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THEMATIC SECTION
Spatial Simulation Models
in Planning for Resilience

How will climate variability interact with long-term climate change to affect the persistence of plant species in fragmented landscapes?

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SUMMARY

As climates change, some plant species will need to migrate across landscapes fragmented by unsuitable environments and human activities to colonize new areas with suitable climates as previously habited areas become uninhabitable. Previous modelling of plant's migration potential has generally assumed that climate changes at a constant rate, but this ignores many potentially important aspects of real climate variability. In this study, a spatially explicit simulation model was used to investigate how interannual climate variability, the occurrence of extreme events and step changes in climate might interact with gradual long-term climate change to affect plant species' capacity to migrate across fragmented landscapes and persist. The considered types of climate variability generally exacerbated the negative effects of long-term climate change, with a few poignant exceptions where persistence of long-lived trees improved. Strategic habitat restoration ameliorated negative effects of climate variability. Plant functional characteristics strongly influenced most results. Any modelling of how climate change may affect species persistence, and how actions such as restoration may help species adapt, should account for both short-term climate variability and long-term change.

Keywords: climate variability, climate change, dispersal, fragmented landscapes, migration, plant persistence, simulation model, spatially explicit

INTRODUCTION

Climate change presents a global threat to the persistence of many plant species (Foden *et al.* 2009). As the climate shifts, so too will the optimal habitat for each species. To persist, species will have to migrate rapidly across landscapes to track their preferred climatic conditions and there is some evidence for this migration having already occurred (Parmesan & Yohe 2003; Walther *et al.* 2005). Rapid migration depends on seed dispersal, germination in suitable habitat, reproduction, and further seed dispersal (Skellam 1951; Turchin 1998). Migration is limited by landscape-scale fragmentation of suitable habitat, both through the patchiness of habitat requirements, such as certain soil types or topographical conditions, as well as human land-use changes such as through agriculture and urbanization (Pitelka 1997).

Much previous work that has considered how plant species distributions might change with climate changes is based on empirical climate envelope modelling. This modelling approach provides predictions of where plant species will have to migrate to persist (see for example Fitzpatrick *et al.* 2008; Yates *et al.* 2010; Maiorano *et al.* 2012), however, it does not deal explicitly with migration processes, which is an important limitation (Thuiller *et al.* 2008). More mechanistic modelling approaches predict whether plant species will be able to make the required migrations, by modelling the dynamic processes involved, such as life cycle dynamics and seed dispersal (see Engler & Guisan 2009; Di Traglia *et al.* 2011; Nathan *et al.* 2011).

The Plant Persistence under Climate Change (PPunCC) model simulates the processes involved in plant species migration under climate change (Renton *et al.* 2011, 2012). We used the model to predict whether different plant functional types would be likely to migrate across a landscape fast enough to track a changing climate, or whether they instead would be likely to become extinct without intervention (Renton *et al.* 2012). The spatially-explicit model accounts for the possibility of the landscape being 'fragmented' by land uses that are not suitable as habitat for the plants, such as urbanization, agriculture, or other unsuitable conditions such as soil type. We considered a wide spectrum of functional types, in order to identify which characteristics were most important, and also considered different levels of landscape fragmentation and rates of climate change. Finally, we used the model to predict whether habitat restoration specifically targeted to reduce the size of gaps between suitable areas would increase the chance of plant species persisting, and found that for some types it did, but for many it did not. (By 'habitat restoration' we mean making areas that were unsuitable for plant establishment suitable again.) Like all models, the original version of PPunCC was based on certain

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*Correspondence: Dr Michael Renton Tel: + 61 8 6488 1959 Fax: +61 8 6488 1108 e-mail: michael.renton@uwa.edu.au assumptions, which could possibly limit the generality of the conclusions that can be drawn from its use. One important assumption was that the key point of vulnerability in a plant's life cycle (the point at which changes in climate would have a significant impact) was seedling establishment. We addressed the importance of this assumption in a second study, considering how the conclusions drawn from the first study varied if, instead of establishment, the key point of vulnerability was instead assumed to be adult mortality, seed production, or a combination of more than one of these (Renton *et al.* 2013). We found that changing the key point of vulnerability had little effect on plant species' migration capacity, meaning that previous results could be generalized more confidently.

Another key assumption of the original study was that climate changes at a constant linear rate, that is, there is no variability from year to year except for a small incremental change that is the same each year. This is clearly an idealization. There is evidence both from modelling exercises (see for example Katz & Brown 1992; Rahmstorf & Coumou 2011) and from historical climate data (for example Collins *et al.* 2000; IPCC [Intergovernmental Panel on Climate Change] 2007) that climatic events such as extended drought, heat waves and extreme hot days have become and will continue to become more frequent under climate change. Increases in the frequency of extreme events may be exacerbated by increasing interannual variability, which leads both to higher extremes within the climatic patterns and less predictability in annual climatic conditions (see Schär *et al.* 2004). Climate may also change in relatively discrete, infrequent, sudden and large 'steps' or 'jumps' as environmental thresholds are reached, rather than in relatively continuous, small changes every year; for example, there is some evidence that rainfall decreased in this sudden step-wise manner in south-west Australia in the mid-1970s (IOCI [Indian Ocean Climate Initiative] 2002; Pitman *et al.* 2004).

Climate variability and step changes can have important implications for ecosystems. For instance, shifted timing in precipitation patterns, as well as sudden decreases in precipitation, can impact ecosystem functions such as net primary productivity (Mearns *et al.* 1996; Fay *et al.* 2003). However, understanding of the importance of climate variability is limited. Extreme events or increased climatic variability may not lead to significant deviation from the natural range of variation within an ecosystem. For example, compensatory behaviour by species adapted to extreme or variable climate can help to prevent dramatic changes to ecosystem functions (Smith 2011).

Little is known about how climate variability will interact with long-term climate change to impact species persistence. At the species level, extreme events potentially play an important part in shaping the ecology and evolution of organisms (Gutschick & BassiriRad 2003). Sudden, dramatic climatic events can cause high individual mortality and vegetation shifts, such as differential tree mortality after drought (Mueller *et al.* 2005). Additionally, extreme events can cause reduced fitness in the affected year, for instance in the loss of reproductive fitness after extreme temperature events (Hedhly *et al.* 2009). Interannual or short-term climatic variability and less frequent, but larger jumps in climate could increase the chance that a species misses its 'window' in which to migrate to more suitable habitat as the long-term climate shifts. Thus, it is important to understand the relative importance of climate extremes and variability to the ability of species to migrate across landscapes during periods of long-term climate change.

Here, we extended the PPunCC model to account for differing amounts of interannual climate variability, in addition to an overall smooth trend of long-term climate change. We also modified the model to be able to account for occasional extreme events, and for non-linear climate change with less frequent, but larger steps. We then conducted a series of analyses to address the questions of whether (1) regular interannual climate variability, (2) occasional extreme events, and (3) non-linear steps would interact with an ongoing trend of climate change to affect the capacity for plant species to migrate fast enough across fragmented landscapes to track suitable climatic conditions.

METHODS

PPunCC model

The PPunCC model (for further details see: Renton *et al.* 2011, 2012, 2013) is a spatially-explicit dynamic model of plant dispersal, establishment and persistence. The model simulates population dynamics and dispersal of plants across a grid-based landscape over several centuries (Fig. 1). Time steps are annual and within each grid cell the following processes are represented at each time step: germination and establishment of new individuals, aging of existing individuals, production of new seeds, dispersal of seeds, and mortality of individuals. Cells can be defined as unsuitable, in which case no establishment can occur. Within each suitable cell, the model tracks the number of individuals, their ages, the number of seeds present and a climatic variable, which here (see later) represents effective rainfall and affects plant establishment in the original version (Renton *et al.* 2012) or various other points of vulnerability within the plant's life cycle in an updated version (Renton *et al.* 2013). A number of parameters define characteristics of the landscape, the climate and plant species being simulated (Table 1). Unless otherwise noted, parameter values for this study were the same as those in the most recent study (Renton *et al.* 2013). The model (Appendix 1, see supplementary material at Journals.cambridge.org/ENC) is implemented in the R programming language (R Core Team 2013).

PPunCC is in part motivated by study of the South Western Australia Floristic Region (SWAFR), which we chose because it has a distinct climate gradient from the Mediterranean coast to the arid inland environment (Searle & Semeniuk 1985); contains landscapes of varying degrees of fragmentation, from

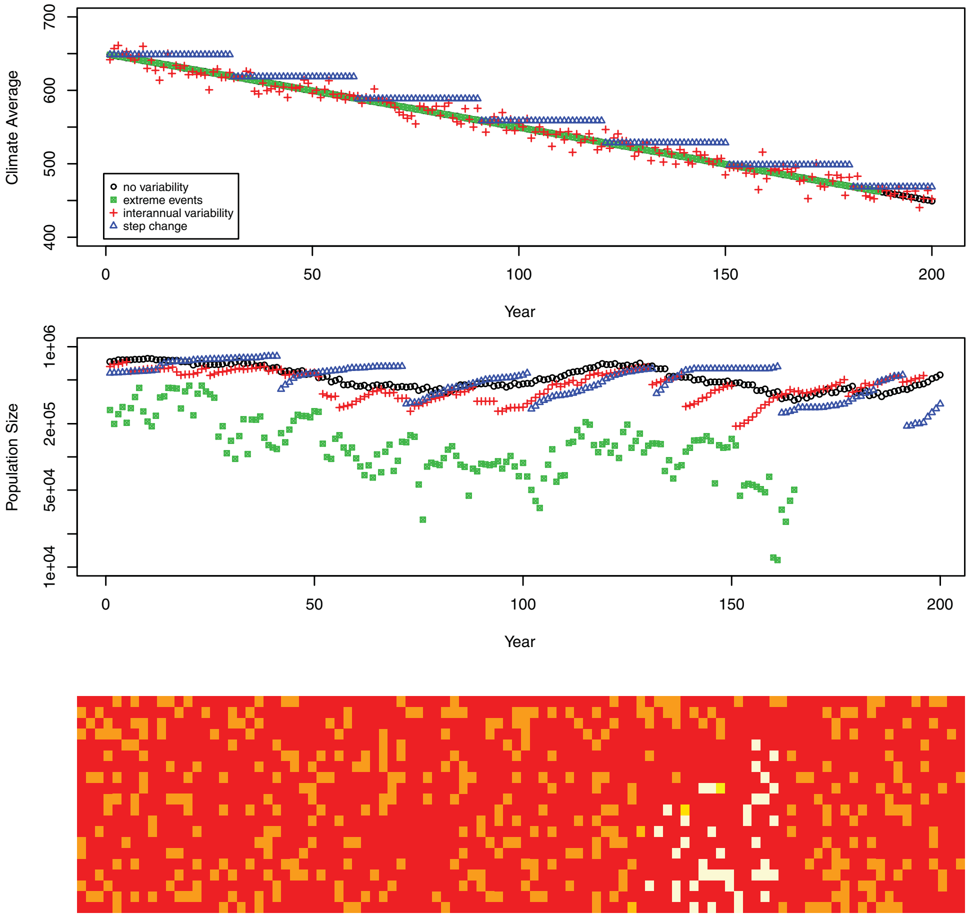

Figure 1 Example outputs from simulations of the annual functional type in the moderately fragmented landscape '80' with different assumptions regarding climate variability, including constant annual change with no variability (as per original model); interannual variability ($\mathrm{clim}_{\mathrm{var}} = 10$), extreme events with combined effects ($p_{\mathrm{ee}} = 0.5$, $p_{\mathrm{eemort}} = 0.4$, $p_{\mathrm{eeseed}} = 0.8$, $p_{\mathrm{eeestab}} = 0.8$), and step changes in climate ($N = 30$). The top subplot shows the average value of climate variable (annual rainfall) across the whole landscape in each year and the middle subplot shows the total population size in each year under each of the climate scenarios. The bottom subplot shows an example output representing the population density across the landscape in one particular year (100 years after climate change begins) from the simulation with step change; the darkest cells represent unsuitable habitat, the lightest cells represent densely populated suitable habitat and the medium cells represent suitable habitat that is not populated due to currently unsuitable climate. As the simulation proceeds, the region of suitable climate is assumed to move from the right to the left of the landscape, and the species must similarly migrate from right to left through seed dispersal over unsuitable habitat if it is to avoid extinction.

intact reserves to areas with as little as 3% remaining native vegetation (Hobbs & Saunders 1993); is a biodiversity hotspot (Hopper & Gioia 2004) characterized by species with generally low dispersal and restricted range (Hopper 2009); is the home of the Gondwana Link restoration project aimed at recreating wide-scale corridors and habitat linkages across different climatic zones (SERI [Society for Ecological Restoration International] 2013); and is undergoing noticeable climate change. From 1975 to 2004, there has been a 14% reduction in mean annual rainfall. Climate models all suggest that this trend will continue over the next half-century, with 2070 rainfall predicted to be 60% lower than mean annual rainfall from 1960–1990 (CSIRO [Commonwealth Scientific and Industrial Research Organization] 2007; Bates *et al.* 2008). The SWAFR case study region underlies this and previous studies in aspects of climate, landscape design and the mapping of habitat suitability within that landscape.

Analysis of SWAFR climate variability

We first considered historical climate records to determine to what extent there was evidence of different types of climatic variability in the SWAFR, in addition to more continuous long-term trends of change. Since rainfall is the main climate factor likely to affect plant persistence in the SWAFR, we analysed rainfall records from two sites representative of the SWAFR and of the Gondwana Link region in particular: Broomehill (33° 50′ 24″ S, 117° 38′ 24″ E), a dry site 248 km inland from the southern Western Australian coast, and Wilgarrup (34° 08′ 59″ S, 116° 10′ 48″ E), a wetter site 108 km from the coast. For each of the sites, we calculated statistics on the recorded annual rainfall, and also on the recorded winter, spring, summer and autumn rainfall. For each of these, we calculated the mean rainfall for the 30 years from 1979 to 2008

Table 1 Parameters of the PPunCC model with description and value(s) used in this study. *Climate variability parameter introduced in the new version of PPunCC created for this study. #The values used for the three functional types (annual, perennial and tree, respectively) used in this study.

Parameters	*Symbol*	*Definition*	*Values*
Landscape and climate parameters	p_f	Proportion of landscape that is unsuitable habitat	0.8 or 0.95
	r_{cc}	Rate of climatic change	1 mm yr^{-1} yr^{-1}
	$clim_{var}$*	Determines the amount of interannual variability in climate	various (see text), 0 by default
	p_{ee}*	Probability of an extreme event	various (see text), 0 by default
	p_{eemort}*	Proportion of adult plants dying in an extreme event	various (see text), 0 by default
	p_{eeseed}*	Reduction in seed set in an extreme event	various (see text), 0 by default
	p_{eestab}*	Reduction in seedling establishment in an extreme event	various (see text), 0 by default
	N*	Climate change step size: a change of $N \times r_{cc}$ occurs each N years	various (see text), 1 by default
Plant functional trait parameters	F	Effective fecundity: $F = N_s \times p_s$ (where N_s is the number of seeds produced by each mature plant each year and p_s is the seed establishment probability in optimal climatic conditions)	100, 1000, 10000 #
	D	Maximum plant density (ha^{-1})	100, 100, 100 #
	T	Threshold dispersal distance (km)	1.26, 1.4, 2.26 #
	p_m	Probability of adult mortality	1, 0.1, 0.04 #
	Y_m	Years to reproductive maturity	1, 4, 10 #
Plant climatic response parameters	c_{opt}	Plant optimal climate value	510 mm yr^{-1}
	c_{tol}	Plant climatic tolerance	4 mm yr^{-1}

(following the mid-1970s 'step-change' in rainfall discussed in the Introduction), the mean rainfall for the previous 50 years from 1929 to 1978, and used a Welch two sample t-test to test whether the difference between these two means was statistically significant. We fitted a linear regression to the rainfall records for the last 30 years to find the linear trend over this period, and also calculated the coefficient of variation (the standard deviation divided by the mean) for these 30-yr and 50-yr periods. Finally we fitted a binomial generalized linear model and looked at whether the chance of a dry period changed significantly over the full 80-yr period, with dry period defined to be rainfall over each period (full year, winter, spring, summer or autumn) being less than 80% of the long-term 80-yr mean.

Adaptations of previous PPunCC model

The existing version of the PPunCC model needed a number of adaptations to enable it be to be used for this study.

Representing climate variability

In the previous version of PPunCC, the climate variable, representing rainfall, was decremented by the same amount in every cell of the landscape every year, thus representing a continuous linear change in rainfall from wetter to drier. For this study, this continuous linear change was still implemented, but, in addition, a temporary extra perturbation could also be applied each year. The size of the perturbation was a random variable, drawn from a normal distribution with mean zero and standard deviation equal to the model parameter $clim_{var}$. One random variable was generated each year and applied to every cell. At the end of the time step, the perturbation was removed, the normal continuous linear change was applied, and a new perturbation generated for the next time step. This meant that if $clim_{var}$ was set to zero, for example, then there was no interannual variability, while if $clim_{var}$ was relatively large then there was a large amount of interannual variability. Whatever value of $clim_{var}$ was used, the overall change was maintained to be approximately r_{cc} per year on average. Setting $clim_{var}$ to be zero thus ensured the model behaved exactly as the previous version, and was the value used by default unless otherwise noted.

Representing extreme events

For this study, we defined an extreme event in terms of its effect on plants, rather than in terms of particular weather conditions. Thus, an extreme event was one in which the acclimatory capacities of a plant were substantially exceeded (Gutschick & BassiriRad 2003). In other words, an extreme event had a negative impact on plant populations, by increased adult mortality or reduced seed production for example, potentially resulting in local extinctions. Nonetheless, in the SWAFR, lack of rainfall (periods of drought that are longer or more intense than normal) is the meteorological factor most likely to negatively affect plants, and so there is a close connection between the occurrence of 'dry periods' defined by the climate and 'extreme events' defined in terms of the effect on plants. The representation of interannual climate variability described above was thus already a representation of extreme events; in years when variable climate is outside its normal range plant establishment will be poor and thus an 'extreme event' occurs. However, to focus on the extreme events themselves, we modified the model to specifically represent three different manifestations of an extreme event. In this modified version of PPunCC, an extreme event occurred in a given year randomly with a probability of p_{ee}. In extreme event years, either (1) massive adult mortality occurred, killing p_{eemort} of all adults at all locations, and/or (2) seed production was reduced by p_{eeseed} at all locations, and/or (3) seedling establishment was reduced by $p_{eeestab}$ at all locations. Setting p_{ee} to be zero thus ensured the model behaved exactly as the previous version, and was the value used by default unless otherwise noted.

Representing non-linear discrete jumps in climate

For this study, we also adapted the model so that, instead of the same change r_{cc} being applied each and every year, a larger change $N \times r_{cc}$ could be applied once every N years. This ensured that the overall change was maintained to be r_{cc} per year on average, but the changes actually occurred in smaller or larger 'steps', depending on the value of N used. Setting N to be one thus ensured the model behaved exactly as the previous version, and was the value used by default unless otherwise noted.

Landscapes and plant functional types

We used four contrasting landscapes for our analysis in this study: a moderately fragmented landscape, the same moderately fragmented landscape with a corridor created by strategic restoration, a highly fragmented landscape, and a highly fragmented landscape with a corridor created by strategic restoration. These four landscapes are referred to as '80', '80r', '95' and '95r', where the percentage refers to the proportion of the area of the landscape that was unsuitable for the plant species. For consistency these were the same landscapes used in previous studies (Renton *et al.* 2012, 2013), where '80' and '90' were generated by randomly choosing cells to have unsuitable habitat until the target fragmentation level was met, and then '80r' and '95r' were generated by converting from unsuitable to suitable the minimal number of cells needed to generate a corridor with no gaps across the landscape. The use of four different landscapes allowed consideration of the effects of different levels of landscape fragmentation and restoration, and their interaction with climate variability on plant species persistence.

We used three particular plant functional types for our analysis, chosen to represent three contrasting life cycles: a long-lived tree, a short-lived annual and an intermediate-lived perennial, defined by particular parameter value combinations (Table 1). For each type, we first specified all parameters except dispersal distance, and then calibrated the dispersal distance parameter to ensure that the plant functional type had an approximately 97% chance of persisting in the unrestored 80% fragmented landscape under the continuously changing climate. This was because we expected the chance of persistence to drop with the introduction of climate variability, so we wanted to start with a good, but not perfect, chance of persistence as a baseline. Thus, any decrease in chance of persistence would be as clear as possible. This calibration is in contrast to previous studies with PPunCC, where we selected a baseline of approximately 50% chance of persisting because we expected our analysis to reveal both increases and decreases in persistence.

Model analyses

In order to investigate how regular climate variability, occasional extreme events with specific effects on plant populations and step-changes in climate would be likely to interact with climate change to impact species persistence, we conducted three separate model analyses. For each of the three analyses, we used a fixed overall rate of long-term climate change $r_c = 1$, and then looked at how varying another climate variable affected the probability of the plant persisting (Fig. 1). We used an adaptive algorithm to efficiently explore values of the climate variable where the chance of persistence was marginal (between zero and one) (Appendix 2, see supplementary material at Journals.cambridge.org/ENC). A binomial generalized linear model was fitted to recorded simulation results, predicting probability of survival as a function of the varied climate variable, as well as its log-transform and exponential-transform. Step-wise model simplification was used to drop terms from the fitted models until a minimum Akaike information criterion (AIC) was achieved, indicating an optimal model fit. The possible inclusion of the log- and exponential-transformed climate variable in the models allowed for increased flexibility in functional form, where this was found to significantly improve the fit to the simulation results. In the simplified fitted models, all apparent differences between landscapes and functional types were found to be significant at $p < 0.001$, indicating that sufficient simulations had been conducted.

Effects of regular interannual climate variability

In order to investigate how regular interannual climate variability is likely to affect the persistence of plant species of different functional types, we looked at the effect of varying the amount of interannual climate variation (namely, varying values of $clim_{var}$). This was repeated for all 12 combinations of the four landscapes and the three plant functional types. Additionally, to investigate whether the effect of climate variability was additional to the effects of an overall continuous trend in climate change, we chose some cases where persistence was marginal and ran 100 simulations both with and without an overall trend of climate change.

Table 2 Results of analysis of rainfall records for inland and coastal site, showing mean and coefficient of variation (CV, the ratio of the standard deviation to the mean) for annual, winter, spring, summer and autumn rainfall (mm) in two different periods: 1979–2008 (new) and 1929–1978 (old); the estimated chance of an extreme event in 1929 (old) and 2008 (new); and the estimated linear rate of change in rainfall over the 1979–2008 period. *Significant difference in rainfall amounts between the two periods; **significant difference in chance of extreme event over time; and #significance of the linear trend over the 1979–2008 period (significance at $p < 0.05$ in each case).

Parameter	*Inland site*					*Coastal site*				
	Annual	*Winter*	*Spring*	*Summer*	*Autumn*	*Annual*	*Winter*	*Spring*	*Summer*	*Autumn*
Old mean	444	193	96	41	108	954	479	202	56	214
New mean	431	180	104	53	101	748^{*}	360^{*}	173^{*}	54	158^{*}
Old CV	0.22	0.28	0.43	0.89	0.47	0.2	0.25	0.33	0.78	0.34
New CV	0.22	0.23	0.35	0.92	0.58	0.17	0.22	0.26	0.73	0.34
Old chance of dry period	0.18	0.07	0.51	0.66	0.3	0.03	0.02	0.18	0.44	0.13
New chance of dry period	0.19	0.42^{**}	0.17	0.36	0.48	0.5^{**}	0.69^{**}	0.33	0.44	0.57^{**}
Change rate	− 1.2	$-0.8^{\#}$	0.1	− 0.3	− 0.1	$-4.4^{\#}$	$-2.5^{\#}$	− 0.5	− 0.1	− 0.8

Effects of extreme events

In order to investigate how occasional extreme climate events might affect the persistence of plant species of different functional types, we looked at the effect of varying the frequency of extreme events (varying values of p_{ee}). We considered eight different types of extreme event, with each type of extreme event having a different effect in the year in which it occurred, as follows:

- adult mortality, $p_{eemort} = 0.4$
- adult mortality, $p_{eemort} = 0.8$
- seed production reduced, $p_{eeseed} = 0.4$
- seed production reduced, $p_{eeseed} = 0.8$
- seed production reduced, $p_{eeseed} = 0.99$
- reduced seedling establishment rate, $p_{eeestab} = 0.4$
- reduced seedling establishment rate, $p_{eeestab} = 0.99$
- adult mortality, $p_{eemort} = 0.4$ and seed production reduced, $p_{eeseed} = 0.8$ and reduced seedling establishment rate, $p_{eeestab} = 0.8$ (the ‘combination’ type)

These eight different types of extreme event were chosen to represent a wide range of severities and points of vulnerability within the plants’ life cycles. The procedure of varying the frequency of extreme events using the adaptive algorithm was repeated for all 96 combinations of the eight types of extreme event, the four landscapes and the three functional types. Additionally, to investigate whether the effect of extreme events was additional to the effects of overall continuous trends in climate change, we chose some cases where persistence was marginal and ran 100 simulations both with and without an overall trend of climate change.

Analysis of effects of non-linear step changes in climate

In order to investigate how non-linear changes in climate are likely to affect the persistence of plant species of different functional types, we looked at the effect of varying the climate change step sizes (varying values of N_{step}). This was repeated for all 12 combinations of the four landscapes and the three functional types.

RESULTS

Analysis of rainfall records for two sites

There were decreases in annual, winter and autumn rainfall between the more recent 30 years and the previous 50 years, which were significant for the coastal site (Table 2). There was also significant reduction in spring rainfall for the coastal site. Variation in rainfall varied from around 20% for annual and winter rainfall, up to 70% for summer rainfall at the coastal site and 90% for summer rainfall at the inland site. Chance of a dry period increased significantly over time for winter rainfall at both sites, and for annual and autumn rainfall at the coastal site. The linear rate of decrease in winter rain over the most recent 30 years was significant at both sites, and the decrease in annual rainfall at the coastal site was more than 4 mm yr^{-1} yr^{-1}.

Model outputs

The relevant output from each PPunCC model run was whether the plant species persisted until the end of the full simulation (270 years of changing climate, the time taken for suitable climate to move from one end of our landscape to the other), with more detailed outputs (Fig. 1) used for diagnostic investigation.

Species persistence in the absence of climate variability

In the absence of interannual variability, step changes or extreme events, with climate simply changing at a constant rate each year, all three functional types had a high, but not 100%, chance of persisting in the unrestored moderately-fragmented landscape (‘80’) (Figs 2–4), as expected. Restoration of this landscape ‘80r’ increased the chance of persistence for all three to effectively 100%. In the unrestored highly fragmented landscape (‘95’), none of the functional types ever persisted, with or without the addition of interannual variability, step changes or extreme events (not shown). Restoring this

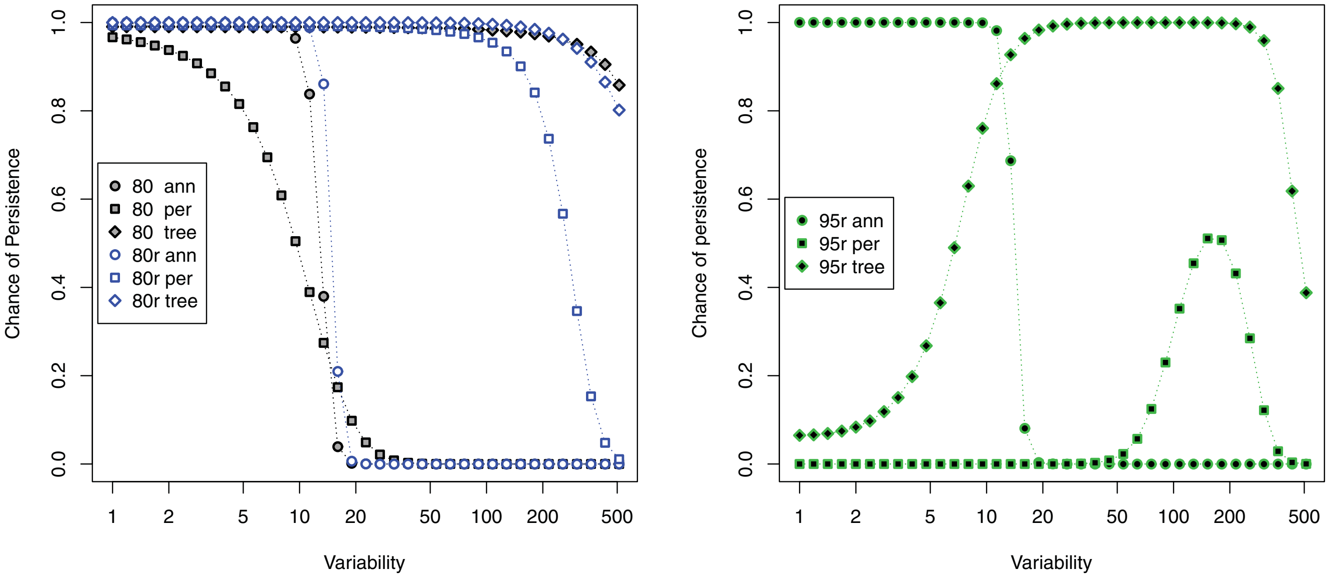

Figure 2 Chance of species persistence as affected by interannual climate variability (clim_{var}); plant functional type (annual, perennial or tree); and landscape (unrestored moderately fragmented '80', restored moderately fragmented '80r' or restored highly fragmented '95r'). Persistence for the unrestored highly fragmented landscape '95' was zero at all levels of variability (results not shown).

highly fragmented landscape ('95r') increased the chance of persistence of the annual to very high, slightly increased the chance of persistence of the tree to *c.* 6% and did not increase the chance of persistence of the perennial.

Interannual climate variability

Increasing interannual climate variability significantly affected persistence (Fig. 2). For the annual functional type, as variability (clim_{var}) increased above a threshold of around 10–20, the chance of persistence quickly dropped from 100% to 0%, for all three landscapes. For the perennial functional type, landscape made a big difference. In both the '80' and '80r' landscapes, the perennial had a high chance of persistence at very low levels of variability, which decreased to zero as variability increased. Restoration greatly increased the threshold of climate variability at which persistence became unlikely. For the tree in '80' landscape, there was a very high level of persistence even up to very high levels of variability, and restoration ('80r') made no significant difference to this result. In the restored highly-fragmented landscape ('95r'), increasing variability had a positive effect on chance of persistence of both the tree and the perennial up to a point, after which further increases had a negative effect. The levels of variability that caused negative effects were similar to those for these two functional types in the other restored landscape '80r'. The effect of variability was in addition to the effect of long-term climate change trends; at the level of variability where the chance of persistence was marginal, reducing the rate of climate change increased the chance of persistence and increasing the rate of climate change decreased the chance of persistence. For example, for the annual in landscape '95r', with $\text{clim}_{\text{var}} = 15$, the chance of persistence was 29% when the rate of climate change was the default of 1 mm yr^{-1} yr^{-1} but 75% when the rate of climate change was set to zero.

Extreme events

Increasing the frequency of extreme events significantly affected persistence in almost all cases, and whenever it did, the chance of persistence declined with increasing frequency of extreme events (Fig. 3). For the annual, the extreme events types that had the greatest effect on the chance of persistence in each of the three landscapes were 99% reduction in fecundity and the combination event, while 40% and 80% adult mortality had no significant effect on persistence in any of the landscapes. Effects of the same reduction in fecundity and establishment were very similar. For the perennial and the tree, 80% adult mortality and the combination were the extreme events types that had the greatest effect on the chance of persistence in the restored and unrestored moderately- fragmented landscapes, while the smaller reduction in fecundity and establishment had the least effect. Effects of reduction in fecundity and establishment were very similar in all landscapes for all plant functional types. Restoration lessened the effect of all extreme event types at all probabilities of occurrence. Comparison of simulations with and without an overall trend of climate change showed that the effect of extreme events was in addition to the effect of overall climate change. For example, for the annual in landscape '95r', when the 'combination' extreme event occurred with frequency of 0.5, the chance of persistence was 39% when the rate of climate change was the default of 1 mm yr^{-1} yr^{-1}, but 100% when climate change rate was set to zero.

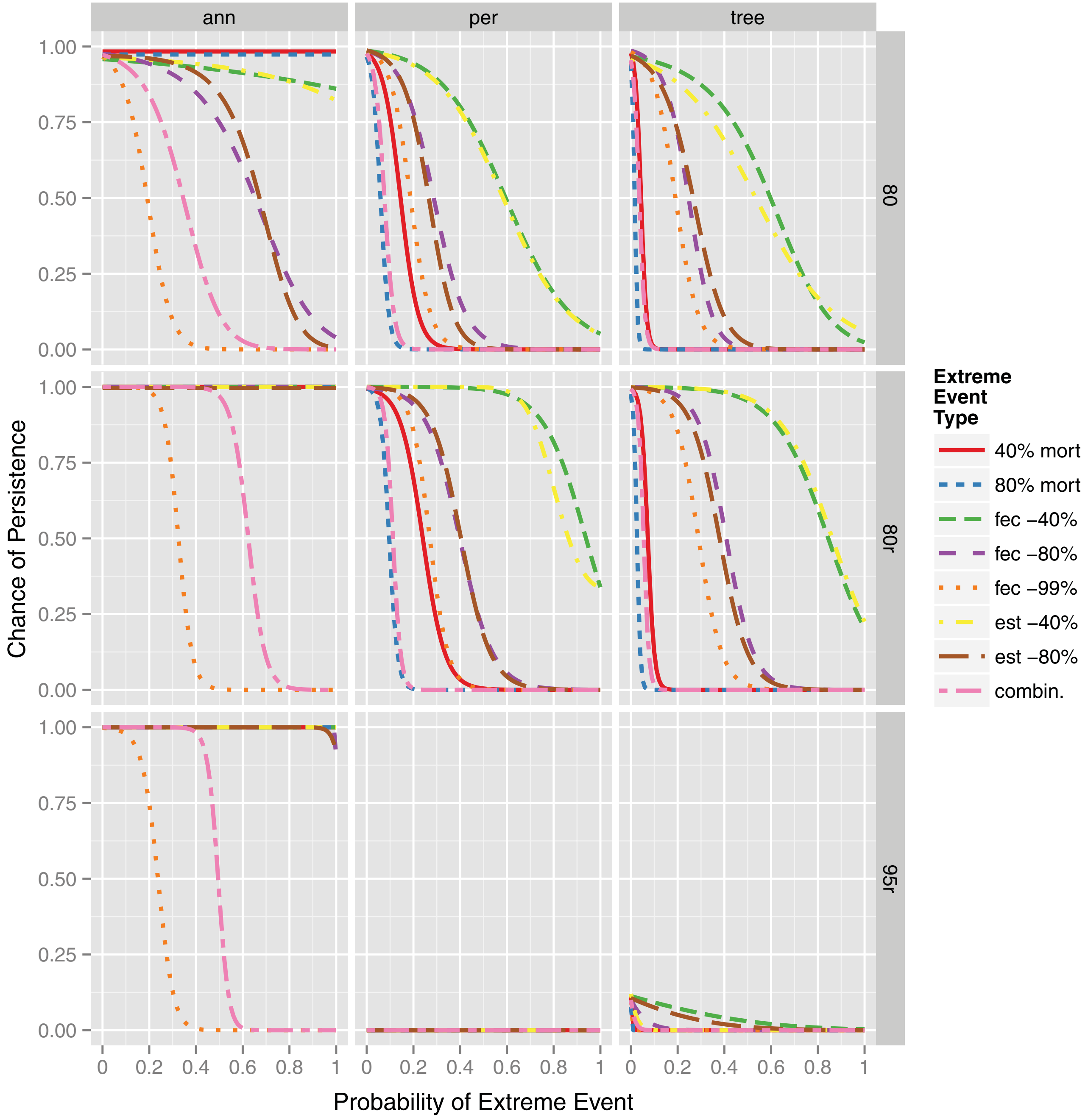

Figure 3 Chance of species persistence as affected by the probability of occurrence of an extreme event; the extreme event type (40% or 80% adult mortality, fecundity i.e. seed production reduced by 40%, 80% or 99%, seedling establishment reduced by 40% or 80%, or a combination of 40% adult mortality with 80% reduction in both fecundity and establishment); plant functional type (annual [ann], perennial [per] or tree); and landscape (unrestored moderately fragmented '80', restored moderately fragmented '80r' or restored highly fragmented '95r'). Persistence for the unrestored highly fragmented landscape '95' was zero at all levels of variability (results not shown).

Non-linear step changes in climate

Increasing the step size of climate change significantly decreased plant persistence in all cases, except when persistence was already zero at the smallest step size (Fig. 4). In the unrestored '80' landscape, the negative effect was greatest on the perennial, occurring more gradually for the annual and only at larger step changes for the tree. When the '80' landscape was restored ('80r'), the effect of changes in step size was generally reduced, that is, there was a greater chance of persistence at similar step change sizes. In the restored, highly-fragmented landscape '95r', the negative effects of step change were evident at similar, but slightly smaller step changes as for '80r'.

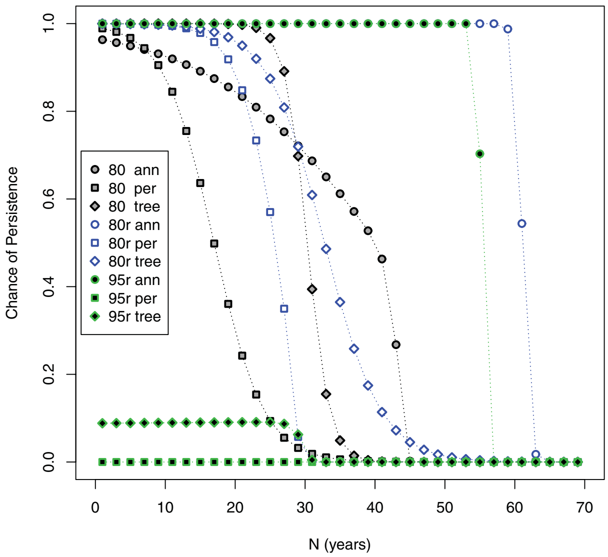

Figure 4 Chance of species persistence as affected by the size of the time steps (in years) at which non-linear climate change occurs (N); plant functional type (annual, perennial or tree); and landscape (unrestored moderately fragmented '80', restored moderately fragmented '80r' or restored highly fragmented '95r'). Persistence for the unrestored highly fragmented landscape '95' was zero at all levels of variability (results not shown).

DISCUSSION

These simulations show that interannual climate variability and discontinuity in climate change could both likely impact plant species' chance of persistence in fragmented landscapes. According to the simulations, the effects also depend on the functional traits of the plant, the extent of the variability and the extent of landscape fragmentation.

This analysis of rainfall records provides evidence of both longer-term climate change and shorter-term variability in the SWAFR region, thus motivating the use of modelling to consider the possible implications of such climatic change and variability. The decreases in spring, autumn and winter rainfall are particularly important; historically this has been the period of reliable rainfall and low evaporation, and so plant species are adapted to rely on rainfall at these periods for establishment, growth and seed production. The increased probability of drier winters over the more recent 30 years is similarly important, as it likely corresponds to 'extreme events' as we have defined them in terms of reducing the size of plant populations.

The three functional types were calibrated to have a similarly high but imperfect chance of persistence in the unrestored moderately-fragmented landscape when there was no climate variability, but this success was a result of varying traits. The annual is short-lived, very quickly reaches reproductive maturity, produces relatively few seeds per individual and its seeds have relatively poor dispersal. The tree is long-lived, slow to reach reproductive maturity, produces many seeds per individual and seeds have relatively good dispersal. The perennial is intermediate for all these traits, although closer to the annual than the tree is terms of dispersal ability. The similar success of these three types in landscape '80' is thus a result of trade-offs between fecundity, dispersal ability and longevity on the one hand (better for the tree, worse for the annual) and time to reach reproductive maturity on the other (better for the annual, worse for the tree). That different strategies achieved similar success in one particular context explains why there were different levels of success in other contexts such as different landscapes and varying levels of different types of interannual variability, step sizes and extreme events.

Restoration generally improved the chance of persistence while greater fragmentation decreased it, as found in other studies of plant migration (see Honnay *et al.* 2002; Higgins *et al.* 2003; Donald & Evans 2006). This result extends our previous studies (Renton *et al.* 2012, 2013) to show that they hold for a wider range of climate change scenarios. Greater landscape fragmentation decreased the chance of species persistence to zero in all cases in the '95' landscape; this shows that increased fragmentation is a major threat, at least for species with marginal chances of persistence at current levels of fragmentation and climate (Ewers & Didham 2007). Restoration greatly improved persistence in some cases, though its level of impact varied dependent on plant functional traits. The annual was similarly successful in both restored landscapes, '80r' and '95r', because its short generation time enabled dispersal over small steps each year, allowing it to follow the restoration corridors in all directions through the landscape. Thus, the annual greatly benefited from restoration in the highly-fragmented landscape. Conversely, the perennial and the tree relied on bigger, but less frequent dispersal steps across the unrestored moderately-fragmented landscape. Restoration in the highly-fragmented landscape was located to minimize the distance between suitable habitats; this created corridors that meandered in many directions, including north-south oriented stretches that potentially created an inefficient path through the east-west shifting climate. The relatively poor persistence of the perennial and tree in the restored highly-fragmented landscape seems to be a result of them not being able to follow the twists and bends in the restoration corridor as quickly as the annual. More strategic restoration along the path of predicted climate change may have more impact on the persistence of perennials and trees in fragmented landscapes.

Interannual climate variability had varying impacts on plant species persistence. A recent study of multi-year demographic data found that long-lived species were significantly less sensitive to climatic variability than short-lived species (Morris *et al.* 2008), and we found similar results among our plant species. The relatively small impact of variability on trees in our study is likely due to the fact that the tree functional type was fecund and long-lived compared to the other types. Therefore occasional 'bad' years with low rainfall, causing a reduction in establishment, did not have a big negative effect on population sizes, since most individuals were adults that were assumed unaffected. The most important effect would have been at the colonization front where most individuals were establishing seedlings, but since there was a persistent population of adults providing propagules to this front, the effect of one or two years of low establishment was negligible. Correspondingly, the relatively extreme impact on the annuals was due to their reliance on establishment every year; one or two 'bad' years with poor or no establishment was enough to cause local extinction.

The positive effect of certain levels of interannual climate variability on the tree and the perennial in the restored highly-fragmented landscape was because the occasional 'good' years at higher levels of variability were frequent enough to offset the 'bad' and 'average' years, even when 'average' was not good enough for persistence. In other words, the good years provided 'temporal refugia' that allowed enough plants to successfully establish even when establishment in most years was poor. At higher levels of interannual variability, the distributions of the perennial and particularly the tree became more variable from year to year, but more widely spread across the climate gradient; this is because for many locations the climate was suitable for recruitment in some years at least. Persistence thus became less about successful migration across the gradient and more about occasional successful recruitment. At very high levels of variability, conditions became so unstable that rainfall within the range for good recruitment was less likely to occur within the plant's life span, even for the trees, and so persistence declined.

Extreme events causing adult mortality had large effects on the perennial and particularly the tree. For these functional types, adult mortality decreases the number of reproductive individuals over the long term, and thus negatively impacts seed production. Except for very large reduction in fecundity (–99%) and the combination of three different effects, no extreme event type had an effect on the persistence of the annual in either of the restored landscapes; this indicates that even when the 'extreme event' happened every year the annual was able to persist, even at these reduced levels of adult survival, fecundity or establishment. We only considered extreme events with negative effects, but it possible that infrequent extreme 'positive' events could play a role in promoting the persistence of populations under climate change, as highlighted by the positive effects of climate variability discussed above.

Non-linear step changes in climate generally had a negative effect on the chance of plant species persistence when the step size reached a certain threshold, and again the location of the threshold depended on the functional type and landscape. The annual was only affected by relatively large step changes. This was a result of its ability to quickly establish dense new colonies in newly suitable areas following big step changes, despite quick extinction in the formerly suitable range. For perennials and trees the extinction in the former range was much slower, but the establishment of populations in new habitat takes much longer due to the longer generation time. These functional types are thus less able to colonize fast enough to persist through several consecutive large step changes. In these scenarios, restoration provided an important increase in the persistence of the perennial and particularly the annual, allowing them to quickly migrate across the landscape despite their short dispersal capabilities.

Like any simulation study, this work involved choices about what factors to consider in more detail and what to leave out to make the study feasible. A few important considerations that might increase plant persistence were not considered here. The current version of PPunCC assumes no persistent (> 1 yr) seed bank. The ability to store seeds in the soil is particularly influential in the face of climate variation. There is strong evidence that soil-stored seeds wait for favourable climatic 'cues' before germination (Thompson & Fenner 2000), allowing them to take advantage of 'good' years and persist dormant in the soil through 'bad' years. Thus, the rate of increase of a population that is capable of seed bank storage is more controlled by favourable than unfavourable conditions (Henle *et al.* 2004). Additionally, PPunCC does not account for phenotypic adaptation or genetic evolution. The three strategies for persistence, migration, adaptation and evolution, are likely to occur in combination (Davis & Shaw 2001), which could increase a species' ability to survive changing climatic conditions. Further extensions to this model or similar models could consider the effects of all three strategies, both individually and in concert. The model does not consider interactions among species. Facilitation and mutualisms among species could be a powerful contributor to persistence through climate change (Suttle *et al.* 2007). Other species interactions with likely negative effects, such as competition and loss of mutualisms, should also be considered in future investigation into the effects of climate change (Brooker *et al.* 2007). It would also be useful to consider the effect of different spatial configurations of restored areas in future.

We studied three specific plant functional types that we acknowledge do not represent all annuals, perennials and trees. Nonetheless, their different responses to the climate and landscape characteristics studied here provide insights that can be cautiously generalized to other plant types. For example, longer generation time is likely to be a disadvantage in migration to keep pace with changing climate and so it seems unlikely that plants with longer generation times will be advantaged by targeted restoration to increase connectivity. Low fecundity and poor dispersal are disadvantages more likely to offset by such targeted restoration. Similarly, annuals with short generation times are likely to be less affected by step changes in climate than plants that take a longer time to reach reproductive maturity. However, work testing a wider range of the interactions between functional traits and climate variability factors, landscape characteristics, and restoration strategies is needed to further increase our understanding of plant persistence under climate change. We have deliberately taken a relatively abstract and theoretical approach in this study to enable us to reach conclusions that can be easily generalized to a wide range of species and scenarios; however similar studies could be conducted for specific cases of interest if required, as discussed in some detail in Renton *et al.* (2012). However, many of the results here could probably be extended to apply to animals as well as plants, at least for those animals that disperse passively and only occasionally within their life cycle, and are relatively stationary at other times.

CONCLUSION

These results have important implications for understanding how climate change is likely to interact with different types of climate variability to impact plant species persistence in fragmented landscapes. Predictive modelling of the effects of climate change on plant distributions and persistence needs to account for short-term climate variability as well as long-term change, particularly when predictions form the basis for planning adaptation activities such as strategic restoration and the creation of conservation reserves. The results confirm that avoiding further landscape fragmentation, restoring landscapes to increase connectivity and action to reduce the speed of climate change are all important factors that, if addressed, could potentially increase the chance of species persistence (Renton *et al.* 2012, 2013). Furthermore, the present results highlight that the negative impacts of these factors are likely to be exacerbated by interannual climate variability, non-linear step changes in climate and extreme events. Indeed, even in the absence of long-term trends of climate change, increased extreme event frequency will likely negatively impact plant persistence, especially for trees and perennials. The results also show that climate variability could possibly provide 'temporal refugia' improving persistence in some cases for longer-lived species. Moreover, restoration seems likely to ameliorate the negative effects of extreme events, interannual variability and step-changes in climate, in addition to those of continuous long-term climate change. The results also show that plant functional traits of different species are likely to interact with all these factors in complex ways, and so predictions and planning need to be tailored for the species of concern. These issues are particularly important in places like the SWAFR, where both plant diversity and landscape fragmentation are very high, and climate change, variability and increasingly frequent extreme events are an observed reality.

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