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Using historic and contemporary data to inform conservation responses to climate change

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USING HISTORIC AND CONTEMPORARY DATA TO INFORM CONSERVATION RESPONSES TO CLIMATE CHANGE

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by

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Table of Contents

List of Figures

Chapter 1

Chapter 2

Chapter 3

List of Tables

Chapter 1

Chapter 2

Chapter 3

Abstract

Using historic and contemporary data to inform conservation responses to climate change

Sarah Skikne

In the face of inevitable and increasing impacts of climate change, the conservation field must adapt its practices. To address this need, my dissertation utilizes untapped historic and contemporary data as empirical evidence to understand climate impacts and potential conservation responses. In my first chapter, I examine the demographic processes underlying range shifts in a California desert ecosystem, using re-photography and unique data extraction methods to track the fate of individual plants over ~35 years. I document uphill range shifts and demonstrate that varying recruitment and survival underlie these patterns in co-occurring species. In my second chapter, I synthesize data from historic avian translocations to uncover lessons relevant to proposals for longer-distance translocations and assisted colonization as potential adaptation tools. I find that post-translocation survival is higher for species with larger body sizes and brain residuals, and for translocations over shorter distances; these results suggest the types of species and sites that might be most feasible for translocation efforts in response to climate change. Finally, in my third chapter, I assess adaptation project proposals from U.S. conservation non-profits in order to determine gaps and strengths in this emerging field. I find that

proposed projects are focused on fish, river ecosystems, and the Atlantic and Pacific coasts, highlighting the need for expansion of the current taxonomic, ecosystem and geographic foci of emerging climate adaptation efforts. Together, these chapters demonstrate the use of historic and contemporary data as fruitful paths for informing our response to climate change in order to promote species persistence and ecosystem integrity.

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Chapter 1:

Uphill shifts and underlying demographic processes in long-lived arid plants

INTRODUCTION

Globally, meta-analyses show that species' ranges have on average shifted poleward and upwards (Parmesan and Yohe 2003, Root et al. 2003), with larger shifts in sites with more warming (Chen et al., 2011a), consistent with expected responses to climate change. Despite these large-scale patterns, individual species show idiosyncratic responses in the directions and rates of range shifts (Chen et al., 2011a; Moritz et al., 2008). Diverse processes potentially underlie this variation (Angert et al. 2011, Chen et al. 2011a, Gibson-Reinemer and Rahel 2015) but are complex and poorly understood.

Species ranges delineate locations where population growth is stable or positive over the long term, i.e. where births and immigration compensate for deaths and emigration (Lawton 1993). Accordingly, a shifting species range is driven by changes in these parameters within parts of the range, due to niche evolution and/or changing environmental conditions (Sexton et al. 2009). For plants, the components of fitness that together contribute to positive population growth – fecundity, recruitment, growth and survival – can each be differently sensitive to one of many climate dimensions (e.g. Doak and Morris, 2010; Ettinger and HilleRisLambers, 2013; McLaughlin and Zavaleta, 2012) as well as species interactions (Hellmann et al. 2012). Identifying the processes underlying an observed plant range shift is important for improving predictions, identifying vulnerable species, and choosing appropriate management responses.

However, for long-lived plants, it is often difficult to directly measure two of these component processes – recruitment and mortality – at the timescale of most research (Cody 2000). As a result, climate-induced range shifts are often inferred without measuring recruitment and mortality, requiring additional assumptions and caveats, and preventing exploration of underlying processes. For example, changes in plant cover over time (e.g. Gottfried et al., 2012; Kelly and Goulden, 2008) may reflect changes in abundance or individual growth, the latter of which may or may not lead to longer-term changes in the former. Inferring range shifts by comparing adult and juvenile distributions requires assuming that juvenile distributions do not include recruitment sinks (Zhu et al. 2012). Studies of changes in presences and absences can obscure instances where long-term persistence is unlikely, such as non-reproductive adult populations (e.g. McLaughlin and Zavaleta, 2012) or demographic compensation, i.e. where vital rates change in opposite directions and thereby compensate for each other (e.g. Doak and Morris, 2010)

Adding to the complexity of range shift dynamics, the processes underlying emergent shifts will be detectable at different time scales depending on species' life histories. Rather than an idealized uphill "march", where leading-edge colonization is matched with trailing edge extinction, range shifts may be initially detected as changing optima within the range, referred to as a “lean” (Breshears et al. 2008). For long-lived plants in particular, leans are expected in the near-term due to lags in migration and population growth at the leading-edge, and long-surviving and/or clonal (but no longer reproductive) individuals at the trailing-edge (Davis 1989, Svenning and Sandel 2013). In the face of ongoing, directional change, leans in long-lived plants likely represent either early stages of a full shifting process, or alternatively, an extinction debt, whereby remnant populations are destined for future extinction (Dullinger et al. 2012). Eventually, such debts are likely to be “paid off” in abrupt, widespread dieback (Lenoir and Svenning 2015).

Desert systems are ideal for detecting and studying these processes in climate-induced range shifts, given the relatively strong role of abiotic factors in controlling species distributions (Belnap et al. 2016). Aridity controls vegetation distributions in California deserts (Belnap et al. 2016) and is projected to increase (Seager et al. 2007, Seager and Vecchi 2010, Cook et al. 2015). Diebacks of very long-lived species have been attributed to episodic drought (Miriti et al. 2007) and large impacts can result from even small changes in precipitation regimes (Brown et al. 1997). Warming minimum temperatures will also decrease freezing (Archer et al. 2008), potentially releasing species from this limiting factor at high elevation sites. In general, desert systems may be more sensitive to climate change than generally appreciated (Foden et al. 2007), so understanding these impacts will be increasingly important into the future.

To explore the mechanisms underlying range shifts in an arid system, here we take advantage of a unique historic dataset from the Deep Canyon Transect, which spans a 2300m elevation gradient in southern California. The transect's steep climatic gradient compresses nearly every terrestrial inland southern California habitat into a short linear distance (Mayhew 1983). Climate has changed rapidly in the area over the last half century, including significant increases in the mean and minimum air temperature, mean precipitation, and interannual precipitation variability. These changes equate to a 56m upwards shift in mean temperature (Kelly and Goulden 2008). The combination of steep elevational gradient and rapid climate change make this an ideal place to expect recent range shifts.

Indeed, resurveys along the Deep Canyon Transect have demonstrated recent and rapid upward shifts in the average elevation of birds (Hargrove et al. 2009) and plants (Kelly and Goulden 2008). This latter study, based on vegetation transects resurveys, showed an average 65m increase in the mean elevations of ten dominant plant species between 1977 and 2006-2007 (Kelly and Goulden 2008). These leans are the net result of changes in spatial patterns of establishment, growth, decline, and mortality (Breshears et al. 2008).

Here we elucidate these varying underlying processes, using unique methods to extract data on the fate of individual plants from paired historic-modern rephotographs. Rephotography has been used before in arid systems (e.g. Bowers et al., 1995; Bullock and Turner, 2010; Hoffman et al., 2010), allowing precise tracking of individual plants over their lifetimes (Bowers et al. 1995) and quantification of demographic rates. Quantification of demographic rates through traditional resurveys (of transects of quadrats) requires that the original collector permanently marked or geolocated each plant. In contrast, rephotography allows historical photographs to be used opportunistically, since demographic rates can be extracted without the foresight of the original photographer. Moreover, a single photographic view can be used to capture data on hundreds of individuals in much larger and steeper areas than would be practical to survey repeatedly using traditional field methods.

Rephotography also presents distinct challenges, including uncertainty about the location and angle of historical photographs, identifying species from a distance, and difficulties quantifying observed patterns due to photo angle geometry (Vellend et al. 2013). Here, we overcame these challenges in a variety of ways. We used permanently marked and therefore readily re-locatable photo sites at the Deep Canyon Transect. In this landscape, it is possible to recreate the precise angle and view of historic photos due to the preponderance of geologic features and sparse vegetation. Almost all of the plant species in the area are conspicuous and identifiable from photographs. Finally, we developed unique methods to quantify physical aspects of the landscape captured in each ground-level photo. We used this rephotography approach to ask (1) which species at Boyd Deep Canyon show uphill shifts in mean elevation consistent with recent climate change, (2) how species' varying recruitment, individual growth and survival contribute to these outcomes, and (3) whether these processes can be predicted by species' life history traits.

METHODS

Site description

The Deep Canyon Transect spans ~2300m in altitude over ~16km in central Riverside County, California, on the slopes of the Santa Rosa Mountains. We studied the lower portion of the Deep Canyon Transect, from ~200m in elevation (116° 21' 54.6" W, 33° 40' 36.9" N) to ~1200m in elevation (116° 26' 6.0" W, 33° 37' 10.5" N, Table S1) over ~9km. Moving upslope, minimum, maximum and mean temperature decrease, while annual precipitation, proportion of precipitation falling as snow, and the incidence of frost increase (Kelly and Goulden 2008). This portion of the Deep Canyon Transect is part of the Colorado desert, and encompasses four habitats defined by Zabriskie (1979) as one moves upslope: alluvial plain, rocky slopes, and the lower and upper plateaus.

Historical and modern photos

We utilized photos originally taken by Dr. Wilbur Mayhew between 1977 and 1982, which we digitized from 35 mm slides stored at Philip L. Boyd Deep Canyon Desert Research Center. We selected 17 photo views out of ~300 available based on several criteria: (1) photos span the elevation gradient, (2) view encompasses a relatively large and undisturbed area, and (3) plants are close enough to the camera to be identifiable to species. In addition, to minimize obstructed views, we often selected views which were either relatively high compared to the landscape, or facing a slope, and we did not choose any views above ~1200m elevation (Table S1), at which point vegetation becomes too dense.

We re-located and photographed permanently marked sites, using a Canon 5D Mark II camera and tripod, in 2015 and 2016 (Table S1). We also took one additional set of photos in April 2017 after the end of a multi-year drought, so we could distinguish dormant form dead individuals of two drought-deciduous species (brittlebush *Encelia farinosa* and white bursage *Ambrosia dumosa*). We sought to approximate the original view as closely as possible in the field, and then later aligned photos digitally.

For each photo view, we chose a single historical and modern photo for analysis based on resolution, contrast and coloration. The mean timespan between paired historic and modern photos was 36 years (Table S1). We perfected the alignment between the paired historical and modern photos in Photoshop by making one photo to semi-transparent, then rotating and re-sizing it while maintaining original aspect ratios.

Data extraction

We extracted data on 13 perennial species (Table 1). We focused on perennials because they integrate climate impacts over a longer period and are visible year-round. We extracted data from the photos in ArcGIS, arranging the paired photos as map layers. We created polygons to delimit a survey area close enough to the camera to identify species; these polygons serve as the “sites” in our subsequent analysis. In some cases, we collected data on larger-bodied or particularly conspicuous species, such as ocotillo (*Fouquieria splendens*) and creosote (*Larrea tridentata*), in a larger site with areas further from the camera than for smaller, less conspicuous species (Table S1).

We recorded whether each plant underwent recruitment, mortality or survival, excluding plants that were dead in the historic period or with bases outside the site polygon. In same cases we consulted other historic and modern photos of the same site to determine species identity or whether an individual was alive. Our methods only captured recruitment events leading to conspicuous individuals visible from a distance but not recently recruited small individuals. Our findings are therefore robust to population sinks of new recruits in unfavorable conditions. We counted and measured clusters of agave (*Agave deserti*) and Mojave yucca (*Yucca schidigera*) as single individuals. On steep faces, we include some pygmy cedar *(Peucephyllum schottii)* in our data on creosote; these two species play the same functional role and are difficult to distinguish from a distance. We aggregated this data to determine the number of survivors, recruits and mortalities for each species at each site.

We measured the relative growth of individual survivors by measuring the height (perpendicular to the ground) and width (the largest horizontal extent of the plant perpendicular to the camera, i.e. canopy width) of surviving plants in both time periods, using the ruler tool in ArcGIS and focusing on woody growth. When dead agave rosettes were surrounded by live rosettes, we did not include the width that was dead if it was >20% the total width. We calculated the relative growth of each plant as $(H_1 – H_0) / H_0$, where H indicates plant height and the subscripts 0 and 1 indicate the historical and modern period, respectively, and an equivalent equation for relative growth in terms of width.

For some species at some sites, we could not track the fate of individuals between the two time periods. This most often occurred for narrow-bodied and relatively short-lived species (e.g. teddy bear cholla *Cylindropuntia bigelovii*) in photo pairs that were difficult to perfectly align, thereby making it difficult to tell whether plants either survived, or died and were replaced by recruits. We therefore designated two kinds of sites for each species: those where we could track the fate of individuals over time, and those where we could only count individuals in each time period (“count only”). If we could not track the fate of at least one third of plants of a given species at a given site, we designated the site as “count only” for that species, and retained the site for analyses of mean elevation shifts but not demographic rates. Because counting (but not tracking the fates of) plants could bias results towards higher resolution modern photos, we removed “count only” sites where counts were drastically higher (>90% of plants in both periods) in the modern vs. historical photos. Our final data set included 7,378 plants, 6,149 of which were tracked through both time periods, and the rest of which were counted but not tracked.

Geophysical data

In order to calculate plant densities and changes with elevation, and to account for other topographic factors that impact arid plant distributions (Parker 1991, Munson et al. 2015), we gathered data on physical aspects of the sites captured in each photo. We used Google Earth Pro “ground level view” to draw polygons matching the extent of the site polygons outlined in the photos. To do so, we first “stood” at the camera’s locality and angle, then used corresponding features (e.g. washes, large creosote, hills) to find the exact site, and finally dropped pins to mark polygon vertices. We used these polygons to extract data on each site’s size, as well as its mean elevation, aspect, slope and annual solar radiation (from here on “insolation”) using USGS NED Contiguous US 1/3 arc-second digital elevation model in ArcGIS. We transformed aspect by taking the cosine to create linear values ranging from -1 (South) to 1 (North).

To determine if five site pairs within 100m of each other captured reasonably different samples and could therefore be considered independent, we compared their aspect, slope and insolation. Where one or more of these metrics differed by 1+ standard deviation, we retained the original sites; one of the pairs did not meet this criterion and so we pooled its data.

Out of the potential geophysical covariates (aspect, slope, insolation), we prioritized including insolation in the models where there was enough data to accommodate additional predictors, based on two analyses. First, we used PCA to determine which of the three variables varied the most in the data set and found that insolation contributed the most to the first principle component (Fig. S1). Second, we examined the correlation of these three variables with elevation and found that insolation was the most correlated with elevation (Pearson's r =0.59, p=0.01). We therefore wanted to include insolation where possible, in order to calculate the effect of elevation that is additional to any effect of insolation.

Detecting range shifts

To determine which species showed an overall upward shift within our sample sites, we calculated the change in each species' density-weighted mean elevation in each time period. We used a two-tailed t-test to determine whether the mean shift across species was statistically different from zero. We also calculated changes in the minimum and maximum elevations between time periods.

Statistical models of demographic processes

To determine which demographic processes contributed to uphill shifts, we created models to test if elevation was related to each of three demographic rates for each species: survival, recruitment, and individual growth. We modeled survival and recruitment at the site-level. We used generalized linear models to model survival as a binomial response (the number of individuals surviving vs. undergoing mortality at each site) and logit link. We modeled the number of recruited individuals at each site using generalized linear models with a Poisson distribution and log link, and an offset of $\log(N_0)$ to weight by the initial population size. We only modeled species with data at 6+ sites, which was chosen as a reasonable minimum sample size in order to avoid very small sample sizes while also allowing for analysis of less widely distributed species. For species with $N_0 = 0$ at any modeled site, we added one to N_0 and the number of recruits at all sites to avoid taking the log of 0. To avoid overfitting, we only included insolation as a covariate for species with data at 10+ sites. We included a random effect for site where there was evidence of over-dispersion.

We modeled the relative growth of individual surviving plant using a linear mixed model with random effect for site when there were 6+ sites (using the R package lme4, Bates et al., 2015), and a linear model otherwise. We only modeled species with data on 6+ plants. Where there was data on 20+ plants, we included insolation as a covariate, and when there was data on 50+ plants, we included slope as a covariate as well. We used equivalent methods to model changes in plant widths.

We rescaled all predictors by subtracting the mean and dividing by two standard deviations (Gelman 2008). For all models, we used visual inspection to look for potential outliers or influential points, as well as plots of Cook's distance for linear models and plots of random effects for linear mixed modes; in all cases, removal of such data did not changed the interpretation of our results. We defined elevation as having a significant impact on outcomes when $p<0.05$. All statistical analysis was done in R (version 3.5.1, R Core Team, 2018).

Comparing detected shifts to species traits

Species with faster life cycles are expected to more quickly respond to directional climate change (Perry et al. 2005, Lenoir et al. 2008, Angert et al. 2011). To test this hypothesis, we first quantified each species' annual per capita mortality and recruitment rates across all sites, as measures of population turnover. We then used visual inspection to compare these values to the detected relationships between elevation and demographic rates from our above analysis.

Because narrow ranges imply greater climate sensitivity (Broennimann et al. 2006), we also used visual inspection to explore whether range shifts aligned with species elevational ranges, using historical elevational ranges (maximum minus minimum elevation) extracted from Zabriskie (1979).

RESULTS

We documented the survival, mortality, and recruitment of 2,385, 1,001 and 915 plants, respectively, of 13 species between the periods 1978-82 and 2015-17 and over a 1,000m elevational gradient (Table S1). Out of 108 species-site combinations, we detected two local colonization and two local extinction events; all other species-site combinations had population persistence.

Seven species had an upward shift in mean elevation of >20m and no species with a sample >10 plants had a downward shifts (Table 1). Across species, there was an average upward shift in mean elevations of 37m (t = 2.87, df = 13, p=0.015). We detected a 143m upward shift in the minimum elevation of one species (Mojave yucca) and did not detect any shifts in maximum elevations; however, sites were not evenly distributed over the elevation gradient and may not adequately capture range limits, so this result should be interpreted with caution.

Three species had increasing recruitment (creosote, brittlebush, Fig. 1 and white bursage) and two species had increasing survival (brittlebush, Fig. 1 and teddy bear cholla) at higher elevations (Table 1). In terms of individual growth, one species grew taller at higher elevations (Mojave yucca), although this result was only marginally significant ($p<0.1$, Table 1), and no species grew wider at higher elevations (results not shown). We did not detect any species with lower recruitment, survival or individual growth at higher elevations.

The three species with the highest overall mortality rates also showed significant increases in survival and/or recruitment with elevation (teddy bear cholla, brittlebush and white bursage). Creosote, which has the lowest per capita annual recruitment rate among the species studied, also showed significant increases in recruitment with elevation (Fig. 2). We did not see any clear patterns between range shift patterns and species elevational range sizes.

DISCUSSION

We detected an overall uphill lean in perennial plant species at the Deep Canyon Transect. These findings corroborate Kelly and Goulden (2008), who documented uphill shifts between 1977 and 2006-2007. Our finding of a mean 37m shift over ~36 years aligns very closely with mean global shifts of 11.0m/decade across taxa (Chen et al., 2011a), is similar in magnitude to the 56m upwards shift in mean temperature between 1947-1976 vs. 1977-2006 in the area (Kelly and Goulden 2008), and is identical to the 37m uphill shift in nearby conifer species attributed to recent drought (Fellows and Goulden 2012). While some species we analyzed were in common with Kelly and Goulden (2008), we also document uphill shifts in mean elevation of >20m in five species unique to our study – four cactus species (teddy bear cholla, Gander's cholla *Cylindropuntia ganderi*, barrel cactus *Ferocactus cylindraceus* and beavertail cactus *Opuntia basilaris*) as well as ocotillo (Table 1). In combination with Kelly and Goulden (2008) and Fellows and Goulden (2012), these results suggest a general pattern in the area.

The uphill shift in percent cover at the Deep Canyon Transect documented by Kelly and Goulden (2008) could conceivably be due to growth responses within the lifetime of standing individuals. However, across species, we found more evidence for increasing survival and recruitment with elevation than we did for increasing individual growth (Table 1). Our finding that uphill shifts in the area include changes in abundance suggests longer-term shifts than if changes were due to individual growth only. The detection of increasing survival and recruitment with elevation over a ~36 year period is especially of note given the "slow motion" population dynamics of desert perennial species (Cody 2000).

For four species, we found an upward shifts in mean elevation >20m but did not detect an underlying demographic process that varied with elevation (Gander's cholla, ocotillo, beavertail cactus and barrel cactus). For these species, a combination of weaker, undetectable processes may have combined to create an overall uphill shift. Moreover, two of these species (beavertail cactus and barrel cactus) had the smallest sample sizes of species with range shifts >20m (Table 1), which may have contributed to low detectability. Finally, the lack of survival response was unsurprising for barrel cactus, which is particularly drought and heat resistant (Smith et al. 1984, Bobich et al. 2014), and for Gander's cholla, which has been shown to have higher post-drought survival at low sites encompassed in our elevational gradient (Bobich et al. 2014).

Our findings demonstrate how similar patterns in co-occurring species – uphill shifts in mean elevation – can be comprised of contrasting underlying demographic processes. Here, creosote and white bursage showed only increases in recruitment at higher elevations, whereas teddy bear cholla showed only increases in survival at higher elevations (Table 1). Such contrasting processes point to life stages with varying climate sensitivities in these species.

The lack of survival response for creosote (Table 1) was unsurprising given this species' longevity and potential to survive long after conditions are suitable for reproduction (Vasek 1980), although we note this contrasts with drought-induced die-offs in nearby Joshua Tree National Park (McAuliffe and Hamerlynck 2010). Future study should compare drought severity and topographic and edaphic factors between the sites we studied and those in Joshua Tree National Park to explore if these factors explain differences in mortality. The uphill shift in creosote recruitment is of note given the species' slow overall recruitment rate (Fig. 2). This shift could reflect increasing soil moisture (due to higher precipitation and lower temperatures) at these sites; creosote recruitment has been shown to be moisture-sensitive (Woods et al. 2011).

The lack of survival response with elevation for white bursage (Table 1) was surprising. Given 100% drought-induced mortality at sites in Joshua Tree National Park in years encompassed by our study (McAuliffe and Hamerlynck 2010), we anticipated lower survival of this species at lower, more drought-prone sites. Moreover, we found increasing survival with elevation for brittlebush (Table 1, Fig. 1) and expected these two species to behave similarly: both are drought deciduous Asteraceae species with similar distributions at the Deep Canyon Transect. In addition to the factors described above for creosote that may have caused this lack of survival response, the relatively small sample size for white bursage (Table 1) may have contributed to this outcome.

Our finding of increasing teddy bear cholla survival at higher elevations (Table 1) aligns with drought-induced mortality patterns described by Bobich et al. (2014), who attributed this to milder temperatures and greater precipitation at higher elevations. The lack of recruitment shift for this species may be related to the fact that its establishment is limited to south-facing slopes at high elevation sites encompassed within our elevation gradient (Bobich et al. 2014). We did not include insolation in the model due to limited data; future studies should attempt to account for this factor while testing for an uphill shift.

Such varying responses of life stages to climate can lead to different outcomes in the face of climate change. Changes in recruitment with elevation could indicate early stages of uphill expansion (if high recruitment at high elevations eventually leads to colonization of new sites), while changes in survival with elevation could indicate early stages of downhill contractions (if low survival at low elevations eventually leads to local extinctions). This underscores the importance of understanding both patterns and underlying demographic processes for successful management under climate change. Understanding varying demographic responses can improve monitoring and management by focusing attention on critical sites and life stages. It also suggests different management priorities; for example, managers might prioritize efforts on species where low survival at low elevations is not being met with high recruitment at high elevations, which could lead to overall range contractions. Such contractions have been documented in both latitudinal (e.g. Zhu et al., 2012) and elevational distributions (e.g. Chen et al., 2011; Moritz et al., 2008), but the specific demographic processes underlying them are not typically known (but see Foden et al., 2007).

We found increasing demographic rates at higher elevations in species with both fast and slow overall mortality and recruitment rates (Fig. 2). However, we note that as a whole, arid perennials are relatively long-lived (Cody 2000), so we might have seen a pattern if we had data on a wider variety of taxa, including annuals. We also did not detect larger range shifts in narrow-range species, perhaps pointing to limitations in their ability to shift ranges even though they are more likely to be vulnerable to climate impacts. Here, we used consistent methods across species to allow for inter-species comparisons, but future research could explore species-specific factors that may explain the lack of response in some species.

It is unlikely that the shifts we detected are due to other confounding impacts. There has been very limited land use change along the Deep Canyon Transect; most of the sites we photographed have been under strict protection as part of UC Natural Reserve System since the 1960s, with the remainder jointly managed by the US Forest Service and Bureau of Land Management as part of the Santa Rosa/San Jacinto National Monument. In addition, we focused on relatively low-elevation sites that have not been subject to historical fire due to low and sparse fuels, thereby avoiding this potentially confounding driver of change (Schwilk and Keeley 2012). However, fire may become more common in such systems due to increasing exotic grasses (Brown and Minnich 1986), potentially altering climate-induced uphill shifts. For example, since post-fire establishment is faster in brittlebush compared to creosote (Brown and Minnich 1986), fire at high elevation sites might promote uphill shifts in the former while counteracting them in the latter.

While the shifts we saw are in line with recent climate change in the area, it is possible that they will be reversed if there is a near-term return to more favorable conditions at lower elevations (Fellows and Goulden 2012). Likewise, we note that results of long-term studies in desert systems depend on the end-point years (Belnap et al. 2016). However, given long-term climate projections (Seager et al. 2007, Seager and Vecchi 2010), at a minimum our results give insight into processes expected to dominate in the future.

Our use of rephotography allowed us to track the fate of >6,000 individual plants over ~36 years, and thereby document both uphill shifts and the varying processes that underlie them. Such a large sample would be exceedingly difficult using more traditional methods such as permanently tagging individual plants. It is likely that many more sources of quantifiable data are currently locked up in historical photos; given the critical importance of historic data for understanding responses to climate change (Vellend et al. 2013), efforts to unlock these additional data sources will be increasingly valuable into the future.

FIGURES AND TABLES

Table 1: Changes in mean elevation between 1978-82 and 2015-17 and the modeled impact of elevation on demographic rates for each species.
Species are listed from largest to smallest number of plants tracked. Shading represents upward shifts in mean elevations of >20m or a significant, positive impact of elevation in models (p<0.05). The first column under each modeled outcome shows the sample size for that model. For recruitment, N plants is the same as N tracked for the species overall. Superscripts i, s and RE indicate that model included a covariate for insolation, covariate for slope, and/or a random effect for site, respectively. Where the impact of elevation was significant or marginally significant, we present the coefficient, SE and p-values (. p<0.1, * p<0.05, ** p < 0.01 and *** p<0.001). "ns" indicates the impact of elevation was not significant. Blank cells indicate insufficient data for modeling. See methods for additional information on model formulations.

Species	**Common name**	**Abbrev**	**N plants tracked**	**Change in mean elevation**	**Modeled impact of elevation**					
					Recruitment		**Survival**		**Individual growth (height)**	
					N sites	Coeff (SE)	N sites, N plants	Coeff (SE)	N sites, N plants	Coeff (SE)
Larrea tridentata	creosote	CRE	1350	+5	11 ^{i}	4.9 (1.1) ***	11, 1338 $^{i, RE}$	ns	10, 393 $^{i, s, RE}$	ns
Encelia farinosa	brittlebush	ENC	761	+134	8 ^{RE}	1.5 (0.65) *	8, 509 ^{RE}	2.2 (0.86) **	5, 27^{i}	ns
Cylindropuntia ganderi	Gander's cholla	DEC	713	+21	14 $^{i, RE}$	ns	14, 435 $^{i, RE}$	ns	14, 100 $^{i, s, RE}$	ns
Fouquieria splendens ssp. *splendens*	ocotillo	OCO	351	+43	10 $^{i, RE}$	ns	9, 287 ^{RE}	ns	7, 24 $^{i, RE}$	ns
Cylindropuntia bigelovii	teddy bear cholla	TBC	333	+129	7 ^{RE}	ns	7, 177	1.7 (0.45) ***	3, 4	
Agave deserti var. *deserti*	agave	AGA	321	+2	9	ns	9, 308	ns	9, 174 $^{i, s, RE}$	ns
Yucca schidigera	Mojave yucca	MYU	141	+7	6	ns	6, 131 ^{RE}	5.1 (2.9) .	5, 95 $^{i, s}$	0.19 (0.10) .
Parkinsonia florida	palo verde	PVE	126	+2	5		4, 91		4, 20^{i}	ns
Ambrosia dumosa	white bursage	AMB	104	+54	8 ^{RE}	2.4 (1.0) *	8, 64 ^{RE}	ns	6, 11RE	ns
Ferocactus cylindraceus	barrel cactus	BAR	35	+32	8	ns	6, 8	ns	2, 2	
Opuntia basilaris var. *basilaris*	beavertail cactus	BEA	28	+64	7	ns	5, 16		2, 2	
Cylindropuntia echinocarpa	silver chola	SIC	28	0	1		1, 16		1, 2	
Echinocereus engelmannii	hedgehog cactus	HHO	10	-5	4		3, 6		1, 1	

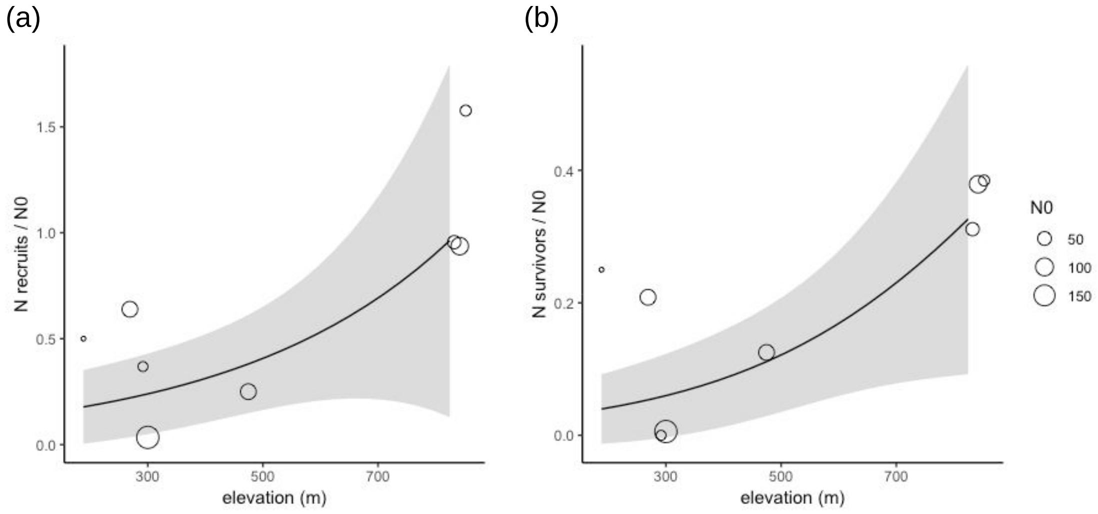

Figure 1: Modeled impact (lines) and 95% confidence intervals (shading; based on fixed effects only) of elevation on brittlebush (Encelia farinosa) recruitment (a) and survival (b).

Raw data (circles) are scaled by the initial population size N_0.

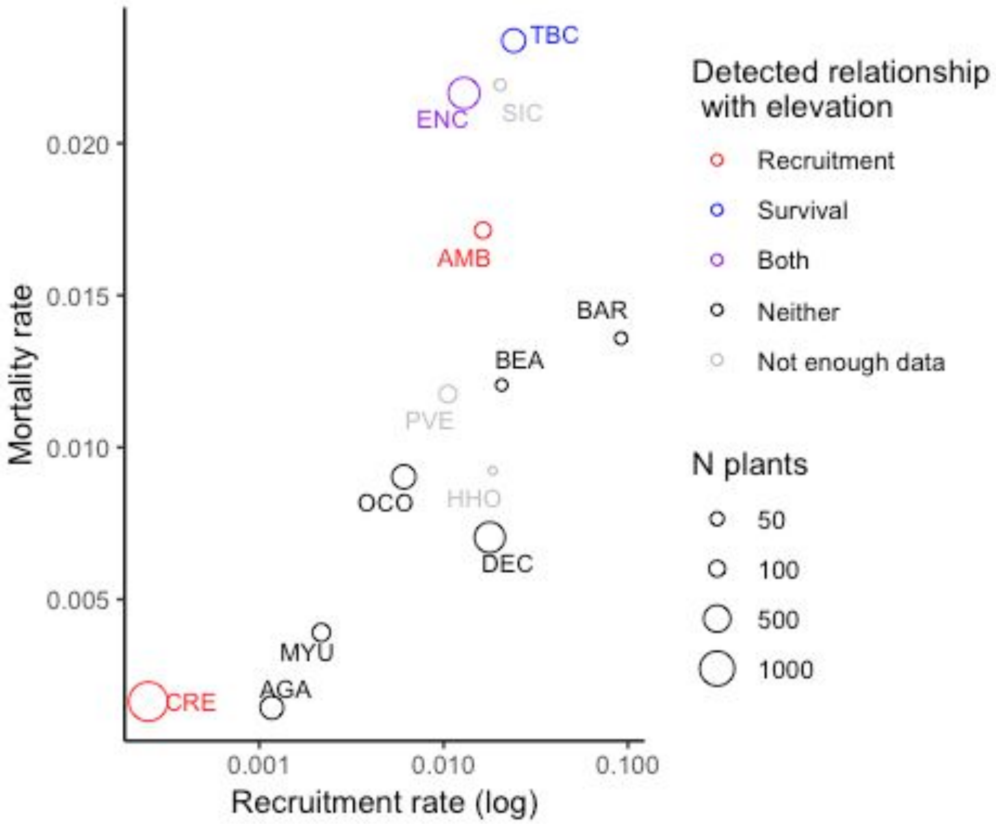

Figure 2: Plot of species' overall annual per capita recruitment and mortality rates. Points are colored by whether we detected a significant increase in survival, recruitment, both, or neither with increasing elevation, or if there was not enough data to construct models for the species. Points are scaled by the number of plants tracked. See Table 1 for species abbreviations.

SUPPORTING INFORMATION

Table S1: Physical characteristics of and timespan captured in historical-modern photo pairs.
Where views were divided into foreground and background sections, the "type" designates the "front" (foreground) area where smaller or less conspicuous plants were surveyed, vs. "all", which refers to the larger site including more background areas where only larger or more conspicuous species were surveyed. For drought deciduous *Encelia farinosa* and *Ambrosia dumosa*, we extracted modern data from photos taken in April 2017, after a multi-year drought, rather than the modern photo date listed (see methods).

Photo view name ("site")	type	Mean elevation (m)	Mean insolation (10^6 Wh/m^2)	Mean slope (°)	Mean aspect (°)	Area (10^3 m^2)	Historic photo date	Modern photo date	Time span (years)
PS16	front	188	1.37	2	58	8.0	5/3/1978	5/16/2015	37.1
PS16	all	189	1.37	2	31	21.2	5/3/1978	5/16/2015	37.1
DCT09		269	1.42	7	176	3.8	2/24/1981	2/7/2016	35.0
PS12SW	front	287	1.40	5	238	24.5	5/3/1978	5/18/2015	37.1
PS12SW	all	288	1.38	4	212	63.7	5/3/1978	5/18/2015	37.1
PS03N		292	1.36	4	39	4.3	4/5/1979	3/21/2015	36.0
PS03E	all	300	1.19	17	58	6.4	4/5/1979	2/5/2016	36.9
PS03E	front	300	1.22	16	18	1.5	4/5/1979	2/5/2016	36.9
PS12E	front	326	1.35	10	267	28.2	5/3/1978	5/18/2015	37.1
PS12E	all	351	1.27	20	244	75.1	5/3/1978	5/18/2015	37.1
PS10	front	475	1.40	6	95	4.1	1/25/1979	3/22/2015	36.2
PS10	all	488	1.36	10	65	18.0	1/25/1979	3/22/2015	36.2
PS11		677	1.15	22	236	2.5	4/20/1978	5/19/2015	37.1
PS05	all	814	1.39	19	82	11.0	7/14/1978	3/22/2015	36.7
PS05	front	819	1.44	18	94	3.7	7/14/1978	3/22/2015	36.7
PS06	front	832	1.53	4	168	1.0	7/14/1978	3/22/2015	36.7
PS07	all	834	1.38	13	244	2.0	4/20/1978	5/17/2015	37.1
PS06	all	836	1.52	9	202	3.0	7/14/1978	3/22/2015	36.7
PS08		842	1.50	13	110	1.0	7/14/1978	5/17/2015	36.9
PS07	front	852	1.29	17	267	0.4	4/20/1978	5/17/2015	37.1
DCT19NE		979	1.47	12	89	4.5	2/15/1979	5/17/2015	36.3
PS17		1,016	1.47	7	57	6.0	2/2/1982	3/22/2015	33.2
DCT19SW		1,061	1.62	15	196	2.7	5/29/1979	5/17/2015	36.0
PS18_60		1,173	1.56	6	133	3.0	10/14/1980	3/22/2015	34.5
PS18_240		1,191	1.53	17	124	9.5	12/2/1980	3/22/2015	34.3

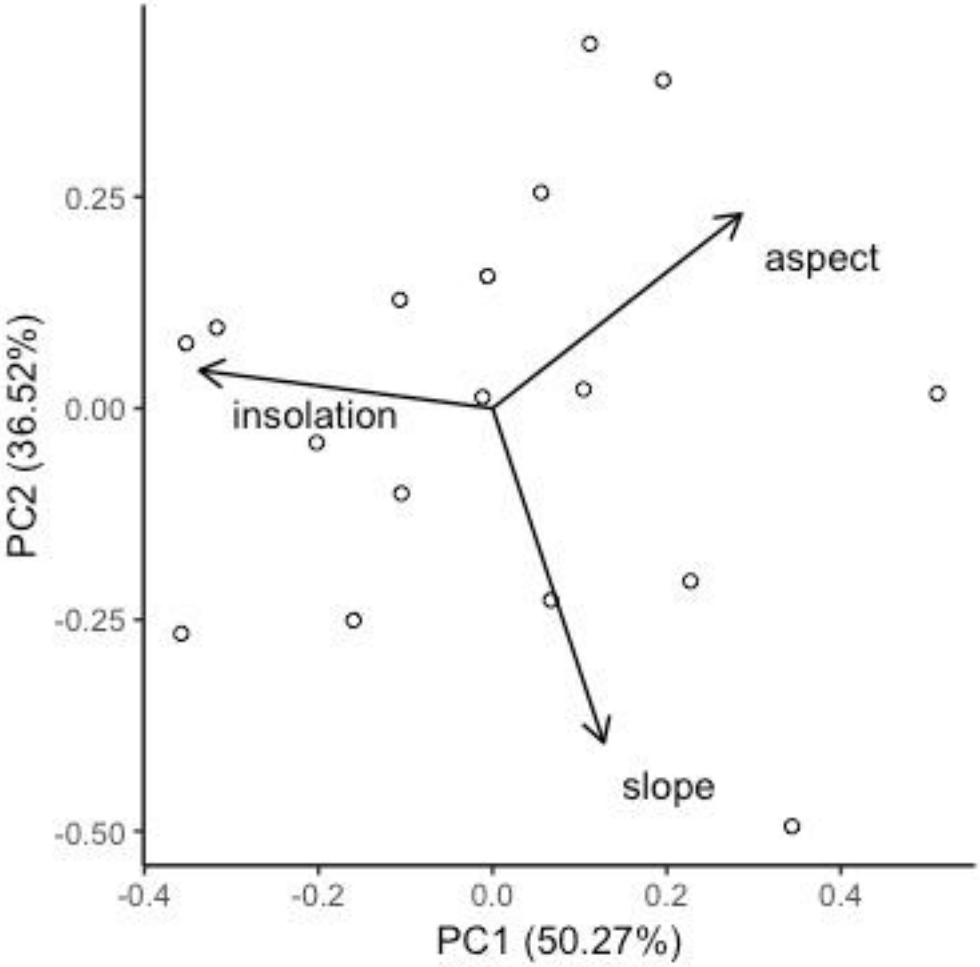

Figure S1: Sites (circles) and variable loadings (arrows) plotted on the first and second principal components of a PCA including insolation, slope, and cosine(aspect) across sites.

Chapter 2:

Lessons from historic avian translocations regarding the potential of longer-distance translocations and assisted colonization as climate adaptation tools

INTRODUCTION

Conservation translocation – the intentional movement of individuals from one area with free release in another for conservation purposes (IUCN/SSC, 2013) – is an increasingly common conservation tool (Seddon et al., 2007). Such efforts are an important tool for securing threatened populations and reducing extinction risks. Documented successes to date include conservation translocations that have prevented global extinction, created additional populations from single-population species, and/or improved species' conservation status (Miskelly and Powlesland, 2013). Building on these successes is critical because in the face of accelerated habitat loss, fragmentation, invasive species and population declines, conservation translocations are expected to become even more widespread (Jachowski et al., 2016).

Translocations focused on conservation of the target species are composed of three types: reinforcement, reintroduction and assisted colonization (also known as "managed relocation" and "assisted migration"). These types are defined, respectively, as translocation into an existing population, to an unoccupied site within the indigenous range, and beyond the indigenous range (IUCN/SSC, 2013).

Longer-distance translocation and assisted colonization are likely to increase as a way of moving populations to locations predicted or already more suitable due to climate change. There are many concerns about assisted colonization, including about risks to recipient ecosystems (reviewed in Hewitt et al., 2011). Here, we do not address these latter concerns, and instead address questions about the feasibility of such an approach with regard to the species being moved – the potential for wasted resources and individuals of rare and endangered species of which there may be precious few and that are the likely targets of such actions (Kreyling et al., 2011). Despite the intensity of debate and open questions about its feasibility, the literature on assisted colonization has been largely philosophical and hypothetical (Liu et al., 2012), with relatively few articles on the topic presenting empirical biophysical research (Hewitt et al., 2011).

However, while relatively rare compared to other conservation translocations, assisted colonization is far from new, having been used in response to a number of non-climate threats such as habitat loss and invasive species. It is particularly well established in New Zealand, where its use may date back as far as the 1890s (Seddon et al., 2012). Moreover, assisted colonization can be viewed as a more extreme action along a spectrum of conservation translocation activities (Seddon, 2010), suggesting that lessons from other conservation translocations can inform assisted colonization. Several authors suggest looking at empirical evidence from historical translocations to inform the debate about assisted colonization (Lawler and Olden, 2011; Mueller and Hellmann, 2008; Olden et al., 2010). However, we know of no systematic synthesis that attempts this.

Here, we synthesize historical conservation translocations in order to address three objectives. Our first objective is to characterize historical conservation translocations in terms of the types of species, sites and management practices used. Synthesizing a fragmented set of efforts can elucidate how relevant our previous experience is to future efforts, and the areas of learning that might be most needed should we increasingly pursue conservation translocations in the future.

In order to improve translocation outcomes, our second objective is to assess the species, site and release factors that predict survival and reproduction in translocated populations. The primary goal of conservation translocations is establishing viable populations, and achieving this goal requires passing through three phases: establishment, growth, and regulation (Sarrazin, 2007). Survival and reproduction correspond to the first two of these phases, respectively, and are therefore preliminary and necessary stages for an ultimately successful translocation. Moreover, using independent metrics of translocation outcomes lessens the impact of differing definitions of success (Robert et al., 2015) and biased reporting (Fischer and Lindenmayer, 2000). Understanding predictors of survival rates is particularly relevant to improving translocation outcomes; survival is often compromised immediately after releases (Tavecchia et al., 2009) and animal mortality is the most commonly listed obstacle to translocation success in North America (Brichieri-Colombi and Moehrenschlager, 2016).

Our third objective is to assess three factors particularly relevant to the feasibility of conservation translocations in a changing climate. Habitat quality is likely critical to translocation outcomes (Osborne and Seddon, 2012), and it is often assumed that high quality habitats are found within the species current range (i.e. reintroductions/reinforcement vs. assisted colonization), nearby (i.e. short geographic distance movements), or in places with similar climates to the capture site. However, these assumptions are rarely tested, and if true, they would present unique challenges for conservation translocations in response to climate change.

The idea that within-range translocations should be more successful than assisted colonizations is partly based on the premise that historical range is a predictor of future habitat suitability, but this premise does not take into account accelerating habitat change (Seddon, 2010), as well as difficulties in delimiting the historical range (Lyman, 2016; Seddon, 2010), especially for rare species (Lomolino and Channell, 1998), and the many factors that can limit species ranges (reviewed in Osborne and Seddon, 2012). Moreover, while Griffith et al. (1989) and Wolf et al. (1996, 1998) found that mammalian and avian translocations into the core of species' indigenous ranges are more successful than those to the periphery or outside of the species' indigenous ranges, this was not found for Psittacines (White et al., 2012).

Geographic distance is a proxy for a variety of environmental gradients, so longer geographic distance between source population sites and release sites may predict worse translocation outcomes. This is especially the case where populations are locally adapted to their environment, and may be a more useful predictor than whether or not a site is within the indigenous range: long-distance translocations may release animals at sites to which they are not locally adapted, even within the species' range; similarly, short-distance translocations to a suitable but previously un-colonized location would nevertheless be assisted colonization. The latter may be especially prevalent amongst dispersal-limited species (exactly those most likely to need assisted colonization). However, for climate-motivated translocations, practitioners may be tempted to translocate populations over longer distances to keep pace with climate change (Leech et al., 2011).

Finally, matching the source and release site climate may be particularly important for translocation success, especially if populations are locally adapted to climatic conditions. There is evidence that climate matching predict establishment success in the invasion biology literature (Hayes and Barry, 2008). If high climate matching predicts translocation outcomes, this would create a tradeoff between needing to match climates to ensure short-term outcomes versus needing to get to a different and more favorable long-term climate. Moreover, given the difficulties in predicting climate change at local scales and its impacts on species (Peterson et al., 2018), it would present a formidable challenge for conservation translocations in the face of climate change.

Given the above challenges and their particular relevance for climate-motivated conservation translocations, here we test whether assisted colonization, geographic distance, and climate matching predict survival in translocated populations.

We focus our analysis on birds, which are an ideal study taxon for several reasons. They are a well-studied (Clark and May, 2002) and disproportionately reintroduced taxon (Seddon et al., 2005). Moreover, these efforts are well documented (Bajomi et al., 2010), as illustrated by our use of a pre-existing database of historical avian conservation translocations in this study. Finally, climate-motivated conservation translocations in birds have already been proposed (e.g. Morrison et al., 2011) and carried out (e.g. VanderWerf et al., 2018). Therefore, improved understanding of the feasibility and ways to translocate birds in the face of climate change relevant to current conservation practice.

There are important parallels between conservation translocations and the intentional and unintentional establishment of exotic species, and we draw upon this literature in formulating our hypotheses. For example, increasing propagule pressure has been shown to improve the establishment of exotic birds (Lockwood et al., 2005), and is therefore likely to impact the outcomes of conservation translocations (Cassey et al., 2008). Non-migratory species (Kolar and Lodge, 2001) and habitat generalists (Cassey et al., 2004) are thought to more readily establish as exotic species and therefore might be considered easier targets for conservation translocations (Cassey et al., 2008). Finally, as with the establishment of exotic species, translocation success is likely to depend on the particular combination of species and site.

However, there are important differences between introduced exotic and threatened species of birds (Cassey et al., 2008), the latter of which are likely candidates for conservation translocations. For example, introduced exotic species tend to be widespread, but it is local endemics that are most often threatened (Cassey et al., 2008). Therefore, while the study of invasive species offers important lessons, studying historical conservation translocations themselves offers a more direct approach for improving future translocation efforts.

Previous synthesis studies have tried to elucidate factors contributing to the success of avian conservation translocations (e.g. Fischer and Lindenmayer, 2000; Griffith et al., 1989; Jones and Kress, 2012; Rummel et al., 2016; White et al., 2012; C. Wolf et al., 1996; Wolf et al., 1998), and we also draw from these in formulating our hypotheses. However, these studies are either taxonomically-limited (e.g. Psittacines) or cover multiple taxa (e.g. both mammals and birds), are geographically-limited (e.g. Mediterranean), incorporate translocations for multiple objectives (e.g. both game and endangered species), use un-quantified self-assessment of success by practitioners (which may be biased) and/or comprise significantly smaller datasets than the database we used. Moreover, none address issues specific to using conservation translocations as an adaptation response to climate change. Here, we synthesize historical conservation translocations using a large, global, single-taxa database, assess the factors predicting translocation success using objective outcome metrics, and address issues of particular relevance for their use in response to climate change.

METHODS

Study sample and data preparation

The publicly-available Avian Reintroduction and Translocation (ART) Database was created and provided by the Lincoln Park Zoo (Lincoln Park Zoo, 2012). The database was collected from a wide range of both peer-reviewed and gray literature as well as personal communication with practitioners (Lincoln Park Zoo, 2012). The database is particularly focused on New Zealand and the United States (see results). We believe that the focus on New Zealand is proportional to historical translocation practice, given >1000 documented translocations of New Zealand fauna, the majority of which are of birds (Armstrong et al., 2015). Similarly, in the peer-reviewed literature, the U.S. has the most documented translocations in North America (Brichieri-Colombi and Moehrenschlager, 2016). Nevertheless, many efforts from non-English speaking countries are missing from the database. However, we do not have reason to think this geographic bias strongly impacts our modeling results.

We accessed the database in 2012, after its most recent update. The data has a nested structure, such that a single species can be released at multiple sites, and at each site a species can be released multiple times. We removed translocations of surrogate species (i.e. practice translocation on a non-target species), reintroductions back to the capture site, and temporary translocations which were not intended to establish a population (see SI for details on database cleaning).

Characterization of conservation translocations

We characterized translocated species by taxonomic order and 2016 International Union for the Conservation of Nature (IUCN) Red List status using data provided by BirdLife International (2017). We distinguished between releases of wild birds only vs. releases including captive-hatched or captive-reared birds (from here on “wild” and “captive”, respectively). For wild releases, we geo-located both release and capture sites; for captive releases, we geo-located release sites only, since they lack capture site data in the ART database. We used these localities to calculate the distance translocated with the law of cosines in the R package geosphere (Hijmans, 2017). We combined data in the ART database with additional datasets (see SI) to determine whether conservation translocations were reinforcements, reintroductions or assisted colonizations. Finally, we calculated the survival of birds one year after release (from here on “survival rate”) and whether released birds successfully fledged young (from here on “breeding success”, see below for how this metric was aggregated) by species and overall.

Survival models

To assess predictors of survival rate, we compiled data on the species, site and release characteristics hypothesized to be important to survival and/or translocation success. We based hypotheses on previous studies, including from the complementary field of invasion biology (Blackburn and Cassey, 2004; Cassey et al.,

2008) and used data included in the ART database as well as a variety of additional sources (Table 1).

We estimated the impact of these predictors on survival rate using generalized linear mixed models with binomial outcomes and a logit link. Much of the ART database (75% of N= 2,259 releases) lacks survival outcomes, and the availability of other predictors of interest varied, so we created two survival models to answer two related questions and best utilize available data. Our first model maximized our sample size ("full model"), and our second used a smaller set of data with available predictors that were particularly relevant to translocations responding to climate change ("distance model", see below). For both models, the binomial outcome was the number of surviving birds vs. the number of deaths one year after release (number of released − number of surviving birds) for each release event. Both models included two random effects, one for species and one for site, to account for non-independence in cases where a species was released at multiple sites and/or over multiple release events at the same site. In all cases we tried to keep release and site data at as fine a spatial and temporal resolution as was possible, but in some cases we collapsed releases and/or sites together in order to retain data.

We removed two kinds of translocations from our models: (1) 18 releases where "reason for action" was recorded as "trial translocations" in the ART database, which had significantly lower survival rates than other translocations (38% survival rate in trials vs. 58% in non-trials, two-sample $t(18.27) = 2.43$, $p = 0.026$, N=557 releases), and (2) 15 releases of seabirds (five species), since most seabirds are translocated before fledging (Jones and Kress, 2012), meaning that it is often not possible to determine survival at one year while they are at sea.

Using R (version 3.4.3, R Core Team, 2017), our modeling procedure was to (1) use visual inspection of predictors to choose between square root, log, or log(x+1) transformations to reduce skewness (Table 1), (2) rescale all continuous variables by subtracting the mean and dividing by two standard deviations, which allows for direct comparison of continuous and binary variable coefficients (Gelman, 2008), (3) fit the model using the lme4 package (Bates et al., 2015), (4) test whether an additional random effect for taxonomic order significantly improved the model fit using a likelihood ratio test; it did not improve the model fit in either model, (5) calculate variance inflation factors to check for collinearity; all were < 1.7, (6) test for significant overdispersion based on the Pearson χ^2 statistic using the aods3 package (Lesnoff and Lancelot, 2013) (7) test for significant non-uniformity of residuals using the DHARMa package; all were uniform (Hartig, 2018), (8) look for extreme site or species random effects by visual inspection, and identify influential releases, sites and species based on visual inspection of Cook's distance plots using the influence.ME package (Nieuwenhuis et al., 2012), and check for substantial changes in the model with these removed, and finally, (9) calculate the marginal and conditional R^2, based on fixed effects alone and fixed and random effects together, respectively (Nakagawa and Schielzeth, 2013), using the piecewiseSEM package (Lefcheck, 2015). In all statistical tests mentioned above, we considered

$p<0.05$ significant, and in our models, we defined fixed effects as significant when 95% confidence intervals did not overlap zero.

Full model

This model focused on widely-available predictors in order to maximize our sample size (Table 1). Body mass and generation length were highly correlated (Pearson's r=0.75, N=68 species, p=2.6e-13), limiting our ability to determine the independent influence of these variable. Therefore, we chose to remove generation length, since body mass is more readily accessible to practitioners. However, in our models body mass should be considered to represent both traits together.

Data on brain residual (relative brain mass adjusted for body mass) and on whether the cause of decline was addressed at the release site was not available for 39 and 38 releases, respectively. However, because these terms substantially improved the model fit using a likelihood ratio test (brain residual: $\chi^2(1)= 7.45$, $p=0.0064$; problem addressed: $\chi^2(1)= 12.89$, $p= 0.00033$), we include them in our model. This resulted in a final sample size of 435 releases of 4,523 birds of 68 species across 136 sites.

We tested for and found very slight overdispersion (ratio of sum of squared Pearson residuals to residual degrees of freedom of 1.26 rather than 1.0, $P(>\chi 2) = 0.00022$), which appears to be driven by one species (whooping crane, *Grus americana*). When we removed this species, coefficient estimates were qualitatively unchanged (Fig S3) and overdispersion ratio was reduced to 1.05 ($P(>\chi 2) = 0.32$), so we feel comfortable that overdispersion does not strongly influence our results and present the original model.

Distance model

This model focused on predictors particularly relevant to the feasibility of conservation translocations in response to climate change. We modeled these predictors separately, rather than including them in the full model, due to limited data availability. We only included releases of wild birds, since very few captive birds have a capture site listed in the ART database, and data on the capture site allows calculation of geographic and climate distance (methods below). We had hoped to include assisted colonization as a predictor in this model, but there were only four cases in this subset of the data and so it was ultimately removed (although it was included in the larger full model).

In order to characterize the difference in climate between capture and release sites ("climate distance"), we first extracted bioclimatic variables for each capture and release site from WorldClim version 2 at 30 arc-second resolution (Fick and Hijmans, 2017). We chose nine variables (BIO2, BIO4-7, BIO12-15) that described temperature and precipitation extremes and variation based on the hypothesis that changes in such variables would negatively impact avian survival. Looking at all sites (both capture and release) together, we then removed variables correlated with a Pearson's $r>0.7$ (Fig S1) so that aspects of climate that covary were not double-counted in our metric of climate distance. This left us with six variables: BIO2, BIO5, BIO6, and BIO13-15. We calculated climate distance as the standardized Euclidian distance between each capture and release site using these variables (Fig S2).

To control for variables found to be important in the full model, we also included five variables that were significant or marginally significant ($p<0.1$) in the full model and that had data for more than 85% of releases (body mass, migratory status, protected area, release year, and release within the first year at the release site). Our final sample size for this model was 117 release events of 1,996 wild birds of 45 species across 74 sites.

Even though neither the correlation between climate and geographic distance nor the variance inflation factors for this model were particularly high (Person's $r<0.50$, 1.64, respectively), climate and geographic distance are theoretically related. Therefore, we also created models that removed these terms one at a time to see how each variable impacted survival independently and in combination.

Post hoc analysis

We found that release year and migratory were significant predictors of survival in the full model (which included both wild and captive birds) but not in the distance model (which included wild birds only). To explore this difference, we added an interaction between wild and migratory and between wild and release year to the full model, to see if such interactions were significant.

Analysis of breeding success

Because of ambiguity in how breeding success was recorded in the database (whether breeding success should be attributed to currently- or previously-released birds) we aggregated breeding success to the level of site, defined as whether or not successful breeding ever took place at the release site.

We plotted and summarized the relationship between breeding success and median values for two variables we hypothesized to most impact breeding success: (1) propagule pressure, which we aggregated across the site as the number of birds released at the site divided by the range of years at the site +1 (to avoid dividing by 0), since releasing more birds should increase the probability of at least one case of successful breeding at a site, and (2) generation length, since short generation lengths are associated with faster breeding rates in birds (Sæther and Bakke, 2000).

Beyond under-reporting of translocation failures in general (Seddon et al., 2007), our aggregation procedures of breeding at the site level further favored successes, since even one success (amidst other missing outcomes for releases at the site) would count as a success, whereas a site needed only failures (and no missing outcomes at the site) to affirmatively be identified as a site with no breeding. On the other hand, breeding success may have happened after primary sources were published or after entry into the database, which would bias results towards lower breeding success. Nevertheless, we felt the above analysis was worthwhile for detecting broad trends.

We removed 24 sites recorded as “trial translocations” by the ART database, which had significantly lower breeding than other sites (percent of sites with successful breeding in trials = 42 vs. 86% in non-trials, $\chi^2(1) = 28.425$, p= 9.7e-08, N=343 sites). Thereafter, our data set for this analysis included 129 species across 315 sites.

RESULTS

Characterization of conservation translocations

The ART database documents the release 70,663 birds of 186 species across 714 sites and 2,259 release events. The earliest translocation in the database was in 1903 and the most recent was in 2010.

The most commonly translocated taxonomic order was Passeriformes (30% of translocated species and 32% of sites, N=186 species and 714 sites, respectively), which make up ~60% of species globally and 48% of extinct, threatened, and near-threatened species. The most disproportionately translocated taxonomic order relative of the number of species globally was Cathartiformes (2 of 7 global species translocated, fig. 1). As of the 2016 IUCN Red List, fifty-eight percent of 186 translocated species were listed as threatened or near-threatened, 40% were considered “least concern”, and three species are extinct or extinct in the wild (Guam Rail *Hypotaenidia owstoni*, Hawaiian Crow *Corvus hawaiiensis* and Bridled White-eye *Zosterops conspicillatus*, BirdLife International, 2016).

Release sites were primarily in New Zealand (41%) and the US (27%), with Australia and the UK each comprising 4% of release sites, and 40 other countries with <3% of release sites each (N=714 sites). The threats that necessitated translocations were habitat loss (61%), invasive species (45%), hunting (35%), poisoning (21%), and disease and reduced food resources (<5% each, N=643 sites).

The median number of birds released per year at a site was 13.0, for a total of 30 birds per site (N=705 sites). 48% of releases were wild vs. captive releases (N= 2,237 releases). The median translocation distance for wild birds was 101 km and ranged from 0 to 4,325 km (N=297 sites). Reintroductions, reinforcements and assisted colonizations comprised 65, 18 and 7% of cases, respectively, while 10% of cases were within the indigenous range but we could not decipher whether they were reinforcements or reintroductions (N=713 sites).

Of 389 sites with data on management practices, the majority (55%) reported using predator control. Other common management practices were the creation of nesting areas and habitat creation or recovery (23% each). Supplemental feeding and acclimatization were both used in the majority of releases with data about these practices (77%, N=1,170 and 70%, N=1,389 releases, respectively.)

Of all 7,155 released birds with survival data, 50% percent survived one year after the release (N=567 release events). Of 92 species with survival data available for 5+ released birds, 11 had an overall survival rate of ≥90% and seven had an overall survival rate of ≤10%.

Of sites with breeding outcome data, 83% report at least one case of successful breeding (N=343 sites). Of 37 species with breeding data available at three or more sites, nineteen had 100% successful breeding and two had 0% successful breeding.

Survival models

Full model

The model had a marginal (fixed effects alone) and a conditional (fixed and random effects together) R^2 of 0.18 and 0.42, respectively. Higher survival rates were predicted by releases of species with larger body mass and brain residuals, sites where the cause of decline had been addressed, releases of wild birds, and releases in more recent years. Releases into protected areas tended to have increased survival, although this result was not significant. In contrast, releases of migratory species and releases within the first year of efforts at a site had decreased survival rates. Habitat generalism, propagule pressure and assisted colonization did not predict survival rates (Fig 2a, Table S1). We interpret the latter result for assisted colonization with caution given their rarity in the modeled data (5% of release events). For predicted survival rates based on the full model, see Table S1.

Distance model

The model had a marginal and conditional R^2 of 0.11 and 0.42, respectively. Increasing geographic distance predicted decreasing survival rates (Fig

2b, Fig 3, Table S1). A similar pattern was found for longer climate distances, although this result was not significant (Fig 2b, Table S1). When geographic distance was removed, climate distance was marginally significant (coefficient -0.76, 95% CI ranging from -1.53 to 0.0089, p =0.053, Fig. S4), suggesting that the impact of these two variables is not independent (Fig S5).

In contrast to the full model, migratory species and years since release did not predict lower survival. Results were qualitatively similar after removing 14 releases that were influential based on Cook's distance (Fig S5).

Post hoc analysis

We found a significant, positive interaction for wild x release year (Fig. S3) suggesting that for wild birds, there is less of an improvement in survival rates for releases in more recent years than for captive birds. Visual inspection of plots suggested a similar pattern (Fig S4).

Breeding success analysis

Excluding trial translocations, 86% of sites with breeding data reported at least one case of successful breeding (N=319 sites). Species with above-median generation lengths at sites with above-median propagule pressure had comparable breeding success (89% success, N=61 sites) to species with below-median generation lengths at sites with below-median propagule pressure (88% success, N=59 sites, Fig 4).

DISCUSSION

Our synthesis of a large, global, single-taxa database of historical conservation translocations, in combination with objective, quantifiable metrics of translocation outcomes, has important implications for the prioritization of species for conservation translocations, the anticipation of translocation outcomes, and the improvement of practice. Below, we first discuss the species, site and release-scale factors that we found to impact survival and breeding success of translocated birds, and then findings that are particularly relevant to assisted colonization and long-distance translocations motivated by climate impacts.

Predictors of survival and breeding

Species traits

We found several species traits – body mass, brain residuals, non-migratory tendency and generation length – that predict survival and breeding in translocated species (Fig 2, Fig 4). These findings should be useful to managers prioritizing species and resources for translocations versus other conservation actions.

Large body mass and high brain residual are thought to buffer individuals from extrinsic factors and be advantageous in novel conditions. Brain residual (relative brain mass adjusted for body mass) in particular has been found to be important to establishment success in introduced birds (Sol et al., 2012, 2005) by enhancing an animal's propensity for behavioral innovation in response to novel ecological challenges (Sol et al., 2005). To illustrate the modeled impact of varying brain residuals, an average translocation of a species with the brain residual of a mean Psittaciformes (amongst the largest brain residuals in our data set) can expect a predicted survival rate of 0.92. This prediction drops to 0.66 for the translocation of a species with the brain residual of a mean Galliformes (amongst the smallest brain residuals in our data set), with all other conditions held equal (Fig S6 and Table S1). To our knowledge, this is the first time brain residual has been tested and confirmed to be predictive of outcomes in the context of conservation translocations. Our findings suggest an additional axis that can be used to prioritize species for translocations and anticipate and compensate for specific translocation outcomes.

Species with shorter generation lengths had increased breeding success (Fig. 4). Since generation length is correlated with body mass, this points to an inherent tension between improved survival and lower breeding rates for larger species, and the opposite for smaller species. This ecological tradeoff is described by a life-history axis that ranges from “highly reproductive species” at one end to “survivor species” at the other end (Sæther and Bakke, 2000). Since both survival and breeding are needed for the establishment of a viable population, this life-history tradeoff impacts management decisions about which species to prioritize for translocation. Another axis that may integrate the need for both survival and successful breeding is “brood value”, which predicted establishment success in invasive birds (Sol et al., 2012) and is worthy of further study in conservation translocations.

Migratory species had lower survival than non-migratory species in the full survival model. This is expected if translocated birds range far from release sites, making it difficult for managers to monitor and protect them, or if birds with strong honing instinct to natal site do not imprint on their release site. However, we interpret this result with caution, since it was not found in the wild-only distance model, and was not explained by an interaction between wild and migratory in the full model.

Site features

We found that birds where the initial cause of decline had been addressed had higher survival rates than other birds, and releases into protected areas tended to have higher survival rates as well (Fig 2). These findings points to the importance of habitat quality in improving translocation outcomes (Griffith et al., 1989; Wolf et al., 1998, 1996). Decreased survival rates in sites where the cause of decline has not been addressed is intuitive, since by definition the driver of decline led to lower survival in the past (thereby necessitating the translocation), and others have found similar patterns (Fischer and Lindenmayer, 2000). Protected areas tended to have a positive impact on survival, providing evidence of improved habitat quality, decreased persecution, and/or protection from other anthropogenic disturbance likely to be present in protected areas.

We also found that increasing geographic distance between capture and release sites decreased survival rates (Fig 2b). Geographic distance is a proxy for many spatially varying factors that might impact translocation success, including differences in biotic (e.g. vegetation and species assemblages) and abiotic (e.g. water availability, substrate, climate) features. In addition, longer distance translocations may also involve longer transit times, increasing stress in releasees and thereby decreasing survival (Parker et al., 2012). This finding has implications for translocations motivated by climate change, which we discuss below.

Release factors

At the release scale, we found that translocations of wild birds, releases after the first year of releases at a site, and more recent translocations had higher survival than others (Fig. 2a).

The improved survival of wild vs. captive releasees aligns with other studies of translocation success (Fischer and Lindenmayer, 2000; Griffith et al., 1989; Rummel et al., 2016; Wolf et al., 1996) and may be due to a variety of additional challenges faced by captive releases (Parker et al., 2012).

We found higher survival rates in more recent translocations (Fig. 2a), which is anticipated given improvements in management over time, the maturation of the field, and the development of the IUCN Reintroduction Specialist Group and 1998 IUCN Reintroduction Guidelines (Seddon and Armstrong, 2016). However, survival rates have only improved with time in the full model (of both captive and wild birds) but not the distance model (which included only wild birds, Fig 2), and we found a significant interaction between wild and release year (Fig S3 and S4), suggesting that most improvements in management over time have benefited captive vs. wild bird translocations.

Birds released during the first year of releases at a site had lower survival than those released in subsequent years, which could be due to two factors. First, it may be that site-specific learning by practitioners improves survival rates. In addition, repeat releases may also allow newly released animals to learn from earlier releasees (IUCN/SSC, 2013), leading to improved survival. Ours is the only study we are aware of to empirically test this predictor. Our finding suggests that poor outcomes in the first year may be best met with commitment to additional years of effort.

The importance of context

Our findings suggest management actions for practitioners tasked with translocating a particular species and/or to a particular site. Practitioners translocating captive birds and/or migratory, small bodied, and/or small-brained species, or faced with a situation where the only available habitat is a long distance away, may be able to compensate for predicted lower survival by focusing on factors that are amenable to management. For example, in such situations it will be all the more important to address the initial cause of decline, release birds into protected area (Fig 3), and commit to more than one year of releases.

For slow-lived species, practitioners may be able to compensate for predicted low breeding by releasing more birds (Fig 4). The importance of propagule pressure overall, as well as its ability to compensate for slow breeding rates, has been shown in introductions of exotic species (Sol 2012). This finding suggests we need a large number of birds to improve translocation outcomes for slow breeders, which is a challenge for rare and endangered species. On the other hand, we interpret our finding with caution, due to the data's coarse resolution (we were unable to calculate the portion of birds that bred, and the more birds released, the more likely there will be at least one case of breeding, see methods), and since low numbers of releasees may be conflated with poorly-resourced efforts and/or practitioners that anticipate failure (Armstrong and Seddon, 2008).

Our models have relatively low marginal R^2 values, suggesting that while the species-, site- and release characteristics we modeled explained some variation, it is difficult to predict outcomes based on these alone. Instead, unidentified factors that impact translocation outcomes should be kept in mind, which is unsurprising given the parallel difficulties in predicting invasive species establishment (Sol et al., 2012). The comparatively large conditional R^2 values and relatively large variance for the random effects of species and sites (Table S1) suggests an important role for understanding how translocation context – the unique combination of species and sites – impact a given translocation outcome.

Implications for translocations under climate change

Our study offers insights pertaining to using translocations in response to climate change. Addressing the initial cause of decline improves survival rates (Fig 2a), but in the face of climate change, practitioners will be forced to continually keep up with climate impacts rather than being able to reverse or remove it. However, the proximate drivers of translocation decisions under climate change will often be familiar ones like invasive species and habitat loss – the two most common drivers of historical translocations – which are both projected to increase with climate change (Settele et al., 2014).

Second**,** we found that assisted colonizations are relatively rare (7% of sites) and did not have different survival than other translocations (Fig 2a), although we note that our ability to detect a pattern may have been hampered by their rarity.

Third, we found that longer distance translocations predict decreased survival in translocated birds (Fig 2b). This suggests a series of shorter translocations over time may be more feasible than longer distance translocations.

However, the distances needed to keep pace with climate change may not be much larger than a typical historical translocation (median 100km translocation distance). Using back-of-the-envelope calculations, we can compare a 100km translocation to the velocity of climate change calculated by Loarie (2009). This exercise shows that a typical translocation distance, in an area with mean climate velocity (0.42 km/yr), and in the direction of climate change, will cover as much distance as the climate will move in ~240 years. In biomes with fast climate velocities (1.26 km/yr) – perhaps those where climate-motivated translocations will be most common – such a translocation will cover as much distance as the climate will move in ~80 years. In other words, the distances we have experience translocating species may be reasonable in terms of their ability to keep up with climate change velocities. The challenge, therefore, may not be the distances themselves, but rather determining which direction to move, given that many climate variables can impact survival, and they may not move in the same direction (Ackerly et al., 2010).

Fourth, geographic distance was a better predictor of survival that climate distance (Fig 2b), suggesting that spatial variations in other, non-climatic dimensions, such as geophysical features, vegetation, and species assemblages impact survival of translocated birds, rather than climate variables *per se*. This suggests that for conservation translocations in response to climate change, the challenges of climate matching may not be as critical as feared. However, the fact that our models did not find an independent impact of climate matching should be interpreted with caution, for several reasons. It may be that under comparatively stable past climates, practitioners have been relatively good at matching source and release site climates, such that there is not variance in our data set to show a strong signal. In addition, we were tasked with finding a generic metric of climate distance for all bird species utilizing globally-available climate data, but any given species will respond uniquely to a specific set of climate variables at a fine-resolution, and so we encourage future studies of individual species with known climatic tolerances and higher-resolution climate data. Moreover, climate distance had improved predictive power when geographic distance was removed from the model (Fig S4), suggesting that the impacts of climate and geographic distance are not independent. Future study should focus on cases where it is possible to tease apart the independent impacts of geographic and climate distance.

Finally, we point out that all translocations in the future – including those motivated by non-climate threats – will need to consider a directionally shifting baseline as species ranges, communities and habitats change. Therefore, regardless of the proximate threat they are responding to, translocation practitioners will need to assess the long-term stability of the climate in the indigenous range (for reintroductions and reinforcements), as well as geographic and climate distance when picking release sites.   In addition to considering these shifting baselines when assessing the feasibility of translocations for target species, they also need to be considered when assessing potential risks to recipient ecosystems.

Future research should expand our approach to include other taxa – mammals could be readily studied since their translocations are common (Seddon et al., 2005) and well documented (Bajomi et al., 2010), and ectothermic taxa should also be studied given the potentially important role of climate matching for such species. Moreover, additional research should explore the impacts of assisted colonization and geographic and climate distance on the longer-term viability of translocation populations. Finally, our analysis looked at the feasibility of translocations for target species but not at potential impacts on recipient ecosystems, the latter of which is a common concern about assisted colonization (Hewitt et al., 2011). Given our longstanding experience with conservation translocations, including assisted colonization, these concerns could be explored using a similar approach to the one we present here.

Conclusions

Conservation translocations are not new to conservation, but are in fact a long-standing strategy for securing threatened populations and reducing extinction risks, with many documented successes. Synthesizing this historical experience is critical to improving current and future efforts in the face of increasing anthropogenic threats. We hope this approach can help move the field about the use of conservation translocation in response to climate change beyond philosophical debates and towards a more nuanced, empirical perspective. Such a perspective will be critical for thoughtfully pursuing their promise as a tool to assist species in responding to climate change.

FIGURES AND TABLES

Table 1. Fixed effect predictors included in survival rate models.
Xs indicate variables that were included based on a priori hypotheses, * indicates variables that were included in the distance model because they were significant or nearly significant (p<0.1) in the full model, and – indicates variables which were considered but ultimately excluded (see text). See text and SI for details on modeling approach and methods for calculating variables.

	Reasoning / example evidence from previous studies	**Variable type (transformation)**	**Full model**	**Distance model**
Species variables				
Body mass (g) [1]	Blackburn et al., 2009	continuous (log)	X	*
Brain residual (log-log brain size [3]–body mass residual)	Sol et al., 2012, 2005	continuous	X	–
Generation length (years) [2]	Slow-lived species have higher survival rates	continuous (log)	–	
Habitat generalism (number of level-2 habitat types) [2]	Cassey et al., 2008; Sol et al., 2012, 2005	continuous (log)	X	
Migratory species[2, 3]	Cassey et al., 2008; Germano and Bishop, 2009	binary	X	*
Site variables				
Problem addressed (problem that caused the initial decline of the population fully vs. partially or not addressed at the release site) [4]	Cassey et al., 2008; Fischer and Lindenmayer, 2000; Wolf et al., 1996	binary	X	–
Within a protected area [4, 5]	A proxy for higher habitat quality and/or decreased persecution: Griffith et al., 1989; Wolf et al., 1996, 1998.	binary	X	*
Assisted colonization (release beyond the indigenous species range) vs. reintroduction or reinforcement [3, 4]	Griffith et al., 1989; Wolf et al., 1996, 1998.	binary	X	–
Geographic distance between capture and release site (wild releases only, km)	Incorporates differences in environmental conditions that vary linearly in space (Cassey et al., 2008) plus potentially longer transit times	continuous (log(x+1))		X
Climate distance between capture and release site (wild releases only, see methods)	Describes differences in climate conditions: Cassey et al., 2008	continuous (square root)		X
Release variables[4]				
Release year	Accounts for improvements in reintroduction science and management (Seddon and Armstrong, 2016)	continuous (log (years before 2018))	X	*
Release within the first year of releases at the site	Within the first year, practitioners use untested protocols and/or face unforeseen circumstances at a new site. Moreover, a lack of prior releasees may limit learning in newly released animals (IUCN/SSC, 2013).	binary	X	*
Propagule pressure (number released including current release, per year since the first release at the site +1)	Cassey et al., 2008; Fischer and Lindenmayer, 2000; Griffith et al., 1989; Sol et al., 2005; Wolf et al., 1998, 1996	continuous (log)	X	
Wild (wild birds only, no captive-hatched or -reared birds)	Fischer and Lindenmayer, 2000; Griffith et al., 1989; Wolf et al., 1996	binary	X	wild-only
1: Dunning, 2007, 2: BirdLife International, 2017, 3: see SI for (additional) sources, 4: Lincoln Park Zoo, 2012, 5: UNEP-WCMC and IUCN, 2017				

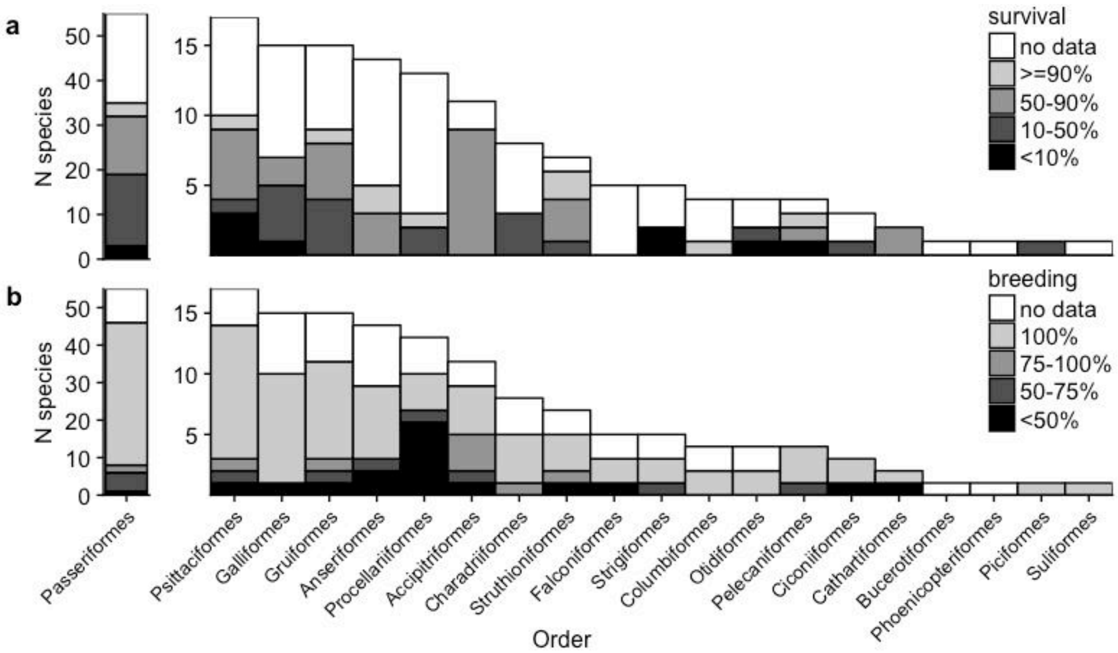

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Figure 1. Number of species translocated by taxonomic order.

(a) For each species, shading indicates percent of birds surviving one year after release out of all birds with survival outcome data.

(b) For each species, shading indicates the percent of sites with successful breeding out of sites with breeding outcome data. Sixty-one percent of species with 100% breeding success had breeding outcome data at only 1 site.

For both, note the separate y-axis scale for Passerines

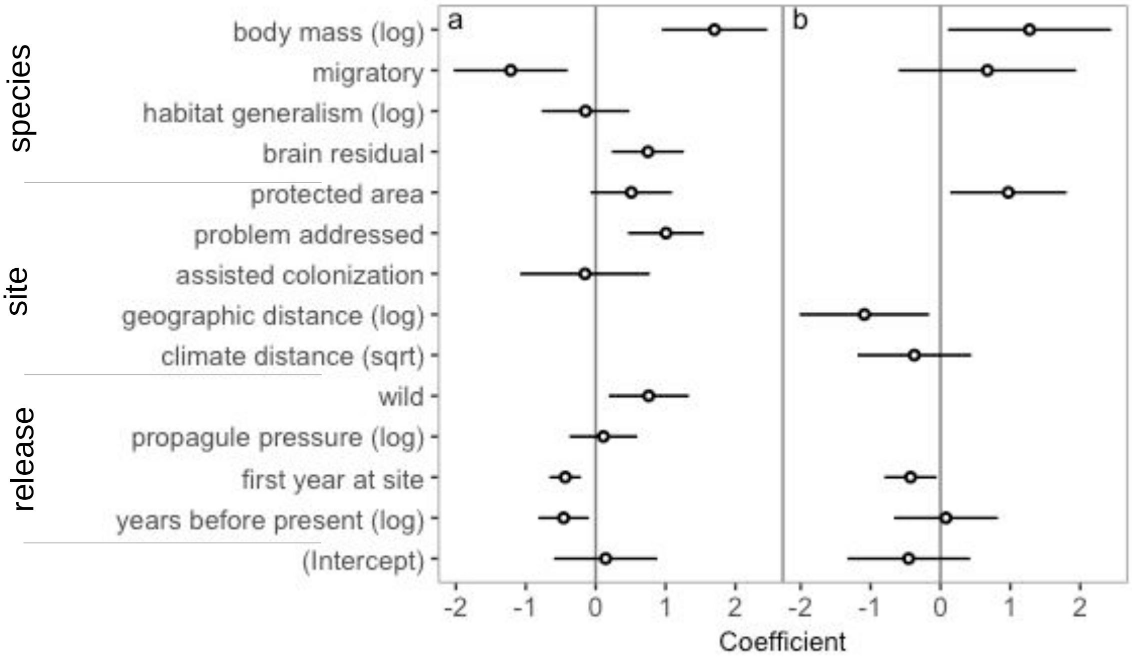


Figure 2. Coefficients and 95% CI of models predicting survival one year after release in translocated birds.

Models include random effects for site and species. Continuous predictors are scaled to allow direct comparison of coefficients (Gelman, 2008), which are on the log-odds scale.

(a) Full model. N= 4,523 birds released over 435 release events across 136 sites and 68 species.

(b) Distance model. N=1,996 birds released over 117 release events across 74 sites and 45 species

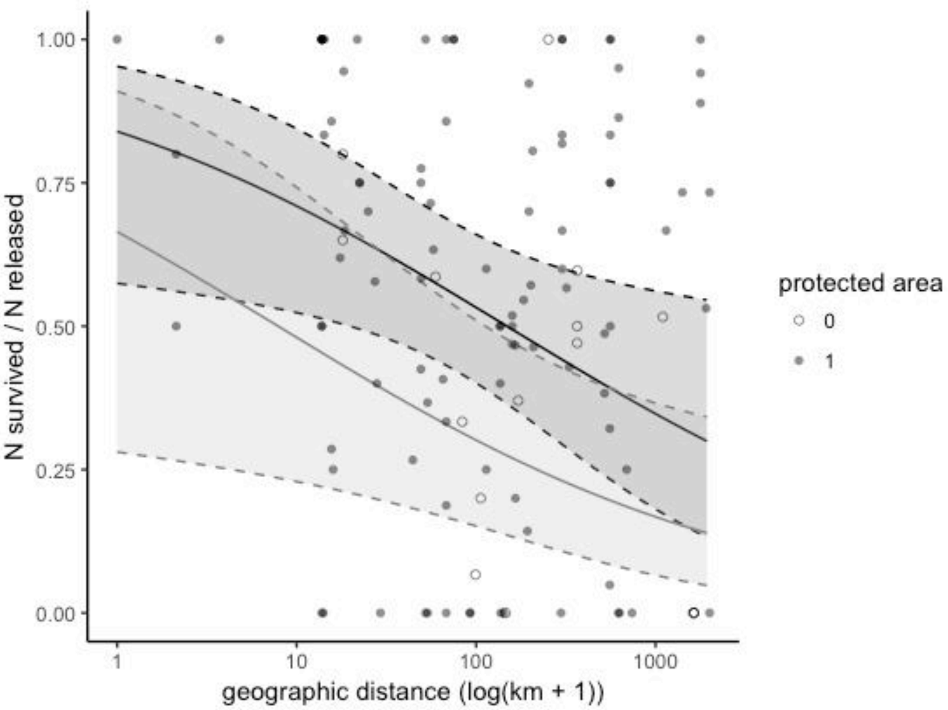


Figure 3: Model-predicted survival rate (lines) and 95% CI (shading and dashed lines) against geographic distance for translocations of birds into (dark grey) and not into (light grey) protected areas, based on the distance model (see text).
CIs are based on fixed effect uncertainty only. Raw data points are open or filled to indicate whether the release was into a protected area.

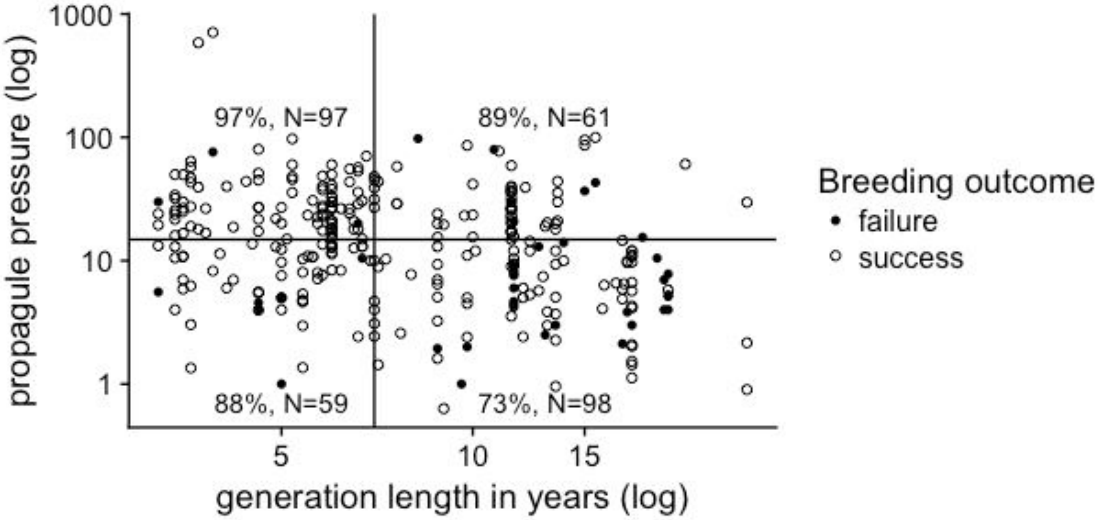


Figure 4: Breeding success (open circle) or failure (solid circles) at each site by species generation length and site propagule pressure.
Vertical and horizontal lines represent median values for each axis (median generation length = 7 years, median propagule pressure = 14.8 birds / year). Labels indicate the percent of sites with successful breeding and sample sizes for each quadrat (N= 129 species at 315 sites total,). Breeding success rates are biased towards success (see text), and this summary does not account for non-independence when a species were released at multiple sites.

SUPPORTING INFORMATION

Supplementary Methods

Body mass

We took body mass values in grams as documented in Dunning (2007). If no species match was found, we took one of the following steps: (1) If an ART database species had a subspecies designation, we took the mean of other sub-species listed in Dunning (2007), (2) if an ART database species did not have a subspecies designation, we took the mean of subspecies that were listed if nothing else was listed, (3) we checked the Dunning (2007) update available online (Dunning, 2017), and (4) we checked the "taxonomic notes" in BirdLife Checklist (BirdLife International, 2016) and Avibase (Lepage) for clues on potential synonyms. For two species (of 186) where we were unable to find body mass values after taking these steps, we took the average of congenerics listed in Dunning (2007). In all cases, we took mean values from Dunning (2007) in the following order of preference based on availability (from first to last choice): mean of female and male values, "both", "unknown sex", female only, male only. We used the midpoint of minimum and maximum values if no mean was reported.

Brain residual

We collected brain size data from a variety of sources (below). We conducted an exhaustive search for species' whose brain size we did not readily find, using Google Scholar to search for each "Genus species" AND ("brain size" OR "brain volume”), including searches using Latin synonyms, as well as communication with experts in comparative avian neuroanatomy (A. Iwaniuk and J. Corfield, personal communication, Sept. 2017). Most publications were searched by hand, however three large databases (Iwaniuk and Nelson 2003, Sayol 2017 and Garenett 2014) were searched automatically for matching Latin names. When reported as volumes, we converted values to mass using 1.036 g/mL brain density, following the methods of Sol et al. (2005). We took the average brain mass of available data from all sources for each species for which we had data (112 species).

To calculate the log-log brain – body relationship we collected mean body mass data for all ART Database species as well as all species in Franklin et al., 2014, Iwaniuk and Nelson, 2003 and Sayol et al., 2016, using the methods above to extract the mean body mass value from Dunning (2007). This resulted in 1,676 body mass-brain mass pairs. We calculated a linear regression between the log(body mass) and log(brain mass) for these pairs, which had an intercept of -1.942 and slope of 0.562, and was strongly positive and significant ($N=1676$ species, $R^2=0.88$, $p < 2.2e-16$). We then extracted the residual brain values for the species in our database. For species where no brain size data was available, we took the mean residual for the genus if available (49 species), again following the methods of Sol et al. (2005).

Brain size data sources

Ashwell, K.W.S., Scofield, R.P., 2008. Big birds and their brains: Paleoneurology of the New Zealand moa. Brain. Behav. Evol. doi:10.1159/000111461

Burton, R.F., 2008. The scaling of eye size in adult birds: Relationship to brain, head and body sizes. Vision Res. doi:10.1016/j.visres.2008.08.001

Carrete, M., Tella, J.L., 2011. Inter-individual variability in fear of humans and relative brain size of the species are related to contemporary urban invasion in birds. PLoS One. doi:10.1371/journal.pone.0018859

Corfield, J.R., Birkhead, T.R., Spottiswoode, C.N., Iwaniuk, A.N., Boogert, N.J., Gutiérrez-Ibáñez, C., Overington, S.E., Wylie, D.R., Lefebvre, L., 2013. Brain size and morphology of the brood-parasitic and cerophagous honeyguides (Aves: Piciformes). Brain. Behav. Evol. doi:10.1159/000348834

Corfield, J.R., Wild, J.M., Hauber, M.E., Parsons, S., Kubke, M.F., 2008. Evolution of brain size in the palaeognath lineage, with an emphasis on New Zealand ratites. Brain. Behav. Evol. doi:10.1159/000111456

Cunningham, S.J., Corfield, J.R., Iwaniuk, A.N., Castro, I., Alley, M.R., Birkhead, T.R., Parsons, S., 2013. The anatomy of the bill tip of kiwi and associated somatosensory regions of the brain: Comparisons with shorebirds. PLoS One. doi:10.1371/journal.pone.0080036

Franklin, D.C., Garnett, S.T., Luck, G.W., Gutierrez-Ibanez, C., Iwaniuk, A.N., 2014. Relative brain size in Australian birds. Emu. doi:10.1071/MU13034

Garamszegi, L.Z., Eens, M., 2004. The evolution of hippocampus volume and brain size in relation to food hoarding in birds. Ecol. Lett. doi:10.1111/j.1461-0248.2004.00685.x

Garamszegi, L.Z., Møller, A.P., Erritzøe, J., 2002. Coevolving avian eye size and brain size in relation to prey capture and nocturnality. Proc. R. Soc. B Biol. Sci. doi:10.1098/rspb.2002.1967

García-Peña, G.E., Sol, D., Iwaniuk, A.N., Székely, T., 2013. Sexual selection on brain size in shorebirds (Charadriiformes). J. Evol. Biol. doi:10.1111/jeb.12104

Guay, P.J., 2008. Behavioural ecology and conservation genetics of the musk duck (Biziura lobata). University of Melbourne.

Guay, P.J., Iwaniuk, A.N., 2008. Interspecific variation in relative brain size is not correlated with intensity of sexual selection in waterfowl (Anseriformes). Aust. J. Zool. doi:10.1071/ZO08082

Guay, P.J., Iwaniuk, A.N., 2008. Captive breeding reduces brain volume in waterfowl (Anseriformes). Condor. doi:10.1525/cond.2008.8424

Iwaniuk, A.N., Nelson, J.E., 2002. Can endocranial volume be used as an estimate of brain size in birds? Can. J. Zool. doi:10.1139/z01-204

Iwaniuk, A.N., Nelson, J.E., 2003. Developmental differences are correlated with relative brain size in birds: a comparative analysis. Can. J. Zool. doi:10.1139/z03-190

Iwaniuk, A.N., Dean, K.M., Nelson, J.E., 2005. Interspecific allometry of the brain and brain regions in parrots (Psittaciformes): Comparisons with other birds and primates. Brain. Behav. Evol. doi:10.1159/000081110

Iwaniuk, A.N., Nelson, J.E., 2001. A comparative analysis of relative brain size in waterfowl (Anseriformes). Brain. Behav. Evol. doi:10.1159/000047228

Iwaniuk, A.N., Nelson, J.E., James, H.F., Olson, S.L., 2004. A comparative test of the correlated evolution of flightlessness and relative brain size in birds. J. Zool. doi:10.1017/S0952836904005308

Iwaniuk, A.N., Wylie, D.R.W., 2006. The evolution of stereopsis and the Wulst in caprimulgiform birds: A comparative analysis. J. Comp. Physiol. A Neuroethol. Sensory, Neural, Behav. Physiol. doi:10.1007/s00359-006-0161-2

Ksepka, D.T., Balanoff, A.M., Walsh, S., Revan, A., Ho, A., 2012. Evolution of the brain and sensory organs in sphenisciformes: New data from the stem penguin Paraptenodytes antarcticus. Zool. J. Linn. Soc. doi:10.1111/j.1096-3642.2012.00835.x

Mlíkovský, J., 1989. Brain size in birds: 2. Falconiformes through Gaviiformes. Věstník Československé společnosti Zool.

Mlíkovský, J., 1989. Brain size in birds: 3. Columbiformes through Piciformes. Věstník Československé společnosti Zool.

Mlíkovský, J., 1989. Brain size in birds: 4. Passeriformes. Acta Soc. Zool. Bohemoslov.

Mlíkovský, J., 1989. Brain size in birds: 1. Tinamiformes through Ciconiiformes. Věstník Československé společnosti Zool.

Mlíkovský, J., 2003. Brain size and foramen magnum area in crow and allies (Aves: Corvidae). Acta Soc. Zool. Bohemoslov. 67, 203–211.

Sayol, F., Maspons, J., Lapiedra, O., Iwaniuk, A.N., Székely, T., Sol, D., 2016. Environmental variation and the evolution of large brains in birds. Nat. Commun. doi:10.1038/ncomms13971

Schuck-Paim, C., Alonso, W.J., Ottoni, E.B., 2008. Cognition in an ever-changing world: Climatic variability is associated with brain size in neotropical parrots. Brain. Behav. Evol. doi:10.1159/000119710

Sol, D., Garcia, N., Iwaniuk, A., Davis, K., Meade, A., Boyle, W.A., Székely, T., 2010. Evolutionary divergence in brain size between migratory and resident birds. PLoS One. doi:10.1371/journal.pone.0009617

Habitat generalism

We defined habitat generalism as number of habitat (level 2) types listed for the species, excluding habitats defined as “marginal” and “non-breeding”, listed in data provided by Birdlife International (2017).

Migratory species

Using data provided by Birdlife International (2017), we coded species listed as "altitudinal migrant", "full migrant", and "nomadic" as 1, and birds listed as “not a migrant” as 0. Birdlife International does not include sub-species, so two non-migratory sub-species (Florida Sandhill Crane, *Antigone canadensis pratensis* and Loggerhead shrike, *Lanius ludovicianus mearnsi*) were changed to 0.

Protected Area

We determined if the release site was protected based on three pieces of evidence gathered for all sites: (1) if it was listed as protected in the ART Database, (2) if the site name indicated it was protected (e.g. includes the words “National Park” or “Protected”), and (3) if the site locality fell within a World Protected Area Database polygon (UNEP-WCMC and IUCN, 2017, excluding “proposed” polygons, those that were designated after the first release year for each site, or did not include a designation year), using the packages sp (Pebesma and Bivand, 2005) and rgdal (Bivand et al., 2018) in R.

As a fourth step, we also coded some sites by hand for two situations: The first was using ArcGIS to see if a site was very near a WDPA polygon but had approximated latitude/longitude data, or near a WDPA point (which were not included in step 3 above), especially if the site name was the same or very similar to the WDPA protected area name. Other data sources used for this process included the Protected Areas Database of the United States (U.S. Geological Survey Gap Analysis Program (GAP), 2016), for areas with "gap status" code 1 or 2, and New Zealand Department of Conservation Maps (New Zealand Department of Conservation). Secondly, we counted sites as protected if there was evidence it was protected for a second species at the same site before or on the same year as the release in question.

If any of the four methods above indicated that the site was protected, we coded the site as protected. Where there was conflicting evidence between these methods, we prioritized what was in the ART Database (1 above) or our “by hand” work.

Assisted colonization, reintroduction or augmentation

We looked at several pieces of evidence in the ART Database to determine if the release of each species at each site was an assisted colonization, reintroduction or augmentation. These variables included “reason for action” (e.g. "Augment existing population", “Return species to former range"), “within known range”, “wild population present”, “wild population size”, and whether the release at the site was “into a wild population”. Where there was enough evidence and internal consistency in the ART Database regarding these variables, we coded sites accordingly.

For sites where there was conflicting information or not enough information in the ART Database, we coded them by hand (148 sites), using a variety of sources regarding native ranges and translocation events. In general, we erred on the side of coding things as augmentation / reintroduction vs. assisted colonization, to be conservative.

There were 133 sites (18%) where we couldn’t distinguish between augmentations and reintroductions using the above methods. For these, we consulted data provided from Miskelly and Powlesland (2013). This comprehensive synthesis of historical New Zealand translocations excludes augmentations, so we took the absence of one of our New Zealand releases in this data set as indicating an “augmentation”, thereby identifying 58 sites as either augmentations or reintroductions. We similarly looked at the synthesis of North American translocations compiled by Brichieri-Colombi and Moehrenschlager (2016) to identify three additional sites as reintroductions.

Climate distance

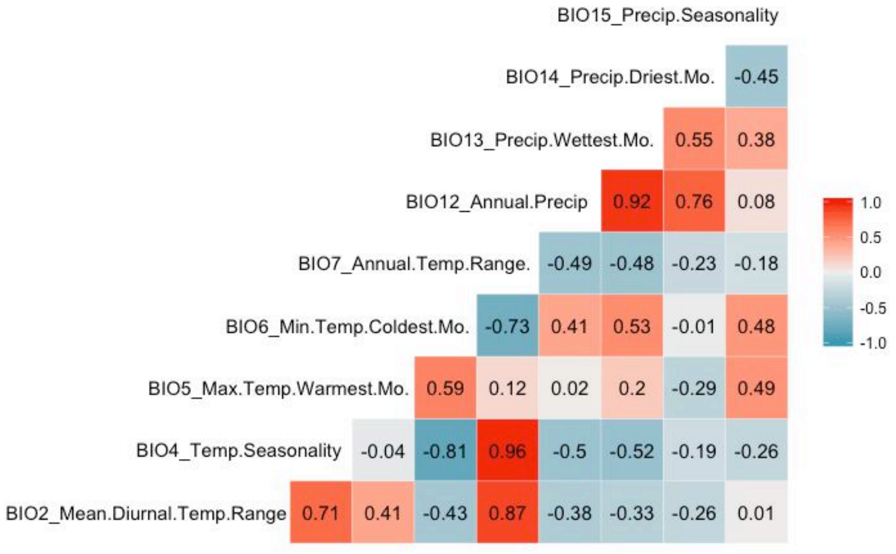


Figure S1: Correlation matrix of climate variables extracted from both capture and release sites and considered for climate distance metric.

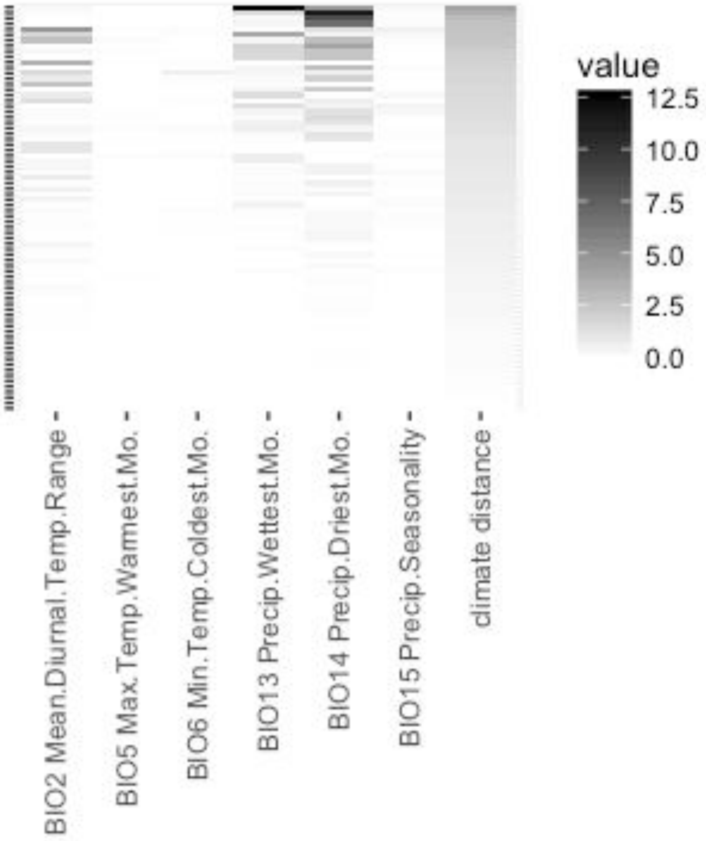


Figure S2: Contribution of each bioclimate variable to climate distance.
Each row represents a release site, and cells are shaded by the standardized distance between capture and release site for that variable, $((c - r)/s)^2$, where *c* is the variable's value at the capture site, *r* is the variable's value at the release site, and *s* is the global standard deviation of the variable. These standardized distances were then summed and the square root was taken to calculate the overall standardized Euclidian distance between the capture and release site ("climate distance"). This value was transformed via the square root to reduce skewness before modeling. Of the six input variables, the standardized distances for BIO14: precipitation in the driest month was most correlated with climate distance (r = 0.66, N=74 capture-release site pairs, p=1.936e-10)

Supplementary Results

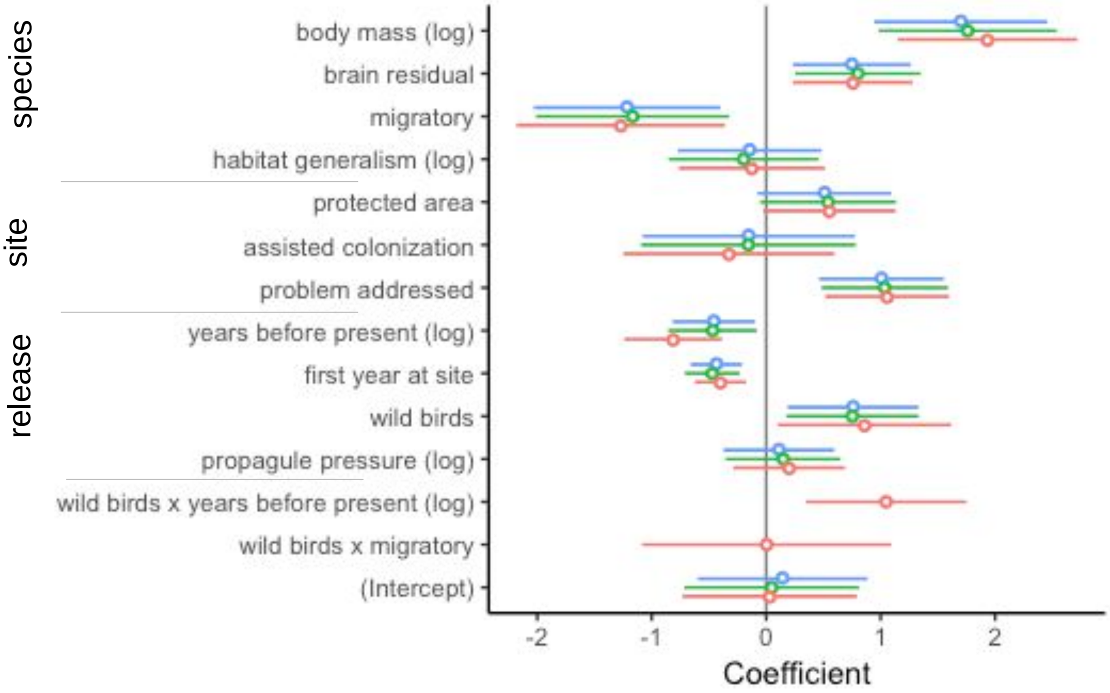


Figure S3: Modeled coefficients for variations on the full model presented in main text (blue, included for comparison).

In green is the full model of survival rates after removing data for one species (whooping crane, *Grus americana*), which fixes slight overdispersion detected in the full model. In red is the full model plus interaction terms, to explore differences between the full model (which includes wild and captive birds) versus the distance model (which includes wild birds only).

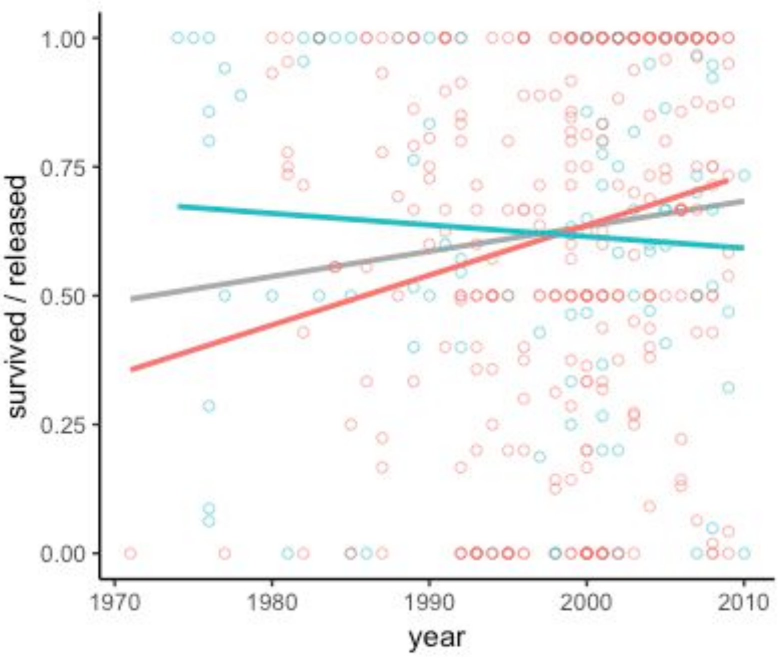


Figure S4: Survival rate by year for releases modeled in full model, for wild (blue) and captive (red) releases.

Lines are best-fit regression lines and are colored the same as the points. Grey line represents the relationship for both captive and wild releases together.

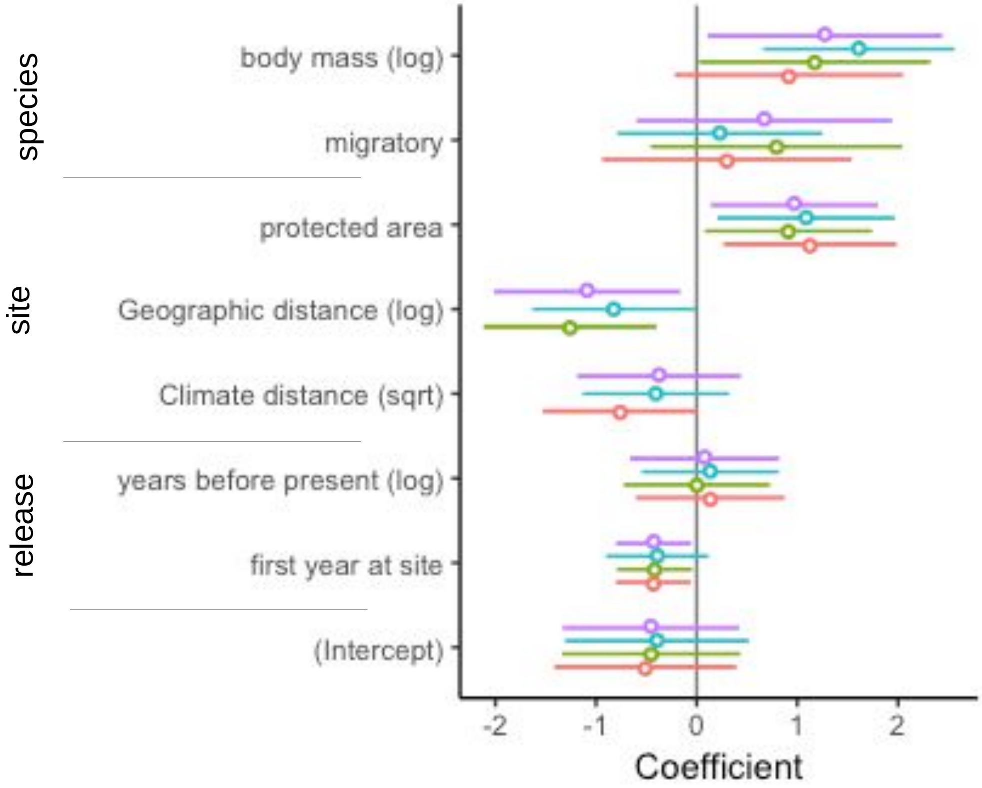


Figure S5: Modeled coefficients for variations on the distance model presented in main text (purple, included for comparison).

The blue model is the distance model after removing 14 releases identified as "influential" using visual inspection of plots of Cook's distance. Here, "first year at site" is no longer a significant predictor of survival. In the green model, climate distance has been removed, which does not change the qualitative interpretation of the other predictors. In the red model, geographic distance has been removed, and the coefficient for climate distance becomes more negative and marginally significant (p=0.053).

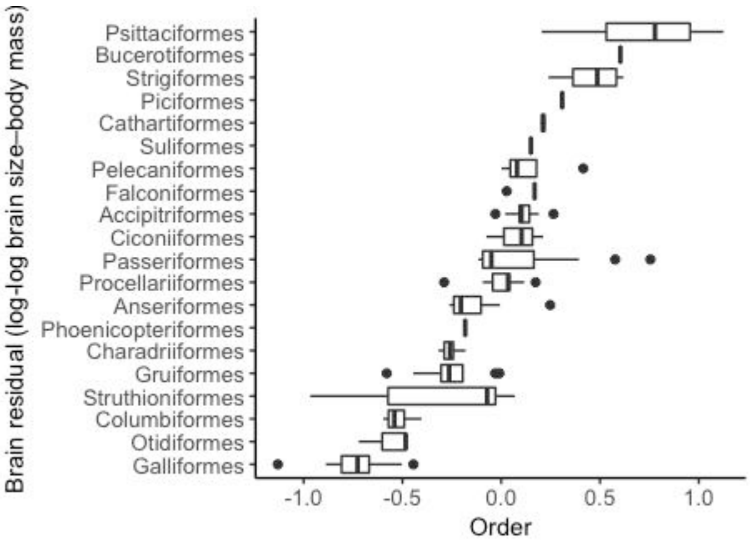


Figure S6: Brain residual (relative brain mass adjusted for body mass, see SI) for species in the ART Database, grouped by taxonomic order.

Table S1. Model coefficients and predictions for survival models.
See Table 1 for predictor definitions and data sources. All predictors are on the log-odds sale, and all continuous predictors are standardized to allow direct comparison of coefficients (Gelman, 2008). Symbols indicate p-values (*** p<.001, ** p<.01, * p<.05 and . p<.1). We present predicted survival rates for significant or marginally significant (p<0.1) predictors. Predictions are based on the full model for all variables except geographic distance, which is based on the distance model. Predictions are calculated with all non-predicted continuous variables set to their mean (=0, since they are rescaled), all non-predicted binary variables set to their most common value in the full model data set (migratory = 0, problem addressed = 1, protected area = 1, assisted colonization = 0, within first year = 0, wild = 0), and represent outcomes for a mean species and site.

	Model coefficients on log-odds scale (standard error)		**Predicted survival rate**	
	Full model	**Distance model**		
(Intercept)	0.14 (0.38)	-0.45 (0.45)		
Species variables				
Body mass, g (log)	1.7 (0.39)***	1.27 (0.6)*	10g:	0.50
			100g:	0.70
			1,000g:	0.85
			10,000g:	0.93
Brain residual	0.75 (0.26)**		mean Galliformes (residual = -0.84):	0.66
			mean Passeriformes (residual = 0.07):	0.85
			mean Psittaciformes (residual = 0.73)	0.92
Habitat generalism (log)	-0.15 (0.32)			
Migratory species	-1.22 (0.42)**	0.67 (0.65)	non-migratory (0):	0.84
			migratory (1):	0.61
Site variables				
Problem addressed	1.01 (0.28)***		problem not addressed (0):	0.66
			problem addressed (1):	0.84
Protected area	0.51 (0.3) .	0.97 (0.42)*	not into protected area (0):	0.76
			into protected area (1):	0.84
Assisted colonization	-0.15 (0.47)			
Geographic distance (log(km +1))		-1.09 (0.47)*	10km:	0.78
			100km:	0.64
			1,000km:	0.45
Climate distance (sqrt)		-0.37 (0.42)		
Release variables				
Release year (log(years before 2018))	-0.46 (0.18)*	0.08 (0.38)	1975:	0.76
			1990:	0.80
			2005:	0.86
Within first year of releases	-0.43 (0.11)***	-0.43 (0.19)*	after first year of releases at site (0):	0.84
			within first year of releases at site (1):	0.77
Propagule pressure (log)	0.11 (0.25)			
Wild	0.76 (0.29)**		captive (0):	0.84
			wild (1):	0.92
Random effect variance				
Species	0.89	1.07		
Site	0.55	0.70		
Sample size				
N Birds	4,523	1,996		
N Releases	435	117		
N Sites	136	74		
N Species	68	45		

Chapter 3:

Progress and gaps in on-the-ground climate change adaptation efforts in the US conservation sector

INTRODUCTION

Conservation research has increasingly focused on adapting conservation in the face of inevitable climate change threats to species persistence and ecosystem integrity (Stein et al., 2013). These efforts focus on predicting ecological impacts, prioritizing species and landscapes based on their vulnerability, and recommending best practices and management frameworks for conservation responses (e.g. Cross et al., 2012; Gardali et al., 2012; Swanston et al., 2016).

Despite a growing imperative to track and evaluate adaptation progress (Ford et al., 2013), we know little about how practitioners are responding to climate change on the ground, for at least three reasons. First, adaptation is inherently hard to measure because it takes place across many different scales and actors (Ford et al., 2013). Second, efforts to operationalize adaptation plans into on-the-ground actions are recently emerging, so little documentation of these efforts exists. This is compounded by the fact that literature on the subject lags behind the field (Glick 2011). Finally, efforts that have emerged have been fragmented (Bierbaum 2013), *ad hoc* and occurring in isolation (Hansen et al., 2013). Together, these features have impeded synthesis of emerging activities, with very few peer-reviewed studies reporting on adaptation actions themselves (Berrang-Ford et al., 2011; Bierbaum et al., 2013) and a limited number of regionally-focused studies on adaptation implementation in U.S. natural resource management (Ontl et al. 2017, Archie et al. 2012).

To address this gap, we took advantage of a national pool of proposed, implementation-ready adaptation projects to synthesize adaptation efforts in the U.S. conservation sector. The dataset is far larger that those in previous studies, in terms of sample size, with >400 project proposals from >250 non-profit organizations, and geographic scope, covering the entire U.S. By analyzing on-the-ground proposals, we sought to address concerns regarding opportunism and specificity in this emerging field. Some practitioners may pursue adaptation funding opportunistically without updating their conservation practices to address new challenges (Stein et al., 2014). Given the broad range of activities that might reduce vulnerability to climate change, it is difficult to distinguish such efforts from those specifically designed to address climate change. We identified patterns that can inform the conversation about this important issue. We also sought to fill a gap in a literature focused on general concepts (Lawler 2009) but lacking the specificity needed for implementation (Heller and Zavaleta, 2009). Here, we illustrate how practitioners are translating general concepts into practical actions to address conservation in the context of climate change.

Our specific objective is to assess the appropriateness of emerging efforts as well as create a baseline for tracking future developments. We focused our analysis on three questions.

What ecosystems, taxa and ecological functions do proposed projects target? Current and predicted impacts to biological systems are widespread and varied (Groffman et al., 2014) but we do not know which are receiving attention from conservation practitioners.

What strategies and activities are proposed? Characterizing the approaches and tools being adopted and utilized by practitioners allows us to determine their uptake, compare them to traditional conservation efforts, and link general adaptation strategies to on-the-ground actions.

What is the distribution of proposed projects relative to geography and specific threats? Identifying regional differences in responses and how these correspond to the diverse climate impacts predicted across the U.S. (USGCRP, 2017) could point to geographic leaders and laggards.

While we cannot (yet) measure the effectiveness of these efforts in reducing vulnerability to climate change, by measuring their self-described targets, approaches, and distribution, we can identify progress and gaps in this emerging field in order to guide efforts to refine adaptation efforts and funding in the US.

METHODS

Study sample

Our sample for this study was 415 pre-proposal applications submitted from 2011-2015 to the Wildlife Conservation Society (WCS) Climate Adaptation Fund (www.wcsclimateadaptationfund.org). Launched in 2011, the fund provides US 501(c)(3) non-profit conservation organizations with grants of between $50,000 and $250,000 for one- to two-year-long implementation-ready adaptation projects in the United States. Made possible by a grant from the Doris Duke Charitable Foundation, the WCS Climate Adaptation Fund is designed to support tangible, on-the-ground conservation projects that are "shovel-ready" (Wildlife Conservation Society, 2012). The pool of proposals to the fund offers a comprehensive indicator of the U.S. non-profit conservation sector's adaptation efforts, with >250 applicant organizations, including all major conservation nonprofits in the US, represented in this pool. Thirteen percent of proposals received funding from WCS for implementation; the vast majority of proposed projects also have other funding committed from one or more additional sources (see results). This indicates that these proposed projects represent feasible and intended activities at the cusp of implementation rather than ideas lacking in substance or potential.

We focused on pre-proposal applications rather than invited full proposals in order to assess the field as a whole rather than the subset of climate adaptation work that WCS was interested in funding. In their three-page pre-proposals, applicants were prompted to describe project activities, outcomes, and partners, and include a project budget describing at least a 1:1 match of their funding request from additional public and private funding sources **(Wildlife Conservation Society, 2011)**. Of 490 pre-proposals submitted to WCS from 2011-2015, we excluded those that did not describe any on-the-ground activities or re-submitted the same proposal over multiple years (in the latter case we only included the most recent proposal). This left 415 proposals submitted by 259 unique organizations for analysis.

Data extraction

We extracted data from proposals for a suite of variables (Table 1). We endeavored to capture how applicants describe their own work, rather than reading between the lines. A single coder extracted variables requiring higher levels of inference. For a more detailed analysis, we extracted additional information from a random subsample of 100 proposals. While we report exact percentages for this subsample, these should be considered close approximations, within ~5% of the true value of the population of proposals as a whole (see Appendix for subsample accuracy calculation methods). Unless noted, we report sample sizes for each variable in Table 1 instead of in-line in the results section.

We categorized proposals' adaptation strategies – their general approach to achieving conservation objectives in the face of climate change (e.g. ensure connectivity, protect refugia) – using categories modified from Stein et al. (2014). We chose these categorizations because they are clearly-defined and applicable across ecosystem types. We also added one category (facilitate change or pick winners) and several subcategories of strategies (Table 2). We also categorized proposed on-the-ground activities, which we define as actions undertaken to implement strategies (e.g. prescribed fire, in-stream engineering).

Bivariate analyses

To determine how strategies and activities were associated, we used a contingency table approach. We calculated the observed - expected number of proposals in each combination of strategy and activity, where expected = sum(row) × sum(column) / overall sum, to determine how many extra (or lacking) proposals there were in each category combination compared to the null hypothesis that the two variables are independent. We excluded activities and strategy categories (or subcategories) described in <15% of proposals in order to focus on categories with larger sample sizes and simplify visualizations.

We also used this approach to see how the climate impacts proposals were responding to were associated with geographic regions (see Fig. S1 for region map), excluding impacts described in <15% of proposals.

Geographic analyses

We characterized the geographic distribution of proposed projects by state by calculating the density of proposed projects per km^2. To assess how much the additional threat of sea level rise drives proposal densities in coastal states, we recalculated the density after removing proposals responding to this threat. Because very few proposals can lead to high proposal densities in the small states of the Northeast, we also ran this analysis by region instead of state (see Fig. S1 for region map).

To assess the alignment between the geographic distribution of proposals and exposure to climate threats, we compared the density or number of proposals that addressed six threats in each state, with state-level metrics of those threats from two sources (Table 3). The USGS National Climate Change Viewer and Climate Central climate data we used are both based on CMIP5 models of the high emissions (RCP 8.5) scenario, using 30 and 29 general circulation models, respectively (Alder and Hostetler, 2013; Climate Central and ICF International, 2015). Consistent state-level climate data covering both the 48 contiguous states as well as Alaska and Hawaii were unavailable for all threats except for sea level rise, so we did not include these two states in this analysis. We calculated all threat metrics as the increase in the threat from the baseline period to 2050. The metric for sea level rise incorporated land area in the calculation, so we compared it to the number of proposals per state; the five other threat metrics were state-level averages, so we compared them to the density of proposals per state. For each threat, we used linear regression to assess whether the threat and response metrics were correlated, first using visual inspection to choose between square root, cube root, log, or log(x+1) transformations to reduce skewness (Table S.2).

To identify states where practitioners lag behind in proposing responses to expected threats, we plotted the response metrics against threat metrics. Since we expect adaptation response to increase with threat, we plotted the predicted adaptation response as a line intersecting the point (0,0) and the mean values for threat and response, since we expect no response to no threat, and an average response to an average threat. We quantified each state’s residual from this line as an indication of how ahead (or behind) practitioners in the state are in their efforts to propose responses to predicted threats. We refer to this residual as their “relative response”, which we also used to rank states.

Post-hoc analyses

We ran several post-hoc tests to explore various outcomes of interest. We used Wilcoxon rank sum tests to test if, compared to other proposals, (1) proposals for projects in streams, rivers, riparian areas and floodplains differed in the number of committed funding sources and amount of committed public funding, (2) proposals focusing on fish differed in the amount of committed federal funding, and (3) proposals describing the “facilitate change or pick winners” strategy had different total project budgets. We used Chi-squared tests to test for associations between (1) proposals with and without a focus on fish and the “protect short-term, in situ refuges” and “ensure connectivity of abiotic elements” strategies, and (2) proposals with and without the “facilitate change or pick winners” strategy and different land ownership types, partnership types, and projects in forest ecosystems.

All analysis and mapping was done in R (version 3.2.4, R Core Team, 2016) with packages reshape2 (Wickham, 2007), ggplot2 (Wickham, 2009), fiftystater (Murphy, 2016) and cowplot (Wilke, 2016).

RESULTS

Project scale, context and funding

The median proposal had a total project budget of $400,000; 9% of proposals had total budgets >$1 million (N=415). The median proposed project was 24 months long and ~200 ha in extent, or 8.4 km for linear projects like stream restorations (N=414, 293 and 139, respectively). More projects were proposed on private than public land (70 vs. 57%, N=349) and in protected areas (65%) than working (39%) or other land uses (N=271). The 259 unique applicant organizations had a median annual organizational budget of $1.2 million, ranging from ~$13,500 to >$500 million (N=415). Proposals described >$84.1 million in total committed funding for the projects in question (N=413); 89% had at least some committed funding and 21% had their entire 1:1 match committed (N=400). For additional findings, see Table S3, S4 and S5.

Ecosystems, taxa and ecological functions

Most proposals (54%) were for projects in streams, rivers, riparian areas and floodplains ("river and riparian", Fig. 1A). Proposals in these ecosystems had more funding sources and marginally more committed public funding than other proposals (number of funding sources, W=16,424, p=0.0013, N=401; public funding, W=10,940, p=0.060, N=316).

Sixty percent of proposed projects focused on one or more named species and 32% focused on listed species or species of concern. Proposed projects focused more on animals than plants (93% vs. 60% of proposals), especially fish (41%) and birds (40%). Twenty-five percent of proposals focused specifically on salmonids (Fig. 1B). Proposals focusing on fish had marginally higher committed federal funding than other proposals (W=679.5, p=0.085; N=85).

Sixty-six percent of proposed projects focused on specific ecological functions. Hydrological functions were the most common (55% of proposals), especially maintaining water quality (30%, e.g. decrease sediment loads) and storage (28%, e.g. groundwater recharge; see Table S6 for these and additional categories).

Strategies and Actions

The most common strategies described were “restore previous structure and function” (72%) and “ensure connectivity” (62%) (Fig. 2 and Table S7).

Compared to proposals focused on other taxa, proposals focused on fish more often described the strategies “protect short-term, in-situ refuges” and “ensure connectivity of abiotic elements” (χ2(1) = 4.85, p=0.028 and χ2(1)=18.47, p=1.7e-05, respectively, N=100).

Proposals for projects in forest ecosystems were more associated with the “facilitate change or pick winners” strategy than projects in other ecosystems (χ2(1, N=100)=6.75, p=0.0094). We found no relationships between this strategy and land ownership, partnership types, or total project budget.

The most common on-the-ground activity was “planting” (55%), followed by “remove invasive or encroaching species” (34%, Table S8). The most positive associations between strategies and activities were “ensure connectivity for organisms” with “acquiring/protecting land”, and “reduce non-climate stressors” with “remove invasive or encroaching species” (Fig. 2).

Geographic distribution of projects and threats

Nineteen of 20 states along the Atlantic or Pacific Ocean had above median proposal densities, and 24 of 30 inland and Gulf coast states had below median proposal densities (Fig. 3A). By region, the Pacific and Northeast regions had the highest and almost identical proposal densities (Fig. S2A). After removing cases responding to sea level rise, proposed project densities remained above median in 15 of 20 states along the Atlantic or Pacific Ocean and below median in 20 of 30 inland and Gulf coast states (Fig. S2B).

Eighty-nine percent of proposed projects responded to direct, abiotic impacts, especially those related to moisture and hydrological cycles (including drying or drought, precipitation amount, timing or form, hydrology and inland flooding, 68%) and warming (63%). Twenty-one percent of proposed projects responded to indirect impacts mediated through other species, including invasive species (11%), disease, pathogens and pests (8%), and human responses to climate change (1%, see Fig. S3 for additional categories).

Responses to climate impacts were not uniform across regions. The most positive associations between the impacts proposals were responding to and regions were sea level rise in the South and drying/drought in the Mountain region (Fig. S3).

The density of proposed projects responding to snow loss increased with increasing snow loss projections (p=0.03, R^2=0.15, N=70 proposals, Fig. 3B). There were no relationships between exposure to the other threats and responses to those threats (warming N=247 proposals, Fig. 3C, fire, N=67, inland flooding N=75, sea level rise N=64, and drought N=157 proposals, Fig. S4).

Kentucky, Mississippi, Ohio and Oklahoma were in the bottom quartile of relative response rankings for 75% or more of the threats assessed in those states (see Table S10 for rankings of all states and all threats assessed).

DISCUSSION

Our synthesis of 415 implementation-ready adaptation project proposals in the U.S. conservation sector illustrates a previously uncharacterized landscape. Some striking overall patterns emerged. First, emerging adaptation efforts have a strong focus on fish, river and riparian areas, and hydrological functions. Second, traditional conservation strategies (e.g. “restore previous structure and function”) are most common, although other forward-looking approaches that attempt to “facilitate change” and “pick winners” are also being considered for implementation. Regardless of strategy, the management actions used to deploy adaptation strategies on-the-ground are traditional, well-established techniques. Third, adaptation efforts are unevenly distributed across the U.S., with little alignment between the geographic distribution of proposed projects and exposure to the threats they are responding to. Some states are particularly behind in proposing adaptation responses given their predicted exposure to climate change.

While our novel data allows for the first synthesis of an otherwise fragmented set of efforts, it also poses some limitations. Activities not funded by the WCS Climate Adaptation Fund (e.g. assisted colonization) are likely underrepresented, as are projects with budgets much larger than grant amounts; only 9% of proposed projects had budgets >$1 million. Forestry projects might be underrepresented if they are funded via timber sales rather than needing external funding. Like most researchers, we are unable to measure efforts that are adaptation in practice but not in name, which might be common due to the politicization of climate change in some regions (Hansen et al., 2013). We are limited to self-descriptions, and applicants likely frame proposals to fit the WCS Climate Adaptation Fund's stated priorities. We were unable to assess the "intentionality" of individual proposed projects – the demonstration of a purposeful and explicit linkage between climate impacts and conservation actions (Stein et al., 2014) – as teasing apart applicants' intentions was beyond the scope of this study. Instead, we focus on how conservation practitioners are approaching and describing adaptation, regardless of whether these projects will truly reduce vulnerability to climate change. Finally, our analysis allows us to describe patterns but does not explain them. Here, we offer hypotheses and speculate on causal factors that could be tested through subsequent research.

What ecosystems, taxa and ecological functions do proposed projects target?

Proposed adaptation projects showed a common focus on fish, river and riparian ecosystems, and hydrological functions (Fig. 1 and Table S6). This was exemplified by the one-quarter of proposed projects focusing on salmonids, which is more than focused on all amphibians and reptiles combined (20%), and vastly disproportionate to the number of such species in the US. These outcomes corroborate Capon et al.'s (2013) prediction that riparian areas will be adaptation foci in the 21st century.

Many factors could contribute to this uneven distribution of focus. First, this focus might be proportional to the importance, true vulnerability and potential adaptive capacity of these species, ecosystems and functions under climate change. Both coldwater fishes (Isaak et al., 2012) and riparian ecosystems (Capon et al., 2013) are thought to be vulnerable to climate impacts. Natural riparian areas are also considered to have high adaptive potential (Capon et al., 2013) and restoration of riparian areas has been championed as an adaptation response because of their resilience (Seavy et al., 2009). Relative to surface area, riparian ecosystems have outsize roles in providing ecosystem functions, and both the connectivity and heterogeneity that underpin this are threatened by (Capon et al., 2013) and critical to adapting to climate change (Seavy et al., 2009). Many multi-benefit adaptation options have also been identified in riparian ecosystems (Capon et al., 2017).

Second, the dominance of river and riparian, hydrological and fish-focused proposals could also reflect established policies and interest groups. Adger et al. (2005) conjectures that climate responses are proportional to the strength and power of the actors that define the problem. The means for adaptation, including developed institutions and networks explicitly concerned with their management, are well established in riparian ecosystems (Capon et al., 2013). Moreover, these ecosystems and taxa attract support from water managers and anglers in addition to conservationists. Our finding that committed federal funding trended higher in proposals focused on fish vs. other proposals aligns with the disproportionate federal spending on endangered and threatened fish (Evans et al., 2016). Similarly, proposals for projects in river and riparian ecosystems had more funding sources and public funding, demonstrating strong support for efforts targeting these systems. The extent to which these patterns are driven by the strength of this sub-sector raises questions about whether these proposals represent real shifts in strategy or are instead reframing existing work that might or might not reduce climate vulnerability.

Finally, long-standing concerns in fish, river and riparian ecology could have enabled early adoption of the concepts, processes and strategies required for developing adaptation projects. Fish ecologists have long focused on short-term refuges from heat (e.g. Swift and Messer, 1971) and connectivity of streams and stream fragmentation (e.g. Sheldon, 1988), issues heightened in the face of climate change. Indeed, we found that compared to other projects, project proposals focused on fish were more often associated with the strategies “protect short-term, in-situ refuges” and “ensure connectivity of abiotic elements”. Moreover, overlapping usage of the terms “refugium” and “refuge” (Davis et al., 2013; Keppel and Wardell-Johnson, 2012) might have facilitated a transition from traditional concerns about short-term refuges (which temporarily buffer climate impacts on ecological timescales) to newer concerns about long-term refugia (which maintain stable climates over evolutionary timescales) in this sub-sector.

Regardless of the reason, this finding suggests that other taxa, ecosystems and ecological functions beyond those associated with river and riparian ecosystems deserve additional attention.

What strategies and activities are proposed?

Strategies

The two most common strategies proposed in our dataset– restore previous structure and function, and ensure connectivity (Fig. 2 and Table S7) – are widely used in conservation in general. Restoration, for example, is a $25 billion industry in the U.S. (BenDor et al., 2015) focused largely on restoring previous structure and function. Some have suggested restoring ecosystem functions as a potential adaptation strategy (Harris et al., 2006; Mawdsley et al., 2009) even if historical conditions are targeted (Hanberry et al., 2015). Others have noted the challenge of restoration to historic targets in the face of climate change (e.g. Harris et al., 2006; Millar et al., 2007). Given this strategy’s dominance in project proposals, we encourage more critical assessment of which structures and functions might sustain themselves while also effectively reducing ecological vulnerability under directional changes.   For example, projects focused on restoring fire might fare well under climate change, while other historic functions could be difficult to maintain long-term without perpetual, intensive management. The frequent use of connectivity as a proposed strategy parallels its prevalence as an adaptation recommendation in the literature (Heller and Zavaleta, 2009) and is unsurprising given its widespread applicability for responding to non-climate stressors like habitat fragmentation (Hanski, 1998). Finally, the WCS Climate Adaptation Fund RFP listed both restoration and connectivity as efforts they would support, perhaps prompting applicants to describe these strategies in particular.

In contrast, the "facilitate change or pick winners" strategy, described in 20% of proposals, is relatively novel. Such efforts include, for example, forestry projects that plant drought-tolerant species or seed sources predicted to succeed in a drier future (e.g., from lower-elevation or lower-latitude areas), or projects to convert coastal agricultural uplands to salt marsh instead of historic wetlands in the face of sea level rise. These efforts actively promote species or ecosystems predicted to do better in the future – or stop supporting those predicted to decline. They are noteworthy because efforts to resist change have heretofore been the focus of most adaptation in the conservation sector (Stein et al., 2013). Such transformative efforts may be considered unconventional (Swanston et al., 2016) and at times appear to violate longstanding and hard-won standardized practices (Kates et al., 2012) such as seed sourcing guidelines. However, they might be more effective over the long-term than those aiming for resistance, especially when focused on the persistent and directional changes we are more certain about (e.g. warming, sea level rise). This strategy could allow for gradual transition to such conditions and avoid catastrophic conversion (Millar et al., 2007) as it works with instead of against changing conditions on the ground.

Given potential barriers to such novel approaches, including institutional and behavioral inflexibility and perceived costs (Kates et al., 2012), we expected to see more limited public partnerships and public land involved in such efforts, as well as higher overall budgets. We did not find any of these associations, indicating that some perceived barriers may not be prevalent. Given the relatively small scale of projects proposed in this pool, efforts of this type can serve as pilots so that in the future practitioners can justify and scale up such approaches in the face of potential institutional pushback.

We also found an association between the "facilitate change or pick winners" strategy and proposals in forest ecosystems and using silviculture activities. Clear economic stakes in managed forestry settings might encourage the use of more experimental, novel strategies, whereas in other settings, practitioners may be more inclined to retain traditional, lower-risk and psychologically-comfortable strategies. In addition, long-lived trees may delay natural responses in forest ecosystems, necessitating more hands-on, forward-looking approaches. This aligns with reports of such approaches in the forestry sector (Ontl et al., 2017), and its early pursuit of assisted colonization (e.g. British Columbia's Assisted Migration Adaptation Trial, which began planning in 2006, Leech et al., 2011). Given these findings, the forestry sector might serve as a source of transformative strategies as they become increasingly needed in other ecosystems.

Activities

The most commonly proposed activities (Fig. 2) were traditional, long-standing management techniques rather than novel activities. This demonstrates that adaptation on-the-ground is currently not a mysterious thing but rather comprised of quite every-day management actions (Lawler, 2009; Mawdsley et al., 2009). This could mean that implementing projects often does not require new skills, tools or techniques. Rather, what makes adaptation unique could be the places, times and reasons these actions are implemented (Lawler, 2009; Mawdsley et al., 2009; Stein et al., 2013). For example, invasive species removal is a long-standing practice, but can be targeted at sites expected to serve as refugia in the future. Fencing to reduce grazing pressure is a well-established conservation tool, but in adaptation projects might be targeted at a movement corridor expected to facilitate species range shifts. In-stream changes and engineering are common components of traditional stream restoration, yet can be designed to help attenuate increasing flood events expected in some regions under advancing climate change. This suggests that the early stages of an adaptive management program – impact and vulnerability assessments, identifying intervention points, and developing and deciding on plans – are where learning and development needs are greatest. Once plans are in place and funding is secured, actually setting plans into motion on the ground might not necessarily require learning new technical skills. Even some skills perceived as novel, such as translocating organisms beyond their native range, have been used for conservation outside of the climate change adaptation context (Schwartz et al., 2012) and are widespread in other sectors (e.g. horticulture). Nevertheless, it could be that novel management techniques remain to be developed that would further enhance efforts to adapt conservation to climate change.

Finally, our analysis illustrates how practitioners are deploying specific strategies on the ground through specific activities (Fig. 2). Some associations are unsurprising – for example, ensuring connectivity for organisms (strategy) by acquiring or protecting land (activity), presumably to form wildlife corridors. Others were weaker but less expected, such as the association between the “facilitate change or pick winners” strategy and silviculture activities (described above). This analysis helps connect the dots between general concepts and the very tangible actions that managers use to translate and actualize them in specific contexts.

What is the distribution of proposed projects relative to geography and specific threats?

Proposed climate adaptation projects were not distributed evenly across the U.S. The higher density of proposals in the states along the Atlantic and Pacific Ocean compared to Gulf coast and inland states (Fig. 3A) could result from several factors. Removing proposals responding to sea level rise decreased but did not eliminate the disparity between proposal densities in Atlantic and Pacific coasts compared to the rest of the country (Fig. S2). Southern states generally had low overall proposal densities (Fig. 3A and Fig. S2A), with the projects that were proposed disproportionately focused on sea level rise (Fig. S3). Despite this focus, states in the South were still underprepared for sea level rise projections: Fig. S4C). Berrang-Ford et al. (2011) hypothesize that dramatic, observable changes lead to more adaptation action than creeping impacts; sea level rise might be considered one such threat.

Low proposal densities in the South and Midwest even after we removed sea level rise proposals (Fig. S2) indicate that additional factors drive the disparity observed among regions. These could include geographic differences in prevailing public opinion and policy preferences about climate change (Mildenberger et al., 2017), regulatory requirements (Hansen et al., 2013) or the presence of conservation resources and organizations. The availability of trust or public lands might also contribute to this distribution. Finally, WCS's network and outreach efforts may be non-uniform across the U.S. While their efforts from 2011-2015 were distributed as widely as possible via their networks and those of their partners, they did not systematically target each state; more recently, they have provided targeted training opportunities in regions that have yielded relatively few applications. Understanding these potential drivers is beyond the scope of this study but deserves further attention to increase adaptation efforts in under-represented geographies.

Proposals also were not distributed evenly across the climate change impacts they addressed. The overall lack of focus on indirect, biotic impacts highlights an area in need of more attention, since such impacts can have wide-ranging effects (Tylianakis et al., 2008). Only 1% of proposals addressed human responses to climate change, which is inconsistent with potentially dramatic impacts of responses such as sea walls, shifts in agriculture and groundwater extraction (Maxwell et al., 2015). We found a distribution of responses to snow loss that was proportional to threat at the national scale (Fig. 3B), but no relationship between proposals and exposure to the other five threats we analyzed (Fig 3C and A.4). This is in some ways unsurprising, since there has been little national or top-down coordination of adaptation efforts (Bierbaum et al., 2013), leaving individual practitioners and agencies to respond independently. Moreover, the ecosystems and locations targeted by conservationists within a state may be impacted by local-scale impacts that differ from those at the state scale. This underscores a need for coordinated identification of the most pressing threats at regional to local scales. Finally, the low relative response rankings for Kentucky, Mississippi, Ohio and Oklahoma (Table S10) highlight a need for more attention and resources to getting adaptation projects launched in these locations.

While our study does not reveal the reasons for these geographic and threat gaps, our analysis highlights places in need of more resources and support, such as capacity building, supportive policies, and/or funding. Given that the causes for these gaps in each place are likely to be unique, the solutions for addressing those gaps might differ as well. We do not suggest shifting resources away from states with high proposal densities or relative responses. Our analysis ranks the state relative to each other, not relative to the problem; while some states are doing better compared to others, their absolute responses to climate change threats may still fall short of the scale of the threats posed. More resources likely need to be directed to all states for this work, but especially those with identified gaps.

Conclusions

By synthesizing a fragmented field, this work addresses a gap in our understanding and can aid in strategic resource allocation and targeted outreach to advance adaptation efforts. Our assessment has also highlighted specific areas where opportunism and rebranding need to be evaluated. For example, the focus on some long-standing conservation strategies (e.g., restore previous structure and function) and targets (fish, river and riparian areas) may be logical and necessary ways to build momentum in the field. On the other hand, these foci invite further assessment to ensure that these efforts are truly adaptive rather than adaptation in name only. Finally, we hope the illustration of specific and traditional management techniques being deployed in the service of adaptation serves to embolden practitioners to incorporate climate change into their on-the-ground strategies for conservation and stewardship.

FIGURES AND TABLES

Table 1. Variables extracted and sample size.

Project scale, context and funding	N
Time and geographic scale	415 [2]
Total project budget	
Land ownership and use [1]	
Applicant's annual organizational budget	
Committed funding: amount and source type [1]	
Partnerships: partner type [1, 3]	265
(1) What ecosystems, taxa and ecological functions do proposed projects target?	
Ecosystem [1]	415
Species focus (y/n)	100
Listed species focus (y/n) [4]	
Taxa [1]	
Ecological function focus (y/n) and type [1]	
(2) What strategies and activities are proposed?	
Strategies [1]	100
On-the-ground activities [1]	
(3) What is the distribution of proposed projects relative to geography and specific threats?	
U.S. State [1]	415
Climate impacts [1]	

[1] Proposals could be coded for >1 non-exclusive category.

[2] Some proposals did not provide enough information to extract these variables; see results for the number successfully extracted and analyzed.

[3] Only extracted for proposal submitted in 2011-2013 due to a change in the wording of the application question in subsequent years.

[4] Based solely on information provided in project proposals (vs. our prior knowledge), and including any species on state lists or "species of concern".

Table 2. Adaptation strategies & definitions, modified from Stein et al. (2014). For differences from Stein et al. (2014) and categorization rules of note, see Table S1

Restore previous structure and function: Rebuild, modify or transform ecosystems that have been lost or compromised, in order to restore desired structures (e.g., habitat complexity) and functions (e.g., nutrient cycling) to a previous condition or state.
Ensure connectivity: Protect, restore and create landscape features that facilitate movement among resource patches. **Movement of organisms** **Movement of abiotic elements** (e.g. water, nutrients) **Movement of habitat**
Protect refugia: Protect, restore, manage or create areas less affected by climate change, as sources of "seed" for recovery in the present, or as destinations for climate-sensitive migrants in the future. **Long-term *in situ* refugia:** Target areas within the species' current range that have long-term stable climates; akin to evolutionary refugia (as described by Keppel et al., 2012). **Short-term *in situ* refuges**: Target areas within the species' current range that provide temporary relief from climate impacts on ecological timescales (as described by Keppel et al., 2012). ***Ex situ* refugia:** Target habitat outside of the species' current range, but likely to be within the future climate space of the species.
Reduce non-climate stressors: Minimize localized human stressors (e.g., pollution) that hinder the ability of species or ecosystems to withstand or adjust to climatic events.
Protect key ecosystem features: Focus management on structural characteristics, organisms, or areas that represent important "underpinnings" or "keystones" of the current or future system of interest **Protect keystone organisms or ecosystem engineers** **Focus on sites with key functions,** especially sites that cannot readily shift (e.g., springs in arid ecosystems, islands, spawning sites, leks). **Protecting geophysical heterogeneity and "nature's stage".** Target geophysical land facets, climatic diversity or "enduring features" that are likely to remain relatively static over time (Anderson and Ferree, 2010; Beier and Brost, 2010).
Facilitate change or pick winners: Actively or passively facilitate community or ecosystem transition away from the current state and towards a more suitable or desired state as climate changes within a site. Target species, community types, genotypes or phenotypes adapted to future conditions, or decrease those least adapted to future condition.
Relocate organisms: Engage in human-facilitated transplanting of organisms from one location to another in order to bypass a barrier.
Support evolutionary potential: Protect a variety of species, populations and ecosystems in multiple places to bet-hedge against losses from climate disturbances, and where possible manage these systems to assist positive evolutionary change.
Other. E.g., enlarge protected areas or habitat, promote recovery after disturbances, eliminate a disease expected to increase with climate change.

Table 3. Metrics used to compare climate threats and conservation response, for 48 contiguous US states unless noted

Threat	**Threat metric** (change between baseline and future period)	Baseline	Future	Response metric
Warming	Average temperature (mean of monthly maximum and minimum, ^{o}C)[1]	1950-2010	2041-2060	Density of proposals responding to warming
Snow loss	Average monthly snow water equivalent (mm) [1, 3]	1950-2010	2041-2060	Density of proposals responding to decreasing snowfall, snowpack, or snowmelt
Dryness	Average monthly evaporative deficit (mm/mo.) [1]	1950-2010	2041-2060	Density of proposals responding to dryness or drought
Wildfire	Average annual number of days with high wildfire potential [2]	1991-2010	2041-2060	Density of proposals responding to wildfire
Inland flooding	Average annual severity of high flow events [2]	1991-2010	2041-2060	Density of proposals responding to inland flooding
Sea level rise	Land area in FEMA 100-year Coastal Flood Plain [2, 4]	2000	2050	Number of proposals responding to sea level rise

[1] Calculated using data from USGS National Climate Change Viewer (Alder and Hostetler, 2013)

[2] Provided by Climate Central (Climate Central and ICF International, 2015)

[3] For 34 contiguous US states with mean monthly snow water equivalent >1 mm in baseline period.

[4] For 22 coastal contiguous U.S. states.

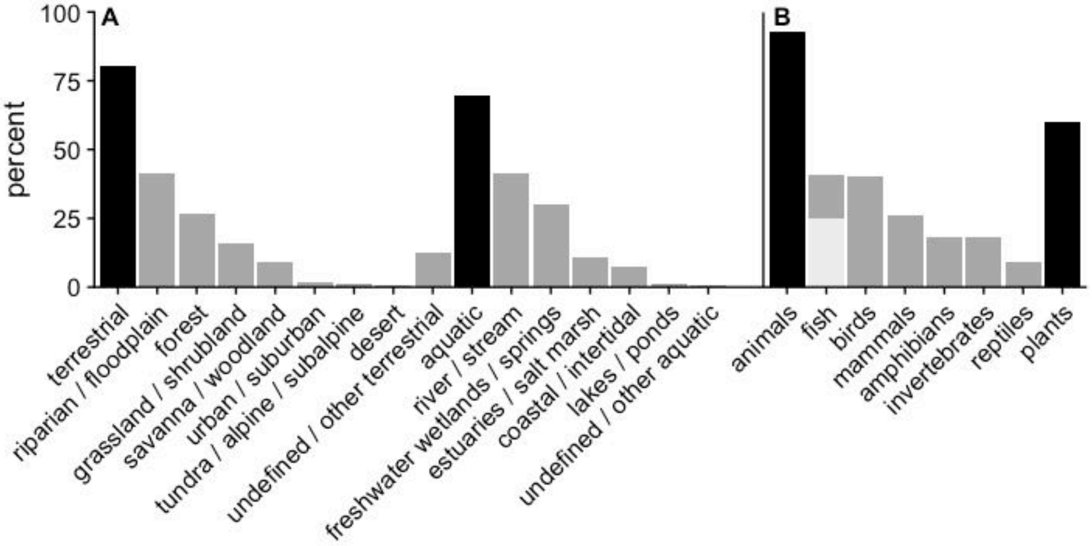
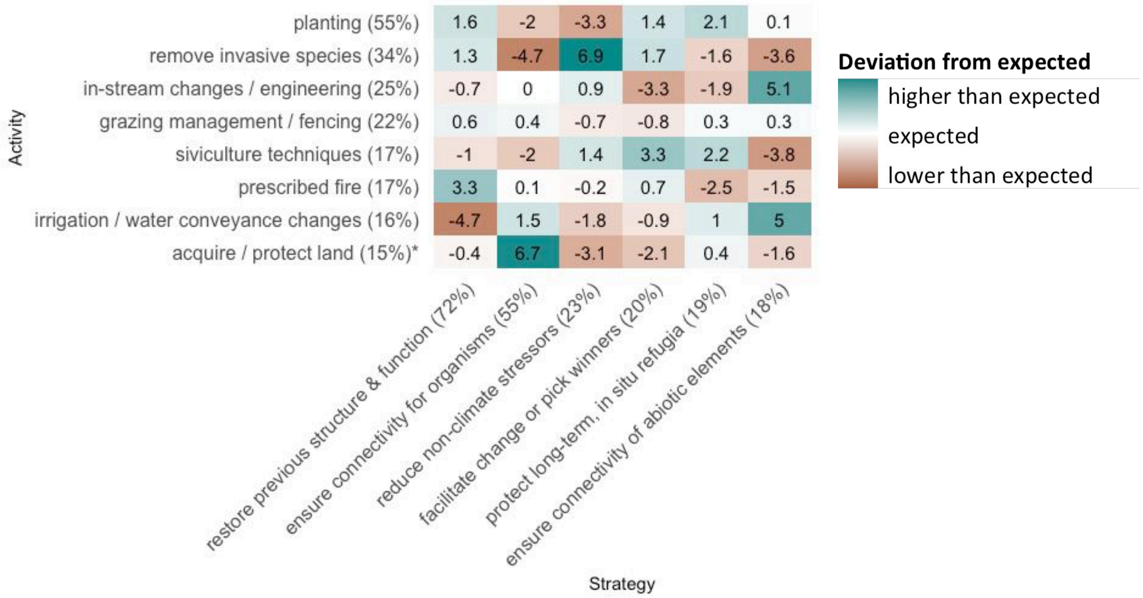


Figure 1
A. Proposed U.S. climate adaptation project ecosystems, grouped by terrestrial and aquatic ecosystems (black) and specific ecosystem types within each black bar (grey). N=415.
B. Taxonomic foci of proposed project, grouped by animals and plants (black) and specific animal types (gray). Light grey indicates proposals that included a focus on salmonids. N=100.
Proposals could fall into >1 category so percentages total to >100%.



	restore previous structure & function (72%)	ensure connectivity for organisms (55%)	reduce non-climate stressors (23%)	facilitate change or pick winners (20%)	protect long-term, in situ refugia (19%)	ensure connectivity of abiotic elements (18%)
planting (55%)	1.6	-2	-3.3	1.4	2.1	0.1
remove invasive species (34%)	1.3	-4.7	6.9	1.7	-1.6	-3.6
in-stream changes / engineering (25%)	-0.7	0	0.9	-3.3	-1.9	5.1
grazing management / fencing (22%)	0.6	0.4	-0.7	-0.8	0.3	0.3
siviculture techniques (17%)	-1	-2	1.4	3.3	2.2	-3.8
prescribed fire (17%)	3.3	0.1	-0.2	0.7	-2.5	-1.5
irrigation / water conveyance changes (16%)	-4.7	1.5	-1.8	-0.9	1	5
acquire / protect land (15%)*	-0.4	6.7	-3.1	-2.1	0.4	-1.6

Figure 2. Contingency table of the observed minus expected number of U.S. climate adaptation project proposals (expected = sum(row) × sum(column) / overall sum) in each combination of strategy and activity.

Cells are colored by their deviation from expected. Percentages in the row and column labels indicate the percentage of proposals describing this activity or strategy overall. Proposals could fall into >1 category so percentages total to >100%. For strategies and activities listed in <15% of proposals, see Tables A7 and A8. N=100.

* The WCS Climate Adaptation Fund only funded easements and land acquisition in 2011-2012; while applicants could list these activities as part of a larger project in subsequent years, they are likely underrepresented in this data set.

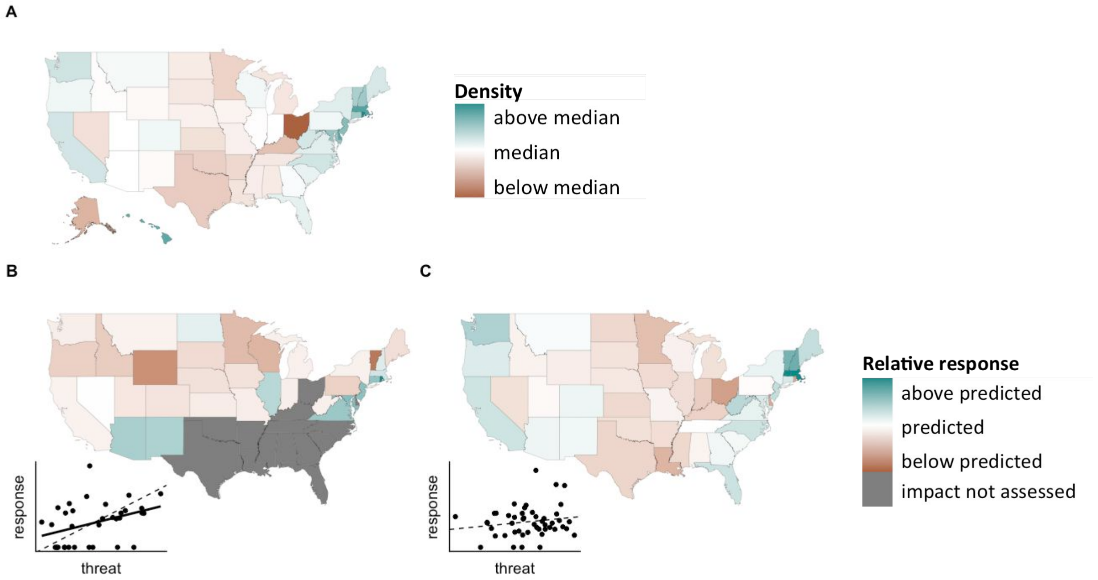


Figure 3.
A. Total climate adaptation proposal density by state (number / km^2).
B-C. Comparison of state-level threats and responses to **(B)** snow loss and (**C**) warming. ***Inset plots*:** Each state is a point. The x-axis is the increase in threat in 2050 from baseline conditions and the y-axis is the response as represented by density of proposed projects in this study (Table 2). The dashed line represents the predicted response (see Methods section 2.4). For (**B**) snow loss, the best-fit regression line through the points is significant (p=0.03, R^2=0.15, N=70 proposals) and shown (solid line). ***Maps:*** States are colored by their relative response (deviation from predicted response).

SUPPORTING INFORMATION

Supplementary Methods

Analysis of subsample accuracy

To determine the accuracy of an N=100 subsample, we re-calculated summary statistics for 1,000 random N=100 subsamples for all categorical and binary variables (except U.S. states) extracted from the full set of 415 applications. We found that the median subsampled variable had 90% of its distribution within -5.0 and +4.9% of the true population percentage.

Table S1: Differences between strategy categorizations and those from Stein et al. (2014), and categorization rules of note.

Restore previous structure and function	Unlike Stein et al. (2014), we only included restoration to previous condition or state in our "restoration" category; restoration to a novel state were included in the "facilitate change or pick winners" strategy.
Reduce non-climate stressors	Does not include improvements to habitat fragmentation (included in "ensure connectivity") nor reducing habitat degradation or fire suppression (include in "restore structure and function")
Facilitate change or pick winners	Added, given focus on changing goals and letting go of past states in the literature (Cole and Yung, 2012; Glick et al., 2011; Heller and Zavaleta, 2009; Millar et al., 2007; Stein et al., 2014, 2013). Focus is within a site; efforts to facilitate movement between sites were classified as "ensuring connectivity".
Support evolutionary potential	Targeting genetic and species diversity and meta-populations are near-universal strategies in traditional conservation, and are often conflated with conservation goals, so we only counted proposals that explained why this strategy would help in the face of climate change. Without this additional standard, almost all applications would have fallen into this category.

Figure S1: Regions used in this study (using U.S. Census-defined divisions, but separating Alaska and the Pacific and Mountain regions)

Table S2: Data transformations applied to climate threat and response metrics.

threat	**threat metric transformation**	**response metric transformation**
snow loss	log	cube root
warming	(no transformation)	square root
fire	cube root	cube root
flooding	(no transformation)	cube root
sea level rise	log	log(x+1)
dryness	square root	square root

Supplementary results

Table S3: Project context before project took place.
Twenty-two percent of projects included a change in land use, and 18% converted non-protected areas to solely protected areas (without additional land uses). Projects could fall into >1 category, so percentages total to >100%.

Land ownership (N=349)		**Subcategory percent**	**Category percent**
Private			71
	Not specified	42	
	Land trust / non-profit, including easements	39	
	Agriculture / ranch	12	
	Other	5	
Public			57
	Federal	34	
	State	16	
	Other (incl. tribal, city, county)	9	
	Not specific	7	
Land use (N= 271)			
Protected area (including easements)			65
Working			39
	Agriculture	19	
	Rangeland / ranch	17	
	Timber	8	
Suburban / urban / residential			8
Other			7
Recreation			4
Ex-situ (gardens, seedbanks)			2

Table S4: Percent of projects with various partnership types.
From prompt to list "other principal individuals / organizations involved". Extracted for 2011-2013 proposals only due to a change in the wording of the application question in subsequent years. Most proposals (51%) had partnerships with two or more of private, federal, state and other public entities. N=265.

Partnership type		Subcategory percent	Category percent
Public			71
	Federal	46	
	State	43	
	Other public (ex. county, tribe)	20	
Private			52
University [1]			19
Total with any type of partner			89

[1] For partnerships, universities were categorized separately to distinguish researchers at state universities from public partnerships such as policymakers and agencies. For funding (below), universities were categorized as state or private as appropriate.

Table S5. Project support.
From applicants' 1:1 match descriptions, which were listed as anticipated or committed. Proposals varied in the amount of detail provided so results represent minimums. Most proposals with committed funding (56%) had funding from two or more of private, federal, state and other public sources.

Funding source [1]	**Percent of projects with some committed funding** from this source		**Median amount committed** for those with this source (thousands USD)				**Total commitment** represented by this pool (millions USD)	
	Sub-category	**Category**	**N**	**Sub-category**	**Category**	**N**	**Sub-category**	**Category**
Public		59	392		99.5	388		49.8
Federal	39		364	60.0		354	20.5	
State	37		371	60.0		365	20.9	
Other public (ex. county, tribe)	18		359	51.5		356	8.5	
Private		83	373		60.0	355		31.3
Unclear		NA	NA		NA	NA		3.0
Total from any source		89	400		108.9	400		84.1

[1] We counted the source as the final granting entity before the proposed project (ex. if the U.S. Fish & Wildlife Service provided a State Wildlife Grant to a state agency, which then allocated funds to a proposed project, we counted this as a "state" funding source.) Therefore our analysis is biased towards local rather than federal funders.

Table S6: Ecological function foci.
Projects could have >1 ecological function foci, so percentages total to >100%.

Rank	Function	Description / examples	Subcategory percent	Category percent
1	Hydrological functions			55
	Water quality	Reduce sediment, nutrient, nitrate, surface runoff and other pollution inputs/loads entering or flowing through streams/rivers; increase infiltration; reduce turbidity	30	
	Catch & store water at or below surface	Increase water/precipitation storage, penetration, retention and release; promote runoff; increase soil water-holding capacity; increase groundwater, aquifer or water table exchange, recharge, filtration, storage or levels; reduce groundwater depletion, seepage or transmissivity.	28	
	Stream flows	Flows or flow duration; allow stream flow to access smaller channels; floodplain connectivity	19	
	Decrease erosion	Decrease eroded sediment, erosive force or washout risk	16	
	Mitigate floods	Mitigate impacts or risks of floods; flood attenuation, control, storage, absorption or protection; provide flood barrier; buffer flood peaks; slow flood flows.	14	
	Sediment transport	Sediment evacuation or redistribution	6	
2	Maintain or buffer temperatures	Maintain temperatures or moderate temperature fluctuations		21
3	Buffering against extremes	Reduce, buffer, absorb, dampen, stabilize or attenuate storms, disturbances or extreme events. Used when there was not enough details to place the application into a more specific category.		11
4	Fire	Maintain fire cycles or regimes; decrease wildfire risk		10
5	Sediment creation or retention	Sediment accretion, deposition, augmentation, storage or accumulation; counter subsidence; increase soil organic matter. Used for cases not falling into the "water quality" category above		7
6	Productivity	Primary or food web productivity		6
6	Resist pests / pathogens / invasives	Ecosystem's intrinsic ability to resist pests, pathogens or invasive species		6
8	Shoreline stabilization / protection	Protect, withstand or buffer against storms or sea level rise		3
	Vague only	Ecosystem/landscape "functionality"; "functional" or "functioning" ecosystems/landscapes; hydrological or geomorphic "processes". Used only for proposals that did not also name specific functions		8
	Other	Ex.: decomposition; food web interactions; trophic energy exchange; mitigating windblown sediment		18

Table S7: Adaptation strategies.
Projects could describe >1 adaptation strategy so percentages total to >100%

Rank	Strategy	Subcategory percent	Category percent
1	Restore previous structure and function		72
2	Ensure connectivity		62
	Movement of organisms	55	
	Movement of abiotic elements	18	
	Movement of habitat	4	
3	Protect refugia		40
	Long-term *in situ* refugia	19	
	Short-term *in situ* refugia	14	
	Ex situ refugia	10	
4	Reduce non-climate stressors		23
5	Protect key ecosystem features		21
	Protect keystone organisms or ecosystem engineers	11	
	Focus on specific sites with key functions	6	
	Protecting geophysical heterogeneity and “nature’s stage”	5	
6	Facilitate change or pick winners		20
7	Relocate organisms [1]		13
8	Support evolutionary potential		9
	Other		20

[1] The Climate Adaptation Fund did not fund introductions nor assisted colonization from 2011-2015, so this strategy is likely underrepresented in this sample.

Table S8: Activities.

Activity categories may not be mutually exclusive, since some applicants provided more specific details than others. Projects could have into >1 so percentages total to >100%.

Rank	Activity	Description / notes	%
1	Planting	Includes seeding, irrigating newly planted plants	55
2	Remove invasive species	Includes encroaching species, “brush control / management”, and preventing invasions.	34
3	In-stream changes / engineering	Includes: • Install boulders, wood debris or structures, simulated beaver dams, stream barbs, baffles, sediment & flow-control structures • Abandon or re-route channels, stabilize channels / banks, dredge creeks • Dam removal • Install or remove fish passage structures, barriers	25
4	Grazing management / fencing	Construct, modify or remove wildlife-friendly fencing. Includes projects for both wild herbivores and livestock.	22
5	Prescribed fire		17
	Silviculture techniques	• Harvest prescriptions, single-tree selection, group selection, no-harvest reserve areas • Fuel management, mechanical fuel reduction, thinning • Diversify age & structure of forests, species mix • Crop-tree release w. canopy gap formation	
7	Irrigation / water conveyance changes	Replace, construct or remove irrigation diversions, reuse pits, tanks, pipelines, culverts, road-stream crossings (incl. bridges), irrigation and other water delivery systems, or drainage tiles, structures and ditches. Includes “coordination of diversion and pumping”	16
8	Acquire / protect land *	Easements, fee acquisition, “habitat protection”.	15
9	Establish wetlands / salt marsh	Includes vernal pools and ponds, installing swales	11
10	Assist, manage or translocate animals		9
	Management restrictions via contracts, existing regulations, ordinance	Includes transfer, purchase or change of water lease or rights, Conservation Reserve Program contracts, coverage under federal and state Endangered Species Acts, forest certification	
12	Berm / levee creation, re-contour, removal		8
	Collect seeds, grow seedlings	Collect, propagate or cross cuttings or pollen; establish orchard	
14	Soil preparation / management / erosion control		6
15	Install flow control devices, water control structures		5
	Install tanks / ponds	Install livestock waters, tanks for wildlife, change or	

		improve tanks / ponds	
17	Remove roads / re-contour abandoned roads / remove infrastructure		4
18	Pollution cleanup		3
20	Build wildlife crossing bridge or remove wildlife barrier		2
	Dam management	Coordinate flows; use attraction flows	
	Farming practices	Inter-plant crops, create windbreaks, permaculture, farm buffer areas	
	Install pumps or wells	Not for tanks / ponds	
	Reduce wildlife conflict or harvest		
	Soil / sediment augmentation	Broadcast dredged material, thin layer deposition	
	Supply with additional water		
27	Challenge planted trees with infection		1
	Leave storm overwash fans in place		
	Trail engineering		
	Vague only	Ex. “habitat restoration”, “rehabilitation” or “improvement”. Used only for proposals that did not also name specific activities.	4

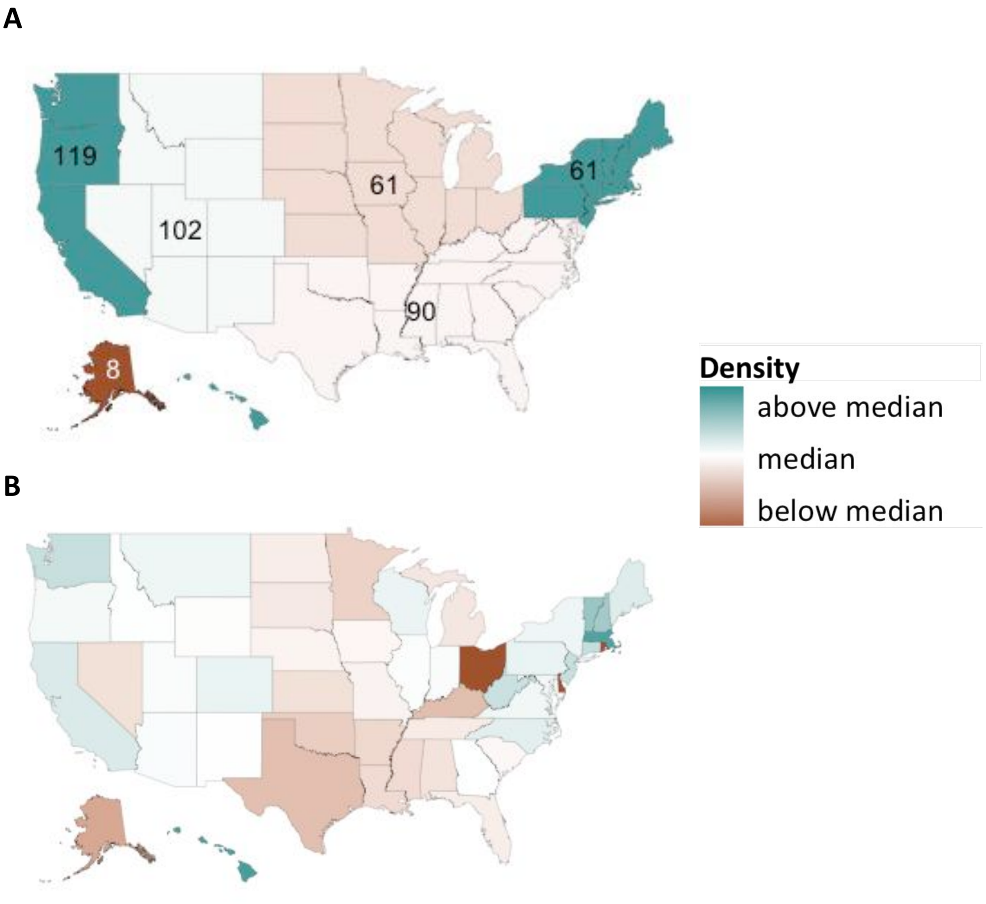
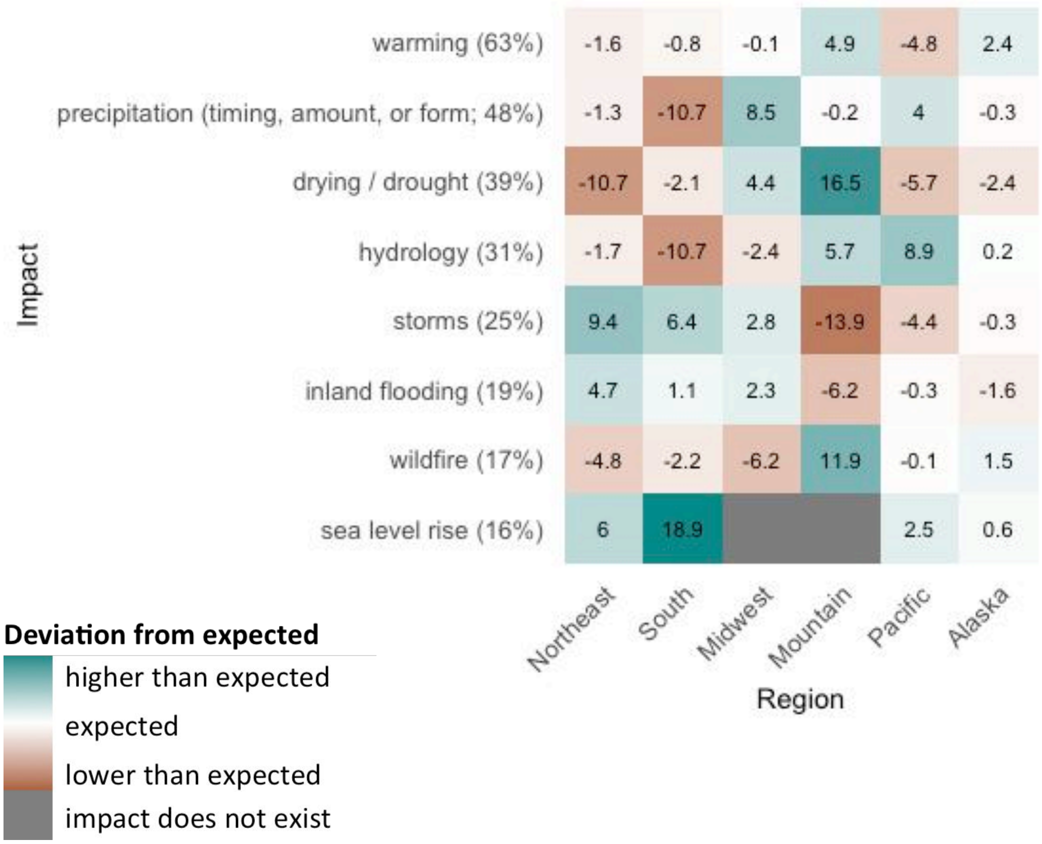


Figure S2: Density of project proposals per km^2.
A. By region. Regions are labeled with the number of proposals included in the study.
B. Excluding projects responding to sea level rise.

Table S9: Climate impact types responded to.
Projects could have into >1 so percentages total to >100%. (N=415)

	Percent
Averages	84
Extreme	58
Variability	19
Documented / current	93
Predicted / future	49



Impact	Northeast	South	Midwest	Mountain	Pacific	Alaska
warming (63%)	-1.6	-0.8	-0.1	4.9	-4.8	2.4
precipitation (timing, amount, or form; 48%)	-1.3	-10.7	8.5	-0.2	4	-0.3
drying / drought (39%)	-10.7	-2.1	4.4	16.5	-5.7	-2.4
hydrology (31%)	-1.7	-10.7	-2.4	5.7	8.9	0.2
storms (25%)	9.4	6.4	2.8	-13.9	-4.4	-0.3
inland flooding (19%)	4.7	1.1	2.3	-6.2	-0.3	-1.6
wildfire (17%)	-4.8	-2.2	-6.2	11.9	-0.1	1.5
sea level rise (16%)	6	18.9			2.5	0.6

Figure S3: Contingency table showing the observed-expected number of projects (expected = sum(row) × sum(column) / overall sum) in each combination of climate impact and region.

Percentages in row labels indicate the percentage of projects responding to this impact overall (N=415). Impacts in <15% of projects are not shown: sediment/erosion (14%), invasive species (11%), disease, pathogens or pests (8%), phenology changes (4%), and human responses to climate change, CO_2 increase and ocean acidification (1% each).

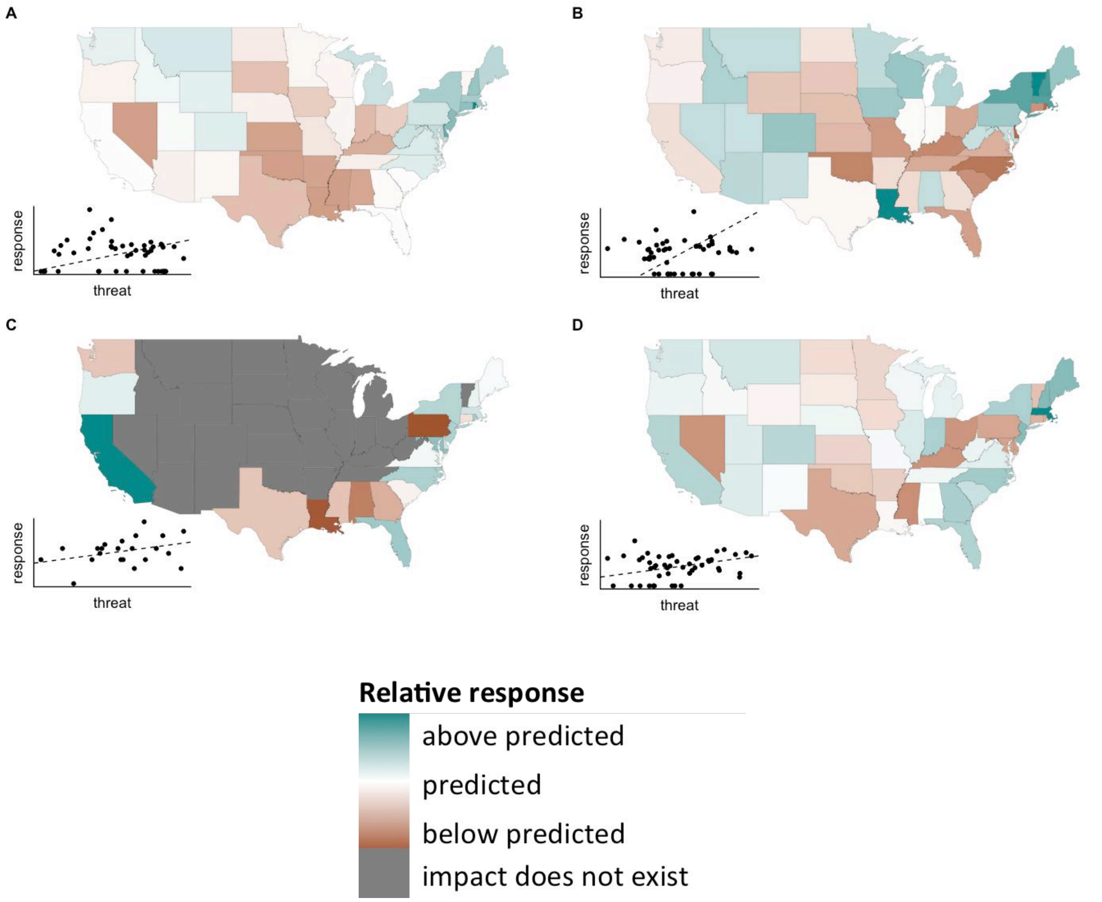


Figure S4: Comparison of state-level threats and conservation responses to (**A**) fire, (**B**) flood, (**C**) sea level rise and (**D**) dryness.

Inset plots: Each state is a point. The x-axis shows the increase in threat in 2050 from 2000 conditions, and the y-axis shows the conservation response as represented by the number of density of project proposals in this data set (see Table 2 for metrics). The dashed line represents the predicted response (see Methods section 2.4). The best-fit regression lines were not significant for these four threats and are not shown. ***Maps****:* States are colored by their relative response (deviation from the predicted response).

Table S10. State rankings by overall project density and relative response for each threat.
Green and red indicate top and bottom quartile ranking for each column, respectively.
Grey boxes indicate threats that were not assessed in that state.

state	Total project density ranking	Relative response ranking					
		snow loss	warming	fire	flood	sea level rise	drying / drought
AK	49						
AL	37		25	42	15	20	28
AR	44		35	43	31		36
AZ	25	6	17	32	13		16
CA	12	13	9	22	29	1	10
CO	20	23	16	16	6		11
CT	8	4	12	4	42	15	39
DE	3		46	2	48	8	43
FL	17		8	21	40	3	9
GA	24		18	24	30	19	6
HI	4						
IA	32	24	37	37	10		32
ID	29	30	27	19	11		26
IL	28	8	36	29	23		15
IN	26	18	43	40	24		8
KS	42	21	38	44	36		35
KY	48		42	41	44		47
LA	41		45	48	2	21	29
MA	2	9	1	6	4	9	1
MD	6	2	11	9	20	2	44
ME	14	26	7	8	8	13	3
MI	40	17	33	10	12		19
MN	45	31	44	27	14		34
MO	34	20	26	35	41		25
MS	35		40	47	32	18	48
MT	23	14	21	13	17		13
NC	11		10	15	46	5	5
ND	36	11	39	34	28		33
NE	33	25	30	31	35		22
NH	7	10	2	5	3	11	2
NJ	5	3	6	3	22	6	4
NM	30	7	19	26	18		27
NV	43	12	32	45	16		46

NY	15	15	15	7	5	7	7
OH	50		48	36	39		45
OK	46		34	46	45		37
OR	19	29	13	30	26	10	20
PA	21	28	23	12	9	22	42
RI	1	1	47	1	47	4	40
SC	18		20	23	43	14	12
SD	39	27	31	38	33		31
TN	38		22	33	38		23
TX	47		41	39	25	17	41
UT	27	22	24	20	21		17
VA	16	5	14	14	37	12	18
VT	9	34	3	25	1		38
WA	10	19	4	18	27	16	14
WI	22	32	28	28	7		24
WV	13	16	5	11	19		21
WY	31	33	29	17	34		30

References

Chapter 1

Angert, A. L., L. G. Crozier, L. J. Rissler, S. E. Gilman, J. J. Tewksbury, and A. J. Chunco. 2011. Do species' traits predict recent shifts at expanding range edges?

Archer, S. R., K. I. Predick, J. C. Chambers, M. Pellant, S. R. Archer, K. I. Predick, J. C. Chambers, M. Pellant, S. R. Archer, and K. I. Predick. 2008. Climate change and ecosystems of the Southwestern United States. Rangelands 30:23–28.

Bates, D., M. Maechler, B. Bolker, and S. Walker. 2015. Fitting linear mixed-effects models using lme4. Journal of Statistical Software 67:1–48.

Belnap, Webb, Esque, Brooks, Defalco, and Macmahon. 2016. California Deserts. Page *in* H. A. Mooney and E. S. Zavaleta, editors. Ecosystems of California. University of California Press.

Bobich, E. G., N. L. Wallace, and K. L. Sartori. 2014. Cholla mortality and extreme drought in the Sonoran Desert. Madroño 61:126–136.

Bowers, J. E., R. H. Webb, and R. J. Rondeau. 1995. Longevity, recruitment and mortality of desert plants in Grand Canyon, Arizona, USA. Journal of Vegetation Science 6:551–564.

Breshears, D. D., T. E. Huxman, H. D. Adams, C. B. Zou, and J. E. Davison. 2008. Vegetation synchronously leans upslope as climate warms. Proceedings of the National Academy of Sciences of the United States of America 105:11591–11592.

Broennimann, O., W. Thuiller, G. Hughes, G. F. Midgley, J. M. R. Alkemade, and A. Guisan. 2006. Do geographic distribution, niche property and life form explain plants' vulnerability to global change? Global Change Biology 12:1079–1093.

Brown, D. E., and R. A. Minnich. 1986. Fire and Changes in Creosote Bush Scrub of the Western Sonoran Desert, California. The American Midland Naturalist 116:411–422.

Brown, J. H., T. J. Valone, and C. G. Curtin. 1997. Reorganization of an arid ecosystem in response to recent climate change. Proceedings of the National Academy of Science 94:9729–9733.

Bullock, S. H., and R. M. Turner. 2010. Plant population fluxes in the Sonoran desert shown by repeat photography. Page *in* R. H. Webb, D. E. Boyer, and R. M. Turner, editors. Repeat Photography: Methods and Applications in the Natural Sciences. Island Press, Washington DC, USA.

Chen, I.-C., J. K. Hill, R. Ohlemüller, D. B. Roy, C. D. Thomas, and R. Ohlemuller. 2011a. Rapid range shifts of species associated with high levels of climate warming. Science (New York, N.Y.) 333:1024–6.

Chen, I.-C., J. K. Hill, H.-J. Shiu, J. D. Holloway, S. Benedick, V. K. Chey, H. S. Barlow, and C. D. Thomas. 2011b. Asymmetric boundary shifts of tropical montane Lepidoptera over four decades of climate warming. Global Ecology and Biogeography 20:34–45.

Cody, M. L. 2000. Slow-motion population dynamics in Mojave Desert perennial plants. Journal of Vegetation Science 11:351–358.

Cook, B. I., T. R. Ault, and J. E. Smerdon. 2015. Unprecedented 21st century drought risk in the American Southwest and Central Plains. Science Advances 1:1–7.

Davis, M. B. 1989. Lags in vegetation response to greenhouse warming. Climatic Change 15:75–82.

Doak, D. F., and W. F. Morris. 2010. Demographic compensation and tipping points in climate-induced range shifts. Nature 467:959–62.

Dullinger, S., A. Gattringer, W. Thuiller, D. Moser, N. E. Zimmermann, A. Guisan, W. Willner, C. Plutzar, M. Leitner, T. Mang, M. Caccianiga, T. Dirnböck, S. Ertl, A. Fischer, J. Lenoir, J. C. Svenning, A. Psomas, D. R. Schmatz, U. Silc, P. Vittoz, and K. Hülber. 2012. Extinction debt of high-mountain plants under twenty-first-century climate change. Nature Climate Change 2:619–622.

Ettinger, A. K., and J. HilleRisLambers. 2013. Climate isn't everything: Competitive interactions and variation by life stage will also affect range shifts in a warming world. American Journal of Botany 100:1344–1355.

Fellows, A. W., and M. L. Goulden. 2012. Rapid vegetation redistribution in Southern California during the early 2000s drought. Journal of Geophysical Research: Biogeosciences 117:1–11.

Foden, W., G. F. Midgley, G. Hughes, W. J. Bond, W. Thuiller, M. T. Hoffman, P. Kaleme, L. G. Underhill, A. Rebelo, and L. Hannah. 2007. A changing climate is eroding the geographical range of the Namib Desert tree Aloe through population declines and dispersal lags. Diversity and Distributions 13:645–653.

Gelman, A. 2008. Scaling regression inputs by dividing by two standard deviations. Statistics in Medicine:2865–2873.

Gibson-Reinemer, D. K., and F. J. Rahel. 2015. Inconsistent range shifts within species highlight idiosyncratic responses to climate warming. PLoS ONE 10:1–15.

Gottfried, M., H. Pauli, A. Futschik, M. Akhalkatsi, P. Barančok, J. L. Benito Alonso, G. Coldea, J. Dick, B. Erschbamer, M. R. Fernández Calzado, G. Kazakis, J. Krajči, P. Larsson, M. Mallaun, O. Michelsen, D. Moiseev, P. Moiseev, U. Molau, A. Merzouki, L. Nagy, G. Nakhutsrishvili, B. Pedersen, G. Pelino, M. Puscas, G. Rossi, A. Stanisci, J. P. Theurillat, M. Tomaselli, L. Villar, P. Vittoz, I. Vogiatzakis, and G. Grabherr. 2012. Continent-wide response of mountain vegetation to climate change. Nature Climate Change 2:111–115.

Hargrove, L., J. T. Rotenberry, and Rotenberry. 2009. Elevational shifts in breeding bird distributions over a 26-year period in a Southern California desert region. Page *in* T. Root, Hall, Herzog, and Howell, editors. Biological Impacts of Climate Change in California: Case Studies Linking Science and Management. California Energy Commission PIER Program.

Hellmann, J. J., K. M. Prior, and S. L. Pelini. 2012. The influence of species interactions on geographic range change under climate change. Annals of the New York Academy of Sciences 1249:18–28.

Hoffman, M. T., R. F. Rohde, J. Duncan, and P. Kaleme. 2010. Repeat photography, climate change, and the long-term population dynamics of tree aloes in Southern Africa. Page *in* R. H. Webb, D. E. Boyer, and R. M. Turner, editors. Repeat Photography: Methods and Applications in the Natural Sciences. Island Press, Washington DC, USA.

Kelly, A. E., and M. L. Goulden. 2008. Rapid shifts in plant distribution with recent climate change. Proceedings of the National Academy of Sciences of the United States of America 105:11823–11826.

Lawton, J. H. 1993. Range, population abundance and conservation. Trends in Ecology and Evolution 8:409–413.

Lenoir, J., J. C. Gégout, P. A. Marquet, P. de Ruffray, and H. Brisse. 2008. A significant upward shift in plant species. Science 320:1768–1772.

Lenoir, J., and J. C. Svenning. 2015. Climate-related range shifts - a global multidimensional synthesis and new research directions. Ecography 38:15–28.

Mayhew, W. W. 1983. Conflicts between the fringe-toed lizard and development in the Coachella Valley. Cal-Neva Wildlife Transactions.

McAuliffe, J. R., and E. P. Hamerlynck. 2010. Perennial plant mortality in the Sonoran and Mojave Deserts in response to severe, multi-year drought. Journal of Arid Environments 74:885–896.

Mclaughlin, B. C., and E. S. Zavaleta. 2012. Predicting species responses to climate change: Demography and climate microrefugia in California valley oak (Quercus lobata). Global Change Biology 18:2301–2312.

Miriti, M. N., S. Rodríguez-Buriticá, S. J. Wright, and H. F. Howe. 2007. Episodic death across species of desert shrubs. Ecology 88:32–36.

Moritz, C., J. L. Patton, C. J. Conroy, J. L. Parra, G. C. White, and S. R. Beissinger. 2008. Impact of a century of climate change on small-mammal communities in Yosemite National Park, USA. Science (New York, N.Y.) 322:261–264.

Munson, S. M., R. H. Webb, D. C. Housman, K. E. Veblen, K. E. Nussear, E. A. Beever, K. B. Hartney, M. N. Miriti, S. L. Phillips, R. E. Fulton, and N. G. Tallent. 2015. Long-term plant responses to climate are moderated by biophysical attributes in a North American desert. Journal of Ecology 103:657–668.

Parker, K. C. 1991. Topography, substrate, and vegetation patterns in the Northern Sonoran Desert. Journal of Biogeography 18:151–163.

Parmesan, C., and G. Yohe. 2003. A globally coherent fingerprint of climate change impacts across natural systems. Nature 421:37–42.

Perry, A. L., P. J. Low, J. R. Ellis, and J. D. Reynolds. 2005. Climate change and distribution shifts in marine fishes. Science 308:1912–1915.

R Core Team. 2018. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Root, T. L., J. T. Price, K. R. Hall, S. H. Schneider, C. Rosenzweig, and J. A. Pounds. 2003. Fingerprints of global warming on wild animals and plants. Nature 421:57–60.

Schwilk, D. W., and J. E. Keeley. 2012. A plant distribution shift: Temperature, drought or past disturbance? PLoS ONE 7.

Seager, R., M. Ting, I. Held, Y. Kushnir, J. Lu, G. Vecchi, H.-P. Huang, N. Harnik, A. Leetmaa, N.-C. Lau, C. Li, J. Velez, and N. Naik. 2007. Model projections of an imminent transition to a more arid climate in southwestern North America. Science (New York, N.Y.) 316:1181–1184.

Seager, R., and G. A. Vecchi. 2010. Greenhouse warming and the 21st century hydroclimate of southwestern North America. Proceedings of the National Academy of Sciences 107:21277–21282.

Sexton, J. P., P. J. McIntyre, A. L. Angert, and K. J. Rice. 2009. Evolution and ecology of species range limits. Annual Review of Ecology, Evolution, and Systematics 40:415–436.

Smith, S. D., B. Didden-Zopfy, and P. S. Nobel. 1984. High-temperature responses of North American cacti. Ecology 65:643–651.

Svenning, J. C., and B. Sandel. 2013. Disequilibrium vegetation dynamics under future climate change. American Journal of Botany 100:1266–1286.

Vasek, F. C. 1980. Creosote bush: Long-lived clones in the Mojave Desert. American Journal of Botany 67:246.

Vellend, M., C. D. Brown, H. M. Kharouba, J. L. McCune, and I. H. Myers-Smith. 2013. Historical ecology: Using unconventional data sources to test for effects of global environmental change. American journal of botany 100:1294–305.

Woods, S. R., S. R. Archer, and S. Schwinning. 2011. Early taproot development of a xeric shrub (Larrea tridentata) is optimized within a narrow range of soil moisture. Plant Ecology 212:507–517.

Zabriskie, J. G. 1979. Plants of Deep Canyon and the Central Coachella Valley, California. Philip L. Boyd Deep Canyon Desert Research Center.

Zhu, K., C. W. Woodall, and J. S. Clark. 2012. Failure to migrate: Lack of tree range expansion in response to climate change. Global Change Biology 18:1042–1052.

Chapter 2

Ackerly, D.D., Loarie, S.R., Cornwell, W.K., Weiss, S.B., Hamilton, H., Branciforte, R., Kraft, N.J.B., 2010. The geography of climate change: implications for conservation biogeography. Divers. Distrib. 16, 476–487. doi:10.1111/j.1472-4642.2010.00654.x

Armstrong, D.P., Moro, D., Hayward, M.W., Seddon, P.J., 2015. Introduction: The development of reintroduction biology in New Zealand and Australia, in: Armstrong, D.P., Hayward, M.W., Moro, D., Seddon, P.J. (Eds.), Advances in Reintroduction Bioogy of Australian and New Zealand Fauna. CSIRO Publishing.

Armstrong, D.P., Seddon, P.J., 2008. Directions in reintroduction biology. Trends Ecol. Evol. 23, 20–5. doi:10.1016/j.tree.2007.10.003

Bajomi, B., Pullin, A.S., Stewart, G.B., Takács-Sánta, A., 2010. Bias and dispersal in the animal reintroduction literature. Oryx 44, 358–365. doi:10.1017/S0030605310000281

Bates, D., Maechler, M., Bolker, B., Walker, S., 2015. Fitting linear mixed-effects models using lme4. J. Stat. Softw. 67, 1–48.

BirdLife International, 2016. Handbook of the Birds of the World and BirdLife International digital checklist of the birds of the world. Version 9.

Bivand, R., Keitt, T., Rowlingson, B., 2018. rgdal: Bindings for the “Geospatial” Data Abstraction Library.

Blackburn, T.M., Cassey, P., 2004. Are introduced and re-introduced species comparable? A case study of birds. Anim. Conserv. 7, 427–433. doi:10.1017/S1367943004001647

Blackburn, T.M., Lockwood, J.L., Cassey, P., Blackburn, T.M., Lockwood, J.L., Cassey, P., 2009. The Role of Species Traits in Establishment Success, in: Avian Invasions: The Ecology and Evolution of Exotic Birds. pp. 1–49. doi:10.1093/acprof

Brichieri-Colombi, T.A., Moehrenschlager, A., 2016. Alignment of threat, effort, and perceived success in North American conservation translocations. Conserv. Biol. 30, 1159–1172. doi:10.1111/cobi.12743

Cassey, P., Blackburn, T., Duncan, R., 2008. Lessons from introductions of exotic species as a possible information source for managing translocations of birds. Wildl. Res. 193–201.

Cassey, P., Blackburn, T.M., Sol, D., Duncan, R.P., Lockwood, J.L., 2004. Global patterns of introduction effort and establishment success in birds. Proc. R. Soc. B Biol. Sci. 271, 405–408. doi:10.1098/rsbl.2004.0199

Clark, J.A., May, R.M., 2002. Taxonomic Bias in Conservation Research. Science (80-.).

Dunning, J., 2017. Data update, in: CRC Handbook of Avian Body Masses.

Dunning, J.B., 2007. CRC Handbook of Avian Body Massess, 2nd Editio. ed. Taylor & Francis.

Fick, S.E., Hijmans, R.J., 2017. WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. Int. J. Climatol. 37, 4302–4315. doi:10.1002/joc.5086

Fischer, J., Lindenmayer, D.., 2000. An assessment of the published results of animal relocations. Biol. Conserv. 96, 1–11. doi:10.1016/S0006-3207(00)00048-3

Franklin, D.C., Garnett, S.T., Luck, G.W., Gutierrez-Ibanez, C., Iwaniuk, A.N., 2014. Relative brain size in Australian birds. Emu. doi:10.1071/MU13034

Gelman, A., 2008. Scaling regression inputs by dividing by two standard deviations. Stat. Med. 2865–2873.

Germano, J.M., Bishop, P.J., 2009. Suitability of amphibians and reptiles for translocation. Conserv. Biol. 23, 7–15. doi:10.1111/j.1523-1739.2008.01123.x

Griffith, B., Scott, J.M., Carpenter, J.W.J., Reed, C., 1989. Translocation as a Species and Conservation Tool: Status and Strategy. Science (80-.). 245, 477–480.

Hartig, F., 2018. DHARMa: Residual Diagnostics for Hierarchical (Multi-Level / Mixed) Regression Models.

Hayes, K.R., Barry, S.C., 2008. Are there any consistent predictors of invasion success? Biol. Invasions 10, 483–506. doi:10.1007/s10530-007-9146-5

Hewitt, N., Klenk, N., Smith, a. L., Bazely, D.R., Yan, N., Wood, S., MacLellan, J.I., Lipsig-Mumme, C., Henriques, I., 2011. Taking stock of the assisted migration debate. Biol. Conserv. 144, 2560–2572. doi:10.1016/j.biocon.2011.04.031

Hijmans, R.J., 2017. geosphere: Spherical Trigonometry.

IUCN/SSC, 2013. Guidelines for Reintroductions and Other Conservation Translocations. Version 1.0. Gland, Switzerland.

Iwaniuk, A.N., Nelson, J.E., 2003. Developmental differences are correlated with relative brain size in birds: a comparative analysis. Can. J. Zool. doi:10.1139/z03-190

Jachowski, D.S., Slotow, R., Angermeier, P.L., Millspaugh, J.J., 2016. Animal Reintroduction in the Antropocene, in: Jachowski, D.S., Millspaugh, J.J., Angermeier, P.L., Slotow, R. (Eds.), Reintroduction of Fish and Wildlife Populations. University of California Press, Oakland, CA, pp. 1–4.

Jones, H.P., Kress, S.W., 2012. A Review of the World's Active Seabird Restoration Projects. J. Wildl. Manage. 76, 2–9. doi:10.1002/jwmg.240

Kolar, C.S., Lodge, D.M., 2001. Progress in invasion biology: predicting invaders. Ecol. Evol. 16, 199–204.

Kreyling, J., Bittner, T., Jaeschke, A., Jentsch, A., Jonas Steinbauer, M., Thiel, D., Beierkuhnlein, C., 2011. Assisted Colonization: A Question of Focal Units and Recipient Localities. Restor. Ecol. 19, 433–440. doi:10.1111/j.1526-100X.2011.00777.x

Lawler, J.J., Olden, J.D., 2011. Reframing the debate over assisted colonization. Front. Ecol. Environ. 110324084539019. doi:10.1890/100106

Leech, S.M., Almuedo, P.L., Neill, G.O., 2011. Assisted Migration : Adapting forest management to a changing climate. BC J. Ecosyst. Manag. 12, 18–34.

Lefcheck, J.S., 2015. piecewiseSEM: Piecewise structural equation modeling in R for ecology, evolution, and systematics. Methods Ecol. Evol. 7, 573–579.

Lepage, D., n.d. Avibase [WWW Document]. URL avibase.bsc-eoc.org/

Lesnoff, M., Lancelot, R., 2013. aods3: analysis of overdispersed data using S3 methods.

Lincoln Park Zoo, 2012. Avian Reintroduction and Translocation Database [WWW Document]. URL http://www.lpzoosites.org/artd (accessed 10.2.12).

Liu, H., Feng, C.-L., Chen, B.-S., Wang, Z.-S., Xie, X.-Q., Deng, Z.-H., Wei, X.-L., Liu, S.-Y., Zhang, Z.-B., Luo, Y.-B., 2012. Overcoming extreme weather challenges: Successful but variable assisted colonization of wild orchids in southwestern China. Biol. Conserv. 150, 68–75. doi:10.1016/j.biocon.2012.02.018

Lockwood, J.L., Cassey, P., Blackburn, T., 2005. The role of propagule pressure in explaining species invasions. Trends Ecol. Evol. 20, 223–228. doi:10.1016/j.tree.2005.02.004

Lomolino, M., Channell, R., 1998. Range Collapse, Re-introductions, and Biogeographic Guidelines for conservation. Conserv. Biol. 12, 481–484.

Lyman, R.L., 2016. A conservation paleobiology perspective on reintroduction, in: Jachowski, D.S., Millspaugh, J.J., Angermeier, P.L., Slotow, R. (Eds.), Reintroduction of Fish and Wildlife Populations. University of California Press, Oakland, CA, pp. 29–51.

Miskelly, C.M., Powlesland, R.G., 2013. Conservation translocations of New Zealand birds, 1863-2012. Notornis 60, 3–28.

Morrison, S.A., Sillett, T.S., Ghalambor, C.K., Fitzpatrick, J.W., Graber, D.M., Bakker, V.J., Bowman, R., Collins, C.T., Collins, P.W., Delaney, K.S., Doak, D.F., Koenig, W.D., Laughrin, L., Lieberman, A. a., Marzluff, J.M., Reynolds, M.D., Scott, J.M., Stallcup, J.A., Vickers, W., Boyce, W.M., 2011. Proactive Conservation Management of an Island-endemic Bird Species in the Face of Global Change. Bioscience 61, 1013–1021. doi:10.1525/bio.2011.61.12.11

Mueller, J.M., Hellmann, J.J., 2008. An assessment of invasion risk from assisted migration. Conserv. Biol. 22, 562–7. doi:10.1111/j.1523-1739.2008.00952.x

Nakagawa, S., Schielzeth, H., 2013. A general and simple method for obtaining R2 from generalized linear mixed-effects models. Methods Ecol. Evol. 4, 133–142. doi:10.1111/j.2041-210x.2012.00261.x

New Zealand Department of Conservation, n.d. Department of Conservation Public Conservation Land [WWW Document]. Dep. Conserv. Maps. URL http://maps.doc.govt.nz/mapviewer/

Nieuwenhuis, R., Te Grotenhuis, M., Pelzer, B., 2012. Influence.ME: tools for detecting influential data in mixed effects models. R J. 4, 38–47.

Olden, J.D., Kennard, M.J., Lawler, J.J., Poff, N.L., 2010. Challenges and opportunities in implementing managed relocation for conservation of freshwater species. Conserv. Biol. 25, 40–7. doi:10.1111/j.1523-1739.2010.01557.x

Osborne, P.E., Seddon, P.J., 2012. Selecting Suitable Habitats for Reintroductions: Variation, Change and the Role of Species Distribution Modelling, in: Ewen, J.G., Armstrong, D.P., Parker, K.A., Seddon, P.J. (Eds.), Reintroduction Biology: Integrating Science and Management. Wiley-Blackwell, pp. 73–104.

Parker, K.A., Dickens, M.J., Clarke, R.H., Lovegrove, T.G., 2012. The theory and practice of catching, holding, moving and releasing animals, in: Ewen, J.G., Armstrong, D.P., Parker, K.A., Seddon, P.J. (Eds.), Reintroduction Biology: Integrating Science and Management. Blackwell Publishing, pp. 105–137.

Pebesma, E.J., Bivand, R.S., 2005. Classes and methods for spatial data in R. R News 5.

Peterson, A.T., Cobos, M.E., Jim, D., 2018. Major challenges for correlational ecological niche model projections to future climate conditions. Ann. N. Y. Acad. Sci. 1–12. doi:10.1111/nyas.13873

R Core Team, 2018. R: A language and environment for statistical computing. doi:10.1007/978-3-540-74686-7

Robert, A., Colas, B., Guigon, I., Kerbiriou, C., Mihoub, J.B., Saint-Jalme, M., Sarrazin, F., 2015. Defining reintroduction success using IUCN criteria for threatened species: A demographic assessment. Anim. Conserv. 18, 397–406. doi:10.1111/acv.12188

Rummel, L., Abraín, A.M., Mayol, J., Olmo, J.R., Mañas, F., Jiménez, J., Gómez, J.A., Oro, D., 2016. Use of wild-caught individuals as a key factor for success in vertebrate translocations. Anim. Biodivers. Conserv. 2, 207–220.

Sæther, B., Bakke, Ø., 2000. Avian Life History Variation and Contribution of Demographic Traits to the Population Growth RSæther, B., Bakke, Ø., 2000. Avian Life History Variation and Contribution of Demographic Traits to the Population Growth Rate. Ecology 81, 642–653.ate. Ecology 81, 642–653.

Sarrazin, F., 2007. Introductory remarks: A demographic frame for reintroduction. Ecoscience. doi:10.2980/1195-6860(2007)14

Sayol, F., Maspons, J., Lapiedra, O., Iwaniuk, A.N., Székely, T., Sol, D., 2016. Environmental variation and the evolution of large brains in birds. Nat. Commun. doi:10.1038/ncomms13971

Seddon, P.J., 2010. From Reintroduction to Assisted Colonization: Moving along the Conservation Translocation Spectrum. Restor. Ecol. 18, 796–802. doi:10.1111/j.1526-100X.2010.00724.x

Seddon, P.J., Armstrong, D.P., 2016. Reintroduction and other conservation translocations: History and future developments, in: Jachowski, D.S., Millspaugh, J.J., Angermeier, P.L., Slotow, R. (Eds.), Reintroduction of Fish and Wildlife Populations. University of California Press, Oakland, CA, pp. 7–28.

Seddon, P.J., Armstrong, D.P., Maloney, R.F., 2007. Developing the science of reintroduction biology. Conserv. Biol. 21, 303–12. doi:10.1111/j.1523-1739.2006.00627.x

Seddon, P.J., Soorae, P.S., Launay, F., 2005. Taxonomic bias in reintroduction projects. Anim. Conserv. 8, 51–58. doi:10.1017/S1367943004001799

Seddon, P.J., Strauss, W.M., Innes, J., 2012. Animal Translocations: What are they and why do we do them?, in: Ewen, J.G., Armstrong, D.P., Parker, K.A., Seddon, P.J. (Eds.), Reintroduction Biology: Integrating Science and Management. Blackwell Publishing Ltd, pp. 1–32.

Settele, J.R., Scholes, R.J., Betts, R.A., Bunn, S., Leadley, P., Nepstad, D., Overpeck, J.T., Toboada, M.A., 2014. Terrestrial and inland water systems, in: Field, C.B., Barros, V.R., Dokken, D.J., Mach, K.J., Mastrandrea, M.D., Bilir, T.E., Chatterjee, M., Ebi, K.L., Estrada, Y.O., Genova, R.C., Girma, B., Kissel, E.S., Levy, A.N., MacCracken, S., Mastrandrea, P.R., White, L.L. (Eds.), Climate Change 2014: Impacts, Adaptation, and Vulnerability. Part A: Global and Sectoral Aspects. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. pp. 271–359. doi:31 March 2014

Sol, D., Duncan, R.P., Blackburn, T.M., Cassey, P., Lefebvre, L., 2005. Big brains, enhanced cognition, and response of birds to novel environments. Proc. Natl. Acadamy Sci. USA.

Sol, D., Maspons, J., Vall-Llosera, M., Bartomeus, I., García-Peña, G.E., Piñol, J., Freckleton, R.P., 2012. Unraveling the life history of successful invaders. Science 337, 580–3. doi:10.1126/science.1221523

Tavecchia, G., Viedma, C., Martínez-abraín, A., Bartolomé, M., Antonio, J., Oro, D., 2009. Maximizing re-introduction success : Assessing the immediate cost of release in a threatened waterfowl. Biol. Conserv. 142, 3005–3012. doi:10.1016/j.biocon.2009.07.035

U.S. Geological Survey Gap Analysis Program (GAP), 2016. Protected Areas Database of the United States (PAD-US), version 1.4 Combined Feature Class.

UNEP-WCMC, IUCN, 2017. Protected Planet: The World Database on Protected Areas (WDPA) [On-line].

VanderWerf, E.A., Young, L.C., Kohley, C.R., Dalton, M., 2018. Translocations of Laysan and black-footed albatrosses in Hawaii, USA, to create new protected breeding colonies safe from climate change, in: Soorae, P.S. (Ed.), Global

Reintroduction Perspectives: 2018. IUCN/SSC Reintroduction Specialist Group & Environment Agency-Abu Dhabi, Gland, Switzerland, pp. 100–105.

White, T.H., Collar, N.J., Moorhouse, R.J., Sanz, V., Stolen, E.D., Brightsmith, D.J., 2012. Psittacine reintroductions: Common denominators of success. Biol. Conserv. 148, 106–115. doi:10.1016/j.biocon.2012.01.044

Wolf, C.M., Griffith, B., Reed, C., Temple, S.S.A., 1996. Avian and Mammalian Translocations: Update and Reanalysis of 1987 Survey Data. Conserv. Biol. 10, 1142–1154.

Wolf, C.M., Jr, T.G., Griffith, B., 1998. Predictors of avian and mammalian translocation success: reanalysis with phylogenetically independent contrasts. Biol. Conserv. 86.

Chapter 3

Adger, W.N., Arnell, N.W., Tompkins, E.L., 2005. Successful adaptation to climate change across scales. Glob. Environ. Chang. 15, 77–86. doi:10.1016/j.gloenvcha.2004.12.005

Alder, J.R., Hostetler, S.W., 2013. USGS National Climate Change Viewer. doi:10.5066/F7W9575T

Anderson, M.G., Ferree, C.E., 2010. Conserving the Stage: Climate Change and the Geophysical Underpinnings of Species Diversity. PLoS One 5, e11554. doi:10.1371/journal.pone.0011554

Beier, P., Brost, B., 2010. Use of land facets to plan for climate change: conserving the arenas, not the actors. Conserv. Biol. 24, 701–10. doi:10.1111/j.1523-1739.2009.01422.x

BenDor, T., Lester, T.W., Livengood, A., Davis, A., Yonavjak, L., 2015. Estimating the Size and Impact of the Ecological Restoration Economy. PLoS One 1–15. doi:10.1371/journal.pone.0128339

Berrang-Ford, L., Ford, J.D., Paterson, J., 2011. Are we adapting to climate change? Glob. Environ. Chang. 21, 25–33. doi:10.1016/j.gloenvcha.2010.09.012

Bierbaum, R., Smith, J.B., Lee, A., Blair, M., Carter, L., Chapin, F.S., Fleming, P., Ruffo, S., Stults, M., McNeeley, S., Wasley, E., Verduzco, L., 2013. A comprehensive review of climate adaptation in the United States: More than before, but less than needed. Mitig. Adapt. Strateg. Glob. Chang. 18, 361–406. doi:10.1007/s11027-012-9423-1

Capon, S.J., Chambers, L.E., Nally, R. Mac, Naiman, R.J., Davies, P., Marshall, N., Pittock, J., Reid, M., Capon, T., Douglas, M., Catford, J., Baldwin, D.S., Stewardson, M., Roberts, J., Parsons, M., Williams, S.E., 2013. Riparian Ecosystems in the 21st Century: Hotspots for Climate Change Adaptation? Ecosystems 16, 359–381. doi:10.1007/sl

Climate Central and ICF International, 2015. States at Risk: America’s Preparedness Report Card Technical Methodology [WWW Document]. URL http://assets.statesatrisk.org/media/TechnicalMethods.pdf

Cross, M.S., Zavaleta, E.S., Bachelet, D., Brooks, M.L., Enquist, C.A.F., Fleishman, E., Graumlich, L.J., Groves, C.R., Hannah, L., Hansen, L., Hayward, G., Koopman, M., Lawler, J.J., Malcolm, J., Nordgren, J., Petersen, B., Rowland, E.L., Scott, D., Shafer, S.L., Shaw, M.R., Tabor, G.M., 2012. The Adaptation for

Conservation Targets (ACT) Framework: A Tool for Incorporating Climate Change into Natural Resource Management. Environ. Manage. doi:10.1007/s00267-012-9893-7

Davis, J., Pavlova, A., Thompson, R., Sunnucks, P., 2013. Evolutionary refugia and ecological refuges: Key concepts for conserving Australian arid zone freshwater biodiversity under climate change. Glob. Chang. Biol. 19, 1970–1984. doi:10.1111/gcb.12203

Evans, D.M., Che-castaldo, J.P., Crouse, D., Davis, F.W., Epanchin-niell, R., Flather, C.H., Frohlich, R.K., Goble, D.D., Li, Y., Male, T.D., Master, L.L., Moskwik, M.P., Neel, M.C., Noon, B.R., Parmesan, C., Schwartz, M.W., Scott, J.M., Williams, B.K., 2016. Species Recovery in the United States: Increasing the Effectiveness of the Endangered Species Act. Ecol. Soc. Am. 28.

Ford, J.D., Berrang-Ford, L., Lesnikowski, A., Barrera, M., Jody Heymann, S., 2013. How to track adaptation to climate change: A typology of approaches for national-level application. Ecol. Soc. 18. doi:10.5751/ES-05732-180340

Gardali, T., Seavy, N.E., DiGaudio, R.T., Comrack, L.A., 2012. A Climate Change Vulnerability Assessment of California’s At-Risk Birds. PLoS One 7, e29507. doi:10.1371/journal.pone.0029507

Groffman, P., Kareiva, P., Carter, S., Grimm, N., Lawler, J., Mack, M., Matzek, V., Tallis, H., 2014. Climate Change Impacts in the United States Chapter 8. Natl. Clim. Assess. 2014 195–219. doi:10.7930/J0TD9V7H.On

Hanberry, B.B., Noss, R.F., Safford, H.D., Allison, S.K., Dey, D.C., 2015. Restoration Is Preparation for the Future. J. For. 113, 1–5. doi:10.5849/jof.15-014

Hansen, L., Gregg, R.., Arroyo, V., Ellsworth, S., Jackson, L., Snover, A., 2013. The State of Adaptation in the United States: An Overview. A report for the John D. and Catherine T. MacArthur Foundation.

Hanski, I., 1998. Metapopulation dynamics. Nature 396, 41–49.

Harris, J.A., Higgs, E.S., Harris, J.A., Hobbs, R.J., Higgs, E., Aronson, J., 2006. Ecological Restoration and Global Climate Change. Restor. Ecol. doi:10.1111/j.1526-100X.2006.00136.x

Heller, N.E., Zavaleta, E.S., 2009. Biodiversity management in the face of climate change: A review of 22 years of recommendations. Biol. Conserv. 142, 14–32. doi:10.1016/j.biocon.2008.10.006

Hoegh-Guldberg, O., Hughes, L., Mcintyre, S., Lindenmayer, D.B., Parmesan, C., Possingham, H.P., Thomas, C.D., 2008. Assisted Colonization and Rapid Climate Change. Science (80-.). 321.

Isaak, D.J., Wollrab, S., Horan, D., Chandler, G., 2012. Climate change effects on stream and river temperatures across the northwest U.S. from 1980-2009 and implications for salmonid fishes. Clim. Change 113, 499–524. doi:10.1007/s10584-011-0326-z

Kates, R.W., Travis, W.R., Wilbanks, T.J., 2012. Transformational adaptation when incremental adaptations to climate change are insufficient. Proc. Natl. Acad. Sci. 109, 7156–7161. doi:10.1073/pnas.1115521109

Keppel, G., Van Niel, K.P., Wardell-Johnson, G.W., Yates, C.J., Byrne, M., Mucina, L., Schut, A.G.T., Hopper, S.D., Franklin, S.E., 2012. Refugia : Identifying and understanding safe havens for biodiversity under climate change. Glob. Ecol. Biogeogr. 21, 393–404. doi:10.1111/j.1466-8238.2011.00686.x

Keppel, G., Wardell-Johnson, G.W., 2012. Refugia: keys to climate change management. Glob. Chang. Biol. 2389–2391. doi:10.1111/j.1365-2486.2012.02729.x

Lawler, J.J., 2009. Climate Change Adaptation Strategies for Resource Management and Conservation Planning. Ann. N. Y. Acad. Sci. 98, 79–98. doi:10.1111/j.1749-6632.2009.04147.x

Leech, S.M., Almuedo, P.L., Neill, G.O., 2011. Assisted Migration : Adapting forest management to a changing climate. BC J. Ecosyst. Manag. 12, 18–34.

Mawdsley, J.R., O’Malley, R., Ojima, D.S., 2009. A review of climate-change adaptation strategies for wildlife management and biodiversity conservation. Conserv. Biol. 23, 1080–1089. doi:10.1111/j.1523-1739.2009.01264.x

Maxwell, S.L., Venter, O., Jones, K.R., Watson, J.E.M., 2015. Integrating human responses to climate change into conservation vulnerability assessments and adaptation planning. Ann. N. Y. Acad. Sci. 1355, 98–116. doi:10.1111/nyas.12952

Mildenberger, M., Marlon, J.R., Howe, P.D., Leiserowitz, A., 2017. The spatial distribution of Republican and Democratic climate opinions at state and local scales 539–548. doi:10.1007/s10584-017-2103-0

Millar, C.I., Stephenson, N.L., Stephens, S.L., 2007. Climate change and forests of the future: managing in the face of uncertainty. Ecol. Appl. 17, 2145–2151.

Murphy, W., 2016. fiftystater: Map Data to Visualize the Fifty U.S. States with Alaska and Hawaii Insets.

Ontl, T.A., Swanston, C., Brandt, L.A., Butler, P.R., D'Amato, A.W., Handler, S.D., Janowiak, M.K., Shannon, P.D., 2017. Adaptation pathways: ecoregion and land ownership influences on climate adaptation decision-making in forest management. Clim. Change. doi:10.1007/s10584-017-1983-3

R Core Team, 2016. R: A language and environment for statistical computing. doi:10.1007/978-3-540-74686-7

Schwartz, M.W., Jessica, J., Jason, M.M., Sax, D.F., Borevitz, J., Brennan, J., Fielder, D., Gill, J., Gonzalez, P., Jamieson, D.W., Javeline, D., Minteer, B., Polasky, S., David, M., Safford, D., Schneider, S., 2012. Managed Relocation: Integrating the Scientific, Regulatory, and Ethical Challenges 62, 732–743. doi:10.1525/bio.2012.62.8.6

Seavy, N.E., Gardali, T., Golet, G.H., Griggs, F.T., Howell, C.A., Kelsey, R., Small, S.L., Viers, J.H., Weigand, J.F., 2009. Why climate change makes riparian restoration more important than ever: Recommendations for practice and research. Ecol. Restor. 27, 330–338. doi:10.3368/er.27.3.330

Sheldon, A.L., 1988. Conservation of Stream Fishes : Patterns of Diversity, Rarity, and Risk. Conserv. Biol. 2, 149–156.

Stein, B.A., Glick, P., Edelson, N., Staudt, A., (eds.), 2014. Climate-Smart Conservation: Putting adaptation principles into practice. National Wildlife Federation, Washington, D.C.

Stein, B.A., Staudt, A., Cross, M.S., Dubois, N.S., Enquist, C., Griffis, R., Hansen, L.J., Hellmann, J.J., Lawler, J.J., Nelson, E.J., Pairis, A., 2013. Preparing for and managing change: Climate adaptation for biodiversity and ecosystems. Front. Ecol. Environ. 11, 502–510. doi:10.1890/120277

Swanston, C.W., Janowiak, M.K., Brandt, L.A., Butler, P.R., Handler, S.D., Shannon, P.D., Lewis, A.D., Hall, K., Fahey, R.T., Scott, L., Kerber, A., Miesbauer, J.W., Darling, L., 2016. Forest Adaptation Resources: Climate Change Tools and Approaches for Land Managers, 2nd edition, General Technical Report NRS-87-2. doi:10.2737/NRS-GTR-87-2

Swift, Jr., L.W., Messer, J.B., 1971. Forest cuttings raise temperatures of small streams in the southern Appalachians. J. Soil Water Conserv. 26, 1–5. doi:10.1007/s13398-014-0173-7.2

Tylianakis, J.M., Didham, R.K., Bascompte, J., Wardle, D.A., 2008. Global change and species interactions in terrestrial ecosystems. Ecol. Lett. 11, 1351–1363. doi:10.1111/j.1461-0248.2008.01250.x

USGCRP, 2017. Climate Science Special Report: Fourth National Climate Assessment, Volume I. U.S. Global Change Research Program, Washington, DC, USA.

Wickham, H., 2009. ggplot2 Elegant Graphics for Data Analysis. Springer-Verlag New York. doi:10.1007/978-0-387-98141-3

Wickham, H., 2007. Reshaping Data with the reshape Package. J. Stat. Softw. doi:10.18637/jss.v021.i12

Wildlife Conservation Society, 2012. Applicant Guidance Document, WCS Climate Adaptation Fund.

Wildlife Conservation Society, 2011. Pre-Proposal Application Form, WCS Climate Adaptation Fund.

Wilke, C.O., 2016. cowplot: Streamlined Plot Theme and Plot Annotations for “ggplot2”.