Synthesising the multiple impacts of climatic variability on community responses to climate change

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Abstract

Recent developments in understanding and predicting species responses to climate change have emphasised the importance of both environmental variability and consideration of the wider biotic community. To date, the interaction between the two has received less attention. However, considerable bodies of theory and empirical results suggest that multi-species consequences of variability can have strong impacts on range limits and the speed of range shifts. Here we demonstrate how biotic interactions and temporal variability can act together to influence range shift dynamics and highlight the need to understand these interactions in order to predict how species will respond to global change. We emphasise the value and utility of partitioning approaches applied to parameterised models to determine the direction and relative importance and direct of these forces in empirical systems.

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JCDT wrote the manuscript and built the models. All authors contributed significantly to the editing and manuscript development.

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25 Data Sharing and Data Accessibility

26 Code to generate all results is publicly available at https://github.com/jcdterry/ClimateVar_BioticInts

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Introduction

Climate change is forcing species across the world to either adapt to different environments in-situ or shift their range to track moving climates. A signal of climate-change induced spatial displacement is clearly visible in shifts in the observed distribution of species across the globe (Parmesan & Yohe 2003; Lenoir *et al.* 2020). Improving our understanding of how range shifts will progress is critical to future conservation efforts and ecosystem management (Pech *et al.* 2017). Here we argue that multiple strands of ecological theory regarding the direct and indirect impacts of climate variability in determining community-level responses can be informative to this wider effort.

Long-term climatic trends are accompanied by higher-frequency variation. This is partly cyclical (seasonal and diurnal) but there is also a considerable stochastic element. Differences in mean temperature between years are often comparable to decades of mean climate change (Huntingford *et al.* 2013). It is well established that environmental variability can have far-reaching impacts on populations (Coulson *et al.* 2004; Lawson *et al.* 2015; Boettiger 2018; Shoemaker *et al.* 2020b). On top of this, interactions with other species strongly influence a species' range (Sexton *et al.* 2009; Kraft *et al.* 2015; Sirén & Morelli 2020). As much as climate driven range shifts are fundamentally driven by the dependence of demographic rates on climatic variables, it is well recognised that the response of an individual species to climatic change cannot be understood in isolation from the rest of the community (Svenning *et al.* 2014; Davis *et al.* 1998; Araújo & Luoto 2007; Gilman *et al.* 2010; Urban *et al.* 2012, 2016; Ettinger & HilleRisLambers 2017; O'Brien *et al.* 2017; Legault *et al.* 2020). Rather than environment and competition acting as independent determinants of range limits, their combined effect is critical (Germain *et al.* 2018).

To date, the direct, systematic analysis of the effect of variability on extinction risk has been dominated by single-species studies (Bennie *et al.* 2013; Renton *et al.* 2014; Vasseur *et al.* 2014; Lawson *et al.* 2015; Bernhardt *et al.* 2018). Likewise, the majority of existing approaches to modelling the impact of climate change on multi-species distributions assume a smooth increase in

the driving climate variable (Urban *et al.* 2012; Thompson & Gonzalez 2017, Alexander *et al.* 2018). However, temporal variability influences species dynamics, and hence response to climate change through multiple direct and indirect routes (Fig 1.)

We propose here that the current discussion around ecological responses to climate change could be missing a key element – the role of temporal variability in determining how interspecific interactions play out (Vasseur & Fox 2009; Gudmundson *et al.* 2015; Fey & Vasseur 2016; Dee *et al.* 2020). Two related questions emerge: firstly, how does considering variability change our expectations for how communities will respond to shifts in mean conditions? And secondly, since increasing interannual variability in vegetation productivity is already detectable in satellite observations (Chen *et al.* 2019) and expected in a number of other environments (Swain *et al.* 2018), what impact would changes in variability patterns have on communities (Vázquez *et al.* 2017)?

We focus on populations near the edges of a species range, which constitute the front-line of climate change impacts - although we note that the geographic range edges are not always the most marginal habitats (Vilà-Cabrera *et al.* 2019, Oldfather *et al.* 2020). For vulnerable species with narrow climatic niches, their overall persistence will typically depend on their ability to advance their ranges. Species range edges are a unifying point of convergence for ecology (Holt & Keitt 2005) and as such the impact of climate change on ranges will require the synthesis of numerous strands of ecological thought (Urban *et al.* 2016). Populations can show greater sensitivity to climate variability towards the edge of their existing range, as observed for butterflies (Mills *et al.* 2017), tundra shrubs (Myers-Smith *et al.* 2015), game birds (Williams *et al.* 2003) and mangroves (Cavanaugh *et al.* 2018).

Within the multi-decadal time horizon relevant to contemporary responses to climate change, temporal variability has many components. One key division is between the impacts of long-term patterns of fluctuations in climatic variables (described by measures such as variance and autocorrelation) and the impacts from individual discrete ‘extreme weather events’ defined either by their statistical unlikeliness or through the breaching of particular physiological thresholds (Smith

2011; Bailey & van de Pol 2016). Drawing a sharp line between long-term and discrete impacts of a variable climate is challenging, as individual extreme events are ultimately part of the ‘background’ variability observed over sufficient time. However, at the intermediate time scales of climate change concern, valuable insights can be gained from considering both aspects.

Variability acts on each species in a community through numerous direct and indirect routes (Figure 1a). We structure our discussion by dividing the diversity of processes into those impacting the long-term viability of a population (Figure 1b), and processes affecting colonisation of new areas, drawing from ideas from invasion ecology. Using simple models, we then show how these processes can interact at all levels and how recent developments in techniques to partition the impact of variability can inform on the importance of different processes. We argue that the interrogation of parameterised models can help overcome the challenge of synthesizing insights from across ecological subfields.

Figure 1. a) Schematic of principal routes by which variability influences a focal species at a site (circled). Climatic variability influences the focal population in three ways: directly influencing its reproductive rate, varying propagule pressure and through impacts of competitors (here represented as conifers). Overall competitive pressure can vary through fluctuating competitor numbers (which can be environmentally driven) and by varying modulation of the impact of competition exerted by the competitor. Variability generating processes internal to the focal population, such as demographic stochasticity, can interact with the externally driven variation. b) Categorisation of impacts of variability in determining species ranges and response to

climate change discussed here. The mechanisms are categorised by organisational scale and whether they influence the ability for a species to persist at a site (its population viability) or the capacity for the species to establish new populations to shift their range.

Variability and single-population growth rate

The direct impacts of climate variability on the viability of individual populations are widely appreciated (Lande 1993; Lawson *et al.* 2015), and so we only briefly review them here. Extensive analytical and experimental work demonstrates a long-term impact of a fluctuating climate on population growth rates (Ruel & Ayres 1999; Drake 2005; Melbourne & Hastings 2008; Thompson *et al.* 2013; Vasseur *et al.* 2014; Lawson *et al.* 2015). Average growth rates over the long term may be considerably different to population growth rates at average environmental conditions. Through non-linear averaging, the net impact of a variable climate on an individual species' growth rate can be either positive or negative (Figure 2). The principal determinant of the direction of the effect is the curvature of the growth rate's response to the relevant climate variable. However, higher-order properties such as temporal autocorrelation can also play a role (Petchey *et al.* 1997; Heino *et al.* 2000). Many populations near the edge of their range show greater population variability and climate sensitivity (Myers-Smith *et al.* 2015; Mills *et al.* 2017) and so may be expected to be particularly responsive to these effects.

Figure 2 How the curvature of environmental performance curves (EPCs) affects average performance. a) The black line shows a classically shaped environmental performance curve where the key environmental variable

is temperature, while the dashed lines show relative frequency of environmental conditions at two sites (yellow and blue). b) shows histograms of observed performances across 1000 random environmental draws at each site. At the yellow site, environmental variability is fairly large, but the curvature of the performance curve is relatively shallow. The long-term average value (dashed line) is therefore very similar to the value under mean conditions (solid line). At the blue site, although the variability is smaller, the local EPC curvature is much larger and downwards. The long-term value average value is considerably lower than the value under mean conditions. It also includes several instances that could be labelled extreme events, where the performance is very markedly below average.

Individual extreme events have most commonly been associated with population declines and heightened extinction risk, in particular when harsh climatic conditions push populations down to a level where they are vulnerable to extinction (Lande 1993; Boyce *et al.* 2006; Jongejans *et al.* 2010; Nadeau *et al.* 2017; Maxwell *et al.* 2019). Extreme events have been associated with extinction risk (Román-Palacios & Wiens 2020) and abrupt changes in community composition (Turner *et al.* 2020). Range contractions and community shifts have also been seen in many communities, including butterflies (de Palma *et al.* 2017), tropical fish (Lenanton *et al.* 2017), kelp (Smale & Wernberg 2013) and bumblebees (Soroye *et al.* 2020). Extreme events have led to extirpations from newly colonised areas, and it has been suggested that this may slow species responses to climate change (Nadeau *et al.* 2017). For example, extreme cold events have been associated with range retractions of invasive marine invertebrates (Canning-Clode *et al.* 2011) and fish (Rehage *et al.* 2016).

Taken together, both long- and short-term impacts of variability are more commonly viewed as having negative consequences for populations of conservation interest. However, as we shall show, when considering the wider community context in which species exist, this baseline assumption may need to be adjusted.

Impacts of variability on longer term coexistence

Where there is biotic control of species distributions, range limits become fundamentally a problem of coexistence (Shea & Chesson 2002; Usinowicz & Levine 2018). This framing unlocks for climate change research a long and rich history of work examining the influence of temporal environmental variability on coexistence (Levins 1979). The potential for temporal variability to enhance coexistence is well attested empirically (Adler *et al.* 2006; Tucker & Cadotte 2013; Tucker & Fukami 2014; Usinowicz *et al.* 2017; Hallett *et al.* 2019). Contrary to conclusions drawn in early and still influential literature (e.g. Hutchinson 1961), environmental fluctuations themselves are not sufficient to support coexistence of competing species (Chesson & Huntly 1997; Fox 2013) and can hinder as much as facilitate coexistence. The framework of modern coexistence theory (MCT, Chesson 2000) has been developed to robustly understand the impact of variability on coexistence. However, this body of theoretical work examining the problem of species coexistence is only recently being applied to climate change in the context of spatially heterogeneous environments (Usinowicz & Levine, 2018).

At its core, MCT defines and investigates coexistence in terms of the capacity for populations to grow from rare in the presence of competing species - the invasion criterion (Grainger *et al.* 2019b). Where all species are able to meet this criterion, they can each resist exclusion by the other species. In order to simplify the following discussion, we assume that only the ability of a particular focal species to persist at a site alongside one or more competitor species is in question. Through MCT, precise principles have been developed to identify how temporal variability influences coexistence by quantifying the effects of temporal variability on the long-term average growth rate when the focal species is at low densities ($\overline{r_{inv}}$, Chesson & Warner 1981; Chesson & Huntly 1997; Amarasekare *et al.* 2004; Snyder 2008).

Since MCT is grounded in analytic results obtained for highly general models it can be applied to most models of population dynamics. This requires conceptually separating direct impacts of the environment on the focal population's growth rate from the impacts exerted by competitors. This separation is delicate because competitors can affect the focal species directly, but also indirectly

through shared resources - defined broadly to include physical resources such as nutrients, water or space, as well as through apparent competition mediated by natural enemy populations (Chesson & Kuang 2008). These routes of impact are the ‘limiting factors’ of MCT and can realise considerable analytical insight but also interpretational challenges (for a recent comprehensive review, see Barabás *et al.* 2018). However, as we shall show below, essential insights can be gained directly from a model that can describe how the growth rate of the population r depends on the environment (E) and the competitive impact (C), $r = f(E, C)$, abstracting over the underlying mechanisms (Ellner *et al.* 2019). Where direct effects of environmental drivers and impacts of competitors contribute linearly and additively to the population growth of the focal species, any variability averages out in the long term. MCT can be used to describe how deviations from the linear, additive base case lead to long-term effects of variability on population growth. These deviations can be understood in terms of two classes of impacts – temporal ‘storage effects’ and non-linearity of competitive effects.

Temporal storage effects arise when the combined effects of the environment and competition allow benefits accrued in certain years to compensate for losses in other years (Chesson & Warner 1981). For this to affect long-term persistence two conditions must be met. Firstly, there must be an interaction between the direct impacts of the environmental conditions and the impacts of the competitor on the growth rate (mathematically this is non-additivity, where $\frac{\partial^2 r}{\partial E \partial C} \neq 0$). For example, a species may suffer proportionally less from competitors in a year of harsh environment if the population is buffered in some way such that the combined effect of a harsh environment and competitive pressure is capped (Fig 3ai). Secondly, the environmental variability must affect the competitive impacts on the focal species (i.e. E and C must co-vary, Figure 3aii). In the classic case with buffered (subadditive) population growth, the more negative this covariance, the greater the beneficial effect to the focal population. However, it is worth noting that temporal storage effects can be reversed if the biotic and abiotic impacts on the focal species growth rate are superadditive,

i.e. the adverse effects of competition are proportionally greater in a harsh year (e.g. Holt & Chesson 2014). In the context of climate change, there is a risk that the current patterns of covariation in species' responses to the environment could change. For example, if climate change results in more frequent universally 'bad' (or equally, universally 'good') periods, instead of a back-and-forth of alternate species being favoured, overall covariance in species responses could become more positive and further undermine coexistence.

The second mechanism arises directly from fluctuations in the impact of other species on the growth rate of the focal species. Non-linear averaging of varying biotic impacts on the focal species' growth can affect $\overline{r_{inv}}$, analogous to the non-linear averaging of abiotic environmental fluctuations on population growth rates described in the section above (Fig 2), and with matching consequences for shifts in climatic variability patterns (Fig 3b). These fluctuations in the biotic pressure can be driven by changes in the abundance of competitor species, or via varying per-capita intensity of the competition exerted by other species through fluctuations in shared resources. When examining coexistence, this is the mechanism of 'relative nonlinearity' that describes how species can differentiate themselves through their capacity to take advantage of variable environments - 'slow-and-steady' versus 'boom-or-bust' dynamics (Armstrong & McGehee 1980). Notably, in contrast to temporal storage effects, this does not directly rely on correlations in species response to the environment and can also derive from other fluctuation generating mechanisms.

a. Temporal 'Storage Effect'

i Non-independence between biotic and abiotic impacts

ii Covariance through time of biotic and abiotic impacts

b. Non-linear averaging of biotic pressures

Figure 3 Illustration of the conditions required for the two multi-species mechanisms by which environmental variability can impact persistence. a) Temporal storage effects describe how species are able to divide niche opportunities afforded by a variable climate between them. For this to influence the long-term average population growth rate, there are two conditions: i) competitors and the environment must interact in how they determine growth rate, and ii) the impact of competition and direct effects of the environment must correlate through time. Here each dot represents a year and pressure from the competitor tends to be lower in a benign year for the focal species. This could derive from the two species prospering in different conditions. b) Non-linear averaging of the impact of biotic pressures can result in an overall impact on average population growth rate that differs from the impact under mean conditions. Here we show a case of environmentally determined impact of competition. The determinants of the net effects of non-linearities of biotic impacts have similar drivers to the single-species mechanisms described in Fig.2, depending on both the pattern of environmental variability and the curvature of species responses.

229 The foundation for identifying the relative strengths of these processes in a real system is the
 230 construction of a simple parameterised model. With that in hand, approaches such as that proposed
 231 by Ellner *et al.* (2019) can be used to partition $\overline{r_{inv}}$ into contributions of different single-species and
 232 multi-species aspects of variability, without the need for complex analytical work and overcoming
 233 limitations incurred by approximations made in the analytic theory. We describe this approach in
 234 Figure 4 and in SI 2. In a recent example, Armitage and Jones (2020) used a model of competition
 235 between two species of duckweed to show that the inferior competitor's poleward range limit is
 236 better predicted when taking into account the impact of temporal fluctuations. Using a partitioning
 237 approach, they found this was dominated by nonlinearity in direct temperature responses, with a
 238 smaller contribution of non-linearities in competition and minimal impact of temporal storage
 239 effects attributable to the positively correlated species responses.

Figure 4. Summary of the steps required to investigate impact of temporal variability through the partitioning method of Ellner et al (2019) and two examples. Full details are given in SI 2. a) Firstly, establish the processes involved and build a model of the population dynamics to calculate the long-term growth rate ($\bar{r}_{inv}$). In our model, rate of population change when rare at each time point is given by Eq (1), where δ = carryover from the previous generation, λ = fecundity in the absence of competitors, α = per-capita competitive coefficient. Since we assume the focal species is rare it includes no intra-specific competition. The impact of a variable climate on competition and intrinsic growth rate at each time step is determined by the two ω terms, which are correlated at each time step t . The population density of the competitor (C_t) also fluctuates through time. $\bar{r}$ is found from the mean of $\log(F_{t+1}/F_t)$ over a sufficiently large number of trials. b) Secondly, systematically alter the inputs of the growth rate model by sequentially fixing different fluctuating terms to their average values or removing correlations between variable components. Choices of which aspects to fix, and in which

combination will allow different partitioning. Here we partition the difference between the growth rate under fully fixed conditions ($\overline{r_0}$) and under the ‘observed’ variable conditions ($\overline{r_{inv}}$) with five Δ -partitions: $\overline{r_{inv}} = \overline{r_0} + \Delta_\lambda + \Delta_N + \Delta_\alpha + \Delta_* + \Delta_{TSE}$, corresponding to the processes identified in a). Differences between the model variants allow the identification of the relative influence of each partition. c) Examples of how the partitioning approach can illustrate how variability can have multiple counteracting consequences for a species’ ability to persist. We use two example parameterisations of the same underlying model, Site 1 (left) and Site 2 (right). At Site 1 without variability, $\overline{r_0}$ is negative, and the focal species would not be expected to persist. The full model (black line) suggests that with a climate variability above 0.08 persistence is possible. Inspection of the partitions (below) shows that the two largest positive impacts are non-linearities in the impact of competition (Δ_α) and temporal storage effects (Δ_{TSE}). Opposing this, variability in the abundance of competitors (Δ_N) is detrimental to the focal species. The impact of variability directly on the growth rate of the focal species (Δ_λ) is here relatively small, and insufficient to lead to persistence in the range of variabilities examined. The interaction term between the processes (Δ_*) is negative but small. Note that at low levels of variability Δ_* is slow to increase, showing that the other partitions identify the main pathways of low variability levels. By contrast, at Site 2, variability in the growth rate of the focal species has a negative impact (Δ_λ), and if it was the only process considered might be expected to prevent persistence at the site. There is also a negative temporal storage effect (Δ_{TSE}), deriving from a positive correlation between competitive impact and intrinsic growth rate in the underlying model. However, these two effects are more than counteracted by strong positive contributions from non-linearities in both competitive effect (Δ_α) and abundance of competitors (Δ_N). In this case the role of interactions between non-linearities (Δ_*) remains small.

Earlier theoretical work placed greater emphasis on temporal storage effects, but in the small number of empirical cases where the relative impact of the two effects on coexistence has been directly compared, relative nonlinearity was found to have comparable, or greater, impact than the more widely appreciated storage effects (Letten *et al.* 2018; Hallett *et al.* 2019; Zepeda & Martorell 2019). Although to date the number of examples is small, it is clear that climate-driven shifts in variability patterns could play a role in determining coexistence between competitors and range limits in the future. While we have focussed here on competitive systems, consumer-resource systems can be analysed in parallel ways (Dee *et al.* 2020; Shoemaker *et al.* 2020a). However, effects

identified in simple communities may not necessarily directly translate to more complex systems (Barabás *et al.* 2018, Song *et al.* 2019). Species respond to different parts of the environment - with a greater diversity of species, it is quite possible that species-level fluctuations in competition may average out at the community level. For example, Clark *et al.* (2010) found that different tree species responded to different aspects of the overall environmental fluctuations. This may suggest that these mechanisms may be strongest where a limited pool of species are involved in constraining the range of the focal species.

Community impacts of discrete events

A species' range expansion in response to climate change is effectively a series of invasions into new communities (Wallingford *et al.* 2020). From this perspective, the significant body of work investigating variability within invasion biology, going back to Elton (1958) and beyond, can offer useful insights. The ability of a species to persist at a site is only one half of the picture – a species must first arrive and establish itself. The spread of a species into new areas can be slowed or even prevented by disadvantages that potential invaders face. For instance, positive density dependence at low population densities (Allee effects, Courchamp *et al.* 1999; Kramer *et al.* 2018) can cause leading range edges to appear 'pinned' in place (Keitt *et al.* 2001) and slow the rate of invasion into newly suitable environments (Taylor & Hastings 2005).

Environmental variability can play a role in shifting a community from one state to another by allowing species to overcome the challenges of Allee effects through intermittent boosts in performance (Dennis 2002). Discrete extreme weather events can have marked influence on the trajectory of species responses to climate change, but pose considerable challenges to investigation and prediction (Bailey & van de Pol 2016). Although direct evidence is challenging to find (see later sections), extreme climatic events have been associated with the arrival into marine communities of species previously found in warmer areas (Wernberg *et al.* 2013). Dispersal is intrinsically episodic (e.g. Kennedy *et al.* 2020) and short term spikes in the number of incoming colonist propagules may

help increase establishment compared to constant dispersal rates by overcoming thresholds induced by Allee effects (Drake & Lodge 2006; Carr *et al.* 2019).

At the community level, biotic resistance from the resident species can slow or prevent a colonist tracking its climatic niche (Urban *et al.* 2012; Legault *et al.* 2020). Whether this resistance is considered a hindrance or beneficial will depend on the conservation status and impact of the colonist and resident species concerned. Over longer time scales, a history of disturbance can shape a community's biotic resistance through selective assembly (Miller *et al.* 2021) or through specific adaptations to the local conditions, which may include levels of variability (Urban & de Meester 2009), although temporal variability in climate could also preclude such local adaptation from occurring (Bridle *et al.* 2010).

Figure 5 Illustration of two ways in which climatic variability can overcome barriers to range shifts. a) through episodic high-dispersal events, and b), by disrupting existing communities and reducing biotic resistance.

Even without local adaptation, priority effects can give residents considerable advantages compared to potential invaders. Where priority effects are strong, an invading species can colonise only if either the density of the resident is brought down from equilibrium, or the invader is otherwise able to reach sufficiently high densities to exert significant competitive pressure on the resident. Individual disturbance events can temporarily break down blocking effects (Davis *et al.* 2000;

Melbourne *et al.* 2007; Diez *et al.* 2012), for example in grasslands (Pinto & Ortega, 2016) and over the longer term there is an expectation that in disturbed environments there are more unused available resources for invaders to take advantage of (Davis *et al.* 2000; Diez *et al.* 2012). Tucker and Fukami (2014) showed experimentally that temperature variability can allow priority effects to be overcome in a nectar-yeast system. Ecological theory can play a key role in identifying cases where individual key events could precipitate the establishment of a climate refugee species. The core results of MCT can be applied to invasions (Shea & Chesson, 2002; MacDougall *et al.*, 2009) and are a useful guide to identifying where priority effects are impactful (Ke & Letten 2018; Grainger *et al.* 2019a; Uricchio *et al.* 2019) particularly where the growth rate of a colonising species can also be affected by variability (Clark & Johnston 2011).

Interactions between influences of variability

There have been frequent calls to improve the representation of communities in ecosystem-change models (Gilman *et al.* 2010; Angert *et al.* 2013; Urban *et al.* 2013). Synthesising the aggregate impact of variability will require an expansion in the scope of models currently used (Felton & Smith 2017). When considering whole communities, the diversity of possible impacts on a focal species due to variability is considerably larger than in the single-species case. The previous three sections demonstrated the breadth of direct and indirect ecological impacts that variability can have on how species will respond to climate change. Faced with such a diverse set of processes, reconciling the assorted influences of variability and determining how they interact is central to determining their influence in practice. There are fundamentally different scales and mechanisms at work, but bottom-up mechanistic modelling can illustrate the key interactions at play. Identifying and (equally importantly) ruling out for practical purposes, interactions between stressors is crucial to meaningful conservation interventions (Côté *et al.* 2016).

To this end, a number of modelling studies have explored the interface between local variability-mediated coexistence and extinction risk (Adler & Drake 2008; Gravel *et al.* 2011; Danino *et al.* 2018;

Pande *et al.* 2019; Schreiber *et al.* 2019; Dean & Shnerb 2020). Populations at low densities may be expected to benefit the most from variability-mediated coexistence mechanisms, but a low population size is also risky if a single bad year could extirpate the population. In these models, the relative strengths of stochastic extinction risk and competitive stabilization change across a gradient of environmental variability. In the largest empirical analysis of this balance to date, Fung *et al.* (2020) used forest plot data to quantify how variability leads to temporal niche partitioning and extinction risk and found that the balance was uneven but more frequently detrimental to coexistence.

A useful way of framing complex climate change responses into a single unified measure of impact is through establishment and extinction lags - differences between climate change and species range responses (Alexander *et al.*, 2018). The core issues can be demonstrated in relatively simple simulation models constructed to capture multiple processes and forms of variability simultaneously. In Figure 6 we demonstrate the potential for complex interactions between mechanisms using a simple model of competition (detailed in SI 3) between a resident species and a climate migrant. As already shown in Figure 4, the response expected from a change in variability due to one mechanism could be countered or even reversed in conjunction with other processes. Given the multitude of theoretically and empirically identified effects of climate variability on colonisation success under climate change, there is a need to develop and investigate such models to understand when interactions between these effects are likely to be influential.

Figure 6 Demonstration of interactions between impacts of environmental fluctuations on climate-driven colonisation in a simple two-species competition model. a) The core model is an extension of that discussed in Figure 4 and is detailed in SI 3. Initially the site is dominated by a resident species and subject to immigration pressure from a potential coloniser. Over time, the environment becomes increasingly favourable for the coloniser and eventually it will displace the resident. We introduce dynamical features or additional sources of variability and observe how average colonisation times respond to changes in certain aspects of variability. Here, we measure the time point from the onset of climate change when the coloniser is permanently established (b). c) Four examples of interaction between model processes, shown with smooth lines through 500 trials: i) as variability in the coloniser's performance rises, colonisation occurs more rapidly with increased variability where there is a negative correlation (blue) between the performance of the resident and the coloniser, as temporal storage effects aid establishment. However, where the competitor responses are positively correlated (yellow) colonisation is slowed by variability, ii) variability in incoming propagule pressure accelerates the colonisation only where there are strong Allee effects to overcome, iii) a colonisation delay with environmental variability can be reversed where there is demographic stochasticity that can lead to extinction at low densities, iv) the beneficial effect of variability for the coloniser can be reversed when it affects both species.

Building on small and focused models, larger, highly generalised and spatially-explicit metacommunity models (O'Sullivan *et al.* 2019; Thompson *et al.* 2020) can also provide insight into potential drivers of community change that emerge from combining processes at multiple scales (Usinowicz & Levine 2018; Chase *et al.* 2020). However, interpreting such models to assess the impact of variability poses distinct challenges, beyond parameterisation. It is rarely possible to directly control multiple aspects of variability simultaneously, even in an artificial model. Temporal variability is inherently multi-faceted and additional qualities beyond direct variance can have significant impacts, e.g. autocorrelation (Levine & Rees 2004). To take one illustrative example, the historical level of variability a community (real or *in silico*) experienced during its assembly contributes to the capacity of the community to respond to future changes, whether that is through direct adaptation of the species in a community to local levels of variability or by the extant species having passed through a previous extinction filter during historical extreme events (Janzen 1967; Nadeau *et al.* 2017; Medeiros *et al.* 2020; Miller *et al.* 2021).

Identifying processes in the real world

The next frontier is directly assessing the magnitude of these effects in real systems. Understanding which aspects of variability are most influential will be key to building models of minimal necessary complexity. Determination of the relative contributions of dispersal, interspecific interactions and environmental dependence has been identified as the key challenge to understanding the dynamics of whole communities (Leibold *et al.* 2020). There is evidence that biotic resistance to invasive species is widespread, but the global contribution of biotic resistance to climate refugee species is challenging to measure (Levine & Rees 2004; Alexander *et al.* 2015, 2016; Louthan *et al.* 2015; Godsoe *et al.* 2017, 2018; Beaury *et al.* 2020). Direct observations demonstrate that species are on the move, but consistent patterns are difficult to determine and influenced by concurrent land use changes (Lenoir *et al.* 2020). The observed rate

of movement of species is highly variable, with many species shifting their ranges considerably faster or slower than the climate velocity and ultimately dependent on availability of habitat (Platts *et al.* 2019). Competitive exclusion at large spatial scales is often very slow (Yackulic 2017), while extirpation by extreme events can be rapid, but not necessarily permanent. Any coupling between species ranges and particular climatic events can be highly idiosyncratic, with multi-year effects of weather events (Harley & Paine 2009). Coupled with the challenge of accurately identifying the pace of range shifts (Bates *et al.* 2015), this makes directly discerning a signal of variability in movement rates an imposing task.

Direct observations of variability in natural populations can highlight how species respond differently to environmental variability (Palmer *et al.*, 2017; Le Coeur *et al.* 2021). Evidence from global satellite data shows that sensitivity to climate variability is itself variable across the globe (Seddon *et al.* 2016). However, to determine the impact in terms of long-term coexistence, model parameterisation of some sort is required (e.g. Fung *et al.* 2020; Usinowicz *et al.* 2021). Species traits hold some promise to identify likely temporal coexistence mechanisms (Adler *et al.* 2013). Life history traits have been found to relate to sensitivity to climate anomalies in herbaceous perennials (Compagioni *et al.* 2021) and amphibians (Cayuela *et al.* 2017), but much work remains to be done in this area.

Mesocosm experiments with manipulation of variability can be illuminating – for example, Zander *et al.* (2017) showed that lower trophic levels of a microbial food web were more strongly affected by variability than top level consumers. However, such an approach is fundamentally limited since variability can be manipulated in many alternative valid dimensions unless it is tied directly to expected climate regimes (Thompson *et al.* 2013). Behavioural adaptation and the role of microclimates pose further challenges to the interpretation of mesocosm work - the realised variability of environmental variables relevant to species may differ from that measured by weather stations (Bladon *et al.* 2020).

Alongside the highly generalised ‘strategic’ models demonstrated in the previous section, multiple impacts of variability need to be tested for in focussed ‘tactical’ case studies of marginal populations in order to build a picture of the real-world prevalence of these processes. Progress will require not just more data, but a connected approach to synthesising the multiple impacts of variability, which in turn requires a reliable model of community dynamics that can incorporate variable conditions. At the core will be robust models of species performance and competitive impact under different environmental conditions. This is no easy task – even in two-species systems with a single environmental variable this requires fitting a multidimensional response surface. Given that species respond to multiple environmental variables (Clark *et al.* 2010; Tingley *et al.* 2012) there are fundamental limits to the resolution such models can aim to achieve. Detailed predictions for individual communities will need to confront measures of environmental performance with observations of current ranges to best estimate future trajectories (Armitage & Jones 2020; Twinaime *et al.* 2020). Observations of communities along climate gradients can provide particularly valuable tests of models designed to investigate climate change (Alexander *et al.* 2016; Tyliaakis & Morris 2017).

With a sufficiently supported model in hand, partitioning of the various impacts of variability on coexistence can be highly informative (Figure 4, Ellner *et al.* 2019; Shoemaker *et al.* 2020a). The method can be extended to the large scales relevant to climate-change responses (Armitage & Jones 2020). Such a simulation-based partitioning approach could also be applied with other response variables, for example colonisation or extirpation lags, or extended to include additional variability terms. Understanding which aspects of variability are most influential can sharpen the focus of investigations, reducing overall problem complexity and concentrate potential mitigation efforts on the most critical fluctuations.

In support of this, a key line of future theoretical enquiry will be determining the minimum data requirements to understand the impact of variability. It is not yet known how sensitive partitioning of variability effects is to model misspecification. The higher-level properties of environmental

performance curves, such as their curvature, are considerably harder to estimate than first order properties such as thermal optima. Empirical estimates for key parameters can be confounded, with each other, with consequences for reliable estimation of species coexistence (Terry *et al.* 2021). The implications of parameter uncertainty need to be explicitly acknowledged and better understood. Since partitioning is algorithmic, it is possible to propagate uncertainties in the underlying model through to uncertainty in the impact of variability on the response of interest.

Conclusion

Process	Key determinant of impact	Possible impact of considering variability in the response to climate change
<i>Single Species</i>		
Non-linear averaging of environmental responses	Curvature of environmental performance curve	Long-term population viability could differ from viability under average conditions
Extreme weather-related population impacts	Population sensitivity and recovery rates	Generally considered detrimental to population persistence
Episodic dispersal	Dispersal limitation of range expansion Allee Effects	Establishment into new areas may be aided
<i>Multi-Species</i>		
Temporal storage effects	Covariance between environmental and competitive impacts on growth rate Non-additivity of environmental and competitive impacts	Consistency of species' environmental responses could be influential in determining persistence
Non-linearity of competition/competitive impact	Curvature of competitive impact on growth rate	Long-term population viability could differ from viability under average conditions
Disruptions overcoming priority effects	Strength of biotic resistance due to priority effects Disturbances reducing biotic resistance	Biotic resistance could be overcome more suddenly than expected

Table 1 Summary of the impacts climate variability can have on species responses to climate change.

Influential interspecific interactions are necessary for the multi-species process to be impactful. Particularly in the multi-species processes, more research is needed to determine their prevalence and influence in real systems.

In Table 1 we summarise the multitude of ecological routes by which underlying temporal variability could influence how a species will fare under climate change. It is not currently clear whether the difference in emphasis of the impact of variability in different ecological subfields represents a lack

of communication, publication bias, or if the relative neglect of the ‘positive’ aspects of variability within global change biology is because they do not leave a widespread strong imprint on real-world dynamics. It would be risky to assume that the impacts of variability are already ‘baked-in’ to current observed species ranges, and so captured by existing distribution models. We reiterate that there will also be evolutionary processes to consider - interactions between variability and adaptation with positive and negative consequences for range shifts has been subject of extensive recent reviews elsewhere (Vázquez et al. 2017; Nadeau & Urban 2019; Thompson & Fronhofer 2019; Coleman & Wernberg 2020; Lyberger et al. 2021; Miller et al. 2020).

At this point in time, we simply do not know whether current assumptions of the impact of variability based on single-population analyses are systematically over or underestimating risks at the community level. What we do know is that climate change will present species with a bumpy and obstacle-filled uphill ride, not a smooth escalator. No single simple theory can predict the effects of climate variability – but, as we have shown, this does not prevent useful insights cannot being synthesised. As with most areas of ecology, both complex and simple verbal and mathematical models have their parts to play. By understanding the linkages between these models, detailed insights can be gained without losing sight of the whole. More examples of quantification of the impact of variability in real communities are needed - it is our belief that the simple modelling frameworks discussed here can meet this need. Building strong bridges between climate change ecology and coexistence theory has never been more possible, or more necessary.

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