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Chapter 1

Roles of the Environment in Plant Life-History Trade-offs

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Abstract

Variation in plant life-history and functional traits at between- and within-species levels has key ecological consequences, in which environmental settings impose strong selective pressures and play a vital role throughout life cycles. Our general notion for plant life-history strategies may be that, relative to tall, long-lived plants, short-lived species have features of small stature, small-seededness, rapid growth, and low seedling survival (*k*- versus *r*-selection). Rate of evolution may be an important agent of selection and annals evolve more rapidly than perennial congeners. These empirical observations prompt a suite of enticing questions, such as how do life-history traits interplay with functional trait at late stages of regeneration? what are the primary trade-offs in a cohort of key life-history traits that may have undergone stabilizing selection? and how do environmental filters differently affect adaptive trait variation in annuals and perennials? In this chapter, we intend to address aforementioned questions via assembling our updated knowledge with emphasis on seed mass and temporal and spatial dimensions of seed dispersal. Through such synthesis, we wish to raise awareness about life-history trade-offs and provide a holistic understanding of the extent to which climate change is likely to impact plant adaptation and eco-evolutionary trajectories of life-history phenotypes.

Keywords: plant life histories, life-history trade-offs, seed mass, seed number, seed dormancy, seed dispersal syndrome, seed emergence, seed persistence, soil seed bank, life-cycle transitions, climate change

1. Introduction

Life-history traits, known as fitness components due to their predictable monotonic relationship with fitness, are related to the timing and success of development, reproduction, and

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senescence throughout the life cycle [1]. The environment has appreciable influences on plant life histories and in the life cycle, the timing of life-history traits (e.g., flowering, seed set, seed mass, seed number, seed dormancy intensity [i.e., delayed onset of germination], seed emergence, etc.) are covaried and thus probably coevolved. Examples for the interplay between the environment and life-history traits at ecological and/or evolutionary levels are instantiated as follows.

- At a global scale, seed dormancy tends to decrease and seed size to increase toward the equator [2–4].
- Life cycles with early flowering, small seeds, deep dormancy, and slow germination are associated with habitats exposed to high temperature, low rainfall, and high radiation [5]. (Note: warming selects for higher optimal photosynthetic temperatures.)
- Lower temperatures with as little as 1°C differences ($T_{critical}$ = 15°C) to the maternal plant in Arabidopsis, on the contrary, tend to enhance final seed dormancy levels [6–9].
- Under natural conditions, a given plant may produce seeds with different levels of dormancy in association with a particular temperature it has experienced during seed development [10].
- Variations in seed dormancy and mass often have a concomitant effect (reviewed by [4]) and are correlated in a negative manner [5, 11–15].
- Species showing very fast germination behavior have (very) small seeds and little or no endosperm, and there is a clear relationship between the phenomenon of very fast germination and high stress habitats (e.g., arid, saline, or in active floodplains), where seeds can rapidly exploit temporarily favorable conditions for germination [16].
- There is a positive correlation of relative embryo length with germination speed and negative correlations with the amount of habitat shade, longevity and precipitation [note that small embryo sizes are typical of primitive taxa] [17].
- Climate change is accelerating plant developmental transitions in temperate environments and advanced flower timing increases dormancy intensities [5, 8, 18].
- Early germination increases seed fecundity due to prolonged vegetative growth and nutrient accumulation but may also bring about high seedling mortality [5].
- There is a strong relatedness between seed mass and the depth of burial from which seedlings emerge [19, 20] and germination of large seeds is strongly facilitated by temperature fluctuations, ensuring germination after deep burial or in litter layers [21–23].
- There exists a negative correlation between seed dormancy and longevity [24] with small seeds persisting longer in soil seed banks than large seeds [25].
- There are strong correlations between seed mass and dispersal syndromes and their correlations hinge on dispersal vectors [26, 27].

Some life-history traits may have reciprocal effects with functional traits at late life stages of regeneration. Environmental challenges, mostly to the maternal plant, influence the resources

Trait one	Trait two	Correlation	References	Notes
Seed dormancy	Seed mass	−	[5, 11–15]	(1)
Seed dormancy	Seed persistence	No?	[143]	(2)
Seed dormancy	Seedling survival	−	[5, 14]	
Seed dormancy	Seed longevity	−	[24]	(3)
Seed mass	Time to seedling emergence given favorable germination conditions	+	[144]	
Seed mass	Seedling growth rate	−	[145–147]	
Seed mass	Maternal plant size	Neutral or +	[28, 148, 149]	(4)
Seed mass	Seed number per lifetime	No	[150]	
Seed mass	Seedling survival	No or weak +	[122, 123]	
Plant size	Time to reproductive maturity	+	[150]	

Notes: (1) In general, species that produce light seeds are more likely to possess some type of seed dormancy [69, 142]. Other correlations were also documented and these inconsistencies may be explained by an incomplete consideration of other covarying factors (e.g., dispersal, fire, and predation) [13] or by phylogenetic constraints [151]. Variation in seed size and dormancy often results from a seed position effect within an inflorescence and within a dispersal unit [35, 50] and this also contributes to uncertainties of their associations. At molecular levels, the parent-of-origin effects on seed traits (e.g., dormancy and size), which are regulated by chromatin remodeling, have been documented for crossing between plants in different ploidy and mutants defective at reproduction [152].

(2) Such correlation remains in the question, as the cited study did not measure whether "the degree of dormancy" was related to persistence. Contrasted with seed release at maturity, canopy seed storage (i.e., serotiny) is reviewed in [153] and we do not extensively discuss canopy-stored seed banks in this chapter. Global warming is expected to reduce seedling emergence for some species [154, 155]. Moreover, the evolution of seed dormancy is favored by high seed persistence in the soil seed bank to alleviate the cost of delayed germination [156]. Both Cohen and Ellner's models suggested that an increase in seed survivorship selects for a low seed germination [88–90]. Soil temperature is the dominant environmental factor controlling the depth of seed dormancy during cycling in imbibed seeds [157]. Climate change engenders long-term exposure to high soil temperatures, which may reduce seed survival, thus selecting for decreased levels of seed dormancy [158]. Taken together, climate change may increase seed numbers in the life cycle and decrease dormancy levels due to increased seed mortality.

(3) Dormancy cycling coupled to seed longevity represents a bet-hedging strategy through persistence in the soil seed bank [159, 160]. As a consequence, seed persistence may be not simply associated with either seed dormancy or longevity.

(4) The mother plant has a significant influence over seed traits and instances have been documented for more than 10 decades. Factors such as age of the mother plant, position of the seed in the fruit, inflorescence, or canopy can affect seed properties, often accompanied by a dimorphism either of the seeds themselves or the fruits in which they arise [161].

Table 1. A summary of correlations of adaptive traits.

that are packaged into seeds (seed size) and may be critical for germination and initial seedling growth. For instance, small-seeded species have small plant size (e.g., a positive correlation between seed mass and plant height [28]). Larger plant size, in turn, has higher annual photosynthetic incomes, giving the plant more energy to allocate to seed yield (increased number, heavier mass, or a trade-off between the two in life cycles). Rather, there are studies reporting that seed mass, nature plant height, and leaf mass per unit area have little intercorrelations [29] and that seed dormancy strategy is largely independent of vegetative functional traits and range characteristics [30]. Those inconsistent reports supply us with clues to studying the interaction between adaptive traits in a broader scope (e.g., controlling for phylogeny, more species from different taxa, and/or more traits at different stages of life cycles).

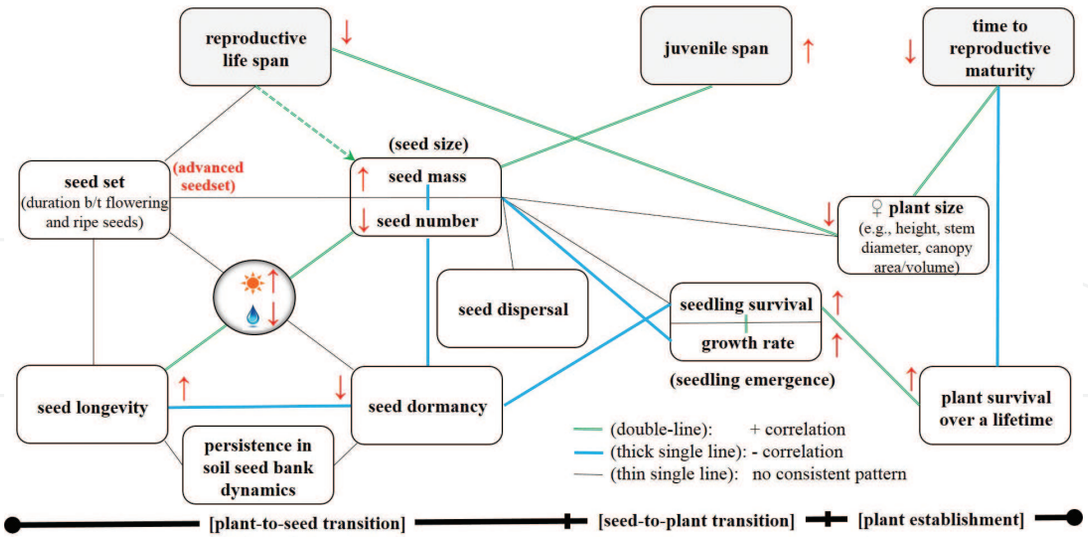


Figure 1. Relatedness among life-history and functional traits and the impact of climate change on the variation (and evolution) of these traits. Note: Lines give interactions between traits (boxes) in a positive or negative manner and the change of direction (↑ or ↓) depends on another trait(s). The arrow linking two traits prompts which trait affects the other. Sun and water drop symbols stand for temperature and rainfall, respectively.

Altered environment (♀)	Affected traits in offspring	Test species	References
Temperature (high or low)	Seed production, seed mass, flowering time	*Arabidopsis thaliana, Plantago lanceolata*	[162–164]
Light (shade or over-exposure)	Seed provisioning, seed mass, germination, seedling survival, biomass, life-history schedule	*Polygonum hydropiper, Campanulastrum americanum*	[165, 166]
Rainfall (drought)	Flowering (select for early flowering and short life cycles), seed provisioning, germination	*Brassica rapa, Polygonum persicaria*	[167–170]
Seasonal environments	Germination timing, life-history schedule	*Arabidopsis thaliana*	[74]
Salinity (high)	Germination, seedling growth	*Arabidopsis thaliana*	[171]
Nutrient (deficiency)	Plant height, biomass	*Oryza sativa*	[172]
Herbivory	Seed mass, germination, seedling growth, flowering, plant height, biomass	*Raphanus raphanistrum, Impatiens capensis*	[137, 138, 173]

Note: When maternal plants are deprived of resources, seed provisioning may be reduced (e.g., [145]), maintained or even increased (e.g., [167, 168, 174]), as trade-offs may exist between increased seed provisioning and decreased persistence in the soil seed bank [145, 167, 174] and thus the benefits may depend on a specific ecological setting.

Progressive global warming leads to widespread shifts toward earlier initiation of flowering in many plant populations, which contributes to an increase in the length of the flowering season in regions where flowering is temperature-dependent [175–177]. Note that longer growing seasons select for later flowering and thus warming and growing season may comprise a trade-off. As the detection of the relatedness between flowering locus and ambient temperature [72, 178], the flowering time diversity is associated with *cis*-regulatory variation [179] and further, flowering time loci restrict potential range size and niche breadth [180].

Table 2. Examples for the effect of different parental environments on offspring adaptive traits.

Last, we provided a summary of interplay patterns between traits (life-history, functional traits, and a combination thereof) as influenced by climatic factors in **Table 1** and **Figure 1**. We also listed examples on adaptive traits with transgenerational plasticity as responses to altered maternal environmental conditions in **Table 2**.

2. Life-history traits and their trade-offs

2.1. Seed size

The reproductive output of an organism is a critical life-history trait defining its fitness and is the result of both offspring number and quality. Seeds are time capsules and receptacles of life and seed mass is a crucial life-history trait that links the ecology of reproduction and seedling establishment with that of vegetative growth. Seed mass commonly varies over 11.5 orders of magnitude among coexisting plant species [31], while within-species variation in seed mass is typically in the range of two- to fourfold [32]. Extant flowering plants exhibit a wider range of seed sizes than nonflowering seed plants, and in particular, some of them can bear very small seeds [31]. Seed mass variation is a type of heteromorphism, which represents a classic trade-off. Production of dimorphic or heteromorphic seeds by a single plant allows plants to decrease temporal variance in offspring success through bet-hedging [i.e., a strategy that reduced temporal variance in fitness at the expense of a lowered arithmetic mean fitness] [33–35], or rather, a blend of plasticity [i.e., a capacity of a genotype to produce different phenotypes when exposed to different environmental conditions] and bet-hedging [36]. Heteromorphism enables a fraction of propagules to adapt to any given environment and may increase long-term reproductive success by reducing the risk of extinction, but it comes at the cost of decreasing immediate fitness [37].

Seed mass is closely correlated with changes in plant form and vegetative type, followed by spatial dispersal syndrome and net primary productivity [27, 38, 39]. Besides, latitude, genome size, forest structure, and life history all have been linked to seed size variation [40–43]. Effects of temperature on seed mass are not consistent, as both increased [44, 45] or decreased [46] seed masses have been documented. Seed mass variation within species is largely related to seed position within pods and fruits [47–49] and upper grains in the spikelet tend to be larger than bottom ones [50]. This is possibly due to physiological or morphological constraints on optimum resource allocation to seeds. The diversity of seed mass may be maintained by tolerance-fecundity trade-offs (i.e., more tolerant (fecund) species gain more (less) stressful regeneration sites, respectively) [51].

Empirical evidence favors the notion that seed production during mast years (i.e., good-seed years) is tightly related to high temperature in the previous spring and summer, late spring frost and summer rainfall of the last two years. The difference in temperature from one growing season to the next effectively predicted the occurrence of mast years [52–54]. Considering yearly climatic variability, Kelly et al. [55] developed a model based on temperature differentials over multiple seasons to predict seed yield [55] and this model was further validated by

Pearse et al. [56]. The robustness of these models is emanated from the hypothesized correlation between seed mass and the environment and, in turn, lends support to the crucial role of climate in seed mass modulations.

From a genetic perspective, seed mass and number can evolve independently. Both traits are affected by a large number of mostly non-overlapping quantitative trait loci (QTLs) in their genetic architecture, which has been manifested by using mapping lines created by two [57–60] and multiple parents [61]. This indicates that the relatedness between seed mass and number may not be invariably direct.

2.2. Seed dispersal in time and space

While seed dormancy is a means to disperse in time, seed dispersal is an important way to disperse in space (hereafter simply referred to as dispersal) and also a risk-spreading strategy [62, 63]. Selection in heterogeneous or unpredictable environments may favor plants to synchronize seed dispersal with environmental conditions allowing or deferring germination until suitable conditions occur [64]. As risk-reducing strategies, can seed dormancy and dispersal substitute for one another so that selection for one may weaken selection for the other? Theoretical expectations support such a trade-off or a negative covariation (reviewed in [62]), but empirical evidence is inconsistent (there are reports on complicated patterns or no relationship, e.g., [65]).

2.2.1. Seed dormancy

Seed dormancy is an innate constraint on germination timing under conditions that would otherwise promote germination in nondormant seeds [66] and prevent germination during periods that are ephemerally favorable [67]. Dormancy is significantly higher in annuals than in perennials (note that perenniality is an alternative risk-reducing strategy; [68]) and dormant seed banks are thus better associated with annuals than perennials [13, 25, 69]. Dormancy is an important adaptive trait that links plant life-history to seasonal change. Dormancy exists as a continuum with multiple layers (blocks to germination completion) that are successively taken off by appropriate environmental signals. These signals inform the seed whether it is in an appropriate habitat and time of the year suitable for the resulting plant to survive and reproduce. Seed germination timing is the earliest trait in plant life-history, which allows plants to regulate when and where they grow. It affects the evolution of other life-history traits that follow in the life cycle, such as fecundity and survival [70]. As such, seed dormancy may be construed as an adaptive strategy for survival during bad seasons and can exert cascading selective pressures on subsequent life stages.

Seeds temporarily block germination through adaptation to the prevailing environments so that germination is timed to avoid unfavorable environmental conditions for subsequent plant establishment and growth and therefore sets the context for the traits that follow [71]. Dormancy levels are maternally manipulated [72, 73] and determined by maternal responses to day length and temperature in many species [6, 74, 75]. Notably, induction of primary dormancy was greatly influenced by the effect of maternal environments on embryo/endosperm

[74, 76, 77] and/or on seed coat properties [78]. Dormancy intensity can be manipulated via controlling the daily circadian clock at reproduction [79]. Such effects can be passed down for multiple generations [80, 81] and have been observed even in long-lived perennials, such as conifers [82]. Dormancy manipulation involves dormancy-specific genomic imprinting programs that mainly occur in mature endosperm [83]. Owing to the similar functionality between plant seed endosperm and mammalian placenta, the kinship or parental conflict theory is often proposed to account for the evolutionary origin of imprinting [84].

Plants distribute their offspring across time, hedging their bets against unpredictable environments [37, 85]. This increases the likelihood that some seeds will survive regardless of environmental perturbations. Seed dormancy variability among individuals is associated with environmental heterogeneity [86] and heterogeneous environments may select for bet-hedging strategies, as population growth is an inherently multiplicative process that is very sensitive to occasionally extreme values [87]. Cohen indicated that low germination probabilities can be expected in harsh environments as individuals can germinate in improved conditions and decrease their average mortality [88]. However, Ellner predicted that increasing the frequency of favorable years may also lead to lower germination rates due to increased density-dependent effects imposed by competitive interactions [89, 90].

Based on mathematical modeling, large nondormant seeds would be selected for under constant unfavorable environments, whereas in temporally unpredictable environments, dormant seeds would be selected for, and their size would rely on the likelihood of predation of large seeds [91]. This alludes to the adaptive value of dormancy that may depend on the variability of the environment and the probability of survival of large seeds in the soil seed bank. Nondormant seeds in legumes can only evolve in climates with long growing seasons and/or in lineages that produce larger seeds; conversely, dormancy should be evolutionarily stable in temperate lineages with small seeds [92]. In light of this, it may be reasonable to extrapolate that, within a given lineage, taxa producing larger, nondormant seeds necessarily predominate in aseasonal environments, while plants bearing small, dormant seeds are dominant under short growing seasons [92].

2.2.2. Seed dispersal syndrome

Spatial aspects are especially important in the global climate change context, as temperature shifts depend on latitude and altitude gradients and species dispersal to higher altitudes and latitudes is thought to be a major constraint to their future survival. The evolution of local adaptation requires low dispersal (and selection against genotypes adapted to other localities) [93]. Also, spatial context influences gene flow and evolutionary dynamics with, again, important consequences for species competition and survival [94]. Differences in dispersal syndrome are likely to affect the shape of the dispersal kernel and the type of environments to which seeds are dispersed [95, 96]. On the one hand, they may evolve as phenotypic plasticity (e.g., bet-hedging) [97–99] in responses to selective factors, including reducing parent-offspring conflict or kin competition, the temporal heterogeneity of the environment, such as local population extinction [100–102] and avoiding inbreeding depression due to mating between related individuals (for dispersal only; [103]). Hence, seed dispersal promotes

adaptation, stability, and persistence [104]. On the other hand, various costs of dispersal have been postulated in theoretical models [such as fleshy fruits dispersed by animals [105], getting lost during displacements, dispersing in fragmented habitats [106], etc.], which end up concluding that increasing the cost of dispersal (certain selective forces) selects for lower dispersal [107]. Collectively, selection acts on trade-offs in temporal and spatial dispersal and eventually maximizes fitness [62]. These trade-offs can, in turn, introduce patterns of covariation among functional and life-history traits that correlate with dispersal (reviewed in [108]).

Further, dispersal syndrome is a consistent predictor of seed size especially in nonflowering seed plant groups [109]. In conifers (serotiny), seeds are generally larger in animal- than wind-dispersed species [110, 111]. This is in alignment with our intuition, because animals should be attracted to large, copious seeds and can be better than wind to disperse large propagules [112–114]. Moreover, spatial differences at the levels of environmental stochasticity, restricted dispersal, increased fragmentation, and intermediate survival during dormancy favor the adaptive diversification of bet-hedging dormancy strategies [115] and spatial heterogeneity and restricted dispersal are essential for evolutionary branching of germination strategies [116]. This suggests that dispersal and above-ground environmental fluctuations have a significant effect on the development of dormancy or germination polymorphisms.

2.3. Trade-offs among multiple life-history traits via stabilizing selection: a compromised strategy to recoup the disadvantage of respective traits

The Smith-Fretwell theory (1974) modeled the optimal seed mass and formalized the concept of a trade-off between producing a few, well provisioned offspring versus producing many poorly nourished individuals. It considers the offspring's lifetime fitness, given the population is stable during their life time. The role of differential seed mass in promoting species coexistence has been stressed in previous theoretical studies [117–119]. Evolution of seed mass results in the fixation of a given strategy and evolved seed mass decreases when seed dormancy is lowered [120]. Large seed mass, on the one hand, confers direct advantages to many fitness-related plant characteristics, including recruitment and survivorship [121, 122] and establishment [32, 122], because large seeds accumulate copious nourishing substances for germination and have better tolerance in face of disturbances (e.g., abiotic stresses) [119, 123]. Furthermore, for a given reproductive investment, seed mass is negatively correlated with seed number [124–126] and large seeds are less dispersible due to their great mass [127]. However, can the survival advantage of large-seeded species really counterbalance the greater seed yield of small-seeded species?

The advantage of large-seededness is generally temporary, probably expiring when all maternal reserves have been deployed [123]. This means large-seeded species have a survival advantage over small-seeded species solely during early seedling establishment [122]. Actually, there is no or even weak negative correlation between seed mass and overall seedling survival [122, 123]. Because slow growth rate (due to slow metabolic rate) increases the capability of persistence under stress and the duration of exposure to juvenile mortality. Greater survival per unit time associated with large-seeded species may be canceled out by the longer time to maturity.

Here, we speculate possible impacts of elements of plant strategy systems (e.g., vegetative functional traits) on seed ecology. Larger plant size has higher annual photosynthetic incomes, giving the plant more energy to allocate to seed production (increased seed number, heavier mass, or a trade-off between the two). A species with a large adult stature will necessarily have a lengthy juvenile period to produce large, well-provisioned offspring, which makes up for a high rate of juvenile mortality. By contrast, smaller plant size of small-seeded species may have less photosynthate to allocate to reproduction. Further, they also tend to have shorter reproductive life span (i.e., less total investment to offspring and lower mortality). Less input from maternal plants further erodes the apparent advantage that small-seeded species harbor during seed production.

In addition to seed dormancy and dispersal, there are other risk-spreading strategies. For instance, there is a negative trade-off between dormancy and longevity (a survival strategy) to reduce risk of reproductive failures in time [69, 128, 129]. Iteroparous (i.e., reproducing more than once in a lifetime) perennial plants increase their probability of encountering favorable conditions for reproduction in time [130–132]. Therefore, the need for seed dormancy in perennials may be negated and perenniality may select against seed dormancy [128, 129].

Additionally, it is reported that dormancy is also dependent on the likelihood of seed predation and nondormancy may evolve as part of a predator avoidance strategy [133, 134] and also with the involvement of environmental pressures [135]. The risk of predation is thought to be proportional to seed size due to its detectability and nutritious contents. However, such risk is lower in large than small seeds, possibly because size is positively correlated with defense mechanisms [136]. Furthermore, maternal herbivory has a major impact on seed size [137, 138] (also see **Table 2**; mediated by phytohormone signaling pathways that affect seed filling [e.g., gibberellins, auxin, brassinosteriod] [139, 140]) and dormancy [141] (mediated by jasmonate signaling pathway and resultant changes in the sensitivity of seed germination to ABA). Thus, whether dormancy or nondormancy is favored by selection ultimately depends on seed size [92].

In a nutshell, there is no prevalent relationship between seed mass and number, in the sense that the advantages that small-seeded species gain during seed production must be counterbalanced somewhere else in the life cycle and seed number is just one of the possibilities to make up the loss of small seededness. Seed mass is determined via a process of stabilizing selection, which may operate through selections on trade-offs among seedling survival, dormancy, dispersal, seed number, and predation [142], and may play a central role among a correlated suite of traits that covaries across a spectrum of life-history strategies.

3. Conclusions

This chapter intends to direct readers' attention to consider multiple life-history traits in the life cycle when studying plant life-history evolution, as selection for one strategy (not necessarily limited to one single trait) may constrain another. Disentangling the trade-offs of how

disadvantages in one studied trait may be made up by being an advantage in another trait(s) helps essentially understand the evolution of a particular trait. Moreover, these trade-offs are essential for understanding the complex response of species to climate change.

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