

Population turnover, habitat use and microclimate at the contracting range margin of a butterfly

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ABSTRACT

Climate change is expected to drive patterns of extinction and colonisation that are correlated with geographic gradients in the climate, such as latitude and elevation. However, local population dynamics also depend on the fine-scale effects of vegetation and topography on resource availability and microclimate. Understanding how this fine-scale variation influences population survival in the face of changing climatic favourability could provide clues for adapting conservation to climate change. Here, we document a long-term decline of the butterfly *Parnassius apollo* in the Sierra de Guadarrama mountain range in central Spain, and examine recent population turnover and habitat use by the species to make inferences about its ecology and conservation. A decline since the 1960s throughout the elevation range suggests a regional deterioration in favourability for the species. Since 2006, local habitat quality has been the main correlate of population persistence, with populations that persisted from 2006 to 2012 associated with high availability of larval host plants. At a finer resolution, the larval distribution in a network of suitable habitat in 2011 and 2012 was most closely related to bare ground cover. Thus, although slope, aspect and elevation lead to considerable variation in microhabitat temperatures during the period of *P. apollo* larval development, vegetation structure appears to have been the most critical factor for local habitat use and population persistence. The results show that site selection and management retain key roles in conservation despite the broad-scale effects of environmental change.

Keywords

Connectivity, extirpation, habitat heterogeneity, metapopulation, range limit, range shift

INTRODUCTION

45 Recent climate change has been accompanied by shifts in species distributions towards higher latitudes and elevations (Parmesan and Yohe 2003; Chen et al. 2011a). The role of climate change in driving these range shifts is supported by evidence for colonisations at or beyond the high-latitude or elevation range limits (the “leading edge”), and local extinctions at low-latitude or elevation limits (the “trailing edge”) (Parmesan et al. 1999; Franco et al. 2006; 50 Thomas 2010). However, there are fewer documented examples in terrestrial environments of contractions at the trailing edge of species distributions than of range expansions at the leading edge (Parmesan 2006; Sunday et al. 2012). In addition, the observed rates at which species have shifted their distributions uphill appear to lag behind rates of warming to a greater extent than poleward shifts in species distributions (Chen et al. 2011a), despite the 55 shorter geographic distances involved, and hence the greater expected likelihood that dispersal can keep pace with patterns of warming over elevation gradients. Understanding these apparent delays to range contractions and elevation range shifts could be important to determine the mechanisms influencing species’ responses to climate change (Merrill et al. 2008; Chen et al. 2011b), and hence to plan adaptive measures for conservation.

60 In addition to changes in range limits, recent climate warming has stabilised population dynamics near the high-latitude range margins of several butterfly species in the UK, suggesting that regional climate conditions have shifted from “marginal” to “core” for the species concerned (Oliver et al. 2012). In contrast, climate warming may be causing regional conditions at lower latitudes to shift from core to marginal, with the consequence that rates of 65 local population extinction increase, and the proportion of habitat that is occupied by species decreases (Hanski 1999). Under such circumstances, extinctions may first occur from sub-optimal habitats whose populations were formerly supported by immigration from populations nearby. As this process occurs, the effects of climate change on observed range

shifts could be masked if coarse-scale spatial patterns of regional climate variation are less
70 correlated with population dynamics than local, fine-scale variation in the microclimates
created by topography and vegetation (Suggitt et al. 2011; Gillingham et al. 2012; Lawson et
al. 2014; O'Connor et al. 2014). For example, despite a recent warming of average
conditions, cool or wet summers may cause local extinctions of upper latitude range margin
populations of the Silver-spotted skipper *Hesperia comma* in England, particularly in habitat
75 patches whose topography or vegetation provide relatively cool microclimates (Lawson et al.
2012; Bennie et al. 2013).

The lowest latitude populations of many species are restricted to high-elevation mountain
regions (e.g. García-Barros et al. 2004; Settele et al. 2008), where temperatures are cooler
than at lower elevations. Ecological communities have responded to global warming by
80 moving to higher elevations (Wilson and Gutiérrez 2012), but rates of elevation shifts vary
among species and locations, with some species persisting at low elevations despite increased
temperatures. One explanation is that some populations are able to persist because
topographic and microhabitat structure provides microclimatic variation which individuals
can exploit to meet their climatic requirements despite unfavourable ambient conditions.
85 Fine-scale studies of population and distribution dynamics at species trailing margins are
needed to understand how such local habitats mediate species responses to climate change,
and thus to inform the types of management, vegetation structure or topography that may
support persistent populations despite a deterioration in regional climatic conditions.

In this paper, we use three complementary approaches to detect factors influencing
90 patterns of persistence by the butterfly *Parnassius apollo* over an elevation gradient near its
low-latitude range margin. We document changes to the elevation range of the species over
four decades, as well as recent patterns of population turnover and fine-scale habitat use in
the Sierra de Guadarrama mountain range (central Spain), where mean annual temperature

has increased by approximately 0.4 °C per decade since 1970 (Wilson et al. 2005). First, we
95 test for longer-term changes to the elevation range of the species by comparing
presence/absence data from transect sites in 2006-2008 and a historical dataset from 1967-
1973 (Montserrat 1976). Second, we test for the factors influencing local population turnover
in *P. apollo*'s remaining network of populations, using data from habitats where the species
was recorded in 2006, and which were resurveyed in 2007, 2008 and 2012. Finally, we
100 examine the influence of fine-scale variation in topography and vegetation on habitat use and
the microclimates experienced by *P. apollo* larvae along a mountain ridge which represents a
stronghold for the species in the region. Overall, we show how local vegetation and
topography can have important effects on microclimate, habitat use and population
persistence, over and above the effects of broad scale gradients in the climate.

105 **METHODS**

Study system

Parnassius apollo (L.) is a mountain butterfly in most of its European range (Tolman and
Lewington 1997; Settele et al. 2008), and its larvae feed predominantly on *Sedum* spp.
(Crassulaceae) (Deschamps-Cottin et al. 1997). The butterfly has one generation per year
110 (June-August), and hibernates as a small larva inside the egg (Tolman and Lewington 1997).
P. apollo is estimated to have declined in Europe by nearly 30% since 2000 (van Swaay et al.
2010), and the pattern of greatest declines at low elevations has been linked to climate change
(Descimon et al. 2005). Land-use change and pollution may also be associated with the
decline (Sánchez-Rodríguez and Baz 1996; Nieminen et al. 2001; Fred and Brommer 2005).
115 The Sierra de Guadarrama mountains run approximately 120 x 50 km in a South-West to
North-East direction around 40°45' N 4°00' W in central Spain. The mountains divide plains
with elevations of *c.* 700 m (to the north) and *c.* 500 m (to the south), with a peak elevation of

2428 m (Fig. 1). The main regional host plant for *P. apollo* is *Sedum amplexicaule* (Sánchez-Rodríguez and Baz 1996), but larvae also feed on *S. brevifolium*, *S. forsterianum* and *S.*
120 *album* (Ashton et al. 2009). Regional distribution surveys in 2006-2008 showed that habitats
around 1500-2000 m elevation, with an intermediate ground cover of shrubs (c. 15-50%), and
widespread *Sedum* larval host plants were most likely to support *P. apollo* populations
(Gutiérrez et al. 2013). These distribution patterns are believed to relate to a requirement for
relatively cool climates at high elevations in Spain, and to habitat use and thermoregulation
125 by *P. apollo* larvae, which alternate their foraging between *Sedum* plants growing on bare
ground and in the shade of shrubs (Ashton et al. 2009; Gutiérrez et al. 2013).

Changes to the elevation range of *P. apollo*

P. apollo was recorded in 1967-73 and 2006-2008 at grassland, scrub and woodland sites
visited to record regional butterfly distributions (Fig. 1). 44 sites (elevation range 620-2040
130 m) were visited at least once during the *P. apollo* flight period in 1967-73 (554 visits in total
in June-August) (Monserrat 1976). In 2006-2008, butterflies were counted on standardised
500 m long by 5 m wide transects (Pollard and Yates 1993) every two weeks at 40 sites
(elevation range 550-2250 m), with an additional three sites sampled in 2006 (246 visits in
total over June-August 2006-2008). These “random sites” were selected as a stratified sample
135 of elevations, without knowledge of whether suitable habitat was present for *P. apollo*. The
butterfly was considered present in either time period at locations where one or more
individuals were counted, and absent where no individuals were observed, an approach
considered valid because the species is large, active during sunny weather, and easy to detect
when present.

140 The location of sample sites in 1967-1973 was determined by inspection of 1:50,000 maps
with V. Monserrat, who carried out the original surveys. In 2006-2008, Universal Transverse
Mercator (UTM) coordinates were taken every 100 m along transects using a handheld

Garmin GPS unit, and used to plot transects in ArcGIS (ESRI 2001). The average elevation of 100 m grid cells crossed by sample sites in both periods was estimated using a digital
145 elevation model (Farr et al. 2007).

Because historical (1967-73) and modern (2006-2008) sites did not match, we used an unpaired-site model (Tingley and Beissinger 2009) to infer any elevation range shift. We modelled the *P. apollo* distribution using a Generalised Linear Model (GLM) with binomial error structure and logit-link function for presence (1) or absence (0) against elevation (km),
150 time (1967-73 = 0, 2006-2008 = 1) and the interaction of time with elevation. The interaction term enabled testing of whether distribution changes had similar intensity across elevations (Moritz et al. 2008). For model selection, we followed the information-theoretic approach based on Akaike's information criterion corrected for small sample size (AIC_c) (Burnham and Anderson 2002). The "best" model, with the lowest AIC_c , is the most parsimonious
155 explanation of observations. We generated all potential models for each response variable, including the null model with only the intercept (five models for *P. apollo* distribution), and subsequently calculated AIC_c and AIC_c differences (ΔAIC_c) for other candidate models.

Several methods involving ΔAIC_c are available to select confidence sets of models whose constituent terms should not be ignored (Burnham and Anderson 2002; Richards 2005, 2008).
160 For analyses shown in this paper, we selected models with $\Delta AIC_c < 2$. Our model confidence set included the model with the lowest AIC_c ; and other models within 2 AIC_c units, as long as they did not add variables to simpler models with lower AIC_c ("nested" in the simpler models). We conducted model-averaging for all models in the confidence set to estimate the effects of variables or interactions that were included, using the MuMIn package (Bartoń
165 2013) in R version 3.0.3 (R Development Core Team 2014). Model-averaged coefficients were calculated by weighting using Akaike weights, and then averaging coefficients over all

models in the confidence set (those included in Table 1), with the coefficient set to zero where a given variable was absent from a constituent model.

Population persistence and turnover

170 In 2006, in addition to the 43 random transects, a further 47 sites were visited where *Sedum*
host plants were known to occur (Gutiérrez et al. 2013). At these additional sites, a 500 m
transect was walked twice (1-2 weeks apart, weather permitting) on dates when *P. apollo* was
expected to be close to its peak flight period based on elevation. *P. apollo* was observed at 26
sites in total of the 90 sampled in 2006 (Gutiérrez et al. 2013), and these 26 sites were
175 revisited using the same protocol in 2007, 2008 and 2012. Flight period over the elevation
gradient was estimated for each year using weekly transects from early June to mid-August in
at least four populations (Ashton et al. 2009).

Habitat data were collected in 2006/2008 and again in 2012 for the 26 sites with *P. apollo*
presence in 2006. In both periods, twenty 50 x 50 cm quadrats were carried out at each site,
180 located every 25 m along the 500 m transect. The proportion of quadrats containing one of
the four *Sedum* species known to be used as host plants in the region (“Host plant *Sedum*
frequency”; recorded in 2006) and the percentage cover of shrubs (recorded in 2008) were
shown to be most strongly related to presence or abundance of *P. apollo* across the total of 90
sites in 2006-2008 (Gutiérrez et al. 2013), so we recorded these variables again in 2012.
185 Vegetation height (in 2006) and bare ground cover (in 2008) were also recorded for each
quadrat in the earlier survey period (see Gutiérrez et al. 2013).

For the 26 sites occupied in 2006, we used a digital elevation model (Farr et al. 2007) to
estimate mean elevation (as above), and mean insolation. Insolation was estimated as the total
direct solar radiation per 100 m grid cell per year (kWh m⁻²), using the Solar Analyst 1.0
190 extension for ArcView GIS (Fu and Rich 2000), based on latitude, slope, aspect, and effects
of shading from the elevations of surrounding cells.

The 26 sites were classified according to whether *P. apollo* was observed in all of the years that the site was visited (“Persistence”) or whether the species was not found by sampling in at least one year (local population “Turnover”). It was not possible to conduct transects near the estimated peak flight period at three sites in 2012, but adult individuals were observed, so all three populations were recorded as persistent. In addition, two sites where the butterfly had been recorded as absent in 2007 were not visited in 2008: the lack of a 2008 visit did not affect the classification of these sites as showing turnover. Hence, slight changes to overall annual sampling do not influence inferred turnover or persistence, but do mean that abundance data are not analysed here (see Gutiérrez et al. 2013 for models of abundance in 2006-2008).

Generalised Linear Models were performed with a binomial error term and logit-link, for Persistence (1) or Turnover (0) against i) mean elevation, mean insolation, host plant *Sedum* frequency, and shrub cover, with the latter two variables recorded in 2006/08; and ii) the same variables, but with *Sedum* frequency and shrub cover measured in 2012, to test for changes in habitat or its effects on occupancy. Possible quadratic terms were included for all variables except *Sedum*, for which we had no expectation that high frequency would reduce persistence (Gutiérrez et al. 2013). The main aim of our analyses was to determine how habitat quality influenced population persistence; although it should be noted that the restriction of our analyses to sites where *P. apollo* was present in 2006 will underestimate absolute levels of population turnover by neglecting colonisations. Nevertheless, two-weekly butterfly transects from March to October were continued at 24 of the random sites from 2009-2012 (see Gutiérrez and Wilson 2014), providing us with information on the wider occurrence of colonisations by *P. apollo* in the region.

215 **Fine-scale habitat associations**

Effects of topography on microclimate, and the fine-scale habitat associations of *P. apollo*, were characterised for an approximately 8 x 5 km mountain ridge (elevation range, 1198-1886 m; Fig. 2) on the border of the provinces of Madrid and Ávila.

Transects for the habitat associations of larvae were conducted in 2011 (13–28 May) and
220 2012 (21–30 April), the differences in dates related to availability of field researchers. A low-intensity transect procedure was established to allow widespread sampling for *P. apollo* larvae despite a relatively remote site and changeable spring weather. Transects were carried out when broadly suitable open habitat with *Sedum*, bare ground and shrubs was encountered. Transects were walked only under dry weather conditions without low cloud, between 1000
225 hours and 1900 hours Central European Summer Time, with the earliest transect on which larvae were observed beginning at 1040 hours, and the latest at 1807 hours. In each transect location, two parallel routes of 100 paces (5 m apart) were carried out through the habitat. Time, weather and GPS grid references (estimated to the nearest m) were recorded at the beginning and end of each transect. During the transect, on every second pace (whenever the
230 surveyor's right foot touched the ground), it was recorded whether the front of the foot was in contact with shrub, bare ground, or neither. Contacts with shrub or bare ground were tallied for each pair of transects to give a percentage frequency. For every two paces, the presence or absence (not cover) of each *Sedum* species was also recorded within a 5 metre wide strip (2.5 metres either side of the walked route). All larvae observed during the transect were recorded,
235 with their length (in millimetres, to the nearest 5 mm) and the perpendicular distance to the transect route (in cm, to the nearest 10 cm). The central point of each transect was calculated as the average of start and end grid references, and it was a proviso for inclusion in analysis that transects in the same or separate years were at least 50 m apart. 50 m was adjudged to represent a distance beyond which larvae would be relatively unlikely to move, so that,

240 although egg laying females could move between some transect locations, the observation of larvae provided evidence for successful overwintering and larval foraging in spring.

To record the microclimate conditions that larvae were exposed to, miniature Hobo TidBit dataloggers were placed in shaded positions beneath the edges of dwarf shrubs (5-10 cm vegetation height; mean = 7.5 cm) to cover the range of elevations and aspects over which *P. apollo* habitat occurred. 21 loggers recorded temperature hourly in the field in March–May 2012, and were used to calculate mean daily maximum and mean daily average temperature (°C) throughout this period.

To model larval habitat associations, we used a Generalised Linear Model with binomial error term and logit-link, for larval presence (1) or absence (0) against frequency of *Sedum*, bare ground and shrub cover, elevation and modelled insolation for March-May. Year (2011 or 2012) was included as a factor, and quadratic terms were tested for variables other than *Sedum* frequency. To model the determinants of spring microclimate conditions, we used General Linear Models with a Gaussian error term for temperature against elevation (km), modelled insolation for March-May (kWh m^{-2}), and vegetation height (cm). We analysed both overall mean temperature, and mean daily maximum temperature (logged to remove model overdispersion). Mean daily maximum temperature is likely to influence whether threshold temperatures are exceeded for larval emergence and activity. To illustrate how topography influenced spring microclimate temperatures on the mountain ridge (Fig 2), we estimated March-May temperatures for the insolation levels estimated for the 100 m grid cells in the landscape with the minimum, 10th percentile, 90th percentile and maximum modelled insolation.

RESULTS

Changes to the elevation range of *P. apollo*

The prevalence of *P. apollo* decreased, and the elevation range contracted between 1967-73
265 and 2006-08 (Fig. 3). The lowest elevation presences in the random sites were at 980 m in
1967-73, and 1450 m in 2006-08, while the species was observed at the highest elevation
sampled in both periods (2040 m and 2250 m respectively). The average elevation of *P.*
apollo presences was 1517 m in 1967-73 (290 m above the average elevation sampled),
versus 1822 m in 2006-08 (477 m above the average sampled). In both periods, *P. apollo* was
270 more frequent at high elevations, but in 1967-73 it was virtually ubiquitous above 1500 m,
whereas in 2006-08 it was rare at all elevations (Fig. 3). *P. apollo* was present at 20 (45%) of
44 sample locations in 1967-73, with 252 individuals recorded, versus 5 (12%) of 43 random
sites in 2006-08, with only 10 individuals recorded from the random transect sites over the
three year period.

275 The best model for *P. apollo*'s elevation range included the effects of elevation, time
period, and an interaction between the two (Table 1), and indicated that relative occupancy by
P. apollo increased with elevation, and decreased from 1967-73 to 2006-08 (Fig. 3). The
negative interaction term between elevation and time indicated that incidence decreased more
markedly at high elevations over time, suggesting a distribution shift to lower elevations (i.e.
280 opposite to that expected under warming). However, the model containing separate effects of
elevation (positive) and time (negative) performed similarly well ($\Delta AIC_c=1.66$), such that
overall there was little evidence for an elevation shift. ΔAIC_c exceeded 29 in all simpler
models.

Population persistence and turnover

285 In addition to the five random sites where *P. apollo* was recorded in 2006, targeted surveys in
2006 found the species in 21 locations. In 17 of this total of 26 occupied sites, adults were
observed in every one of the following survey years (2007, 2008 and 2012), suggesting the
existence of persistent populations during the survey period. The remaining nine sites showed
evidence of population turnover after 2006, with adults absent in two or three of the survey
290 years at six sites, and one of the survey years at three sites. Between 2009 and 2012, *P. apollo*
was only observed at one of the 19 random transect sites from which the species had been
absent in 2006-08, with a single individual seen at 1220 m elevation in 2011.

Confidence sets of models for persistence versus turnover included positive effects of
Sedum host plant frequency using habitat data from either 2006 (Table 1b) or 2012 (Table
295 1c). Analysis using the 2012 data also showed a positive effect of shrub cover (Table 1c).
However, these models were relatively weakly supported relative to the null model ($\Delta AIC_c =$
2.6-2.9). Average *Sedum* host plant frequency at the 26 sites was 0.48 in 2006, and 0.43 in
2012; while average shrub cover was 26% in 2008, and 23% in 2012, but neither host plant
frequency nor shrub cover at the sites changed significantly between 2006/08 and 2012
300 (Wilcoxon signed-rank tests, $P = 0.09$ for *Sedum* frequency, $P = 0.32$ for shrub cover). There
was strong consistency between the two surveys in the relative *Sedum* host plant frequency
and shrub cover per site ($n = 26$ sites, Pearson's $r = 0.80$, $p < 0.001$ for *Sedum*; $r = 0.63$, $p <$
0.001 for shrubs). *Sedum* host plant frequency and shrub cover were not significantly
correlated with each other in either period. We found no evidence that elevation or modelled
305 insolation were related to population turnover.

Fine-scale habitat associations

P. apollo was recorded on 23 out of 68 larval habitat transects (12 out of 31 in 2011, and 11
out of 37 in 2012; Fig 2). The model with the lowest AIC_c for larval presence versus absence

showed an association of larvae with intermediate bare ground cover (Logit probability of
310 presence = $-12.03 (\pm SE 4.00) + 0.65 \text{ Bare ground} (\pm SE 0.23) - 0.008 \text{ Bare ground}^2 (\pm SE$
0.003)) (Fig 4). Two further models had ΔAIC_c of <2 (one showed a positive effect of *Sedum*
frequency, and the other a negative effect of modelled insolation in March-May), but each of
these included the bare ground cover effect (i.e. they were nested in the simpler model), so
the additional variables were excluded from the final model. The highest ranked model which
315 did not include the effect of intermediate bare ground cover instead had a positive effect of
shrub cover and a negative effect of shrub cover², with ΔAIC_c of 7.8; while the null model
had ΔAIC_c of 9.49. The best model predicted a greater than 50% probability of larval
presence for 30-45% bare ground cover, with a maximum at 39% bare ground cover (Fig 4).

The best models for March – May daily mean temperature, and for log mean daily
320 maximum temperature, included a negative effect of elevation, and a positive effect of
modelled March – May insolation (Table 2). In both cases the next best model also included a
negative effect of vegetation height ($\Delta AIC_c = 3.22$ for daily mean; $\Delta AIC_c = 1.77$ for daily
maximum), but these models were nested within the simpler models of altitude and modelled
insolation. AIC_c differences of the best model from the null model were 25.19 for mean, and
325 15.22 for maximum temperatures. The 10% of grid cells in the landscape with the lowest
modelled insolation during March-May had aspects of 274° - 86° , whereas the 10% of grid
cells with highest modelled insolation had aspects of 112° - 254° . At equivalent elevations,
estimated average temperatures during March-May were 1.7-4.2 °C warmer for the top tenth
percentile of modelled insolation cells than for the lowest tenth percentile, and mean daily
330 maxima were 3.1-14.9 °C warmer (Fig 5).

DISCUSSION

The elevation range of *Parnassius apollo* contracted between 1967-1973 and 2006-2008 in the Sierra de Guadarrama, as regional temperatures warmed. Declines occurred throughout the elevation range, with some evidence for greater decline at higher elevations, suggesting an overall decrease in regional favourability for the species. Patterns of population turnover since 2006 indicate the importance of local habitat quality for population persistence, in this case related to host plant frequency and shrub cover. At a fine resolution, habitat structure and topography are likely to play important roles in determining both resource availability and the microclimate conditions experienced by larvae, potentially influencing population dynamics and the future conservation prospects of the species.

Changes to the elevation range of *Parnassius apollo*

In 1967-73 and 2006-08, *P. apollo* had an upper range limit apparently established by the maximum elevation of the mountains, and a lower limit well above the minimum elevation sampled (Fig. 3). In both periods, low elevations were very patchily occupied (900-1400 m in 1967-73; 1300-2000 m in 2006-08). The increase in minimum elevation by 470 m (based on comparable sampling in 1967-73 and 2006-08) greatly exceeds the average uphill shift for montane butterflies in the region (212 m), or that crudely expected based on a 1.3 °C increase in mean annual temperatures (*c.* 225 m in isotherms) (Wilson et al. 2005).

However, we found no indication of greater loss from low elevations, despite expectations that climate warming may first extirpate low-elevation parts of species ranges (Franco et al. 2006; Thomas et al. 2006; Thomas 2010). Indeed, the best supported model included an interaction term suggesting greater relative loss of populations from high elevations. For *P. apollo*, the fact that populations were sparsely distributed below *c.* 1500 m in 1967-73 means that relatively few extinctions could lead to the observed uphill contraction in the low-elevation limit. In contrast, at higher elevations in 1967-73 the relatively abundant and widespread populations may have produced sufficient numbers of dispersing individuals to

support some populations by immigration into sub-optimal habitats. The marked decline at high elevations could stem partly from a decline in favourability throughout the region (possibly related to climate), that has reduced population sizes even at high elevations: as a result, populations in sub-optimal habitats would be less likely to be bolstered by immigration, leading to local extinctions. In a comparable example, Beever et al. (2003) found greater recent population loss for the mountain pika *Ochotona princeps* at high than low latitudes, and suggested that low-latitude populations in marginal habitats may have been extirpated long ago, whereas recent changes to the climate have increased the extinction risk of high-latitude populations.

In relatively restricted mountain regions, unfavourable weather may have the potential to act broadly over population networks, leading to regionally correlated declines (e.g. Roland and Matter 2013 for the butterfly *Parnassius smintheus*). Hence, even though regional distributions of species may be related to broad-scale environmental correlates of the climate (e.g. elevation, Gutiérrez Illán et al. 2010), changes to occupancy patterns during periods of climate change may be mediated by effects of local habitat or microclimate on population dynamics, together with the effects of relative connectivity on rates of population rescue or recolonisation (Lawson et al. 2012).

375 **Population persistence and turnover**

In areas with sufficiently widespread larval host plants and available shrub cover, *P. apollo* populations have been able to persist since 2006 throughout the elevation range of the species. The associations of the species with high larval host plant frequency and shrub cover seem robust (see also Gutiérrez et al. 2013), and are probably related to observations that eggs are not laid directly on *Sedum* leaves, so larvae must locate sufficiently widespread suitable plants; and shrubs can act both as egg-laying substrates, and to provide shelter for larvae (Ashton et al. 2009).

Without an exhaustive survey of populations in the region, we have not been able to quantify connectivity for *P. apollo*, but the increasing restriction of the species to isolated
385 ridges and peaks has probably reduced connectivity between populations, leading both to reduced chances of rescue or recolonisation following local declines or extinctions, and potentially an increased risk of local inbreeding depression (see Schmeller et al. 2011). Recent increases in tree cover in the Sierra de Guadarrama (de las Heras et al. 2011) might also contribute to reduced connectivity for the species, such as has been found among
390 populations of *Parnassius smintheus* in the Rocky Mountains (Roland and Matter 2007).

Declines in local population density, potentially linked to climate conditions, are also likely to contribute to reduced population connectivity. One of the few random transects to record *P. apollo* in 2006 (at 1450 m elevation: four individuals were seen in total from 2004 to 2006) corresponds to an area where previous researchers sighted 27-61 *P. apollo* each year
395 between 1994 and 1997 (Sánchez-Rodríguez and Baz 1996; Baz 2002). Regular two-weekly transects throughout 2007-2013 (D. Gutiérrez and R.J. Wilson, unpublished data) provide robust evidence that *P. apollo* is now extinct from this location. Sites such as this that contain favourable quantities of host plants and shrubs but are small and isolated from the core parts of the species distribution probably stand little long-term chance of persistence. Single
400 individuals of *P. apollo* have been seen sporadically at one 1220 m elevation site from among the random transect sites that were not occupied in 2006, suggesting dispersal either from known populations 5-7 kilometres away, or from unknown populations shorter distances away. The lack of observations of *P. apollo* in other regularly-sampled sites, combined with the evidence of turnover from known populations, suggest that local extinctions are more
405 frequent than new colonisations in the region.

Fine-scale habitat associations

In an earlier study, we found that larvae use both bare ground and shrub cover for thermoregulating and foraging, with apparently stronger associations with shrubs at lower elevations (Ashton et al. 2009). The larval transects conducted here did not have the
410 statistical power to detect variation in habitat use over local climate gradients, but did indicate an association of *P. apollo* larvae with bare ground cover of 30-45% (Fig 4). This intermediate to high cover of bare ground may provide opportunities for larvae to thermoregulate by moving relatively short distances between bare ground and shrubs. Springtime temperatures on bare ground are on average 2-3°C warmer than temperatures
415 beneath vegetation (Ashton et al. 2009), such that variation in habitat structure could have a comparable effect on the average temperatures experienced by larvae to that caused by differences between shallow south-facing versus north-facing slopes (Fig 5a).

Nevertheless, variation in habitat structure is unlikely to compensate for the 3-15 °C warmer daily maxima experienced on south-facing versus north-facing slopes. We found a
420 weak indication that larvae were negatively associated with modelled insolation, which might be expected if larvae whose springtime emergence is advanced by warm temperatures on steep south-facing slopes are at greater risk of mortality if cold conditions return. Such “false-spring” events have been linked with *P. apollo* declines elsewhere in Europe (e.g. Descimon et al. 2005; Schmeller et al. 2011). For other montane butterflies, earlier snowmelt dates have
425 been implicated in increased larval mortality, and in declining larval host plant or nectar plant quality (Boggs and Inouye 2012; Roland and Matter 2013). Whilst we do not have evidence to link snowmelt date to the declines observed in *P. apollo* in the Sierra de Guadarrama, we note that the annual period of snow cover has decreased by 20-30 days since *P. apollo* was widespread in the region in 1967-1973 (Giménez-Benavides et al. 2007). In this context, the
430 protection of topographically heterogeneous habitats that include some sheltered north-facing

locations where cool conditions or snow cover remain more reliably until later in the year, as well as warm south-facing slopes where larvae are able to develop relatively quickly in cool years, could act as an insurance for *P. apollo* against climate variability (see Weiss et al. 1988).

435 **Conclusion**

Despite a widespread recent decline by *P. apollo* in the Sierra de Guadarrama, suitable local habitats can enable populations to survive throughout the remnant elevation range occupied by the species. The results show that identifying and maintaining suitable habitat, and monitoring population responses, remain fundamental for conservation in the face of climate
440 change. In the case of *P. apollo*, regional conservation in the short term will depend on maintenance of open areas with bare ground, shrubs, and larval host plants, probably through continued low-intensity livestock grazing. Determining the longer term prospects of this species and others at low-latitude range margins requires continued research into how resource availability, local microclimate and population connectivity interact to determine
445 population and metapopulation persistence in a warming climate.

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Table 1 Model confidence sets for a) changes to the elevation range of *P. apollo* between 1967-73 and 2006-08; and b+c) population persistence versus turnover between 2006 and 2012. a) n = 25 presences (20 in 1967-1973, and 5 in 2006-2008) and 62 absences (24 in 1967-1973, and 38 in 2006-2008). b+c) n = 17 persistent populations, 9 populations showing turnover between 2006, 2007, 2008 and 2012. Analyses show the results for host plant frequency and shrub cover measured b) in 2006, or c) in 2012. GLMs were derived using a logit-link and binomial error. K is the number of parameters in the model, including the intercept. AIC_c: Aikaike Information Criterion for small sample size; ΔAIC_c: AIC_c difference from the “best” model.

Model	K	Log Likelihood	AIC _c	ΔAIC _c	Model weight
a) Elevation range, 1967-1973 versus 2006-2008					
Time + Elevation + Time:Elevation	4	-25.01	58.50	0	0.70
Time + Elevation	3	-26.94	60.16	1.66	0.30
b) Population persistence versus turnover, 2006-2012; 2006 habitat data					
Host plant frequency	2	-14.30	33.10	0	1
c) Population persistence versus turnover, 2006-2012; 2012 habitat data					
Shrub cover + Host plant frequency	3	-12.85	32.80	0	0.55
Shrub cover	2	-14.34	33.19	0.39	0.45

Parameter estimates (± adjusted SE) for the model averaged confidence sets were:

- a) Logit (probability of presence) = -10.70 (±3.72) + 8.68 (±3.10) Elevation (km) + 1.54 (±5.64) Time – 4.24 (±3.42) Elevation:Time
- b) Logit (probability of persistence) = -1.39 (±1.09) + 4.56 (±2.35) Host plant frequency

600 c) Logit (probability of persistence) = $-2.27 (\pm 1.70) + 2.10 (\pm 2.56)$ Host plant frequency
+ $0.10 (\pm 0.05)$ Shrub cover

For b and c, AIC_c for the null model was 35.7 ($\Delta AIC_c = 2.6$ for b, $\Delta AIC_c = 2.9$ for c).

605 **Table 2** Best fitting models for spring temperatures in the habitat where *P. apollo* larval transects were conducted. 21 dataloggers recorded hourly temperatures throughout March – May 2012. “Elev” = elevation (km); “Insol” = total direct solar radiation in March – May estimated per 100 m grid cell (kWh m⁻²).

Model coefficients (\pm SE)	Log Likelihood	AIC _c	R ²
a) Mean daily temperature (°C)			
26.01 (\pm 4.79) – 15.14 Elev (\pm 2.21) + 2.3 x 10 ⁻⁵ Insol (\pm 7.2 x 10 ⁻⁶)	-25.98	62.5	0.77
b) Log mean daily maximum (°C)			
5.49 (\pm 0.99) – 2.21 Elev (\pm 0.46) + 3.5 x 10 ⁻⁶ Insol (\pm 1.5 x 10 ⁻⁶)	7.140	-3.8	0.63

Legends to figures

Figure 1 Site distribution for *P. apollo* in 1967-73 and 2006-12. Triangles show 1967-73 sites (n = 44), squares 2006-2008 random sites (n = 43) and circles additional 2006 sites with *P. apollo* presence (n = 21). Filled symbols are sites where *P. apollo* was observed, open symbols where absent; crosses indicate turnover, 2006-2012. Elevation bands are shown as 250 m increments from < 0.75 km (pale grey) to > 2 km (black). White frame shows location of larval transects (see Fig 2). The inset map shows geographical context in Spain. Georeferencing units are in UTM (30T; ED50)

Figure 2 Location of larval transects for *P. apollo*. Filled symbols indicate larval presence, and open symbols larval absence, for 2011 (squares) and 2012 (circles). Elevation is shown in 100 m increments from < 1.2 km (pale grey) to > 1.7 km (black); pixel size 100 x 100 m. Area corresponds to white frame in Fig 1. Georeferencing units are in UTM (30T, ED50)

Figure 3 Proportion of occupied sites in 250 m elevation bands for *P. apollo* in 1967-73 (n = 44 sites) (black) and 2006-08 (n = 43 sites) (white). Number of sites per elevation band shown above each bar (n for 1967-73 and 2006-2008 separated by hyphens). Lines fitted based on equation in Table 1a), for 1967-73 (solid) and 2006-08 (dashed)

Figure 4 Probability of presence of larvae as a function of bare ground cover on transects. Outline bars show proportion of transects where larvae were present for 10% increments of bare ground cover (minimum 10-20%; maximum 60-70%; sample sizes above bars). Smooth curve shows best-fitting model for probability of larval presence (Logit probability = $-12.03 + 0.65 \text{ Bare ground} - 0.008 \text{ Bare ground}^2$)

Figure 5 Effects of topography on March-May microclimate in *P. apollo* larval habitat. a) Mean temperature and b) Mean daily maximum (both °C) against elevation for 21 dataloggers located beneath 5-10 cm dwarf shrub vegetation. Lines show modelled temperature based on the equations in Table 2 applied to the 100 m grid cells shown in Fig 2. 640 Solid lines show maximum (upper line) to 90th percentile (lower line) of modelled insolation in March-May, corresponding to south-facing slopes. Dotted lines show minimum (lower line) to 10th percentile (upper line) of modelled insolation, corresponding to north-facing slopes

Fig. 1

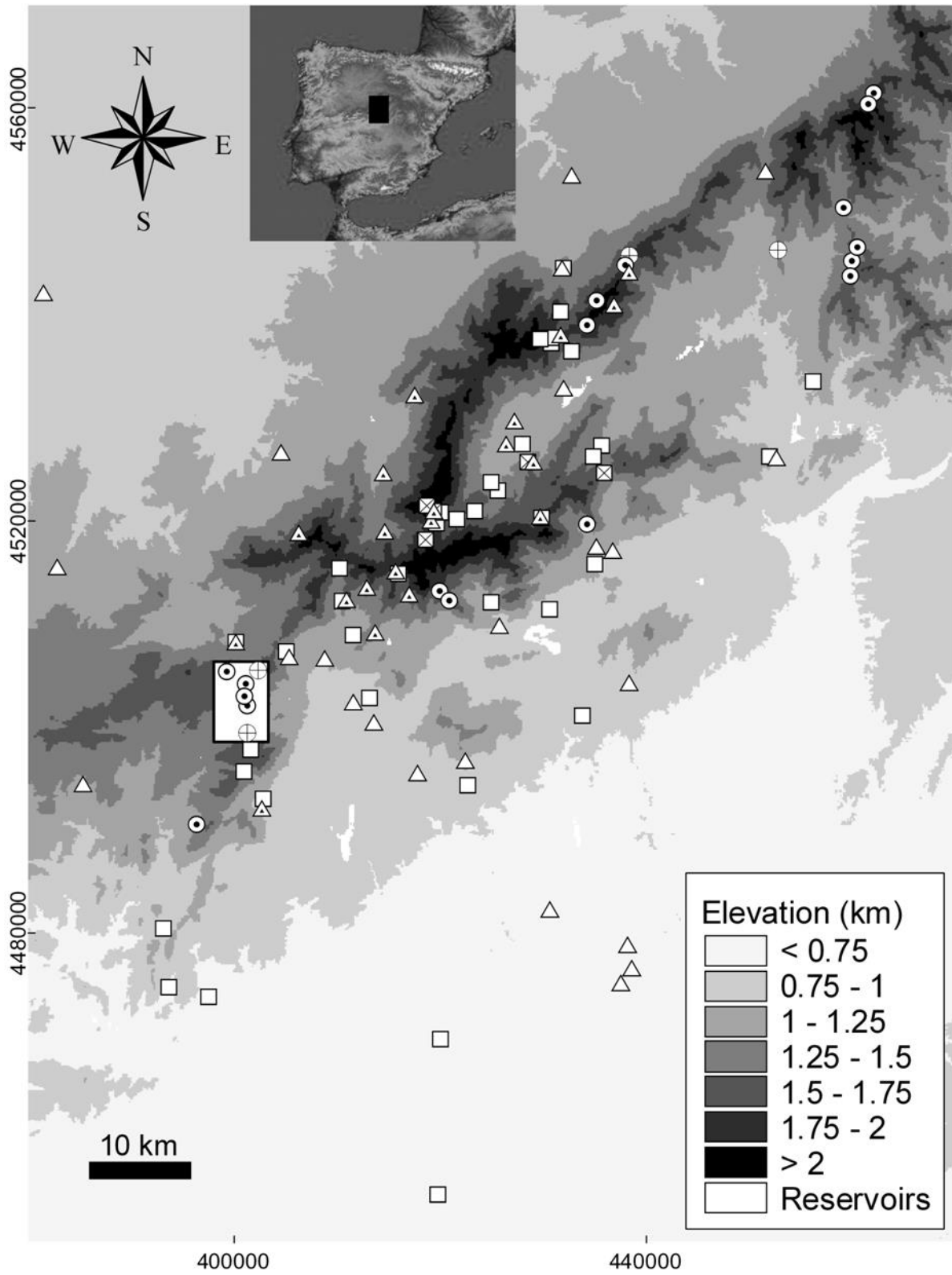
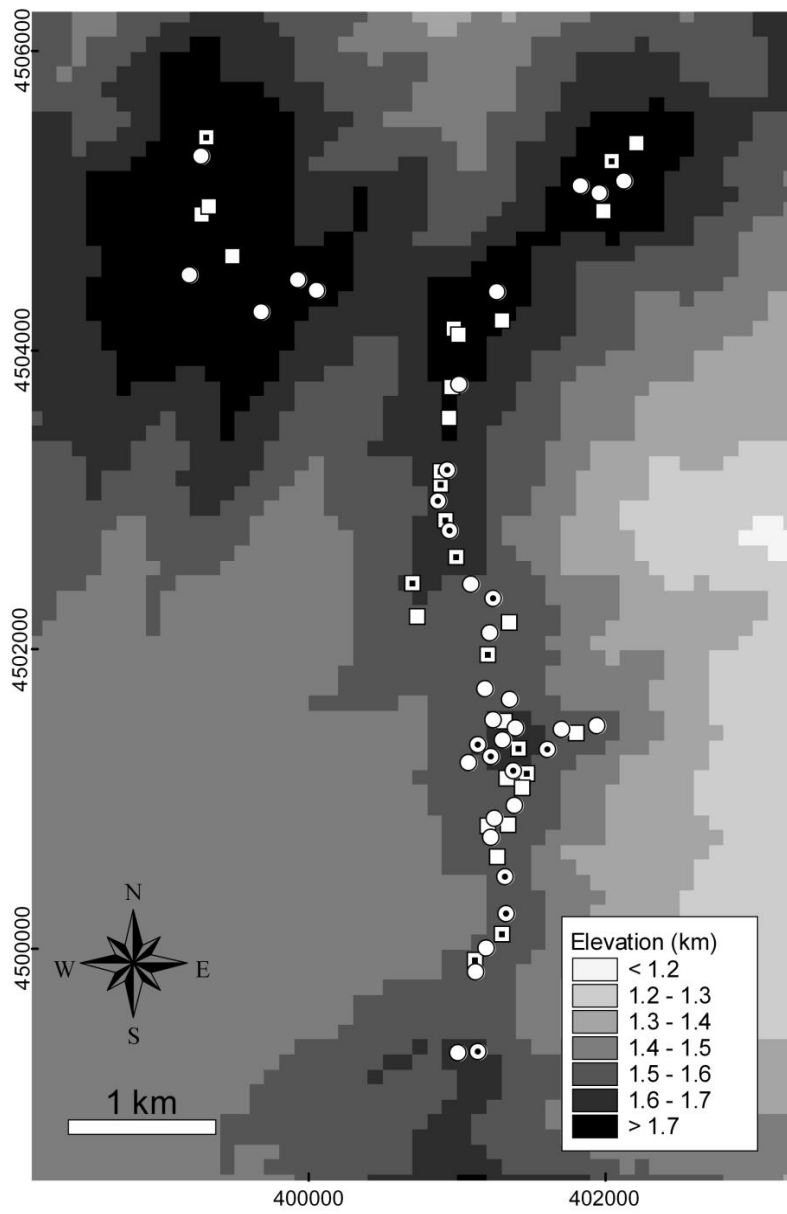


Fig. 2



650

Fig. 3

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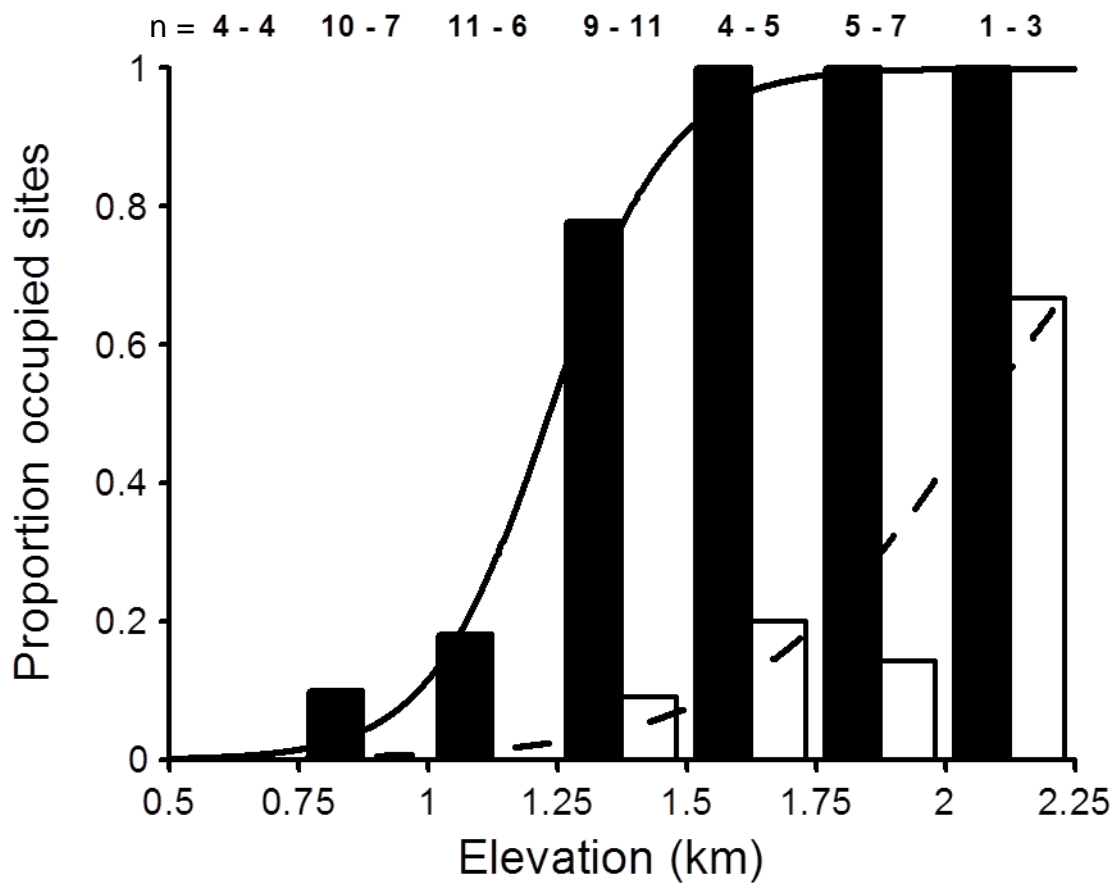
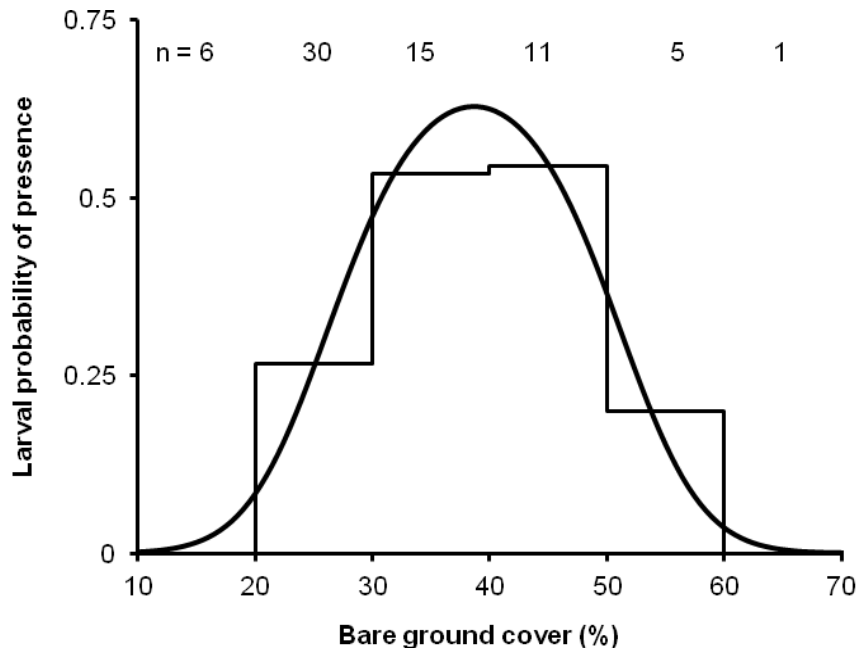


Fig 4

660



665 Fig 5

