1 Synthesising the multiple impacts of climatic variability on

2 community responses to climate change

3 Authors

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9 Abstract

10 Recent developments in understanding and predicting species responses to climate change have

11 emphasised the importance of both environmental variability and consideration of the wider biotic

12 community. To date, the interaction between the two has received less attention. However,

13 considerable bodies of theory and empirical results suggest that multi-species consequences of

14 variability can have strong impacts on range limits and the speed of range shifts. Here we

15 demonstrate how biotic interactions and temporal variability can act together to influence range

16 shift dynamics and highlight the need to understand these interactions in order to predict how

17 species will respond to global change. We emphasise the value and utility of partitioning approaches

18 applied to parameterised models to determine the direction and relative importance and direct of

19 these forces in empirical systems.

20 Authorship

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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

27   and should the manuscript be accepted will be permanently archived. The paper contains no new

28   datasets.

29   Running title

30   *Temporal variability and community responses*

31   Keywords

32   Range shifts, temporal variation, community responses, coexistence theory, climate change

Introduction

34   Climate change is forcing species across the world to either adapt to different environments in-situ

35   or shift their range to track moving climates. A signal of climate-change induced spatial displacement

36   is clearly visible in shifts in the observed distribution of species across the globe (Parmesan & Yohe

37   2003; Lenoir *et al.* 2020). Improving our understanding of how range shifts will progress is critical to

38   future conservation efforts and ecosystem management (Pecl *et al.* 2017). Here we argue that

39   multiple strands of ecological theory regarding the direct and indirect impacts of climate variability

40   in determining community-level responses can be informative to this wider effort.

41   Long-term climatic trends are accompanied by higher-frequency variation. This is partly cyclical

42   (seasonal and diurnal) but there is also a considerable stochastic element. Differences in mean

43   temperature between years are often comparable to decades of mean climate change (Huntingford

44   *et al.* 2013). It is well established that environmental variability can have far-reaching impacts on

45   populations (Coulson *et al.* 2004; Lawson *et al.* 2015; Boettiger 2018; Shoemaker *et al.* 2020b). On

46   top of this, interactions with other species strongly influence a species' range (Sexton *et al.* 2009;

47   Kraft *et al.* 2015; Sirén & Morelli 2020). As much as climate driven range shifts are fundamentally

48   driven by the dependence of demographic rates on climatic variables, it is well recognised that the

49   response of an individual species to climatic change cannot be understood in isolation from the rest

50   of the community (Svenning *et al.* 2014; Davis *et al.* 1998; Araújo & Luoto 2007; Gilman *et al.* 2010;

51   Urban *et al.* 2012, 2016; Ettinger & HilleRisLambers 2017; O'Brien *et al.* 2017; Legault *et al.* 2020).

52   Rather than environment and competition acting as independent determinants of range limits, their

53   combined effect is critical (Germain *et al.* 2018).

54   To date, the direct, systematic analysis of the effect of variability on extinction risk has been

55   dominated by single-species studies (Bennie *et al.* 2013; Renton *et al.* 2014; Vasseur *et al.* 2014;

56   Lawson *et al.* 2015; Bernhardt *et al.* 2018). Likewise, the majority of existing approaches to

57   modelling the impact of climate change on multi-species distributions assume a smooth increase in

3

58   the driving climate variable (Urban *et al.* 2012; Thompson & Gonzalez 2017, Alexander *et al.* 2018).

59   However, temporal variability influences species dynamics, and hence response to climate change

60   through multiple direct and indirect routes (Fig 1.)

61   We propose here that the current discussion around ecological responses to climate change could

62   be missing a key element – the role of temporal variability in determining how interspecific

63   interactions play out (Vasseur & Fox 2009; Gudmundson *et al.* 2015; Fey & Vasseur 2016; Dee *et al.*

64   2020). Two related questions emerge: firstly, how does considering variability change our

65   expectations for how communities will respond to shifts in mean conditions? And secondly, since

66   increasing interannual variability in vegetation productivity is already detectable in satellite

67   observations (Chen et al 2019) and expected in a number of other environments (Swain *et al.* 2018),

68   what impact would changes in variability patterns have on communities (Vázquez *et al.* 2017)?

69   We focus on populations near the edges of a species range, which constitute the front-line of

70   climate change impacts - although we note that the geographic range edges are not always the most

71   marginal habitats (Vilà-Cabrera *et al.* 2019, Oldfather et al 2020). For vulnerable species with narrow

72   climatic niches, their overall persistence will typically depend on their ability to advance their ranges.

73   Species range edges are a unifying point of convergence for ecology (Holt & Keitt 2005) and as such

74   the impact of climate change on ranges will require the synthesis of numerous strands of ecological

75   thought (Urban *et al.* 2016). Populations can show greater sensitivity to climate variability towards

76   the edge of their existing range, as observed for butterflies (Mills *et al.* 2017), tundra shrubs (Myers-

77   Smith *et al.* 2015), game birds (Williams *et al.* 2003) and mangroves (Cavanaugh *et al.* 2018).

78   Within the multi-decadal time horizon relevant to contemporary responses to climate change,

79   temporal variability has many components. One key division is between the impacts of long-term

80   patterns of fluctuations in climatic variables (described by measures such as variance and

81   autocorrelation) and the impacts from individual discrete 'extreme weather events' defined either

82   by their statistical unlikeliness or through the breaching of particular physiological thresholds (Smith

83   2011; Bailey & van de Pol 2016). Drawing a sharp line between long-term and discrete impacts of a

84   variable climate is challenging, as individual extreme events are ultimately part of the 'background'

85   variability observed over sufficient time. However, at the intermediate time scales of climate change

86   concern, valuable insights can be gained from considering both aspects.

87   Variability acts on each species in a community through numerous direct and indirect routes (Figure

88   1a). We structure our discussion by dividing the diversity of processes into those impacting the long-

89   term viability of a population (Figure 1b), and processes affecting colonisation of new areas, drawing

90   from ideas from invasion ecology. Using simple models, we then show how these processes can

91   interact at all levels and how recent developments in techniques to partition the impact of variability

92   can inform on the importance of different processes. We argue that the interrogation of

93   parameterised models can help overcome the challenge of synthesizing insights from across

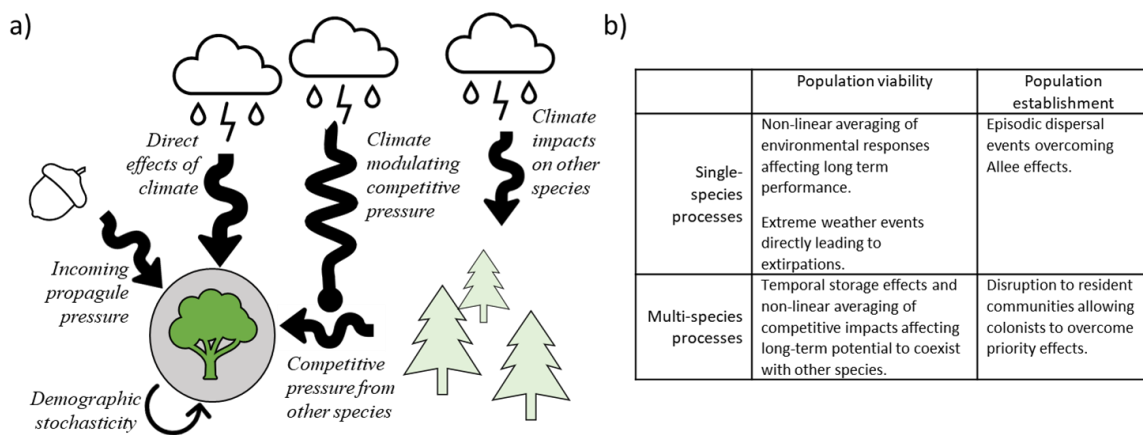94   ecological subfields.

95

96   **Figure 1.** a) Schematic of principal routes by which variability influences a focal species at a site (circled).

97   Climatic variability influences the focal population in three ways: directly influencing its reproductive rate,

98   varying propagule pressure and through impacts of competitors (here represented as conifers). Overall

99   competitive pressure can vary through fluctuating competitor numbers (which can be environmentally driven)

100   and by varying modulation of the impact of competition exerted by the competitor. Variability generating

101   processes internal to the focal population, such as demographic stochasticity, can interact with the externally

102   driven variation. b) Categorisation of impacts of variability in determining species ranges and response to

103 climate change discussed here. The mechanisms are categorised by organisational scale and whether they

104 influence the ability for a species to persist at a site (its population viability) or the capacity for the species to

105 establish new populations to shift their range.

Variability and single-population growth rate

107 The direct impacts of climate variability on the viability of individual populations are widely

108 appreciated (Lande 1993; Lawson *et al.* 2015), and so we only briefly review them here. Extensive

109 analytical and experimental work demonstrates a long-term impact of a fluctuating climate on

110 population growth rates (Ruel & Ayres 1999; Drake 2005; Melbourne & Hastings 2008; Thompson *et*

111 *al.* 2013; Vasseur *et al.* 2014; Lawson *et al.* 2015). Average growth rates over the long term may be

112 considerably different to population growth rates at average environmental conditions. Through

113 non-linear averaging, the net impact of a variable climate on an individual species' growth rate can

114 be either positive or negative (Figure 2). The principal determinant of the direction of the effect is

115 the curvature of the growth rate's response to the relevant climate variable. However, higher-order

116 properties such as temporal autocorrelation can also play a role (Petchey *et al.* 1997; Heino *et al.*

117 2000). Many populations near the edge of their range show greater population variability and

118 climate sensitivity (Myers-Smith *et al.* 2015; Mills *et al.* 2017) and so may be expected to be

119 particularly responsive to these effects.
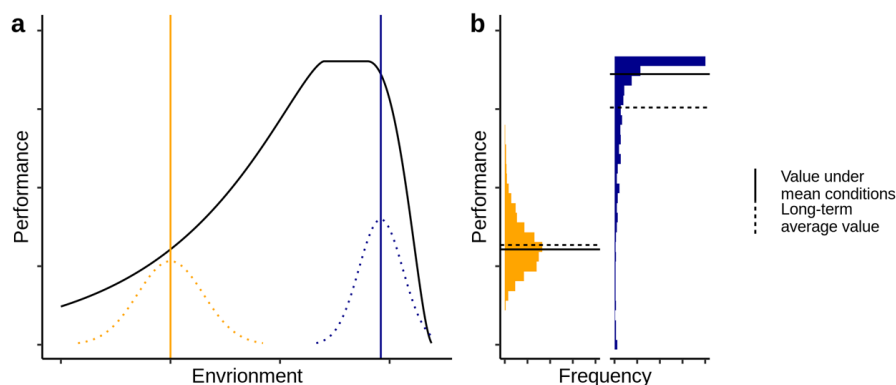
121 **Figure 2** How the curvature of environmental performance curves (EPCs) affects average performance. a) The

122 black line shows a classically shaped environmental performance curve where the key environmental variable

123   is temperature, while the dashed lines show relative frequency of environmental conditions at two sites

124   (yellow and blue). b) shows histograms of observed performances across 1000 random environmental draws

125   at each site. At the yellow site, environmental variability is fairly large, but the curvature of the performance

126   curve is relatively shallow. The long-term average value (dashed line) is therefore very similar to the value

127   under mean conditions (solid line). At the blue site, although the variability is smaller, the local EPC curvature

128   is much larger and downwards. The long-term value average value is considerably lower than the value under

129   mean conditions. It also includes several instances that could be labelled extreme events, where the

130   performance is very markedly below average.

131   Individual extreme events have most commonly been associated with population declines and

132   heightened extinction risk, in particular when harsh climatic conditions push populations down to a

133   level where they are vulnerable to extinction (Lande 1993; Boyce *et al.* 2006; Jongejans *et al.* 2010;

134   Nadeau *et al.* 2017; Maxwell *et al.* 2019). Extreme events have been associated with extinction risk

135   (Román-Palacios & Wiens 2020) and abrupt changes in community composition (Turner *et al.* 2020).

136   Range contractions and community shifts have also been seen in many communities, including

137   butterflies (de Palma *et al.* 2017), tropical fish (Lenanton *et al.* 2017), kelp (Smale & Wernberg 2013)

138   and bumblebees (Soroye *et al.* 2020). Extreme events have led to extirpations from newly colonised

139   areas, and it has been suggested that this may slow species responses to climate change (Nadeau *et*

140   *al.* 2017). For example, extreme cold events have been associated with range retractions of invasive

141   marine invertebrates (Canning-Clode *et al.* 2011) and fish (Rehage *et al.* 2016).

142   Taken together, both long- and short-term impacts of variability are more commonly viewed as

143   having negative consequences for populations of conservation interest. However, as we shall show,

144   when considering the wider community context in which species exist, this baseline assumption may

145   need to be adjusted.

146   # Impacts of variability on longer term coexistence

147 Where there is biotic control of species distributions, range limits become fundamentally a problem

148 of coexistence (Shea & Chesson 2002; Usinowicz & Levine 2018). This framing unlocks for climate

149 change research a long and rich history of work examining the influence of temporal environmental

150 variability on coexistence (Levins 1979). The potential for temporal variability to enhance

151 coexistence is well attested empirically (Adler *et al.* 2006; Tucker & Cadotte 2013; Tucker & Fukami

152 2014; Usinowicz *et al.* 2017; Hallett *et al.* 2019). Contrary to conclusions drawn in early and still

153 influential literature (e.g. Hutchinson 1961), environmental fluctuations themselves are not

154 sufficient to support coexistence of competing species (Chesson & Huntly 1997; Fox 2013) and can

155 hinder as much as facilitate coexistence. The framework of modern coexistence theory (MCT,

156 Chesson 2000) has been developed to robustly understand the impact of variability on coexistence.

157 However, this body of theoretical work examining the problem of species coexistence is only

158 recently being applied to climate change in the context of spatially heterogeneous environments

159 (Usinowicz & Levine, 2018).

160 At its core, MCT defines and investigates coexistence in terms of the capacity for populations to

161 grow from rare in the presence of competing species - the invasion criterion (Grainger *et al.* 2019b).

162 Where all species are able to meet this criterion, they can each resist exclusion by the other species.

163 In order to simplify the following discussion, we assume that only the ability of a particular focal

164 species to persist at a site alongside one or more competitor species is in question. Through MCT,

165 precise principles have been developed to identify how temporal variability influences coexistence

166 by quantifying the effects of temporal variability on the long-term average growth rate when the

167 focal species is at low densities ($\overline{r_{inv}}$, Chesson & Warner 1981; Chesson & Huntly 1997; Amarasekare

168 *et al.* 2004; Snyder 2008).

169 Since MCT is grounded in analytic results obtained for highly general models it can be applied to

170 most models of population dynamics. This requires conceptually separating direct impacts of the

171 environment on the focal population's growth rate from the impacts exerted by competitors. This

172 separation is delicate because competitors can affect the focal species directly, but also indirectly

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173   through shared resources - defined broadly to include physical resources such as nutrients, water or

174   space, as well as through apparent competition mediated by natural enemy populations (Chesson &

175   Kuang 2008). These routes of impact are the 'limiting factors' of MCT and can realise considerable

176   analytical insight but also interpretational challenges (for a recent comprehensive review, see

177   Barabás *et al.* 2018). However, as we shall show below, essential insights can be gained directly

178   from a model that can describe how the growth rate of the population r depends on the

179   environment (E) and the competitive impact (C), $r = f(E, C)$, abstracting over the underlying

180   mechanisms (Ellner *et al.* 2019). Where direct effects of environmental drivers and impacts of

181   competitors contribute linearly and additively to the population growth of the focal species, any

182   variability averages out in the long term. MCT can be used to describe how deviations from the

183   linear, additive base case lead to long-term effects of variability on population growth. These

184   deviations can be understood in terms of two classes of impacts – temporal 'storage effects' and

185   non-linearity of competitive effects.

186   Temporal storage effects arise when the combined effects of the environment and competition

187   allow benefits accrued in certain years to compensate for losses in other years (Chesson & Warner

188   1981). For this to affect long-term persistence two conditions must be met. Firstly, there must be an

189   interaction between the direct impacts of the environmental conditions and the impacts of the

190   competitor on the growth rate (mathematically this is non-additivity, where $\frac{\partial^2 r}{\partial E\, \partial C} \neq 0$). For

191   example, a species may suffer proportionally less from competitors in a year of harsh environment if

192   the population is buffered in some way such that the combined effect of a harsh environment and

193   competitive pressure is capped (Fig 3ai). Secondly, the environmental variability must affect the

194   competitive impacts on the focal species (i.e. *E* and *C* must co-vary, Figure 3aii). In the classic case

195   with buffered (subadditive) population growth, the more negative this covariance, the greater the

196   beneficial effect to the focal population. However, it is worth noting that temporal storage effects

197   can be reversed if the biotic and abiotic impacts on the focal species growth rate are superaddictive,

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198   i.e. the adverse effects of competition are proportionally greater in a harsh year (e.g. Holt & Chesson

199   2014). In the context of climate change, there is a risk that the current patterns of covariation in

200   species' responses to the environment could change. For example, if climate change results in more

201   frequent universally 'bad' (or equally, universally 'good') periods, instead of a back-and-forth of

202   alternate species being favoured, overall covariance in species responses could become more

203   positive and further undermine coexistence.

204   The second mechanism arises directly from fluctuations in the impact of other species on the growth

205   rate of the focal species. Non-linear averaging of varying biotic impacts on the focal species' growth

206   can affect $\overline{r_{inv}}$, analogous to the non-linear averaging of abiotic environmental fluctuations on

207   population growth rates described in the section above (Fig 2), and with matching consequences for

208   shifts in climatic variability patterns (Fig 3b). These fluctuations in the biotic pressure can be driven

209   by changes in the abundance of competitor species, or via varying per-capita intensity of the

210   competition exerted by other species through fluctuations in shared resources. When examining

211   coexistence, this is the mechanism of 'relative nonlinearity' that describes how species can

212   differentiate themselves through their capacity to take advantage of variable environments - 'slow-

213   and-steady' versus 'boom-or-bust' dynamics (Armstrong & Mcgehee 1980). Notably, in contrast to

214   temporal storage effects, this does not directly rely on correlations in species response to the

215   environment and can also derive from other fluctuation generating mechanisms.
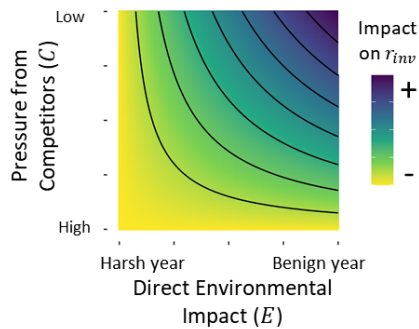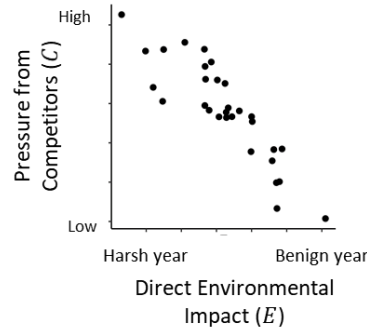
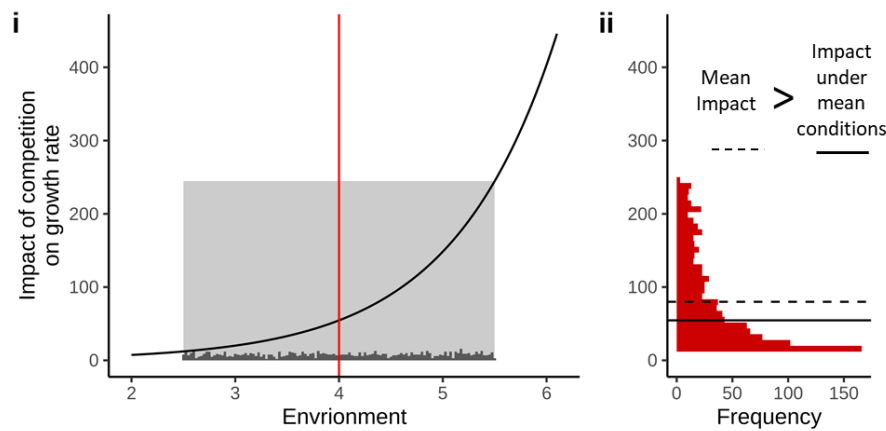**Figure 3** Illustration of the conditions required for the two multi-species mechanisms by which environmental variability can impact persistence. a) Temporal storage effects describe how species are able to divide niche opportunities afforded by a variable climate between them. For this to influence 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.

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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.

a)

$$\frac{F_{t+1}}{F_t} = \delta + \frac{\lambda \, \omega_{\lambda,t}}{1 + (\alpha \, \omega_{\alpha,t} \, C_t)} \quad (1)$$

b)
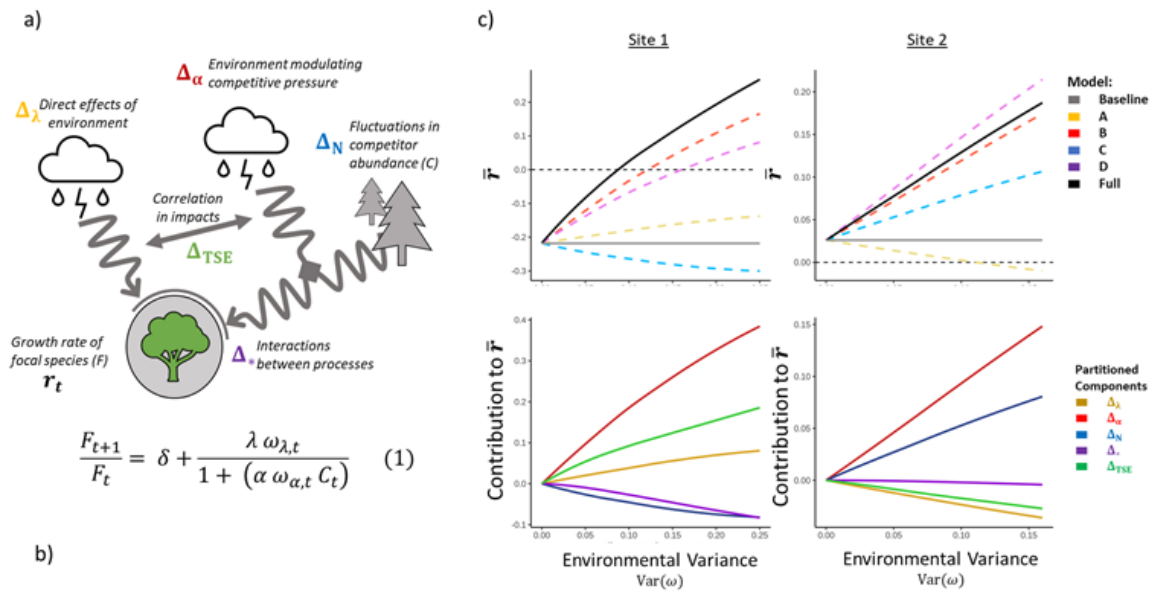
Model	Components:	Direct effects of environment	Environment effect on per-capita competition	Competitor abundance	Interactions between non-linearities	Correlation in impacts
Baseline	$\bar{r}_0$	Fixed	Fixed	Fixed	Absent	Absent
A	$\bar{r}_0 + \Delta_\lambda$	Variable	Fixed	Fixed	Absent	Absent
B	$\bar{r}_0 + \Delta_\alpha$	Fixed	Variable	Fixed	Absent	Absent
C	$\bar{r}_0 + \Delta_N$	Fixed	Fixed	Variable	Absent	Absent
D	$\bar{r}_0 + \Delta_\lambda + \Delta_N + \Delta_\alpha + \Delta_.$	Variable	Variable	Variable	Present	Set to zero
Full	$\bar{r}_0 + \Delta_\lambda + \Delta_N + \Delta_\alpha + \Delta_. + \Delta_{TSE}$	Variable	Variable	Variable	Present	Present

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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 ($\overline{r_{inv}}$). 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

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252   combination will allow different partitioning. Here we partition the difference between the growth rate under

253   fully fixed conditions ($\overline{r_0}$) and under the 'observed' variable conditions ($\overline{r_{inv}}$) with five Δ-partitions: $\overline{r_{inv}} =$

254    $\overline{r_0} + \Delta_\lambda + \Delta_N + \Delta_\alpha + \Delta_* + \Delta_{TSE}$, corresponding to the processes identified in a). Differences between the

255   model variants allow the identification of the relative influence of each partition. c) Examples of how the

256   partitioning approach can illustrate how variability can have multiple counteracting consequences for a

257   species' ability to persist. We use two example parameterisations of the same underlying model, Site 1 (left)

258   and Site 2 (right). At Site 1 without variability, $\overline{r_0}$ is negative, and the focal species would not be expected to

259   persist. The full model (black line) suggests that with a climate variability above 0.08 persistence is possible.

260   Inspection of the partitions (below) shows that the two largest positive impacts are non-linearities in the

261   impact of competition (Δ_α) and temporal storage effects (Δ_{TSE}). Opposing this, variability in the abundance of

262   competitors (Δ_N) is detrimental to the focal species. The impact of variability directly on the growth rate of the

263   focal species (Δ_λ) is here relatively small, and insufficient to lead to persistence in the range of variabilities

264   examined. The interaction term between the processes (Δ_*) is negative but small. Note that at low levels of

265   variability Δ_* is slow to increase, showing that the other partitions identify the main pathways of low variability

266   levels. By contrast, at Site 2, variability in the growth rate of the focal species has a negative impact (Δ_λ), and if

267   it was the only process considered might be expected to prevent persistence at the site. There is also a

268   negative temporal storage effect (Δ_{TSE}), deriving from a positive correlation between competitive impact and

269   intrinsic growth rate in the underlying model. However, these two effects are more than counteracted by

270   strong positive contributions from non-linearities in both competitive effect (Δ_α) and abundance of

271   competitors (Δ_N). In this case the role of interactions between non-linearities (Δ_*) remains small.

272   Earlier theoretical work placed greater emphasis on temporal storage effects, but in the small

273   number of empirical cases where the relative impact of the two effects on coexistence has been

274   directly compared, relative nonlinearity was found to have comparable, or greater, impact than the

275   more widely appreciated storage effects (Letten *et al.* 2018; Hallett *et al.* 2019; Zepeda & Martorell

276   2019). Although to date the number of examples is small, it is clear that climate-driven shifts in

277   variability patterns could play a role in determining coexistence between competitors and range

278   limits in the future. While we have focussed here on competitive systems, consumer-resource

279   systems can be analysed in parallel ways (Dee *et al.* 2020; Shoemaker *et al.* 2020a). However, effects

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280   identified in simple communities may not necessarily directly translate to more complex systems

281   (Barabás *et al.* 2018, Song *et al.* 2019). Species respond to different parts of the environment - with a

282   greater diversity of species, it is quite possible that species-level fluctuations in competition may

283   average out at the community level. For example, Clark *et al.* (2010) found that different tree species

284   responded to different aspects of the overall environmental fluctuations. This may suggest that

285   these mechanisms may be strongest where a limited pool of species are involved in constraining the

286   range of the focal species.

Community impacts of discrete events

288   A species' range expansion in response to climate change is effectively a series of invasions into new

289   communities (Wallingford *et al.* 2020). From this perspective, the significant body of work

290   investigating variability within invasion biology, going back to Elton (1958) and beyond, can offer

291   useful insights. The ability of a species to persist at a site is only one half of the picture – a species

292   must first arrive and establish itself. The spread of a species into new areas can be slowed or even

293   prevented by disadvantages that potential invaders face. For instance, positive density dependence

294   at low population densities (Allee effects, Courchamp *et al.* 1999; Kramer *et al.* 2018) can cause

295   leading range edges to appear 'pinned' in place (Keitt *et al.* 2001) and slow the rate of invasion into

296   newly suitable environments (Taylor & Hastings 2005).

297   Environmental variability can play a role in shifting a community from one state to another by

298   allowing species to overcome the challenges of Allee effects through intermittent boosts in

299   performance (Dennis 2002). Discrete extreme weather events can have marked influence on the

300   trajectory of species responses to climate change, but pose considerable challenges to investigation

301   and prediction (Bailey & van de Pol 2016). Although direct evidence is challenging to find (see later

302   sections), extreme climatic events have been associated with the arrival into marine communities of

303   species previously found in warmer areas (Wernberg *et al.* 2013). Dispersal is intrinsically episodic

304   (e.g. Kennedy *et al.* 2020) and short term spikes in the number of incoming colonist propagules may

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305   help increase establishment compared to constant dispersal rates by overcoming thresholds induced

306   by Allee effects (Drake & Lodge 2006; Carr *et al.* 2019).

307   At the community level, biotic resistance from the resident species can slow or prevent a colonist

308   tracking its climatic niche (Urban *et al.* 2012; Legault *et al.* 2020). Whether this resistance is

309   considered a hindrance or beneficial will depend on the conservation status and impact of the

310   colonist and resident species concerned. Over longer time scales, a history of disturbance can shape

311   a community's biotic resistance through selective assembly (Miller *et al.* 2021) or through specific

312   adaptations to the local conditions, which may include levels of variability (Urban & de Meester

313   2009), although temporal variability in climate could also preclude such local adaptation from

314   occurring (Bridle *et al.* 2010).
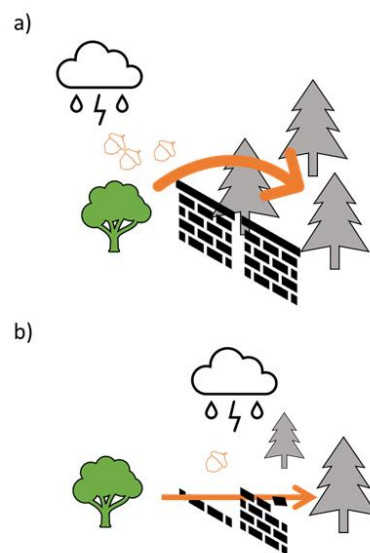
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316   **Figure 5** Illustration of two ways in which climatic variability can overcome barriers to range shifts. a) through

317   episodic high-dispersal events, and b), by disrupting existing communities and reducing biotic resistance.

318   Even without local adaptation, priority effects can give residents considerable advantages compared

319   to potential invaders. Where priority effects are strong, an invading species can colonise only if

320   either the density of the resident is brought down from equilibrium, or the invader is otherwise able

321   to reach sufficiently high densities to exert significant competitive pressure on the resident.

322   Individual disturbance events can temporarily break down blocking effects (Davis *et al.* 2000;

323   Melbourne *et al.* 2007; Diez *et al.* 2012), for example in grasslands (Pinto & Ortega, 2016) and over

324   the longer term there is an expectation that in disturbed environments there are more unused

325   available resources for invaders to take advantage of (Davis *et al.* 2000; Diez *et al.* 2012). Tucker and

326   Fukami (2014) showed experimentally that temperature variability can allow priority effects to be

327   overcome in a nectar-yeast system. Ecological theory can play a key role in identifying cases where

328   individual key events could precipitate the establishment of a climate refugee species. The core

329   results of MCT can be applied to invasions (Shea & Chesson, 2002; MacDougall et al., 2009) and are a

330   useful guide to identifying where priority effects are impactful (Ke & Letten 2018; Grainger et al.

331   2019a; Uricchio et al. 2019) particularly where the growth rate of a colonising species can also be

332   affected by variability (Clark & Johnston 2011).

## Interactions between influences of variability

334   There have been frequent calls to improve the representation of communities in ecosystem-change

335   models (Gilman *et al.* 2010; Angert *et al.* 2013; Urban *et al.* 2013). Synthesising the aggregate impact

336   of variability will require an expansion in the scope of models currently used (Felton & Smith

337   2017). When considering whole communities, the diversity of possible impacts on a focal species

338   due to variability is considerably larger than in the single-species case. The previous three sections

339   demonstrated the breadth of direct and indirect ecological impacts that variability can have on how

340   species will respond to climate change. Faced with such a diverse set of processes, reconciling the

341   assorted influences of variability and determining how they interact is central to determining their

342   influence in practice. There are fundamentally different scales and mechanisms at work, but bottom-

343   up mechanistic modelling can illustrate the key interactions at play. Identifying and (equally

344   importantly) ruling out for practical purposes, interactions between stressors is crucial to meaningful

345   conservation interventions (Côté *et al.* 2016).

346   To this end, a number of modelling studies have explored the interface between local variability-

347   mediated coexistence and extinction risk (Adler & Drake 2008; Gravel *et al.* 2011; Danino *et al.* 2018;

17

348   Pande *et al.* 2019; Schreiber *et al.* 2019; Dean & Shnerb 2020). Populations at low densities may be

349   expected to benefit the most from variability-mediated coexistence mechanisms, but a low

350   population size is also risky if a single bad year could extirpate the population. In these models, the

351   relative strengths of stochastic extinction risk and competitive stabilization change across a gradient

352   of environmental variability. In the largest empirical analysis of this balance to date, Fung *et al.*

353   (2020) used forest plot data to quantify how variability leads to temporal niche partitioning and

354   extinction risk and found that the balance was uneven but more frequently detrimental to

355   coexistence.

356   A useful way of framing complex climate change responses into a single unified measure of impact is

357   through establishment and extinction lags - differences between climate change and species range

358   responses (Alexander et al., 2018). The core issues can be demonstrated in relatively simple

359   simulation models constructed to capture multiple processes and forms of variability

360   simultaneously. In Figure 6 we demonstrate the potential for complex interactions between

361   mechanisms using a simple model of competition (detailed in SI 3) between a resident species and a

362   climate migrant. As already shown in Figure 4, the response expected from a change in variability

363   due to one mechanism could be countered or even reversed in conjunction with other processes.

364   Given the multitude of theoretically and empirically identified effects of climate variability on

365   colonisation success under climate change, there is a need to develop and investigate such models

366   to understand when interactions between these effects are likely to be influential.

367
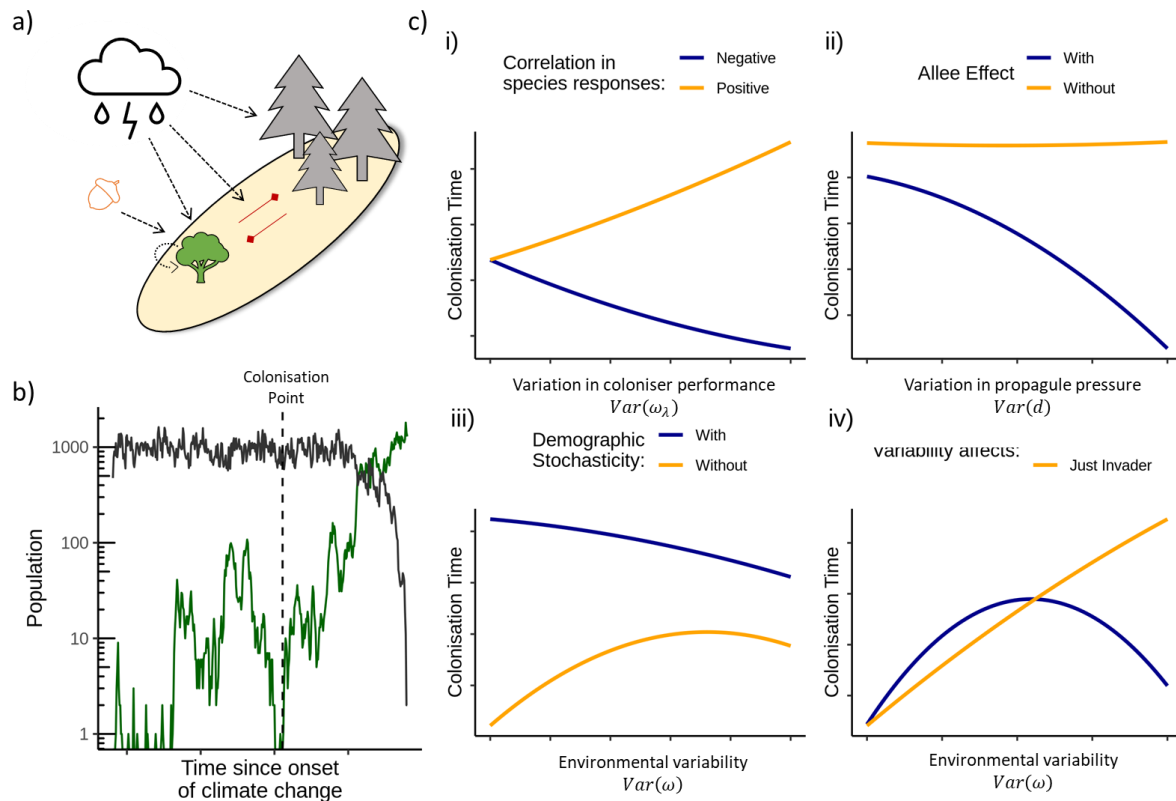
Figure 6 Demonstration of interactions between impacts of environmental fluctuations on climate-driven colonisation in a simple two-species competition model. a) The core model is an extension of that discussed in Figure 4 and is detailed in SI 3. Initially the site is dominated by a resident species 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.

19

385   Building on small and focused models, larger, highly generalised and spatially-explicit

386   metacommunity models (O'Sullivan *et al.* 2019; Thompson *et al.* 2020) can also provide insight into

387   potential drivers of community change that emerge from combining processes at multiple scales

388   (Usinowicz & Levine 2018; Chase *et al.* 2020). However, interpreting such models to assess the

389   impact of variability poses distinct challenges, beyond parameterisation. It is rarely possible to

390   directly control multiple aspects of variability simultaneously, even in an artificial model. Temporal

391   variability is inherently multi-facetted and additional qualities beyond direct variance can have

392   significant impacts, e.g. autocorrelation (Levine & Rees 2004). To take one illustrative example, the

393   historical level of variability a community (real or *in silico*) experienced during its assembly

394   contributes to the capacity of the community to respond to future changes, whether that is through

395   direct adaptation of the species in a community to local levels of variability or by the extant species

396   having passed through a previous extinction filter during historical extreme events (Janzen 1967;

397   Nadeau *et al.* 2017; Medeiros *et al.* 2020; Miller *et al.* 2021).

Identifying processes in the real world

399   The next frontier is directly assessing the magnitude of these effects in real systems. Understanding

400   which aspects of variability are most influential will be key to building models of minimal necessary

401   complexity. Determination of the relative contributions of dispersal, interspecific interactions and

402   environmental dependence has been identified as the key challenge to understanding the dynamics

403   of whole communities (Leibold *et al.* 2020). There is evidence that biotic resistance to invasive

404   species is widespread, but the global contribution of biotic resistance to climate refugee species is

405   challenging to measure (Levine & Rees 2004; Alexander *et al.* 2015, 2016; Louthan *et al.* 2015;

406   Godsoe *et al.* 2017, 2018; Beaury *et al.* 2020).

407   Direct observations demonstrate that species are on the move, but consistent patterns are difficult

408   to determine and influenced by concurrent land use changes (Lenoir *et al.* 2020). The observed rate

20

409   of movement of species is highly variable, with many species shifting their ranges considerably faster

410   or slower than the climate velocity and ultimately dependent on availability of habitat (Platts *et al.*

411   2019). Competitive exclusion at large spatial scales is often very slow (Yackulic 2017), while

412   extirpation by extreme events can be rapid, but not necessarily permanent. Any coupling between

413   species ranges and particular climatic events can be highly idiosyncratic, with multi-year effects of

414   weather events (Harley & Paine 2009). Coupled with the challenge of accurately identifying the pace

415   of range shifts (Bates *et al.* 2015), this makes directly discerning a signal of variability in movement

416   rates an imposing task.

417   Direct observations of variability in natural populations can highlight how species respond differently

418   to environmental variability (Palmer *et al*., 2017; Le Coeur *et al*. 2021). Evidence from global satellite

419   data shows that sensitivity to climate variability is itself variable across the globe (Seddon *et al.*

420   2016). However, to determine the impact in terms of long-term coexistence, model

421   parameterisation of some sort is required (e.g. Fung *et al.* 2020; Usinowicz *et al.* 2021). Species traits

422   hold some promise to identify likely temporal coexistence mechanisms (Adler *et al.* 2013). Life

423   history traits have been found to relate to sensitivity to climate anomalies in herbaceous perennials

424   (Compagoni *et al*. 2021) and amphibians (Cayuela *et al*. 2017), but much work remains to be done in

425   this area.

426   Mesocosm experiments with manipulation of variability can be illuminating – for example, Zander *et*

427   *al.* (2017) showed that lower trophic levels of a microbial food web were more strongly affected by

428   variability than top level consumers. However, such an approach is fundamentally limited since

429   variability can be manipulated in many alternative valid dimensions unless it is tied directly to

430   expected climate regimes (Thompson *et al.* 2013). Behavioural adaptation and the role of

431   microclimates pose further challenges to the interpretation of mesocosm work - the realised

432   variability of environmental variables relevant to species may differ from that measured by weather

433   stations (Bladon et al. 2020).

21

434   Alongside the highly generalised 'strategic' models demonstrated in the previous section, multiple

435   impacts of variability need to be tested for in focussed 'tactical' case studies of marginal populations

436   in order to build a picture of the real-world prevalence of these processes. Progress will require not

437   just more data, but a connected approach to synthesising the multiple impacts of variability, which

438   in turn requires a reliable model of community dynamics that can incorporate variable conditions. At

439   the core will be robust models of species performance and competitive impact under different

440   environmental conditions. This is no easy task – even in two-species systems with a single

441   environmental variable this requires fitting a multidimensional response surface. Given that species

442   respond to multiple environmental variables (Clark *et al.* 2010; Tingley *et al.* 2012) there are

443   fundamental limits to the resolution such models can aim to achieve. Detailed predictions for

444   individual communities will need to confront measures of environmental performance with

445   observations of current ranges to best estimate future trajectories (Armitage & Jones 2020;

446   Twiname *et al.* 2020). Observations of communities along climate gradients can provide particularly

447   valuable tests of models designed to investigate climate change (Alexander *et al.* 2016; Tylianakis &

448   Morris 2017).

449   With a sufficiently supported model in hand, partitioning of the various impacts of variability on

450   coexistence can be highly informative (Figure 4, Ellner *et al.* 2019; Shoemaker *et al.* 2020a). The

451   method can be extended to the large scales relevant to climate-change responses (Armitage & Jones

452   2020). Such a simulation-based partitioning approach could also be applied with other response

453   variables, for example colonisation or extirpation lags, or extended to include additional variability

454   terms. Understanding which aspects of variability are most influential can sharpen the focus of

455   investigations, reducing overall problem complexity and concentrate potential mitigation efforts on

456   the most critical fluctuations.

457   In support of this, a key line of future theoretical enquiry will be determining the minimum data

458   requirements to understand the impact of variability. It is not yet known how sensitive partitioning

459   of variability effects is to model misspecification. The higher-level properties of environmental

460   performance curves, such as their curvature, are considerably harder to estimate than first order

461   properties such as thermal optima. Empirical estimates for key parameters can be confounded, with

462   each other, with consequences for reliable estimation of species coexistence (Terry *et al.* 2021). The

463   implications of parameter uncertainty need to be explicitly acknowledged and better understood.

464   Since partitioning is algorithmic, it is possible to propagate uncertainties in the underlying model

465   through to uncertainty in the impact of variability on the response of interest.

Conclusion

466

Process	Key determinant of impact	Possible impact of considering variability in the response to climate change
Single Species		
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
Multi-Species		
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

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

468   Influential interspecific interactions are necessary for the multi-species process to be impactful. Particularly in

469   the multi-species processes, more research is needed to determine their prevalence and influence in real

470   systems.

471   In Table 1 we summarise the multitude of ecological routes by which underlying temporal variability

472   could influence how a species will fare under climate change. It is not currently clear whether the

473   difference in emphasis of the impact of variability in different ecological subfields represents a lack

474   of communication, publication bias, or if the relative neglect of the 'positive' aspects of variability

475   within global change biology is because they do not leave a widespread strong imprint on real-world

476   dynamics. It would be risky to assume that the impacts of variability are already 'baked-in' to current

477   observed species ranges, and so captured by existing distribution models. We reiterate that there

478   will also be evolutionary processes to consider - interactions between variability and adaptation with

479   positive and negative consequences for range shifts has been subject of extensive recent reviews

480   elsewhere (Vázquez et al. 2017; Nadeau & Urban 2019; Thompson & Fronhofer 2019; Coleman &

481   Wernberg 2020; Lyberger et al. 2021; Miller et al. 2020).

482   At this point in time, we simply do not know whether current assumptions of the impact of

483   variability based on single-population analyses are systematically over or underestimating risks at

484   the community level. What we do know is that climate change will present species with a bumpy and

485   obstacle-filled uphill ride, not a smooth escalator. No single simple theory can predict the effects of

486   climate variability – but, as we have shown, this does not prevent useful insights cannot being

487   synthesised. As with most areas of ecology, both complex and simple verbal and mathematical

488   models have their parts to play. By understanding the linkages between these models, detailed

489   insights can be gained without losing sight of the whole. More examples of quantification of the

490   impact of variability in real communities are needed - it is our belief that the simple modelling

491   frameworks discussed here can meet this need. Building strong bridges between climate change

492   ecology and coexistence theory has never been more possible, or more necessary.

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