Brevia

Averaged 30 year climate change projections mask opportunities for species establishment

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Survival of early life stages is key for population expansion into new locations and for persistence of current populations (Grubb 1977, Harper 1977). Relative to adults, these early life stages are very sensitive to climate fluctuations (Ropert-Coudert et al. 2015), which often drive episodic or 'event-limited' regeneration (e.g. pulses) in long-lived plant species (Jackson et al. 2009). Thus, it is difficult to mechanistically associate 30-yr climate norms to dynamic processes involved in species range shifts (e.g. seedling survival). What are the consequences of temporal aggregation for estimating areas of potential establishment? We modeled seedling survival for three widespread tree species in California, USA (*Quercus douglasii, Q. kelloggii, Pinus sabiniana*) by coupling a large-scale, multi-year common garden experiment to high-resolution downscaled grids of climatic water deficit and air temperature (Flint and Flint 2012, Supplementary material Appendix 1). We projected seedling survival for nine climate change projections in two mountain landscapes spanning wide elevation and moisture gradients. We compared areas with windows of opportunity for seedling survival – defined as three consecutive years of seedling survival in our species, a period selected based on studies of tree niche ontogeny (Supplementary material Appendix 1) – to areas of 30-yr averaged estimates of seedling survival. We found that temporal aggregation greatly underestimated the potential for species establishment (e.g. seedling survival) under climate change scenarios.

Windows of opportunity for seedling survival were predicted in many areas where 30-yr averaged climate change predictions estimated losses or null suitability for seedling survival (Fig. 1). These areas of overlooked potential establishment represented, on median, 357% of the area predicted by the 30-yr averaged estimates (median across species, sites, climate projections, time projections and survival thresholds). Interestingly, the majority of masked windows of opportunity were concentrated in areas that were predicted as unsuitable for seedling survival based on 30-yr averaged projections (355%; null establishment in Fig. 1). Masked opportunities for establishment varied considerably across species, climate scenarios and study sites, but they were present in most cases (Fig. 1). Our results were robust to differences in the length of the survival period considered for seedling establishment (1-yr versus 3-yr) and the frequency of windows of opportunity during 21st century climate change (1 versus 3; Supplementary material Appendix 2).

Our results imply that areas that are climatically suitable for early-stage survival may be more extensive than previously estimated using averaged climate scenarios. Indeed, limited time periods of cooler and wetter conditions may enhance species persistence and migration during global warming (Hannah et al. 2014), and such limited-time conditions have been shown to influence modeled species distributions shifts (Bennie et al. 2013).

Matching the temporal resolution of the data used in models to the ecological processes involved in species distribution shifts is key to understanding how individuals and populations may persist or migrate. Our results support the importance of considering the role of pulsed colonization and extinction events in impact analysis of species vulnerability to climate change (IUCN 2010). Additionally, better framing of the temporal resolution in our datasets to match the ecological process under examination may boost our
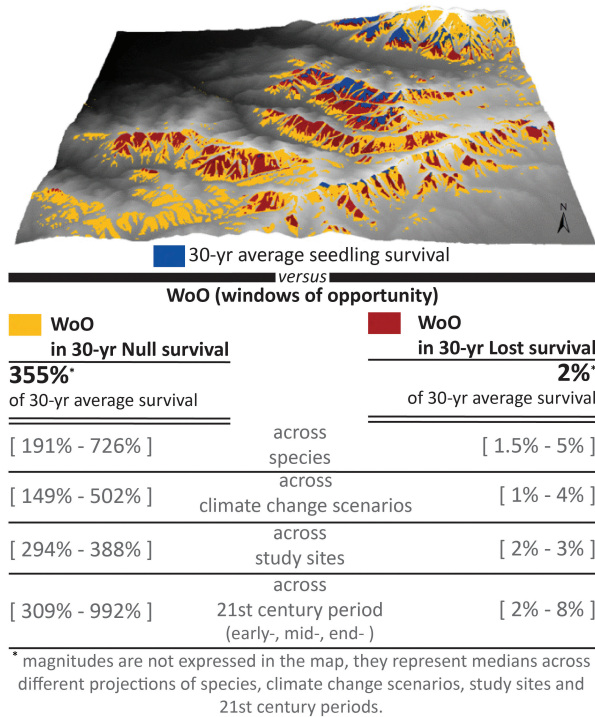
	30-yr average seedling survival	
	versus	
	WoO (windows of opportunity)	

WoO **in 30-yr Null survival**		**WoO** **in 30-yr Lost survival**
355%[*] of 30-yr average survival		**2%**[*] of 30-yr average survival
[191% - 726%]	across species	[1.5% - 5%]
[149% - 502%]	across climate change scenarios	[1% - 4%]
[294% - 388%]	across study sites	[2% - 3%]
[309% - 992%]	across 21st century period (early-, mid-, end-)	[2% - 8%]

[*] magnitudes are not expressed in the map, they represent medians across different projections of species, climate change scenarios, study sites and 21st century periods.

Figure 1. Mismatch in potential seedling establishment areas when comparing areas of 30-yr averaged projections of seedling survival to areas of windows of opportunity for establishment (3 consecutive year of climate suitable for seedling survival). Map shows *Quercus kelloggii* dynamics for the period 1980–2040 (e.g. early-century MIROC RCP 4.5 projection) in the Tejon Ranch study area. Values given in bold below the map are the median percentages of 3-yr windows of opportunity for establishment relative to the 30-yr seedling survival average areas among species (3), climate scenarios (9), study sites (2) and 30-yr periods of 21st century projections (3) considered.

predictive ability. For instance, in studies using correlative species distributions models, extreme climate variables have been shown to increase model accuracy (Zimmermann et al. 2009), and matching weather – not climate – conditions to species occurrence can provide a better picture of habitat suitability and competitive interactions (Bateman et al. 2012).

Windows of opportunity for establishment are tightly linked to climate variability, which may have positive or negative consequences at the population and species range level (Higgins et al. 2000, Saltré et al. 2015). Nevertheless, there is considerable uncertainty in climate change projections of short-term climatic variability (Deser et al. 2012), calling for greater attention to deviation from the historic range of variability when selecting climate change scenarios for ecological forecasting. Our results show that large areas favoring potential establishment could be ignored by temporal aggregation of data for the lifestage of trees with the narrowest survival span (e.g. seedlings, Young et al. 2005). Further work, however, is needed to account for the roles of seed source, dispersal capacities, biotic interactions and disturbance dynamics affecting microsite conditions (Conlisk et al. 2012, Serra-Diaz et al. 2015).

Ultimately, predicting the ability of species to colonize and persist in rapidly changing environments will require a comprehensive understanding of ontogenic niche shifts – changes in species requirements across life stages – together with modeling efforts that can accommodate spatially and temporally varying scales when integrating ecological processes.

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Supplementary material (Appendix ECOG-02074 at <www.ecography.org/appendix/ecog-02074>). Appendix 1–2.