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Life history trade-offs, the intensity of competition, and coexistence in novel and evolving communities under climate change.

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3 Life history trade-offs, the intensity of competition, and coexistence in novel and
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5 evolving communities under climate change.
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26 Keywords: range shifts, no-analogue communities, global warming, trophic
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28 interactions and competition, community assembly, ecological niche.
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Summary

The consequences of climate change for local biodiversity are little understood in process or mechanism, but these changes are likely to reflect both changing regional species pools and changing competitive interactions. Previous empirical work largely supports the idea that competition will intensify under climate change, promoting competitive exclusions and local extinction, while theory and conceptual work indicate that relaxed competition may in fact buffer communities from biodiversity losses that are typically witnessed at broader spatial scales. In this review, we apply life history theory to understand the conditions under which these alternative scenarios may play out in the context of a range-shifting biota undergoing rapid evolutionary and environmental change, and at both leading-edge and trailing-edge communities. We conclude that in general, warming temperatures are likely to reduce life history variation among competitors, intensifying competition in both established and novel communities. However, longer growing seasons, severe environmental stress, and increased climatic variability associated with climate change may buffer these communities against biodiversity loss. The role of life history plasticity and evolution has been previously underappreciated in community ecology, but may hold the key to understanding changing species interactions and local biodiversity under changing climates.

Introduction

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3 Anthropogenic climate change is a primary risk to global biodiversity [1–
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5 3]. While most projections for future changes in biodiversity indicate that global
6
7 warming will contribute significantly to biodiversity loss over the next decades
8
9 (e.g., [2,4]), such projections often have wide error margins [5], particularly
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11 because we still have little insight into the roles of biotic interactions and
12
13 evolutionary change. Multiple studies demonstrate that many species possess
14
15 some capacity to persist under climate change, through a combination of
16
17 phenotypic plasticity and evolutionary adaptation [6]. However it is still largely
18
19 unknown how rates and modes of phenotypic change and adaptation will vary
20
21 between interacting species, and how these evolutionary responses will affect
22
23 biotic interactions, communities, and ecosystems. Much work in this area has
24
25 focused on the potential for mismatches between species across trophic levels
26
27 [7,8]. Potentially equally or more important to future community diversity are
28
29 effects of warming on changes in the outcomes of competitive interactions, but
30
31 these have received much less attention to date. Like trophic interactions,
32
33 competitive interactions may intensify or diminish under climate change [9,10],
34
35 with important consequences for local biodiversity and ecosystem services.
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41 Here I propose a novel framework to predict effects of climate change on
42
43 competition intensities, based on general life history theory. The framework
44
45 rests on the observation that the strength of competition among species with
46
47 similar ecological niches (such as within a guild) is often mediated by their
48
49 degree of similarity in their evolved life histories, including strategies for
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51 survival, reproduction, and dispersal [11,12]. Life history traits are
52
53 fundamentally limited in nature by evolutionary and ecological trade-offs [13],
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55 and differences among species in how these trade-offs are resolved
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3 evolutionarily can allow fine partitioning of shared niches [14] and promote
4
5 coexistence of competitors [15]. Moreover, the particular way that an individual
6
7 or species resolves this trade-off (i.e., which dimensions are favoured over
8
9 others) often reflects the species' historical legacy of biotic interactions and its
10
11 colonization history [16,17]. By identifying patterns of coevolved life history
12
13 trade-off strategies within communities that facilitate or limit coexistence of
14
15 competing species, now and under future conditions [11,18,19], we can derive
16
17 more general principles of coexistence under rapid environmental change and in
18
19 evolving species assemblages (Fig. 1).
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25 26 *Climate change and competitive interactions* 27 28 29

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31 Competition is a well-known driver of local (alpha) biodiversity [20], and
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33 thus effects of climate change on competitive interactions are likely to be critical
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35 mediators of biodiversity responses. While numerous studies have provided
36
37 evidence of changing competitive interactions in response to climate change
38
39 [10,21,22], it is more difficult to identify how climatic warming affects the overall
40
41 importance of competition for shaping communities [23]. In general, changes in
42
43 the intensity of interspecific competition under climate change are likely to be
44
45 driven by several distinct, but sometimes synergistic, processes: first, changes in
46
47 the extent and diversity of favourable habitats may alter patterns of competition
48
49 for remaining space and resources [10,24–27]. Second, climate change may
50
51 directly affect the competitive abilities of interacting species, via plastic or
52
53 evolved effects on growth rates, body sizes, and phenologies, and these changes
54
55 can alter patterns of competitive dominance within or competitive exclusion
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3 from communities [21]. Third, competitive interactions may be influenced by the
4
5 direct effects of climate on numerical abundances of each species [28]. Finally,
6
7 range shifts mediated by climate change can directly impact the strength of
8
9 competition within communities by changing the biodiversity of the regional
10
11 species pool, altering the total potential number and identity of species
12
13 interacting at each site [29,30]. Here I review the evidence for how these factors
14
15 may interactively contribute to changing competitive interactions and
16
17 biodiversity in different environments, and suggest how life history theory can
18
19 help inform predictions for future loss of community diversity and ecosystem
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21 services.
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28 *Life history trade-offs and coexistence*

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32 All species face the problem of being limited in their ability to
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34 simultaneously maximize all components of fitness [31]. Such trade-offs are
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36 often mediated by extrinsic limits to the time or energy, so that, for example,
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38 energy allocated to reproduction detracts from energy available for survival and
39
40 maintenance. Individuals solve this dilemma by investing in some traits (such as
41
42 growth rate, body size, stress response, timing of reproduction, offspring
43
44 quantity and quality, longevity, and dispersal), which are related to primary
45
46 energy allocation and which are closely linked to fitness, at the expense of other
47
48 such traits. The nature of trade-off functions among these traits can be quite
49
50 complex, involving multidimensional allocation decisions or higher order
51
52 properties of trait values [32]. Despite these complexities, a simplistic “Y” model
53
54 is often a useful heuristic to depict the essence of individual allocation decisions,
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3 with the caveat that many trade-offs do not conform to this simple structure [13]
4
5 (Fig. 1A). Life history trade-offs are often strong determinants of competitive
6
7 abilities under both stable and changing ecological conditions [21,33,34], and
8
9 thus climate change-induced shifts in life history traits may be partially
10
11 responsible for changing competitive interactions under climate change (see
12
13 below).

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16 Traditional community assembly theory suggests that species that occupy
17
18 similar niche space will compete most intensely and will exclude each other from
19
20 communities unless each can increase when rare [35,36]. Central to this theory
21
22 is the tenet that the structuring of resource availability, and the strategies used
23
24 to garner resources, are critical predictors of interspecific competition and
25
26 coexistence within communities [15,37]. Also implicit in coexistence theory is
27
28 the role of demographic trade-offs; i.e., coexistence occurs within communities
29
30 because no species can simultaneously optimize all strategies for monopolizing
31
32 the shared resource(s) [15]. This theory bears striking resemblance to life
33
34 history theory in evolutionary biology, however these parallels have rarely been
35
36 acknowledged (but see [11,15]), in part because classic community ecology often
37
38 ignores the evolutionary processes occurring within communities (but see [38]).

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41 Recent theory suggests that coexistence of competitors can occur on the
42
43 basis of evolved differences in life history strategies [11]. Interspecific life
44
45 history divergence can support coexistence for a variety of reasons. First, an oft-
46
47 reported trade-off between competitive ability and longevity will favour the
48
49 coexistence of species able to achieve quick numerical abundance, and species
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51 with slower growth but better persistence through time [15,39]. This mechanism
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53 is particularly salient when the environment fluctuates over time [19], but
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3 intransitive dynamics mediated by interspecific differences in density-
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5 dependent regulation can also maintain the coexistence of competitors with
6
7 divergent life history strategies along the slow-fast continuum within
8
9 communities, even in the absence of environmental fluctuations [40]. Note that
10
11 this coexistence mechanism does not depend on competitors diverging in their
12
13 resource requirements or resource acquisition abilities. Second, trade-offs
14
15 between survival and growth rate (and contributing, for example, to variation in
16
17 age and size at maturity, longevity, and lifetime reproductive success) may be
18
19 resolved differently among competing species, leading to phenological
20
21 divergence of feeding and breeding times between competitors. This occurs
22
23 because individuals of each species experience some measure of stabilizing
24
25 selection to converge on particular strategies that ensure synchronization or
26
27 overlap between mates or other cooperative strategies. When members of each
28
29 species group together in life history trait space to ensure beneficial intraspecific
30
31 interactions, temporal niches are made available for other species to fill. Once
32
33 filled, each species' temporal niche may also be maintained by selection to avoid
34
35 competition (character displacement). This mechanism is particularly relevant
36
37 when there are external limits or guides on the life cycle imposed by seasonality,
38
39 such that fast strategies automatically correlate to earlier emergence/peak
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41 feeding times, whereas slower strategies may monopolise later opportunities
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43 [17]. Under this mechanism, divergent life histories within communities
44
45 facilitates temporal partitioning of a shared resource niche among competing
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47 species [14,41,42].
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55 Empirical evidence from damselflies, plants, parasitoids, fig wasps, fish,
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57 and *Drosophila* all indicate that life history divergence is often a critical
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3 coexistence mechanism within guilds, where species overlap very closely in
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5 specific resource requirement and acquisition traits [14,15,18,19,39,40,43]. Life
6
7 history traits are also well-characterised mediators of competition and
8
9 coexistence even amongst more diffuse competitors [37,44]. Despite this, little
10
11 consideration has been given to the evolution of life history strategies (in other
12
13 words, towards optimal allocation of resources across different, competing
14
15 components of fitness) in the context of interspecific competitive interactions
16
17 (but see [11]).
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21 Life history traits are typically highly sensitive to climatic temperature
22
23 changes, exhibiting typically high levels of thermal plasticity (for example,
24
25 thermal dependence of growth rates in ectotherms and plants, and thermal
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27 reaction norms for survival and immune response across many species [45,46]).
28
29 Furthermore, most of the best-documented examples of evolutionary responses
30
31 to climate change also primarily involve shifts in life history traits, rather than
32
33 shifts in environmental tolerances or resource requirements [47]. Thus an
34
35 important but largely unasked question is how ongoing climate change will affect
36
37 competitive intensities and local biodiversity via its rapid effects on life histories
38
39 of constituent species. If climate change drives convergence of life histories
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41 among competitors, competition for shared resources may intensify and
42
43 competitive exclusion and local extirpations are likely to ensue (Fig. 1C).
44
45 However, if climate change leads to life history divergence among competing
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47 species within communities, this may buffer communities from biodiversity loss
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49 but potentially leave them vulnerable to invasion (Fig. 1D). These alternative
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51 scenarios are discussed below.
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Climate warming and life history convergence within communities

There are good reasons to expect that climate change will lead many species to adopt a 'faster' life history strategy, whether through evolutionary change or phenotypic plasticity [48]. This occurs for a number of reasons: first, climate change is in many cases resulting in the earlier or shortened growing seasons in many biotas, selecting for both plastic and evolved responses towards earlier and faster growth, maturation, and reproduction [7,8]. Evolutionary change under selection for faster life histories may occur under climate change to adaptively allow species to capitalize on earlier opportunities for reproduction, or to track changes in timing of resource abundances [49]. Depending on the degree of reliability of thermal cues to predict peak breeding or feeding opportunities, selection for faster life histories under warming climates may act on the trait values, or on the thermal dependence of the underlying traits (reaction norm evolution [50]), in either case producing evolutionary change. Second, many life history traits are inherently thermally-dependent, and thus increasing temperatures will automatically result in acceleration of these processes purely via plasticity, which may or may not be adaptive [51] and may or may not affect future evolutionary change [52]. For example, the growth rate of ectotherms relates directly to temperature, e.g., via Dyer's Law [53], so higher temperatures automatically equate to faster growth rates and changes, typically but not always resulting in shifts to smaller adult body sizes [45]. This shift towards faster life histories, whether through plasticity or evolutionary change, often invokes life history trade-offs with survival or dispersal abilities [54]. A recent meta-analysis suggests that plants,

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3 fish, birds, mammals, and terrestrial ectotherms have all tended to shift towards
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5 faster life histories and smaller body sizes under climate change [55].
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8 The pressures of climate change to 'speed up' the life histories of most
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10 species may result in convergence of life history strategies among species within
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12 communities, increasing the opportunity for competition. This can occur for
13
14 several, often simultaneous, reasons. First, coexistence is commonly maintained
15
16 in part by selection to promote life history divergence among competing species
17
18 (as reviewed above). Thus, advancing or accelerating life histories caused by
19
20 climate change could result in more convergent strategies on average,
21
22 particularly if life history shifts are purely plastic, and if the plasticity the trait is
23
24 negatively correlated with its mean value (as is often reported for life history
25
26 and thermally-sensitive traits [56,57]). In this scenario, all species are shifted to
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28 faster life history strategies, but species exhibiting slower values for a particular
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30 trait experience greatest rates of plastic change, resulting in life history
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32 convergence and increased opportunities for competition. If shifts towards faster
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34 life histories are evolutionary, however, then adaptive patterns of life history
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36 divergence may be preserved among interacting species under ongoing selection
37
38 for reduced interspecific competition, providing that selection for faster life
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40 histories under climate change is very weak in comparison to ongoing selection
41
42 to preserve life history divergence from interspecific competitors. Second, life
43
44 history convergence within communities is likely to be even more pronounced if
45
46 competitors share similar hard physiological or genetic constraints on the extent
47
48 to which they can undergo climate change-driven changes in trait values [58].
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50 Several previous studies have indicated that individuals or populations with
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52 more extreme life history trait values are less likely to exhibit significant genetic
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3 variation for or ability to plastically increase these traits [59,60]. Thus, warming-
4
5 induced increases in life histories of interacting species will potentially promote
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7 convergence on the most extreme strategy observed in the community under
8
9 current conditions. Finally, given that shifts towards faster life histories are often
10
11 adaptive for tracking advancing conditions under climate change, species best
12
13 able to rapidly respond to this novel source of selection on life history may thus
14
15 gain an increased evolutionary advantage over more obligately slow-developing
16
17 species, as climates continue to change. This process could result in life history
18
19 convergence within communities via species-level selection imposed by
20
21 changing abiotic conditions. In other words, only species able to alter their life
22
23 histories to match changing conditions will persist within communities. The loss
24
25 of competitors with more divergent life histories frees up resources to allow
26
27 numerical increases in the remaining species. These remaining species now
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29 compete more intensely because they are now dominating the resource and they
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31 overlap in their life history strategies [61,62].
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37 If convergence of life histories occurs via any of the above mechanisms,
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39 interspecific competition will be more intense within these replacement
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41 communities, where the strength of competition is not alleviated by among-
42
43 species life history diversification (Fig. 1C). It is worth noting that both plastic
44
45 and evolutionary changes in life history allocations under climate change can
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47 produce changes in the variances as well as mean life history strategies within
48
49 each population, and changes in intrapopulation variances may temper
50
51 outcomes for predicted competitive intensities based on trait means. For
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53 instance, increased life history variability within species (such as via stress-
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55 induced expression of cryptic genetic variation for life history traits) could
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3 temper increases in interspecific competition. In contrast, reduced life history
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5 variability within populations (such as under strong selection for extreme
6
7 values) could compound effects of convergence to produce even greater
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9 intensities of interspecific competition [63].
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14 *Life history convergence and increased competition in the context of changing*
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16 *regional species pools*
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21 Within the Anthropocene, we are witnessing a mass reorganization of
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23 global, regional, and local biotas [64]. Range expansions of many terrestrial and
24
25 marine taxa are currently underway as climates warm to surpass minimally-
26
27 suitable temperatures just beyond their historical poleward or peak-ward range
28
29 margins [65], however the relationship between these range movements and
30
31 local (alpha) biodiversity is poorly understood. Increased competitive
32
33 interactions under climate change may at least temporarily strengthen
34
35 communities against colonization from lower latitudes [64] because it is more
36
37 difficult for species to establish in novel habitats where existing competitors are
38
39 already monopolizing the niche [66]. This protective feature of native
40
41 competition could benefit native species by preventing interaction with novel
42
43 competitors, but may have detrimental effects on range shifting species by
44
45 preventing their poleward movement [67]. However, it has been well
46
47 documented that range expansions select for faster life history strategies
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49 [16,68,69], and the same traits associated with a successful range expansion are
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51 also favoured under competition during periods of rapid environmental change
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53 [21,34,70,71]. Thus competition between native species and novel competitors
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3 that have already gathered momentum in their poleward shifts will likely be
4
5 fierce, because all are experiencing faster (converged) life histories (Fig. 1C). In
6
7 other words, due to the special, evolved properties of range shifting species
8
9 combined with detrimental effects of warming on native species, priority effects
10
11 may be insufficient to protect native species from novel competitive interactions
12
13 created by widespread range expansions.
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17 While intensified competition does not always lead to competitive
18
19 exclusion [72], most empirical evidence suggests that incoming species will
20
21 dominate in novel competitive interactions driven by climate change-induced
22
23 range shifts [34,70], and competition between native and range shifting species
24
25 will contribute to native species population declines [26]. Thus life history
26
27 convergence and novel competitive interactions may play a significant role in the
28
29 erosion of native biodiversity at high latitudes and contribute to biotic
30
31 homogenization of the global flora and fauna [3]. Changes in the competitive
32
33 outcomes between native and range-shifting species may also take time to
34
35 resolve—a range-expanding species of damselfly in Scotland (*Ischnura elegans*)
36
37 does not produce noticeable impacts on native community composition until it
38
39 has naturalized for several generations in the new part of its range [73]. Thus life
40
41 history convergence among historic and novel competitors, resulting in
42
43 intensified competitive interactions in the wake of climate change-mediated
44
45 range expansions, could represent a major contribution to lingering extinction
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47 debt at high latitudes [30].
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55 *Climatic change and life history divergence within communities*
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3 Previous work has largely focused on the role of intensified competition
4 under climate change [24–26,67], and relatively less effort has been expended to
5 investigate the possibility that climate change reduces the intensity of
6 competitive interactions (but see [29,74,75]). Competitive intensity may be
7 reduced within communities if changing climates produce diverse effects on the
8 life history of constituent species, resulting in life history divergence among
9 close competitors (Fig. 1D). Divergence in life histories within communities may
10 occur as a by-product of longer growing seasons (particularly at high latitudes),
11 or increased climate variability, both of which are important features of ongoing
12 climate change [76,77]. For instance, at high latitudes where growing seasons
13 are relatively short (with historically limited opportunities for temporal niche
14 partitioning), climate change-mediated increases in growing season length may
15 provide greater opportunity for a variety of growth rate and body size strategies
16 to exist and coexist [78]. Similarly, increased climatic variability associated with
17 global warming may support more diverse life history strategies, particularly
18 because more variable climates allow persistence of species with life histories
19 characterized by flexibility and opportunism, which can then coexist with species
20 that exhibit intrinsically high growth rates [39]. Note that either intra- or inter-
21 specific life history variability can alleviate interspecific competition and support
22 coexistence in principle [63], although there is little empirical evidence for the
23 former as a coexistence mechanism.

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26 Life history divergence might also be related to the numerical abundance
27 of each species at starting conditions—species at relatively low abundance with
28 lower levels of intraspecific competition may have a greater opportunity to
29 respond to climate warming by increasing growth rates or decreasing adult body
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3 sizes (via rapid evolutionary change during periods of demographic growth, or
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5 because soft-selection against plastic life history shifts is weaker), while more
6
7 abundant species may be limited in this response due to higher levels of
8
9 intraspecific competition and higher levels of soft-selection against life history
10
11 shifts [79]. Effects of different relative abundances on populations' potential
12
13 responses to climate change may reinforce pre-existing interspecific variation in
14
15 life history strategies.
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19 Finally, climate change may promote life history divergence within
20
21 communities by magnifying interspecific differences along pre-existing thermal
22
23 reaction norms for underlying life history traits. Nearly all species have very
24
25 slow growth rates or low survival at very low temperatures, but thermal optima
26
27 may be more variable among competing species [80]. Given that many temperate
28
29 species inhabit environmental temperatures which are cooler than their thermal
30
31 optima [81], warming temperatures may move each species closer to its own,
32
33 evolved thermal optimum. Differences among competing species in the degree of
34
35 phenotypic plasticity or evolutionary potential to respond to climate may
36
37 reinforce life history variation as climates warm [74]; such divergence can
38
39 support continued coexistence within communities facing environmental
40
41 change, provided that there remain opportunities for multiple life history
42
43 strategies to obtain high fitness under the new conditions (in other words,
44
45 opportunities provided by longer growing seasons or increased climatic
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47 fluctuations).
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55 *Life history divergence and decreased competition in the context of changing*
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57 *regional species pools*
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5 Because, globally, range expansions in response to climate change are
6
7 more prevalent than contractions, the large-scale movement of species currently
8
9 underway is generally resulting in an increase in regional biodiversity,
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11 particularly at high latitudes, even while global biodiversity declines [1,2,82,83].
12
13 Life history divergence under climate change may allow high latitude
14
15 communities to be more open to accepting these regional colonisers, if the
16
17 process of life history divergence leaves gaps in life history trait space that can
18
19 be filled by previously excluded species (Fig. 1D). If this occurs, then the regional
20
21 increase in biodiversity currently witnessed at high latitudes will be supported
22
23 at the community level as well as climates continue to warm, and we can expect
24
25 to see net benefits to high latitude biodiversity over time at multiple scales
26
27 [2,83]. This process may critically depend on range-expanding species
28
29 possessing life history traits that fill the developing gaps within communities as
30
31 climates change. If incoming species overlap strongly with native species in life
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33 history traits and outcompete them for shared resources [26], then species
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35 replacement and biotic homogenization may occur instead of enhanced
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37 biodiversity (Fig. 1C,D).
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44 Life history divergence and associated relaxation of competition
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46 intensities may also occur under increasing drought or heat stress at lower
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48 latitudes and at the trailing edge of many species' ranges. However, the role of
49
50 life history divergence to buffer these exceptionally stressed communities from
51
52 biodiversity loss remains to be formally tested. A recent meta-analysis of plant
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54 communities along stress gradients indicated a role for life history in this
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56 process: the switch from competition to facilitation was more often observed
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3 under stressful conditions for adult life stages than juveniles within perennial
4 plant communities, and more often in perennial than annual communities [75].
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7 However, the role of life history *shifts* within these communities was not
8 investigated for its effects on changing competitive interactions. Recent
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10 conceptual work suggests that high stress does not in fact alleviate competitive
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12 intensities when competing species overlap strongly in their life history
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14 strategies [12], and future studies should therefore focus on the role of
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16 evolutionarily diverging life histories as drivers of relaxed competition in
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18 stressed communities.
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25 26 *Taking the framework forward: a case study*

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30 While identifying the community-level consequences of evolved life
31 history responses to climate change will require detailed, long-term,
32 demographic and quantitative genetic studies in wild communities or mesocosm
33 experiments, the effects of thermal plasticity in life history strategies on
34 competition intensities in novel or threatened communities may be evaluated
35 more readily, using laboratory temperature manipulations. We conducted a
36 preliminary investigation of these effects using three damselfly species that
37 commonly interact and compete within local guilds of ecologically similar
38 species across NE Scotland. One of our study species (*Ischnura elegans*, Odonata:
39 Coenagrionidae) is a recent immigrant to the region, and warming climates have
40 facilitated its colonisation of northern Britain [84]. The other two species are
41 historic residents of the area [85] (*Enallagma cyathigerum*, Odonata:
42 Coenagrionidae, and *Lestes sponsa*, Odonata: Lestidae).
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3 We reared larvae of these species under present and projected
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5 freshwater temperatures, and identified changes in the phenotypic responses to
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7 the trade-off between survival and growth rate, and cascading effects of these
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9 changes on competitive interactions. Rearing at current freshwater
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11 temperatures for the Scottish Highlands (15° C, [86]) revealed divergent life
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13 histories among both resident and colonizing, coexisting competitors along the
14
15 growth rate vs. survival trade off axis (effect of species on growth rates at 15° C
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17 = -0.07 ± 0.002 , $t = 2.79$, $P = 0.008$, Fig. 2A; effect of species on survival at 15° C =
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19 2.52 ± 0.83 , $z = 3.02$, $P = 0.003$, Fig. 2B). Rearing under temperatures projected for
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21 2080 under a warming scenario (20° C, [86]), however, resulted in reduced
22
23 interspecific variability in both growth rates (effect of species on growth rate at
24
25 20° C = -0.03 ± 0.03 , $t = 1.17$, $P = 0.25$, Fig. 2A) and survival (effect of species on
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27 survival at 20° C = 1.15 ± 0.72 , $z = 1.62$, $P = 0.11$, Fig. 2B), suggestive of life history
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29 convergence between colonizing and resident species as climates continue to
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31 warm.
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37 Faster growth at higher temperatures led to larger body sizes for all
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39 species (effect of growth rate on emergence size = 16.76 ± 5.49 , $t = 3.05$, $P =$
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41 0.003), and this affected larval competitive outcomes. At smaller sizes, resident
42
43 and colonizing species are competitively equivalent. However, the larger size
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45 classes produced by warmer temperatures resulted in competitive asymmetry
46
47 between resident (*Enallagma cyathigerum*) and colonizing species (*I. elegans*)
48
49 (effect of species x body size on aggressive behaviours = 0.86 ± 0.31 , $z = 2.80$, $P =$
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51 0.005 ; Fig. 2C), which was resolved in favour of the colonising species.
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55 Together, these results suggestively illustrate one potential mechanism
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57 by which climate change may influence interspecific competition via thermal
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3 plasticity in life history strategies, such that life history divergence between
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5 colonizing and native species initially supports coexistence, but further climatic
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7 warming may promote life history convergence via shared physiological limits
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9 among all interacting species, or via inherently low thermal plasticity of non-
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11 range expanding, high latitude populations. Converged life histories increased
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13 opportunity for competition, and also increased the asymmetry in competitive
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15 outcomes among these species, with the range-shifting species exhibiting the
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17 greatest increases in growth rate, adult body size and competitive advantage
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19 under a warming scenario (Fig. 2). Greater thermal plasticity observed in *I.*
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21 *elegans* in comparison to its local competitors is likely to contribute to its
22
23 advantage under future warming conditions. Such plasticity may have adaptively
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25 evolved during the course of this species' range expansion [70,69,87], however,
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27 more detailed investigations and comparative work are needed to draw firmer
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29 conclusions.
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35 This preliminary study suggests one way that warming climates may
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37 directly affect life history trade-offs and competitive abilities. Future efforts to
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39 identify links between climate change, life history, and competition in a
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41 laboratory context should incorporate more species, a broader range of
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43 experimental temperatures, and larger sample sizes to investigate the generality
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45 and robustness of these preliminary effects. Furthermore, all such temperature
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47 manipulation experiments should be integrated with detailed ecological data or
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49 mesocosm studies to identify reciprocal demographic effects of each species'
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51 changing life history strategy under environmental change. This approach can
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53 generate short term predictions for the effects of life history plasticity on
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55 community interactions as climate change, and combined with further breeding
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3 studies, may also reveal the genetic potential for rapid evolutionary change in
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5 the distribution of life histories within communities.
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10 *Knowledge gaps and future directions*
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14 This paper provides a conceptual framework for identifying and
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16 predicting changing strengths of competition and patterns of coexistence within
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18 communities under ongoing climate change. The framework is based on the role
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20 of life history trade-offs to enforce resource allocation decisions, and the
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22 predictable consequences of divergence or convergence of these allocation
23
24 decisions within communities. The framework is relevant both within existing
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26 communities and in the context of ‘no-analogue communities’ created by shifting
27
28 regional biodiversity pools [64]. The strength of this framework lies in its solid
29
30 reliance on a well-developed set of principles for time and energy allocation
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32 [31,88], and the clear, predictable relationship between the directions of evolved
33
34 or plastic life history shifts and the resulting intensities of competition within
35
36 communities. However, before this framework can be effectively implemented in
37
38 a predictive context to understand the links between climate change and local
39
40 biodiversity, a number of critical issues must be addressed.
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46 Primarily, more work is needed to understand how changing intensities
47
48 of competition derive from contributions of climate change to life history
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50 syndrome evolution and development, vs. contributions of climate change to
51
52 changes in other, non-life history traits such as environmental tolerances,
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54 nutritional requirements, or feeding preferences. In general, little work has been
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56 done to understand how different coexistence mechanisms interact—for
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3 example, how do predators affect the limiting similarity in resource use (e.g.,
4 [89]), and how do these affect limiting similarities of life history? To what extent
5 is coexistence mediated by trait divergence along any of these axes [72,90]?
6
7 Within close-knit guilds of plants, insects, and parasites, life history variation has
8 proved to be a critical coexistence mechanism (as reviewed above), and evolved
9 variation in life history strategies is likely to be an important driver of local
10 diversity in other communities as well. Life history traits are often highly
11 responsive to changing climates [7,49,55,65,68], and have predictable properties
12 of trade-offs and underlying constraints that facilitate predicting links between
13 environmental variation, life history shifts, and community change—this is the
14 potential promise of the proposed framework.
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28 Second, better evidence is needed to describe interspecific variation in
29 effects of climate change on life history traits. Most previous studies support the
30 hypothesis that warming will influence or select for ‘faster’ life histories in most
31 species, and thus promote convergence and intensified competition, but this
32 conclusion may reflect research and reporting biases [74]. Understanding the
33 conditions and support for this pattern will help refine further predictions for
34 changing community interactions. More work is also needed to discover how
35 often physiological limits (i.e., the total extent to which climate change can shift
36 life history traits towards extremes) are similar for closely interacting species.
37
38 Finally, and potentially most critically, more work is needed to track plastic and
39 evolving life histories in wild populations [7], how these changes respond to
40 different features of environmental change (for example, climatic warming vs.
41 increased climate variability), and how these life history shifts affect local
42 interaction strengths and community diversity.
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3 So far the observed changes in community diversity under changing
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5 climates remain poorly understood in terms of both process and mechanism
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7 [1,3]. It is hoped that applying life history theory to understand changing and
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9 evolving competitive interactions can pave the way to a more general
10
11 understanding of community assembly under changing environmental
12
13 conditions. These research efforts will facilitate the development of effective
14
15 climate change adaptation strategies for preservation of local biodiversity and to
16
17 protect the wide array of valuable ecosystem services that rely on particular
18
19 patterns of local biodiversity for their effective delivery [91].
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Figure 1: A conceptual model of how life history shifts within communities may affect the future of coexistence under ongoing climate change, in both existing species assemblages and novel assemblages resulting from colonization events and range shifts.

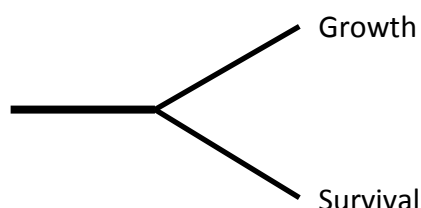
Figure 2: Effects of warming on life history and competitive outcomes in Scottish damselfly communities. A: Larval growth rates under current (15° C) and projected (20° C) Scottish freshwater temperatures, for range-shifting species (*Ischnura elegans*) and resident species (*Enallagma cyathigerum* and *Lestes sponsa*). B: Survival rates for larvae of these species when reared under current and projected conditions. C: Effects of body size (positively correlated with

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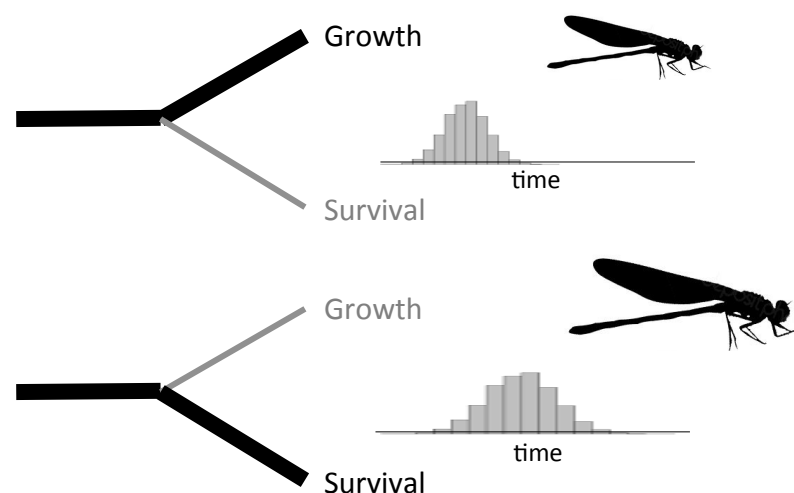
growth rates, see text) on competitive outcomes. Error bars represent standard errors. Data reproduced from Lancaster, Morrison, and Fitt, unpublished.

For Review Only

A. Typical, simplified “Y” trade-off structure among, e.g., growth rate and survival, in which ecological or physiological constraints imply that a species must allocate resources into one or the other of these life history trajectories, but that it cannot simultaneously maximize both strategies:



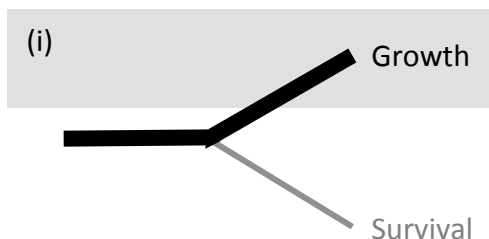
B. In the case of co-existing competitors, selection to avoid competition may cause interacting species to resolve trade-offs differently:



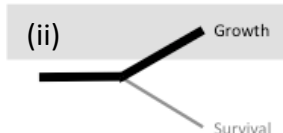
This process produces interspecific divergence in e.g., body size or phenology.

C. Climate change may influence trade-offs allocation in the same direction in all species, resulting in reduced opportunity for coexistence (grey bars represent positively selected traits in each hypothetical species):

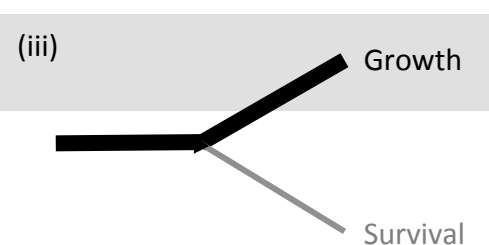
E.g. a warming climate favors fast growth in all species (i), increasing interspecific competition within this strategy:



Obligately slow-growing species (ii) may be disadvantaged (lost) under climate change:

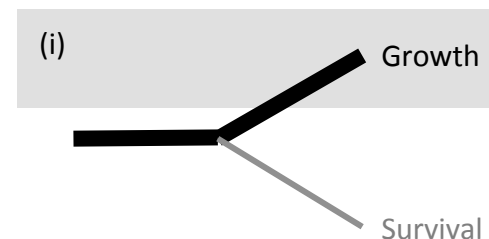


New colonists (iii) typically also exhibit fast growth rate and therefore compete strongly with the remaining, dominant residents (i):

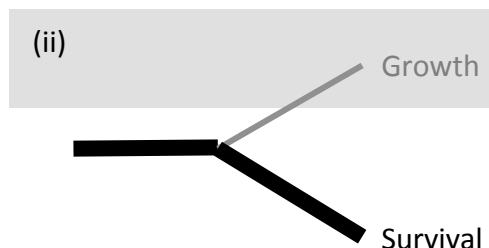


D. Alternatively, climate change may reinforce differences in trade-offs allocations among interacting species, resulting in continued coexistence and opportunity for incoming, range expanding-species to enhance local biodiversity:

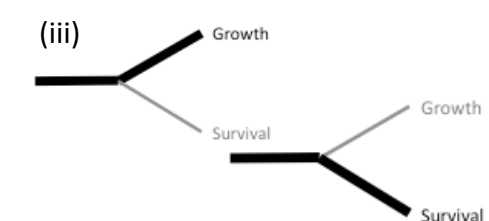
E.g., a warming climate leads to faster growth in already fast-growing species (i):



but may lead to increased investment in survival in slow-growing species (ii):



This process may also leave gaps in life-history trait space to be filled by a variety of new colonists (iii):



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