

Terrestrial insects along elevation gradients: species and community responses to altitude

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ABSTRACT

The literature on the response of insect species to the changing environments experienced along altitudinal gradients is diverse and widely dispersed. There is a growing awareness that such responses may serve as analogues for climate warming effects occurring at a particular fixed altitude or latitude over time. This review seeks, therefore, to synthesise information on the responses of insects and allied groups to increasing altitude and provide a platform for future research. It focuses on those functional aspects of insect biology that show positive or negative reaction to altitudinal changes but avoids emphasising adaptation to high altitude *per se*. Reactions can be direct, with insect characteristics or performance responding to changing environmental parameters, or they can be indirect and mediated through the insect's interaction with other organisms. These organisms include the host plant in the case of herbivorous insects, and also competitor species, specific parasitoids, predators and pathogens. The manner in which these various factors individually and collectively influence the morphology, behaviour, ecophysiology, growth and development, survival, reproduction, and spatial distribution of insect species is considered in detail. Resultant patterns in the abundance of individual species populations and of community species richness are examined. Attempts are made throughout to provide mechanistic explanations of trends and to place each topic, where appropriate, into the broader theoretical context by appropriate reference to key literature. The paper concludes by considering how montane insect species will respond to climate warming.

Key words: adaptation, ecophysiology, behaviour, life history, genetics, performance, host plant, population dynamics, community dynamics, climate change.

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I. INTRODUCTION

Many insect species are broadly distributed along elevation gradients, such that populations living at the upper and lower altitudinal extremes experience quite different environmental conditions, especially with respect to local climate. This has clear implications for our general understanding of the biology of species and their distributions. The comparative study of species ecology along altitudinal or latitudinal transects/gradients may provide clues to the likely response of both species and communities to climate change at any one point over time. Pickett (1989) referred to this analogue approach as space for time substitution. There are, however, significant differences between the characteristics of typical altitudinal and latitudinal gradients. The former are usually characterised by rapid environmental change over short horizontal distances (in km), whereas the latter usually represent relatively gradual change of the same approximate magnitude over much longer horizontal distances (in 100 km). This in turn accentuates differences in latitude-dependent parameters along the gradient, particularly light availability and day length, with altitudinal gradients having comparatively minimal variability.

This paper investigates the way that species of insects and allied groups living on mountains respond to the steep environmental gradients that define their habitat. The nature of mountain gradients is initially characterised, with the important individual physical parameters that vary along altitudinal gradients examined in isolation and combination. The responses of insect species to these gradients, both directly and mediated through their host plant, are then discussed at the levels of the individual, population and community. The intention is to provide an overview of changing adaptations and variations in insect biology along altitudinal gradients and not to discuss adaptation to the high mountain environment *per se*, which is already adequately documented (Mani, 1962, 1968; Coulson & Whittaker, 1978). Adaptations for survival in cold montane environments are particularly well covered elsewhere and are not discussed in detail (Sömme, 1999; Bale, 2002).

Emphasis is placed, therefore, on the functional aspects of insect biology that show clear measurable responses to changing altitude. Consideration is also given to the particular vulnerability of mountain insects to global warming.

II. PHYSICAL GRADIENTS ON MOUNTAINS

The main general changes observed as one ascends an altitudinal transect are well known, potentially involving changes in temperature, precipitation as rain or snow, partial pressure of atmospheric gases, atmospheric turbulence and wind speed, and radiation input, including short-wave ultra violet (UV) radiation at different wavelengths (Barry, 1992). These parameters, as described briefly below, are often strongly interactive and together they create the environmental envelope within which montane insect species survive and reproduce. Furthermore, they combine to produce a general decrease in the overall structural complexity of the insects' habitat with increasing altitude.

(1) Temperature lapse rate

The temperature lapse rate (decrease) with respect to increasing altitude in the free atmosphere is generally taken to lie between 5.5 and 6.5 °C for each 1000 m of ascent (Anslow & Shawn, 2002) and this range has often been applied to mountain ecosystems. While this range holds true as a generality, the lapse rate on mountains varies significantly with respect to both local topography and conditions and to the wider meteorological circumstances (Dodson & Marks, 1997; Lookingbill & Urban, 2003; Rolland, 2003). Variation can result from time of year or day, aspect, vertical atmospheric mixing and wind speed, atmospheric moisture, cloud cover and surface radiation balance (Pepin, Benham & Taylor, 1999; Pepin, 2001). Thus lapse rates may differ for example between areas with continental climates, characterised by hot summers and reduced cloud cover, and maritime areas with cooler, cloudier summer conditions (Pepin, 2001). Seasonal differences may also become accentuated,

and thus increasingly important, during the active growth phase of an insect. Vertical temperature profiles can be disrupted locally by cold winds from glaciers and by temperature inversions, in which a cold body of air becomes trapped in a valley below a layer of warmer air, thereby giving higher temperatures at higher elevations (Tenow & Nilssen, 1990). Furthermore, temperatures within vegetation or the surface soil layers may differ significantly from ambient air temperature and this may be increasingly important for insects at higher elevations (Geiger, Aron & Todhunter, 1995). In general, however, an insect species will experience a decreasing annual thermal budget for growth and development and an increased exposure to temperature extremes with increasing elevation. Mean temperatures will be lower on average, meaning that critical temperature thresholds for growth, development and activity will be exceeded less frequently and for shorter periods.

(2) Short-wave radiation input

Short-wave radiation within the UV band is known to have potentially deleterious effects on living organisms (Caldwell *et al.*, 1998). The general tendency is for UV radiation input to rise with increasing altitude (Tenow & Nilssen, 1990; Dvorkin & Steinberger, 1999; Iziomon & Mayer, 2002; Schmucki & Philipona, 2002). The extent of the rise at any one location varies, dependent on wavelength. Comparisons between alpine stations at 3576 m (Jungfraujoch) and (577 m) (Innsbruck) suggest rises of around 8–9, 9–11 and 18–19% 1000 m^{-1} in annual total UV, UV-B and UV-A radiation, respectively (Blumthaler, Ambach & Rehwald, 1992). Similar comparisons between Mauna Loa (Hawaii, 3400 m) and Lauder (New Zealand, 370 m) show increases of 17 and 26% for UV-A and UV-B over the entire gradient (McKenzie *et al.*, 2001). This increase is greater than the maximum rise in incident UV-B associated with the ozone hole over countries such as New Zealand. Total measured UV is further modified by several factors, particularly solar zenith angle, cloud cover, surface albedo effects and atmospheric levels of aerosol pollutants (Blumthaler, Ambach & Salzgeber, 1994; Alados-Arboledas *et al.*, 2003; Piacentini, Cede & Barcena, 2003).

(3) Partial pressure of respiratory gases

The partial pressure of atmospheric gases, including oxygen and carbon dioxide, decreases approximately linearly with increasing altitude (Peacock, 1998). Thus, for any insect the availability of oxygen falls by around 11, 31 and 46% at 1000, 3000 and 5000 m altitude, respectively, compared with sea level. The thinner air at higher altitudes has implications for both convective energy transfer in exothermic organisms and their ability to maintain flight performance. Similarly, reduced CO_2 levels have implications for the growth of insect host plants.

(4) Precipitation

Precipitation is a major factor affecting the diversity, distribution and productivity of insect host plants and the nature of the associated soils. Orographic precipitation in the form

of rain or snow often rises significantly along an altitudinal gradient (Egger & Hoinka, 1992). This in turn leads to increased nutrient leaching from the soil or, where rainfall input is consistently high, the formation of organic peat soils that provide larval habitats for many insect species. Conversely, larval insects inhabiting such habitats are highly susceptible to sporadic drought that may result in local population extinction (Coulson, 1962).

While the mechanisms producing orographic rain are well understood, the accurate prediction of rainfall patterns over complex mountain topography is less precise and may be subject to long-term change (Ueyoshi & Han, 1991; Weltzin *et al.*, 2003). The stable generation of orographic precipitation can be best illustrated using the example of an isolated high mountain such as Teide (3718 m) on Tenerife. Here moist air carried by the North East Trade Winds hits the land and rises, producing a layer of cloud and a sharp peak in precipitation at intermediate altitudes of between 400 and 1900 m. Cloud cover in turn reduces surface temperatures. Above and below the cloud layer precipitation is greatly reduced and temperatures are often much higher and the conditions for insects very different.

The presence of a thermally protective snow blanket can protect insects from extremes of air temperature (Coulson *et al.*, 1995; Bird & Hodkinson, 1999). The amount and extent of snowfall, however, may vary significantly between years (Latarnser & Schneebeli, 2003). The annual variation in snowfall may be overlaid by longer term trends, although the direction of these trends may differ between altitudes (Latarnser & Schneebeli, 2003). Persistence of snow cover during the spring significantly affects early-season growing temperatures and the duration of the growing period for insects (Coulson *et al.*, 1995).

(5) Turbulence and wind speed

Wind speed generally increases significantly with increasing altitude but varies locally, being highly dependent on surface topography. Sustained high wind speeds have important implications for small organisms such as insects that normally undertake routine local flight activity – there is a tendency for the population to be blown away. However, the impact of moving air is not always negative. It may also serve to move and disperse insects around to their particular benefit and, in addition, many montane habitats receive a continual rain of allochthonous insects and/or detritus that provides energy subsidies that support the resident species (Hodkinson, Webb & Coulson, 2002).

III. DIRECT ALTITUDINAL EFFECTS ON INSECT SPECIES

(1) Wing size polymorphism and variation

Several studies suggest that insect communities living at higher altitude show a greater incidence of brachypterous or apterous forms compared with equivalent communities at lower elevation and that this is associated with reduced flight activity in harsh cold environments (Strathdee & Bale, 1998).

Examples include aphids (Strathdee *et al.*, 1995), carabid beetles (Honek, 1981; Liebherr, 1992), grasshoppers (Dearn, 1977), lacewing flies (Neuroptera) (Oswald, 1996), scorpion flies (Boreidae: Mecoptera) and some groups of Diptera, especially Tipulidae and Chironomidae (Hadley, 1969; Byers, 1983). One specialised flightless order of insects the Grylloblattodea is adapted solely to montane habitats. Wing reduction may be observed both as a polymorphism within a single species or among an increasing proportion of species within a community. In the carabid beetle *Agonum retractum* in the Rocky Mountains of Canada, both males and females exist as fully winged and brachypterous forms within the same population (Carter, 1976). Heterozygous long-winged females produce both long- and short-winged forms that probably play different roles in migration and colonization. The direct link between increasing brachyptery and altitude, however, is contentious as it clearly involves an energy trade off between the advantages of flight for dispersal and mate finding, and the conservation of scarce energy resources for investment in reproduction when ambient temperatures are rarely conducive to flight activity (Zera & Harshman, 2001). Brachyptery, however, is also common at low altitudes and may in reality be more often associated with habitat stability and age rather than altitude *per se* (Roff, 1990; Wagner & Liebherr, 1992; Denno *et al.*, 1996). It is probably an important determinant of geographical and regional distribution patterns as demonstrated for carabid beetles in northern Spain (Gutierrez & Menendez, 1997). Brachyptery and consequent loss of flight ability also has important implications for gene flow and body size within species (see later).

One might predict that wing size, of fully winged individuals, will be proportionately greater in high-altitude populations, to cope with the thinner air encountered during flight. In actively flying insects, wing loading will be higher at greater elevations, suggesting that populations are subjected to stronger selection for wings of increased surface area, linked to thinner air (Norry, Bubbly & Loeschke, 2001). Such differences are seen in males of the fly *Drosophila flavopilosa* in Chile, in which both wing length and breadth increased with elevation (Budnik, Brncic & Acuna, 1988). Wing size for females, perhaps subject to different selection pressures, was, however, greatest at mid-altitudes.

(2) Colour polymorphisms, absorbance and spectral reflectance

For ectothermic insect species living under the varying temperature regimes on mountains it is potentially advantageous to adjust body temperature to exploit particular altitudes. In part this may be achieved behaviourally through thermal basking, as in many butterfly, grasshopper and tiger beetle species whose thermally related behaviour may vary at different elevations (Kingsolver, 1983b; Gillis & Smeigh, 1987; Schultz, Quinlan & Hadley, 1992). For other species it is principally achieved passively through the spectral reflectance/absorbance properties of the body surface. Put simply, dark colouration at high altitudes maximises heat absorbed: lighter or reflective colouration minimises heat gain under warmer conditions at lower elevations (Heinrich,

1996). Several insect species exhibit colour pattern polymorphism or body colour variation with respect to altitude. The most widely studied example is the polymorphic spittlebug *Philaenus spumarius* in which the proportion of melanistic morphs in the population often, but not invariably, tends to increase with altitude (Halkka, Vilbaste & Raatikainen, 1980; Honek, 1984; Berry & Willmer, 1986). Similar altitude-related colour polymorphisms are seen in *Eupteryx* leafhoppers (Stewart, 1986), ladybirds (Scali & Creed, 1975; Brakefield & Willmer, 1985) and grasshoppers (Guerrucci & Voisin, 1988). Alpine butterfly species of the genus *Colias* likewise show parallel altitudinal variation in the spectral reflectance of their ventral surface (wings folded) related to colour (Roland, 1978), which when combined with increased fur insulation on the ventral thorax and solar basking, raises the body temperature to the 30–40 °C required for flight (Kingsolver, 1983b). The adaptive significance of other altitudinal clines in insect morphology, however, such as the reduced hind-wing spot number in the satyrid butterfly *Coenonympha corinna*, are less obvious (Brunton *et al.*, 1991). The extent of atmospheric pollution, by absorbing radiation, and non-prescribed habitat effects, may also influence the proportions of colour polymorphs present in the population (Scali & Creed, 1975; Boucelham & Raatikainen, 1987; Boucelham, Hokkanen & Raatikainen, 1988). It has been suggested that among phytophagous chrysomelid beetle species, feeding on exposed leaf surfaces in mountainous areas of Europe, Russia and Japan, differences in metallic colouration may relate directly to UV exposure (Fujiyama, 1979; Mikhailov, 2001). Species, such as *Oreina sulcata*, for example, which is normally green at low elevations, show significantly increased percentages of darker and more reflective metallic morphs at higher elevations across a broad geographical area, leading to the suggestion that such species might serve as indicators of enhanced UV radiation input (Mikhailov, 2001).

(3) Variation in insect size

The literature contains many examples showing that the mean body size of an insect species may change along an altitudinal (or latitudinal) gradient. Differences arise from variation in rates of growth and development at different temperatures and this has important implications for overall reproductive success. The problem is that some species show increasing size with increased altitude while others show the reverse trend (Hawkins & deVries, 1996; Chown & Klok, 2003). Size increases are generally explained by a negative relationship between developmental temperature and size among ectothermic animals in a non-resource-limited environment (Atkinson, 1994; Smith *et al.*, 2000). Size decreases, by contrast, as in the *Cacopsylla* species feeding on *Salix lapponum* in Norway, are generally thought to result from resource limitations, often linked to seasonal resource availability, restricting potential growth (Hill, Hamer & Hodkinson, 1998). Support for these explanations comes from trends in body size of several common weevil species over a 1000 m altitudinal range on subantarctic islands (Chown & Klok, 2003). In the warmer, but still cool, non-seasonal environment (Marion Island) mean size increased

with altitude but in the colder seasonal environment (Heard Island) more likely to impose significant resource limitation at higher altitude, size decreased. By contrast, both body size increases and decreases with increasing altitude were found in tenebrionid beetle populations in the Negev Desert along similar gradients, although here the effect of rainfall on productivity may have been a confounding factor (Krasnov, Ward & Shenbrot, 1996). Costa Rican butterfly species show similar contrasting trends in wing size with altitude, with some even reaching maximum wing length at intermediate elevations (Hawkins & de Vries, 1996).

Different life-history strategies within a seasonal environment may potentially produce either stepped or continuous clines in body size along altitudinal gradients (Roff, 1980). Continuous clines tend to be produced where a species maintains a univoltine life history throughout its altitudinal range. Stepped clines, by contrast, may occur where a species switches from a uni- to a bivoltine life cycle. At the altitudinal point of transition the time available for development within the growing season is abruptly halved, resulting in the bivoltine population tending to produce smaller individuals.

At the community level there is evidence from carabid beetles in Spain that among brachypterous, but not macropterous species, body size is positively correlated with the extent of their regional distribution (Gutierrez & Menendez, 1997). Often there is a general decrease in the mean size of individual species within insect communities with increasing elevation (Janzen *et al.*, 1976).

(4) Thermal tolerance and thermal requirements

The upper and lower altitudinal distributional limits of any insect species will, unless other factors intervene, be determined by the capacity of the species to match its thermal tolerance range to the altitudinal temperature profile of its habitat (Hodkinson *et al.*, 1999). This is particularly important for long-lived cold-adapted species confined to high altitudes, such as the Grylloblattodea, which rapidly succumb to heat stress at lower elevations (Morrissey & Edwards, 1979) and for warm-adapted species at their altitudinal limit. In practice, however, it is usually the ability of a species to gain sufficient heat energy from its environment to complete development within a restricted period, an effect often mediated through its host plant, that often determines the upper distributional limits (Roff, 1980; Bird & Hodkinson, 1999).

Buse, Hadley & Sparks (2001) compared the distribution range of species along a 400 m transect on Snowdon, Wales, with their wider distribution within the UK. Optimal body temperature and supercooling point were used to indicate thermal tolerance. Mountain-dwelling and more widespread species differed little in their abilities to withstand lethal cold temperatures, with both freezing between -5.8 and -6.9 °C. Freeze tolerance was surprisingly more evident among the widespread species. The main difference lay in the optimal body temperature, which in the smaller mountain-dwelling carabids *Patrobus assimilis* and *Nebria rufescens* was 5.6 and 7.1 °C, respectively, compared with values of 12.9 – 15.5 °C in the widespread species. The mountain-dwelling species were thought to survive by a

combination of moderate cold tolerance and selection of thermally favourable winter microhabitats, coupled with an optimum metabolism suited to lower ambient temperatures.

Similarly, overwintering rosebay willow herb psyllids *Craspedolepta nebulosa* and *C. subpunctata* in upland Norway can withstand both short- and long-term exposure to low temperatures below -17.5 °C and short-term exposures to high temperatures of over 40 °C (Bird & Hodkinson, 1999). These temperatures are rarely encountered in the insects' preferred habitat where, for example, winter temperatures below a protective deep snow blanket rarely fall much below 0 °C, despite potentially lethally cold air temperatures. Their distribution correlates strongly with their minimum heat budget for development rather than extreme temperatures.

Gaston & Chown (1999), using an assemblage of 26 species of African dung beetles along a 2500 m elevation transect, showed that altitudinal ranges of individual species within the overall assemblage became wider as elevation increased. The explanation seems to lie in the critical thermal minima of species changing more rapidly than the critical thermal maxima, producing a wider tolerance band. It is suggested that this wider tolerance band allows species to withstand wider variations in the climate they experience. This perhaps should be set against the consequences of possible global warming where it is predicted that the altitudinal range of some host plant species and communities will effectively increase as temperatures rise (Woodward, 1993).

One consequence of temporal variation in temperature is that the upper distributional limits of species may fluctuate on a seasonal or annual basis. The upper altitudinal limit of the spittlebug *Neophilaenus lineatus* on Ben Lomond, Scotland, for example, varied from 530 to 900 m over a 10 year period (Whittaker & Tribe, 1996). Similar distributional effects are found in checkerspot butterflies, with larval distribution and relative times of adult emergence varying between years along the same slope (Weiss *et al.*, 1993). Effects of fluctuating annual mean temperature on development, rather than lethal temperature extremes, provided the most plausible explanation.

(5) Response to declining oxygen availability

Populations of insect species faced with declining oxygen availability per unit volume of air may need to increase their rate of air intake through their tracheal system if they are to maintain normal activity levels. This in turn might lead to an increased rate of water loss through the respiratory exchange pathway, although this might be partially offset by a lower frequency of discontinuous gas exchange cycles and/or the potentially moister conditions pertaining at higher elevations (Chown, 2002). In parallel, selection may favour high-altitude populations, which when faced with a lower mean temperature, are able to respire more effectively at a given temperature than their lowland counterparts (Chown & Gaston, 1999). Conversely, if the insect is unable to compensate for decreased oxygen availability then this might be reflected in its energy allocation budget and growth performance.

Evidence to test these ideas is sparse. Populations of the Californian grasshopper *Melanoplus sanguinipes* from high

altitude exhibit, as predicted, greater water loss and higher mass specific rates of respiration at a given temperature than lowland populations (Rourke, 2000). Similar altitudinal differences were found among populations of the montane grasshoppers *Melanoplus dodgei*, *Trimerotropis pallidipennis* and *Aeropedullus clavatus* (Suanraksa, 1956; Massion, 1983). In the latter species there were, however, no significant differences in the total cuticular lipids and hydrocarbons linked to the prevention of water loss, suggesting that water was lost mainly through the spiracles (Hadley & Massion, 1985). Populations of the Antarctic beetles *Perimylops antarcticus* and *Hydromedion sparsutum* on South Georgia showed little difference in respiration rate over a small altitudinal range of 200 m, except for larvae of *P. antarcticus*, which exhibited the predicted increased respiration at higher altitude (Sömme *et al.*, 1989). Limited evidence also exists for differences in respiration per unit body mass and/or temperature sensitivity of respiration rate among closely related species of harvester ant (*Pogonomyrmex* spp.) distributed along an altitudinal gradient in California (Mackay, 1982) and in the cicindelid beetle *Cicindela longilabris* over a 3000 m altitude range in the USA (Schultz *et al.*, 1992).

(6) Variation in insect life history and the significance of diapause

Insects with a broad altitudinal distribution face the general problem of adapting their life history to compensate for deteriorating environmental conditions for growth and reproduction, particularly decreasing temperatures, with increasing altitude. Different species respond to this challenge in different ways, depending on their particular biology. The opportunities for adaptation are governed by the need to maintain synchrony with the seasons, and in the case of herbivorous insects, with the phenology of their host plant (Tauber, Tauber & Masaki, 1986). Adaptation can involve: (a) reduced number of instars; (b) reduced number of generations per annum; (c) extending life cycles beyond one year; (d) reduced temperature thresholds for development; (e) accelerated development at lower temperatures; (f) shorter diapause at lower temperatures. In each case the control mechanisms that maintain seasonal or host-plant synchrony need to remain intact. Often the response is mainly phenotypic rather than genetic, thus displaying the inherent plasticity achieved within insect life histories (Blanckenhorn, 1997).

Some insects such as the alpine collembolan *Isotomurus alticola* and the cricket *Allonemobius fasciatus* compensate for a shorter growing season at higher altitude by reducing the number of instars during their development (Tanaka & Brookes, 1983; Zettel, 2000). This has clear implications for body size achieved, with the resulting adult insects being smaller and having potentially reduced fecundity. Instar reduction in *A. fasciatus*, in common with some other crickets, is triggered by the delayed start of development within the growing season. Nymphs at higher altitude are exposed, during their developmental phase, to shorter declining day lengths than those at lower altitudes (Tanaka & Brookes, 1983).

Reduction in the number of generations per annum with increasing altitude is observed in many insect species. Adult sepsid flies, for example, show two separate seasonal peaks of abundance at high elevations in northern England, compared with four or more at lower elevations, suggesting a marked reduction in the number of generations (Randall, Coulson & Butterfield, 1981). Several species of butterfly in Britain show a similar altitudinal trend in voltinism (Pollard & Yates, 1993). The lycaenid *Aricia agestis* in N. Wales, for example, has two generations per annum at warmer low-elevation locations but only one generation at cooler higher elevations (I. R. Wynne, personal communication), although in this case the picture is slightly complicated by the ameliorating effects of aspect.

For any species the growing season will be shorter at higher compared with lower altitudes. Species at higher altitude may well enter overwintering diapause sooner (or terminate later) than those at low altitude, although slow-growing species at low altitude may similarly enter diapause early. Given the fact that day length tends to be constant along a short altitudinal gradient one might predict that if species are locally adapted and diapause is determined by photoperiod, then the day length triggering diapause would be significantly longer in high- *versus* low-altitude populations of the same species. There is little evidence to support this suggestion. Among populations of the dung flies *Scathophaga stercoraria* and *Sepsis cynipsea* in Switzerland, the critical day length varied only slightly, indicating weak genetic differentiation, with respect to altitude (Blanckenhorn, 1998). Both species appeared primarily to use temperature rather than photoperiod as the timing cue. Entry into diapause was, however, more rapid at high elevation in *S. stercoraria*.

For some insects with a univoltine life history the potential exists to extend the life cycle with increasing altitude over two or more years. For herbivorous insects feeding on deciduous plants this creates a particular problem in that the ability to synchronise with the annual phenology of its host is potentially lost. The most successful insects tend to be those feeding on evergreen plants or polyphagous species that are not dependent on a single plant host. For example, the heather psyllid, *Strophingia ericae* Curtis, feeding on heather, *Calluna vulgaris*, throughout its range, has a one year life history at low elevation but is semivoltine at higher elevations in the UK (Hodkinson, 1973*a,b*; Hodkinson *et al.*, 1999; Butterfield, Whittaker & Fielding, 2001). Life cycle duration is controlled by the effects of day length and temperature on the rate of development of nymphs, which hatch over an extended summer period. The moult to instar 3 is delayed at long day length and that to instar 5 is delayed by short day length. Together this ensures that nymphs complete their development within one year at warmer lower elevations whereas at cooler higher elevations nymphs overwinter twice, first predominantly in instar 2 and then mainly in instar 5. This in turn ensures that, despite the two year duration of the life cycle, adults are produced every year and the insect is able to occupy the full altitudinal range of its host plant (Miles, Bale & Hodkinson, 1998; Butterfield *et al.*, 2001). This control mechanism appears to be species specific, as the closely related species *S. cinerea* on *Erica*

cinerea does not, despite the availability of its host at higher altitudes, exhibit a switch from annual to biennial life history and as a result its distribution is greatly restricted within the altitudinal range of its host plant (Hodkinson *et al.*, 1999). Similar, extensions of life cycles at higher altitudes are known for several insect groups including predatory carabid beetles (Butterfield, 1986, 1996; Refseth, 1988; Sparks, Buse & Gadsden, 1995; Sota, 1996), scarab beetles (Fujiyama, 1997) and bibionid flies (Skartveit & Solhoy, 1997). The converse occurs in the montane crane fly *Tipula montana*, which normally has a two year life cycle in the UK, but where some individuals within the population complete their cycle in one year at warmer lower altitudes (Todd, 1996). An important consequence of moving from an annual to a biennial life cycle is the requirement to overwinter in two different life stages, with the resulting implications for cold-hardiness (Sota, 1996).

The timing and synchronicity of the life cycles of montane insects is thus primarily determined by a photoperiod or temperature-controlled diapause acting during the insects' development, thereby ensuring that species only become active when conditions are suitable for growth, development and reproduction (Butterfield, 1976*a*; Butterfield & Coulson, 1988; Butterfield *et al.*, 1999, 2001; Fielding *et al.*, 1999). In widespread species, such as the grasshopper *Melanoplus sanguinipes* in the USA, which ranges from sea level to 3000 m, and with a life cycle ranging from biannual through annual to biennial, variation in diapause responses in the egg, and occasionally the second-stage larvae, are crucial in matching the life history to the varying habitat template (Dingle, Mousseau & Scott, 1990; Köhler, 1991).

Many insect species that maintain an annual life cycle over a wide altitudinal range have additional physiological mechanisms that enable them to maintain synchronicity and minimize, as far as possible, variation in the timing of the life cycle. Good examples include the montane crane flies *Tipula subnodicornis* and *Molophilus ater* in northern England (Coulson *et al.*, 1976). *T. subnodicornis* displays a gradual reduction in the (Q_{10}) rate for development in final-instar larvae as mean temperature increases. This ensures that development rates are slowed towards the end of the life cycle in warmer conditions, thereby minimising the effect of temperature variation on the duration of larval development over the species altitudinal range (Butterfield, 1976*b*). The rate of larval development of *M. ater*, by contrast, appears to be largely independent of temperature (Coulson *et al.*, 1976). Similarly, over an altitudinal range of 440 m, date of egg hatch in the spittlebug *Neophilaenus lineatus* varied by up to four weeks. However, because of the later hatch, larvae at higher altitudes developed more rapidly at higher mean temperatures than if they had hatched earlier. This partially compensated for their late start and allowed them by the time of adult emergence to narrow significantly the phenological timing difference compared with the lower elevation population (Fielding *et al.*, 1999). Conversely, at their lower temperature limits some insect species appear to compensate for low mean temperatures by completing their development within a lower thermal budget (measured as day degrees above 0 °C) than under warmer conditions. Good examples include the psyllids feeding on *Salix* spp. and

Epilobium angustifolium (Hill & Hodkinson, 1995; Hodkinson, 1997; J. M. Bird & I. D. Hodkinson, unpublished data). The extent to which these different responses result from variations in lower development threshold temperatures (LDT) or in the sums of effective temperatures (SET) remains largely unestablished. However, an inverse relationship between LDT and SET is suggested by Honek (1996), based on latitudinal trends.

For animals with usually short, free-running, non-synchronous life histories, such as the collembolan *Folsomia octoculata*, the duration of the life cycle tends to increase gradually with increasing elevation (Tamura & Mihara, 1977).

(7) Fecundity

Insects might be predicted to show declining fecundity with increasing altitude. This may be related to decreasing body size as discussed earlier, to lower food quality or to the shorter time available for oviposition. However, evidence from altitudinal transects to test these predictions is surprisingly scarce. The grasshoppers *Kosciuscola conatus*, *K. usitatus* and *Praxibulus* sp. in Australia, for example, all show a pattern of decreasing egg production per female with increasing elevation (Dearn, 1977). The reduction results from a decrease in number of egg batches laid: mean number of eggs per batch actually increased while egg size remained constant. Egg production in *Cotias* butterflies at high elevations can be less than half that at lower elevations (Kingsolver, 1983*a*). This is attributed to females operating at below their physiological maximum owing to altitudinal limitation of flight activity, together with heritable differences in resource allocation to oocytes (Springer & Bloggs, 1986; Bloggs & Murphy, 1997). The fly *Drosophila teissieri* shows a similar smooth decline in fecundity with increasing altitude. Crosses between allopatric populations from high and low elevation, produce flies of intermediate fecundity, suggesting a genetic component to fecundity. Interestingly, a congeneric species, *D. yakuba*, displays rising fecundity with increasing altitude in a stepwise manner, perhaps linked to abrupt changes in the availability of particular habitat types (Devaux & Lachaise, 1987).

(8) Additional genetic considerations

Harsh environmental conditions, combined with the isolated and fragmented nature of many montane habitats, means that such areas serve as foci of micro-evolution and adaptation in insects (Haslett, 1997*a*). In particular, mountain ranges serve as major barriers to gene flow between populations of the same species, potentially producing genetic differentiation between subpopulations, as in the grasshopper *Melanoplus bivittatus* in Colorado (Baker & Williams, 1988). Genetic differences arise through limited gene exchange and local selection and may apply to many of the characteristics already discussed. Such differentiation also may occur along single steep altitudinal gradients and can usually be linked to the dispersal abilities of the species. In some, presumably weak dispersers, such as the montane willow-feeding leaf beetle *Chrysomela aenicollis*, measurable

genetic differences (five enzyme loci) occur among willow patches and even between individual willow trees, as well as between populations in different drainage basins (Rank, 1992). The fly *Drosophila subobscura* in the Swiss Alps shows differences in the frequency patterns of gene arrangement on chromosome I that reflect the steepness of its habitat gradient (Burla, Jungen & Bächli, 1986). The population was structured on a coarse scale between altitudes but on a finer scale within altitudes. Populations of the related species *D. robusta* in the USA were more genetically distinct, as measured by inversion frequencies, at the upper and lower elevational extremes than at mid elevations (Etges, 1984). Among montane carabid beetles in the eastern USA the fully winged *Platynus tenuicollis* displayed clinal genetic variation between populations, suggesting stepwise gene transfer (Liebherr, 1986). By contrast, its less dispersive brachypterous congener *P. angustatus*, showed strong correlations between allele frequencies and altitude, with erratic gene frequencies and heterozygote deficiencies suggesting a low level of gene flow and evidence of inbreeding. The butterfly *Euphilotes enoptes*, whose movements track plant phenology, not unsurprisingly, shows clinal genetic differentiation along altitudinal gradients, suggesting continuous stepwise gene transfer, even though individuals from the top and bottom of the transect may never meet (Peterson, 1995).

Temporal isolation, linked to environmental temperatures at different altitudes, may also be important in maintaining the genetic integrity of closely related species that are capable of hybridization. For example, the crickets *Gryllus firmus* (lower elevation) and *Gryllus pennsylvanicus* (higher elevation) hybridise along the eastern slope of the Blue Ridge and Appalachian Mountains, USA. Separation of the species outside the hybrid zone is maintained by the differential effects of temperature on development rates leading to temporal isolation (Harrison, 1985).

Variation in life cycle duration may potentially lead to genetic differentiation within species with biennial life cycles, such as butterflies of the genus *Erebia* (Vila & Björklund, 2004). Individual year cohorts may potentially become temporally and thus genetically isolated. Strong experimental evidence to support this contention is, however, lacking (Vila & Björklund, 2004).

IV. ALTITUDINAL EFFECTS ON INSECT HOST PLANTS

Many insect host plants occupy wide altitudinal ranges. Environmental variation over that range produces variation in their suitability to support insect growth and development. In particular, exposure to lower partial pressures of CO₂, lower mean temperatures, increased UV exposure, shorter growing season, poorer soils and increasingly strong winds will affect the phenology, size, morphology, physiology, chemistry and spatial configuration of the host plant, with consequences for the dependent insect population (Kronfuss & Havranek, 1999). Upland mineral soils are likely to be shallower and less mature, often with lower

water retention capacity and lower nutrient status, and this is likely to affect resource allocation within the plants, particularly by increasing root to shoot biomass ratios (Oleksyn *et al.*, 1998; Kronfuss & Havranek, 1999; Blionis & Vokou, 2002), thereby increasing the potential impact of root-feeding insects (Brown & Gange, 1990). Alternatively, in upland peat soils waterlogging may restrict plant growth. The effects of individual factors linked to altitude are, however, complex and difficult to tease apart in the field, with plants integrating the impacts of several factors simultaneously (Smith & Donahue, 1991).

(1) Growth and morphology

Historically it was assumed that reduced partial pressure of CO₂ at higher altitude would impair photosynthesis and reduce plant growth and productivity proportionally (Friend & Woodward, 1990; Terashima *et al.*, 1995). Recent evidence, however, suggests that many plant species at higher altitude are able to photosynthesise more efficiently than their lower elevation counterparts and that this extends to altitudinal compensation within some species, including species as diverse as the herbaceous *Potentilla crantzii* in Austria and the woody *Metrosideros polymorpha* in Hawaii (Korner & Diemer, 1994; Diemer & Korner, 1996; Cordell *et al.*, 1999). To some extent this partly offsets the impact of lower mean temperatures reducing overall growth. Evidence for the effect of CO₂ enrichment on tree species, linked to global warming, also suggests changes in host plant quality and consequent effects on plant palatability to insects related to varying ambient CO₂ levels (Buse *et al.*, 1998; Kruger, Volin & Lindroth, 1998; Hattenschwiler & Schafellner, 1999; Agrell, McDonald & Lindroth, 2000).

Wind may strongly influence the size and morphology of host plants. The growth of the pine *Pinus cembra* grown in standard experimental plots along an altitudinal gradient in Austria, for example, was strongly correlated with wind speed, with annual height growth reduced by 5–6 % for each 100 m of altitude (Kronfuss & Havranek, 1999).

Thus in general, host plants at higher altitude, such as *Salix lapponum* and *Epilobium angustifolium* in Norway and *Metrosideros polymorpha* in Hawaii tend to be smaller, often more prostrate, less compact and more widely separated spatially than their lower altitude counterparts and thus possibly less easily located by their insect herbivores (Bird & Hodkinson, 1999; Cordell *et al.*, 1999; Hodkinson *et al.*, 2001). Frequently this is associated with other morphological traits that are known to influence insect feeding, such as smaller leaves or needles, higher or lower leaf mass area, greater leaf thickness, increased depth and changed composition of the waxy cuticle, altered size of resin ducts and reduced intercellular airspace in the leaf mesophyll (Sase, Takamatsu & Yoshida, 1998; Suzuki, 1998; Hengxiao *et al.*, 1999; Kogami *et al.*, 2001). In *Oreganum vulgare*, densities of stomata and non-glandular hairs increase with altitude whereas those of glandular hairs decrease (Kofidis, Bosabalidis & Moustakas, 2003). Such hairs often confer resistance to insect feeding (Bernays & Chapman, 1994).

Table 1. Seasonal phenology of *Epilobium angustifolium* (Onagraceae) along an altitudinal transect in Norway in 1994 (J. M. Bird & I. D. Hodkinson, unpublished data). Data are for date of first appearance. Early season data for 1993 and 1995 at a lowland site, Ainsdale National Nature Reserve, UK, are added for comparison

	Ainsdale 1993	Ainsdale 1995	Geilo	Haugastol	Finse
Altitude (m)	10	10	749	988	1222
First shoot	14 Apr	4 Apr	20 May	20 May	3 Jun
First leaf	20 Apr	11 Apr	10 Jun	17 Jun	24 Jun
First flower bud			17 Jun	17 Jun	15 July
First flower			22 Jul	30 Jul	12 Aug
First seed capsule			30 Jul	12 Aug	None set

(2) Phenology and timing

Climatic variability along an altitudinal transect inevitably produces variation in the seasonal phenology of insect host plants. Key phenological events for insects include the timing of bud burst, leaf flushing, leaf maturity, leaf senescence and fall, flowering, seed set and seed maturity and dispersal (Watt & McFarlane, 1991; Hunter, 1992; Hill & Hodkinson, 1995; Hodkinson, 1997; Hill *et al.*, 1998; Virtanen & Neuvonen, 1999; Hodkinson *et al.*, 2001).

The effect of altitude on plant seasonal phenology is illustrated by the example of *Epilobium angustifolium*, the host plant for several insects (Hodkinson & Hughes, 1982) in the Hardangervidda area of Norway (749–1222 m above sea level) (Table 1) and at a low-altitude site (10 m) (Ainsdale National Nature Reserve) in the UK. These major phenological timing differences, extending to several weeks in some instances, also produced significant declining trends with increasing altitude for maximum stem height achieved, number of leaves and flowers produced, and the number of seed capsules developed (J. M. Bird & I. D. Hodkinson, unpublished data).

(3) Nutrient composition

The overall performance of herbivorous insects depends on the nutritional qualities of their host plants, particularly the available nitrogen concentrations of leaves or other target tissues (Bernays & Chapman, 1994). Non-nutritive chemicals, including plant secondary compounds, also determine host-plant choice and insect feeding behaviour. Many plant species show variation in chemical composition along altitudinal transects, with inevitable consequences for insect nutrition. Despite growing in comparatively nutrient-poor soils, plant populations at higher altitude often exhibit higher nitrogen concentrations than their counterparts growing in more nutrient-rich soils at lower elevations. Examples range from the leaves of herbaceous perennials such as *Alchemilla alpina* and *Saguisorba tenuifolia* to those of trees such as *Picea alba*, *Metrosideros polymorpha* and others (Niemelä, Rousi & Saarenmaa, 1987; Bernays & Chapman, 1994; Morecroft & Woodward, 1996; Erelli, Ayres & Eaton, 1998; Oleksyn *et al.*, 1998; Cordell *et al.*, 1999). By contrast, in *Salix lapponum*, the tissues fed on by sap-sucking insects, namely female catkins and growing shoots, showed only marginal differences in total soluble nitrogen concentrations

(Hodkinson *et al.*, 2001). A similar exception is found in the conifer *Pinus yunnanensis* in which nitrogen concentration of needles decreased with rising altitude (Hengxiao *et al.*, 1999).

The mechanisms producing these nutritional differences are not clear and may vary among species. It has been suggested that it results from enhanced nitrogen input in precipitation at higher altitude or alternatively, from slower growth at lower temperatures, producing smaller leaves with a higher carbon and nitrogen concentration (Morecroft & Woodward, 1996; Erelli *et al.*, 1998). A third explanation might be that plants growing at lower densities at higher elevations along an altitudinal transect may suffer less competition for nitrogen than plants at lower altitudes growing at higher densities and are thus more successful at incorporating nitrogen into their tissues. Evidence from *Pinus ponderosa* in Arizona supports this contention (McMillin & Wagner, 1998).

(4) Secondary compounds and defensive chemicals

In parallel with nutritive chemicals, both insect digestibility inhibitors and feeding deterrents may vary within plant species along altitudinal gradients. Concentrations of condensed tannins in mature *Betula papyrifera* foliage at low elevations in New Hampshire were around twice those at 800–1400 m, suggesting that plants growing under greater stress at higher altitude may invest less in defensive compounds (Erelli *et al.*, 1998). Similarly, total sesquiterpenes in the needles of *Pinus yunnanensis* in China decreased with altitude while those of oxygenated monoterpenes increased (Hengxiao *et al.*, 1999). Parallel altitudinal increases are also recorded in chlorophyll concentrations and protective plant pigments such as carotene that may affect insect feeding behaviour (Oleksyn *et al.*, 1998).

(5) Plant age and stress

Differences in population age structure, related to altitudinal factors, can influence the susceptibility of long-lived plants to insect feeding. This presumably derives from differences in the nutritive and defensive chemical composition of the tissues and to the relative levels of environmental stress to which they are exposed (Niemelä *et al.*, 1987). Water stress in particular is known to result in increased levels of soluble nitrogen that favour the growth and survival of sap-sucking or tissue-boring insects but may detrimentally affect the

growth performance, but not necessarily the leaf consumption, of leaf-chewing species (Koricheva, Larsson & Haukioja, 1998). Old populations of the birch *Betula pubescens*, for example, growing at higher altitude in Finnish Lapland are particularly susceptible to insect damage (Ruohomäki *et al.*, 1997). Equally, hemlocks (*Tsuga* spp.) in Japan, growing at altitudes beyond the normal range are especially vulnerable to attack by the scale insect *Nuculaspis tsugae* (McClure, 1985).

(6) Seed availability

Many montane insects are specialised for feeding on the reproductive structures of their host plant (Molau, Eriksen & Knudsen, 1989) but plants often exhibit declining reproductive output with increasing altitude. Examples include *Juncus squarrosus* in England, *Solidago macrophylla* in New Hampshire, *Festuca novae-zealandiae* in New Zealand, and *Epilobium angustifolium* and *Ranunculus acris* in Norway (Randall, 1986; Molau *et al.*, 1989; Totland, 1997; Kelly, 1998; Lord & Kelly, 1999; J. M. Bird & I. D. Hodkinson, unpublished data). Generally this is associated with a restricted heat budget limiting reproductive success. However, in *Silene vulgaris* the effect may be linked more directly with UV-B exposure. Plants exposed to UV-B levels equivalent to 1600 m altitude produced significantly less seed than those exposed to UV-B levels equivalent to 2 m elevation (Van de Staaij *et al.*, 1997). By contrast, some plant species, such as *Chionochloa rubra* exhibit seed masting (sporadic high levels of reproduction) at altitude, a possible mechanism for avoiding predation (Sullivan & Kelly, 2000).

(7) Genetic basis of variation

Experiments in common gardens and elsewhere, using material of the same plant species collected from different altitudes provides evidence for genetically-based ecotypic variation in size, morphology and chemistry in several plant species such as *Achillea millefolium* (= *lanulosa*) (Clausen, Keck & Hiesey, 1948), *Campanula spatula* (Blionis & Vokou, 2002) and *Picea abies* (Oleksyn *et al.*, 1998). To what extent this influences host plant acceptability and insect performance is largely unknown, although the relationship between provenance and insect damage susceptibility is well established for forest trees (Day, Leather & Lines, 1991; Xie, Johnstone & Ying, 1995). In insect-pollinated plants, particularly those pollinated by far-ranging insects such as bumblebees, efficient pollination may limit genetic diversification along altitudinal transects (Bingham & Ranker, 2000).

V. EFFECTS OF ALTITUDE ON INSECT PERFORMANCE, POPULATION DENSITY AND COMMUNITY COMPOSITION

One might presume that the altitudinal distribution of an insect species is controlled by its environmental tolerances, with maximum population size being achieved at some optimum elevation and population density declining with

altitude above and below the optimum. However, things are rarely that simple and the determinants of abundance, particularly in the case of herbivorous insects, include interactions with one or more species of living organisms and integral life-history variations that override or modify simple climatic effects. Thus, the population density pattern of a particular species reflects changing host plant phenology, quality and density and variation in the populations of specific parasitoids and predators.

(1) Phenology effects and growth performance

For many species of herbivorous insect, particularly those with an annual life cycle in which adult emergence is promoted by temperature or temperature combined with photoperiod, seasonal development, flight activity and the timing of reproduction is often progressively delayed with increasing altitude (Hill & Hodkinson, 1995; Bird & Hodkinson, 1999; Fielding *et al.*, 1999). Furthermore, the period of activity may become progressively curtailed. A good example is the butterfly species in the Picos de Europa of N. Spain, which display a consistent year-to-year pattern in flight activity, with maximum activity concentrated within the warmest summer period but its commencement becoming later at increasingly higher elevations (Gutierrez & Menendez, 1998). The flight season becomes later and shorter with increasing altitude, with the fewest species active at the highest elevation, suggesting that many species are temperature limited at their upper altitudinal range boundary. By contrast, in some autumn-emerging species such as *Tipula paludosa* in Britain, flight activity may begin earlier at higher elevations than in the lowlands (Coulson, 1962).

Phytophagous insect species, to complete their life cycle successfully, must select a particular plant tissue at an appropriate state of development. Failure to synchronise their life cycle with the period of optimum food plant quality/availability at a particular altitude often results in reduced performance. For the sap-feeding psyllids on *Salix lapponum*, the soluble nitrogen content of their food source, the catkins, declines progressively over time and the catkin rapidly becomes unsuitable as the seeds develop and dehiscence occurs (Hill & Hodkinson, 1995; Hill *et al.*, 1998; Hodkinson *et al.*, 2001). Psyllids only achieve optimum growth performance if egg hatch coincides with initial maximum soluble nitrogen concentrations. Larvae hatching from eggs laid late usually fail to mature. Low temperatures and short growing period at higher altitude may, however, reduce significantly the ability of some insects, such as the leaf beetle *Galerucella grisea*, to exploit its host plant, despite better leaf quality at higher elevation (Suzuki, 1998). In other species, such as the moth *Epirrita autumnata* on mountain birch *Betula pubescens*, the phenological state of the buds reflecting topographic variation, rather than temperature linked to altitude *per se*, was the main determinant of reproductive success and larval growth (Virtanen & Neuvonen, 1999).

Inherent altitudinal differences in host-plant quality produce similar effects on insect performance. Growth of the moths *Lymantria dispar* and *Orgyia leucostigma*, for example, was significantly enhanced when fed *Betula papyrifera* leaves from higher altitudes compared with those from lower

elevations, reflecting the altitudinal variations in levels of available nitrogen and condensed tannins (Erelli *et al.*, 1998). Similar host-plant quality effects on performance, linked to altitude, are found in the pine sawflies *Neodiprion xiangyunicus* and *Neodiprion sertifer* on *Pinus yunnanensis* and *P. sylvestris*, respectively (Niemelä *et al.* 1987; Hengxiao *et al.*, 1999) and in the beetle *Galerucella grisescens* on *Sanguisorba tenuifolia* (Suzuki, 1998). Such effects are however not ubiquitous: there was no significant effect of variation in foliar nitrogen levels related to increasing altitude on the sawfly *Neodiprion autumnalis* on *Pinus ponderosa* in the USA (McMillin & Wagner, 1998).

Local topography, by creating significant microclimatic variation, may have a major modifying effect on the reproductive success and distribution of insects, by producing effects over short vertical distances that override the more general altitudinal trends (Weiss, Murphy & White, 1988). This is particularly true of herbivorous insects in which changes to host phenology and growing season, linked to aspect and or shelter, result in significantly modified insect growth performance. Variation in the timing of leaf flushing in *Quercus ilicifolia*, over a vertical distance of 15 m up the side of a small depression, produced closer synchrony with the feeding activity of Thysanoptera in the bottom of the depression than at the top, resulting in higher populations and greater damage to the plant despite the significantly lower mean temperature (Aizen & Patterson, 1995). The upper altitudinal distributional limit of the psyllid *Craspedolepta subpunctata* in Norway was extended significantly along a 1 m strip at the top of a south-facing railway embankment. Here, snow melted early and the growing season of its host plant *Epilobium angustifolium* was significantly enhanced compared with the lower slopes of the same embankment and other adjacent sites at the same elevation (Bird & Hodkinson, 1999).

The lack of synchrony within plant populations along an altitudinal gradient may significantly limit the ability of insects to disperse and reproduce successfully on plants at higher or lower elevations. However, in insects with good dispersal abilities, such as the north American lycaenid butterfly *Euphilotes enoptes*, feeding and reproducing on the flowers and seeds of *Eriogonum compositum*, adult females tend to move uphill over time, tracking the flowering phenology of the host (Peterson, 1997). This in turn can lead to a concentration of reproduction on plants at the higher altitudes and provide the opportunity to resynchronise a life cycle that may have become less synchronous with the host plant at lower altitudes.

(2) Responses to increased UV radiation

For plant-feeding insects it is difficult to separate the direct effects of UV-B on the insect from the indirect effects mediated through the host plant and thus the importance of UV-B is here considered separately (Buck & Callaghan, 1999; Paul & Gwynn-Jones, 2003). An increase in UV-B equivalent to a 15% depletion in atmospheric ozone, for example, produced a significant decrease in populations of phloem feeding heather psyllid *Strophingia ericae* under standardised conditions (Salt *et al.*, 1998). However, all but one of the physical and chemical measurements of treated and

control host plants were similar, leaving a 28% decrease in levels of the amino acid isoleucine as a sole possible explanation. A direct effect of UV-B, although unlikely, could not be dismissed.

Increased exposure to UV-B in many insect host plants results in changes (> 25%) in plant growth and this is often associated with changes in plant morphology and biochemistry that may influence insect feeding (Buck & Callaghan, 1999; Newsham, Greenslade & McLeod, 1999). For example, *Quercus ilex* at 1200 m has a greater leaf thickness, a higher specific leaf weight and a higher leaf trichome density than at 200 m, attributes that confer enhanced UV-B protection (Filella & Penuelas, 1999). Concentrations of UV-B-absorbing pigments, mainly carotenes, were similarly 15% higher. Larvae of the moth *Trichoplusia ni* developed more slowly on foliage of the host plant *Citrus jambhiri* exposed to enhanced UV-B levels than when fed on control leaves. This appears related to increased concentrations of fouranocoumerins in the UV-B-treated plants (McCloud & Berenbaum, 1994).

There is some evidence that increased experimental exposure to UV-B, in sub-arctic forest heath communities and *Quercus robur* leads to higher levels of herbivory by chewing insects, as measured by leaf area removal (Newsham *et al.*, 1999; Gwynn-Jones, 2001). However, this is not necessarily reflected in insect performance. Growth rate, mortality and fecundity in larvae of the moth *Epirrita autumnata* fed on mountain birch *Betula pubescens* ssp. *tortuosa* all showed slight but non-significant reductions in UV-B treatments (25% enhancement) despite consuming three times the amount of leaves compared with controls. By contrast, the effects of 30% UV-B enhancement on four non-woody species of grass (*Lolium* and *Festuca* spp.) produced no measurable differences in the amounts consumed during feeding trials with the polyphagous locust *Schistocerca gregaria*. However, in one instance (*F. pratensis*) there was a significant interaction with the presence of endophytic fungi (McLeod *et al.*, 2001). Specialist insects, such as the willow beetle *Phratora vitellinae*, may exhibit differential responses to UV-B-induced changes in the chemistry of different related host species (Veteli *et al.*, 2003).

There is some limited evidence for a direct behavioural response to enhanced UV-B: the thrip *Calicothrips phaseoli*, for example, selectively chooses low UV-B intensity environments (Mazza *et al.*, 2002). The nature of the insect cuticle is important in determining penetration of UV-B into the insects' bodies and species differ in their capability of responding to and mitigating its effects. Species, such as larval *Epirrita autumnata*, may increase their resistance to UV-B penetration following initial exposure whereas others, such as *Operophtera brumata*, do not and remain equally susceptible (Buck & Callaghan, 1999).

(3) Population density and feeding damage to plants

Table 2 summarises the population responses to altitude in examples of insects representing a range of taxonomic orders and feeding habits. Some insects, such as the heather psyllid *S. ericae*, maintain high population densities to the

Table 2. Altitudinal trends in abundance for selected insect species, excluding host-specific parasitoids and predators

Species	Order	Host plant	Locality	Altitudinal trend	Reference
<i>Strophingia ericae</i>	Hemiptera	<i>Calluna vulgaris</i>	UK	None	Hodkinson <i>et al.</i> (1999)
<i>Strophingia cinerea</i>	Hemiptera	<i>Erica cinerea</i>	UK	Decreasing	Hodkinson <i>et al.</i> (1999)
<i>Yponomeuta mahalebella</i>	Lepidoptera	<i>Prunus mahleb</i>	Spain	Decreasing	Alonso (1999)
<i>Ditropis pteridis</i>	Diptera	<i>Pteridium aquilinum</i>	UK	Decreasing at four sites	Lawton <i>et al.</i> (1987)
<i>Chirosia parvicornis</i>	Diptera	<i>Pteridium aquilinum</i>	UK	Decreasing at two out of three sites, none at remainder	Lawton <i>et al.</i> (1987)
<i>Dasineura filicina</i>	Diptera	<i>Pteridium aquilinum</i>	UK	Decreasing at one out of four sites, none at remainder	Lawton <i>et al.</i> (1987)
<i>Dasineura pteridicola</i>	Diptera	<i>Pteridium aquilinum</i>	UK	Decreasing at one out of three sites, none at remainder	Lawton <i>et al.</i> (1987)
<i>Strongylogaster lineata</i>	Hymenoptera	<i>Pteridium aquilinum</i>	UK	None	Lawton <i>et al.</i> (1987)
<i>Tephritis arnicae</i>	Diptera	<i>Arnica montana</i>	Germany	Increasing	Scheidel <i>et al.</i> (2003)
<i>Acyrtosiphon brivicornis</i>	Homoptera	<i>Dryas octopetala</i>	Sweden	Increasing	Strathdee <i>et al.</i> (1995)
<i>Galerucella griseocens</i>	Coleoptera	<i>Sanguisorba tenuifolia</i>	Japan	Decreasing	Suzuki (1998)
<i>Kaltenbachia strobi</i>	Diptera	<i>Picea abies</i>	Switzerland	Increasing	Wermelinger <i>et al.</i> (1995)
<i>Torymus sp.</i>	Hymenoptera	<i>Picea abies</i>	Switzerland	Increasing	Wermelinger <i>et al.</i> (1995)
<i>Cydia strobilella</i>	Lepidoptera	<i>Picea abies</i>	Switzerland	Decreasing	Wermelinger <i>et al.</i> (1995)
<i>Leptocarabus procerulus</i>	Coleoptera	Predator	Japan	Decreasing	Sota (1996)
<i>Leptocarabus arboreus</i>	Coleoptera	Predator	Japan	Increasing	Sota (1996)
<i>Cacopsylla palmeni</i>	Homoptera	<i>Salix lapponum</i>	Norway	Decreasing	Hill & Hodkinson (1995)
<i>Cacopsylla brunneipennis</i>	Homoptera	<i>Salix lapponum</i>	Norway	Decreasing	Hill & Hodkinson (1995)
<i>Neodiprion sertifer</i>	Hymenoptera	<i>Pinus sylvestris</i>	Finland	Increasing	Niemelä <i>et al.</i> (1987)
<i>Dactynotus sp.</i>	Homoptera	<i>Solidago macrophylla</i>	USA	Decreasing	Kelly (1998)
<i>Campiglossa albiceps</i>	Diptera	<i>Solidago macrophylla</i>	USA	None	Kelly (1998)
<i>Aphid</i>	Homoptera	<i>Polemonium viscosum</i>	USA	Decreasing	Galen (1990)
<i>Lymantria monacha</i>	Lepidoptera	<i>Pinus abies</i>	Italy	Decreasing	Cescatti & Battisti (1992)
<i>Drosophila</i> (12 spp.)	Diptera		Japan	Decreasing	Ichijō <i>et al.</i> (1982)
<i>Drosophila</i> (six spp.)	Diptera		Japan	None	Ichijō <i>et al.</i> (1982)
<i>Drosophila makinai</i>	Diptera		Japan	Increasing	Ichijō <i>et al.</i> (1982)
<i>Nuculaspis tsugae</i>	Homoptera	<i>Tsuga</i> spp.	Japan	None	McClure (1985)

very edge of their altitudinal range through life history modification. Others, such as its congener, *S. cinerea*, lack such flexibility, and decline in density with increasing altitude (Hodkinson *et al.*, 1999). Several insects show similar declining densities with increasing altitude, including the moth *Yponomeuta mahalebella* (Alonso, 1999) and the delphacid bug *Ditropis pteridis* (Lawton, Macgarvin & Heads, 1987). Other species show increased densities, or at least increasing evidence of feeding activity at higher densities, such as in the sawfly *Neodiprion sertifer* on *Pinus sylvestris* (Niemelä *et al.*, 1987) and the tephretid fly *Tephritis arnicae* on *Arnica montana* (Scheidel, Rohl & Bruelheide, 2003). By contrast, several species show no altitudinal trends in abundance. These include *Strongylogaster lineata* and *Campiglossa albiceps* on bracken and goldenrod, respectively (Lawton *et al.*, 1987; Kelly, 1998).

It is notable that among the polyphagous predatory carabid beetles, which although often associated with a specific vegetation type, are less strongly tied to a particular plant species, altitudinal distribution more closely reflects the physiological tolerances and preferences of the particular species (Sota, 1996). One of the problems with all these abundance data, however, is that the insect species involved are rarely studied over their entire altitudinal range and the data may often represent fragments of a larger pattern.

One consequence of population variation in herbivorous insect species along altitudinal gradients is a change in the apparent levels of feeding damage to their host plant (Reynolds & Crossley, 1997; Alonso, 1999). Again, however, there is no consistency of trend. Paradoxically, an improvement in insect performance linked to enhanced nutritional suitability of leaves, at least in the short term, may produce apparently reduced levels of defoliation as the insects begin to assimilate food more efficiently (Suzuki, 1998). Trends in levels of species-specific seed predation by insects are also highly variable with respect to increasing altitude, ranging from a decrease in *Chionochloa rubra* and *Festuca novae-zealandiae* (Lord & Kelly, 1999; Sullivan & Kelly, 2000) to peaks at mid altitude in *Juncus squarrosus* (Randall, 1986). Care, however, is again needed in interpreting these tendencies as a decreasing trend in seed predation may be offset by a decrease in seed set, such that overall seed production may appear constant with respect to elevation (Lord & Kelly 1999).

Local topography may again produce unexpected altitudinal effects on insect populations, resulting from differential temperature-related mortality. This is vividly illustrated in the patterns of defoliation of mountain birch trees by the moth *Epirrita autumnata* in northern Scandinavia during 1955 and 1964–65 (Tenow & Nilssen, 1990; Virtanen, Neuvonen & Nikula, 1998). During severe

outbreaks, extensive areas of forest were defoliated but others remained relatively untouched. Non-defoliated areas were confined to valley bottoms and upland plateaus, with severe damage concentrated at intermediate altitudes. The explanation lies in the critical winter temperature (around -36°C) required to kill overwintering eggs. Lethally cold air ($< -37^{\circ}\text{C}$) formed 'lakes' within the valley or 'domes' over the plateau, resulting in poor egg survival. By contrast, at intermediate altitudes, eggs survived low ($> -36^{\circ}\text{C}$) but sub-lethal temperatures, larvae hatched, and caused defoliation the following year.

Altitudinal variation in insect density, and consequent feeding intensity, may have direct effects on other ecosystem processes such as nutrient flow and decomposition through varying inputs of insect faeces, in the form of frasse or honeydew (Crozier, 1981; Hunter, Linnen & Reynolds, 2003). Similarly, populations of soil-dwelling Collembola may vary with altitude and contribute to differences in the rate of leaf litter breakdown or accumulation within a particular vegetation type, such as holm oak forest in the Atlas Mountains (Hoover & Crossley, 1995; Sadaka & Ponge, 2003a, b).

(4) Tritrophic interactions and the importance of parasitism and predation

A full understanding of the tritrophic interaction between host plant-herbivorous insect and parasitism/predation is usually necessary for a clear understanding of the population dynamics of species along altitudinal gradients. Such studies are infrequent but where complete often provide elegant explanations for changes in insect abundance of the target species over its altitudinal range. A good example is the rush moth *Coleophora alticolella* that feeds on the seeds of *Juncus squarrosus* and occupies an elevation range of 600 m in N. England (Randall, 1982a, b, 1986). Abundance in any one year tends to follow a parabolic trend with respect to altitude (Fig. 1). This consistent pattern of distribution derives from a series of often opposing trends. Mortality associated with parasitism decreases with rising altitude whereas failure of the host to produce suitable seed capsules increases. Mortality associated with larval competition for food, however increases rapidly at lower altitudes but declines beyond peak at mid elevations. These three superimposed trends produce the characteristic parabolic altitudinal pattern of abundance. Similar tritrophic studies along altitudinal gradients include the moth *Phyllonorycter* sp. on *Quercus gambelii* (Preszler & Boecklen, 1996), the sawfly *Neodiprion autumnalis* on *Pinus ponderosa* (McMillin & Wagner, 1998) and the moth *Epirrita autumnata* on *Betula pubescens* (Virtanen & Neuvonen, 1999).

When examined individually, levels of parasitism by various host-specific insect parasitoids, within host species representing several insect orders, generally appear to decline with increasing altitude (Table 3). In some species, such as the upland crane fly *Molophilus ater*, evidence of parasitism is absent from large samples (Hadley, 1969, 1971). In other species such as *Coleophora alticolella* cited above, parasitism declines to zero before the moth's altitudinal limit is reached, leaving the upper distribution zone

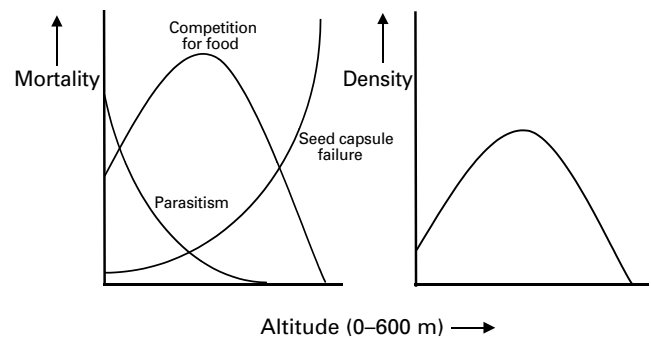


Fig. 1. Tritrophic interactions in the moth *Coleophora alticolella* on its host plant *Juncus squarrosus* along an altitudinal gradient (after Randall, 1982a, b, 1986). The left diagram shows how levels of parasitism, competition for food and failure of the host to set seed vary with altitude. The right diagram shows the resulting effect on the population density of the moth.

as a parasitoid-free space (Randall, 1982b). Coulson & Whittaker (1978) suggested that the searching efficiency and thus the efficacy of parasitoids is impaired under cooler and often misty conditions at higher elevations. This is supported by several experimental studies that show a decrease in parasitoid functional efficiency with declining temperature below the optimum (Enkegaard, 1994; Mills & Getz, 1996; Van Roermund, Van Lenteren & Rabbinge, 1996; Menon, Flinn & Dover, 2002). In some species, such as the moth *Epirrita autumnata* on birch in Finland, the dominant parasitoid differs with altitude: with *Eulophus larvarum* and *Cotesia jucunda* dominant at higher and lower sites, respectively (Virtanen & Neuvonen, 1999). Davis *et al.* (1998), basing their arguments on laboratory studies of *Drosophila* species and their parasitoids, suggested that insect range limits might be modified by interactions of species with their parasitoids. Field evidence to support this conclusion is at best flimsy, at least in the case of altitudinal limits for individual species (Hodkinson, 1999). Where it may have some relevance is where a complex of parasitoids which overlap in their host ranges and altitudinal distributions attacks a complex of closely related host species themselves exhibiting altitudinal zonation. For example, tephritid fruit flies belonging to the genus *Anastrepha* in Veracruz, Mexico are distributed along an altitudinal gradient together with 10 species of hymenopterous parasitoid (Sivinski, Pinero & Aluja, 2000). Here there is opportunity for parasitoid species to act differentially on shared hosts at different elevations, with different hosts and parasitoids having peak abundances at different altitudes.

Reliable data on changes in predation rate with altitude are fewer than for rates of parasitism. Available data for relatively specific predators and their hosts (Table 3) again suggest declining predation with increasing altitude. However, most predators are opportunistic generalists, such as spiders, and it is difficult to draw general conclusions as to their overall impact on a particular prey species along altitudinal transects.

Table 3. Altitudinal trends in levels of parasitism and predation among selected species of insect with a wide altitudinal range

Host	Parasite/predator	Locality	Altitudinal response	Reference
Parasitoids				
<i>Strophingia ericae</i>	<i>Tetrastichus actis</i>	UK	Decrease	Hodkinson (1973 <i>a, b</i>); Whittaker (1985)
<i>Operophtera brumata</i>	<i>Phobocampe neglecta</i>	UK	Decrease	Kerslake <i>et al.</i> (1996)
<i>Eutreta xanthochaeta</i>	<i>Diachasmimorpha tyroni</i>	Hawaii	No trend	Duan <i>et al.</i> (1998)
<i>Cydia</i> spp.	<i>Calliephialtes grapholithae</i> , <i>Diadegma blackburni</i> , <i>Pristomerus hawaiiensis</i> , <i>Euderus metallicus</i>	Hawaii	All decreased	Brenner <i>et al.</i> (2002)
<i>Kaltenbachiola strobi</i>	<i>Triplatygaster contorticornis</i> , <i>Torymus azureus</i> , <i>Tetrastichus stroblinae</i>	Poland	General decrease	Kozioł (1998)
<i>Neophilaenus lineatus</i>	<i>Verallia aucta</i>	UK	Decrease	Whittaker (1971)
<i>Coleophora alticolella</i>	<i>Elachertus olivaceus</i> , <i>Euderus viridis</i> , <i>Pteromalus semotus</i> , <i>Scambus brevicornis</i> , <i>Gelis</i> sp., <i>Gonotypus melanostoma</i>	UK	All decreased	Randall (1982 <i>b</i>)
<i>Molophilus ater</i>		UK	Absent at altitude	Hadley (1971)
<i>Cacopsylla palmeni</i>		Norway	Absent at altitude	I.D. Hodkinson (unpublished data)
<i>Cacopsylla propinqua</i>		Norway	Absent at altitude	I.D. Hodkinson (unpublished data)
<i>Craspedolepta nebulosa</i>		Norway	Absent at altitude	I.D. Hodkinson (unpublished data)
<i>Craspedolepta subpunctata</i>		Norway	Absent at altitude	I.D. Hodkinson (unpublished data)
<i>Tipula subnodicornis</i>	<i>Crocota geniculata</i>	UK	Virtually absent at altitude	Coulson (1962)
<i>Coccinella septempunctata</i>	<i>Dinocampus coccinellae</i>	Poland	Decrease	Ceryngier (2000)
<i>Phyllonorycter</i> sp.	Not stated	USA	Decreasing, absent at altitude	Preszler & Boecklen (1996)
<i>Lithocolletis messaniella</i>	Several species	Europe	Decreasing	Delucchi (1958)
Predators				
<i>Cryptococcus fagisuga</i>	<i>Allothrombium mitchelli</i>	USA	Decrease	Wiggins <i>et al.</i> (2001)
<i>Dendroctonus micans</i>	<i>Rhizophagus grandis</i>	France	Decrease	Gilbert & Gregoire (2003)

(5) Community composition and altitude

Altitudinal patterns in insect taxonomic diversity may be apparent on a range of spatial scales (Gaston & Williams, 1996). At the finest scale the number of insect species associated with a particular plant species may decline with rising altitude. The insect fauna of birch *Betula pubescens*, for example, shows a general decline in Heteroptera, Homoptera and Coleoptera species from 0 to 900 m in Sogndal, Norway (Hägvar, 1976). Bracken, *Pteridium aquilinum*, in the UK, by contrast, showed little difference in associated insect species richness over an altitudinal range of 350 m (Lawton *et al.*, 1987) while the Psocoptera on mango, *Mangifera indica*, showed a general increase in species richness over an altitudinal range of approximately 1100 m in Jamaica (Turner & Broadhead, 1974). This latter trend was explained by the increasing abundance of micro-epiphytes at higher elevations. A similar increase in species richness with increasing altitude occurs in some groups with soil-dwelling larvae, such as craneflies (Tipulidae), in which the high levels of soil moisture, particularly in organic soils, favour larval survival (Coulson & Whittaker, 1978). Variation in precipitation can also produce opposite altitudinal effects on diversity within different groups. Free-living herbivore species richness often declines in drier habitats whereas that of gall-forming insects increases, particularly on sclerophyllous plants (Whittaker,

1952; Warren & Harper, 1994; Ribeiro, Carneiro & Frenandes, 1998).

Altitude affects not only the species richness but also the species composition of insect communities (Whittaker, 1952). Many phytophagous insect species, as noted earlier, are found only within a limited altitudinal range within the broader elevational distribution of their host plant: others occupy the full range. Thus species with a broad altitudinal distribution are likely to encounter different potential competitors in different parts of their elevational range. For example, the gall-forming tephritid fly *Acurina idahoensis* feeding on *Chrysothamnus viscidiflorus* in the USA co-occurs with its congener *A. semilucida* at lower elevations but with *A. ferruginea* and *A. michaeli* at higher altitudes (Goeden & Teerink, 1996). Similarly, the sap-feeding psyllid *Craspedolepta nebulosa* living on *Epilobium angustifolium* in Canada co-occurs with its congeners *C. schwarzi* and *C. subpunctata*, but at high and low elevations, respectively (Hodkinson & Bird, 1998). Equivalent examples of species replacement along altitudinal gradients are found among such diverse groups as grassland bugs (Auchenorrhyncha) and dung-feeding flies (Sepsidae) in northern England (Randall *et al.*, 1981; Eyre, Woodward & Luff, 2001), horseflies and grasshoppers in the French mountains (Claridge & Singrao, 1978; Raymond, 1979) and satyrid butterflies in Venezuela (Adams & Bernard, 1981).

Table 4. Selected examples of insect communities showing altitudinal variation in species richness on a local scale. Examples are selected to demonstrate the range of responses recorded

Insect group	Habitat types	Location	Altitudinal range (m) of transect	Species richness trend	Reference
All insects	<i>Acacia/Metrosideros</i> tree community	Hawaii	2400	Peaking mid-altitude	Gagne (1979)
All insects	Tropical forest	Panama	2100	Decreasing	Wolda (1987)
All insects	Open fields	USA	1600	Peaking mid-altitude	McCoy (1990)
Geometridae moths	Montane rainforest	Ecuador	1800	None or increasing	Brehm & Fiedler (2004)
Galling insects	Mixed vegetation	Brasil	700	Decreasing or none	Lara <i>et al.</i> (2002)
Scarabaeidae beetles	Various habitats	Spain		Increasing	Romero & Avila (2000)
Scarabaeidae beetles	Various habitats	Indonesia	2300	Generally decreasing	Hanski (1983)
Moths	Montane rainforest		600	Decreasing	Hebert (1980)
Gall-forming insects (several groups)	Various habitats	Indonesia	3400	All decreasing	Fernandes & Lara (1993)
General insects	Bryophytes	Australia and New Zealand	1750	No overall trend – suggestion of peak at mid altitude	Andrew <i>et al.</i> (2003)
Orthoptera	Open habitats	France	1600	No overall trend	Claridge & Singrao (1978)
Hemiptera	Tropical rainforest	Indonesia	1600	No clear pattern	Casson & Hodgkinson (1991)

The availability of particular host plant species to a particular set of related insect species can also change with altitude, as in the bruchid beetle *Bruchidius* complex feeding on *Acacia* species in Saudi Arabia (Abdullah & Abulfatih, 1995). In this situation the relative performance of insect species is likely to vary between different host plants, potentially shifting the competitive balance between the insect species present at any particular altitude.

Some observed altitudinal patterns may result in part from mutualistic interactions among species. Ant-tended treehoppers (Membracidae) in Colombia, for example, exhibit declining species richness with rising altitude resulting from lower ant densities, whereas similar non-attended colonial species do not (Olmstead & Wood, 1990). It is, therefore, unsurprising, given the complex interplay of determining factors, that there is little consistency in the altitudinal trends in species richness recorded for different insect communities. Table 4, reinforcing the earlier conclusions of McCoy (1990), summarises the wide variety of responses of species richness to altitude, with different taxa showing contrasting increasing or decreasing trends or no trend at all. Other taxa exhibit peak richness at intermediate elevations. These mid-altitude peaks in species richness are thought to result as artifacts of short-term sampling or from disturbance at lower altitudes (Wolda, 1987; McCoy, 1990). Similarly, peaks at high altitude may reflect more effective sampling of a seasonally compressed community (Whittaker, 1952).

Wider scale distribution effects also compound the problems of assessing species richness trends along local altitudinal gradients. For example, among the butterflies of the Iberian Peninsula a significant percentage of the variation in the geographic range of species, but not of their abundance, can be explained by their altitudinal range, suggesting that species are limited primarily by their climate tolerances (Gutierrez & Menendez, 1995).

Mountain habitats are, however, spatially complex and in certain areas subject to human disturbance through recreation or grazing, producing a mosaic of different habitat types, often with their own particular vegetation and/or microclimate (Haslett, 1997a). This is especially true where trees or larger shrubs form part of the landscape, adding to the structural complexity. Utilization of these mosaic patches by particular insect species in groups such as hoverflies (Syrphidae), ground beetles (Carabidae) or dung beetles (Aphodiidae) may reflect more on particular insects' life strategies and ability to exploit a particular habitat type, rather than on the total taxonomic diversity present at a selected altitude (Menendez & Gutierrez, 1996; Ottesen, 1996; Haslett, 1997a).

Such factors may thus blur or distort overall altitudinal trends. High mountain habitats, furthermore, often support their own characteristic but spatially fragmented faunas resulting from species becoming isolated on mountains following the Pleistocene glaciations. The species composition of the high-altitude passalid beetle fauna of Central America, for example, is similar on different isolated mountain tops, suggesting that the mountains act as separate postglacial or even interglacial refugia (Macvean & Schuster, 1981).

(6) Pollinator communities and pollination

Mountain-dwelling insect species often display mutualistic relationships with plants and many alpine plant species are highly dependent on insects for pollination (Bingham & Orthner, 1998). It has been hypothesised that pollination limitation restricts the reproductive success of many plant species at higher altitudes (Totland, 1993). At high altitudes in temperate regions anthophilous flies are often the sole insect pollinators (Warren, Harper & Booth, 1988; Kearns, 1992; Totland, 1993) but at lower altitudes the significance

of Lepidoptera and particularly Hymenoptera increases, such that they become the dominant pollinators. Coleoptera play a minor role in pollination and their importance tends to decrease with rising altitude (Warren *et al.*, 1988). Temperature influences the flight ability and activity of insect taxa and this in turn determines their success as pollinators (Totland, 1994). For plants with a wide altitudinal distribution the insect community potentially available for pollination may vary with altitude (Arroyo, Primack & Armesto, 1982). Despite an overall decline in the species richness of plants and their insect pollinator systems with increasing altitude, the level of connectance, measured through an interaction matrix, did not appear to change significantly within such systems at high-altitude sites in Argentina (Medan *et al.*, 2002).

In insect-pollinated plant species with specialist flowers, such as Leguminosae, which are predominantly bee pollinated, there may be significant trends in both flower and pollinator characteristics along elevational gradients. For example, in Central Spain mean flower size of broom, *Cytisus scoparius*, increases with altitude as does the mean size of its bee pollinators. Pollination success, however, decreases (Malo & Baonza, 2002).

VI. EFFECTS OF CLIMATE CHANGE ON MONTANE INSECT SPECIES

Changing climate has profound implications for the distribution and abundance of montane insects. Evidence from sub-fossil quaternary insect remains clearly illustrates the major shifts that have occurred in montane insect communities within the Quaternary and recent time periods in response to climatic amelioration or deterioration (Elias, 1994; Coope, 1995; Ashworth, 1996). Such studies have tended to focus on generalist insects such as carabid beetles and herbivorous insects have been largely dismissed as proxies for their host plant. Recently, however, it has been argued that altitudinal range shifts in herbivorous insect species, within the broader distribution range limits of their host plant, can serve as a sensitive indicator of changing climate (Hodkinson & Bird, 1998). The likely responsiveness of a species to such change will depend on the flexibility of many of their life-history characteristics already discussed. Bale *et al.* (2002) suggest a predictive framework of how insects with differing growth rates, life cycles and diapause requirements, including low temperature responses, might react to climate warming. Potential responses include range expansion and contraction and/or altitudinal and latitudinal shifts in distribution. Slow-growing species, for example, with a required exposure to low temperature invoking diapause, are unlikely to respond positively to rising temperatures and may in fact suffer range contraction. Fast-growing, non-diapausing species, with annual or multivoltine life cycles are the likeliest to display range expansion. Clearly for many alpine insect species their relative specialization to naturally harsh conditions makes them particularly vulnerable, as they are unable to expand their altitudinal

distribution beyond the summits of the mountains on which they live (Haslett, 1997b). Montane butterfly species with weak powers of dispersal and which exploit already fragmented habitats appear especially susceptible (Bloggs & Murphy, 1997).

Evidence for the possible effects of climate warming on montane species comes from field experiments using passive warming involving some form of cloche or chamber and from modelling studies based on a prior knowledge of the population dynamics and ecophysiology of the species. For example, in the multivoltine aphid *Acyrtosiphon brevicornis* populations at both lower and higher elevations responded positively to warming by approximately 2 °C but end of season egg production was significantly greater at the higher site (Strathdee *et al.*, 1995). The population of the univoltine spittle bug *Neophilaenus lineatus* similarly increased by 50% at higher altitude under a 1 °C enhancement but a lowland density-regulated population remained unaffected (Whittaker & Tribe, 1998). This change in the upland population corresponded closely with the predicted change from a population model in which mean minimum September temperature was the main climatic driver. Among insects with optional annual/biennial life cycles, such as *Strophingia ericae*, there is parallel experimental evidence for a population increase in the biennial population when warmed by 2 °C, although the switch to an annual cycle is constrained by winter diapause requirements (Miles, Bale & Hodkinson, 1997, 1998).

Differential effects of raised temperature on the relative growth and phenology of the host plant has important consequences for herbivorous insects. Among the psyllids (Psylloidea), for example, which feed on the catkins of *Salix lapponum* throughout its altitudinal range in Norway, the relative rate of development of the insects was accelerated more than that of the host plant in field cloche experiments at different altitudes (Hill & Hodkinson, 1995). For the high-altitude species *Cacopsylla palmeni*, with the lower thermal requirement for development, mean size of adults and survival from egg to adult increased under warming. By contrast, in the low-altitude species *Cacopsylla brunneipennis*, with the greater thermal requirement, adult insects were significantly smaller but survival rate remained unchanged. For these two insects the lower and upper altitudinal limits respectively appear to be set by the catkins or the insect species developing too slowly or too rapidly for the insect to synchronise its life cycle with the optimum period of catkin growth. Overall, these results support the broader prediction that insect populations at altitude are more thermally restricted and are likely to respond most sensitively to rising temperature.

Climatically induced altitudinal range shifts can sometimes produce unexpected consequences. Relict populations of Scots pine *Pinus sylvestris*, growing at higher altitude in the Sierra Nevada and Sierra de Baza of southern Spain, are increasingly being damaged by larvae of the Pine processionary moth *Thaumetopoea pityocampa* (Hodar, Castro & Zamora, 2003). The moth normally feeds on other Mediterranean pines growing at lower altitudes but is expanding its distribution to higher altitudes as mean temperatures increase.

VII. CONCLUSIONS

(1) Insect species experience significant changes in environmental conditions along elevational gradients, particularly temperature, radiation input (including UV-B), precipitation, oxygen availability and wind turbulence.

(2) Responses can be direct or mediated through or by other organisms such as host plants, competitor species or parasitoids and predators.

(3) Direct responses include increased levels of wing-size polymorphism, including brachyptery and an increasing proportion of individuals with darker heat-absorbing or UV-B-reflective colouration.

(4) Species often show altitudinal trends of size but this may be positive or negative, depending on their biology.

(5) In many species, thermal requirements for growth rather than temperature tolerance limits appears to set distribution limits.

(6) Limited data suggest that populations at higher altitudes tend to have higher mass-specific metabolism at a set temperature and higher respiratory water loss.

(7) Species extend their altitudinal distributions by altering their life-history pattern. This may involve reducing the number of instars, developing more efficiently at lower temperatures, reducing the number of generations per year or extending the life cycle beyond one year.

(8) Insect host plants vary with altitude. Variations occur in growth rates, morphology, phenology, nutrient composition, concentrations of secondary and plant defensive compounds, extent of flowering and seed production. Plants at different altitudes may represent different genetic provenances. Insects' responses to these differences include changes in food consumption, food conversion efficiency, growth rates, survival and fecundity.

(9) Phenological synchrony between insect and host plant and between insects and seasons is essential for the successful growth and reproduction of montane insects. Synchrony may change with altitude. Diapause plays an important role in maintaining synchrony.

(10) Local environmental variation linked to topography and aspect ameliorates the effects of altitude on insect biology.

(11) Significant effects of UV-B on insect performance can be direct, or more usually mediated through host plant quality.

(12) Species vary in their population response to altitude with different species showing increasing, declining or no altitudinal trends in abundance. Population densities, particularly of herbivorous insects at any given altitude are ultimately determined by the tritrophic interaction between the host plant, the insect and its parasitoids and predators. Levels of parasitism and predation tend to decline with increasing altitude.

(13) Dispersal ability largely determines the comparative patterns of genetic variation within the insect population along vertical and horizontal gradients.

(14) The species composition of insect communities changes with altitude. Species richness may peak at the highest, lowest or mid altitude or display no trend, depending

on the community studied and location. Mechanisms determining altitudinal variation in species richness are poorly understood.

(15) Insect pollinator communities change significantly with altitude and absence of specific pollinators at higher altitudes may restrict successful sexual reproduction in some plant species.

(16) The response of montane insects to climate change, particularly rising temperature, will vary significantly among species, depending on characteristics of their life history. Some species will expand their altitudinal range: others are likely to contract.

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