

## Review and synthesis

### Spatial and temporal heterogeneity in climate change limits species' dispersal capabilities and adaptive potential

RUNNER-UP

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Global climate change has already caused local declines and extinctions. These losses are generally thought to occur because climate change is progressing too rapidly for populations to keep pace. Based on this hypothesis, numerous predictive frameworks have been developed to project future range shifts and changes in population dynamics resulting from global climate change. However, recent empirical work has demonstrated that seasonally asynchronous climate change regimes – when a region is warming during some parts of the year, but cooling in others – are constraining species' responses to climate change more strongly than rapid warming, leading to intra-specific variation in responses to climate change and local population declines. Here, we couple a review of the literature related to asynchronous climate change regimes with meta-population simulations and an analysis of long-term North American climate trends to show that seasonally asynchronous regimes are occurring throughout most of North America and that their current spatial distribution may be a strong barrier to dispersal and gene flow across many species' ranges. Thus, even though adaptation to climate change may potentially be more common and rapid than previously thought, species whose ranges overlap with asynchronous regimes will likely succumb to local declines that may be difficult to mitigate via dispersal. Future climate-related predictive frameworks should therefore incorporate asynchronous regimes as well as more traditional measures of climate velocity in order to fully capture the array of potential future climate change scenarios.

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#### Introduction

As global climate change accelerates, there is an increasing urgency to identify the species and populations most likely to succumb to future climate-related declines and extinctions (Wiens 2016). In recognition of this urgency, there have been myriad empirical and theoretical attempts to characterize the ways in which climate change is already impacting species and how such impacts may affect the population dynamics of those species in the coming century (Cahill et al. 2012, Moritz and Agudo 2013, Urban 2015). Nonetheless, there remains a strong disconnect between empirical data



and current theoretical frameworks. This disconnect arises from the fact that the theoretical models developed to project future range shifts and extinctions currently incorporate only a subset of the mechanisms by which empirical studies have shown climate change to be affecting species (Webster et al. 2017). In turn, this discrepancy limits our ability to identify vulnerable species and hampers the implementation of conservation actions where they are needed most.

One of the most important differences between the current collection of climate change-related predictive frameworks and the empirical literature is the reliance of these frameworks on climate velocity – the speed with which climatic zones are shifting spatially – as a metric to predict the rate at which species must respond to climate change (Loarie et al. 2009, Burrows et al. 2011, Hamann et al. 2015). This focus presents a problem, as the standard formulas used to calculate climate velocity rely on mean annual rates of temperature change (Hamann et al. 2015), which can mask seasonally asynchronous climate change regimes – e.g. when a region is warming during one portion of the year, but cooling in another. Unlike spatially asynchronous dynamics, which can increase the persistence of meta-populations (Heino et al. 1997), asynchronous climate change regimes are temporally asynchronous and can therefore impose contrasting selection pressures to which populations have difficulty responding (Senner et al. 2017). Accordingly, recent empirical work has demonstrated that asynchronous regimes can adversely affect many species (Straile et al. 2015), limiting the ability of some populations to respond to climatic changes (Both and Visser 2001) and causing intra-specific variation in vulnerability to climate change (Visser et al. 2003) that leads to local population declines (Both et al. 2006). As such, asynchronous regimes represent a frequently overlooked, but critical component of global climate change that should be incorporated into climate-related predictive frameworks.

Here we review the recent empirical literature on asynchronous regimes, and then couple that review with novel meta-population simulations and an analysis of long-term climate data to more fully document the range of effects asynchronous regimes are likely having on species and populations. Our results indicate that seasonally asynchronous climate change regimes are occurring throughout much of North America and likely disrupt dispersal and gene flow for many species. As a result, although rapid adaptations to climate change may not be especially rare, species whose ranges overlap with regions exhibiting asynchronous regimes will likely soon experience local declines and extinctions that may be difficult to reverse by evolutionary rescue.

## The effects of asynchronous climate change regimes

Although they have yet to be incorporated into climate-related predictive frameworks, the detrimental effects of asynchronous regimes on population dynamics have been widely documented in the ornithological (Visser et al.

1998), entomological (Doi et al. 2008), limnological (Straile et al. 2015), and broader ecological literature (Burrows et al. 2011). Across these studies, asynchronous regimes have frequently been found to disrupt population dynamics by causing phenological mismatches. Mismatches arise when the environmental conditions occurring when an individual initiates a process become decoupled from the conditions occurring when the fitness consequences of that process are determined (Durant et al. 2007). Most commonly, this leads individuals to initiate their reproductive efforts too late and thus raise their young in a resource poor environment. For instance, in the classic example of Dutch-breeding great tits *Parus major*, rates of temperature change in March – when tits initiate reproduction – have been outpaced by those occurring in May – when tits rely on the emergence of winter moth *Opheroptera brumata* larvae to feed their young (Visser et al. 1998). This disparity in rates of temperature change has caused a mismatch between the two species, as winter moth emergence has shifted earlier as a result of the warming May temperatures (van Asch et al. 2007), but tit reproduction has not as a result of the stagnant March temperatures (Visser et al. 1998).

Phenological mismatches are common across trophic levels and can arise via a number of different mechanisms (Ovaskainen et al. 2013). In general, though, mismatches result from either the imposition of physiological constraints – e.g. if cooling early spring temperatures reduce an individual's body condition, delaying the onset of reproduction (Stevenson and Bryant 2000) – or the disruption of the environmental cues triggering phenological events – e.g. when rates of temperature change influence the timing of reproduction, but temperatures now increase more slowly than in the past (Schaper et al. 2012) – or both (Lof et al. 2012). In turn, once a mismatch has been initiated between two trophic levels, it becomes more likely that mismatches will arise at other trophic levels within that community as well, with those mismatches being exacerbated and potentially more harmful at higher trophic levels (Both et al. 2009).

Although phenological mismatches are not the only way in which asynchronous regimes can detrimentally affect populations, the mechanisms by which they arise are representative of the broader effects that asynchronous regimes can have across taxa. For example, cooling trends in late winter can prolong winter conditions and potentially exacerbate regular food shortages. This can lead to heightened mortality rates during this period (Brommer et al. 2000) or cause delays in the emergence of hibernating individuals such that they are unable to accumulate sufficient fat stores before the onset of the following winter (Lane et al. 2012). Likewise, cooling spring conditions can result in cold snaps that limit reproductive success in early breeders through direct mortality and reductions in food supplies (Winkler et al. 2013). Additionally, both within- and trans-generational plasticity – when the parents' environmental exposure influences the phenotype of their offspring – have been identified as potential mechanisms facilitating responses to climate change (Chevin et al. 2010, Bonduriansky et al.

2012). However, individuals raised in cooling conditions may have reduced thermal tolerances if exposed to warming conditions during subsequent life-history stages (Allen et al. 2012) or maladaptively influence the phenotype of their offspring via parental effects (Shama et al. 2016).

Potentially one of the most underappreciated mechanisms by which asynchronous regimes can disrupt population dynamics is through the induction of developmental traps in species that cycle through multiple generations during a single year (Forrest 2016). In these species, warming spring and summer temperatures that are counteracted by cooling fall conditions can initiate the production of 'lost generations' (Chinellato et al. 2014, van Dyck et al. 2015, Glazacow et al. 2016). This situation occurs when temperature cues override a species' photoperiod cues, inducing them to develop to adulthood when they would normally overwinter at earlier developmental stages (van Dyck et al. 2015). When these adults subsequently fail to mate because of cooling temperatures, they leave no generation to overwinter and reproduce the next spring (Chinellato et al. 2014). While only recently recognized as a possible consequence of climate change (van Dyck et al. 2015), the scenario is analogous to those experienced by many invasive species in novel environments and may thus be a common occurrence among invertebrate taxa (Musolin 2007).

Ultimately, the unifying feature among these scenarios is that asynchronous regimes are imposing contrasting selection regimes that are difficult to reconcile via either phenotypic plasticity or rapid evolutionary adaptation (Gienapp et al. 2014). Plasticity allows populations to track changes in both mean environmental conditions and the variance around that mean under certain circumstances – such as climate change regimes in which warm years are followed by cool years, but there is a uniform trend for warming across seasons and years (Nussey et al. 2005). However, plasticity is unlikely to be beneficial in situations in which the cues used by an individual to induce plastic changes are no longer predictive of future environmental conditions (McNamara et al. 2016). Such scenarios should instead lead to the development of bet-hedging strategies, but these may be slow to evolve in all but the most dramatically unpredictable and resource-limited environments (Poethke et al. 2016). Similarly, only the introduction of novel genetic variation may be able to adaptively resolve situations in which two antagonistic traits are experiencing directional selection in opposing directions (Careau et al. 2015), suggesting that evolutionary responses to the contrasting selection pressures imposed by asynchronous regimes may be especially slow. Asynchronous regimes thus pose a significant hurdle to the ability of species to respond to climate change and may help explain some persistent climate-related patterns observed across species.

## Asynchronous regimes and the potential for rapid adaptation

A common hypothesis presented to explain the danger posed by climate change to global biodiversity is that climate

change is progressing too rapidly for species to keep pace, meaning they can neither adapt quickly enough nor disperse far enough to maintain viable populations throughout their range (Etterson and Shaw 2001). There is increasing evidence, however, that both rapid plastic and evolutionary changes can occur in response to even relatively weak selection pressures. Experimental and laboratory studies have demonstrated appreciable changes in population allele frequencies within a single generation (Gompert et al. 2014), with complex life-history traits evolving in only 20–30 generations (Cameron et al. 2013, de Roissart et al. 2016). Although rates of change in the wild are generally expected to be slower than in experimental settings (Kinnison and Hendry 2001, Barrick et al. 2009), examples of rapid phenotypic and evolutionary change over short time periods do exist. For instance, following the extremely cold mid-winter conditions experienced by much of continental North America in January–February 2014, surviving green anoles *Anolis carolinensis* exhibited both marked increases in their cold tolerances and signatures of selection across the genome (Campbell-Staton et al. 2017). Similarly, rapid plastic and evolutionary responses to global climate change have already been observed across taxa ranging from migratory birds (Gill et al. 2013) to anadromous fish (Kovach et al. 2012), arthropods (Kreherwinkel et al. 2016), annual plants (Franks et al. 2016), and soil (Bataillon et al. 2016) and aquatic invertebrates (Oexle et al. 2016). In fact, rapid, directional climatic changes may even facilitate rapid responses (Phillips et al. 2016). Thus, although niche conservatism may ultimately constrain the extent and rate at which populations can adapt evolutionarily to climate change (Quintero and Wiens 2013), rapid climate-driven adaptations may not be as rare as once thought (Moran and Alexander 2014).

Nonetheless, many species are incapable of adequately responding to climate change. A recent quantitative review covering a wide range of taxa found that 47% of the species surveyed have already experienced local climate-related declines or extinctions (Wiens 2016). Unfortunately, beyond broad characterizations of the vulnerability of species with different traits or life-history strategies (Comte et al. 2014, Nadeau and Fuller 2016), there is currently little understanding as to what determines which species are most susceptible to climatic change. Consideration of the extent and severity of asynchronous climate change regimes, however, may provide a useful lens through which to view such assessments.

As an example, consider the responses to climate change of two populations of a long-distance migratory bird, the Hudsonian godwit *Limosa haemastica*, that are both experiencing rapid climatic changes. These two populations breed on opposite sides of the Nearctic – one in Alaska and the other in the Hudson Bay Lowlands of eastern Manitoba – but share a common migratory corridor through mid-continental North America along which they pass one month apart during northward migration (Senner 2012). Despite sharing a migratory corridor and breeding at similar latitudes, the two populations exhibit contrasting responses to recent climatic changes. The Alaska population

has accelerated its arrival at its breeding grounds by nine days over the past three decades, while the Hudson Bay population has retarded its arrival by nearly 11 d during that time. These divergent trends in arrival timing mean that although the Alaskan population has kept pace with local phenological changes on its breeding grounds, the Hudson Bay population now experiences a phenological mismatch with the resources its young rely on for food, leading to dramatic reductions in reproductive success on a nearly annual basis (Senner et al. 2017). Neither genetic differences, nor differences in phenotypic plasticity or flexibility, can explain these trends (Senner et al. 2014, unpubl.). Instead they result from the climate change regimes experienced by the two populations: the Alaska population experiences synchronous warming throughout their migration and breeding season, while the Hudson Bay population encounters cooling trends during the latter part of its northward migration, followed by dramatic warming during the breeding season (Senner 2012).

Although differences in genetic variation and trait architecture have the potential to strongly influence the extent to which separate populations can respond to climatic change, it is also critical to understand a population's current selective environment and the potential for that selective environment to constrain their response to what would otherwise be strong climate-driven selection pressures. When assessing differences in vulnerability to climate change, the question therefore should not necessarily be, 'Is climate change progressing too rapidly?' but rather, 'What is the selection regime being experienced by a population?'. Reframing the question in this manner refocuses attention on the general features of a population's selection regime rather than assuming a specific selection pressure.

### Asynchronous regimes, dispersal, and intra-specific variation in climate resilience

The Hudsonian godwit example suggests that spatial variation in climate change regimes may also be a strong driver of intra-specific variation in climate change vulnerability (Senner et al. 2017). This insight has potentially far-reaching consequences. For instance, many studies predict that endemic or range-limited species will be most vulnerable to climate change (Urban 2015). This increased vulnerability may be related to the limited intra-specific trait variation and inherent demographic instability of small populations (Urban 2015, Gilroy et al. 2016). Species with smaller geographic ranges, however, are also more likely to experience a single climate change regime (Liebold et al. 2004). They may therefore become trapped if an asynchronous regime encompasses the entirety of their range and poses contrasting selection pressures that are potentially irreconcilable on short time scales, irrespective of the amount of trait variation present in the population (Heino et al. 1997, Koenig and Liebhold 2016).

As they are likely to encounter more than one climate change regime across their geographic range, species with larger ranges face a different challenge. Although heterogeneity in climate change regimes may reduce the likelihood that species with large ranges become trapped by a single asynchronous regime, the occurrence of even isolated asynchronous regimes within a species' range may cause local declines and extinctions (Both et al. 2006). In this context, dispersal becomes a key response mechanism that may mitigate the effects of asynchronous regimes. Dispersal and gene flow can facilitate evolutionary rescue, whereby beneficial alleles present in one portion of a species' range spread into other portions of its range and halt or reverse local population declines (Gonzalez et al. 2013). Although empirical evidence for the occurrence of evolutionary rescue is rare, it is growing (Reid et al. 2016). Moreover, recent work suggests that dispersal propensity itself can evolve rapidly, increasing the rate of gene flow across a species' range (Ochocki and Miller 2017).

Spatial heterogeneity in climate change regimes, however, has the potential to disrupt dispersal patterns, limiting gene flow and constraining the movement of potentially beneficial alleles across a species' range (Angert et al. 2011, D'Angelo et al. 2015, Logan et al. 2016). In this scenario, the heterogeneous spatial pattern of climate change regimes may mimic classical habitat mosaics, with some regions being more hospitable to particular genotypes than others (Barros et al. 2016). In general, dispersal across heterogeneous landscapes is more difficult than across homogeneous ones, with patterns of local adaptation exacerbating this disparity (Zhang and Buckling 2016). This could result when locally adapted populations are able to resist gene flow either because their fitness is sufficiently higher than that of immigrants (Logan et al. 2016) or the social structure of the local population makes it difficult for immigrants to establish (Ingleby et al. 2016). The opposite can also be true as well, and the introgression of alleles beneficial in other environments can lead to high migration loads, swamping local adaptations, and leading to the extinction of locally adapted populations (Farkas et al. 2016). Predicting the likelihood of successful occurrences of evolutionary rescue is thus difficult at best (Marshall et al. 2016). As such, there is a considerable need to quantify how common asynchronous regimes actually are and determine how their distribution may affect dispersal and gene flow among populations.

### The effects of asynchronous regimes on dispersal: a model simulation

As a first attempt at characterizing the frequency with which asynchronous climate change regimes are occurring, we obtained interpolated monthly mean temperature data from 1979–2016 for northern South America and continental North America through the North American Regional Reanalysis dataset (Mesinger et al. 2006), which provides climate

data for  $32 \times 32$  km grid cells ranging from 1.00N, 145.5W in the southwest to 46.63N, 148.64E in the northeast. To assess annual rates of change in monthly temperatures across the region during this 37-yr period, we ran separate linear regressions with year as the predictor variable and mean temperature as the dependent variable for each month of the year within each terrestrial grid cell using the package 'ncdf4' (Pierce 2015) in Program R (R Core Development Team). We found that 70.6% of all terrestrial grid cells are exhibiting cooling trends (e.g. negative beta coefficients) during at least one month of the year, while 99.6% are displaying warming trends during at least one month ( $n = 28\,023$  total cells; Fig. 1). When only considering grid cells that have significant trends ( $p < 0.05$ ), March, June, and July are experiencing the most cooling (Fig. 2, Supplementary material Appendix 1 Fig. A1), while August–October are exhibiting the most warming (Fig. 2).

Next, we determined 1) the spatial scale at which climate change regimes vary across the continent by calculating Moran's I for distance classes ranging from 32–12 000 km using the R package 'ape' (Paradis et al. 2016) and 2) the proportion of months during which each grid cell is cooling. We found that terrestrial grid cells throughout the entire region have a global Moran's I of 0.15, but that there is a precipitous decline in spatial autocorrelation as distances increase, with I-values falling below 0.5 after a distance of  $1169 \pm 387$  km

(Fig. 3). There is thus considerable heterogeneity in the occurrence of asynchronous regimes both within and across regions. Accordingly, a patchwork of climate change regimes is occurring across the continent (Fig. 4), with some cells cooling throughout the year (darker purple) and others synchronously warming (lighter orange).

We then used these results to parameterize a model simulating how the spatial distribution of asynchronous regimes can influence patterns of gene flow and the potential for evolutionary rescue within a meta-population. To do this, we compared the spread of alleles that are beneficial under asynchronous regimes across three landscapes, each representing a different spatial configuration of climate change regimes. As a null hypothesis, we first constructed a landscape in which areas with asynchronous regimes were randomly distributed (Fig. 5). Rates of climate change, however, generally vary latitudinally, with more rapid rates of warming occurring farther north (Rawlins et al. 2016). Therefore, we also constructed a landscape characterized by a gradient, whereby the landscape transitions linearly from a synchronous environment to an asynchronous one (e.g. an environment that is both warming and cooling during a single year). Finally, we generated a spatially autocorrelated landscape with a Moran's I of 0.15, which was derived from our analyses of the current distribution of asynchronous regimes in the northern Western Hemisphere. We then used these landscapes to

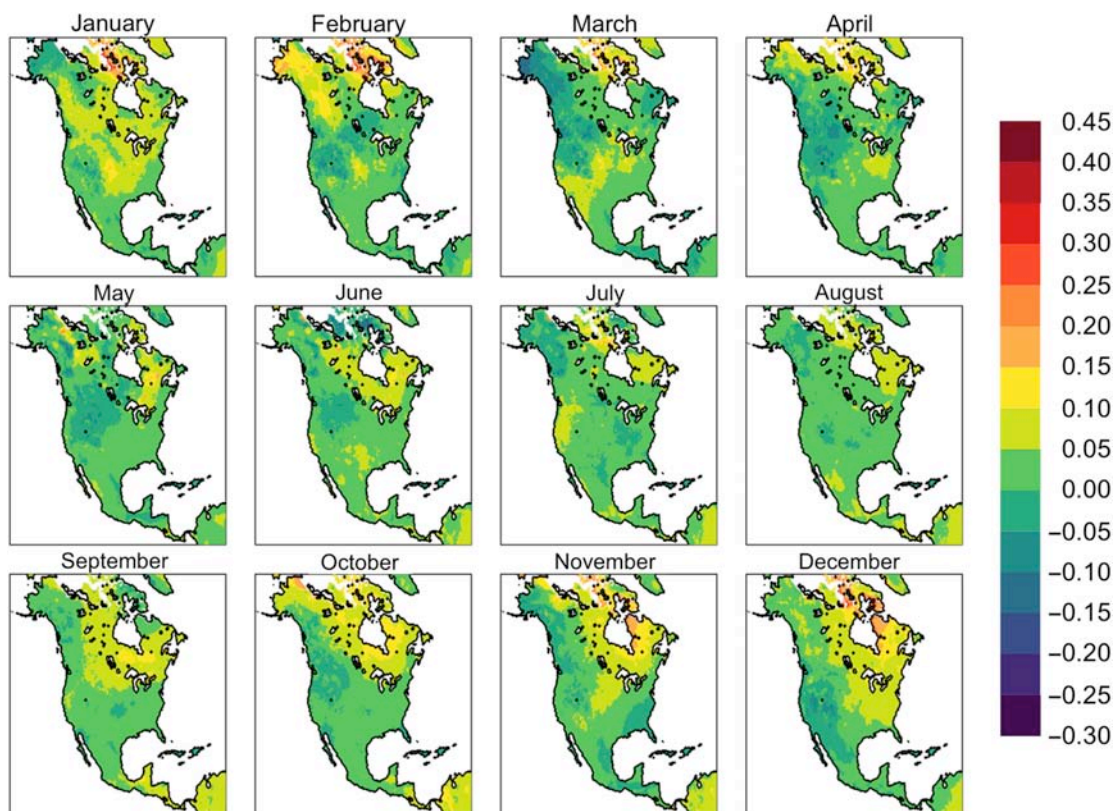


Figure 1. Monthly North American terrestrial temperature trends, 1979–2016. Trends were calculated with data from the North American Regional Reanalysis dataset for  $32 \times 32$  km grid cells using linear regression models. Colors represent changes in degrees Celsius per year.

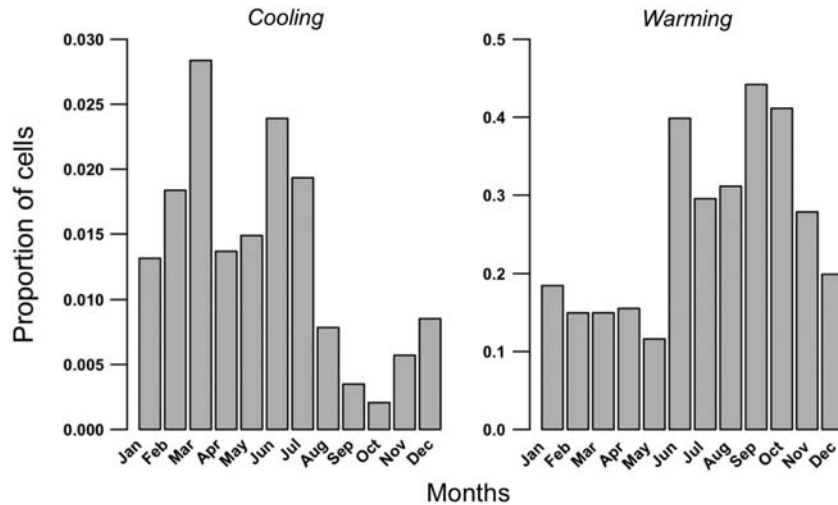


Figure 2. Proportion of terrestrial grid cells in North America significantly cooling or warming during each month, 1979–2016. Trends were calculated with data from the North American Regional Reanalysis dataset for  $32 \times 32$  km grid cells using linear regression models. Only grid cells with trends having p-values  $< 0.05$  are presented.

perform simulations with the program ‘Nemo’ (ver. 2.3.46), a spatially explicit platform for modeling demographic scenarios incorporating heterogeneous rates of gene flow across different habitat types (Guillaume and Rougemont 2006).

We tested the effects of variation in dispersal rates, strength of selection, and levels of genetic diversity on rates of gene flow and phenotypic variation across our three landscapes (see Table 1 for parameter values). In each simulation, a  $10 \times 10$  grid was evenly populated with 10 000 diploid individuals with phenotypes for a quantitative trait ranging from  $-1$  to  $1$  – more negative values were beneficial in synchronous environments, while more positive ones were beneficial in asynchronous environments. Genotypes at each locus had an additive effect on the quantitative trait value, with each additional copy of the beneficial allele resulting in an incremental change in the trait value. We then developed three different potential scenarios related to a population’s genetic diversity – a de novo mutation scenario, in which a mutation occurs at a single locus producing an allele beneficial in asynchronous regimes, and two scenarios representing standing genetic

variation for a quantitative trait beneficial in asynchronous regimes, one in which the trait is controlled by 10 independent and recombining loci and the other by 100. In the de novo mutation scenario, all individuals were homozygous for the ancestral allele except for a single individual, which was heterozygous for a derived, beneficial allele appearing at time point  $t=0$ . In the two standing genetic variation scenarios, all loci coding the quantitative trait were considered unlinked, and the beneficial allele at each locus was distributed evenly across the landscape at a low frequency (1%).

For each landscape and genetic scenario, we additionally varied the strength of selection by altering the amount of variation around the local phenotypic optimum selected for (0.1, 1, and 5% of the phenotypic trait value), as well as the proportion of individuals dispersing outside of a grid cell per generation (0.01, 0.1, and 0.5). We then ran each simulation for 100 generations and replicated it 10 times to enable comparisons with climate-related frameworks making predictions about changes in population dynamics over the coming century. To compare across landscapes,

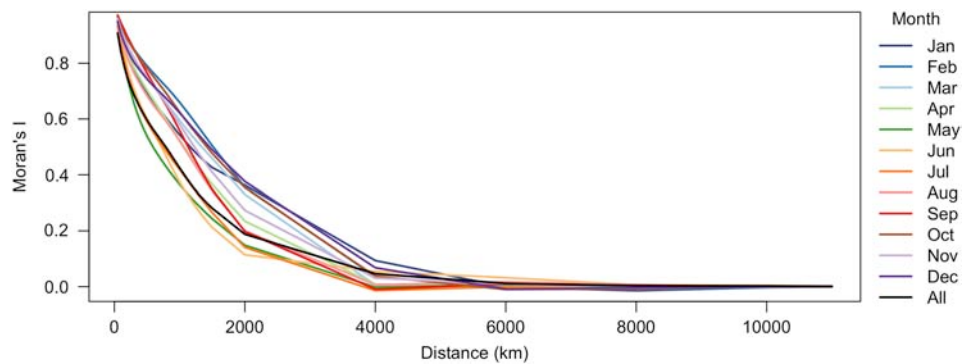


Figure 3. Spatial correlation in monthly temperature trends across terrestrial North America, 1979–2016. Lines represent changes in the Moran’s I value across distance classes ranging from 32 km (a single grid cell) to 12 000 km (the entire NARR region).

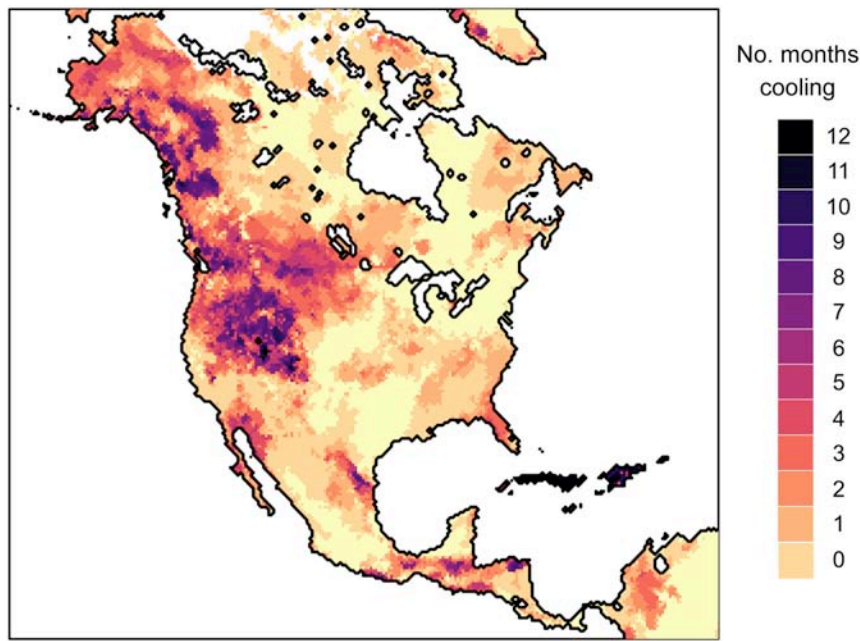


Figure 4. Spatial heterogeneity in climate change regimes across terrestrial North America, 1979–2016. Trends were calculated with data from the North American Regional Reanalysis dataset for  $32 \times 32$  km grid cells using linear regression models. Colors represent the proportion of months for which each grid cell exhibited a cooling trend.

we quantified the allele frequency of the beneficial allele(s), mean phenotype, and total population size within asynchronous cells.

We found that under strong selection, neither the spread of the beneficial allele(s) nor evolutionary rescue of populations occupying asynchronous regimes occurred in most demographic scenarios, resulting in widespread local extinctions (Supplementary material Appendix 1 Fig. A2). However, when there was standing variation for a relatively simple quantitative trait (10 loci), the landscape affected the outcome of the simulation, with the gradient landscape having a more locally adapted population and larger population size (Supplementary material Appendix 1 Fig. A2). In contrast, under weak selection, the beneficial allele(s) spread in all scenarios, but remained at relatively low frequencies even in

asynchronous cells. As a result, populations in asynchronous cells generally failed to reach the local phenotypic optimum, but nonetheless remained at or near carrying capacity. At an intermediate strength of selection, dispersal rate played an important role: low dispersal rates consistently resulted in local extinctions across landscape types, but moderate and high dispersal rates led to the extensive spread of the beneficial allele(s) (Fig. 6). In general, no single landscape type consistently exhibited higher population sizes or a more complete spread of the beneficial allele(s). Instead, the demographic scenario considered was a stronger determinant of the likelihood of evolutionary rescue – the single-locus de novo mutation and less complex quantitative trait spread more rapidly and completely than did the more complex quantitative trait.

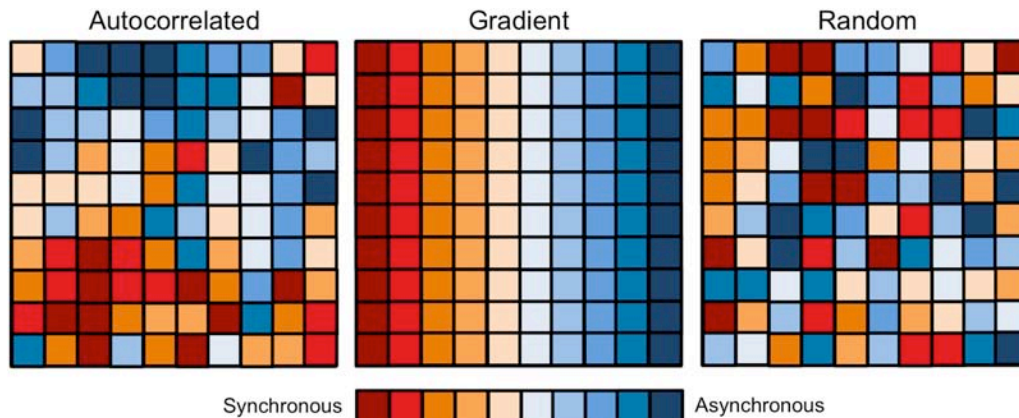


Figure 5. Spatial configuration of simulated landscapes. Colors represent degree of climatic asynchrony.

Table 1. Parameter values for models simulating the spread of alleles beneficial in asynchronous climate change regimes across three landscapes – a gradient, a random landscape, and a spatially autocorrelated landscape. Simulations performed with Nemo (ver. 2.3.46).

Parameter	Values
Replicates	10
Generations	100
Number of patches	100
Patch carrying capacity	100
Dispersal rate	0.01; 0.1; 0.5
Dispersal model	lattice, reflective boundaries
Phenotypic trait values	-1 to 1
Selection trait	quantitative
Selection local optima landscape	random; gradient; autocorrelated
Selection model	Gaussian
Selection variance	0.1; 1; 5
Number of quantitative trait loci	1; 10; 100
Mutation rate	0
Quantitative allele model	diallelic

## Discussion

Recent advances have demonstrated that rapid, directional climatic change is not necessarily the insurmountable challenge for populations it was once believed to be (Kovach et al. 2012, Gill et al. 2013, Bataillon et al. 2016, Franks et al. 2016, Krehenwinkel et al. 2016, Oexle et al. 2016). Instead the difficulty posed by climate change is that rates of climatic change can vary both across time within a single region, as well across regions during a single time period (Ebi et al. 2016). This spatial and temporal heterogeneity can, in turn, impose contrasting selection pressures that are difficult for populations to reconcile on short time scales (Senner et al. 2017). Our results add to the growing body of literature highlighting the importance of asynchronous climate change regimes (Visser et al. 1998, Both et al. 2006, Straile et al. 2015, Senner et al. 2017) by revealing that they occur across much of North and Central America and may be an important mediator

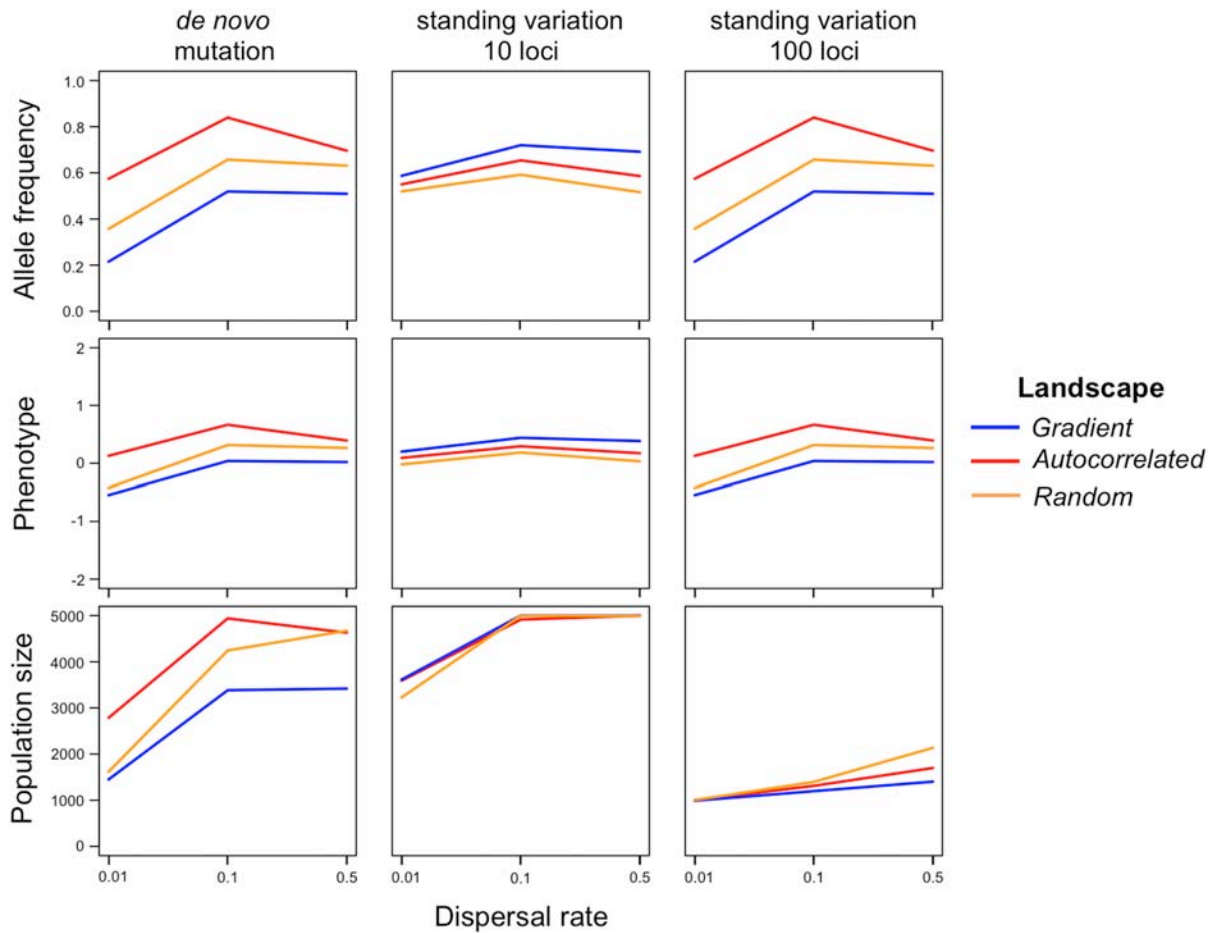


Figure 6. Model simulation results quantifying the allele frequency of beneficial alleles, mean phenotype, and total population size in asynchronous grid cells under a selection variance of 1. Models were run in program Nemo (ver. 2.3.46) on a  $10 \times 10$  grid, with 50 cells corresponding to asynchronous climatic regimes and a carrying capacity of 100 individuals per grid cell.



of gene flow. Given that asynchronous regimes are rarely incorporated into predictive models of potential biotic responses to climate change, our findings suggest the need to reconsider the selective pressures that underlie these theoretical frameworks.

### The distribution of asynchronous regimes

Our results demonstrate that asynchronous regimes are common throughout North and Central America, occurring across just over 70% of the terrestrial land mass. These results are consistent with local-scale studies on other continents (Chen et al. 2005, Rebetz and Reinhard 2008) and, together, indicate that asynchronous regimes are likely common across the globe. Furthermore, our results indicate that cooling trends are most prevalent from March through July, which means that asynchronous regimes may be particularly problematic for the many north temperate and arctic species that either breed or transition into breeding readiness during the boreal spring and summer. These species have likely experienced an evolutionary history of strong selection to properly time their phenological events during this period and thus may be especially sensitive to even relatively small heterogeneity in spring temperature trends (Visser and Both 2005).

At the same time, previous studies have found large-scale spatial synchrony in climatic conditions (Koenig 2002). Similarly, we found that some entire regions, such as eastern North America, were synchronously warming. Species whose distributions are confined to these regions may therefore experience selection regimes that facilitate rapid climate-driven phenotypic responses and adaptive evolution. Accordingly, a number of studies have found evidence of rapid evolutionary responses to climate change in species living in eastern North America (van Buskirk et al. 2010, 2012) and these responses tend to be more rapid than those for species living elsewhere on the continent (Langham et al. 2015). Given that many species are broadly distributed throughout this region (Ricklefs 2015), and that its precipitation regime is expected to remain relatively constant (Walsh et al. 2014), eastern North America may thus be more buffered from the effects of climate change than other regions.

In general, however, our results indicate that regional climatic heterogeneity occurs at relatively small spatial scales, smaller even than the range sizes of many range-limited species (Pfrender et al. 1998, Orme et al. 2006). For instance, almost the entire spectrum of climate change regimes – from nearly synchronous cooling regimes to synchronously warming ones – occurs within a ~600 km radius in the Great Basin region of the western United States. While this reduces the likelihood that species with small range sizes will become trapped under a single asynchronous regime (Pouteau and Birnbaum 2016), it highlights the importance of dispersal as a means to facilitate evolutionary rescue within the region (Gonzalez et al. 2013).

### Spatial heterogeneity in climate change regimes limits dispersal

Dispersal has long been recognized as an important component of a species' ability to respond to climate change (Parmesan and Yohe 2003). Dispersal, however, is most frequently considered in the context of range shifts that allow a species to track movements in its fundamental niche and not the potential spread of beneficial alleles. The effects of asynchronous regimes, though, make clear that it is not only the future distribution of thermal regimes that makes dispersal propensity an important trait for mediating resilience to climate change, but also the current spatial heterogeneity in climate change regimes. While our model results do not indicate that the current distribution of asynchronous regimes represents a more pronounced barrier to dispersal and gene flow than would other spatial configurations of asynchronous regimes, they do suggest that the existence of any spatial heterogeneity in climate change regimes can strongly constrain the movement of individuals across a species' range and result in local extinctions over short time scales.

While informative, we note a few general caveats about our simulations. First, the progress of gene flow across our simulated landscapes was likely much more rapid than would be possible in nature. Our simulated landscape was evenly populated, and only varied in one habitat parameter – climate asynchronicity. Natural habitat matrices are far more complex and it is unlikely that even the most abundant species are distributed evenly across their range (Barros et al. 2016). Similarly, the genetic architecture of our simulated quantitative trait was simplistic. Complex physiological traits that are relevant for climate adaptation are likely to be highly polygenic (Shao et al. 2008), and our simulations demonstrated that genetic architecture influences the spread of adaptive alleles across heterogeneous landscapes. Our simulations necessarily assumed relatively simple genetic architectures (i.e. relatively few, completely unlinked loci, with uniform phenotypic effects) because the genetic architecture of climate-related traits has yet to be fully described for any natural, free-ranging species (McCairns et al. 2016). Furthermore, in some cases asynchronous climate change regimes may impose selection on multiple separate traits – such as upper and lower thermal tolerances – that vary in their genetic architecture and, therefore, evolvability (Araújo et al. 2013). A better understanding of the genetic architectures of relevant traits is thus needed to inform predictive models of the potential for evolutionary rescue in the wild, and to better evaluate our simulation results.

Another potential caveat of our simulations stems from the fact that climate change is projected to accelerate over the coming century (IPCC 2014). Because we did not explicitly model such potential variation in the rate of climatic change over the course of our simulations, we may have underestimated the lag load – the distance between the theoretical fitness peak and the fitness of the average genotype in a population (Maynard Smith 1976) – and thus overestimated the rate at which populations can adapt to environmental

change. However, accelerating rates of climate change are likely to increase the strength of selection experienced by a population. Our inclusion of three different strengths of selection can therefore be seen as analogous to modeling the effects of accelerating rates of climatic change. As with previous studies (Bolnick and Nosil 2007, Duputié et al. 2012, Kirkpatrick and Peischl 2013), our simulations suggest that under strong selection/rapid rates of change, moderate dispersal rates generally result in the fastest pace of adaptation. This occurs because high dispersal rates can result in high migration loads, disrupting the migration-selection balance (Bolnick and Nosil 2007), while low dispersal rates can strongly limit gene flow and the input of new and beneficial genetic variation (Lenormand 2002, Duputié et al. 2012). As the rate of global climate change accelerates, a precise combination of traits and circumstances may therefore be necessary to minimize rates of local extinctions and population declines.

Finally, our results are also broadly consistent with recent studies demonstrating that complex genetic architectures can constrain rapid evolutionary responses and prevent the fixation of beneficial alleles (Chevin and Hospital 2008) and that standing genetic variation can result in parallel adaptations to shared selection pressures across fragmented landscapes (Ralph and Coop 2015). Thus, ultimately, a trait's genetic architecture, potential plasticity, variation within a population, and distribution across a population's range must all be considered in addition to the degree of habitat fragmentation in a population's dispersal matrix when assessing the potential for evolutionary rescue (Kopp and Matuszewski 2014).

### Improving climate-related predictive frameworks

Processes as complex as global climate change are inherently difficult to distill into theoretical models that can generate workable predictive frameworks. Nonetheless, the theoretical models used to predict the consequences of global climate change are developing rapidly and employing an increasingly diverse array of information to forecast changes in population dynamics (Bush et al. 2016). For instance, genetically and physiologically informed ecological niche models have recently been developed and are a major improvement, as they incorporate information on population genetic structure and variation in levels of local adaptation into projections of future range shifts (Ikeda et al. 2017). Similarly, efforts to make use of spatially explicit population data, such as avian abundance and population trend information generated by the Breeding Bird Survey and Christmas Bird Count, are an important development that can help identify vulnerable local populations (Langham et al. 2015). Our results emphasize that additionally incorporating asynchronous regimes and the potential for evolutionary rescue (Marshall et al. 2016) into future predictive frameworks is critical to our ability to make accurate assessments of inter- and intra-specific variation in climate vulnerability.

Given the difficulty of incorporating the complexity of global climate change into predictive frameworks, however,

there is also increasingly a push to do away with predictive frameworks altogether (Webster et al. 2017). Instead, recent studies have advocated for the establishment of 'adaptation networks'. These networks rely on the preservation of interconnected mosaics of managed habitats that contain enough diversity – genetic, functional, community, or climatic – to allow for in situ adaptation and climate-driven range shifts irrespective of which future climate change scenario proves most accurate (Anderson et al. 2015). Our findings broadly support the establishment of such networks as a conservation strategy, especially considering that the potential for rapid adaptation to climate change may be greater than previously thought. Nonetheless, our results also indicate that the spatial scale at which climate change regimes are correlated is at once larger than traditional matrices of protected areas (Cantú-Salazar and Gaston 2010), but also smaller than the range sizes of many species (Pfrender et al. 1998, Orme et al. 2006). This means that adaptation networks must be large enough to encompass this climatic heterogeneity and allow for potential gene flow among disparate patches with similar climate change regimes (Ricketts 2001). Thus, practical application of our results towards the creation of adaptation networks will be dependent on studies that can empirically measure how regional climate heterogeneity may currently be mediating gene flow among populations.

### Conclusions

Our results suggest that in order to fully understand the potential ramifications of climate change, we must work to better understand both the ways in which climate change can impact species and the ways in which species can potentially respond. This means continuing the movement away from assuming that climate change will act as a linear process that can solely be described by changes in temperature means (Ebi et al. 2016), and undertaking more studies that assess the effects of not only asynchronous regimes, but also changes in the occurrence of extreme weather events (Senner et al. 2015), temperature extremes rather than temperature means (Long et al. 2016), and precipitation regimes (Brawn et al. 2016). It also means working towards a mechanistic framework that explains why species respond to climate change the way they do and further developing our understanding of eco-evolutionary dynamics within the context of life-history trade-offs (Ellner 2013). Together these efforts can lead us toward a more holistic approach to mitigating the current and future effects of global climate change.

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## References

- Allen, J. L. et al. 2012. The effects of acclimation and rates of temperature change on critical thermal limits in *Tenebrio molitor* (Tenebrionidae) and *Cyrtobagous salviniae* (Curculionidae). – *J. Insect Physiol.* 58: 669–678.
- Anderson, S. C. et al. 2015. Portfolio conservation of metapopulations under climate change. – *Ecol. Appl.* 25: 559–572.
- Angert, A. M. et al. 2011. Incorporating population-level variation in thermal performance into predictions of geographic range shifts. – *Integr. Comp. Biol.* 51: 733–750.
- Araújo, M. B. et al. 2013. Heat freezes niche evolution. – *Ecol. Lett.* 16: 1206–1219.
- Barrick, J. E. et al. 2009. Genome evolution and adaptation in a long-term experiment with *Escherichia coli*. – *Nature* 461: 1242–1247.
- Barros, C. et al. 2016. Spread rates on fragmented landscapes: the interacting roles of demography, dispersal and habitat availability. – *Divers. Distrib.* 22: 1266–1275.
- Bataillon, T. et al. 2016. A replicated climate change field experiment reveals rapid evolutionary response in an ecologically important soil invertebrate. – *Global Change Biol.* 22: 2370–2379.
- Bolnick, D. I. and Nosil, P. 2007. Natural selection in populations subject to a migration load. – *Evolution* 61: 2229–2243.
- Bonduriansky, R. et al. 2012. The implications of nongenetic inheritance for evolution in changing environments. – *Evol. Appl.* 5: 192–201.
- Both, C. and Visser, M. E. 2001. Adjustment to climate change is constrained by arrival date in a long-distance migrant bird. – *Nature* 411: 296–298.
- Both, C. et al. 2006. Climate change and population declines in a long-distance migratory bird. – *Nature* 44: 81–83.
- Both, C. et al. 2009. Climate change and unequal phenological changes across four trophic levels: constraints or adaptations? – *J. Anim. Ecol.* 78: 73–83.
- Brawn, J. D. et al. 2016. Impacts of changing rainfall regime on the demography of tropical birds. – *Nat. Clim. Change* 7: 133–136.
- Brommer, J. et al. 2000. Reproductive effort and reproductive values in periodic environments. – *Am. Nat.* 155: 454–472.
- Burrows, M. T. et al. 2011. The pace of shifting climate in marine and terrestrial ecosystems. – *Science* 334: 652–655.
- Bush, A. et al. 2016. Incorporating evolutionary adaptation in species distribution modelling reduces projected vulnerability to climate change. – *Ecol. Lett.* 19: 1468–1478.
- Cahill, A. E. et al. 2012. How does climate change cause extinction? – *Proc. R. Soc. B* 280: 20121890.
- Cameron, T. C. et al. 2013. Eco-evolutionary dynamics in response to selection on life-history. – *Ecol. Lett.* 16: 754–763.
- Campbell-Staton, S. C. et al. 2017. Winter storms drive rapid phenotypic, regulatory and genomic shifts in the green anole lizard. – *Science* 357: 495–498.
- Cantú-Salazar, L. and Gaston, K. J. 2010. Very large protected areas and their contribution to terrestrial biological conservation. – *Bioscience* 60: 808–818.
- Careau, V. et al. 2015. Evolution of the additive genetic variance–covariance matrix under continuous directional selection on a complex behavioural phenotype. – *Proc. R. Soc. B* 2015: 20151119.
- Chen, X. et al. 2005. Spatial and temporal variation of phenological growing season and climate change impacts in temperate eastern China. – *Global Change Biol.* 11: 1118–1130.
- Chevin, L.-M. and Hospital, F. 2008. Selective sweep at a quantitative trait locus in the presence of background genetic variation. – *Genetics* 180: 1645–1660.
- Chevin, L.-M. et al. 2010. Adaptation, plasticity, and extinction in a changing environment: towards a predictive theory. – *PLoS Biol.* 8: e1000357.
- Chinellato, F. et al. 2014. Better today but worse tomorrow: how warm summers affect breeding performance of a Scots pine pest. – *Agrochimica* 18: 133–145.
- Comte, L. et al. 2014. Species traits and phylogenetic conservatism of climate-induced range shifts in stream fishes. – *Nat. Comm.* 5: 5023.
- D’Angelo, C. et al. 2015. Local adaptation constrains the distribution potential of heat-tolerant *Symbiodinium* from the Persian/Arabian Gulf. – *ISME J.* 9: 2551–2560.
- de Roissart, A. et al. 2016. Life-history evolution in response to changes in metapopulation structure in an arthropod herbivore. – *Funct. Ecol.* 30: 1408–1417.
- Doi, H. et al. 2008. Heterogeneous intra-annual climatic changes drive different phenological responses at two trophic levels. – *Clim. Res.* 36: 181–190.
- Duputié, A. et al. 2012. How do genetic correlations affect species range shifts in a changing environment? – *Ecol. Lett.* 15: 251–259.
- Durant, J. M. et al. 2007. Climate and the match or mismatch between predator requirements and resource availability. – *Clim. Res.* 33: 271–283.
- Ebi, K. L. et al. 2016. The shape of impacts to come: lessons and opportunities for adaptation from uneven increases in global and regional temperatures. – *Clim. Change* 139: 341–349.
- Ellner, S. P. 2013. Rapid evolution: from genes to communities, and back again? – *Funct. Ecol.* 27: 1087–1099.
- Etterson, J. R. and Shaw, R. G. 2001. Constraint to adaptive evolution in response to global warming. – *Science* 294: 151–154.
- Farkas, T. E. et al. 2016. Observational evidence that maladaptive gene flow reduces patch occupancy in a wild insect metapopulation. – *Evolution* 70: 2879–2888.
- Forrest, J. R. K. 2016. Complex responses of insect phenology to climate change. – *Curr. Opin. Insect Sci.* 17: 49–54.
- Franks, S. J. et al. 2016. Rapid genome-wide evolution in *Brassica rapa* populations following drought revealed by sequencing of ancestral and descendant gene pools. – *Mol. Ecol.* 25: 3622–3631.
- Gienapp, P. et al. 2014. Why climate change will invariably alter selection pressures on phenology. – *Proc. R. Soc. B* 281: 20141611.
- Gill, J. A. et al. 2013. Why is timing of bird migration advancing when individuals are not? – *Proc. R. Soc. B* 281: 20132161.
- Gilroy, J. J. et al. 2016. Migratory diversity predicts population declines in birds. – *Ecol. Lett.* 19: 308–317.
- Glazaczow, A. et al. 2016. Increased temperature delays the late-season phenology of multivoltine insect. – *Sci. Rep.* 6: 38022.

- Gompert, Z. et al. 2014. Experimental evidence for ecological selection on genome variation in the wild. – *Ecol. Lett.* 17: 369–379.
- Gonzalez, A. et al. 2013. Evolutionary rescue: an emerging focus at the intersection between ecology and evolution. – *Phil. Trans. R. Soc. B* 368: 20120404.
- Guillaume, F. and Rougemont, J. 2006. Nemo: an evolutionary and population genetics programming framework. – *Bioinformatics* 22: 2556–2557.
- Hamann, A. et al. 2015. Velocity of climate change algorithms for guiding conservation and management. – *Global Change Biol.* 21: 997–1004.
- Heino, M. et al. 1997. Synchronous dynamics and rates of extinction in spatially structured populations. – *Proc. R. Soc. B* 264: 481–486.
- Ikeda, D. H. et al. 2017. Genetically informed ecological niche models improve climate change predictions. – *Global Change Biol.* 23: 164–176.
- Ingle, S. J. et al. 2016. Social context, but not individual personality, alters immigrant viability in a spider with mixed social structure. – *Anim. Behav.* 120: 153–161.
- IPCC 2014. Climate change 2014: synthesis report. – Inter-governmental Panel on Climate Change, Geneva, Switzerland.
- Kinnison, M. T. and Hendry, A. P. 2001. The pace of modern life II: from rates of contemporary microevolution to pattern and process. – *Genetica* 112–113: 145–164.
- Kirkpatrick, M. and Peischl, S. 2013. Evolutionary rescue by beneficial mutations in environments that change in space and time. – *Phil. Trans. R. Soc. B* 368: 20120082.
- Koenig, W. D. 2002. Global patterns of environmental synchrony and the Moran effect. – *Ecography* 25: 283–288.
- Koenig, W. D. and Liebhold, A. M. 2016. Temporally increasing spatial synchrony of North American temperature and bird populations. – *Nat. Clim. Change* 6: 614–617.
- Kopp, M. and Matuszewski, S. 2014. Rapid evolution of quantitative traits: theoretical perspectives. – *Evol. Appl.* 7: 169–191.
- Kovach, R. P. et al. 2012. Genetic change for earlier migration timing in a pink salmon population. – *Proc. R. Soc. B* 279: 2870–2878.
- Krehenwinkel, H. et al. 2016. Rapid genetic and ecological differentiation during the northern range expansion of the venomous yellow sac spider *Cheiracanthium punctorium* in Europe. – *Evol. Appl.* 9: 1229–1240.
- Lane, J. E. et al. 2012. Delayed phenology and reduced fitness associated with climate change in a wild hibernator. – *Nature* 489: 554–557.
- Langham, G. M. et al. 2015. Conservation status of North American birds in the face of future climate change. – *PLoS One* 10: e0135350.
- Lenormand, T. 2002. Gene flow and the limits to natural selection. – *Trends Ecol. Evol.* 4: 183–189.
- Liebold, M. A. et al. 2004. The metacommunity concept: a framework for multi-scale community ecology. – *Ecol. Lett.* 7: 601–613.
- Loarie, S. R. et al. 2009. The velocity of climate change. – *Nature* 462: 1052–1055.
- Lof, M. E. et al. 2012. Timing in a fluctuating environment: environmental variability and asymmetric fitness curves can lead to adaptively mismatched avian reproduction. – *Proc. R. Soc. B* 279: 3161–3169.
- Logan, M. L. et al. 2016. Spatial variation in climate mediates gene flow across an island archipelago. – *Evolution* 70: 2395–2403.
- Long, O. M. et al. 2016. Sensitivity of UK butterflies to local climatic extremes: which life stages are most at risk? – *J. Anim. Ecol.* 86: 108–116.
- Marshall, D. J. et al. 2016. Global change, life-history complexity and the potential for evolutionary rescue. – *Evol. Appl.* 9: 1189–1201.
- Maynard Smith, J. 1976. What determines the rate of evolution? – *Am. Nat.* 110: 331–338.
- McCairns, R. J. S. et al. 2016. The adaptive potential of subtropical rainbowfish in the face of climate change: heritability and heritable plasticity for the expression of candidate genes. – *Evol. Appl.* 9: 531–545.
- McNamara, J. M. et al. 2016. Detection vs. selection: integration of genetic, epigenetic and environmental cues in fluctuating environments. – *Ecol. Lett.* 19: 1267–1276.
- Mesinger, F. et al. 2006. North American regional reanalysis. – *Bull. Am. Meteorol. Soc.* 87: 343–360.
- Moran, E. V. and Alexander, J. M. 2014. Evolutionary responses to global change: lessons from invasive species. – *Ecol. Lett.* 17: 637–649.
- Moritz, C. and Agudo, R. 2013. The future of species under climate change: resilience or decline? – *Science* 341: 504–508.
- Musolin, D. L. 2007. Insects in a warmer world: ecological, physiological and life-history responses of true bugs (Heteroptera) to climate change. – *Global Change Biol.* 13: 1565–1585.
- Nadeau, C. P. and Fuller, A. K. 2016. Combining landscape variables and species traits can improve the utility of climate change vulnerability assessments. – *Biol. Conserv.* 202: 30–38.
- Nussey, D. H. et al. 2005. Selection on heritable phenotypic plasticity in a wild bird population. – *Science* 310: 304–306.
- Ochocki, B. M. and Miller, T. E. X. 2017. Rapid evolution of dispersal ability makes biological invasions faster and more variable. – *Nat. Comm.* 8: 14315.
- Oexle, S. et al. 2016. Rapid evolution of antioxidant defence in a natural population of *Daphnia magna*. – *J. Evol. Biol.* 29: 1328–1337.
- Orme, C. D. L. et al. 2006. Global patterns of geographic range size in birds. – *PLoS Biol.* 4: e208.
- Ovaskainen, O. et al. 2013. Community-level phenological response to climate change. – *Proc. Natl Acad. Sci. USA* 110: 13434–13439.
- Paradis, E. et al. 2016. Analyses of phylogenetics and evolution. – <www.r-project.org>.
- Parmesan, C. and Yohe, G. 2003. A globally coherent fingerprint of climate change impacts across natural systems. – *Nature* 421: 37–42.
- Pfrender, M. E. et al. 1998. Patterns in the geographical range sizes of ectotherms in North America. – *Oecologia* 115: 439–444.
- Phillips, B. L. et al. 2016. Heat hardening in a tropical lizard: geographic variation explained by the predictability and variance in environmental temperatures. – *Funct. Ecol.* 30: 1161–1168.
- Pierce, D. 2015. Interface to unidata netCDF (version 4 or earlier) format data files. – <www.r-project.org>.
- Poethke, H. J. et al. 2016. The evolution of optimal emergence times: bet hedging and the quest for an ideal free temporal distribution of individuals. – *Oikos* 125: 1647–1656.
- Pouteau, R. and Birnbaum, P. 2016. Island biodiversity hotspots are getting hotter: vulnerability of tree species to climate change in New Caledonia. – *Biol. Conserv.* 201: 111–119.

- Quintero, I. and Wiens, J. J. 2013. Rates of projected climate change dramatically exceed past rates of climatic niche evolution among vertebrate species. – *Ecol. Lett.* 16: 1095–1103.
- Ralph, P. L. and Coop, G. 2015. The role of standing variation in geographic convergent adaptation. – *Am. Nat.* 186: S5–S23.
- Rawlins, M. A. et al. 2016. Future decreases in freezing days across North America. – *J. Clim.* 29: 6923–6935.
- Rebetz, M. and Reinhard, M. 2008. Monthly air temperature trends in Switzerland 1901–2000 and 1975–2004. – *Theor. Appl. Clim.* 91: 27–34.
- Reid, N. M. et al. 2016. The genomic landscape of rapid repeated evolutionary adaptation to toxic pollution in wild fish. – *Science* 354: 1305–1308.
- Ricketts, T. H. 2001. The matrix matters: effective isolation in fragmented landscapes. – *Am. Nat.* 158: 87–99.
- Ricklefs, R. 2015. How tree species fill geographic and ecological space in eastern North America. – *Ann. Bot.* 115: 949–959.
- Schaper, S. V. et al. 2012. Increasing temperature, not mean temperature, is a cue for avian timing of reproduction. – *Am. Nat.* 179: E55–E69.
- Senner, N. R. 2012. One species but two patterns: populations of the Hudsonian godwit (*Limosa haemastica*) differ in spring migration timing. – *Auk* 129: 670–682.
- Senner, N. R. et al. 2014. An exception to the rule: carry-over effects do not accumulate in a long-distance migratory bird. – *PLoS One* 9: e86588.
- Senner, N. R. et al. 2015. When Siberia came to the Netherlands: the response of continental black-tailed godwits to a rare spring weather event. – *J. Anim. Ecol.* 84: 1164–1176.
- Senner, N. R. et al. 2017. Ecological mismatches are moderated by local conditions for two populations of a long-distance migratory bird. – *Oikos* 126: 61–72.
- Shama, L. N. S. et al. 2016. Transgenerational effects persist down the maternal line in marine sticklebacks: gene expression matches physiology in a warming ocean. – *Evol. Appl.* 9: 1096–1111.
- Shao, H. et al. 2008. Genetic architecture of complex traits: large phenotypic effects and pervasive epistasis. – *Proc. Natl Acad. Sci. USA* 105: 19910–19914.
- Stevenson, I. R. and Bryant, D. M. 2000. Climate change and constraints on breeding. – *Nature* 406: 366–367.
- Straile, D. et al. 2015. Trophic mismatch requires seasonal heterogeneity of warming. – *Ecology* 10: 2794–2805.
- Urban, M. C. 2015. Accelerating extinction risk from climate change. – *Science* 348: 571–573.
- van Asch, M. et al. 2007. Predicting adaptation of phenology in response to climate change, an insect herbivore example. – *Global Change Biol.* 13: 1596–1604.
- van Buskirk, J. et al. 2010. Declining body sizes in North American birds associated with climate change. – *Oikos* 119: 1047–1055.
- van Buskirk, J. et al. 2012. Phenotypic plasticity alone cannot explain climate-induced change in avian migration timing. – *Ecol. Evol.* 2: 2430–2437.
- van Dyck, H. et al. 2015. The lost generation hypothesis: could climate change drive ectotherms into a developmental trap? – *Oikos* 124: 54–61.
- Visser, M. E. and Both, C. 2005. Shifts in phenology due to global climate change: the need for a yardstick. – *Proc. R. Soc. B* 272: 2561–2569.
- Visser, M. E. et al. 1998. Warmer springs lead to mistimed reproduction in great tits (*Parus major*). – *Proc. R. Soc. B* 265: 1867–1870.
- Visser, M. E. et al. 2003. Variable responses to large-scale climate change in European *Parus* populations. – *Proc. R. Soc. B* 270: 367–372.
- Walsh, J. et al. 2014. Chapter 2: our changing climate. – In: Mellillo, J. M. et al. (eds), *Climate change impacts in the United States: the third national climate assessment*. US Global Change Research Program, pp. 19–67.
- Webster, M. S. et al. 2017. Who should pick the winners of climate change? – *Trends Ecol. Evol.* doi:10.1016/j.tree.2016.12.007
- Wiens, J. J. 2016. Climate-related local extinctions are already widespread among plant and animal species. – *PLoS Biol.* 14: e2001104.
- Winkler, D. W. et al. 2013. Temperature effects on food supply and chick mortality in tree swallows (*Tachycineta bicolor*). – *Oecologia* 173: 129–138.
- Zhang, Q.-G. and Buckling, A. 2016. Migration highways and migration barriers created by host–parasite interactions. – *Ecol. Lett.* 19: 1479–1485.

Supplementary material (Appendix ECOG-03234 at < [www.ecography.org/appendix/ecog-03234](http://www.ecography.org/appendix/ecog-03234) >). Appendix 1.