure) between pairs of sites as a function of environmental differences and geographic separation between sites. GDM is a nonlinear extension of matrix regression designed to accommodate the problem of realistically

modeling two types of nonlinearity common in ecological data sets: (1) the curvilinear relationship between ecological separation and compositional dissimilarity between sites and (2) the variation in the rate of compositional turnover at different positions along environmental gradients. Thus, GDM represent an improvement on the Mantel test, which has been used previously to examine spatial covariation between changes in species composition and environmental change, and offers a more robust statistical method to assess complex patterns of climate-biota covariation in space. See Ferrier *et al.* (2007) for details and applications.

GDM provides two primary forms of output relevant to our analysis: (1) percent deviance explained and (2) an indication of the rate and total amount of turnover in species composition for each environmental variable. The amount of explained deviance provides a measure of the relative strength of climate-biota covariation and an indication of differences in equilibrium between groups of species, with greater deviance explained indicating higher degree of equilibrium. The rate and total amount of turnover in species composition provide an indication of the primary variables influencing changes in species composition and how this varies by dispersal mode.

Because environmental conditions are spatially autocorrelated, we used GDM to construct a set of three models to parse the relative importance of change in the environment and geographic distance in explaining spatial turnover in each dispersal mode. For each model and dispersal mode, the response variable consisted of a site-by-species matrix, with rows corresponding to the 605 sites and a column for each species (e.g., this matrix contained 947 columns for ant-dispersed species and 1155 columns for passively-dispersed species), which was modeled against: (1) environmental distance only, (2) geographic separation only, and (3) both geographic separation and environmental distance. We then compared how much additional percent deviance was explained by adding geographical distance between sites to a model already containing the environmental predictors. If a group of species is not in equilibrium with the environment, it is expected that geographic separation should have greater explanatory power because sites with similar environmental conditions will become increasingly dissimilar in biological composition with increasing geographical separation. For all models, we used the "standard" weighting function within GDM. The standard weighting approach is likely the safest option to use if sampling effort is known to have varied substantially between sites. Standard weighting weights sites proportionally to the number of species observed at that site, such that sites with few species carried less weight, and therefore less influence, in model fitting than sites with larger numbers of species. Nonetheless, we also ran models without weighting and found results were virtually indistinguishable from those obtained using standard weighting. To calculate the total amount of turnover along each environmental gradient, we summed the coefficients of the I-spline basis functions used by GDM to model turnover as described in Ferrier *et al.* (2007).

Niche characteristics

To examine niche characteristics, we compared niche breadth and geographic range size of species among dispersal modes along the gradient of winter precipitation (See Results). We defined geographic range size as the north-south span in kilometers,

which transverses the mainly east-west precipitation gradient in southwestern Australia (Fig. 5.1) and which was strongly related to east-west range size (r = 0.79). We calculated niche breadth using the maximum and minimum values of winter precipitation found within the range of the species. It is important to note that our measures of both range size and niche breadth quantify realized, not potential characteristics of distributions of species and when coupled with results from GDM, provide a sense of the relationship between realized and potential ranges. Because the assumptions of normality and equality of variances required for ANOVA were violated, we made pair-wise comparisons of means across dispersal modes using Wilcoxon tests in R 2.6.0 (R Development Core Team 2006).

Plant distribution and dispersal data

We obtained over 57,000 georeferenced, presence-only distribution data for 2,543 species of plants representing 22 families occurring in southwestern Australia from the Western Australia Herbarium (PERTH, data provided May 2005). We assigned species to one of four dispersal modes: ant, passive, vertebrate, or wind, using morphological adaptations of seeds for dispersal (hereafter "dispersal morphology"). We assigned dispersal morphology at the level of plant genera, except for *Acacia* which was split at the species level, due to a large degree of within-genus variation of dispersal mode, based on a combination of observations of seeds and the consultation of systematic revisions, regional floras, interactive keys and publications explicitly focusing on seed dispersal. When seeds possessed white, or more generally pale, fleshy appendages smaller in size than the "body" of the seed, these appendages were considered to be elaiosomes and the seeds were considered to be ant-dispersed. When seeds possessed larger, more brightly colored appendages, or were covered in flesh, they were coded as vertebrate-dispersed. When seeds possessed wings or wing-like appendages they were coded as wind-dispersed. All other species were coded as passively dispersed. Note that we use the term seed throughout for convenience, but technically the relevant dispersal unit (diaspore) varies from seeds to multi-seeded fruits. Of the 2,543 species, we characterized 945 as ant-dispersed, 1153 as passively-dispersed, 335 and wind-dispersed, and 110 as vertebrate-dispersed. Phylogenies are not available for most of the families we considered. However, because each of these dispersal modes has evolved many times in southwestern Australia (e.g. Beattie 1985; Dunn *et al.* in press) our results should be relatively robust to phylogenic dependence.

Although we used an extensive database of distribution data, we addressed potential differences in collection effort (sampling bias) associated with presence-only distribution data in several ways. First, we performed our analysis at a resolution of 25 km. This resulted in 605 sites within southwestern Western Australia and ensured that although individual locations may be poorly sampled at local scales, broad-scale patterns of species composition likely are not. Second, we removed from the analysis 42 sites that had fewer than five individual records and so focused only on comparisons among better sampled pairs of sites. Finally, we weighted sites proportionally to the number of records at that site, such that sites with few records carried less weight, and therefore less influence, in model fitting than sites with larger numbers of species records.

Environmental data

We modelled changes in species composition using five uncorrelated ($r < 0.75$) environmental variables considered critical to the physiological function (and thus the broad-scale distribution) of plants generally (Woodward 1987) and of plants in Western Australia in particular (Hopper and Maslin 1978; Hnatiuk and Maslin 1988; Beard 1990; Groom and Lamont 1996; Keighery 1996; Lamont and Connell 1996; Cowling and Lamont 1998; B. Lamont, *pers. comm*.). These included: mean annual temperature, minimum temperature of the coldest month, maximum temperature of the warmest month, and winter (June, July, August) and summer (December, January, February) precipitation (Australian Bureau of Meteorology (http://www.bom.gov.au/). The native resolution of the digital data layers was 0.025^{o} (approximately 2.5 km × 2.5 km in Australia), which was decreased to 0.25^{o} (25 km × 25 km) to match the aggregated distribution data by calculating the mean of surrounding cells using ArcGIS 9.2 (ESRI 2006).

RESULTS & DISCUSSION

Range equilibrium

In contrast to the hypothesized relationship, ant- and passively-dispersed species exhibited better model fits (greater explained deviance) and therefore higher covariation between species composition and climate than did wind- and vertebrate-dispersed species (Table 5.1, Fig. 5.2). Passively-dispersed species had the highest overall explained deviance with climate (53.8%) followed by ant- (47.7%), vertebrate (43.1%), and wind-dispersed species (39.8%). Thus, the distributions of wind- and vertebrate-dispersed species tended to be more random with respect to environmental transitions than did the distributions of ant- and passively-dispersed species, suggesting ant- and passively-dispersed species fill more of their potential distributions and are closer to equilibrium with the climate variables we considered.

We also predicted that geographic distance would be relatively more important in explaining turnover than would change in environmental conditions for dispersal-limited species than vertebrate- and wind-dispersed species. However, we found no clear change in the relative importance of environmental conditions and geographic distance in explained deviance across dispersal modes (Fig. 5.2), nor was it possible to readily assign explained deviance to either environment or distance, given the sizeable proportion of explained deviance shared between these variables (Table 5.1). Taken together, our results indicate that (1) the ostensibly dispersal-limited groups are closer to equilibrium with climate than either wind- or vertebrate-dispersed species and that (2) adaptations of species for dispersal indicate the opposite pattern expected between seed morphology and the ability of species to attain equilibrium with climate in southwestern Australia.

Turnover and dispersal mode

The greatest rates and amounts of turnover in species composition and the greatest differences between dispersal modes generally occurred along the gradient of winter precipitation (Fig. 5.3b). To a lesser extent maximum temperature was also important, but

Table 5.1: Percent deviance explained for each Generalized Dissimilarity Model.

	Ant	Passive	Vertebrate	Wind
Geographic distance	34.9	44.0	31.7	32.2
Environment	47.7	53.8	43.1	39.8
Environment + geography	52.5	58.4	44.7	46.5

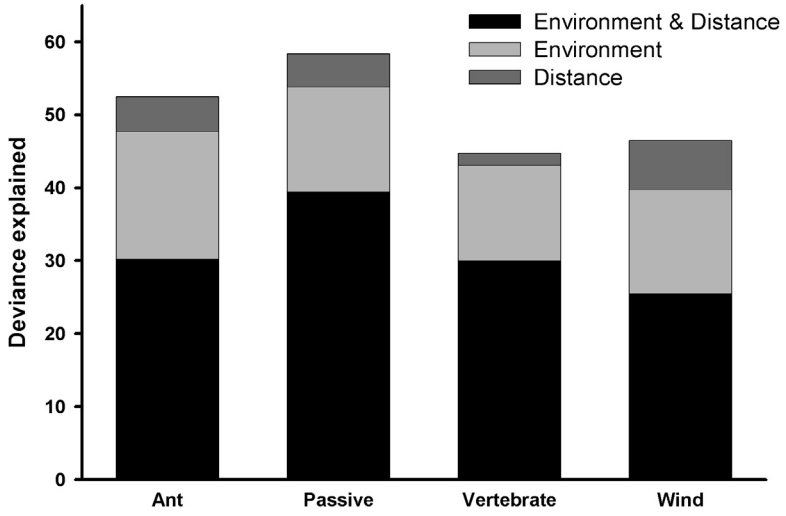

Figure 5.2: Predictive performance of generalized dissimilarity models in terms of percent deviance explained, partitioned into three components: (black) percent deviance shared by the environmental predictors and geographic distance, (light grey) percent deviance explained by the environmental predictors while controlling for geographic distance, and (dark grey) percent deviance explained by the geographic distance while controlling for environment. The height of each bar represents the total percent deviance explained by a model containing the five environmental predictors and geographic distance.

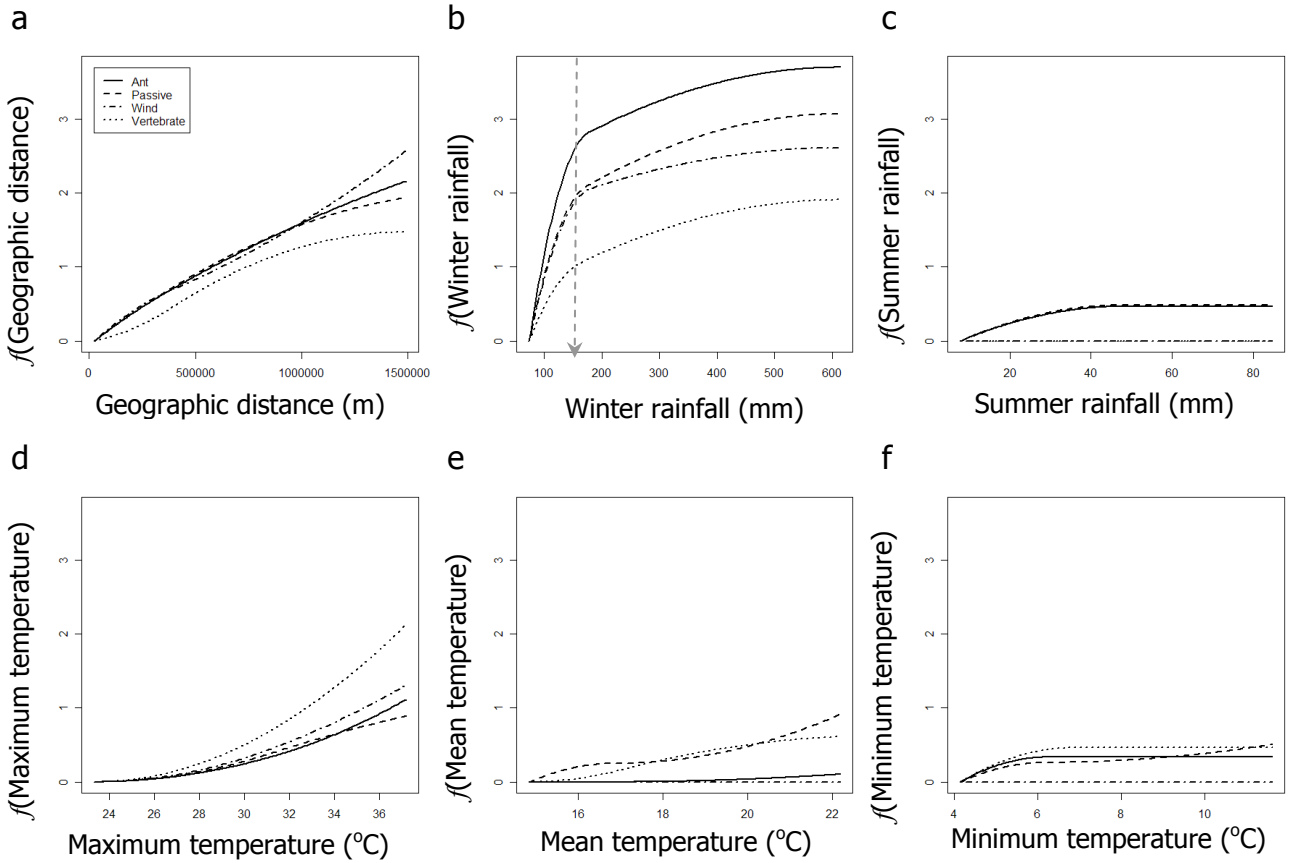

Figure 5.3: Fitted functions of turnover in species composition by each dispersal mode for a Generalized Dissimilarity Model using geographic distance and the five environmental variables as predictor variables. The maximum height reached by each function provides an indication of the total amount of compositional turnover for each dispersal mode associated with that variable, holding all other variables constant. The slope of each function provides an indication of the rate of compositional turnover and how this rate varies along the gradient.

Table 5.2. The rate (slope) and percent of the total change in species composition by region and dispersal mode along the gradient of winter precipitation.

	Ant	Passive	Vertebrate	Wind
Arid (< 180 mm)				
Turnover	78.9	73.1	58.9	81.0
Slope	0.022	0.017	0.0092	0.017
Mediterranean (> 180 mm)				
Turnover	21.1	26.9	41.0	19.0
Slope	0.002	0.0022	0.0022	0.0013

mainly to turnover in vertebrate-dispersed species (Fig. 5.3d). In general, there was little relative change in species composition or differences between dispersal modes along the other environmental variables considered.

Across all four dispersal modes and along the gradient of winter precipitation, the greatest change in species composition occurred between sites that receive less than 180 mm of precipitation, as indicated by the abrupt decrease in the rate of turnover before 180 mm of winter precipitation (dashed gray arrow, Fig. 5.3b). Sites that received more than 180 mm of precipitation showed comparatively little turnover. The rate of turnover between sites (as indicated by the slope of the line for each dispersal mode, Table 5.2) that receive less than 180 mm of precipitation was greatest in ant-dispersed species and least for vertebrate-dispersed species. However, vertebrate- and passively-dispersed species showed the most change in composition per unit of precipitation between sites receiving more than 180 mm of precipitation, whereas wind-dispersed species exhibited the lowest rate of turnover.

The patterns of turnover along the gradient of winter precipitation suggest several major characteristics of the biota. First, the abrupt change in the rate of turnover identified by the models indicates a major biogeographical transition at an ecotone occurring near the 180 mm isopleth (highlighted dotted line, Fig. 5.3b). To the east of this ecotone (values less than 180 in Fig. 5.3b), the climate is arid and turnover is very rapid between sites even though they differ little in rainfall. To the west of this ecotone (values greater than 180 in Figure 3b) the climate is Mediterranean and the rate and amount turnover is generally low, despite large changes in the environment. When mapped (highlighted dotted line, Fig. 5.1), this line corresponds almost exactly to the boundary between the Jarrah Forest and the Avon Wheatbelt bioregions identified using a qualitative approach (Hobbs and McIntyre 2005). Second, differences in the rate of turnover by region suggest that species that occur in the arid region tended have narrower precipitation niches than those that occur in more Mediterranean areas near the coast. Thus, spatial variation in water availability may be a key factor structuring plant communities in the drier interior, whereas other climatic factors increase in relative importance nearer the coast. Finally, differences in the rate of turnover between dispersal

modes suggest that ant-dispersed species in the arid region tended to have the narrowest niche overall and vertebrate-dispersed species tended to have the broadest windows of winter precipitation over which they occurred. In the Mediterranean region, wind-dispersed species tended to have the broadest niche overall and vertebrate- and passively-dispersed species tended to have the narrowest niche.

Niche characteristics and geographic range size

Given the obvious differences in niche breadth by position along the precipitation gradient and by dispersal mode, we pursued our analysis of niche characteristics and geographic range size by dividing each dispersal mode into two classes: (1) species occurring entirely to the east of the 180 mm ecotone (arid) and (2) species occurring entirely to the west of the 180 mm ecotone (Mediterranean). For species occurring in arid sites that receive less than 180 mm of winter precipitation (east of the 180 mm ecotone), we found no significant differences between precipitation niche breadth among dispersal modes ($P > 0.45$). Although the mean values of precipitation niche breadth were not significantly different, the rank order of the mean values was reconcilable with the pattern of turnover. Ant-dispersed species had the smallest mean niche breadth (24.5 mm), vertebrate the largest (31.3 mm) and wind- and passively-dispersed species in the middle (28.2 and 26.0 mm respectively). Spatial arrangement and overlap of geographic ranges of species in the arid region may also explain differences in the patterns of turnover exhibited between dispersal modes.

We did find significant differences in mean niche breadth among dispersal modes for species occurring in sites that receive more than 180 mm of winter precipitation (west of the 180 mm ecotone). Ant- and wind-dispersed species tended to have broader precipitation niches than passively-dispersed species (Fig. 5.4b, $P < 0.042$). These findings are generally congruent with the patterns of turnover in these groups as well, with ant- and wind-dispersed species exhibiting lower amounts of turnover west of the 180 mm ecotone than passively- and vertebrate-dispersed species.

In nearly all instances, realized niche breadths were broader west of the 180 mm ecotone in Mediterranean environments than those in arid environments to the east ($P < 0.002$). However, niche breadth did not differ between arid or Mediterranean environments for vertebrate-dispersed species. Also, the niche breadth of wind-dispersed species in arid environments did not differ from the niche breadth of vertebrate-dispersed species in Mediterranean environments.

We found few significant differences in geographic range size either among dispersal modes or between arid and Mediterranean environments (Fig. 5.5). This finding is consistent with the similar patterns of turnover exhibited between dispersal modes with increasing geographic separation (Fig. 5.3a). Within arid environments, species did not differ in range size by dispersal mode (Fig. 5.5a). Within Mediterranean environments, ant- and wind-dispersed species had larger geographic ranges than passively-dispersed species (Fig 5.5b). When comparing between regions, we found no differences in range size. Therefore, region primarily had an effect on niche breadth, rather than geographic range size (Gove *et al.* in press).

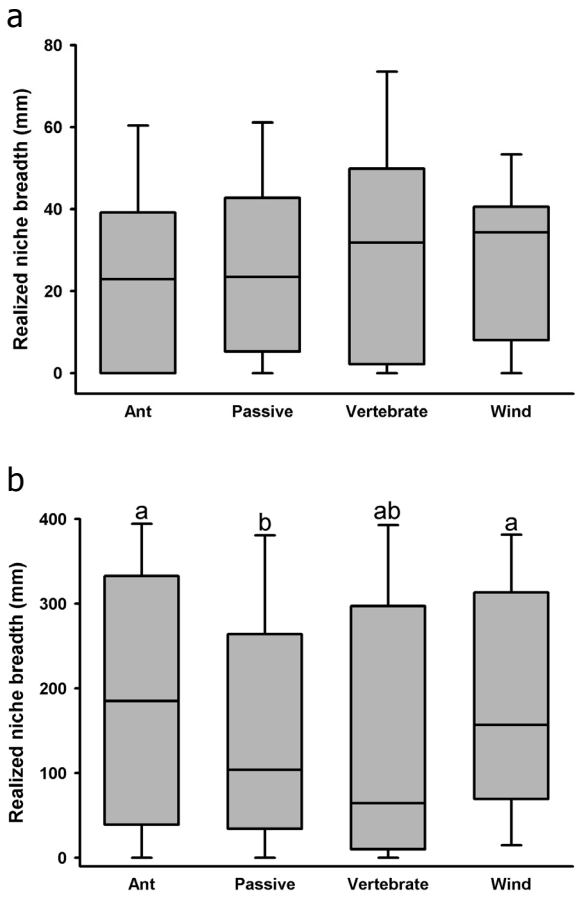

Figure 5.4: Mean realized precipitation niche breadth for each dispersal mode in (a) arid and (b) Mediterranean habitats.

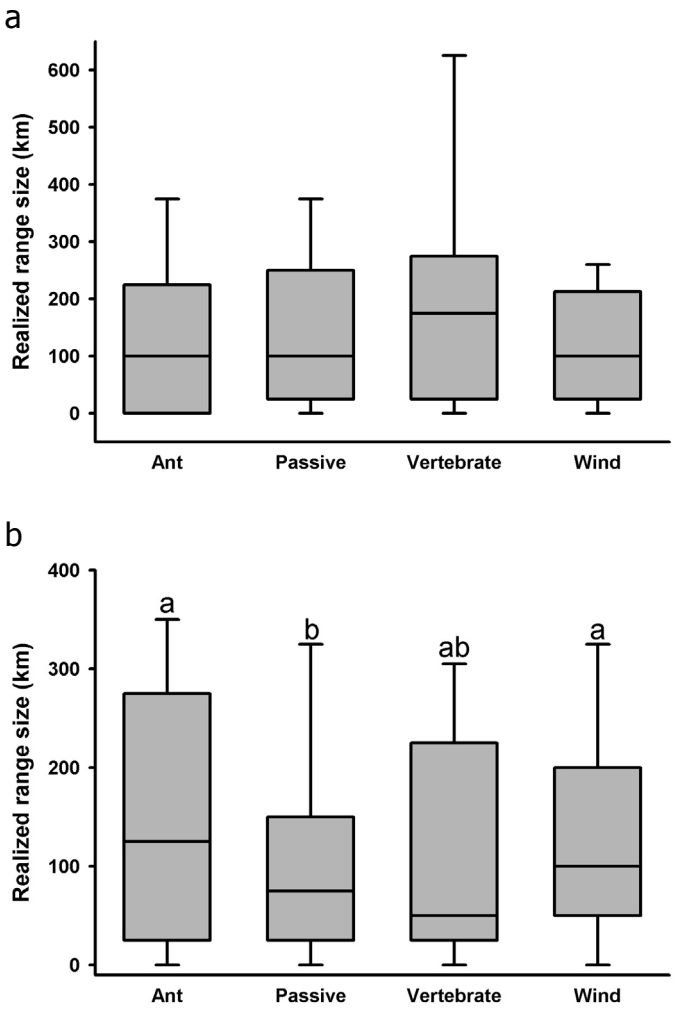

Figure 5.5: Mean realized geographic range size for each dispersal mode in (a) arid and (b) Mediterranean habitats.

Seed dispersal and range equilibrium

In contrast to our prediction that better dispersers should fill more of their potential distribution and therefore be closer to equilibrium, we found that species dispersed by wind or vertebrates were relatively more distant from equilibrium than ant- and passively-dispersed species with ostensibly limited dispersal abilities. Why might seed dispersal mode represent a poor predictor of how close species are to equilibrium? Among the many possible explanations, we explore three key possibilities here: (1) the degree to which seed morphology and dispersal mode represent dispersal ability, (2) factors unaccounted for in our analysis but which influence the distributions of species, and (3) interactions between seed dispersal mode, niche characteristics and the spatial structure of environment gradients.

Seed morphology and dispersal ability

The simplest explanation for why dispersal mode does not predict range equilibrium is that seed morphology and mode and associated mean dispersal distances are not an indication of the ability of species to disperse across the landscape. Seeds can also be dispersed by non-standard mechanisms, which may transport seeds much greater distances than those suggested by morphological adaptations (Higgins *et al.* 2003) and which are extremely difficult to quantify (Nathan *et al.* 2003). Such long-distance dispersal events, though rare, could disproportionately influence range dynamics (Cain *et al.* 1998) and may ameliorate relationships between dispersal morphology and range equilibrium. For example, in Western Australia, both Emu (*Dromaius novaehollandiae*) and kangaroo (*Macropus fuliginosus*) feces contain viable seeds of each of the dispersal modes we considered (Calvino-Cancela *et al.* 2006; Calvino-Cancela *et al.* 2008). Long-distance movements by such non-standard means might yield occasional dispersal events much longer than those implied by morphology alone and may allow species with otherwise limited dispersal abilities to maintain equilibrium. Although this explanation is satisfying for ant- and passively-dispersed species, it is not clear why non-standard mechanisms should be more important for these dispersal modes than wind- or vertebrate-dispersed species, when presumably these latter groups have the greatest potential for long-distance movements via their standard means of dispersal. Finally, dispersal rates are also a function of population abundance, with more abundant populations producing more propagules. Although we did not have abundance data at our disposal, we can think of no reason why there should be any consistent relationship between dispersal mode and population size.

Non-climatic factors that influence distributions

The ability of species to attain equilibrium is ultimately a function of three processes: (1) the amount of suitable habitat, (2) the ability of species to colonize this habitat, and (3) the rate at which species go extinct from occupied patches. Like dispersal rates, extinction rates are also a function of abundance, with larger population less likely to suffer extinction. Of more importance however is the frequency and spatial extent of disturbances that cause extinction. In southwestern Australia, brushfires are an important

and frequent disturbance that influence the distributions of plant species (Beard 1990), yet reliable data describing fire were not available for our study, nor is it obvious at which scale such a variable would be relevant. The same can be said of soil type, which is also important for species composition and turnover in southwestern Australia (Beard 1990; Hopper and Gioia 2004). Further, anthropogenic factors such as land use change can also influence biogeographical patterns (La Sorte 2006). Over 40% of land in southwestern Australia currently is under agriculture and therefore actual current ranges are likely smaller than those analyzed here (Gove *et al.* in press). Agriculture is particularly concentrated in the arid region, where nearly 100% of the land is under agriculture. The greater rates and total amount of turnover in this region across all dispersal modes may be attributed to the intensity of fragmentation as populations may highly dissected, unlikely to colonize suitable patches, and more prone to extinction. Indeed, many abandoned fields in this region have not been re-colonized by native species after 45 years owing to dispersal limitation (Standish *et al.* 2007). However, because we consider relative distance from equilibrium, these factors would only alter our results to the extent that they impact one dispersal mode more than another. For example, many species in southwestern Australia rely on fire for germination (Roche *et al.* 1998), whereas the size and frequency of bushfires ultimately set colonization potential by limiting germination opportunities and rare long-distance dispersal events (e.g., serotinous *Banksia*, Lamont *et al.* 2007).

Dispersal mode and range dynamics in climatic and geographic space

Our preferred explanation for why dispersal mode does not predict range equilibrium invokes both the ecological and evolutionary implications of dispersal ability and range dynamics (e.g., Thompson *et al.* 1999; Lester *et al.* 2007). We assessed range equilibrium by exploring patterns of turnover in species composition along environmental gradients and how well change in the environment explained change in species composition. Nekola and White (1999) argued that rates of change in species composition will be related to several key factors: characteristics of the environment (spatial arrangement and geographic extent of suitable habitats) and two characteristics of the organism: niche breadth and dispersal ability. Besides influencing range dynamics by hindering attainment of potential distributions in geographic space, dispersal limitation can also influence potential distributions by facilitating adaptation in climatic space (i.e., niche breadth) if there is no benefit to long distance dispersal. In this sense, dispersal acts on geographic ranges not only by influencing the ability of species to attain their potential distribution, but also by determining the spatial extent of the potential distribution through its impacts on environmental tolerances and the diversity of suitable habitats that can be exploited. For example, one of the consequences of short distance dispersal may be smaller realized ranges and disequilibrium. A second possibility, however, is that short distance dispersal may tend to concentrate seeds in a particular habitat and allow for habitat specialization to evolve more easily than if seeds are constantly being distributed across habitats. Such habitat specialization might be particularly prevalent where climate has been relatively stable, such that narrow endemics do not go extinct (Jansson 2003). In our analyses, habitat specialization due to short distance dispersal would manifest as smaller niches and small geographic ranges.

Beyond niche and dispersal characteristics of species, we also find that spatial structure of the environment also influences on biogeographic patterns in southwestern Australia. Like Steinitz *et al.* (2006), who found that species turnover in both snails and birds occurred more rapidly in arid versus Mediterranean regions, we find that precipitation distance had a stronger per-unit effect on species turnover in inland arid regions versus wetter Mediterranean areas near the coast. Because the precipitation gradient is shallow in the arid region and steep in the Mediterranean region, one unit of change in precipitation will cover a relatively large geographic area in the arid region, whereas one unit of change in precipitation will cover a relatively small geographic area in the Mediterranean region. Therefore, both where species are distributed along this gradient and their niche breadth will influence the amount of geographic space they must cover via dispersal to attain equilibrium.

For example, we found that passively-dispersed species were the closest to equilibrium relative to other groups. Passively-dispersed species tended to have narrow niches and small geographic ranges in both wet and dry habitats. Given their narrow niches and their correspondingly small projection of these niches into geographic space, passively-dispersed species need to traverse a relatively small geographic distance to attain equilibrium. Therefore, short distance dispersal can allow equilibrium if it leads to a narrow niche because of selection and that niche tends to encompass a small geographic area. Conversely, long distance dispersal can prevent equilibrium if selection leads to a broad niche and the projection of that niche covers a large geographic extent. This may explain the lower equilibrium in vertebrate dispersed species that tended to have the broadest niche in dry habits, which, given the shallow nature of the gradient, would cover a much large geographic area than a similarly broad niche in the Mediterranean region.

The relatively high degree of equilibrium in ant-dispersed species, which tended to have a comparatively broad niche in Mediterranean habitats, is somewhat more puzzling but potentially reconcilable with the nature of ant-mediated dispersal in southwestern Australia. Despite preventing frequent long-distance dispersal, ant-mediated dispersal allows "dispersal in time" by storing seeds underground and thus protecting them from fire (Auld 1986). Dispersal in time, coupled with climate-stability and rare long-distance dispersal events (Calvino-Cancela *et al.* 2006; Calvino-Cancela *et al.* 2008) may allow ants to realize and maintain a relatively broad climate niche. This would be particularly true in wet habitats where ant-dispersed species wait belowground protected from fire for winter rain in order to germinate once fire has removed competing species (including seeds exposed on the surface). Further, because the precipitation gradient is steep in wet habitats, having a broad niche in climate space does not necessarily translate into a large geographic range.

Given the abrupt ecotone near 180 mm of winter precipitation, a simple method to approximate range equilibrium is to calculate the proportion of species of each dispersal mode with ranges that extend to, but not beyond, this boundary. In the dry region, this would constitute the proportion of species with a maximum precipitation value at or near 180 mm. In the Mediterranean region, this would correspond to a minimum precipitation value at or near 180 mm. In performing this analysis, we found that ant- and passively-dispersed species had distributions that most often coincided with, but did not cross, this boundary. These groups were also closest equilibrium. In contrast, vertebrate- and wind-

dispersed species had the lowest proportion of species that extend to the ecotone, and therefore tended to be more distant from equilibrium. This pattern was consistent at precipitation values within 5, 10, and 20% of the ecotone. Further, the distributions of wind-dispersed species extended beyond the ecotone most frequently. Therefore, the low degree of equilibrium in this group may be additionally attributed to the possibility that immigration from suitable habitats is sufficiently large to allow persistence unsuitable habitats beyond their potential range (Pulliam 2000), thereby reducing the amount of turnover between sites as well as model fit. In other words, well-dispersed species may colonize more marginal areas beyond their potential range, yet this possibility is rarely discussed in the context of range equilibrium or patterns of species turnover.

Range equilibrium and climatic change in southwestern Australia

When projected in either space or time, species distribution models generally assume that the distributions of modeled species are at equilibrium with climate. Araújo and Pearson (2005) argued that the extent to which this assumption is met will influence the validity of model projections, with projections being least certain for species that do not attain equilibrium. Following this logic, our analysis allows us to draw two general conclusions regarding the projection of climate change impacts on biodiversity in southwestern Australia using species distributions models. First, our results suggest that future projections may be most valid for ant- and passively-dispersed species and least valid for vertebrate- and wind-dispersed species. However, given the relatively small difference between groups in model fit, uncertainties regarding range equilibrium may be relatively minor compared to other sources of uncertainty, such as scenario of future climate change. Second, given the drastic change in species composition when crossing the 180 mm ecotone, we argue that the coastward movement of this ecotone with climate change will have disproportionate effects on biodiversity, an outcome demonstrated by projection of species distribution models (Fitzpatrick *et al.* in press).

Araújo and Pearson (2005) additionally proposed that species that are unable to attain equilibrium under current climate may also be most threatened by climatic change. Though this is likely true for many species because disequilibrium reflects dispersal limitation, it may not be true for well-dispersed species that are in disequilibrium because they explore marginal areas beyond their potential range. If identified, such species could serve as indicators of climatic change since they would likely disappear rapidly from marginal areas (e.g., Midgley *et al.* 2006).

CONCLUSIONS

We found that characteristics of the environment, niche breadth and dispersal ability of species all exert some influence on patterns of species turnover and range equilibrium in southwestern Australia. Taken as a whole, our results suggest an ecotone along the gradient of winter precipitation is an important driver of patterns of range equilibrium in southwestern Australia. Given their relatively high-rates of turnover, better model fits, we suggest that passively-dispersed species tend to have smaller niches and correspondingly smaller geographic ranges than ant-, vertebrate-, or wind-dispersed species, but are closer to equilibrium within their small geographic ranges than these

groups. The relationships between seed dispersal mode and range equilibrium in groups other than passively-dispersed species is less clear. Thus, more generally, we argue that the ecological and evolutionary implications of dispersal ability, coupled with spatial structure of the environment and the propensity for long-distance dispersal events by non-standard means, forgo simple extrapolations of range equilibrium based on categorical measures of dispersal ability.

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APPENDIX A

Supplemental material for Chapter 4

Table 1.A.1: Species-specific classification of 100 Western Australian endemic *Banksia* (Proteaceae) species into range loss categories under three future climate scenarios and three assumptions regarding migration rate. 'Sim' refers to simulated-migration of 5 km decade^{-1}. Percentages refer to the amount of range loss projected to occur by 2080 (i.e., 0% refers to a range loss between 0 and 30%), whereas '+' and 'EX' refer to range expansion and to extinction (projected loss of range equal to 100%) respectively. Species projected to suffer range losses equal to 100% (EX) in at least one of the nine climate × migration scenario are in bold font.

	Low-severity (B1)			Mid-severity (A1B)			High-severity (A1F)		
Species	Full	Sim	No	Full	Sim	No	Full	Sim	No
Banksia ashbyi	+	+	0%	+	+	0%	+	+	0%
Banksia attenuata	0%	0%	0%	0%	0%	0%	80%	80%	80%
Banksia baueri	+	+	0%	+	+	0%	+	30%	50%
Banksia baxteri	+	+	0%	+	+	0%	30%	50%	50%
Banksia benthamiana	0%	0%	30%	0%	0%	0%	0%	30%	50%
Banksia blechnifolia	0%	0%	0%	80%	80%	80%	80%	80%	80%
Banksia brownii	30%	30%	30%	50%	50%	50%	50%	50%	50%
Banksia candolleana	0%	0%	30%	+	+	0%	80%	80%	EX
Banksia chamaephyton	0%	0%	0%	0%	0%	0%	50%	50%	50%
Banksia coccinea	0%	0%	0%	30%	30%	30%	50%	50%	80%
Banksia cuneata	80%	80%	80%	0%	0%	50%	EX	EX	EX
Banksia dryandroides	30%	30%	30%	80%	80%	80%	80%	80%	80%
Banksia elderiana	80%	80%	80%	80%	80%	80%	EX	EX	EX
Banksia elegans	+	+	0%	+	+	0%	+	+	0%
Banksia gardneri	+	+	0%	0%	0%	0%	30%	30%	30%
Banksia grandis	0%	0%	0%	30%	30%	30%	80%	80%	80%
Banksia grossa	+	+	0%	+	+	0%	30%	30%	50%
Banksia hookeriana	0%	0%	30%	+	+	0%	+	+	0%
Banksia ilicifolia	+	+	0%	0%	0%	0%	50%	50%	80%
Banksia incana	0%	0%	0%	0%	0%	0%	80%	80%	80%
Banksia laevigata	0%	0%	50%	80%	80%	80%	50%	80%	80%
Banksia lanata	30%	30%	30%	+	+	0%	+	+	0%
Banksia lemanniana	+	+	0%	+	+	0%	+	+	30%
Banksia leptophylla	0%	0%	0%	+	+	0%	0%	0%	0%
Banksia littoralis	0%	0%	0%	30%	30%	30%	80%	80%	80%
Banksia media	0%	0%	0%	30%	30%	30%	50%	50%	80%
Banksia meisneri	50%	50%	50%	50%	50%	50%	EX	EX	EX
Banksia menziesii	0%	0%	0%	+	0%	0%	0%	0%	30%
Banksia micrantha	0%	0%	30%	50%	50%	80%	80%	EX	EX
Banksia nutans	30%	30%	30%	50%	50%	50%	80%	80%	80%
Banksia occidentalis	0%	0%	0%	30%	30%	30%	50%	50%	50%
Banksia petiolaris	30%	30%	30%	50%	50%	50%	80%	80%	80%
Banksia pilostylis	0%	0%	0%	50%	50%	50%	80%	80%	80%
Banksia prionotes	30%	30%	30%	+	0%	0%	50%	50%	50%
Banksia pulchella	+	+	0%	+	0%	0%	50%	50%	80%
Banksia quercifolia	50%	50%	50%	80%	80%	80%	80%	80%	80%
Banksia repens	+	+	0%	0%	0%	0%	50%	50%	80%
Banksia scabrella	+	+	0%	+	+	0%	+	+	0%
Banksia sceptrum	+	0%	0%	+	+	0%	+	+	0%
Banksia seminuda	30%	30%	30%	50%	50%	50%	80%	80%	80%
Banksia speciosa	+	+	0%	+	+	0%	30%	30%	30%
Banksia sphaerocarpa	0%	0%	0%	30%	30%	30%	80%	80%	80%
Banksia telmatiaea	50%	50%	50%	+	+	30%	EX	EX	EX
Banksia verticillata	80%	80%	80%	80%	80%	80%	EX	EX	EX

continued

	Low (B1)			Mid (A1B)			High (A1F)		
Species	Full	Sim	No	Full	Sim	No	Full	Sim	No
Banksia violacea	+	+	0%	0%	0%	0%	0%	50%	50%
Dryandra arborea	50%	50%	50%	80%	80%	80%	80%	80%	80%
Dryandra arctotidis	50%	50%	50%	50%	50%	50%	80%	80%	80%
Dryandra armata	0%	0%	0%	30%	30%	50%	80%	80%	80%
Dryandra bipinnatifida	0%	0%	0%	0%	0%	0%	50%	50%	50%
Dryandra blechnifolia	50%	50%	50%	80%	80%	80%	80%	80%	80%
Dryandra brownii	30%	30%	30%	50%	50%	50%	80%	80%	80%
Dryandra carlinoides	0%	0%	0%	+	+	0%	0%	0%	30%
Dryandra cirsioides	0%	0%	0%	50%	50%	50%	80%	80%	80%
Dryandra conferta	50%	50%	50%	50%	50%	50%	80%	80%	80%
Dryandra cuneata	0%	0%	0%	0%	0%	0%	50%	50%	50%
Dryandra cynaroides	EX	EX	EX	EX	EX	EX	EX	EX	EX
Dryandra cypholoba	0%	0%	50%	30%	50%	80%	EX	EX	EX
Dryandra drummondii	50%	50%	50%	80%	80%	80%	80%	80%	80%
Dryandra echinata	30%	30%	50%	+	50%	80%	80%	EX	EX
Dryandra erythrocephala	EX	EX	EX	EX	EX	EX	EX	EX	EX
Dryandra falcata	0%	0%	0%	50%	50%	50%	50%	50%	80%
Dryandra ferruginea	80%	80%	80%	80%	80%	80%	80%	80%	80%
Dryandra formosa	50%	50%	50%	80%	80%	80%	80%	80%	80%
Dryandra fraseri	0%	0%	0%	0%	0%	0%	30%	30%	50%
Dryandra glauca	30%	30%	30%	0%	0%	30%	80%	80%	80%
Dryandra hewardiana	0%	30%	50%	+	50%	80%	80%	EX	EX
Dryandra horrida	80%	80%	80%	30%	30%	50%	EX	EX	EX
Dryandra kippistiana	+	+	0%	+	+	30%	80%	80%	80%
Dryandra lindleyana	30%	30%	30%	30%	30%	30%	80%	80%	80%
Dryandra meganotia	EX	EX	EX	EX	EX	EX	EX	EX	EX
Dryandra mucronulata	80%	80%	80%	80%	80%	EX	EX	EX	EX
Dryandra nervosa	0%	0%	0%	30%	30%	30%	50%	50%	50%
Dryandra nivea	0%	0%	30%	30%	30%	30%	80%	80%	80%
Dryandra nobilis	0%	0%	30%	+	0%	30%	80%	80%	80%
Dryandra obtusa	+	+	0%	0%	0%	30%	50%	50%	80%
Dryandra octotriginta	EX	EX	EX	EX	EX	EX	EX	EX	EX
Dryandra pallida	80%	80%	80%	EX	EX	EX	80%	EX	EX
Dryandra platycarpa	80%	80%	80%	80%	80%	80%	EX	EX	EX
Dryandra plumosa	30%	30%	30%	80%	80%	80%	80%	80%	80%
Dryandra polycephala	+	0%	50%	+	0%	50%	80%	80%	EX
Dryandra porrecta	50%	50%	50%	50%	50%	50%	80%	80%	80%
Dryandra praemorsa	50%	50%	50%	50%	50%	50%	80%	80%	80%
Dryandra preissii	EX	EX	EX	EX	EX	EX	EX	EX	EX
Dryandra pteridifolia	+	+	0%	30%	30%	30%	80%	80%	80%
Dryandra purdieana	0%	0%	30%	30%	30%	30%	80%	80%	80%
Dryandra quercifolia	+	+	0%	+	+	0%	+	+	30%
Dryandra sclerophylla	+	+	0%	+	+	0%	80%	80%	80%
Dryandra serra	30%	30%	30%	80%	80%	80%	80%	80%	80%
Dryandra sessilis	0%	0%	0%	0%	0%	0%	50%	50%	50%
Dryandra shanklandiorum	80%	80%	80%	80%	80%	80%	80%	80%	80%
Dryandra shuttleworthiana	0%	0%	30%	+	+	0%	80%	80%	80%
Dryandra speciosa	30%	30%	30%	30%	30%	50%	EX	EX	EX
Dryandra squarrosa	0%	0%	30%	0%	0%	30%	80%	80%	80%
Dryandra stricta	0%	0%	0%	+	+	0%	30%	30%	50%
Dryandra stuposa	80%	80%	80%	80%	80%	80%	EX	EX	EX
Dryandra subpinnatifida	50%	50%	50%	30%	30%	30%	EX	EX	EX
Dryandra tenuifolia	30%	30%	30%	50%	50%	50%	80%	80%	80%
Dryandra tridentata	+	+	0%	+	+	0%	+	+	0%
Dryandra vestita	30%	30%	30%	30%	30%	30%	80%	80%	80%
Dryandra xylothemelia	50%	50%	50%	EX	EX	EX	80%	EX	EX

VITA

Matthew Charles Fitzpatrick was born October 10th, 1975 in Baltimore, Maryland. The day was drizzly, 0.6 inches of precipitation fell and the mean temperature was 59°F (i.e., six heating degree days). He soon moved with his family to rural southeastern Pennsylvania where they lived in simple structure for nearly two years with a single hand pump for water. He attended grade school in the farming community of Fawn Grove, Pennsylvania before entering the Pennsylvania State University in 1993. After completing a Bachelor of Science degree in Mechanical Engineering in 1997, he moved to Connecticut to work as an aerospace engineer, designing advanced gas turbine engines for commercial and military aircraft. This work did not suite him, so he moved to Montana under the ruse of pursuing a graduate degree in Environmental Studies. However, his main pursuits included photography, down-hill and cross-country skiing, and fly-fishing streams, lakes and rivers in the mountains of western Montana. Nonetheless, he completed a Master of Science degree in 2003 and immediately began a PhD at the University of Tennessee, which he completed in February of 2008. He plans to continue his research at Harvard Forest in Petersham, Massachusetts before obtaining a permanent research position in a place with mountains where he will build a house of his own design.