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Tritrophic interactions in a changing climate: a seed-feeding moth and its larval ectoparasitoids along an elevational gradient

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Research Article

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Abstract

Anthropogenic climate change is having measurable effects on the phenology and distribution of organisms, with many species moving polewards or to higher elevations. Temperature-driven elevational range shifts can vary between species and therefore interactions within multitrophic systems are expected to alter along elevational gradients, however there is limited empirical evidence to test this hypothesis. The tritrophic interactions between the seed-feeding moth *Coleophora alticolella*, its larval ectoparasitoids and its host plant, the rush *Juncus squarrosus*, were surveyed along the same elevational gradient in northern England in 1977 and 1978, and again in 2019 and 2021. Spatio-temporal changes in these trophic levels over the intervening forty-year period were more complex than a simple synchronous upslope shift of the whole system. Seed production by *J. squarrosus* greatly increased at equivalent elevations since 1977/1978. Floret production by inflorescences was significantly higher than expected from recent temperature changes. Seed capsule ripening was also greater at higher elevations in the warmer summers of 2019 and 2021.

The elevational limit of *C. alticolella* distribution and the elevation of peak larval densities both rose more than the change in the isotherm recorded for this area since 1977. The rate of larval parasitisation was greater at equivalent sites in 2019 and 2021 than previously and the structure of the ectoparasitoid community on *C. alticolella* larvae had changed. The ectoparasitoids also occurred at higher elevations but their elevational gains were less than for their host.

Implications for insect conservation:

Understanding the impact of climate-related changes on insects is currently of major importance for insect conservation. In addition to assessing the effect of these changes on an individual species, this study shows that measuring longer-term changes within a multitrophic system across a spatial dimension can reveal additional insights for conservation and management strategies.

INTRODUCTION

The global climate is changing at an historically rapid rate, driven by increasing atmospheric greenhouse gases, with the average global surface temperature currently about 1.1°C warmer compared with pre-industrial levels (IPCC,2023). This temperature change is having a significant measurable impact on natural systems (IPCC,2014) including changes to individual species' phenology and distribution, mostly consistent with that expected from increasing environmental temperatures (Parmesan & Yohe,2003; Root *et al.*,2003; Menzel *et al.*,2006; Hickling *et al.*,2006; Chen *et al.*,2011a; Mason *et al.*,2015; Büntgen *et al.*,2022). Most distributional changes are poleward and to higher elevations. However, at a community level, climate-related changes can be complex and non-linear (Walther *et al.*, 2002; Baranov *et al.*,2020). Understanding the impact of these temperature, and other climate-related, changes on insects within natural systems is therefore of crucial importance for insect conservation (Cardoso *et al.*2020; Harvey *et al.*2023).

At mid to high latitudes, temperature primarily drives phenological responses to climate change, with ectotherms generally exhibiting stronger phenological responses than endotherms (Cohen *et al.*,2018; Visser & Gienapp,2019). Although phenological events tend to be earlier, there is evidence that the amount of advancement differs between trophic levels (Voigt *et al.*,2003), with secondary consumers affected less than the primary producers and consumers (Thackeray *et al.*,2010,2016; Cohen *et al.*,2018). These temperature-driven differences can affect phenological synchrony between trophic levels, including insect herbivores, their food plants and host-parasitoid relationships (Godfray *et al.*,1994; Hodgson *et al.*,2011; Jeffs & Lewis,2013; Damien & Tougeron,2019; Kankaanpää *et al.*,2021).

Recorded rates of elevational range shifts also vary between species and taxonomic groups (Menéndez,2007, Chen *et al.*,2011b; Mason *et al.*,2015), with those differential changes applying both to boundaries and 'optimal' elevations of species' distributions (Vitasse *et al.*,2021). These elevational changes can result in spatial mismatches or novel recombinations within communities, for example among montane butterflies and dung beetles (Wilson *et.al.*,2007; Nieto-Sánchez *et.al.*,2015; Birkett *et al.*,2018; Cuesta & Lobo, 2019). Elevational and phenological changes could act together to also affect interrelationships between host plants, herbivorous insects and their parasitoids (Hance *et al.*,2007; Menéndez *et al.*,2008; Walther, 2010; Rasmann *et al.*,2014) leading to consequential effects on populations and their dynamics (Tylianakis *et al.*,2008; Shah *et al.*,2020; Wilson & Fox,2021). While spatial differences in the relative roles of bottom-up and top-down impacts in tritrophic interactions have been recorded previously (e.g. Whittaker,1971; Preszler & Boecklen,1996), empirical studies to examine longer-term changes in population dynamics and community structure within multitrophic relationships across a spatial dimension are rare (Lawton,1994a,1995; Harrington *et al.*,1999; Gilman *et al.*,2010; Van der Putten *et al.*,2010; Abdala-Roberts *et al.*,2019; Visser & Gienapp,2019; Jamieson *et al.*,2012).

A 1°C temperature change is equivalent to about a 150m difference in elevation using average lapse rates (Manley,1952; Barry & Chorley,2009), although there are seasonal, diurnal and topographical variations (Coulson *et al.*,1976; Pepin,2001; Hodkinson,2005). As temperature is a dominant environmental factor affecting insects (Bale *et al.*,2002; Rasmann *et al.*,2014), an elevational gradient provides the opportunity to study its effects with the benefit of eliminating some other abiotic factors, such as photoperiod, whilst maintaining natural diurnal climatic variations that are difficult to replicate in a laboratory (Fielding *et al.*,1999; Hodkinson,2005; Moreira *et al.*,2018). Precipitation patterns can also alter when higher global temperatures increase atmospheric water content (IPCC,2021), but current temperature effects are likely to have a greater direct impact on insects within multitrophic systems, at least in temperate systems (Bale *et al.*,2002; Jeffs & Lewis,2013; McDermott Long *et al.*,2017). Traits of a system that show a relationship with elevation are therefore expected to respond to increasing environmental temperatures. Consequently, longer-term studies of multi-trophic systems along elevational gradients may be instructive in predicting potential spatio-temporal effects of climate change on insect communities and their population dynamics (Butterfield,1996; Whittaker & Tribe,1996, 1998; Hodkinson & Bird,1998; Fielding *et al.*,1999; Sundqvist *et al.*,2013; Corcos *et al.*,2018; Kankaanpää *et al.*,2021). However, finding a suitable system to compare historical data with new field research can be a

challenge and earlier studies may be limited to data collected to answer different questions (Didham *et al.*,2020; McCain & Garfinkel,2021).

Coleophora alticolella Zeller (Lepidoptera: Coleophoridae) is a widespread moth recorded over an elevational range to 660m in the UK (Kimber,2024). Its larvae feed on the seeds of several rush species, notably *Juncus squarrosus* L. (Pearsall,1950; Jordan,1958; Kimber, 2024). The biology and population ecology of *C.alticolella*, and its larval ectoparasitoids, on *J.squarrosus* have been studied on a number of occasions since the 1940s (Pearsall,1950; Jordan,1958,1962; Cragg,1961; Reay,1964; Welch,1965; Randall,1982a,b). Three mortality factors affecting the moth population were found to change systematically along an elevational gradient in northern England (Randall,1982a). Failure of newly hatched larvae to become established in a food supply occurred when rush florets did not set seed. This early larval mortality increased in severity with increasing elevation, whilst the incidence of attack by ectoparasitoids reduced (Randall,1982b). The combined effect of these bottom-up and top-down factors left a region at mid elevations where the density of unparasitised moth larvae, in relation to the food supply, was highest, leading to greater competition for food and mortality. This relatively simple tritrophic system, along an elevational gradient, can be seen as an illustration of the influence that climate-related temperature change may have on the moth's population dynamics and species interactions (Butterfield & Coulson,1997; Sundqvist *et al.*,2013). However if increasing environmental temperatures affect trophic levels differentially, in their distribution and phenology, then the expectation is for a complex change in these bottom-up and top-down factors, rather than a simple uphill shift of the system. This paper compares the tritrophic system along the same elevational gradient in 2019 and 2021 with that in 1977 and 1978 (and also draws from older records since the 1940s). It examines how the *C.alticolella* larval food supply and rates of attack by ectoparasitoids changed between these two study periods, with a consequential effect on the moth population, to test if the system simply moved uphill, commensurate with increasing local temperatures, or whether any changes were more complex and asynchronous.

METHODS

Sample sites and study system

Surveys of the three trophic levels were carried out in two study periods (1977 & 1978 and 2019 & 2021) along the same elevational gradient on the western escarpment of the Dun Fell area of the Pennine uplands of northern England; the majority lying within the Moor House National Nature Reserve. The sites extended from 215m asl to 845m near the summit of Great Dun Fell, a distance of about 5km, (54.6755°, -2.5267° to 54.6833°, -2.4503°; Figure S1) and along the transect used by Jordan (1962) in his studies of *C.alticolella*.

The moor rush, *Juncus squarrosus*, is a widely distributed, sward-forming, perennial, found on damp acidic soils from sea level to over 1,000m in the British Isles (Welch,1966a). Flowering starts in late May, through July at higher elevations. The inflorescences carry a number of florets some of which develop

into seed capsules in August. Seed capsules and unfertilised florets are retained on the inflorescence throughout this period. In this paper, both the flowering and fruiting stems are referred to as inflorescences.

Coleophora alticolella lay eggs on the developing rush florets. Eggs are laid singly on these oviposition sites, except at the highest densities (Reay,1964). On hatching, the first of four larval instars burrows through the pericarp of the seed capsule to start feeding on the developing seeds. Towards the end of the third or beginning of the fourth instar the larva produces a characteristic papery case. It then moves around the inflorescence to feed on seeds in additional capsules. The larvae overwinter in the leaf litter in diapause (Jordan,1958; Butterfield *et al.*,1999) with survivors pupating the following spring.

Five species of hymenopterous parasitoids (ectoparasitic idiobionts) attacked *C.alticolella* larvae on Dun Fell in 1977 and 1978 (Randall,1982b). Moth larvae parasitised by these enemies remain on the inflorescences. Most of the parasitisation was by three species; the polyphagous ichneumon *Scambus brevicornis* (Gravenhorst), and two eulophids, *Euderus viridis* Thomson and *Hyssopus olivaceus* Thomson. *Pteromalus semotus* (Walker) and a *Gelis* species (Ichneumonidae) were also present, but only rarely. *Euderus viridis* overwinter as larvae and were found singly on second and third instar *C. alticolella* larvae inside their first seed capsule. *Scambus brevicornis* attack later in the season than the eulophids and, being larger, were on fourth instar hosts mostly in the moth larval cases, usually overwintering as larvae. *Hyssopus olivaceus* is restricted to *Coleophora* species on rushes (Askew,1971), attacking second, third and fourth instar *C.alticolella*, with up to five parasites per host. It overwinters as a pupa; however, as it is bivoltine (Askew,1964), pupal exuviae of first generation *H.olivaceus* are found with the remains of host larvae inside the seed capsules and *C.alticolella* larval cases.

One species of obligatory hyperparasitoid, *Baryscapus endemus* Walker, was also found in 1977 and 1978 but only at a site 70km west of Dun Fell at 15m asl. Its larvae are endophagous and visible within in the first generation *H.olivaceus* pupae on early instar *C.alticolella* inside the *J.squarrosus* seed capsules. Sixty percent of these *H.olivaceus* pupae had been parasitised by *B.endemus* at 15m in 1978 (Randall,1982b).

Survey methods and statistical analyses

J.squarrosus inflorescences were collected on several occasions over the four years to examine floret and seed production, moth larval numbers and parasitisation. The density of the inflorescences was measured in 1977 and 1978 in late June or early July, depending on their development, which was retarded at higher elevations. Density was again measured in August, and inflorescence samples taken, by which time the larvae were established in the developing seed capsules. Inflorescences were also collected in early November 1977 and 1978 to measure parasitisation rates. In the 1970s, sampling extended to higher elevations in 1978 than in 1977. Inflorescence density measurements and sample collections were made in October of 2019 and 2021. Site elevations are detailed in Table S1 with inflorescence collection dates and sample sizes.

Sample sites in both the 1977/1978 and 2019/2021 study periods were on extensive areas of *J.squarrosus*-dominated sward on near-level ground and not in sheltered positions, to eliminate the effects of local microclimatic variations, other than elevation, which can affect the performance of the plant (Jordan,1962; Welch,1966b). Inflorescence density was measured with 50x50 cm quadrats cast randomly (n = 16, except 2021 n = 8) over the *J.squarrosus* sward and inflorescences lying nearest to quadrat corners selected, to avoid over-sampling those with the more conspicuous *C.alticolella* larval cases. These samples were examined under a low-power microscope to record the number of *C.alticolella* larvae present and those that had been parasitised. The numbers of *J.squarrosus* florets and seed capsules per inflorescence were also counted, as well as those that had had their seeds eaten (damaged capsules). As *C.alticolella* larvae were the only seed predators present, the number of damaged capsules provides additional evidence of infestation and parasitisation levels (Southwood & Henderson,2000; Brewer & Gaston,2003; Kankaanpää *et al.*,2021).

Statistical analyses were performed using R (version 4.2.1, R Core Team,2022).

Temperature and rainfall records

Monthly temperature (T_{max} and T_{min}) and rainfall (mm) data are from Newton Rigg meteorological station (54.670^{o}, -2.786^{o}); at 169m asl and 16km west of the 235m sample site. Average temperatures (monthly (T_{max}+T_{min})/2) are used to calculate mean annual temperatures, and mean temperatures for the 'summer' months (April to September), for each year from 1977 to 2021. Changes in the local isotherm since 1977 are calculated using the temperature values predicted from linear regressions, between mean temperature and time (year), by using the mean adiabatic lapse rates (annual: 0.77–0.78^{o}C, April-September: 0.80–0.83 ^{o}C, per 100m change in elevation) provided by Holden & Rose (2011) from data for Moor House and several other weather stations in northern England. Changes in annual and summer (April to September) rainfall are also examined using linear regression between rainfall and time (year).

Juncus squarrosus seed production

The reproductive performance of *J.squarrosus* along the gradient was measured using four variables; the density of inflorescences, the number of florets per inflorescence, the proportion of florets that had developed into seed capsules and the seeds per capsule. Counts of inflorescences per ¼m^{2}, florets per inflorescence and seeds per capsule and their respective relationships with elevation are examined for 2019 and 2021 using separate Generalised Linear Models (GLMs) with quasipoisson distributions for each year. Individual counts of those three parameters are not available for the 1977/1978 period, only the mean numbers per sample site. Where a significant relationship between elevation and the 2019 and 2021 variable counts was found, the mean numbers along the elevational gradient are compared between the two study periods using a linear model and analysis of covariance (ANCOVA), followed by post-hoc pairwise comparisons of estimated marginal means with a Bonferroni adjustment.

The relationships between the proportion of florets that developed into seed capsules and elevation in each of the four years are described by GLMs with quasibinomial distributions. The predicted point of 50% seed capsule development, used as a measure of the relative success of seed-setting along the transect each year, is compared with the average of the June and July mean temperatures at Newton Rigg, to test whether the development of *J.squarrosus* seed capsules was related to temperature at the time of flowering and seed setting.

Parasitisation of the moth larvae

The incidence of ectoparasitoid attack in 1977 and 1978 was estimated using data for the number of parasitised larvae in early November and relating this to the larvae present in August, when ectoparasitoids were first detected on the transect. Ectoparasitoid larvae were scarce in 1977 and 1978; additional samples of inflorescences were therefore taken in November of those years to detect them, breed out some adults and record larval and pupal characteristics. Samples were not taken in August 2019 or 2021, therefore there was no equivalent measure to estimate parasitisation on the previous basis. As an alternative, a proxy has been used. The moth larvae tend to eat the contents of a similar number of seed capsules during their development (Jordan,1958). Thus larval densities will be related to the number of seed capsules with their seeds eaten (damaged capsules) at the end of the season; therefore the number of parasitised larvae per damaged capsule in the sample should be related to the actual rate of parasitisation. This hypothesis was tested using the 1977 and 1978 data fitted to the non linear model y = 1-(exp(-b*x)), and the results from the relationship used to assess the level of parasitisation in the 2019 and 2021 samples. The rates of parasitisation of the *C.alticolella* larvae along the elevational gradient in each of the two periods are described by GLMs with quasibinomial distributions.

Moth larval distribution and abundance

The combined effect of changes in food supply and parasitisation upon the moth larvae along the gradient is measured as the number of *C.alticolella* larvae remaining after the attack by ectoparasitoids; calculated as the unparasitised larvae per seed capsule and also as the number per square metre. Those measures along the elevational gradient are compared between the two study periods using LOESS regression. Changes in the upper limit of the moth's distribution are also taken from other records published since the 1940's.

RESULTS

Temperature and rainfall changes

Both the mean annual temperature and the mean summer temperature at Newton Rigg increased significantly from 1977 to 2021 but there was no significant change in annual or summer rainfall here over this period (Table 1). The temperature changes represent an increase of 0.88 ^{O}C in mean annual

temperature and 0.71 ^{o}C in mean summer temperature; equivalent to a rise of 113–114m in the annual isotherm and 86–90m in the summer isotherm in the Dun Fell area between 1977 and 2021.

Changes in the larval food supply

Inflorescence density and seeds per capsule.

There were no significant correlations either between counts of *J. squarrosus* inflorescence density and elevation or seeds per capsule and elevation in either 2019 or 2021 (Table 2). The mean density of inflorescences and of seeds per capsules varied between sites in the 1997/1978 study period but in neither case was there a correlation with elevation, indicating that temperature along the transect had little effect upon them. Median values of inflorescence density (per ¼ m ^{2}) along the transect were 39.7 in 1977 and 15.8 in 1978; then 20.8 and 18.6 in 2019 and 2021 respectively. Median seeds per capsule: 83.7 in 1977; then 64.6 and 69.0 in 2019 and 2021. (Tables S2 and S3).

Florets per inflorescence.

The number of florets per inflorescence reduced with increasing elevation in 2019 and 2021 with no significant differences in the GLM linear model estimates between the two years (elevation: z=1.829, p=0.068; intercept: z= -1.619, p=0.105; Table 2). Similarly, the mean number of florets (y) reduced with increasing elevation (x) in the 1977/1978 period but the mean values were lower at comparable sites than in the later period (Figure 1A; linear models for the two periods: 1977/1978 y = 17.6 ± 0.7SE – 0.009x ± 0.002SE, $F_{[1,42]}$34.34 p<0.001. 2019/2021 y = 25.5 ± 0.7SE – 0.013x ± 0.001SE, $F_{[1,21]}$141.1 p<0.001). There was homogeneity of the regression slopes (interaction term $F_{[1,63]}$=2.83 p>0.05), with the covariate, elevation, having a significant effect on the mean floret number (β = -0.0113 ± 0.002SE; t=10.51, 64 d.f., p<0.001). After adjustment for this elevation effect, there was a significant difference in the number of florets per inflorescence between the two periods (ANCOVA, $F_{[1,64]}$=221.2, p<0.001), with a mean of 6.2 florets per inflorescence more in the latter period (Bonferroni adjusted marginal means: 13.1 ± 0.23SE in 1977/78 and 19.3 ± 0.37SE in 2019/2021).

Seed capsules.

Seed capsule production reduced with increasing elevation each year (Table 3), with a greater proportion of florets developing into seed capsules at equivalent sites in each of the two later years, apart from at the lowest elevations where capsule development approaches 100% (Figure 1B). Fewer than 1% of florets developed to seed capsules at 610m in 1978. In contrast, there was 58% capsule formation at 610m, 14% at 815m and 3% at the summit of Great Dun Fell in 2019. Seed capsule development was even more successful in 2021, with 83% of florets developing to seed capsules at 610m and 58% at 815m.

There was a direct significant relationship between the elevation of 50% seed capsules development, as predicted from the quasibinomial GLMs, and the mean average temperature at the time the florets were

opening and seed capsules developing each year, indicating a 190m change in the mid point for every degree Celsius change (Table 3).

Changes in the parasitisation of the moth larvae

Attack by ectoparasitoids reduced from 50% at 215m in 1978 to 2% at 305m and 0.3% at 335m; parasitisation rates were similar in 1977 (Figure 1C). Ectoparasitoids were not detected above 365m in 1978 nor above 395m in 1977. There was a significant positive relationship between larval parasitisation rates (y) and the number of parasitised larvae per damaged capsule (x) in 1977 and 1978 ($y = 1 - (\exp(-2.253 \pm 0.226\ SE)x)$; t=9.989, $p<0.001$; residual standard error 0.0685). This proxy shows the incidence of parasitisation to be considerably higher at equivalent elevations in 2019 and 2021 compared with the earlier years (Table S4); equivalent to 68% and 64% parasitisation in 2019 and 2021 respectively at 235m, compared to 18% in 1977 and 21% in 1978. Parasitisation rates were significantly greater in the second study period along the elevational gradient, with ectoparasitoids found on *C. alticolella* larvae as high as 520m in 2021(Figure 1C and Table 4).

In addition to the increased rate of parasitisation, the relative proportion of the three main parasitoid species altered (Table 5). The striking difference compared to the earlier years is the change from the prevalence of *S.brevicornis* to *H.olivaceus*, with over seventy percent of parasitised *C. alticolella* larvae attacked by *H.olivaceus* in the later perioda at the two lowest sites, compared to fewer than thirty percent previously. Although *C.alticolella* densities were lower in 2021 compared to 2019, three of the larvae in the 455m sample and one at 520m had been parasitised. *S.brevicornis* was the only species of parasitoid found on *C. alticolella* above 305m in the 1970s, but only up to 395m. In contrast, and although more frequent, *H.olivaceus*, appears not to have gained as much in elevational range since 1978. No hyperparasitisation of *H.olivaceus* by *B. endemus* was found at sites on Dun Fell in either study period.

Changes in the distribution and abundance of the moth larvae

In both 2019 and 2021, *C.alticolella* larvae were found in samples from as high as 750m on the Dun Fell transect. Larval cases were also seen on rush seed heads at 815m in 2019 at very low densities, although none were present in the sample taken from that site. In 1977, larvae were found up to 610m but the upper limit reduced to 520m in 1978 after *J.squarrosus* failed to set sufficient seed above that elevation in 1978. In various studies prior to 1977, and since 1942, *C.alticolella* had not been recorded above 610m on the west of the Pennines or the nearby Lake District of Cumbria (Table S5).

The highest densities of larvae after parasitoid attack, in relation to the seed capsules, were around 520m in 2019 and 2021, an increase from 300m during the earlier period (Figure 1D). There was a similar elevational increase in relation to unit area (Figure 1E). For example, in 1978 there were 0.81 larvae per seed capsule (359 per m^2)at 335m and 0.11 per seed capsule (17 per m^2) at 520m; in 2019 there were 0.11 larvae per seed capsule (129 per m^2) at 340m and 0.26 per seed capsule (250 per m^2) at 520m. The increase in the number of florets per inflorescence and the greater proportion developing to

seed capsules in 2019 and 2021, compared to the 1970s, reduced the differential between the LOESS trends for density per unit area between the two periods, compared to the trends for larvae per seed capsule. Variation in Inflorescence density between years and sample sites did not, alone, account for most of these differences in larval densities. In 1978 there were 15.1(±1.2SE) inflorescences per ¼m^2 at 335m and 21.9(±1.9SE) per ¼m^2 in 2019 at 340m. There was, however, no significant difference in inflorescence density at 520m between 1978 and 2019 (21.5(±1.6SE) and 23.4(±2.1SE) per ¼m^2 respectively).

Larval numbers recorded in 2019 and 2021 are likely to be underestimates because there will have been some migration of unparasitised larvae from the inflorescences by the time the samples were taken. The majority of the *J.squarrosus* seeds are eaten where larval densities are high. In 1977 and 1978 the seeds from more than 95% of the capsules had been eaten between 275 and 365m (Randall,1986). In 2019 over 90% of the capsules had their seeds eaten at 455m, further indicating that the peak of this measure of population density is now at a higher elevation than previously.

DISCUSSION

The larval food plant

The density of *J.squarrosus* inflorescences was not significantly correlated with elevation in any of the four years nor was there a correlation between elevation and the number of seeds per seed capsule. No previous relationship has been found between the number or dry weight of seeds per capsule and elevation (Reay,1964; Welch,1966b). Summer rainfall and drainage at any particular location may be more important for inflorescence production than variations in temperature over this elevation range (Welch,1966b). Future summer droughts (Slingo,2021) could therefore affect inflorescence production of this rush, particularly at lower elevations and on leeward slopes due to orographic effects.

Whilst florets per inflorescence of *J.squarrosus* reduce with progressively lower temperatures at higher elevations, the mean number per inflorescence was greater in both 2019 and 2021 than at equivalent sites in the 1970s. Welch (1966b) measured the reproductive capacity of *J.squarrosus* in 1962 and 1963 at various sites above 470m in the Pennines. He found the number of florets reduced from about 14 per inflorescence at 472m to about seven per inflorescence at 892m, similar to floret numbers at equivalent elevations in the late 1970s (Fig. 1A). There was also little variation in floret numbers from season to season at equivalent sites in the 1960s (Welch,1966b). The increase in florets recorded by 2019 and 2021 is greater than expected from the isotherm increase on Dun Fell since 1977. This temperature change alone would provide an increase of only one to two florets per inflorescence at equivalent elevations, many fewer than observed, which suggests a more complex and longer-term response by *J.squarrosus*. The growing season in Europe has extended since the 1960s (Menzel & Fabian,1999) and during the decade to 2021 the number of growing degree days in the UK increased by 17% compared with the period from 1961–1990 (Kendon *et al.*,2022). This sustained temperature rise over a longer growing period has possibly had a relatively greater impact on floret production by this rush plant.

Global atmospheric CO_2 increased from 334ppm in 1977 to 410ppm in 2019 (Dunn *et al.*,2020). Higher levels of CO_2 in controlled environments have been found to increase plant reproductive performance in annual crop plants, separately from temperature effects (Lawlor & Mitchell,1991; Amthor,2001; Hampton *et al.*,2016). Similarly, for some wild graminoids and forbs, experimental exposure to elevated CO_2 resulted in increased flowering shoot density, inflorescence size and the number of seeds per inflorescence (Edwards *et al.*,2001;Thürig *et al.*,2003).

In addition to increasing atmospheric CO_2, atmospheric nitrogen deposition derived from agriculture and vehicle traffic has increased in recent years, particularly in upland areas (Lee *et al.*,1988; Newton,2020). Nitrogen deposition has a greater fertilising effect on above ground biomass in grassland areas of higher precipitation (Lee *et al.*,2010) and can stimulate the growth of dominant plants on moorlands (Bobbink *et al.*,1998), with potential consequences for higher tropic levels (Stevens *et al.*,2018).

Clearly there has been a temperature effect on the production of florets per inflorescence by *J.squarrosus* since previous studies. However it is not possible to say whether, nor to what extent, recent changes in atmospheric CO_2 and nitrogen might have contributed to this increase.

Maturation of the *J.squarrosus* florets to seed capsules declines with increasing elevation although, as a wind-pollinated species (Welch,1966a; Michalski & Durka,2010), microclimate and local weather will affect pollination success and subsequent seed setting. Consequently, seed capsule production varies due to year-on-year variation in weather conditions at the time of flowering, resulting in fluctuations in the upper limit of seed setting from year to year. Previously, the upper limit of seed setting varied between 400 and 750m on the Dun Fell transect – but with generally higher summer temperatures since the 1970s, more consistent seed setting is expected at higher elevations.

The combination of the greater proportion of florets developing into seed capsules, and the significant increase in florets produced per inflorescence, since 1977/1978, has resulted in a greater number of seed capsules per inflorescence at higher elevations. Thus, for example, in 1978 there were 9.5 (± 0.61SE) seed capsules per inflorescence at 305m and only 1.8 (± 0.36SE) at 520m, whilst there were 10.6 (± 0.55SE) at 610m in 2019 and 9.9 (± 0.67SE) at 750m in 2021.

The ectoparasitoids

Other studies have shown the rate of parasitisation of phytophagous insects, and the diversity of those parasitoids species, increases at lower elevations (e.g. Whittaker,1971; Preszler & Boecklen,1996; Péré *et al.*,2013; Maunsell *et al.*,2015; Moreira *et al.*,2018; Corcos *et al.*,2018). These changes with elevation may be variously attributed to the effects of increasing temperature *per se* (Hance *et al.*,2007; Jeffs & Lewis,2013; Chen *et al.*,2019); as well as climatic variability (Juillet,1964; Virtanen & Neuvonen,1999; Stiremann *et al.*,2005), and community structure altering both the availability of alternative hosts and interactions with other species (Davis *et al.*,1998; Tylianakis *et al.*,2008; Moreira *et al.*,2018). All of these factors are expected to be impacted by a changing climate, which could also affect phenological synchrony between host and parasitoids (Van Nouhuys & Lei,2004; Jeffs & Lewis,2013; Wetherington *et*

al.,2017; Tougeron *et al.*,2019). However, the latter may be more complex, either increasing or reducing synchrony, or reordering the impact of different linkages within the system (Tylianakis *et al.*,2008; Maunsell *et al.*,2015; Damien & Tougeron,2019). Furthermore, since host-parasitoid systems share co-evolutionary histories, host-specific parasitoids may show a different response to changing environmental temperatures compared to generalist species with a wider host range (Damien & Tougeron,2019; LeLann *et al.*,2021). At lower elevations parasitisation of *C.alticolella* larvae had an increasingly greater effect on the moth population, but with several changes in 2019 and 2021 compared with the earlier study period. The rate of parasitisation was much higher than previously at equivalent sites. Further, just as the host larvae have increased their upslope range, so too have the three main ectoparasitoid species attacking them, though not to the same extent. The polyphagous ichneumon, *S. brevicornis*, was recorded on this host 125m higher than during 1977 and 1978, whilst the two eulophids showed smaller elevational gains. Jordan (1962) found only *S.brevicornis* above 260m on the Dun Fell transect, with no parasitisation above 305m. Another significant change was in the relative abundance of the different species of ectoparasitoids, with the eulophid *H.olivaceus* now being predominant. It is possible that additional parasitoid species now attack *C.alticolella* at the low elevations although, if so, their relative incidence is likely to be small.

Temporal synchrony is a key component of host-parasitoid dynamics (Godfray *et al.*,1994; Wetherington *et al.*,2017). *H.olivaceus* started attacking *C.alticolella* larvae at an earlier date than the other ectoparasitoids at Dun Fell in the 1970s (Randall,1982b). Further, unlike those other species, the onset of attack by *H.olivaceus* was not delayed at higher sites. By attacking earlier, *H.olivaceus* will have little competition from other species. Field observations of *H.olivaceus* searching for the host larvae inside seed capsules, found they injected the ovipositor through the pericarp to lay on the moth larva within. Successful oviposition would rely on the host larva being within reach, close to the inside wall of the pericarp. Later in the season *H.olivaceus* were seen ovipositing through the larval cases of fourth instar larvae. Consequently, if host larval development is advanced due to higher summer temperatures, larger hosts could be available sooner, particularly if phenological advancement was not as marked at the higher trophic level. Larger hosts would also have a positive effect on parasitoid brood size. Additionally, as the hyperparasitoid, *B.endemus*, was not present at Dun Fell, a greater number of *H.olivaceus* would emerge in the second generation to attack later hosts, resulting in higher parasitisation rates. It is also possible that, with the high rate of parasitisation at 235m, in excess of 60%, few unparasitised larvae remained on the seed heads, with the early developing larvae having suffered the majority of the parasitisation. At higher parasitisation levels, earlier attacking parasitoids are at a competitive advantage compared to those attacking later (Teder *et al.*,2013), which could explain the increased prevalence of *H.olivaceus*, compared to the other ectoparasitoid species.

The moth larvae

Coleophora alticolella larvae were found on *J.squarrosus* at a higher elevations in 2019 and 2021 than previously. Until the 1980s, most surveys recorded the upper limit at about 600m (Jordan,1962; Reay,1964; Welch,1965; Coulson & Whittaker,1978; Randall,1982a). Indeed, Pearsall (1950) commented

that in the 1940s, there were no signs of the moth above 550m "*except in the abnormal summer of 1947"*, a year with unusually warm summer temperatures (Royal Meteorological Society,1948), when some larval cases were found on a south-facing slope at 610m. Current recording schemes show *C.alticolella* occurring up to 660m in some years (Kimber,2024), following the discovery of larvae at 655m in 1991 in the Knock Ore Gill area of Dun Fell (Welch,1992) and with one record, in 1953, at 660m on the less exposed eastern slope of the Pennines (Welch,1965).

Two recorded events (1954 and 1978) when adverse weather reduced the upper limit of seed production led to a reduced upper limit of *C.alticolella* (Table S5). The adults are not active fliers and upward recolonisation was slow, at less than 50m in three years after the 1954 event, even though *J.squarrosus* seed was available at higher sites (Cragg,1961). Survival of newly hatched *C.alticolella* larvae is directly related to the proportion of florets developing to seed capsules (Randall, 1982a); consequently, mortality at this larval stage will have been much lower at higher elevations in 2019 and 2021 than previously. The upper limit of *C.alticolella* larvae has now increased to between 750 and 815m, with low densities almost to the summit of Dun Fell, due, in part, to the availability of rush seeds at these higher elevations. However, the upper limit of *J.squarrosus* seed production was recorded to 750m in several years in the 1940s and early 1950s but *C.alticolella* were absent, suggesting that the latest increase in the upper limit of the moth is not merely the result of successful seed production at the highest sites.

The presence of insect larvae at higher elevations does not necessarily mean their lifecycle can be successfully completed here, because the thermal budget may be insufficient (Hodgkinson & Bird,1998; Bale *et al.*,2002; Battisti *et al.*,2005). Larvae of *C.alticolella* found at the new limit could be the result of occasional immigration of adults from lower on the hillside, where they are more abundant. Jordan (1958) recorded larvae on *J.squarrosus* during the spring adult emergence period, and suggested that some require additional time feeding, after diapause, before pupating. In laboratory studies, Butterfield *et al.*(1999) found some *C.alticolella* larvae remained in diapause after various photoperiod and chilling treatments. They suggested 'cohort splitting' might allow *C.alticolella* to survive in localities where all seed had been eaten, because of high larval numbers, with some emerging the next season. Altering life history patterns by extending insect lifecycles beyond a year can also be an adaptation to cooler conditions at high elevations (Butterfield & Coulson,1997; Bale *et al.*,2002; Hodkinson,2005, Salman *et al.*,2019). Such a polymorphic adaptation, enabling continued larval development in the second year, could allow the *C.alticolella* population to persist at the high elevational margin of its range.

Thus identifying the range boundary is not straightforward, since it is often dynamic (Andrewartha & Birch,1954; Brown *et al.*,1996; Whittaker & Tribe,1998; Gaston,2003; Rafajlović *et al.*,2022), particularly at low population densities (Battisti & Larsson,2015). Consequently, concentrating on changes at the boundary does not necessarily reveal the full extent of climate impacts on a species (Ehrlén & Morris,2015; McCain & Garfinkel,2021). Although there are some exceptions (e.g. Sagarin *et al.*,2006), species tend to be more abundant away from their range edges (Lawton,1993,1996; Brown *et al.*,1996) and their population dynamics can vary across their distribution (Haldane,1953,1956; Lawton,1994b; Gaston,2009). Therefore, when assessing climate change impacts on distribution and dynamics,

consideration should also be given to any changes within the 'internal structure' (Brown *et al.*,1996) of the range.

Below its elevational limit, the density of *C.alticolella* larvae is higher until, at the lowest elevations, parasitoids have an increasing impact on the moth population. In 2019 and 2021 the highest densities of unparasitised larvae were around 500m; an increase from 1977/1978 when the highest larval densities were around 320m, which resulted in density-dependent over-winter mortality and reduction in natality (Randall 1982a). Similarly, during the 1950s, the larval densities on *J.squarrosus* were highest around 300m on the western escarpment of Dun Fell, with infestation rates of seed capsules about 70% in 1953 (Jordan,1962), and over 90% at this elevation in 1955 and 1956 (Reay,1959).

CONCLUSION

The elevation of peak *C. alticolella* larval abundance, and the pattern of larval parasitisation and floret production by *J. squarrosus* along the Dun Fell gradient at the end of the 1970s showed consistency with records available from earlier studies. In 2019 and 2021 the upper limit of moth larval distribution and peak densities had moved to higher elevations and, in contrast to some other studies of insect elevational distributions (e.g. Wilson *et al.*,2005; Menéndez *et al.*,2014; Lenoir *et al.*,2020), these increases for *C.alticolella* were greater than expected from the local isotherm change since 1977. There was also a greater rate of larval parasitisation, extending to higher elevations, than previously at equivalent sites, with a change in the structure of the parasitoid community. However, elevational gains by ectoparasitoids were less than for the host and, in the case of the now predominant specialist species, *H.olivaceus*, apparently less than the isotherm change. In addition, in this later period, *J.squarrosus*, produced more florets per inflorescence at equivalent elevations than expected from the change in temperature alone, a greater proportion of which developed to seed capsules at the highest elevations, and beyond the new upper distributional limit of the moth larvae. Thus, early larval mortality, due to seed capsule failure, would be much reduced which, together with the other changes, would alter the moth's population dynamics along the elevational gradient.

Changes in insect populations at a time of increasing environmental temperatures do not necessarily demonstrate causality with climate change, particularly when considering abundance at two points in time. Observed differences may merely be a reflection of inter-annual variation in a particular location at the time of the surveys and care is therefore needed when examining trends (Wilson *et al.*,2005; Didham *et al.*,2020). However, as Didham *et al. (loc cit)* also point out, climate-driven range expansions may be detected from differences in occupancy using paired comparisons through time at multiple reference sites. Whilst bearing in mind that note of caution, the results reported here show that, over a time when environmental temperatures have been increasing, there have been measurable spatio-temporal changes within all three of the trophic levels between *C.alticolella* and its ectoparasitoids on *J. squarrosus* along the elevational gradient. Furthermore those changes are more complex than a simple synchronous upslope shift of the whole tritrophic system.

In some situations upward shifts in elevational distribution of insect species linked to climate change may be due to a contraction at lower range boundaries (Hill e*t al.*,2002; Wilson *et al.*,2005; Merrill *et al.*,2008; Chen *et al.*,2011b; Marshall *et al.*,2020). For example, Birkett *et.al.*(2018) found an increase in the lower elevational limit of the cold-adapted dung beetle *Agoliinus lapponum* (Gyllenhal) of around 177m between surveys in 1956 and 2013 along an elevational gradient on the western escarpment of the Pennines adjacent to the Dun Fell area. This change was consistent with the increase in the local isotherm recorded for the intervening 57-year period. Similar climate-driven changes to the distribution the mountain ringlet butterfly (*Erebia epiphron* Knoch.) has led to its loss from low elevation sites in the UK (Franco *et al.*,2006), whilst other montane, and more widely distributed, butterfly species have been more significantly impacted by habitat degradation (Warren *et al.*,2001; Franco *et al.*,2006). Host-parasitoid food web structure decreases with increasing elevation (Maunsell *et al.*,2014, Morris *et al.*,2015) but spatio-temporal changes in the distribution of insect parasitoids are not well documented (Colwell, 2023). DiMarco *et al.*,(2023) examined the distribution of European parasitoid bristle flies (Diptera, Tachinidae) from various elevations over a six decade period and found that parasitoid specialisation within the community changed over time along the gradient. At low elevations, the proportion of specialist feeders increased but showed a slower upward shift in elevation compared to generalists, whilst the range of highland specialist feeders tended to contract consistent with the increase in local temperatures.

Coleophora alticolella is not a species restricted to highland elevations and therefore the moth, and the interactions with its natural enemies, could persist where suitable habitats remain available at low elevations in the UK, even under future warming scenarios. Nevertheless, the interactions within and between the trophic levels in this relatively simple system are expected to change substantially. It is recognised that fully investigating longer-term complex interactions within other multi-trophic systems, beyond pairwise interactions, will be taxing (Harrington *et al*,1999; Parmesan & Mattews,2006; Ehrlén & Morris,2015). However such investigations are needed to monitor changes to the diversity and distribution of insect species and their inter-relationships, because complex non-synchronous changes are likely have significant effects on the responses of insect populations and communities to changing environmental temperatures. For example, higher densities of insect pests may occur when natural enemies are unable to keep pace with an increasing population of their hosts at higher elevations (Menéndez *et al.*,2008, Tougeron *et al.*, 2019, Hódar *et al.*,2021), whilst differential evolutionary pressures between species could affect the dynamics of host-parasitoid relationships within food webs, and some parasitoid species may be lost due to inter-specific competition or lack of alternative hosts (Hance *et al.*2007; Wetherington *et al.*2017; LeLann *et al.* 2021). Thus, in addition to assessing the effect of climate-related changes on an individual species, measuring longer-term changes within multitrophic systems across a spatial dimension can reveal additional insights for insect management and conservation strategies.

Declarations

Author Contribution

The data from the 1970s were collected during an NERC studentship. The research since 2019 received no grant from any funding agency nor from any commercial or not-for-profit sectors. The manuscript and figures were written and prepared by the author.

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Tables

Table 1: Linear regression analyses describing the changes in average mean temperatures and total rainfall each year from 1977 to 2021 at Netwon Rigg weather station. Analyses are for annual and summer (April to September) data from

https://www.metoffice.gov.uk/pub/data/weather/uk/climate/stationdata/newtonriggdata.txt

		Estimate	SE	t	*p*	r^2	d.f.
Annual temperature (^oC)	Intercept	- 31.282	10.988	-2.847	0.007	0.48	43
	Year	0.020	0.005	3.643	0.0007		
Summer temperature (^oC)	Intercept	-20.390	10.750	-1.897	0.065	0.47	43
	Year	0.016	0.005	3.023	0.004		
Annual rainfall (mm)	Intercept	-4445.26	3149.46	-1.411	0.165	0.064	43
	Year	2.709	1.575	1.720	0.093		
Summer rainfall (mm)	Intercept	-2998.47	2096.59	-1.430	0.160	0.057	43
	Year	1.697	1.049	1.618	0.113		

Table 2: Quasipoisson GLM analyses describing the relationship between each of three components of *J. squarrosus* reproductive performance and elevation (m) from samples taken at the various sites on Dun Fell in 2019 and 2021.

			2019	2021
Florets per inflorescence	Intercept	Estimate	3.242	3.340
		SE	0.037	0.043
		t	88.56	78.49
		p	<0.001	<0.001
	Elevation (m)	Estimate	-6.212E-04	-8.127E-04
		SE	6.436E-05	7.470E-05
		t	-9.79	-10.88
		p	<0.001	<0.001
	df		358	218
Inflorescence density (per ¼m^2)	Intercept	Estimate	2.967	2.984
		SE	0.108	0.081
		t	27.50	36.70
		p	<0.001	<0.001
	Elevation (m)	Estimate	1.489E-05	-5.27E-05
		SE	1.888E-04	1.431E-04
		t	0.079	-0.37
		p	0.937	0.714
	df		174	78
Seeds per seed capsule	Intercept	Estimate	4.136	4.299
		SE	0.056	0.071
		t	73.26	60.31
		p	<0.001	<0.001
	Elevation (m)	Estimate	6.557E-05	1.021E-04
		SE	1.095E-04	1.195E-04
		t	0.60	-0.85
		p	0.55	0.395
	df		171	108

Table 3: Quasibinomial GLM analyses describing the relationship between the proportion of *J.squarrosus* florets developing into seed capsules and elevation (m) on Dun Fell in each of the four years of the study. The elevation (m) at which the GLMs predict 50% seed capsule development and the average of the mean temperatures in June and July at Newton Rigg (169m asl) are also given. The linear relationship between the 50% point (*y*) and average mean temperature (*x*) is $y = 189.7x$ (±32.9SE) – 2109.4 (±466.1SE), $F_{[1,2]}$ =33.3, p=0.03.

		1977	1978	2019	2021
Intercept	Estimate	2.978	5.600	3.826	4.063
	SE	0.524	0.250	0.511	0.401
	t	5.68	22.38	7.48	10.13
	p	<0.001	<0.001	<0.001	<0.001
Elevation (m)	Estimate	-0.0065	-0.0155	-0.0065	-0.0046
	SE	0.0014	0.0007	0.0008	0.0006
	t	-4.82	-21.58	-7.75	-7.83
	p	<0.001	<0.001	<0.001	<0.001
	df	10	28	10	9
	Pseudo r^2	0.724	0.976	0.883	0.897

Elevation with predicted 50% seed capsule development (m)	456	362	590	885
Average mean June + July temperature ^{o}C	13.35	13.03	14.63	15.55

Table 4: Quasibinomial GLM analyses describing the rate of ectoparasitisation of *C.alticolella* larvae and elevation (m) along the elevational gradient in the two study periods.

Study period		Estimate	SE	t value	*p*	d.f.	Pseudo r^2
1977 & 1978	Intercept	8.275	1.223	6.76	<0.001	15	0.968
	Elevation (m)	-0.039	0.005	-7.97	<0.001		
2019 & 2021	Intercept	4.177	0.672	6.22	<0.001	17	0.905
	Elevation (m)	-0.016	0.002	-7.43	<0.001		

Table 5: The number of *C. alticolella* larvae parasitised by various species of ectoparasitoids in samples taken from equivalent sites on Little Dun Fell in November 1977 and 1978, and October 2019 and

2021. The ‘other’ column relates to other species identified in 1977 and 1978 and those that could not be confidently identified in the 2019 and 2021 samples.

Elevation (m)	Year	*Scambus brevicornis*	*Hyssopus olivaceus*	*Euderus viridis*	Other	Total
245	1977	53	23	14	3	93
245	1978	66	40	20	11	137
235	2019	5	156	17	28	206
235	2021	2	24	1	13	40
305	1977	26	2	0	0	28
305	1978	22	7	0	0	29
300	2019	2	64	7	10	83
300	2021	0	4	0	1	5
335	1977	5	0	0	0	5
335	1978	5	0	0	0	5
340	2019	0	11	0	0	11
340	2021	2	3	0	2	7
455	2021	3	0	0	0	3
520	2021	1	0	0	0	1
Sample sizes: 2019 *n*=30, 2021 *n*=20, *J. squarrosus* inflorescences at each site; sample size in 1977 *n*=80 at 245m, 305m and 335m; 1978 *n* =100 at 245m, 150 at 305m and 200 at 335m. Up to five *H. olivaceus* can be present on each parasitised host larva.						

Figures

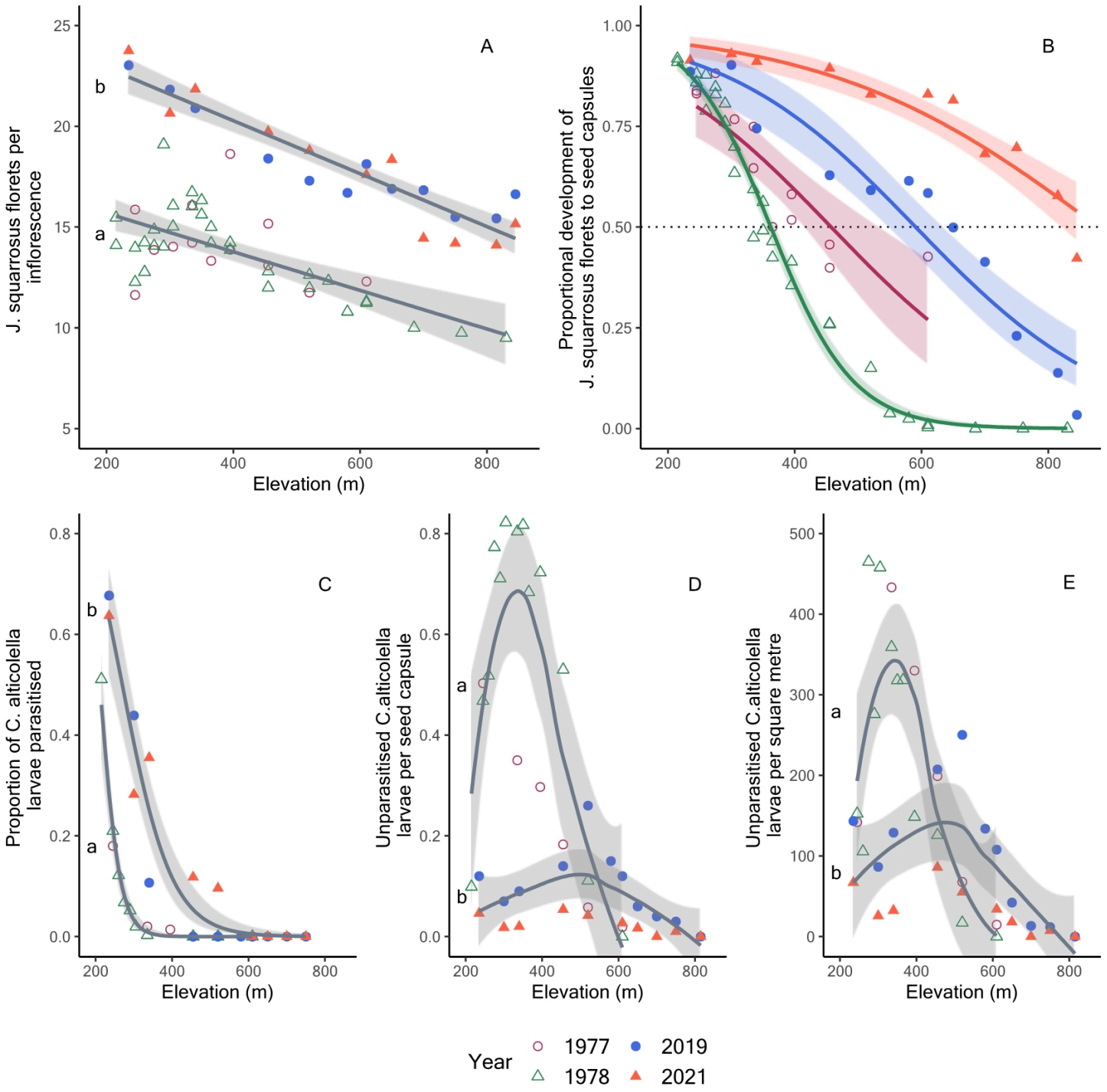


Figure 1

Changes in the *Juncus squarrosus* > *Coleophora alticolella* > ectoparasitoid system along the elevational gradient on Dun Fell between the two periods (a) 1977/1978 and (b) 2019/2021. Panel (A): the mean number of florets per inflorescence of *J. squarrosus* at the various sites, from samples taken in each year of the two study periods. The linear model for each of the two periods is shown with 95% confidence limits. Panel (B): The proportion of those *J. squarrosus* florets that developed into seed

capsules in each of the four years. The quasibinomial GLMs are shown with 95% confidence limits shaded. Panel (C): The proportion of *C. alticolella* parasitised by ectoparasitoids along the gradient; (a) shows the rates recorded in 1977 and 1978. The rates of ectoparasitisation in 2019 and 2021 (b) are the predicted values from the proxy measure (see text). The quasibinomial GLMs are shown with 95% confidence limits shaded. Panel (D): The number *C. alticolella* larvae per seed capsule of *J. squarrosus* after ectoparasitisation attack along the elevational gradient in the two study periods. The data in period (a) are the number of *C. alticolella* larvae in August reduced by the parasitisation rates for the relevant sample sites. The data for the period (b) are the unparasitised larvae still present in the October 2019 and 2012. Panel (E): The density of *C.alticolella* larvae after ectoparasitisation attack, calculated from the larval data in Panel (D) with *J.squarrosus* seed capsule production and inflorescence density (per m^2) at each site. In panels (D) and (E) the solid lines are the trends using the LOESS method with 95% confidence intervals shaded.

Supplementary Files

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- RandallOctober2024Supportingmaterial.docx