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The effects of climate change and land-use change on demographic rates and population viability

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ABSTRACT

Understanding the processes that lead to species extinctions is vital for lessening pressures on biodiversity. While species diversity, presence and abundance are most commonly used to measure the effects of human pressures, demographic responses give a more proximal indication of how pressures affect population viability and contribute to extinction risk. We reviewed how demographic rates are affected by the major anthropogenic pressures, changed landscape condition caused by human land use, and climate change. We synthesized the results of 147 empirical studies to compare the relative effect size of climate and landscape condition on birth, death, immigration and emigration rates in plant and animal populations. While changed landscape condition is recognized as the major driver of species declines and losses worldwide, we found that, on average, climate variables had equally strong effects on demographic rates in plant and animal populations. This is significant given that the pressures of climate change will continue to intensify in coming decades. The effects of climate change on some populations may be underestimated because changes in climate conditions during critical windows of species life cycles may have disproportionate effects on demographic rates. The combined pressures of land-use change and climate change may result in species declines and extinctions occurring faster than otherwise predicted, particularly if their effects are multiplicative.

Key words: climate variation, extinction risk, extirpation, emigration, immigration, land-use intensification, landscape condition, mortality, natality.

CONTENTS

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I. INTRODUCTION

Biodiversity continues to decline; of species that have been assessed for extinction risk around the world, 38% are considered to be under threat (Vié, Hilton-Taylor & Stuart, 2009). The abundances of vertebrate populations fell by one-third between 1970 and 2006, and continue to decline; 70% of assessed plant species have been classified as threatened by the IUCN (Vié *et al.*, 2009). The principal pressures causing biodiversity loss are unabated, and, in most cases, are increasing (Butchart *et al.*, 2010). Human land-use change, leading to the loss, fragmentation and degradation of native vegetation, is the predominant driver of terrestrial species decline (Sala *et al.*, 2000). Climate change has been recognized comparatively recently as a major driver, and its effect on plant and animal populations is increasing (Bellard *et al.*, 2012; Foden *et al.*, 2013).

The most widely used measure of biodiversity is species richness, although subspecies, races and genotypes are important components. However, it is the extinction of individual species, especially iconic ones, that causes most consternation among practitioners and the public, so that it is important to understand the processes leading to species extinction. While there is a relatively good understanding of the identity of the pressures acting on species, the mechanisms by which these pressures operate and interact to affect the viability of species and populations is poorly understood (Akçakaya *et al.*, 2006). Understanding the processes that ultimately cause species extinctions is critical for deciding on the most appropriate actions for conservation management (Cushman, 2006).

The effects of land-use change have been a focus for conservation biology for several decades, particularly the effects of habitat fragmentation (Fischer & Lindenmayer, 2007). The most common measures for quantifying the effects on biota are species richness, species occurrence and the abundance patterns of individual species (Debinski & Holt, 2000). Few studies on fragmentation measure demographic responses, with most studies measuring presence/absence, diversity, or abundance (McGarigal & Cushman, 2002); these are 'static' rather than dynamic measures, and so generally do not provide much information on the trajectories of change. There has been much less focus on the demographic effects of land-use change on populations, which provide indications of trajectories of change (Lampila, Mönkkönen & Desrochers, 2005).

Climate change is expected to become an equally, or more important, driver of global biodiversity loss over the next century (Heller & Zavaleta, 2009). Climate change and climatic events (e.g. drought) have already caused range shifts (Chen *et al.*, 2011), severe and long-term population declines (Sanderson *et al.*, 2006; Newton, 2008*b*) and extinctions (Thomas, Franco & Hill, 2006). While interest in the effects of climate on biodiversity has escalated in recent decades, studies on the effects of climate have predominantly focused on observed and potential shifts in species ranges (Dawson *et al.*, 2011) and changes in species phenology (Parmesan, 2006; Chambers & Keatley, 2010) and physiology (Buckley, Nufio & Kingsolver, 2013). These factors may indicate or lead to a change in the likelihood of a species' persistence, but they do not directly reveal the changes in demographic rates that determine the chances that a population will persist. Changes in the phenology, such as timing of breeding, do not in themselves indicate a deleterious effect on population viability. The population is affected when these changes alter demographic rates.

Geographic distribution is the spatial expression of demographic rates, but change in distribution is one of the last signals to be detected as a species declines (Martinez-Meyer, 2012). Focusing on shifts in species ranges misses the population-level processes leading to these shifts, including local extinctions and recolonizations, and the changes in demographic rates that lead to these. While species-distribution models may predict range expansions with climate change, demographic studies may indicate the opposite effect (Campbell *et al.*, 2012). Organisms may colonize or remain in poor-quality habitat if there is asynchrony between the cues used for habitat selection and declines in habitat suitability caused by climate change (van de Pol *et al.*, 2010), so that distributions do not necessarily inform population viability.

We refer to 'pressure' as a human-induced perturbation that negatively affects a population and that may be transient (pulse), persistent (press), or monotonically changing in magnitude (ramping) over time. We synonymize pressure with 'stressor' and 'threat'. Pressures have causative effects on demographic rates (e.g. decreased seed germination, increased nest predation), while associations between pressures and changes in species richness, species occurrence and abundance are correlative. The close connection between a pressure and a demographic-rate response means that measuring the changes in demographic rates should offer a more accurate indication of the mechanisms through which anthropogenic pressures affect population viability (Fig. 1).

Here, we review the effects of some of the major anthropogenic pressures on population viability, and we present a conceptual model to describe these relationships. We focus on the processes through which climate change and changed landscape condition induced by human land use affect population viability in terrestrial plant and animal populations. Last, we quantify these relationships by synthesizing the results of empirical studies to provide a comparison of the effects of these major pressures on population viability. For tractability, this review concentrates on terrestrial systems; different sets of pressures may predominate for freshwater (Ficke, Myrick & Hansen, 2007) and marine (Halpern *et al.*, 2008) systems. There are other pressures on biodiversity such as direct harvest (including fisheries), pollution, invasive species and disease (Mace, Masundire & Baillie, 2005). These are vast topics, so we do not consider them further; instead we focus on the influence of landscape condition and climate change as the main pressures of interest, given their pervasive influence.

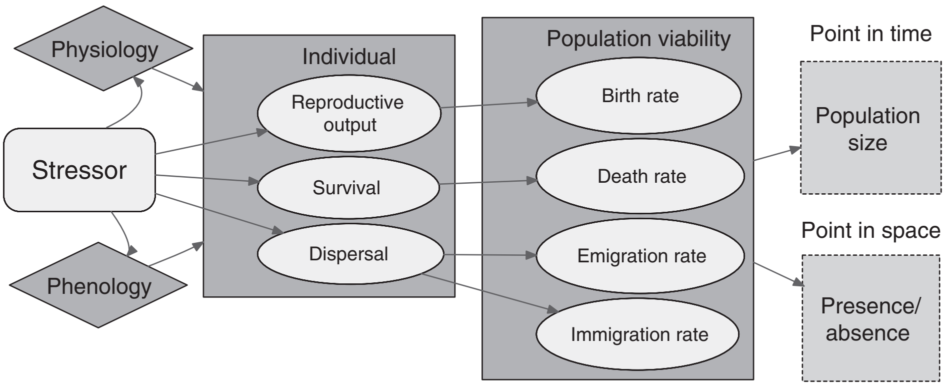

Fig. 1. A general representation of the linkages between the effects of a pressure, such as vegetation loss, and commonly used measures of populations.

(1) Factors affecting population viability

Population viability is a quantitative measure of the capacity of a population to persist, typically the probability of persistence for 100 years, which indicates the risk of extinction (Boyce, 1992). Population viability analyses often are used to quantify extinction risks for individual populations, which can include the identification of minimum viable population size (Reed *et al.*, 2003). The processes that lead to the extinction of a population arise from deleterious changes to demographic rates, which occur through changes in reproductive output, survival and dispersal of individuals in response to a pressure (Fig. 1). Population viability is based on likely changes in population size over time, with the component demographic rates contributing to changes in population size. Birth, death, immigration and emigration are the four fundamental demographic parameters that determine changes in population size (Begon, Mortimer & Thompson, 1996). The dynamics of a population can be represented by (Cohen, 1969):

$$N_{t+1} = N_t \left(1 + b + i - d - e\right),$$

where: N_t is the abundance of a population at time *t*, *b* and *d* are the *per capita* birth and death rates, and *i* and *e* are *per capita* immigration and emigration rates during time interval $(t+1)-t$. The effective population size will be affected by the sex ratios of individuals contributing to these demographic rates (Frankham, 1995). If one or more of these demographic rates is affected by a proximal pressure, arising from a distal driver, then this will affect the size of the population, and may decrease its viability, unless offset by changes to another demographic rate (i.e. consistently have $N_{t+1} < N_t$, Fig. 2). Once populations become small, stochastic events, inbreeding depression and genetic erosion further affect demographic rates and steepen the rate of decline in population viability (Young *et al.*, 2000; Keller & Waller, 2002). Given the direct effects on population dynamics, measuring changes in demographic rates allows us to infer likely changes to a population's viability in response to human pressures.

II. CONCEPTUAL MODEL

(1) Overview of land-use change and climate change

Changes in human land use for food and resource production and urbanization affect landscape condition through the loss and fragmentation of native vegetation (Fahrig, 1997) and the degradation of remnant vegetation (Fischer & Lindenmayer, 2007). Climate change can further degrade vegetation condition through changes to the frequency and intensity of disturbances that can affect vegetation composition, structure and function (Cunningham *et al.*, 2009; Bennett *et al.*, 2013), decrease plant growth and cause disruptions to plant–pollinator interactions (Memmott *et al.*, 2007). In some locations, increased temperature or carbon dioxide levels may enhance plant growth (Reich & Oleksyn, 2008; Wigley, Bond & Hoffman, 2010).

Barriers to movement caused by vegetation loss and fragmentation affect the movement of individuals and propagules (Cunningham, 2000*a*; Schtickzelle & Baguette, 2003). Vegetation loss and degradation alter microclimates, habitat quality and habitat structure, affecting conditions for survival and reproduction and modify species interactions (Mac Nally, Bennett & Horrocks, 2000). Resources for survival and reproduction are diminished in degraded and fragmented vegetation (Zanette, Doyle & Tremont, 2000).

Changes to the global climate include increased global temperature and sea levels, decreased extent of snow and ice (both sea and ice-caps) and increased prevalence and intensity of drought (IPCC, 2013). Changes to climate alter demographic rates because of the physiological responses of organisms to environmental variables such as temperature, which affect survival and reproduction (Chown *et al.*, 2010). Climate conditions affect dispersal behaviour (Altermatt, Pajunen & Ebert, 2008) and pathways (Kuparinen *et al.*, 2009). Climate-induced changes to phenology are well documented (Parmesan, 2006), and these affect demographic rates through their effects on reproduction and survival (Lehikoinen, Kilpi & Öst, 2006; Briscoe *et al.*, 2012), through mismatches in trophic relationships and species interactions (Durant *et al.*, 2007; Miller-Rushing *et al.*, 2010).

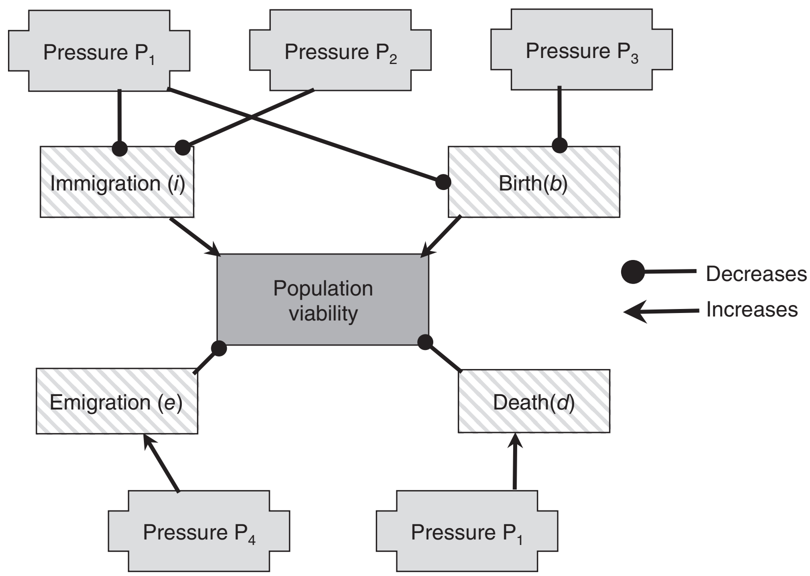

Fig. 2. A general model of the how anthropogenic pressures (P_1-P_4) impinge on demographic rates (*i*, *e*, *b*, *d*) in complex networks of effects. The quantification of the strengths of the relationships is key to managing population viability. 'Pressure' refers to a human-induced perturbation that negatively affects a population and that may be transient (pulse), persistent (press), or monotonically changing in magnitude (ramping) over time (Mac Nally *et al.*, 2011). A population may be exposed to multiple pressures and the one pressure may affect multiple syntopic populations of different species. We synonymize pressure with 'stressor' and 'threat'.

Demographic rates are controlled by resource availability (Skogland, 1985), such as food, which depends on climate (Previtali *et al.*, 2009; Tian *et al.*, 2010). Some populations may benefit from climate change, perhaps through an increase in survival or growth with warmer temperatures (Reich & Oleksyn, 2008). Climate-induced changes to species interactions may benefit some populations by competitor or predator release, while others may be adversely affected by, for example, weakened mutualistic relationships (Tylianakis *et al.*, 2008).

Despite the numerous mechanisms through which land-use change and climate change affect demographic rates, there has been little attention to the relationships between these pressures and demographic responses. Identifying and quantifying the pathways through which anthropogenic pressures affect population viability is important for framing management actions to contribute to population persistence.

(2) Model description

Multiple pressures need to be considered together because pressures rarely occur singly and interactions among pressures may be multiplicative rather than additive (Dawson *et al.*, 2011; Mantyka-Pringle, Martin & Rhodes, 2012). The relationships among pressures and demographic rates are shown in Fig. 2.

Depending on biological characteristics such as longevity, sexual maturity, and propensity to disperse, changes in one or more demographic rates may have a greater influence on population viability than a proportionally similar change in others (Harper, Rittenhouse & Semlitsch, 2008). For example, long-lived species are most affected by changes in death rates because adult survivorship contributes most to population persistence (Li *et al.*, 2009).

By populating the general model of Fig. 2 with empirical information, we show how the principal human pressures (Mace *et al.*, 2005) impinge on demographic rates in plant and animal populations (Fig. 3). The model emphasizes the large roles that land-use change and climate change play in affecting population viability, which we quantify in Section III.

The loss, fragmentation and degradation of native vegetation are proximal ecological pressures stemming from land-use change, which affect demographic rates and population viability through their effects on landscape condition and resource availability. We refer to 'landscape condition' as the degree to which a landscape resembles its natural condition prior to substantial human disturbance or alteration, consisting of native vegetation cover, connectivity and quality. Climate change and changed landscape condition decrease resource availability, such as food, shelter, soil, nutrients, water and other resources necessary for population survival.

III. QUANTIFYING THE EFFECTS OF HUMAN PRESSURES ON DEMOGRAPHIC RATES

Here, we parameterized the strength of the linkages in the conceptual model (Fig. 3) using a representative set of literature estimates. We quantified the effects of changed landscape condition and climate variation on

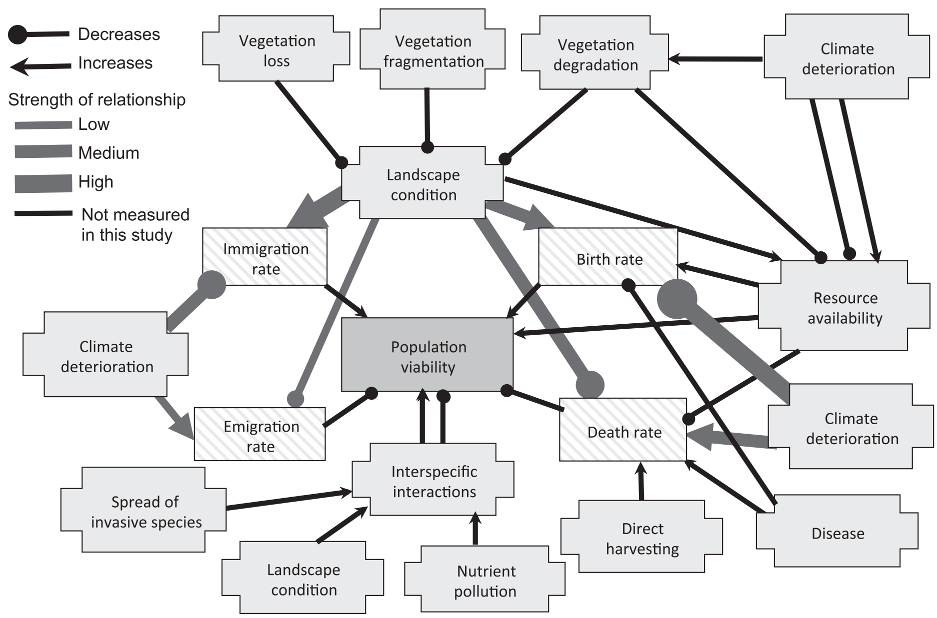

Fig. 3. Empirical application of the general model of Fig. 2 to effects on population dynamics in terrestrial landscapes; the same conventions apply. Grey arrows represent relationships reviewed here. Arrow width represents the mean effect size of the relationship for reviewed studies: low = $0.2 < r < 0.4$; medium $0.4 < r < 0.6$; high = $0.6 < r < 0.8$. No mean effect sizes were <0.2 (very low) or >0.8 (very high).

demographic rates, which provides an assessment of the relative importance of changed landscape condition and climate change on population viability.

(1) Literature search

We searched for papers published between 1970 and 2012 using search terms consisting of descriptors for these pressures and demographic rates under TOPIC (i.e. title, abstract and key words) in Thomson–ISI *Web of Science* (Science Citation Index Expanded) (see online supporting information, Table S1), which returned 206 papers. We examined the titles and abstracts of the papers and retained those that provided quantitative relationships between pressures arising from climate or landscape condition and demographic variables, resulting in the retention of 24 papers. A second search, including broader terms for demography (see online Table S2) was conducted to find other studies that measured variables related to demographic rates. Searching for these terms within TOPIC returned >75000 papers; a random selection of 300 of these revealed no studies that provided quantitative information on the effects of a pressure on a demographic rate. The search was restricted to titles, returning 2324 papers, of which 209 were retained. Another 60 studies were found by using the reference lists of the 233 papers found during both searches.

We examined the results of the 294 studies to obtain statistics that were appropriate for calculating the r correlation coefficient (Rosenthal, 1994) for relationships between demographic variables and landscape condition or climate; this was possible for 147 studies. We used the r correlation coefficient because of its generality and simplicity of interpretation and consistency of meaning (Rosenthal, 1994). While r is most appropriate for relationships between continuous variables, it can also be calculated from pairwise comparisons (Rosenthal, 1994). We included empirical, field-based or experimental studies that directly measured the effects of variables of climate and landscape condition on demographic variables in native plant and animal populations. Only 19 studies looked specifically at *per capita* demographic rates, so we included studies that measured variables that were related to these rates, such as clutch size, fruit production, juvenile survival, and genetic differentiation.

(2) Quantification of effect sizes

Values of the correlation coefficient r (including linear and rank correlations: Pearson's r, Spearman's r, Kendall's τ, point-biserial r, and phi) range between -1 and $+1$, and indicate the strength of the association between variables; the sign indicates the direction of the monotonic association (De Veaux, Velleman & Bock, 2008). Where no correlation coefficient was presented, we calculated r following standard methods (Rosenthal, 1994; Nakagawa & Cuthill, 2007) from reported test statistics (t-statistic, F-statistic, χ^2, Z-score, coefficient of determination R^2, Hedge's d). Where the P-value was the only statistic reported, we transformed these to Z-scores using a standard normal variate (De Veaux *et al.*, 2008).

The correlation coefficient r for each documented relationship between a climate variable (e.g. rainfall, temperature) or landscape-condition variable (e.g. vegetation cover, patch size) and the demographic response was obtained from all species in each study. If >1 variable related to a particular demographic rate was measured (e.g. number of eggs and number of fledglings, or number of seeds and number of seedlings), we used the variable that would contribute most to the number of adult individuals in that population, usually the more advanced life stage (e.g. number of fledglings or number of seedlings). If >1 variable related to climate (e.g. rainfall and temperature) or to landscape condition (e.g. fragment size and isolation) was measured, we included the variable that had the largest effect size on the demographic response variable. Details of included studies and their effect sizes are in Table S3. Thirty-six studies measured >1 species, demographic rate and/or driver, and so, contributed >1 datum to the analysis.

For landscape condition, values of r ranged between -1 and $+1$, with positive values being associated with a positive effect of measures such as vegetation cover or contiguity on a demographic rate. For example, if fragmentation had a negative effect on a measure of birth rates in a study, the correlation coefficient for landscape condition on birth rates for that relationship would be positive.

We did not estimate the direction of relationships between climate variables (e.g. temperature, rainfall) and demographic rates because there is difficulty in generalizing the effects of climate variables on population viability given that directional climate deviations do not uniformly affect demographic rates (Glenn *et al.*, 2011). Changes in climate depend on region, so that generalizations are not appropriate. For example, there may be increases in precipitation in some regions and decreases in others, so that decreased rainfall cannot be considered to be a consistent climate-change effect (IPCC, 2013). The effects of climate variables on demographic rates may differ among seasons (Reed & Slade, 2009) and many studies measured within-year climate measures (e.g. winter rainfall) making it inappropriate to extrapolate to general trends given the scope of this review. We considered the correlation coefficient to be an absolute value for climate variables on demographic rates when calculating an average effect size, with r ranging from 0 to 1. This provides an indication of the size of the effect that climate may have on demographic rates rather than generalizing the effects of climate variables.

We converted all r values to Z_r using Fisher's transformation, which transforms r to a near-normal distribution, because the distribution of r values becomes skewed as r becomes absolutely larger (Rosenthal, 1994). We calculated the mean effect size and standard error for the effect of landscape condition and climate on demographic rates using the Z_r values to gauge the size of the effect that climate and landscape condition have on demographic processes and, in the case of pressures arising from landscape condition, the direction of this effect. Means were calculated for plants and animals separately. The means and upper and lower confidence interval values (95% confidence interval) were then back-transformed to r, so that the effect size could be between 0 and 1 for the effect of climate, and between -1 and $+1$ for the effect of landscape condition (Rosenthal, 1994).

(3) Results

Most studies on climate and landscape condition were from North America and Europe (see online Table S4). Birds were the most studied animals, followed by mammals, with other groups poorly represented (see online Table S3). There were few studies on the effects of climate on plant demographic rates (see online Table S3).

Landscape condition had a mean positive effect on birth rates in plant ($\bar{r} = 0.3$) and animal populations ($\bar{r} = 0.5$), a negative effect on death rates in animal populations ($\bar{r} = -0.6$), and a positive effect on plant dispersal and animal immigration ($\bar{r} = 0.6$ for both). Landscape condition had a mean negative effect on death rates in plant populations ($\bar{r} = -0.6$) and emigration in animal populations ($\bar{r} = -0.2$), but studies were few ($N = 2$ and 5) and confidence intervals overlapped zero, indicating that these effects were not significantly different from zero (Harrison, 2011) (Fig. 4A). The mean absolute effect sizes of climate on demographic rates were similar, for birth rates in plants ($\bar{r} = 0.7$) and animals ($\bar{r} = 0.6$), and plant ($\bar{r} = 0.7$) and animal death rates ($\bar{r} = 0.6$) (Fig. 4B).

There was a small mean effect size on animal emigration ($\bar{r} = 0.2$), but there were only three studies, each of which reported increased measures of emigration with higher temperatures. There was just one study on animal immigration ($\bar{r} = 0.6$) (Fig. 4B). There were no studies that provided statistics for calculating the effect size of climate on plant dispersal.

Studies that measured the effects of temperature and rainfall used a wide variety of temporal measures of climate (e.g. week, month, season, year, life-cycle stage), so we cannot extrapolate to responses to climate change (see online Table S5). For studies that reported an effect of rainfall, most were lower birth rates (11 of 13 studies) and increased death rates (five of eight studies) with decreasing rainfall (see online Table S5). For those assessing temperature effects, most showed a negative effect on birth rates (13 of 17 studies) and survival (five of five studies) with increasing temperatures (see online Table S5).

Landscape condition and climate appear to have substantial effects on demographic rates in plant and animal populations, with absolute effect sizes of 0.5–0.7 for all demographic rates except animal emigration (Fig. 4B). Given the large number of studies, there is good support for the positive effect of landscape condition on plant and animal birth rates and animal immigration (Fig. 4A). There were ≤ 5 studies on the effect of landscape condition on plant death rates, animal emigration and plant dispersal, but the directions of the relationships from these studies supported the conceptual model (Fig. 3).

IV. MECHANISMS AFFECTING DEMOGRAPHIC RATES

Here, we qualitatively review the mechanisms through which demographic rates in plant and animal populations are affected by changed landscape condition and climate change.

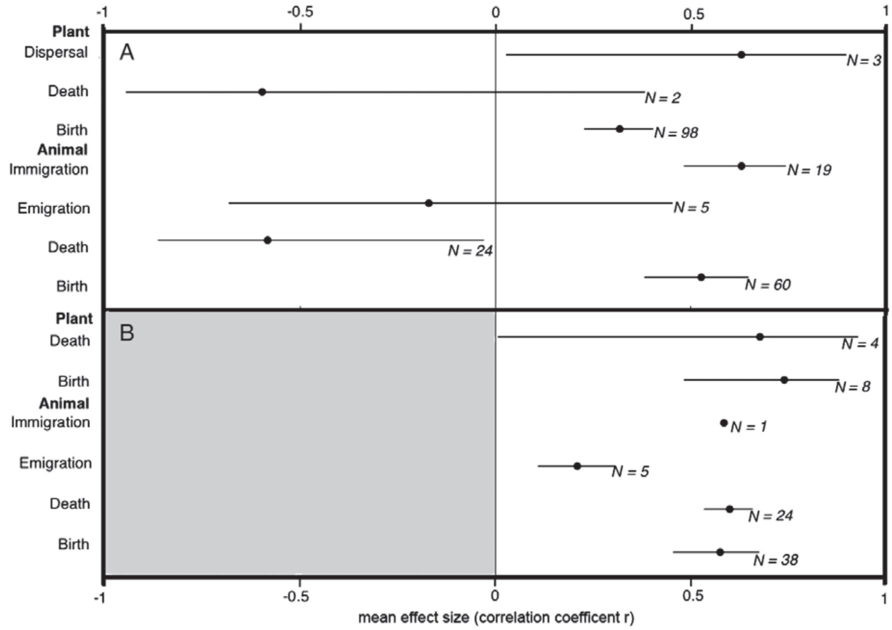

Fig. 4. (A) Mean effect sizes ($\bar{r}$) of landscape condition parameters and (B) mean absolute effect sizes ($\bar{r}$; values between 0 and 1 only) of climate parameters on measures of birth rates, death rates, immigration, emigration and dispersal in plant and animal populations. Error bars are 95% confidence intervals. The number of data points (study × species) is shown by *N*.

(1) Birth rates

Our quantitative review shows strong evidence for a negative effect of changed landscape condition on birth rates in plant and animal populations. The most proximate effect on plant reproduction in changed landscapes is usually pollination limitation (Aguilar *et al.*, 2006). Changed landscape condition results in declines in native pollinator populations and reduced pollinator visitation due to isolation, which reduces fruit production and seed set (Wilcock & Neiland, 2002; Gómez *et al.*, 2010). Allee effects, including inbreeding and genetic erosion, affect mate availability and seed set and interact with pollen limitation to reduce population viability (Wagenius, Lonsdorf & Neuhauser, 2007; Young, Broadhurst & Thrall, 2012). Wind-pollination may be disrupted by fragmentation, possibly causing inbreeding (Jump & Peñuelas, 2006). Reduced seed dispersal or increased seed predation occur in modified landscapes (Benitez-Malvido, 1998; Tallmon *et al.*, 2003). Loss and degradation of vegetation alters the conditions for germination and seedling establishment, including light environments (Uriarte *et al.*, 2010), microclimatic conditions (Jacquemyn *et al.*, 2003; Werner & Gradstein, 2008), and wind erosion (Li *et al.*, 2009). Grazing by domestic stock causes trampling and herbivory of seedlings (Jansen & Robertson, 2001). These declines in plant recruitment have large effects on population viability (Bruna & Oli, 2005).

Vegetation loss and fragmentation influence birth rates in animal populations by affecting access to food resources (Mbora, Wieczkowski & Munene, 2009) and by reducing food and resource levels in vegetation remnants (Zanette *et al.*, 2000). Increased nest predation and parasitism are common in much-modified landscapes, particularly near vegetation boundaries (Lampila *et al.*, 2005). Decreased vegetation connectivity reduces mate availability (Cooper & Walters, 2002), including through inbreeding avoidance (Boudjemadi, Lecomte & Clobert, 1999; Stow & Sunnucks, 2004). Some plant and animal populations experience higher birth rates in changed landscapes, especially those with a preference for open or edge habitat (Mac Nally *et al.*, 2012), or through decreased competition for resources such as light (Neal, Hardner & Gross, 2010).

Climate had a strong effect on birth rates, affecting rates in several ways. Most studies reported decreased birth rates with increased temperature and decreased precipitation. Global temperatures have risen, and the frequency of hot days and of heat waves is likely increasing (IPCC, 2013). Increased annual temperatures and short-term heat waves may reduce germination of plants (Chidumayo, 2008; Shevtsova *et al.*, 2009). In animals, heat stress of parents may induce declines in neonatal survival (Griffin *et al.*, 2011) and decreased fecundity (Neveu, 2009). Higher temperatures may cause heat stress in young animals, leading to lower survival rates of young (Steenhof, Kochert & McDonald, 1997). Warm and dry conditions, such as those associated with El Niño events, may harm eggs and hatchlings by altering microclimate conditions in nests (Tomillo *et al.*, 2012), although warmer temperatures may increase hatching success (Beissinger, Cook & Arendt, 2005). Warmer temperatures may enhance the breeding success and survival of young and seedlings by reducing energy needs (Nielsen & Møller, 2006; Milbau *et al.*, 2009) and reducing the occurrence of severe winters that limit reproductive success (McIntyre & Schmidt, 2012). Warming may lengthen periods suitable for breeding and result in increased birth rates and additional generations within an annual cycle (Jönsson *et al.*, 2009; Clarke & Zani, 2012).

Lower rainfall and increased drought frequency may affect plant birth rates through decreased fruit set (Ågren, Ehrlén & Solbreck, 2008) and seedling survival (Hallett, Standish & Hobbs, 2011). Reduced food-plant productivity and food availability during periods of low rainfall, such as in El Niño events, may depress fecundity (Dunham, Erhart & Wright, 2010), prevent reproductive maturation (Lima *et al.*, 2001), and lessen offspring survival (Sillett, Holmes & Sherry, 2000). Limited water availability for lactating females may affect juvenile survival (Dunham *et al.*, 2010). Lower water levels at aquatic breeding sites may result in increased ultraviolet radiation and heat exposure, which can affect hatching success (Blaustein *et al.*, 2012), increase the vulnerability of embryos to pathogens (Kiesecker, Blaustein & Belden, 2001), and desiccate tadpoles (Pechmann *et al.*, 1991). Heavy rains or snowfalls, which are expected to increase in frequency even in areas with decreased annual precipitation (IPCC, 2013), stress gestating females (Dunham *et al.*, 2010), and increase juvenile and egg mortality (Skagen & Adams, 2012).

Phenological changes triggered by climate changes such as earlier warming, may increase self-fertilization in monoecious plants or cause mistiming in the flowering of dioecious plants (Miller-Rushing *et al.*, 2010). While earlier breeding may benefit birth rates of some species (Nielsen & Møller, 2006), advances in breeding and flowering expose flower buds (Inouye, 2000, 2008), eggs and young (Lehikoinen *et al.*, 2009) to poor or more variable weather conditions (e.g. frosts or heavy rain) if seasonal climate patterns do not advance in concert. Changed climate conditions may delay breeding so that the young may experience adverse conditions later in the season (Waite & Strickland, 2006; Senapathi *et al.*, 2011), and may inhibit breeding altogether (Pankhurst & Munday, 2011). Phenological changes in plants can cause asynchrony with pollinators, increase exposure to florivores and granivores, and increase synchrony of flowering among species competing for pollinators (Miller-Rushing *et al.*, 2010). Phenological changes to a population or its biotic resource may affect birth rates if the two do not change in synchrony. Asynchrony between food needs during breeding and food availability arises from earlier breeding (Moss, Oswald & Baines, 2001), advancement of peak prey availability (Sanz *et al.*, 2003), advanced phenology of food and larval host plants (Parmesan, 2005; Post & Forchhammer, 2008), or changed timing of food peaks (Wolf *et al.*, 2009). Climate-induced asynchronies in resource availability and resource needs during breeding have caused population extinctions (McLaughlin *et al.*, 2002). For some species, earlier warming may increase synchrony with food resources, which can increase birth rates (Vatka, Orell & Rytkönen, 2011).

Spring snow cover is decreasing in the northern hemisphere (Werner, 2011). Reduction of snow cover may decrease seedling survival by permitting increased herbivory (Brodie *et al.*, 2012) and by increasing exposure to frost (Bannister *et al.*, 2005). Sea levels are rising (IPCC, 2013), and this can affect birth rates through more frequent flooding of coastal nesting sites (van de Pol *et al.*, 2010). Physiological stress from severe weather limits reproductive success of many animals (Dunham *et al.*, 2010).

Within species, the extents to which birth rates are affected by climate changes differ depending on the elevational (Munier *et al.*, 2010; Hargrove & Rotenberry, 2011) or latitudinal (Ontiveros & Pleguezuelos, 2003; Sanz, 2003) location of populations, with some populations experiencing opposite effects of climate on birth rates in different locations (Gaston, Gilchrist & Hipfner, 2005). Climate effects on other demographic characteristics, such as death rates or sex ratios can dampen or counter positive effects (Zani, 2008; Schwanz *et al.*, 2010).

The effects of both landscape change and climate are diverse, and it is possible that there will be interactions or additive effects of these pressures on birth rates. However, while studies on variables related to birth rates were the most numerous of the demographic rates, this does not necessarily reflect the proportional importance of birth rates to population viability. In many species, rates of adult survival have a greater influence on population growth rates than do birth rates (Sæther & Bakke, 2000; Bruna, Fiske & Trager, 2009).

(2) Death rates

Although rates of survivorship in established plants usually contribute more to plant population growth rates than reproduction and seedling dynamics, there has been more focus on the effects of landscape condition on plant reproduction (Bruna *et al.*, 2009). There have been few studies on the effects of landscape condition on plant death rates, but mortality increases in many species due to transformation of native forest to plantations (Jules, 1998), and increased wind turbulence and microclimate changes near vegetation boundaries with agricultural land (Laurance *et al.*, 1998; Werner, 2011).

Elevated death rates in changed landscapes may reduce population viability for animal species (Harper *et al.*, 2008; Li *et al.*, 2009). Diminished availability of resources can contribute to higher death rates in fragmented landscapes and in small vegetation remnants (Boudjemadi *et al.*, 1999; Doherty & Grubb, 2002). Death rates may be affected by higher predation and desiccation in degraded or cleared vegetation (Rothermel & Semlitsch, 2002; Harper *et al.*, 2008), including during dispersal (Cushman, 2006). Mortality during dispersal through much-modified landscapes affects sex ratios, birth rates (Banks *et al.*, 2005) and the persistence of populations (Brooker & Brooker, 2002).

High temperatures and heat waves (Jakalaniemi, 2011; Andrello *et al.*, 2012) and low rainfall and drought (Toräng, Ehrlén & Ågren, 2010) increase plant death rates through physiological stress. Drought increases susceptibility and exposure to pest species that cause mortality (Kloeppel *et al.*, 2003). Mortality of trees from increased drought occurs in many forests around the world and is expected to become more frequent (Van Mantgem & Stephenson, 2007; Horner *et al.*, 2009).

Warmer temperatures and low rainfall can accelerate water loss and energy expenditure in animals, leading to chronic stress, desiccation or hyperthermia (Grafe *et al.*, 2004; Moses, Frey & Roemer, 2012), particularly if these climate changes occur during energetically demanding phases of a species annual cycle (Grosbois *et al.*, 2006), or if temperatures approach or exceed the upper lethal limit of a species (Bale & Hayward, 2010). High temperatures increase population death rates (Grosbois *et al.*, 2006; Griffiths, Sewell & McCrea, 2010) and the frequency of catastrophic mortality events (McKechnie & Wolf, 2010). While increased temperatures may improve survival rates in some animals that experience cold stress, earlier melting of protective snow layers increases death rates by exposing animals to deleterious weather conditions, such as freezing rain and cool air temperatures (Bale & Hayward, 2010; Fisher & Davis, 2011) and increases predation risk (Lindström & Hörnfeldt, 1994). In cooler climates, elevated temperatures may increase survival rates for organisms near their lower thermal limits (Walther *et al.*, 2002; Frenot *et al.*, 2005). Asynchronies in the life cycles of predator and prey may increase the survival of the prey species, particularly if the prey is limited by predation rather than by food availability (Miller-Rushing *et al.*, 2010).

Increased frequency of high-energy weather events, such as hurricanes, storms and heavy rainfall, increase death rates in plants (Van Mantgem & Stephenson, 2007) and animals (Langtimm & Beck, 2003). Severe rain, snow or wind events cause mass mortality events (Newton, 2008*a*). Death rates increase with fewer food and foraging resources in the aftermath of intense weather events (Wiley & Wunderle, 1993).

Drought and much reduced rainfall can increase death rates through decreased food availability for terrestrial animals (Sillett *et al.*, 2000; Frick, Reynolds & Kunz, 2010), particularly when these occur during crucial times of breeding and survival. Climate oscillations affect food availability, and therefore death rates (Sandvik *et al.*, 2005; Morrison *et al.*, 2011).

While we have detailed several predicted and observed effects of both landscape condition and climate change on mortality, there has been relatively little research that measures the effects of these processes on death rates, and their subsequent effect on population viability. A better understanding of the effects of major anthropogenic pressures on death rates will be particularly important for those species whose population viability is most acutely affected by death rates, such as long-lived species (Sæther & Bakke, 2000).

(3) Emigration and immigration

Given that adult terrestrial plants are sedentary, emigration and immigration mostly is through the transport of seeds, fruits or vegetative propagules by animals, wind or water (Raulings *et al.*, 2011) and does not constitute the loss of an adult from the donor population *per se*. Increased isolation of plant populations and declines in seed-disperser populations (Cordeiro & Howe, 2003) inhibit biotic and abiotic seed dispersal, particularly for heavy-seeded species (Hewitt & Kellman, 2002; McEuen & Curran, 2004), with potentially substantial effects on population viability (Hewitt & Kellman, 2002). Gene flow of plants predominantly is through the dispersal of pollen by biotic vectors and physical transmission (Ellstrand, 1992), which can be impeded by declines in landscape condition and climate change (Section IV.1).

The loss, fragmentation and degradation of native vegetation increase emigration rates and decrease immigration rates in animal populations, which affect population size and hence population viability, but the evidence for these expectations is weak (Section III). Reduced immigration can lead to skewed sex ratios (Harrisson *et al.*, 2012), inbreeding (Daniels, Priddy & Walters, 2000), disruption of mating systems (Pavlova *et al.*, 2012) and mate limitations (Stow & Sunnucks, 2004), which decrease population viability.

Low emigration rates generally occur when habitat and resources are ample (Baguette, Petit & Queva, 2000). If a site is rich in resources, immigration is likely to be higher because the immigrants are attracted by the presence of numerous conspecifics (Buechner, 1987) and highly suitable habitat (for the species) increases the 'attractiveness' of sites for recolonizing individuals (Doerr, Doerr & Jenkins, 2006).

Populations in high-intensity human land-use areas or that are experiencing low resource availability are more likely to experience emigration, and, in extreme circumstances, this can cause extinction (Lin & Batzli, 2001; Mac Nally *et al.*, 2009). Individuals are more likely to emigrate if they experience low reproductive or pairing success (Bayne & Hobson, 2002; Zitske, Betts & Diamond, 2011).

Small and isolated vegetation remnants generally attract fewer immigrants (Wauters *et al.*, 1994; Holland & Bennett, 2010). Decreased dispersal success caused by death during dispersal or the inability to locate appropriate habitat in high-intensity land-use areas lowers immigration rates (Matthysen, 1999; Püttker *et al.*, 2011) and reduces population viability, even in mobile animals, such as birds (Cooper & Walters, 2002; Robles *et al.*, 2008). Measurements of genetic connectivity among populations suggest decreases in dispersal in fragmented landscapes (Vos *et al.*, 2001). These measures, when combined with direct measures of movement, have the potential to help tease out the effects of landscape condition and other pressures on immigration and emigration rates (Lowe & Allendorf, 2010).

Warmer temperatures can increase animal emigration rates (Pärn *et al.*, 2011; Franzén & Nilsson, 2012) and dispersal distances (Cormont *et al.*, 2011), but may cause disparities in dispersal between the sexes (Merckx, Karlsson & Van Dyck, 2006). Increased atmospheric instability caused by warmer temperatures induces long-distance wind dispersal of seeds (Kuparinen *et al.*, 2009) and small invertebrates (Coulson *et al.*, 2002) by increasing convective turbulent airflow. Warmer temperatures may discourage juvenile dispersal (Massot, Clobert & Ferrière, 2008) and increase dispersal mortality due to heat stress (Henry, Sim & Russello, 2012). Lower rainfall can decrease vegetation quality in high-intensity land-use areas, discouraging emigration between fragments of native vegetation (Blaum *et al.*, 2012). Climatic events such as El Niño Southern Oscillation (ENSO) phases and consequent declines in food resources may trigger irruptive migrations of animals (Holmgren *et al.*, 2006; Lindén *et al.*, 2011).

Studies that use niche models to predict changes in species distributions predict elevational and latitudinal shifts in response to climate exposure, assuming colonization of newly suitable climate conditions (Fordham *et al.*, 2012). The structure and condition of many human-dominated landscapes are likely to impede colonization (Opdam & Wascher, 2004). Although organisms have responded to climate changes through migration and adaptation in the past, the barriers imposed by human land use and the unprecedented rate of climate change are unlikely to allow the predicted range shifts in many species to occur (Davis & Shaw, 2001). Range shifts are inhibited in much-modified landscapes, and may stall where the amount or cohesion of habitat is below thresholds necessary for population persistence (Opdam & Wascher, 2004). Fragmented vegetation may be disproportionately affected (higher mortality or die-back) by climate change (Bennett *et al.*, 2013), creating further barriers to climate-induced range shifts. Some species may be unimpeded by modified landscapes and this will affect species interactions in receiving habitats (Menéndez *et al.*, 2008). For example, landscape and climate change have increased the distribution and abundance of the despotic noisy miner (*Manorina melanocephala*) in eastern Australia. This has caused local emigration and a lack of immigration of small-bodied birds in fragmented vegetation where the species is present (Maron *et al.*, 2013).

To gauge the effects of climate change on species distributions, an understanding of the effects of climate on immigration and emigration rates and the processes of dispersal is vital, particularly in changed landscapes where these rates are already affected.

V. SYNTHESIS AND FUTURE WORK

Demographic rates are rarely the focus of studies on the effects of human pressures on native populations of plants and animals. However, these effects can be substantial and their identification enables a better understanding of the mechanisms through which pressures affect population viability. That vegetation loss, fragmentation and degradation affect demographic rates in plant and animal populations is not unexpected given the widespread declines in biodiversity that have been seen as a result of these pressures (Foley *et al.*, 2005; Butchart *et al.*, 2010). Our finding that the mean effect of climate on demographic rates is of comparable magnitude to changes in landscape condition is significant and supports recent assertions that climate change will become as, or more, important in species declines and extinctions in coming decades (e.g. Mantyka-Pringle *et al.*, 2012).

The relative effects of climate on demographic rates probably are underestimates. Most studies assess relationships between general climate measures, such as annual temperature or seasonal precipitation within average ranges of year-to-year variation. The characteristics of relationships between demographic variables and climate variations are likely to change once changes in climate fall outside the average range. The effects of climate variables on demographic rates may become greater, new effects may emerge, or the direction of relationships may change. There are likely to be critical windows of climate effects on population parameters, where climate conditions at very specific times in species life cycles are disproportionally important to population viability (Lada *et al.*, 2013). Assessing general trends in climate and demographic rates may not detect the true size of the effects on population viability that will occur if changes in climate occur during critical windows. Critical thresholds may exist, such as where temperatures exceed lethal limits (Somero, 2010). Studies that measure demographic responses to climate conditions within the average range are unlikely to detect such responses. While the studies we reviewed assumed monotonic relationships between pressures and demographic variables, physiological responses to temperature are commonly asymmetric, such that a positive response to temperature may be reversed once an optimal level is reached (Sinclair & Chown, 2003).

Climate change may introduce new pressures to otherwise viable populations, or may cause the decline of populations in changed landscapes faster than otherwise expected. Decreases in rainfall and increases in temperature probably will have deleterious effects on many populations, although some taxa almost certainly will benefit. Small populations have less capacity to evolve rapidly to changed conditions (Willi, Buskirk & Hoffmann, 2006), so climate change may have a cascading effect on the viability of populations that have been affected by changed landscape condition. Some species will have increased population viability with the amelioration of limiting climate conditions. Changes in population viability in either direction will affect species interactions, with disruptions for communities (Sorte & White, 2013). A greater focus on the relationships between climate conditions and demographic rates is needed to produce better predictions for likely impacts of climate changes on animal and plant populations. A more complete understanding of the effects on immigration and emigration must improve predictions of range shifts. Identification of the demographic rates most affected by projected climate changes will assist with better planning for climate adaptation.

Populations in changed landscapes may decline faster than expected with the added pressures arising from climate change. This is important in making predictions about population size in response to pressures such as habitat loss, including considerations of critical thresholds (Swift & Hannon, 2010), which could be reached earlier than expected with the added imposts of climate pressures and their effects may be synergistic (Mantyka-Pringle *et al.*, 2012). Landscape modification may hinder or reverse the expected population growth in response to changed climate conditions (Warren *et al.*, 2001). Whether the effects of landscape condition and climate on demographic rates are additive or multiplicative (or for some species, opposing), is a core question.

While our review highlights some mechanisms through which the major anthropogenic pressures affect population viability, there is a clear need for more data. A more comprehensive understanding of these relationships will contribute greatly to improving the effectiveness of conservation policies and management actions. Specifically, there is a need for expanding research beyond North America and Europe, and we suggest that the most important areas for conducting this research are those that are predicted to experience the greatest changes in climate conditions. Warming is likely to occur most rapidly in the polar regions, while mid-latitude and sub-tropical dry regions are likely to be most affected by decreased precipitation (IPCC, 2013). There is a dearth of research into the effects of climate on plant demographic rates despite climate change being the most commonly cited factor in the extinction and endangerment of plant species (Mora & Zapata, 2013).

VI. CONCLUSIONS

(1) Given their intimate connection with population viability, demographic responses provide a critical indication of likely changes in extinction risk in response to human pressures.

(2) Changes in landscape condition generally have a negative effect on birth and immigration rates in plant and animal populations, and increase death and emigration rates. We predict that climate change will have a negative effect on birth and immigration rates, and a positive effect on death and emigration rates, although we did not quantitatively assess this.

(3) Despite the recognition of landscape change as the major driver of biodiversity loss, the effects of climate on demographic rates in plant and animal populations are of equivalent magnitude. This supports consideration of climate change as a major driver of population viability, of similar importance to human land-use change.

(4) A more comprehensive understanding of the rate and size of the effects of pressures on demographic rates among taxa and regions will greatly assist management attempts to arrest species declines and extinctions.

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IX. SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article.

Table S1. Search terms used to locate studies that measured the effect of climate and landscape condition on demographic rates.

Table S2. Search terms used to locate studies that measured the effect of climate and landscape condition on variables related to demographic rates.

Table S3. List of species used for the calculation of mean effect sizes for climate and landscape condition on population vital rates.

Table S4. Breakdown of individual studies (December 2012 and earlier) that measured demographic responses to landscape condition and climate by region and taxonomic group.

Table S5. Subset of studies (from online Table S3) that showed effects of temperature and rainfall variables on birth or death rates.

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