

Chapter 11

Life-History Responses to the Altitudinal Gradient

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Abstract We review life-history variation along elevation in animals and plants and illustrate its drivers, mechanisms and constraints. Elevation shapes life histories into suites of correlated traits that are often remarkably convergent among organisms facing the same environmental challenges. Much of the variation observed along elevation is the result of direct physiological sensitivity to temperature and nutrient supply. As a general rule, alpine populations adopt ‘slow’ life cycles, involving long lifespan, delayed maturity, slow reproductive rates and strong inversions in parental care to enhance the chance of recruitment. Exceptions in both animals and plants are often rooted in evolutionary legacies (e.g. constraints to prolonging cycles in obligatory univoltine taxa) or biogeographic history (e.g. location near trailing or leading edges). Predicting evolutionary trajectories into the future must take into account genetic variability, gene flow and selection strength, which define the potential for local adaptation, as well as the rate of anthropogenic environmental change and species’ idiosyncratic reaction norms. Shifts up and down elevation in the past helped maintain genetic differentiation in alpine populations, with slow life cycles contributing to the accumulation of genetic diversity during upward migrations. Gene flow is facilitated by the proximity of neighbouring populations, and global warming is likely to move fast genotypes upwards and reduce some of those constraints dominating alpine life. Demographic buffering or compensation may protect local alpine populations against trends in environmental conditions, but such mechanisms may not last indefinitely if evolutionary trajectories cannot keep pace with rapid changes.

Keywords Bet hedging · Centre-periphery hypothesis · Local adaptation · Ontogeny · Phenotypic plasticity · Reproductive allocation · Slow-fast life-history continuum · Survival

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11.1 Introduction

Mountain environments present a challenge to any living organism, and elevation gradients, with their sharp physical and ecological transitions, have been a favourite scenario for approaching general questions about adaptive change in life histories. Growth, development, maturation, reproduction and survival patterns of organisms are remarkably diversified along elevation, but also tend to converge in similar environmental conditions. Literature on the subject is abundant, but also widely dispersed and poorly integrated with respect to the plant and animal realms, and also between endotherms (animals that primarily produce their own heat) and ectotherms (in which body temperature tends to match environmental temperature, or requires behavioural thermoregulation). Undeniably, focal organisms differ in substantial ways, but the similarities in scope, objective, and often in findings among studies along elevation gradients provide an opportunity for a synergic appraisal with insights from both vascular plants and animals. Here, we first highlight those abiotic and biotic factors that are major determinants of life-history variation in elevation. We then illustrate the primary mechanisms of evolutionary adaptation to such variation, involving environmental and genotypic variation, their interaction and covariation. We discuss the limitations to environmental fit within and among species, like those imposed by intrinsic or evolutionary constraints. We review published literature on elevation patterns in growth, reproduction and survival in populations and species of plants and animals, and discuss the elevation life-history continuum in these taxonomic contexts. Our intention is neither to provide an extensive survey of literature on specific taxonomic groups, which in some cases are adequately covered (e.g. insects and birds: Hodkinson 2005; Hille and Cooper 2015; Boyle et al. 2015), nor to perform a meta-analysis given the literature bias towards specific taxa. Rather, we aim to provide a broad and synthetic appraisal of life-history variation along elevation. We discuss whether the climatic and ecological shifts occurring along elevation select some strategy within the life-history continuum and whether responses are, to a certain degree, comparable within and between unitary animals and modular plants. In spite of obvious connections with life histories, we intentionally omit to canter on seasonality of plant and animal life-cycle events, i.e. phenology per se, as this would require different spatial and temporal perspectives from those adopted here.

11.2 Environmental Variation in Elevation

11.2.1 *Temperature*

Among the abiotic factors that vary among mountainsides, temperature is the most critical for both plants and animals given the magnitude of variation it displays, and its profound effect on biochemical or physiological processes (Sibly and Calow 1986).

It decreases at a rate of 0.54–0.65 °C per 100 m of ascent, but significant variation is introduced by meteorology, local topography and height above the ground (Barry and Chorley 1987; Körner 2003; Rolland 2003). At cold temperatures, physical and chemical reactions slow down, as do the assimilation of energy and metabolic activity (Schmidt-Nielsen 1997). This process has the most remarkable consequences for plants and ectotherms, and either leads to reduced activity or triggers costly homeostatic responses to offset the passive reaction to reduced temperature and freezing (Sakai and Larker 1987; Gillooly et al. 2001). Endotherms may be affected in a similar way when they are outside their thermoneutral zone (Angilletta et al. 2010), and lower critical temperatures are reached more frequently at high elevations. Dormancy (including diapause and hibernation) is a mechanism to escape cold weather or resource shortage over the winter and corresponds to a period when growth, development and physical activity are temporarily arrested. Through its effect on metabolism, temperature limits the rates of production throughout ontogeny and reproduction, thus directly influencing phenology, growth and reproductive patterns, and life-history correlates such as body size (Atkinson 1996; Atkinson and Sibly 1996; Angilletta et al. 2004). Temperature is also tightly associated with seasonality, and in turn, with productivity, and thus also controls the above processes indirectly via these variables.

11.2.2 Atmospheric Pressure

Atmospheric pressure, the moisture content of air and the partial pressures of biologically relevant gases, such as oxygen and carbon dioxide, decrease relatively uniformly with increasing elevation, and impact gas exchanges in plants and respiration in animals. Pressure effects on photosynthesis are, however, smaller than predicted from the decline in the ambient $p\text{CO}_2$ alone because the increased rate of molecular diffusivity, induced by thinner air, is counteracted by the descent of atmospheric temperature, decelerating diffusion. Moreover, up to 80% of the total CO_2 transfer resistance between air and the chloroplasts is in the liquid phase, which is not influenced by pressure (Körner 2007). An improvement in the rate of oxygen intake with elevation has been observed in animals through ventilation or changes in blood composition (Rourke 2000), as well as increased porosity of bird eggshells to facilitate O_2 diffusion to the embryo (Körner 2007).

11.2.3 Precipitation

Unlike temperature and atmospheric pressure, precipitation exhibits non-linear relationships with elevation, and regional, rather than global, patterns. Precipitation tends to increase with altitude at low elevations, but exhibits no pattern at very high elevations, or declines above the cloud zone in tropical areas (Nagy and Grabherr 2009). Orographic precipitation in the form of snow typically characterises high

elevations and dictates, together with seasonal changes in temperature and photoperiod, the duration of the growing and/or breeding seasons of alpine organisms, apart from providing thermally protective snow blankets (Hodkinson 2005). Since evapotranspiration declines with elevation, the balance for plant water supplies is rarely critical. However, in periods of high evaporative demand or prolonged soil moisture depletion, the need to reduce transpiration may affect the rates of CO₂ photosynthetic uptake and nutrient assimilation (Schulze and Chapin 1987). This trade-off has direct consequences for alpine plant recruitment, survival and growth patterns, and ultimately shapes their phenology and morphology (Körner 2003), as well those of the fauna they host (Hodkinson 2005).

11.2.4 Primary Productivity

Mountain environments display sharp gradients in soil fertility, largely dependent on climate, bedrock, soil structure and age, micro-topography and soil fertilisation by primary consumers. At high elevations, low temperatures (or a short duration of mild temperatures) negatively affect soil enzymatic activities, the rate of nutrient mineralisation and turnover, thus reducing nutrient availability for primary producers with consequences for upper trophic levels (Laiolo et al. 2015a). In some mountain areas, shorter grazing seasons and reduced nutrient inputs from herbivores also contribute to lower productivity, and the permanence of nutrients shortens in steep and shallow soils (Mariotti et al. 1980; Huber et al. 2007). Alpine plants may respond by reducing their size and enhancing mineral nutrient concentration (Körner 2003), although there are exceptions (Laiolo et al. 2015a). It is also worth mentioning that soil nutrient concentration does not always reflect availability for organisms, as nutrients may be in a form that cannot be absorbed. Nutrient availability unquestionably affects the overall performance of plants up to higher trophic levels and plays a key role in life-history evolution (Stearns 1992).

11.2.5 Biotic Interactions

The above factors, together with land area and history, are evoked as the primary drivers of the decline in species richness observed in many taxa on mountains, as well as of the decrease of biotic interactions (McCain and Grytnes 2010). Under the Stress Gradient Hypothesis, negative interactions should decline with environmental harshness while positive ones should increase (Brooker 2006). Negative trends of competition, predation and parasitism with elevation have indeed been documented in a large number of studies (Hodkinson 2005; Boyle 2008; Meléndez et al. 2014), but some positive relationships have as well (e.g. Abbate and Antonovics 2014).

Greater agreement exists on the enhancement of plant facilitation with elevation, documented in floral communities across the globe (Callaway et al. 2002). Together with productivity, variation in extrinsic mortality related to interactions is a major driver of organisms' life strategies, influencing patterns of growth, development, age and size at maturity, allocation in self-maintenance and parental care, as detailed further in the text.

11.3 The Process of Life-History Evolution

11.3.1 Mechanisms

Life-history variation among mountain populations can be explained by both phenotypic plasticity and local adaptation. The former, by means of which organisms with the same genetic constitution adjust their development to the current conditions, is generally considered poorly efficient for coping with extreme environments (Grime 1974; DeWitt et al. 1998). Some studies have shown that plastic genotypes bear a cost of low performance in unfavourable alpine habitats when compared to locally adapted genotypes (Emery et al. 1994; Stöcklin et al. 2009; Fischer and Karl 2010). However, purely plastic life-history responses to changes in resource availability among elevations have been described (Dobson and Murie 1987; Blanckenhorn 1997; Sears and Angilletta 2003; Yeh and Price 2004).

More frequently, selection for stress tolerance induces ecotypic differentiation in the form of local adaptations, exemplified by significant non-additive gene–environment interactions and populations that show genetic differences, and performances, corresponding to the conditions met along the gradient (Törang et al. 2015; Muir et al. 2014). Since environmental variation occurs at small spatial scales across elevations, strong local selection and limited gene flow are required to promote local adaptation *sensu strictu* (i.e. demonstrated by comparing performances after reciprocal transplants; Kawecki and Ebert 2004), and population size may also matter (Leimu and Fischer 2008). Local adaptation also results in gene–environment covariation and non-random distributions of genotypes along the gradient, an evolutionary pathway fairly well documented in mountain species. If, for instance, slow-growing genotypes are favoured at high elevations, where low temperatures also act to slow organisms' growth rates, then genetic and environmental influences on phenotypic expression covary positively. This process of co-gradient selection explains size reduction in alpine plants, with genotypes for small size found primarily on uplands where the environment also hampers somatic growth (Aarssen and Clauss 1992; Byars et al. 2007). The same environmental context may however select for genetically rapid growth and development to compensate for environmental conditions that slow down these processes (Conover and Schultz 1995), a countergradient pattern often adopted by ectotherms in cool environments.

Across populations or species, life histories can be interpreted as the result of the optimisation of individual phenotypes, or the development of evolutionarily stable strategies, with respect to the environment (Stearns 1992). This process should lead to similar elevation trends within and among species. The greatest variability among species in organismal design, evolutionary history and ecological niche enhances the opportunity for differentiation as compared to variation within species, but these factors also constrain environmental fit proportionally more among species, as detailed below.

11.3.2 Constraints

Body size is one of the most crucial intrinsic constraints to differentiation in life histories and should always be accounted for when analysing the fit of life histories to the environment. It engenders a continuum with, at one extreme, large species that grow slowly, mature late, and live long, and at the other extreme, small species adopting the opposite strategy (Sibly and Brown 2007). Biological rates, such as growth rates or reproductive biomass production, tend to obey simple allometric scaling laws regardless of the living conditions or taxonomic group (Enquist et al. 1999; Laiolo et al. 2015b). Trade-offs in resource allocation among competing functions foster a second dimension of correlated traits, also known as the ‘slow-fast life-history continuum’, rooted in the concept of *r/K*-selection. The cost of reproduction, i.e. the reduction in future reproduction resulting from current investments in reproduction, is the most prominent trade-off, describing the constraining relationships between growth, survival and reproduction (Reznick 1985; Obeso 2002). Great allocation in reproduction is associated with fast and short lives even when the effect of body mass or environment is controlled for, a correlation also defined as the ‘pace-of-life’ syndrome in comparative animal studies (Ricklefs and Wikelski 2002). In plants, vegetative growth is strongly hampered by investment in sexual reproduction, and is a crucial component of this continuum. Within species, this trade-off lies beneath the population process of ‘demographic compensation’, or negative correlations of fitness components across environmental gradients and towards species’ range margins (Villellas et al. 2015). At margins, vital rates tend to decline because of poorer conditions of the environment (‘centre-periphery’ hypothesis: Lawton 1993; Vucetich and Waite 2003; Angert and Schemske 2005).

Evolutionary history, relatively unimportant at the intraspecific level, dictates the options available to selection, with traits of more closely related species responding more similarly to environmental factors (Harvey and Clutton-Brock 1985).

11.3.3 *Drivers*

Beyond these constraints, natural selection shapes life histories into suites of correlated traits, often remarkably convergent among alpine organisms facing the same environmental challenges. Life-history theory predicts that components of the environment, such as resources, predation, herbivory, competition, disease or physical stresses, favour different combinations of life histories and yield general patterns in their variation. Altogether, these factors can be grouped in two major extrinsic drivers of variation, associated broadly with resource availability and disturbance, respectively. Abundant resources, such as food and light, and competitive environments foster fast growth, short life cycles and high levels of reproduction, thus a ‘fast’ strategy (Clark and Clark 1992; Ghalambor and Martin 2001). This ‘fast’ strategy is also favoured when a disturbance, for instance, disease and predation, increases juvenile extrinsic mortality (Franco and Silvertown 1996). The investment in parental care reflects responses to perceived risks and environmental stresses. High juvenile (extrinsic) mortality or reduced recruitment may yield greater allocation in offspring quality instead of quantity to enhance (intrinsic) juvenile survival and recruitment (Clutton-Brock 1991; Armstrong and Westoby 1993). Life-history theory also predicts that where environmental conditions are not constant across years, individuals should favour a bet-hedging strategy. This strategy involves a reduction in annual breeding performance to reduce the probability of investing too much in reproduction during poor years, and an increase in self-maintenance so that reproduction can be attempted over multiple years (Stearns 1976).

As we detailed above, mortality risk (especially for juveniles) associated with disease, competition and predation tends to decline, while those associated with abiotic stress or a paucity of resources increases in alpine environments. These factors are expected to tilt the life-history continuum towards slower life cycles and enhanced offspring quality vs. quantity, thus a ‘slow’ strategy. Moreover, the environmental variability of alpine regions, consisting both of predictable (seasonality) and less predictable components (e.g. between-year variability), should also favour the evolution of bet-hedging strategies and longer lifespan. This combination of longevity and limited reproductive effort reduces the deleterious effects of environmental stochasticity on population growth and persistence.

In the next section, we present an assessment of the above predictions, reviewing literature that measured responses of life histories along elevation clines in major taxonomic groups, as summarised in Table 11.1.

Table 11.1 Summary of the main life-history characteristics of upland populations and species of different taxonomic groups

Taxonomic group	Responses in uplands (or at the cold extreme of the gradient)	References
Insects and other arthropods	Prolonged generation time	Hodkinson (2005), Schmolter (1970)
	Short larval stage	Tanaka and Brookes (1983), Zettel (2000)
	Fast growth	Dingle et al. (1990), Berner et al. (2004), Laiolo and Obeso (2015), Chown and Klok (2003)
	Small adult size	Laiolo et al. (2013)
	Low fecundity	Reviewed by Hönek (1993)
	Fewer but larger eggs	Fischer et al. (2003), Hayashi and Hamano (1984), Mashiko (1990), Hancock et al. (1998), Wilhelm and Schindler (2000)
	Parthenogenesis	Wachter et al. (2012)
Fishes	Increased longevity	Pauly (1980), Beverton (1987)
	Fewer but larger eggs	Sternberg and Kennard (2013)
	Egg guarding	Sternberg and Kennard (2013)
Amphibians	Increased longevity	Zhang and Lu (2012)
	Larger eggs and reduced offspring size	Liao et al. (2014)
	Fast growth in common garden experiments	Berven et al. (1979), Berven (1982)
Reptiles	Increased adult survival	Adolph and Porter (1993)
	Viviparity	Braña et al. (1991), Tinkle and Gibbons (1977)
	Reduced eggshell thickness	Mathies and Andrews (1995)
	Increased offspring size (oviparous species)	Sinervo et al. (1992)
	Infrequent reproduction	Shine (2005)
Birds	Reduced fecundity	Badyaev (1997a), Badyaev and Ghalambor (2001), Boyle et al. (2015), Laiolo et al. (2015b)
	Prolonged parental care	Badyaev (1997a), Badyaev and Ghalambor (2001), Boyle et al. (2015)
	Shift from sexual to parental behaviour in males	Badyaev (1997b), Snell-Rood and Badyaev (2008), Apfelbeck and Goymann (2011), Bastianelli et al. (2015)
Mammals	Longer lifespan of adults, older age at reproduction	Bronson (1979), Zammuto and Millar (1985), Yoccoz and Ims (1999)
	Lower litter size	Dunmire (1960), Fleming and Rauscher (1978), Smith and McGinnis (1968)
	Increased parental care	Festa-Bianchet et al. (1994)

(continued)

Table 11.1 (continued)

Taxonomic group	Responses in uplands (or at the cold extreme of the gradient)	References
Vascular plants	More investment in maintenance and less in reproduction	Jónsdóttir (2011)
	Clonal growth and vegetative reproduction	Stöcklin (1992), Klimes et al. (1997)
	Iteroparity; high adult survival	Bliss (1971), Hautier et al. (2009), Milla et al. (2009), García and Zamora (2003), Arx et al. (2006), Kim and Donohue (2011)
	Reduction in seed bank size	Molau and Larsson (2000)
	Low seedling recruitment, high seedling mortality	Bliss (1971), Hautier et al. (2009), Milla et al. (2009)
	Pseudoviviparity	Sarapul'tsev (2001)

11.4 Empirical Evidence in Animals

11.4.1 *Insects and Other Arthropods*

Two major obstacles are faced by ectotherms in uplands or with broad altitudinal distribution: low or decreasing ambient temperature and short or decreasing growing/breeding seasons. Insect growth, development, reproduction, dormancy and diapause are timed in relation to these constraints through alternative strategies. The most common are the reduction of the length of the larval stage and the acceleration of growth. Insects from collembolans to orthopterans have been shown to reduce the number of instars (i.e. the number of moults to achieve the adult stage) or the timing of diapause to complete their annual cycle earlier in uplands (Tanaka and Brookes 1983; Zettel 2000). This response is typically associated with thermal conditions close to a species' tolerance range at either low or high extremes (Esperk et al. 2007). Growing faster at high elevations is a widespread alternative (Dingle et al. 1990; Berner et al. 2004; Laiolo and Obeso 2015), and represents one of the best examples of countergradient genotypic variation opposing physiological responses to temperature.

The reduction of instar number or development time lead to smaller adult body sizes, a pattern commonly observed in upland insect populations and species (Laiolo et al. 2013). Body size constrains fecundity, thus these strategies may carry direct fecundity costs (Hönek 1993). These costs are obviated when prolonging development or generation time over the years rather than restraining them within a single year. This strategy has been described in alpine populations of both holo- and hemimetabolous insects (Hodkinson 2005) and is more commonly associated with seasonal but non-resource-limited environments. Meanwhile, resource limitation together with high seasonality tends to favour fast growth at the expense of body

size and overall reproductive output (Chown and Klok 2003). Prolonged development is achieved either by increasing instar numbers or by extending instar growth over 2 years, which involves passing from pluri- or univoltinism in lowlands, to semivoltinism in highlands, with individuals overwintering at different instar stages over the years (Miles et al. 1997), or entering diapause at different stages (Dingle et al. 1990).

The allometric reduction in egg number with elevation is often accompanied by increased egg size to enhance embryo viability at low temperatures, whereas, at higher temperatures, it pays off to produce more and smaller eggs since offspring mortality is lower (Fischer et al. 2003). Increased adult survival with elevation has been observed in fruit flies (Duyck et al. 2010) and is explained by trade-offs between fecundity and longevity (Norry et al. 2006) or increasing rates of damage from by-products of metabolism in hot temperatures (Leiser et al. 2011). In annual species, however, selection on reproductive schedules may induce the opposite patterns, with accelerated senescence at the completion of reproduction (Tatar et al. 1997).

Asexual, or parthenogenetic, populations frequently appear in high-altitude habitats. This strategy, favoured in areas with few sexual competitors (Peck et al. 1998), permitted persistence in isolated ice-free summits surrounded by glaciers ('nunataks') during the Pleistocene glaciation periods (Wachter et al. 2012).

The optimal life strategies of crustaceans also vary along elevation, and females from stream head or alpine waters, for instance, lay larger eggs but smaller clutches than those from lowlands (decapods: Hayashi and Hamano 1984; Mashiko 1990; Hancock et al. 1998; amphipods: Wilhelm and Schindler 2000). Among arachnids, alpine tundra *Pardosa* wolf spiders display no interpopulation variation in egg number per cocoon, but generation time is twofold than that in lowlands (Schmoller 1970).

11.4.2 *Fishes*

Despite the high thermal conductivity of water buffers thermal fluctuations over time and space, and thus reduces the opportunities for sharp temperature-driven selection, temperature has a pervasive influence on developmental traits of fishes and adaptation to local thermal regimes as well as plastic responses are well documented (Haugen and Vøllestad 2000). Factors such as water flow or predation risk also affect fish life-history decisions and, in particular, recruitment is a key trait in determining fish allocation to contrasting life-history traits. As a general rule, larger sizes, later maturity and long reproductive lifespans are selected for when recruitment is low (Kennedy et al. 2003; Parra et al. 2014). Sternberg and Kennard (2013) found that among Australian freshwater fishes, egg guarding species that reach maturity at a small size were more frequent in environments with perennial flow and low mean annual temperatures typical of uplands. Conversely, larger-bodied,

non-egg guarding, highly fecund fish with small eggs and late maturity were more frequent in environments with high mean annual temperature and temporary flow. This pattern indicates that it may be advantageous to increase parental care or produce fewer but larger eggs in low-temperature stream heads, as also observed in crustaceans. Another consistent intraspecific pattern with temperature is that of longevity, which declines at increasing temperatures (Pauly 1980; Beverton 1987).

Many fish species continue somatic growth after sexual maturation and growth is typically highly plastic (Gotthard 2001). However, there is evidence that developmental decisions and growth patterns of populations are locally adapted (Niecieza et al. 1994; Haugen and Vøllestad 2000) and respond to climate, for instance, along latitudes, in a countergradient fashion as for other ectotherms (Conover and Present 1990).

11.4.3 Amphibians

Juvenile development to metamorphosis or sexual maturity strongly influences amphibian adult fitness and has been the target of a large number of studies along climate gradients (Berven and Gill 1983; Altwegg and Reyer 2003; Laugen et al. 2003; Muir et al. 2014). These have shown that ontogenetic traits tend to adjust to a countergradient variation pattern across elevations. Berven et al. (1979) and Berven (1982) showed, for instance, that the mountain larvae of the green frog (*Rana clamitans*) and wood frog (*R. sylvatica*) complete metamorphosis faster and at a larger size than their lowland counterparts in a common environment. Despite their higher genetic growth capacity, however, in nature they metamorphose later because of strong climatic constraints.

Again, similar to other taxonomic groups, anurans and urodeles from high-altitudes invest in larger eggs but reduce offspring number (Liao et al. 2014) and increase mean and maximum age, as well as maturation age (Zhang and Lu 2012). Apart from intrinsic trade-offs, hypoxia has been evoked as a possible cause of increased longevity in high-altitude regions (Zhang and Lu 2012).

11.4.4 Reptiles

Viviparity in squamate reptiles has been explained in terms of climate selection for longer periods of egg retention where juvenile mortality is high because of extended cold exposure (Tinkle and Gibbons 1977). However, this does not apply to the independent evolution of viviparity in freshwater fishes (Pollux et al. 2009) and amphibians (Vitt and Caldwell 2013). In viviparous lizards and snakes, gravid females actively thermoregulate and provide embryos of higher temperatures for development, a behaviour that reduces juvenile mortality as compared to conditions in nest regimes (Braña et al. 1991). Viviparity, however, requires modifications to

other reproductive features, such as eggshell thickness and clutch size, both decreasing with the degree of viviparity and elevation (Mathies and Andrews 1995). Moreover, pregnant females pay metabolic costs for maintaining higher body temperatures, as visibly appreciable in postpartum body condition. However, the ultimate consequences for survival depend upon a combination of factors, from stored reserves and thermal conditions to the capability of using current food intake during reproduction (Lourdais et al. 2002; Cox et al. 2010). Many reptiles are in fact predominant ‘capital breeders’, i.e. they use reserves gathered over long periods prior to the year of reproduction, but nevertheless are able to optionally integrate energy from current feeding (‘income’) (Shine 2005).

In oviparous species, a decrease in clutch size translates into an increase in offspring size (Sinervo et al. 1992), infrequent reproduction (Shine 2005) and enhanced annual survival rate (Adolph and Porter 1993). Lizards exhibit indeterminate and fully plastic growth (Sears and Angilletta 2003) with a few documented cases of countergradient variation (Sinervo 1990). Although no comparative analyses have addressed interspecific variation along elevation gradients, a trend for ‘slow’ life strategies in cold-environment or slow-metabolism taxa, in contrast to ‘fast’ strategies in hot-environment or fast-metabolism taxa, has been highlighted (Bauwens and Diaz-Uriarte 1997; Shine 2005).

11.4.5 Birds

Several comparative reviews on avian intra- and interspecific patterns highlight a strategy of reduced annual fecundity, e.g. reduced clutch size or reproductive attempts per year, with elevation. As an opposite pattern, the duration of the incubation and nesting phases increase with elevation (Krementz and Handford 1984; Badyaev 1997a; Badyaev and Ghalambor 2001; Boyle et al. 2015; Hille and Cooper 2015; Laiolo et al. 2015b). Ruling out the effect of body size, low predation pressures and poor food availability likely contribute to prolonged parental care, as a result of bird parents spending increasingly longer periods outside the nest (Boersma 1982). This fact inevitably slows the development of young, but protects parental survival (Martin 2002) and improves food provisioning where resources are scarce and scattered and where chicks have increased metabolic demands because of cold weather.

At the intraspecific level, survival has been shown to increase with elevation in some study cases (e.g. Bears et al. 2009), but pairwise comparisons of closely related species, subspecies or populations are not conclusive in this respect (Badyaev and Ghalambor 2001; Boyle et al. 2015). It is possible that large variations in extrinsic (environmental) mortality, essentially independent of the choices made by individuals, override slight differences in intrinsic mortality between entities with a great degree of shared history. Tests with phylogenetically and functionally diverse bird assemblages indeed suggest remarkable variation in survival patterns (Laiolo et al. 2015b; Bastianelli et al. 2017).

Elevation clines in reproductive allocation and parental care have crucial consequences for the expression of costly sexual characters in passerines with bi-parental care (Badyaev and Ghalambor 2001). Males from upland grounds have to shift rapidly from sexual to parental behaviours, which requires that testosterone be maintained at low levels, or to rapidly decline, to avoid an undermining of reproductive success by testosterone-driven aggressiveness (Apfelbeck and Goymann 2011). These conditions should tilt the balance between parental and mating effort of males towards the former, considering that opportunities for additional mating and extra-pair fertilizations may decline with elevation, because of low densities or synchronic reproduction. As a matter of evidence, Badyaev (1997b) and Snell-Rood and Badyaev (2008) found reduced plumage dimorphism and shorter and simpler songs in high elevation Cardueline species, while Apfelbeck and Goymann (2011) and Bastianelli et al. (2015) highlighted weaker male territorial aggressiveness in *Phoenicurus* and *Anthus* species.

11.4.6 Mammals

Literature is limited in mammals compared to other taxonomic groups. One possible explanation is that life-history strategies are constrained by aspects of the ecological niche (e.g. aquatic, aerial or terrestrial life; diurnal vs. nocturnal habits) with a poor relationship with elevation (Fisher et al. 2001; Bielby et al. 2007; Sibly and Brown 2007). Mammal growth and reproduction tend to be highly plastic (Hansen and Boonstra 2000), and temporal patterns are often more divergent than spatial ones. Seasonality is a strong driver of life-history diversification. Thus, elevational clines should be envisioned, but high latitudes have instead been the favourite scenario for analysing major temperature and photoperiod influences. Polyestrous rodents represent one of the best examples of seasonal diversification: spring-born young grow fast, mature early and reproduce in the year of birth, while those born later grow slowly, overwinter as immature and reproduce the next year (Bronson 1989).

When analysing variation across elevation, Bronson (1979), Zammuto and Millar (1985) and Yoccoz and Ims (1999) found that highland populations of ground squirrel (*Spermophilus columbianus*) and voles (*Chionomys nivalis*) have longer lifespans, lower litter sizes and later ages at reproduction than those from lowlands. Lower litter size in ground squirrels depends on reduced ovulation rates because embryonic mortality is low and decreases with elevation (Bronson 1979). A reduction in litter size with altitude has also been recorded in the deer mice *Peromyscus maniculatus* (Dunmire 1960; Fleming and Rauscher 1978) and holds at the interspecific level among species of this genus (Smith and McGinnis 1968). In the alpine collared pika *Ochotona collaris*, adult survival is the trait that contributes most to population growth rate, and fecundity is less variable than in other lagomorphs (Morrison and Hik 2007). As previously mentioned, buffering of survival and bet hedging are thought to secure persistence in alpine environments.

Among mountain goats (*Oreamnos americanus*), females augment parental care to enhance juvenile survival in high elevations (Festa-Bianchet et al. 1994). Male parental care, although rare in mammals, emerges as a facultative behaviour at very low population densities (Barash 1975) and in extreme cold, arid or seasonal environments (Kleiman and Malcolm 1981). In the dwarf hamster *Phodopus campbelli*, for instance, male presence is essential to guarantee pup survival and growth, because it alleviates female thermoregulatory stress and thus water loss due to maternal hyperthermia, which compromises milking (Wynne-Edwards 1995, 1998). Similarly, pups of the alpine marmot *Marmota marmota*, due to small sizes, have reduced thermal inertia and take advantage of the energy spent by all family members during hibernation ('social thermoregulation'; Arnold 1988). Young survival, in particular, is positively associated with the number of subordinate males, which also participate in the surveillance of the family's territory (Arnold 1993; Allainé and Theuriau 2004).

11.5 Empirical Evidence in Plants

11.5.1 *Interspecific Variation*

In mountain and alpine environments, life histories are often characterised by long-lived iteroparous perennial life cycles. A trade-off between allocation to vegetative growth and sexual reproduction is expected as a consequence of nutrient limitation. Thus, the increased allocation to vegetative growth should reduce the availability of resources for reproduction (Obeso 2002). In general terms, alpine and arctic plants invest more in maintenance and less in reproduction (Jónsdóttir 2011).

In the harsh climatic environment of high altitudes, new plant establishment is a particularly risky (unsuccessful) mode of reproduction because of the high nutrient demand of seed production (Watson 1984), infrequent germination and low seedling survival (Bliss 1971; Scherff et al. 1994). Accordingly, there may be a reduction in seed rain and seed bank size as elevation increases (Molau and Larsson 2000). The demography of alpine plant populations is often characterised by low seedling recruitment and high seedling mortality at early developmental stages compared with lower-elevation populations (Bliss 1971; Hautier et al. 2009; Milla et al. 2009). In general terms, this implies that the successful establishment ex-novo of new genets (independent physiological units, or clonal colonies, sensu Watson and Casper 1984) is infrequent. However, these paradigms regarding alpine plants are currently changing and seedling establishment may be more common and successful than previously thought (Jolls and Bock 1983; Chambers et al. 1990; Forbis 2003, Forbis and Doak 2004; Giménez-Benavides et al. 2007; Venn and Morgan 2009; Kim and Donohue 2011).

The main evidence of the rarity of seedling establishment in alpine plants is the fact that the size-class distributions within the populations are often characterised

by the absence of the smaller size-classes (Philipp 1997; Jónsdóttir 2011). These distributions may also be a consequence of longer intervals between ‘windows’ of regeneration by seeds in the extremely variable alpine conditions (Eriksson 1997). Additionally, taking into account that long-lived alpine plants may reach ages of one thousand years or more, the selective pressures that conditioned the establishment of the parent plant were likely not the same that seeds and seedlings currently face.

Persistence of established genets, through somatic maintenance, clonal growth and vegetative reproduction is thought to be one of the most remarkable adaptations to the conditions of high mountain habitats and its importance tends to increase with altitude. Survival of adult plants has been suggested to be a key demographic parameter for maintaining alpine plant populations, and their demography is often characterised by high adult survival compared with lower-elevation populations (Bliss 1971; Hautier et al. 2009; Milla et al. 2009; García and Zamora 2003; Kim and Donouhe 2011). As a consequence, the decline of annual species with increasing altitude is remarkable, as it is the number of long-lived species that relies on clonal reproduction for population maintenance (Stöcklin 1992; Klimes et al. 1997).

Despite the above generalisations, life histories of alpine plants are highly diverse due to a great variety of growth and multiplication models. This diversity may be associated with different growth forms and varying degrees of physiological integration within genets. Most alpine plants are clonal perennials, the lifespan of which is one order of magnitude longer than that of non-clonal perennials (de Witte and Stöcklin 2010). Clonal perennials range from ‘splitters’ to ‘extensive integrators’. In the former case, the new clonal individuals (ramets) split from the parental genet shortly after their development (seeds produced by agamospermy, bulbils, plantlets, and some bulbs and tubers) and in the latter, the offspring ramets (normally rhizomes) remain physiologically integrated with the parent genet throughout their lifetime. There is an intermediate situation (‘intermediate integrators’) in which the offspring ramets remain connected to the parental plant for a time, as is the case of stolons, rosettes, rhizomes and root shoots (Jónsdóttir 2011).

Arctic and alpine non-clonal perennial lifespans from several decades to more than one hundred years are common (Callaghan and Emanuelsson 1985) and genet age of ‘extensive integrator’ clonal perennials may reach over one thousand years or more. As an expected consequence of a trade-off between longevity and sexual reproduction, the allocation to sexual reproduction is generally lower in clonal than in non-clonal plants (Jónsdóttir 1995; Stenström 1999; Stenström and Jónsdóttir 2006).

Taking into account the reduction in reproductive allocation at high elevations, we can expect that plants have developed some adaptations in their life histories to reduce the risk of costly reproductive investment. In this sense, we can expect alpine plants to increase offspring survival throughout life-history variables related to parent care: larger seed size to produce larger seedlings, pseudovivipary (Lee and Harmer 1980) and nursing of seedlings to increase their survival. Established cushion plants (such as *Silene acaulis*) can act as nurses of seedlings increasing

their survival (Bliss 1971). This nursing effect has been mostly observed in an interspecific context. However, we can predict that this may be an important phenomenon from an intraspecific perspective, as has been proposed in environmental contexts others than alpine ones (Fajardo and McIntire 2011).

Pseudoviviparity consists of the formation of vegetative diaspores in inflorescences, with the already developed flower parts undergoing proliferation and transformation into leaf-like structures (Pijl 1972). Species with pseudovivipary are mostly found in arctic, alpine and arid environments. In the local high-altitude floras, the proportion of pseudoviviparous species reaches 10% and, in exceptional cases, even up to 25% (Sarapul'tsev 2001). These habitats may favour pseudovivipary because they are extraordinarily coarse-grained for seedling establishment and the probability of an offspring being dispersed to a suitable patch is very low. The success of pseudovivipary may also be related to the problems of establishment and growth in the short, cold growing seasons of these regions (Lee and Harmer 1980; Elmqvist and Cox 1996). Furthermore, parental care is not restricted to seedling establishment, as the survival of daughter ramets may be greatly enhanced by translocation of resources from the parental plant through the vascular connections. This extended parental care depends on the degree of physiological integration or independence and is prolonged in the case of 'extensive integrators' (Callaghan 1984; Jónsdóttir 2011). As a rather general trend, parental care to seeds is substituted by parental care to daughter ramets, which are much more costly to produce but exhibit much higher survival. Seedling survival is probably the most critical stage in the life histories of long-lived perennial alpine plants, determining species' distribution and range shifts (Kitajima and Fenner 2000).

Seed weight should be affected by altitude because heavier seeds are more likely to produce larger seedlings that successfully establish in harsh conditions (Westoby et al. 1992), which is in accordance with the 'stress-tolerance' hypothesis (survival depends on plant stress resistance). However, despite the fact that elevation gradients in seed mass have repeatedly been reported (Baker 1972; Blionis and Vokou 2005), findings were often conflicting and had not revealed any consistent pattern thus far. Although an increase in seed mass with elevation was reported by Pluess et al. (2005), there is also evidence of negative relationships between seed mass and elevation supporting the 'energy constraints' hypothesis, which states that lower temperatures and shorter growing seasons at higher elevations may reduce resource acquisition and the energy available for seed development and seed provisioning (Baker 1972; Körner 2003; Bu et al. 2007). Additionally, seed size is subjected to allometric constraints and thus determined by plant size variation with altitude.

In detail, Pluess et al. (2005) tested the hypotheses that between related species-pairs and among populations of single species a similar trend for increasing seed weight with increasing altitude should be present. These authors determined seed weights from 29 species-pairs, with each pair consisting of one species occurring in a lowland area and a congeneric species from a high altitude area. Compared to the related lowland species, 55% of the alpine species had heavier seeds, 3% (one species) had lighter seeds and 41% had seeds of approximately

equal weight. However, Wu and Du (2009), who examined the hypothesis of a positive effect of altitude on both interspecific and intraspecific variation in seed mass, found that in 50% of the 44 species that occurred in both low and high altitudes, seed mass increased with altitude, but decreased in the other 50%. Moreover, Wang et al. (2014) examined seed mass variation in 42 species of *Rhododendron* along an altitudinal gradient from a few hundred metres to 5500 m above sea level on the Tibetan Plateau. They found that seed length, width, surface area and wing length were negatively correlated with altitude, and positively with plant height. Conversely, Qi et al. (2014), using a large database involving 1355 species from the Tibetan Plateau, found a non-significant seed mass-elevation relationship across all species after controlling for phylogeny and plant height. These authors also found a mass-dependent response to the elevation gradient: smaller seeds tended to increase in mass with elevation but large seeds tended to decrease.

11.5.2 *Intraspecific Variation*

When the same plant species occurs along a mountainside, within-species variation in life histories is expected since a suitability gradient is found within each mountain range (Körner 2003). Depending on the biogeographic origin of the species, plants occurring at the highest or lowest altitudinal limits should face especially harsh constraints on reproduction and establishment via seeds (Hampe and Petit 2005; Arrieta and Suárez 2006; Giménez-Benavides et al. 2007). In this sense, the ‘centre–periphery’ hypothesis proposes that conditions for the regeneration of plant populations are less suitable in the boundaries than in the centre of the distribution area, and at the same time, life cycles should slow down at high altitudes (Lawton 1993; Vucetich and Waite 2003; Angert and Schemske 2005).

Arx et al. (2006) used the width of annual rings in roots to study plant demography along an altitude gradient after determining plant age and lifetime growth in three perennial forbs. For all three species, the plants from the highest altitudes tended to be considerably older and produced more flowering shoots than lowland plants. Highland plant growth, estimated by ring width, was approximately half that of lowland plants. However, ring width of the high-altitude plants increased during the first years and later decreased. These results highlight the importance of investing resources in plant growth during the first years to ensure plant establishment. This initial investment in growth is a characteristic behaviour of life cycles in which mortality decreases considerably with the age of the individual.

When comparing demography and life-history traits of populations of *Erysimum capitatum* from alpine and low-elevation populations, Kim and Donohue (2011) found that mortality of all life stages was higher at lower elevations than at an alpine site. At the same time, they found that low-elevation plants reproduced more quickly and were more frequently semelparous than alpine plants.

Thus, low-elevation semelparous populations depended primarily on seedling recruitment and precocious reproduction, whereas alpine plants tended to be iteroparous and to produce more vegetative rosettes. These results showed an altitudinal variation in parity (number of reproductive events), and its demographic consequences, indicating that plastic or evolutionary changes in this trait have a clear influence on population performance along altitudinal gradients.

As the allocation of resources to reproduction results in a reduction of allocation to vegetative growth and, therefore, an impact on future reproductive success, the trade-off between allocation to reproduction and vegetative growth is also a determinant of iteroparous perennial cycles within species. Hautier et al. (2009) conducted a transplant experiment to assess the influence of both the altitudinal origin of populations and the altitude of the growing site on vegetative growth and reproductive investment in *Poa alpina*. According to the general trend in plants, the variation in reproductive investment was mainly explained by plant size. However, the vegetative growth and the relative reproductive allocation decreased in populations originating from higher altitudes compared to populations originating from lower altitudes. They also found that the importance of plasticity was scarce in relation to genetic effects and interpreted these results as a consequence of local adaptations.

Gao-Lin et al. (2011) tested the hypothesis that seed mass was positively correlated with altitude within species in four congeneric *Saussurea* (Asteraceae) that occur in the Tibetan Plateau. They found a general trend of a significant increase in seed mass with altitude. Contrarily, Meng et al. (2014) showed that along an altitudinal gradient in the Hengduan Mountains, mean seed weight of *Sinopodophyllum hexandrum* decreased significantly. Pluess et al. (2005) compared seed weights among populations of four species from different habitats and with different life histories along an altitude gradient (*Scabiosa lucida*, *Saxifraga oppositifolia*, *Epilobium fleischeri* and *Carex flacca*). In all the four species, they found no indication for heavier seeds at higher altitudes. Similarly, in the cactus *Gymnocalycium monvillei* seedling height increased with altitude, whereas seed mass was not related to this variable (Bauk et al. 2015).

Assessing adaptive differentiation of plant populations along altitude gradients is useful for predicting how they may respond to climatic change. Local adaptation along altitudinal gradients has been demonstrated in several alpine plant species after reciprocal transplant experiments (Byars et al. 2007; Kim and Donohue 2013; Torång et al. 2015) or transplants to a common garden (Stenström et al. 2002). However, information about local adaptation in traits related directly to life history is still scarce. Leimu and Fischer (2008) reviewed the information about local adaptations and found that although local plants performed better than foreign plants in 71% of the studies, local adaptation, *sensu stricto*, was demonstrated in approximately 40% of the case studies.

Surprisingly, genetic diversity of alpine plant populations is not as depleted as predicted from small population sizes and repeated vegetative multiplication,

a fact that suggests that gene flow and repeated seedling recruitment during succession might be more frequent than commonly thought (Diggle et al. 1998; Pliess and Stöcklin 2004; Reisch et al. 2007).

11.6 Discussion

11.6.1 Current Patterns

This review shows that much of life-history variation in elevation is the result of direct physiological sensitivity to temperature and nutrient supply, which is then modified secondarily by evolutionary responses that refine the relationship with the environment. Generally, organisms as diverse as animal ectotherms, endotherms and plants inhabit mountaintops by adopting ‘slow’ life cycles, involving longer lifespan, delayed maturity, slow reproductive rates, including clonal or parthenogenetic spreading and strong inversions in parental care to augment juvenile survival where recruitment is limited. There are however exceptions, for instance, slow life cycles are precluded to obligatory annual organisms in seasonal environments. Moreover, traits may not reflect optimality at lower and upper margins of species ranges, also depending on the position of the mountain ridge with respect to species’ overall geographic distribution (Fig. 11.1). Jiménez-Alfaro et al. (2014) showed, for instance, that plant species from different geographic regions are filtered in different ways by altitude, and that constraints on reproduction and establishment via seeds may vary, being generally strong for lowland species at their highest elevation or arctic and alpine species at their lowest limits (Hampe and Petit 2005; Arrieta and Suárez 2006; Giménez-Benavides et al. 2007).

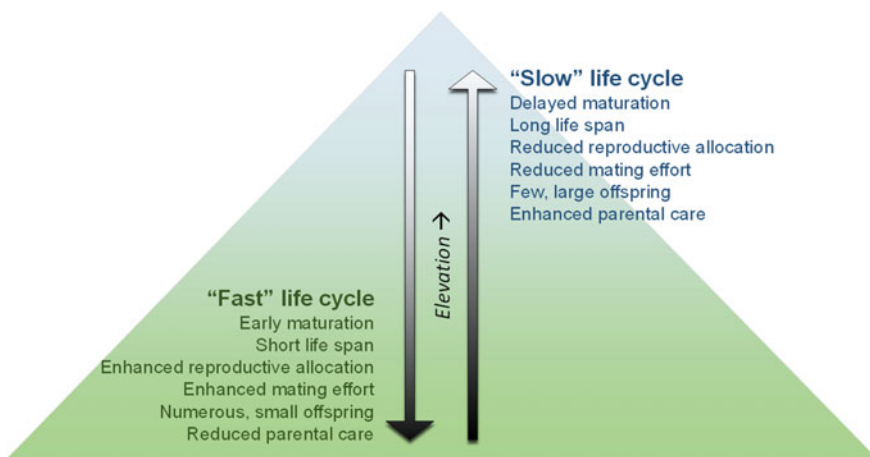
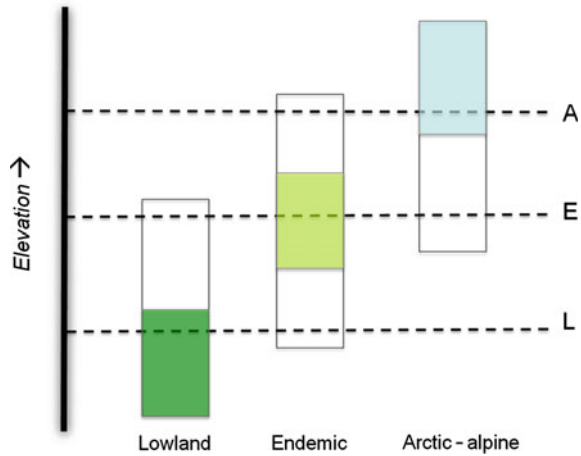


Fig. 11.1 Main trends of life-history variation observed along the elevation gradients

Fig. 11.2 Rectangles showing the distribution area of different species depending on their biogeographic origin. The centre of the distribution is depicted in *black* and the periphery in *white*. Letters A, E, L indicate locations with optimal conditions for regeneration of Arctic-alpine, Endemic and Lowland species, respectively, but non-optimal conditions for the other groups



Contrarily, species at the centre of their distribution areas (e.g. endemic species) should face optimal conditions for regeneration (Fig. 11.2).

11.6.2 Evolutionary and Plastic Responses to Environmental Change

A frequent assumption is that populations negatively affected by ongoing climate change, when lacking the plasticity to tolerate it, will migrate more readily than undergoing evolutionary change to produce new phenotypes. Implicit in this view is the observation that modern populations of many species that shifted ranges in the past display life-history adaptations to current climatic conditions. However, the tolerance ranges of migrating species are not ‘static’ during distribution shifts: differential survival of migrating individuals, or their propagules, sieve out genotypes that do not tolerate local conditions, and differential growth and reproduction further promote adaptation of physiological characteristics (Davis and Shaw 2001). In this scenario, negative genetic correlations among life-history traits, such as those between survival and reproduction, may slow (or impede) the responses to selection of single traits, as compared, for instance, to the responses of unrelated traits, as those conferring physiological tolerance (Davis and Shaw 2001).

Apart from dispersal and selection, gene flow and recombination are essential elements in evolutionary change during range shifts. When dealing with altitudinal migration, gene flow is facilitated by the proximity of neighbouring populations. In the case of species with broad elevational distribution, if the upper elevation limit is the leading edge of the migrating front, adaptations to the novel environment may be enhanced by gene transfer from the centre of the range. This feature would likely lead to the spread of ‘fast’ genotypes that may allow persistence in warmer conditions.

Although a ‘fast’ strategy may enhance the speed of range expansion (Burton et al. 2010), ‘slow’ cycles protect species from the dramatic loss of genetic variability during upward migration: when a few founders colonise a remote patch, delayed maturation allows genetic diversity to accumulate through recruitment of additional individuals (Austerlitz et al. 2000). It is also often argued that alpine specialists inhabiting narrow elevation bands may lack substantial genetic variability for traits under selection, but evidence of this phenomenon is not strong, because the distribution of these species is the result of past climate-driven shifts up and down elevation gradients that helped maintain genetic differentiation (Galbreath et al. 2009; Wachter et al. 2012). Hence, predicting evolutionary trajectories into the future must take into account the past persistence of many relict species (Hampe and Petit 2005).

The interactions between climate shifts with phenotypic plasticity or heritable variation in reaction norms are also crucial to envisage species responses to changing environmental conditions (Winkler et al. 2002; Both and Visser 2005; Jensen et al. 2008; Williams et al. 2015). Temperature increases may not necessarily have the expected worst impact on ectotherm metabolism because they may adjust thermoregulation and activity to prevailing temperatures (Aguado and Braña 2014), as alpine plants do with respiration (Larigauderie and Körner 1995). It is also worth stressing that warming reduces some of those constraints dominating alpine life, as evidenced by improved survival or reproductive output of a number of species (e.g. Day et al. 1999; Erschbamer 2007; Ozgul et al. 2010). Similarly, Barrett et al. (2015), using data from a long-term research project in the Arctic, demonstrated enhanced reproductive allocation in connection with improved air and soil temperature. Differences in species’ responses are, however, huge, making generalisations of responses and predictions of effects very weak. Experiments and observations within the same community or environmental context often highlight highly idiosyncratic responses in growth and reproduction to changing temperature and resource availability (Wookey et al. 1993; Arft et al. 1999; Dorman and Woodin 2002; Wipf et al. 2009).

11.6.3 Demographic Responses to Environmental Change

Patterns of life history determine the dynamics of populations when facing environmental variation, and life-history traits have a differential influence in this process. Perturbations (either cyclic or stochastic) can trigger substantial fluctuations in population size when reproductive parameters have the greatest influence on the finite rate of population growth, corresponding to a ‘fast’ life strategy. In contrast, perturbations are buffered when survival parameters have the largest relative influence on growth rate, i.e. a ‘slow’ strategy (Sæther and Bakke 2000; Oli and Dobson 2003). Therefore, when facing environmental change, a ‘slow’ life strategy is expected to confer more stable dynamics, high resistance and low resilience, as opposed to a ‘fast’ life strategy, which induces more cyclic or chaotic

population dynamics and low resistance, but a greater chance of recovery. Processes like demographic buffering (temporal stability) and demographic compensation (spatial compensation) may buffer local alpine populations against trends in environmental conditions (such as climate warming) (Villemas et al. 2015), although such compensatory responses may not last indefinitely (Doak and Morris 2010).

11.6.4 Future Research

In spite of widespread evidence of adaptations to climate in the past, there is a need to assess whether these changes will occur as readily during the present period of climate change since the range shifts documented in the past are below the rates required to track climate in the future (Davis and Shaw 2001). More experiments coupled with quantitative genetics are required to appreciate the magnitude of genetic constraints and genetic variation for traits critical to survival and reproduction, as well as molecular and demographic studies assessing the potential for dispersal and gene flow.

This overview highlights the scarcity of information and the gaps in our knowledge about life-history variation along elevation gradients. There is a need to expand the taxonomic focus because there has been a disproportionate effort on northern-latitude cold environments (such as the Arctic) compared to mountain and alpine systems in many groups. Life-history knowledge should also be improved: reproductive variables such as seed, clutch or litter size or number have been a favourite target of research, but lifespan and age at first reproduction are virtually unknown for the majority of alpine species. Ultimately, processes within and among species should be integrated, such that their changes can be linked to community-wide processes. This integration will improve our capability for predicting the response of alpine flora and fauna to the combinations of current, novel environmental drivers.

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