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Reduced variability in range-edge butterfly populations over three decades of climate warming

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Running title: Population variability and climate change

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Keywords

Population dynamics, climate change, geographic range, niche space, interannual fluctuations

Abstract

Populations at the high latitude edge of species' geographic ranges are thought to show larger interannual population fluctuations, with subsequent higher local extinction risk, than those within the 'core' climatic range. As climate envelopes shift northwards under climate warming, however, we would expect populations to show dampened variability. We test this hypothesis using annual abundance indices from 19 butterfly species across 79 British monitoring sites between 1976 and 2009, a period of climatic warming. We found that populations in the latter (warmer) half of the recording period show reduced interannual population variability. Species with more southerly European distributions showed the greatest dampening in population variability over time. Our results suggest that increases in population variability occur towards climatic range boundaries. British sites, previously existing at the margins of suitable climate space, now appear to fall closer to the core climatic range for many butterfly species.

Introduction

Understanding changes in the abundance of populations over time has long fascinated ecologists. Some populations show regular cycles whilst many others appear to fluctuate about some stable mean or long term trajectory; others reject characterisation by any obvious pattern and are described as ‘chaotic’ (May, 1974). Population dynamics are known to arise from a combination of demographic and environmental stochasticity and non-linear effects from intra- and inter-specific interactions (Bjørnstad & Grenfell, 2001). The relative importance of these factors for different populations has long been debated. What is clear from empirical and theoretical studies, however, is that populations that show large fluctuations in abundance over time often face higher extinction risk (Karr, 1982, Pimm *et al.*, 1988, Lande, 1993, Inchausti & Halley, 2003). The consistency of this relationship has led to the presence of extreme population fluctuations being used as one of the IUCN Red List criteria to assess extinction risk (IUCN, 2001, Mace *et al.*, 2008).

Variability in population abundance over time is also known to change intraspecifically across geographic ranges. Hansson & Henttonen (1985) showed that two species of microtine rodent showed increased variation at higher latitudes. Curnutt, Pimm & Maurer (1996) showed that across six species of sparrow, bird populations tended to be more variable towards the edge of their geographic range. In some cases, population fluctuations are cyclic (Hansson & Henttonen, 1985, Ruohomäki *et al.*, 2000, Revels, 2006). In most cases, however, populations do not show clear cycles and the exact causes of fluctuations in abundance are unknown. As a result of increases in these fluctuations, however, and in addition to the lower mean abundances which sometimes occur at range edges (Brown, 1984, Sagarin & Gaines, 2002), populations face increased local extinction risk in these locations. The frequency of these local extinctions contributes to defining the edge of species’ geographic ranges (Gaston, 2003). Perhaps, the most extensive demonstration of increased

population fluctuations towards geographic range edges comes from Thomas, Moss & Pollard (1994), who showed that across 24 species of butterfly in Britain, which comprises the northern European distribution limits for many of the species, there was a consistent trend of increased population variability with latitude.

The paucity of examples of this phenomenon probably stems from the rarity of suitable time-series that both span a large number of generations and have suitable spatial replication across ranges. Because of this lack of appropriate data there has also been, to our knowledge, no exploration of how the variability of populations changes over time, i.e. by this, we mean whether populations in one time period are more or less variable than a subsequent time period of the same length. We are aware that certain studies have considered how measures of population variability change with increasing length of the time-series (Pimm & Redfearn, 1988, Curnutt *et al.*, 1996, Cyr, 1997, Inchausti & Halley, 2003). However, this is different from considering how population variability might change between two subsequent discrete time periods in which the abiotic environment (e.g. climate) has changed, independent of time-series length. This is the question we explore in this study.

Our main hypothesis is that increased population variability at geographic range edges is ultimately caused by populations existing at the threshold of their fundamental niche due to unsuitable macroclimatic conditions (Hutchinson, 1957). For example, high latitude range-edge populations typically occupy narrow niches that are constrained by micro-temperature (Thomas, 1993, Lennon *et al.*, 2002, Oliver *et al.*, 2009). In warm years, these populations expand to occupy a wider range of previously unsuitable micro-sites, thereby temporarily broadening the available resource base and increasing the carrying capacity of populations (Weiss *et al.*, 1988, Davies *et al.*, 2006). Fluctuations in carrying capacity with weather at northern range limits would lead to highly variable population dynamics. In contrast, lower latitude populations, closer to the centre of their fundamental niche spaces, would only rarely

be constrained by the availability of climatically suitable micro-sites, and a large proportion of their micro-sites would be consistently above the minimum temperature thresholds for occupancy. Hence, regardless of changes in weather, the carrying capacity of these populations would remain relatively stable.

If this hypothesis is correct, we would expect range-edge populations to show dampened variability over time as climate envelopes shift northwards under climate warming. Populations that were previously climatically ‘marginal’ will shift their position in niche space closer to the ‘core’ (i.e. from the edge of fundamental niche space towards the centre). We test this hypothesis using annual abundance indices from 19 butterfly species across 79 British monitoring sites between 1976 and 2009, a period spanning 34-68 discrete generations of the short-lived study species. We split time-series into two 17-year recording periods 1976-1992 and 1993-2009. Between these periods, mean seasonal temperatures have increased, whilst temperature variability has remain relatively unchanged (e.g. mean spring temperatures have increased from $8.44 \pm 0.17^{\circ}\text{C}$ to $9.19 \pm 0.16^{\circ}\text{C}$; Table S1). We test for changes in butterfly population variability between the two periods. In addition, we test for an interaction effect between recording period and latitude. We predict that populations closest to the edge of their species’ overall climatic niche space (highest latitude) will show the greatest dampening in population dynamics over time. We also test for this space-time interaction by considering the location of species’ high-latitude European range margins. We predict that species that are closest to their range edge in Britain will show the greatest dampening in population dynamics over time.

Materials and Methods

Data collation

Annual indices of butterfly abundance were obtained from the UK Butterfly Monitoring scheme (<http://www.ukbms.org/>). The scheme has operated since 1976 and involves weekly visits along set transect routes ('sites') between April and September each year. Full details of the recording methods can be found in Pollard and Yates (1993). An index of annual abundance of each species at each site was calculated allowing for missing counts (Rothery & Roy, 2001). To allow comparison of results with a previous study by Thomas *et al.* (1994), for species that overwinter as adults, we used the first of the two annual flight periods to estimate our abundance index; for those that are usually bivoltine we used the second, typically larger, generation index (Thomas *et al.*, 1994). We then split the UKBMS data into two 17-year recording periods: 1976-1992 and 1993-2009. We followed criteria from Thomas *et al.* (1994), to select sites and species with sufficient data to assess population variability. Hence, only sites recorded for at least eight consecutive years and with a mean index exceeding nine in each separate period were included in our analysis. In addition, we only used species with at least seven populations fulfilling the above criteria. This filtering resulted in a dataset containing 19 species from 79 different sites (mean = 62.3 ± 7.0 sites per species, Table S3). Species had been *a priori* classified into three categories, depending on the location of their high-latitude European range margin (from Thomas, 2007): 1) north of the Arctic circle, 2) north of the UK but below Arctic circle, or 3) range margin within UK latitudes.

Calculating population variability

For each species, we calculated the variability of time-series separately for each recording period at each site. Two measures of variability were used: a) coefficient of variation (CV,

the standard deviation of time-series divided by mean abundance), and b) standard deviation of \log_{10} annual abundance values omitting zero counts; $SD[\log(N)]$. Care must be taken when assessing the variability of time-series because we are interested in interannual fluctuations in abundance, yet measures of variability such as CV and $SD[\log(N)]$ are also influenced by biases such as length of time-series and long-term trends in abundance (Pimm & Redfearn, 1988, McArdle *et al.*, 1990, Lepš, 1993). Therefore, for each time-series we calculated the magnitude of the log-linear trend of abundance over time and the total number of years the site was recorded (mean time series length = 13.8 ± 0.08) and included these as control explanatory variables in our statistical models.

In addition, mean abundance can affect population variability, often in a Power Law relationship (Taylor, 1961, Kilpatrick & Ives, 2003). We were interested in whether the spatial and temporal patterns in population variability that we observed could be explained solely by differences in mean abundance. Therefore, each statistical model was fitted twice, once with and once without log mean abundance as a covariate (mean abundance was logged along with the response variable to account for the Power Law relationship between the two). Hence, if, for example, populations at the northern edge of a species' range show greater interannual variability in abundance simply because population sizes are much smaller, then the significant effect of latitude on variability would be expected to drop out when mean abundance is included as a covariate.

Statistical analysis

With population variability (CV or $SD[\log(N)]$) as our response variable, our explanatory variables of interest were site northing (km north, Great Britain Ordinance Survey system) and recording period (1976-1992 or 1993-2009). Additional control explanatory variables were time-series duration, log mean abundance of time-series and the magnitude of the log-

linear trend of abundance over time. We conducted two types of analysis: first, a statistical model was fitted to all species and sites as an overall test of our hypotheses; second, a separate statistical model was fitted to each species, to explore variation between species and to obtain species-specific parameters.

For the multispecies models, we fitted linear mixed models using the *MCMCglmm* package in the program R (R Development Core Team, 2009, Hadfield, 2010). Population variability can vary across species and also across the geographic range depending on landscape structure (Oliver *et al.*, 2010). Therefore, site and species were included as normally distributed random effects with zero mean. In our first model we tested for the interaction effect between site northing and recording period on CV (as fixed effects). Time-series duration and the magnitude of the log-linear trend in abundance over time were included as control explanatory variables. In the absence of strong evidence for an interaction between site northing and recording period on CV, we fitted a simpler second model with additive effects between the two explanatory variables of interest. The two statistical models were then repeated with $SD[\log(N)]$ as the response variable. Finally, all models were repeated including log mean abundance as an additional control explanatory variable. We tested for spatial autocorrelation by fitting linear mixed effects models using the *lme4* package in R (Bates *et al.*, 2008) and plotting correlograms of model residuals using the *ncf* package (Bjornstad, 2009). In no cases were significant spatial autocorrelation in residuals apparent.

For the single species analyses, we fitted separate linear mixed models to each species. With CV as the response variable, we fitted a full model including the interaction term between site northing and recording period. Control explanatory variables were time-series duration, log mean abundance of time-series and the magnitude of the log-linear trend of abundance over time. Site was included as a normally distributed random effect with zero

mean. This model was repeated with $SD[\log(N)]$ as the response variable. Finally, we removed the interaction term and fitted additive models to the CV and $SD[\log(N)]$ response variables.

For the comparative analyses, we related species' change in population variability over either space or time to the location of species' high-latitude European range margins using ANOVAS. The response variables comprised either species' slope coefficients for the trend in population variability over space within Britain or species' slope coefficients over time. The explanatory variable was a categorical factor describing the northern range limit of each species' European distribution. We tested for phylogenetic autocorrelation in the residuals using a Moran's I test with Geary randomizations (1000 iterations for each of 1000 trees; Paradis, 2006). We created a phylogeny from Genbank nucleotide sequences from the mitochondrial cytochrome oxidase subunit I (COI) gene. We used a relaxed-clock Bayesian approach implemented in Beast v1.5.4, and obtained a posterior sample of 1000 trees (Drummond *et al.*, 2006a, Drummond & Rambaut, 2007). Sequences were not available for two of the 19 species (*Erynnis tages* and *Ochlodes venata*), so we used sequences from congeners (*Erynnis tristis* and *Ochlodes ochracea*). Detailed information on the phylogeny reconstruction can be found in the Supplementary Information. In the absence of phylogenetic autocorrelation in the model residuals, we proceeded with a standard ordinary least squares ANOVA (Kunin, 2008).

Results

Multispecies models

In the multispecies model using CV as the measure of population variability there was no evidence for an interaction effect between site northing and recording period (early versus late) on population variability (Table 1). In an additive model, with the interaction term

removed, there were significant main effects of both site northing and recording period on CV (Table 1). Sites further north tended to show greater population variability and time-series from the later recording period showed less population variability. All the control variables that we included also had significant effects on CV (Table 1); longer time-series had higher values of CV, as did time-series with long term trends in abundance.

When mean abundance was included as a control variable the results were qualitatively similar; indeed, relationships with the other explanatory variables of interest and CV were even stronger (Table S2), indicating that differences in population variability across the geographic range and between recording periods were not an artefact of differences in mean population abundance between sites or between recording periods.

Results using $SD[\log(N)]$ as the measure of population variability were similar (Table 1), the only difference was that when mean abundance was included as a control variable there was some evidence for an interaction effect between site northing and recording period on population variability. This interaction is further explored in the single species analyses results below.

Single species models

The overall results from the single species analyses confirmed those of the combined multispecies analysis. An example result is shown for the meadow brown butterfly *Maniola jurtina* L. (Fig 1). From the additive models using CV as a measure of population variability, site northing and recording period had significant effects on population variability. Species tended to have positive relationships between site northing and CV (Wilcoxon signed ranks test on species' slope values: $V = 146$, $n = 19$, $p = 0.040$). Four species had individually significant relationships, all of which were positive (Fig 2, Table S3). Species tended to have negative relationships with recording period and CV (i.e. decreased variability in the later

recording period, $V = 40$, $n = 19$, $p = 0.026$). Five species had individually significant relationships, four negative and one positive (Fig 2, Table S3). Using $SD[\log(N)]$ as a measure of population variability, the effect of site northing was non-significant using a Wilcoxon signed rank test, although 15 out of 19 species had positive slopes (with two individually significant; Wilcoxon signed ranks test on species' slope values: $V = 142$, $n = 19$, $p = 0.060$; Fig. 2, Table S4). Recording period once again had a significant negative relationship with $SD[\log(N)]$ ($V = 42$, $n = 19$, $p = 0.032$). Fourteen out of 19 slopes were negative (eight slopes were significant, seven of which were negative; Fig. 2, Table S4).

Considering the models including the interaction term between site northing and recording period on CV, only one out of 19 species demonstrated a significant interaction effect. With $SD[\log(N)]$ as the response variable three species had a significant interaction terms. Given the large number of tests carried out, these results provide little evidence of multiplicative effects between position in range and recording period on population variability.

Finally, we related the change in population variability over space (within Britain) or time (over three decades) to the location of species' European range margins using ANOVAS. There was little evidence of phylogenetic structuring in model residuals (for the comparative analysis of temporal trends in population variability the Moran's I test with Geary randomizations on 1000 trees showed significant phylogenetic autocorrelation in 0% cases with CV and 4.8% cases with $SD[\log(N)]$); for the comparative analysis of spatial gradients in population variability the respective values were 5.2% and 0%). Species with more southerly European distributions tended to show steeper latitudinal gradients in population variability within Britain as expected, although the result was not statistically significant (Fig 3 panels a and b; CV response: $F_{2,16} = 0.35$, $p = 0.72$; $SD[\log(N)]$ response: $F_{2,16} = 0.60$, $p = 0.56$). However, these inter-specific differences in latitudinal gradients may be obscured by

the fact that southerly-distributed species also showed the greatest dampening in population dynamics over time (i.e. between the two recording periods 1976-1993 and 1994-2009). The relationship was significant with $SD[\log(N)]$ as the measure of variability and marginally non-significant with CV as the response (Fig 3 panels c and d; $SD[\log(N)]$ response: $F_{2,16} = 4.76$, $p = 0.024$); CV response: $F_{2,16} = 3.01$, $p = 0.077$).

Discussion

This study shows that the interannual population variability of British butterflies has declined over three decades of climate warming. It also supports the contention that interannual population variability increases towards geographic range edges. Spatial patterns in population variability have been found in case studies of certain species of other taxa (e.g. north American sparrows- Curnutt, Pimm & Maurer 1996; Fennoscandian rodents- Hansson & Henttonen 1985) and our results extend those of a previous study on British butterflies between 1976 and 1992 (Thomas *et al.*, 1994). However, the addition of a subsequent 17 years of monitoring using the same methodology also allowed us to test for changes in population variability over time. We found a significant reduction in species' interannual population variabilities in the later (17 year) recording period.

To account for potential biases in the measurement of interannual variability, we reviewed previous studies to identify control variables to include in our statistical analyses (Pimm & Redfearn, 1988, McArdle *et al.*, 1990, Lepš, 1993, Cyr, 1997, Inchausti & Halley, 2003). Our results confirmed that longer time-series, long-term trends in population abundance and lower mean abundance all produced significantly higher values of CV or $SD[\log(N)]$; hence, accounting for all these biases is important in studies of population variability. We ran all our analyses optionally excluding mean abundance as a control variable, in order to explore whether differences in mean abundance across the range and

over time might be responsible for differences in our measures of population variability. For populations experiencing constant per capita variability, a regression of log variance versus log mean abundance gives a line with a slope of 2 (Taylor, 1961, Kilpatrick & Ives, 2003). This is why CV or SD[log(N)] are often used to assess population variability, because both transformations produce measures that are independent of mean abundance (McArdle *et al.*, 1990). Yet, from empirical data, many populations show a slope of less than 2, indicating that larger populations are less variable than expected (Taylor *et al.*, 1978, Taylor & Woiwod, 1982, Hanski & Tiainen, 1989). In these cases, using CV or SD[log(N)] as response variables does not adequately account for the relationship between variance and mean abundance (McArdle *et al.*, 1990, Lepš, 1993). However, additionally including mean abundance as a covariate in a log-log transformed model can account for slope coefficients different to 2 (Lepš, 1993, Oliver *et al.*, 2010). Our results show that the spatial and temporal patterns in interannual population variability that we observed were not simply a result of differences in mean abundance between populations; for example, the smaller population sizes that might occur at range edges (Brown 1984, Sagarin & Gaines 2002; even though, for butterflies, large populations can often be found at range edges; Isaac *et al.* 2010, Päävinen *et al.* 2005). Moreover, differences in mean abundance would be unlikely to explain decreases in population variability over time, because many British butterfly populations have decreased in size over the last few decades, which one would expect to lead to increased variability (Fox *et al.*, 2011). Therefore, the decrease in variability over time that we observed in this study is not caused by changes in mean abundance.

In our analysis, we tested for an interaction effect between site northing and recording period, because we thought that more northerly sites closest to the species' range edge may have shown the greatest reduction in population variability over time. We found little evidence of such an effect. The only multispecies model which showed a significant

interaction term was the model with $SD[\log(N)]$ as the response variable and including log mean abundance as covariate (Table S2). In this case, there was a weak negative interaction effect suggesting that the slope of variability against northing has become less positive over time. This is in line with our hypothesis that population dynamics at more northerly sites have become most dampened. However, the multispecies models with CV as the response variable did not show significant interaction effects, and there was little evidence of consistent interaction effects in the single species models. Therefore, the balance of evidence suggests no strong spatial patterning in the dampening of population variability over time within Britain. This may be because Britain covers too narrow a latitudinal band relative to species' geographic ranges to be able to effectively detect spatial variation in the dampening in population dynamics over time. However, our comparative analysis, relating change in population variability over space or time to the location of species' high-latitude European range margins allowed us to explore changes in population variability across species' geographic ranges (i.e. depending on whether species were at the edge or towards the centre of their geographic range in Britain).

We found that those species for which Britain was at the northern edge of the European distribution showed the greatest reduction in variability over time. The fact that these range edge populations show disproportionate reductions in population variability is consistent with our hypothesis that fluctuations in abundance are strongly driven by the suitability of climatic conditions. Towards the 'core' of the climatic range (i.e. potentially within Britain for species whose ranges extend northwards beyond the Arctic circle), there was little effect of climate warming on interannual population variability. These species still show shallow latitudinal gradients in population variability that did not change substantially over the three decades studied. In contrast, species for which Britain constitutes the northern edge of their European distribution tended to have steeper latitudinal gradients in population variability that showed

greater dampening over time. Hence, population parameters appear much more constant within the core region of species' climatic envelopes and marked changes in population dynamics occur towards climatic range boundaries. This mirrors results from analyses of niche breadth across geographic ranges, which suggest that niche breadth is relatively constant across the 'core' of the range with rapid declines in niche breadth towards climatic range boundaries (Oliver *et al.*, 2009).

What are the mechanisms by which changes to climatic conditions might alter population variability at range edges? One possibility is that latitudinal gradients in the density of specialist natural enemies cause increased population variability in northern populations (Hansson & Henttonen, 1985). However, for population variability to increase over time across many butterfly species would require consistent parallel increases in their specialist natural enemies. We currently have no direct evidence for or against this hypothesis. A second possibility is that climatic variability drives population variability (Garcia-Carreras & Reuman, 2011). For example, the frequency of extreme weather events (cold winters, droughts etc.) is likely to influence the frequency of population crashes (Bjørnstad & Grenfell, 2001). However, for population variability at range edges to decrease over time would suggest reductions in climatic variability in the last 17 years, yet there is no evidence for this (Fig S1; Table S1); indeed, the frequency of climatic extremes are expected to increase with global warming (IPCC, 2007, Jenkins *et al.*, 2009). A third possibility is that incremental warming in temperatures has a large effect on population dynamics when populations exist close to the threshold of their fundamental niche. We suggest three (non-mutually exclusive) mechanisms by which this may occur: 1) *Climatic extremes*- years of below-average suitability may have a much greater effect on populations at range edges by pushing them beyond the threshold of the fundamental niche, causing populations to plummet. An intra-annual parallel of such population 'bottlenecks' are the seasonal

expansion and contractions in abundance of the summer and autumn/ spring feeding generations of the bi-voltine butterfly *Polyommatus bellargus* Rott. (Roy & Thomas, 2003),

2) *Microclimatic buffering*- populations at range edges are often constrained to a limited range of suitable microclimates (Thomas, 1993, Lennon *et al.*, 2002, Davies *et al.*, 2006, Oliver *et al.*, 2009). In contrast, in the climatic ‘core’ of the range, individuals can occupy a broader range of microclimates. In unfavourable years, the ability to move along a broader range of environmental gradients allows additional buffering against the impact of climatic extremes. In favourable years, a broader range of microclimates may mean more resources are available leading to higher population carrying capacities (Weiss *et al.*, 1988, Davies *et al.*, 2006),

3) *Variation in growth rates*- in favourable years, populations at range edges may be far from their maximum carrying capacity and grow relatively more quickly than ‘core’ populations that exist closer to carrying capacities (assuming growth slows as the carrying capacity is approached; Nicholson, 1933, Begon *et al.*, 1996). In poor years, range edge populations may be resource limited, due to fewer resources available in suitable microclimates, resulting in much lower growth rates (Pollard & Rothery, 1994). We suspect that, to some extent, all these mechanisms may be implicated in the way that macroclimatic conditions drive population dynamics.

In conclusion, our results are consistent with the hypothesis that populations at the edges of their climatic niche show increased temporal population variability. Mean temperature rises in Britain over the last three decades appear to have favoured many butterfly species. Hence, British populations now appear to have more stable population dynamics, perhaps because they occupy a more central position in their fundamental niche space. Reassuringly, dampening of population fluctuations in Britain may mean populations are more robust to local extinction events (Leigh, 1981, Pimm *et al.*, 1988, Lande, 1993, Inchausti & Halley, 2003). More worrying, however, is the apparent increasing disconnect between the climatic

niche (i.e. potential suitable climate space) and the actual geographic ranges that species occupy. If we are correct that species now occupy a more core position in their climatic range within Britain, then the climatic range boundary should have shifted much further north. Many different species have been shown to track climatic envelopes and to shift their high-latitude range edges closer towards the poles (Chen *et al.*, 2011). However, only a subset of (generally more dispersive) butterfly species are achieving this niche space-distribution equilibrium and expanding their distributions northwards in Britain (Hill *et al.*, 2002, Menéndez *et al.*, 2006, Willis *et al.*, 2009). Although populations may now be more stable, they may not be large enough to provide sufficient propagules to facilitate range expansion. In addition, British landscapes with highly fragmented semi-natural habitats are likely to have low functional connectivity (Hill *et al.*, 2001, Travis, 2003, Powney *et al.*, 2011). The fact that British populations seem to be more robust in the current climate but still lack the ability to expand reinforces the importance of both increasing current population sizes and increasing landscape quality (i.e. a combination of both site based and landscape-scale approaches; Lawton *et al.*, 2010).

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Tables

Table 1, Coefficients for predictors of population variability measured by CV or SD[log(*N*)] from a multispecies analysis (n = 19 species; 1150 species: site: recording period combinations), with only duration of time-series and log-linear abundance trend included as control variables (i.e. mean abundance was not accounted for). Models a and c contain interaction terms between site northing (km) and recording period. Models b and d are additive models without interaction terms. A negative coefficient for recording period indicates lower population variability in the later recording period (1993-2009). Significance of model coefficients are indicated by asterisks (0.05 > p > 0.01 * ; 0.01 > p > 0.001 ** ; p < 0.001 ***)

Model	Response	Explanatory variable	Coefficient	Lower 95% interval	Upper 95% interval	
a	CV	Site northing: recording period	0.0000	-0.0003	0.0003	NS
b	CV	Site northing	0.0003	0.0001	0.0005	*
b	CV	Recording period	-0.0581	-0.0896	-0.0261	***
b	CV	Duration recorded	0.0245	0.0196	0.0324	***
b	CV	Log-linear abundance trend	2.0924	1.8411	2.2585	***
c	SD[log(<i>N</i>)]	Site northing: recording period	-0.0001	-0.0002	0.0000	NS
d	SD[log(<i>N</i>)]	Site northing	0.0001	0.0000	0.0002	**
d	SD[log(<i>N</i>)]	Recording period	-0.0308	-0.0437	-0.0217	***
d	SD[log(<i>N</i>)]	Duration recorded	0.0107	0.0081	0.0133	***
d	SD[log(<i>N</i>)]	Log-linear abundance trend	1.0031	0.9205	1.0877	***

Figures

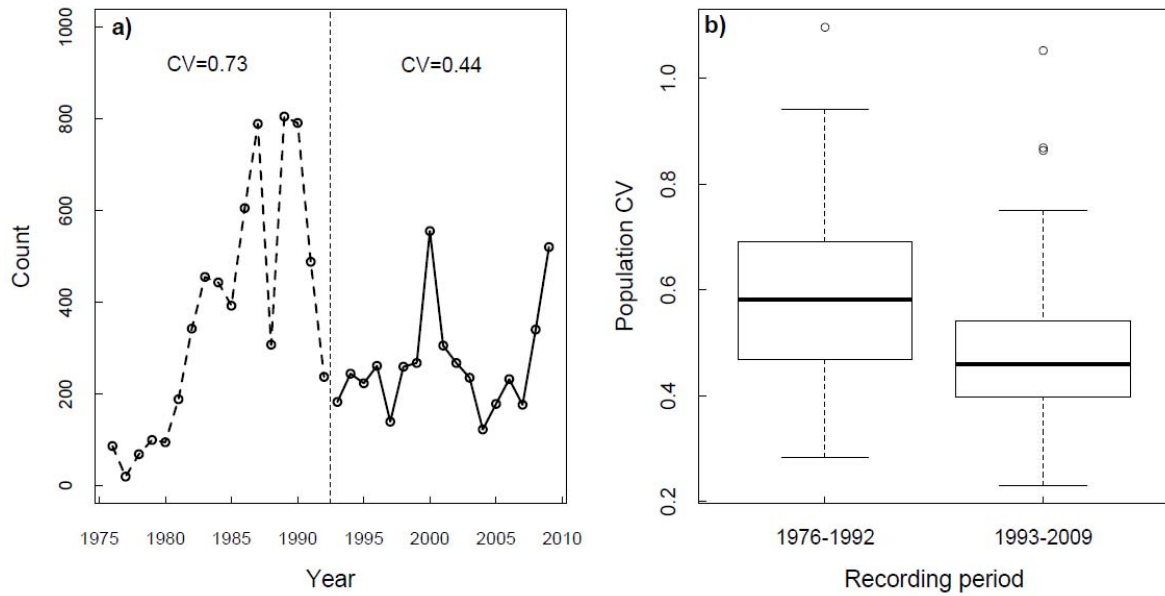


Figure 1 Population variability of the meadow brown butterfly *Maniola jurtina* has dampened over the past three decades. Panel **a** shows an example of count data from a monitoring site (Holme fen, Cambridgeshire, UK, OS gridref. TL2189) with the coefficient of variation in population size (CV) calculated for two periods 1976-1992 and 1993-2009. Panel **b** shows a Box and Whisker plot of CV across all UKBMS monitoring sites in the two recording periods.

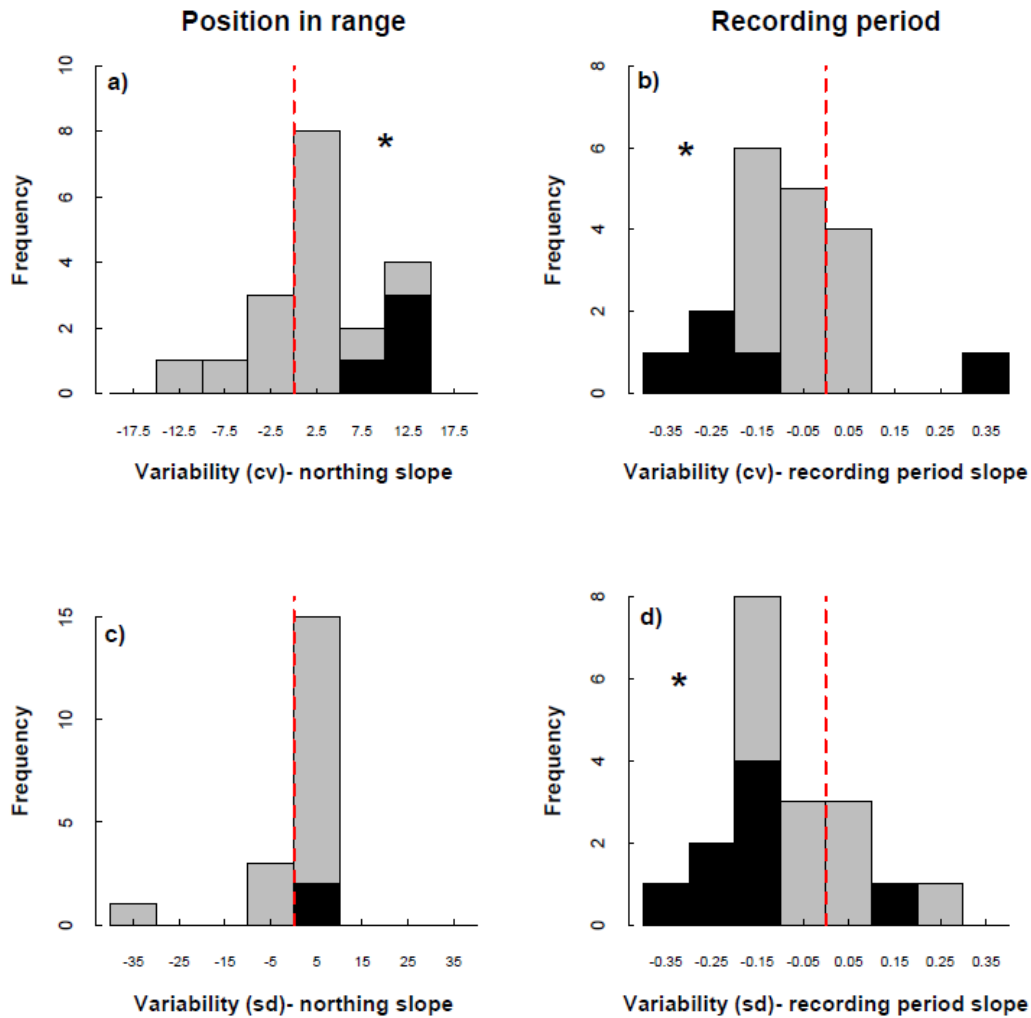


Figure 2 Histogram of coefficients for individual species relationships between site northing (panels a and c) and recording period (panels b and d) on population variability, measured using CV (panels a and b) or SD[log(*N*)] (panels c and d). The dashed vertical line indicates a coefficient of zero. Slopes for the site northing-variability relationship were transformed by multiplying by 10^4 to ensure axes legends were legible. Species with individually significant coefficients are highlighted as black bars ($p < 0.05$). For each panel, the overall significance of a consistent trend across species was tested by a Wilcoxon signed ranked tests, comparing the pooled coefficients to zero ($p < 0.05$ indicated by an asterisk).

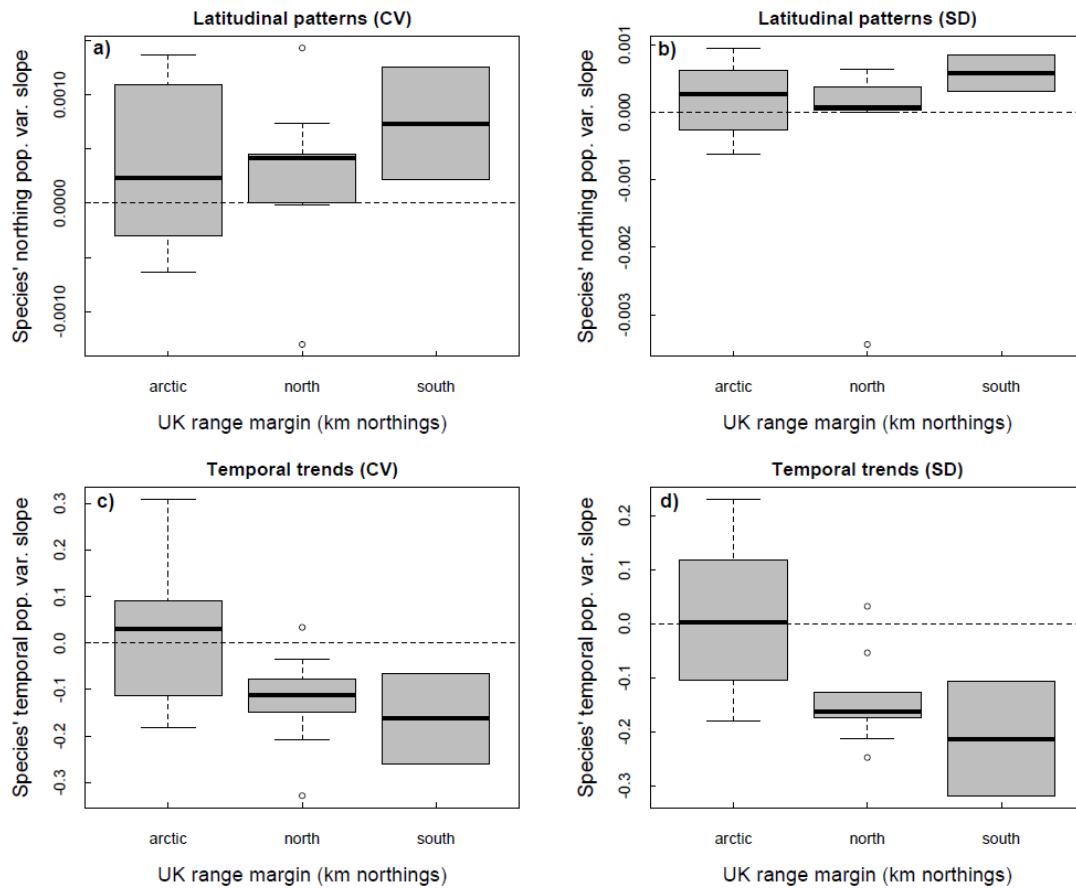


Figure 3 Change in species' population variability with northing (panels a and b) and over time (panels c and d; between recording periods 1976-1992 and 1993-2009), versus the locations of species' high-latitude European range margins (3 categories: beyond Arctic circle, beyond UK but below Arctic circle, not beyond UK). Panels a and c show slope values for population variability measured using CV and panels b and d for population variability measured using $SD[\log(N)]$. Southerly-distributed species show the steepest latitudinal gradients in population variability within Britain and the greatest dampening of population dynamics between the two recording periods.

Supporting Information

Additional supporting Information is available for this article:

Figure S1, Mean seasonal temperatures 1976-2009 from the Central England Temperature Series

Details of phylogeny construction

Table S1, Mean seasonal temperatures (\pm SE) in the two recording periods

Table S2, Coefficients for predictors of population variability with log mean abundance included as a control variable

Table S3, Species relationships between site northing (km) and recording period on population variability (measured using CV)

Table S4, Species relationships between site northing (km) and recording period on population variability (measured using SD)

Supporting Information

Supporting Information

This supporting information contains the following:

- Figure S1, Mean seasonal temperatures 1976-2009 from the Central England Temperature Series
- Details of phylogeny construction
- Table S1, Mean seasonal temperatures (\pm SE) in the two recording periods.
- Table S2, Coefficients for predictors of population variability with log mean abundance included as a control variable
- Table S3, Species relationships between site northing (km) and recording period on population variability (measured using CV)
- Table S4, Species relationships between site northing (km) and recording period on population variability (measured using SD)

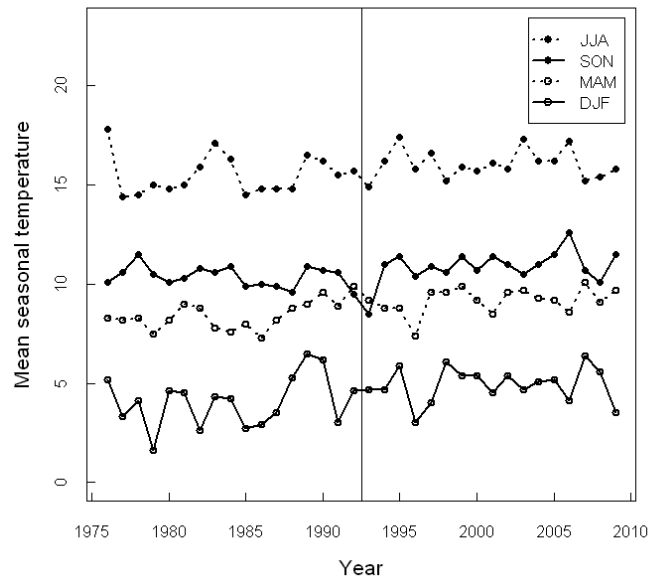


Figure S1, Mean seasonal temperatures 1976-2009 from the Central England Temperature Series (Parker *et al.*, 1992). See Table S1 for summary statistics.

Details of phylogeny construction

We created a phylogeny for 59 butterfly species commonly occurring Britain. We used Geneious (Drummond *et al.*, 2006b) to search Genbank for nucleotide sequences from the mitochondrial cytochrome oxidase subunit I (COI) gene. We were able to find sequences for 54 British species, for a further five species we included the sequence of a congener. Sequences ranging from 406-1450bp long were aligned by eye in Se-AL (<http://tree.bio.ed.ac.uk/software/seal/>). Phylogeny reconstruction used a relaxed-clock Bayesian approach (Drummond *et al.*, 2006a) implemented in Beast v1.5.4 (Drummond & Rambaut, 2007). We constrained several sets of species that correspond to well-supported clades in two recent higher level phylogenies of butterflies that used multiple genes and morphological data (Wahlberg *et al.*, 2009, Mutanen *et al.*, 2010) (constrained nodes are indicated on phylogeny). We used the SRD06 codon model that allows the substitution rates to differ between codon position 3 versus positions 1 and 2 (Shapiro *et al.*, 2006). We used a pure birth tree prior and random starting tree and a HKY + Γ substitution model. We assumed that substitution rate heterogeneity was lognormally distributed and uncorrelated, with the mean substitution rate set at 1. We conducted four runs of 50 million generations, sampling from the posterior distribution every 5000 generations. To assess mixing, that all independent runs were sampling from the posterior distribution and that the estimated sample sizes for all parameters were adequate (>200) we used Tracer v1.5 (<http://tree.bio.ed.ac.uk/software/tracer/>) after removing the first 5million generations as burnin. We built a maximum clade credibility tree from 36,000 samples drawn from the posterior distribution. For use in comparative analyses we obtained a posterior sample of 1000 trees from which we selected only the 19 species that we analysed in this study (Table S1).

Table S1, Mean seasonal temperatures (\pm SE) in the two recording periods. Temperature variability was not significantly different between the two periods, but mean winter spring and autumn temperatures were significantly higher.

Season	Temperature measure ($^{\circ}$ C)		Variance F-test		Means t-test		
	1976-1992	1993-2009	$F_{16,16}$	p	t	df	p
DJF	4.06 (0.32)	4.92 (0.22)	0.48	0.157	2.43	16	0.027
MAM	8.44 (0.17)	9.19 (0.16)	0.81	0.679	4.39	16	<0.001
JJA	15.51 (0.24)	16.05 (0.18)	0.54	0.232	1.54	16	0.143
SON	10.38 (0.13)	10.89 (0.20)	2.59	0.065	2.34	16	0.033

Table S2, Coefficients for predictors of population variability measured by CV or SD[log(*N*)] from a multispecies analysis (n = 19 species; 1150 species: site: recording period combinations), with log mean abundance included as a control variable along with duration of time-series and log-linear abundance trend. Models a and c contain interaction terms between site northing (km) and recording period. Models b and d are additive models without interaction terms. A negative coefficient for recording period indicates lower population variability in the later recording period (1993-2009). Significance of model coefficients are indicated by asterisks (0.05 > p > 0.01 * ; 0.01 > p > 0.001 ** ; p < 0.001 ***)

Model	Response	Explanatory variable	Coefficient	Lower 95% int erv al	Upper 95% int erv al	
a	CV	Site northing: recording period	0.0000	-0.0003	0.0003	
b	CV	Site northing	0.0002	0.0001	0.0004	**
b	CV	Recording period	-0.0632	-0.0981	-0.0359	***
b	CV	Duration recorded	0.0259	0.0189	0.0318	***
b	CV	Log(mean abundance)	-0.0631	-0.0796	-0.0438	***
b	CV	Log-linear abundance trend	1.9599	1.7226	2.1671	***
c	SD[log(<i>N</i>)]	Site northing: recording period	-0.0001	-0.0002	0.0000	*
d	SD[log(<i>N</i>)]	Site northing	0.0001	0.0000	0.0002	*
d	SD[log(<i>N</i>)]	Recording period	-0.0389	-0.0492	-0.0256	***
d	SD[log(<i>N</i>)]	Duration recorded	0.0110	0.0077	0.0130	***
d	SD[log(<i>N</i>)]	Log(mean abundance)	-0.0346	-0.0408	-0.0278	***
d	SD[log(<i>N</i>)]	Log-linear abundance trend	0.9343	0.8810	1.0357	***

Table S3, Results from single species models considering relationship between site northing (km) and recording period on population variability (measured using CV). Log mean abundance, duration of time-series and log-linear abundance trend were included as control variables. Model 1 contains interaction terms between site northing (km) and recording period. Model 2 is an additive model without an interaction term. A negative coefficient for recording period indicates lower population variability in the later recording period (1993-2009). Significance regression coefficients are highlighted in bold font ($p < 0.05$). The number of data points analysed for each species is given as N (with two recording periods per site, the total number of sites per species is N/2).

Species	N	Model 1		Model 2					
		Northing:period interaction coef.	t	Site northing coef.	se	t	Recording peri od coef.	se	t
<i>Aglais urticae</i>	82	0.0007	0.9342	-0.0002	0.0004	-0.4357	0.0811	0.0760	1.0674
<i>Anthocaris cardamines</i>	42	0.0009	1.3173	0.0004	0.0005	0.9070	-0.1095	0.0784	-1.3962
<i>Aphantopus hyperantus</i>	80	0.0005	0.7383	0.0014	0.0004	3.5834	-0.0351	0.0584	-0.6012
<i>Callophrys rubi</i>	14	-0.0026	-1.4839	0.0014	0.0006	2.1194	0.0757	0.1317	0.5747
<i>Coenonympha pamphilus</i>	60	-0.0007	-1.4281	-0.0004	0.0003	-1.2884	0.0984	0.0723	1.3601
<i>Erynnis tages</i>	24	-0.0006	-0.1232	-0.0013	0.0024	-0.5347	-0.0787	0.1094	-0.7192
<i>Gonepteryx rhamni</i>	76	-0.0005	-0.9471	0.0005	0.0003	1.3722	-0.2076	0.0537	-3.8665
<i>Lycaena phlaeas</i>	18	0.0006	0.4936	0.0003	0.0007	0.4778	0.3088	0.1512	2.0427
<i>Maniola jurtina</i>	118	0.0000	-0.0805	0.0000	0.0002	0.1659	-0.1490	0.0481	-3.0973
<i>Pyronia tithonus</i>	108	0.0009	1.4325	0.0002	0.0004	0.6220	-0.2594	0.0490	-5.2956
<i>Ochlodes venata</i>	98	-0.0005	-0.8321	0.0004	0.0004	1.2026	-0.1235	0.0668	-1.8486
<i>Pararge aegeria</i>	94	-0.0002	-0.4355	0.0000	0.0002	0.0073	-0.1123	0.0573	-1.9614
<i>Pieris brassicae</i>	50	-0.0001	-0.1060	0.0012	0.0006	2.1800	-0.1820	0.0975	-1.8659
<i>Pieris napi</i>	46	-0.0006	-0.8011	-0.0006	0.0005	-1.2524	-0.0160	0.0842	-0.1895
<i>Pieris rapae</i>	58	0.0019	2.2955	0.0001	0.0006	0.2695	-0.0993	0.0816	-1.2161
<i>Polygonum c-album</i>	48	0.0005	0.6132	0.0007	0.0005	1.5941	0.0334	0.0678	0.4923
<i>Polyommatus icarus</i>	38	-0.0010	-1.1477	0.0000	0.0007	-0.0168	-0.3289	0.0866	-3.7988
<i>Thymelicus sylvestris</i>	64	0.0010	1.0417	0.0013	0.0007	1.9125	-0.0658	0.0904	-0.7285
<i>Vanessa atalanta</i>	66	-0.0001	-0.2513	0.0009	0.0003	3.2744	-0.1249	0.0859	-1.4536

Table S4, Results from single species models considering relationship between site northing (km) and recording period on population variability (measured using $SD[\log(N)]$). Log mean abundance, duration of time-series and log-linear abundance trend were included as control variables. Model 1 contains interaction terms between site northing (km) and recording period. Model 2 is an additive model without an interaction term. A negative coefficient for recording period indicates lower population variability in the later recording period (1993-2009). Significance regression coefficients are highlighted in bold font ($p < 0.05$). The number of data points analysed for each species is given as N (with two recording periods per site, the total number of sites per species is $N/2$).

Species	N	Model 1		Model 2					
		Northing:period interaction coef.	t	Site northing coef.	se	t	Recording period coef.	se	t
<i>Aglais urticae</i>	82	-0.0010	-2.0719	-0.0004	0.0003	-1.2876	0.0294	0.0550	0.5351
<i>Anthocaris cardamines</i>	42	0.0010	1.2145	0.0001	0.0005	0.1214	-0.0541	0.0908	-0.5962
<i>Aphantopus hyperantus</i>	80	-0.0003	-0.4125	0.0006	0.0004	1.4033	-0.1279	0.0721	-1.7746
<i>Callophrys rubi</i>	14	-0.0006	-0.3073	0.0004	0.0007	0.5494	-0.0241	0.1402	-0.1720
<i>Coenonympha pamphilus</i>	60	-0.0004	-0.7693	-0.0001	0.0003	-0.5124	0.1810	0.0733	2.4706
<i>Erynnis tages</i>	24	0.0067	1.2641	-0.0034	0.0028	-1.2244	-0.1528	0.1324	-1.1540
<i>Gonepteryx rhamni</i>	76	-0.0007	-1.0625	0.0006	0.0004	1.6164	-0.2131	0.0689	-3.0927
<i>Lycaena phlaeas</i>	18	0.0008	0.7338	0.0005	0.0007	0.6566	0.2302	0.1501	1.5330
<i>Maniola jurtina</i>	118	-0.0010	-2.4872	0.0002	0.0002	0.8908	-0.1627	0.0527	-3.0852
<i>Pyronia tithonus</i>	108	0.0004	0.6556	0.0003	0.0003	0.9003	-0.3190	0.0502	-6.3513
<i>Ochlodes venata</i>	98	-0.0008	-1.4371	0.0004	0.0004	0.9470	-0.1644	0.0620	-2.6503
<i>Pararge aegeria</i>	94	0.0005	0.9585	0.0000	0.0003	0.1094	-0.1748	0.0612	-2.8547
<i>Pieris brassicae</i>	50	-0.0005	-0.8541	0.0010	0.0005	2.0323	0.0568	0.0695	0.8180
<i>Pieris napi</i>	46	-0.0006	-1.1036	-0.0006	0.0004	-1.4222	-0.1331	0.0685	-1.9425
<i>Pieris rapae</i>	58	0.0004	0.5856	0.0002	0.0005	0.3129	-0.0759	0.0620	-1.2237
<i>Polygonum c-album</i>	48	-0.0001	-0.1539	0.0001	0.0005	0.1145	0.0321	0.0724	0.4434
<i>Polyommatus icarus</i>	38	-0.0016	-2.6524	0.0000	0.0006	0.0060	-0.2480	0.0712	-3.4830
<i>Thymelicus sylvestris</i>	64	0.0009	0.9895	0.0008	0.0008	1.1030	-0.1075	0.0843	-1.2762
<i>Vanessa atalanta</i>	66	0.0001	0.2527	0.0008	0.0002	3.3426	-0.1807	0.0699	-2.5855

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