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Climatic factors and species range position predict sexually antagonistic selection across taxa

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Sex differences in selection are ubiquitous in sexually reproducing organisms. When the genetic basis of traits is shared between the sexes, such sexually antagonistic selection (SAS) creates a potential constraint on adaptive evolution. Theory and laboratory experiments suggest that environmental variation and the degree of local adaptation may all affect the frequency and intensity of SAS. Here, we capitalize on a large database of over 700 spatially or temporally replicated estimates of sex-specific phenotypic selection from wild populations, combined with data on microclimates and geographical range information. We performed a meta-analysis to test three predictions from SAS theory, that selection becomes more concordant between males and females: (1) in more stressful environments, (2) in more variable environments and (3) closer to the edge of the species' range. We find partial empirical support for all three predictions. Within-study analyses indicate SAS decreases in extreme environments, as indicated by a relationship with maximum temperature, minimum precipitation and evaporative potential (PET). Across studies, we found that the average level of SAS at high latitudes was lower, where environmental conditions are typically less stable. Finally, we found evidence for reduced SAS in populations that are far from the centre of their geographical range. However, and notably, we also found some evidence of reduced average strength of selection in these populations, which is in contrast to predictions from classical theoretical models on range limit evolution. Our results suggest that environmental lability and species range position predictably influence sex-specific selection and sexual antagonism in the wild.

This article is part of the theme issue 'Linking local adaptation with the evolution of sex differences'.

1. Introduction

The striking diversity of sexual dimorphisms in animals and plants suggest that patterns of selection and evolution often differ between the sexes. Sex-specific selection is common in nature [1] and is expected to result in sexual antagonism, and specifically intralocus sexual conflict, that impedes adaptation when traits with shared inheritance between the sexes have differing effects on male and female fitness [2]. Sex-specific selection is most extreme when selection acts in opposing directions on the same trait in males and females [1,3], a situation commonly referred to as sexually antagonistic selection (SAS). However, any sex difference in directional selection is expected to lead to genetic conflicts between the sexes that constrain adaptation [4], and a broader definition of SAS would include any situation where selection acts differentially on males and females. As such, SAS and resulting sexual conflict is increasingly recognized as a major evolutionary force shaping adaptation in all organisms

with two sexes [5] and understanding the factors that affect the strength of SAS is a critical and yet open question in evolutionary biology [2]. In spite of a rapidly growing number of studies of sexual antagonism in the wild [6–8] and laboratory [9–12], the environmental drivers and ecological causes of variation in sexual antagonism and SAS remain poorly understood.

Recent theory and laboratory experiments point to factors that may influence the presence or degree of SAS in different environmental contexts. The magnitude and direction of sex-specific selection is expected to be strongly influenced by environmental conditions and local ecological factors [10,13–16]. More specifically, the extent to which selection is sexually antagonistic is expected to increase as a population becomes more adapted to its local environment and both sexes become closer to their phenotypic optima [15]. This effect arises because, even if male and female optima differ for a shared trait, extreme mal adaptation caused by both sexes being displaced far from their optima will mask such SAS and instead align selection for both sexes [15,16]. This expectation leads to several specific predictions for the association between environmental conditions and the pattern of SAS. For instance, stressful environmental conditions are expected to reduce SAS as the respective distributions of a shared male and female trait will be displaced from the phenotypic optima in both sexes. A recent experimental study in seed beetles (*Callosobruchus maculatus*) directly tested this hypothesis and found that although sexual antagonism was strong under benign conditions, sexual antagonism was reduced when individuals were subjected to harsh thermal conditions [17]. Similarly, fluctuating environmental conditions are also predicted to reduce SAS, as populations, on average, will not inhabit stable adaptive peaks and hence will tend to be perennially displaced from their optima [16].

Only recently have sexual antagonism and SAS been considered in theoretical models of local adaptation in heterogeneous environments [16,18–21]. New theory merging SAS with classic models [22,23] of local adaptation suggest that factors such as distance from population mean phenotype to an optimum, and the geographical position in a species' range can affect the degree and strength of SAS [15,16,21]. The distance from the range centre should strongly influence the degree of SAS because populations residing in the centre of a species' range are expected to be locally adapted and both sexes are expected to be closer to their respective fitness optima, and so SAS would then be strong [21]. By contrast, males and females in populations at the range edge are expected to be less locally adapted, due to maladaptive gene flow outward from the centre of the species' range. Hence, at the extremes of a species range, selection is expected to be largely congruent across the sexes [21]. These models and data strongly suggest that sexual antagonism and its resolution may go hand in hand with local adaptation.

In this study, we examine global ecological drivers of sex-specific selection in wild populations to test predictions about how environmental factors influence sexual antagonism, at a large geographical scale and across a broad range of taxa. We used a large dataset from a recently published meta-analysis on environmental drivers of phenotypic selection on a global scale [24] to address the question of environmental and geographical influences on SAS. Specifically, we tested three predictions from sexual conflict theory: (1) SAS will become

reduced under harsh environmental conditions, (2) SAS should become reduced in variable environments and (3) SAS will decrease with distance from the centre of a species' range. Our novel analyses using a large database of temporally and spatially replicated phenotypic selection studies combined with independently obtained local environmental data [24], allowed us to test the first prediction at the level of within-study variance. We then tested the second and third predictions analysing variation across studies. We find varying levels of support for all three predictions, suggesting that environmental influences on sex-specific selection lead to partly predictable patterns of biogeographic and temporal variation in SAS.

2. Material and methods

(a) Data acquisition

We extracted all studies from the database compiled by Siepelski *et al.* [24] (henceforth Siepelski database) that contained estimates of phenotypic selection (variance-standardized multivariate selection gradients or univariate differentials) for both males and females, or male and female fitness components in the case of hermaphrodites. Because sex was coded arbitrarily in the Siepelski database, we recoded each as male or female, revisiting the original study when necessary. We then matched male and female selection estimates for the same trait that were estimated at the same time and in the same population. Our final dataset contained 722 paired and replicated estimates of male and female phenotypic selection from 28 studies (average number of replicates within trait \times study combination = 9.4) representing 25 species, with corresponding estimates of local environmental conditions also compiled by Siepelski *et al.* [24]. These local climate data from the CRU-TS 3.1 Climate Database are on 0.5×0.5 degree resolution and were used to generate annual mean, variation (measured as the standard deviation), and monthly maximum and minimum values for temperature, precipitation and potential evapotranspiration (PET) corresponding to each study year and location. PET is a climatic measure of environmental productivity that integrates temperature and humidity to indicate the potential for evaporation [24,25]. Although defining environmental harshness in a meaningful way is difficult, deviations from mean environmental conditions are likely to affect fitness for a variety of organisms; maximum and minimum environmental conditions can express extremes of organisms' niche, and variation can indicate either the need to cope with a greater range of conditions or with the unpredictability of the environment. Our final dataset of male and female selection estimates and corresponding environmental and range data is available in the electronic supplementary material.

We obtained a time calibrated phylogeny for the taxa in our dataset from the TimeTree database (<http://www.timetree.org>). We placed three unresolved orchid species (*Myrmecophila christinae*, *Geoblasta pennicillata*, *Changnienia amoena*) as a polytomy on the crown node of the Orchidaceae. We placed an unresolved dipteran (*Sepsis cynipsea*) as a polytomy on the crown node of the Diptera. Our phylogeny is available in the electronic supplementary material.

Species' distribution records were obtained from the Global Biodiversity Information Facility (GBIF: <https://www.gbif.org/>) using the function 'gbif' from the package *dismo* (v. 1.1-4; [26]). As this function limits the download of the data to a maximum of 200 000 observations, we therefore downloaded the data for species with a larger number of data points directly from the GBIF website. Because for some of these species the datasets included millions of records, we reduced the number of data points by subsetting the dataset to records from 2015 to 2017.

Visual comparison of the mapped data between the full dataset and the reduced one suggested this data reduction caused no loss of information. We further compared the datasets obtained with previously described distribution ranges of the IUCN (<http://www.iucnredlist.org>) when available, or other sources we could find. We excluded data points that seemed incorrectly coded and were not supported by any additional source of information. We limited the range of widespread birds to reflect their breeding range (e.g. *Hirundo rustica*), as it is during reproduction when we primarily expect SAS to operate [27]. Since some species (e.g. *Oncorhynchus kisutch*) present larger ranges than their native ones as a consequence of human introduction, we also removed data points that represented observations in introduced sites. Finally, because some species have discontinuous distributions, we restricted our analyses to the continuous range that included the locations where the actual selection studies were conducted. For instance, for an organism with a range that would include North America and West Europe, if the selection study was conducted in North America, we excluded West Europe data points for the estimation of distribution range.

We created a convex polygon as the species distribution range, and calculated its area (A) using the package *geosphere* (v. 1.5-5; [28]). We used the following equations to calculate the centroid coordinates (C_x , C_y) of the species distribution range polygon:

$$\left. \begin{aligned} C_x &= \frac{1}{6A} \sum_{i=0}^{n-1} (x_i + x_{i+1})(x_i y_{i+1} - x_{i+1} y_i) \\ C_y &= \frac{1}{6A} \sum_{i=0}^{n-1} (y_i + y_{i+1})(x_i y_{i+1} - x_{i+1} y_i), \end{aligned} \right\} \quad (2.1)$$

where:

$$A = \frac{1}{2} \sum_{i=0}^{n-1} (x_i y_{i+1} - x_{i+1} y_i), \quad (2.2)$$

where x is longitude, y is latitude, and n is the number of vertices of the polygon. We then used these estimates and the coordinates for each population in our selection database to calculate the Euclidean distance of each population from the centre of the species' range. For our analyses, described below, we use the raw distance from the range centre (in kilometres). This measure is preferable, because variation in adaption across a range is not expected for organisms with extremely restricted ranges, where a population residing on the edge would be expected to experience similar environmental conditions as populations in the centre of the small range. Nonetheless, we also performed our analyses (described below) using absolute distance divided by the square root of the range area and we present results from both analyses.

The potential for sexual antagonism occurs whenever there is additive genetic variance for a trait that is shared by both sexes [3]. However, sexual antagonism will only be realized when selection on these traits differs as well, resulting in a selective constraint on the evolution of sexual dimorphism [2]. Thus, the extent of realized sexual antagonism in a population will depend on both SAS across many traits and the intersexual genetic correlations of those traits [4,29], both of which can be captured in a single parameter, the cross-sex genetic correlation for fitness, which estimates the strength of intralocus sexual conflict at the level of the entire genome [2]. Unfortunately, estimation of intersexual genetic correlations in the wild remains a significant challenge, and to date has only been performed in a few vertebrate populations where reproductive success can be determined and pedigree information is available [6,7]. Conversely, estimates of sex-specific phenotypic selection in the wild are easier to estimate, exist for many taxa [1], and provide key

information on the strength of sexual antagonism because SAS plays a critical role in generating intralocus sexual conflict.

A further issue then arises in how to characterize SAS so that it can provide a relevant proxy for the strength of sexual antagonism. Past researchers [1] have often characterized SAS as the absolute difference between male and female selection coefficients (either differentials or gradients), $|\beta_m - \beta_f|$. This estimator has the desirable property that it is the strength of selection on sexual dimorphism itself [4,29]. Thus $|\beta_m - \beta_f|$ captures the degree to which the sexes are selectively constrained if sharing a common intersexual genetic correlation structure. Moreover, sex differences in the strength of selection on single traits will lead to sex differences in the direction of multivariate selection vectors, even if selection acts in the same direction on univariate traits (e.g. [30]). As an alternative to this traditional estimate of SAS, other researchers have advocated using the product of male and female selection ($\beta_m \beta_f$) either in its raw form or standardized by some measure of the magnitude of selection [3,31]. This alternative product estimator of SAS has the desirable property that it captures the sign of sex differences in selection. In particular, when the product is negative, selection is acting in opposing directions in males and females, indicating high SAS. A major drawback with this alternative estimate, however, is that it fails to represent sexual antagonism whenever one sex is at or near its optimum while the other is experiencing directional selection towards a different optimum [3]. In this case, directional selection in the sex which is at its current optimum would be low (and the corresponding estimate of SAS near zero), yet sexual antagonism could nonetheless be high as selection in one sex tends to pull the other off of its current optimum. Given that this is a scenario that is precisely how the evolution of sexually selected traits are often envisioned [4], the drawback of this alternative SAS estimate is potentially substantial. Because of these issues, we present results from separate analyses of SAS treated as $|\beta_m - \beta_f|$ ([1]; henceforth, 'difference estimator'), or as $\beta_m \beta_f / \sqrt{(\beta_m^2 + \beta_f^2)/2}$ ([3]; henceforth, 'product estimator'). For each study, we calculated these metrics using selection differentials when available and for gradients when differentials were unreported, as more studies reported differentials than gradients. Note that differentials and gradients are equivalent in univariate variance-standardized (as is typical) analyses [32]. Separate analyses conducted on gradients and differentials yielded similar qualitative results (electronic supplementary material, tables S2 and S3).

(b) Statistical analysis

Our database contained variance estimates (standard errors) for male and female selection coefficients for only 111 trait \times study combinations, restricting our ability to fit random regression models (see below) that explicitly model measurement error. Ignoring measurement error can have critical consequences for interpretation of meta-analyses [31]. In particular, the difference estimator will be biased upwards as variation in sex-specific selection due to sampling error is ignored, and the variance in both difference and product estimators of SAS will be inflated [31]. The former issue suggests interpreting average values of the difference estimator in informal meta-analysis should be avoided, while the latter suggests that ascribing importance to residual variation in SAS should be avoided. For our study, where a key goal is ascertaining the extent to which environmental variables predict variation in SAS, rather than estimate a mean strength of SAS, informal meta-analysis is less problematic. If unaccounted for, measurement error in the dependent variable of regression models is subsumed in the residual variance [33], and in this case interpretations of effect sizes are likely to be conservative. Measurement error in predictor variables is rarely or never accounted for in meta-analyses (and

was not in previous analyses of the Siepelski database; [24]). Although covariance in measurement errors between estimates of SAS and environmental variables would bias estimates of the relationship between the two, we expect such measurement error covariance to be non-existent, because the datasets contributing to selection and environmental factors are entirely independent from each other.

Being aware of the caveats discussed above, we used informal random-effects meta-analysis to determine the relationship between SAS and climatic and geographical factors. For the analysis of climatic factors, our model structure followed previous analyses of these data [24]. Owing to the limited within-study replication, we follow Siepelski *et al.* [24] and perform multiple univariate analyses rather than a single multivariate analysis; high dimensional random effect variance-covariance matrices (a feature of such a multivariate approach) would not be estimable. For each climatic predictor variable, we fit the following univariate linear random regression model:

$$y_{i,j,k} = \mu_a + a_j + (\mu_b + b_j) * x_{i,j} + e_k + e_{i,j}, \quad (2.3)$$

where $y_{i,j,k}$ is the estimate of SAS for replicate i in trait (trait \times study combination) j from species k , μ_a is the mean strength of SAS across all trait \times study combinations, a_j is the deviation in intercept or mean value of SAS for trait j , μ_b is the average slope relating SAS and climatic predictor x , and b_j is the trait-specific deviation in the relationship, e_k is the deviation in SAS due to evolutionary history and $e_{i,j}$ is the residual. Note that because our models did not incorporate measurement error in parameter estimation, the residual variance represents a mixture of real, and interesting, biological variation ([24,33]; here, deviation in the strength of sexual antagonism) and sampling error. Random variance in intercepts a_j and slopes b_j was modelled via an unstructured variance-covariance matrix with among-trait variance in slopes and intercepts and covariance between them. Variance in e_k was modelled as $\sigma^2 C$, where σ^2 is the phylogenetic variance component (Brownian motion rate) and C is the similarity matrix (phylogenetic correlation matrix) summarizing shared evolutionary history between species. For these models, following Siepelski *et al.* [24], each climatic variable was standardized to zero mean and unit variance within each trait \times study combination. Thus, our models examine how variation in environmental variables at the scale of the study impact estimates of SAS. Although Siepelski *et al.* [24] were able to examine spatial and temporal effects separately, due to the much larger sample size of their database, we were unable to achieve this with our more limited dataset (only seven studies reported spatial replication) and we, therefore, chose to pool the spatial and temporal replicates in a single analysis.

For analyses of geographical range and latitude, we fitted simplified univariate mixed models that excluded the random slopes among trait \times study combination. This is because for almost all studies in our database, we lacked sufficient within-study variation in the geographical predictors to fit such a model. Thus, we fit the following linear mixed model with random variation in intercepts, but not slopes, among trait \times study combination:

$$y_{i,j} = \mu_a + a_j + \mu_b * x_{i,j} + e_k + e_{i,j}, \quad (2.4)$$

where x in this case is a geographical predictor, either in the form of latitude or distance (absolute or relative; see above) from the centre of the species' range.

For the random slope models for climatic predictors, Gaussian error was assumed and the models were fit by restricted maximum likelihood (REML). Although distributions of the raw data were clearly non-Gaussian for analysis of the difference estimator, which is bounded at 0, inspection of the distributions of conditional residuals from the mixed models indicated that violations of normality were not severe, and attempts to fit

models assuming alternative error distributions failed to converge for our random slopes models. We therefore assumed Gaussian error in all microclimatic models. For the simplified random-intercept models used for analysis of geographical data, we were able to fit models with more appropriate error distributions and assumed an over-dispersed Poisson for analyses of the difference estimator. Note that use of Poisson regression is not restricted to count data [34] and might be ideal for these data as zeros are accommodated. Poisson models were fit by restricted maximum pseudo-likelihood. Finally, phylogenetic variance components were constrained to be non-negative. All mixed models were fit using the glimmix procedure in S.A.S. v. 9.3 (S.A.S. Institute, Cary, NC), and code is provided in the electronic supplementary material.

Previous analyses of the full database of replicated selection estimates have interpreted the random-effect variance components; specifically, Siepelski *et al.* [24] interpret the among-trait variance in slopes as an indicator of the variance in selection explained by within-study variance in climatic factors. This is an appropriate approach to interpret their models, as in this case there is no clear biological expectation for the magnitude and sign of fixed-effect slopes (mean slope). This is because there is no reason to expect the sign of such a relationship between a climatic factor and the strength of phenotypic selection to be conserved across taxa and traits. In our analyses, however, we have explicit theoretical predictions for how SA and environmental variables should be associated with each other, and so we take the traditional meta-analytical approach and interpret the estimates of the fixed effects. Note that because the distribution of the response variable is the same across all analyses with the same SAS estimator, and because predictors were standardized within studies, the fixed effects are comparable estimates of effect size across models with the same SAS response variable.

3. Results

Within-study variation in measures of temperature, precipitation and evaporative potential (PET) were associated with the strength of sex-specific selection for both the difference and product estimators of SAS. The relative importance and contribution of variation in the variance and mean values, however, differed depending on the estimator of SAS that was used (figure 1). Climatic variables were generally stronger predictors of the difference estimator than for the product estimator (figure 1, electronic supplementary material, tables S1–S3), and phylogenetic signal was generally higher in analyses of the product estimator. For the difference estimator of SAS, temperature variation and maximum were the strongest predictor variables of SAS, although minimum PET and precipitation were also significant (figure 1*a,c,e*). Importantly, these analyses all indicate negative effect sizes, where the magnitude of SAS became reduced at extreme (within-study) values of temperature, precipitation and PET. Thus, SAS was reduced in extremely dry, wet, hot and cold environments, as well as in environments with low or high values of PET. This is consistent with our first prediction of reduced SAS in harsh environments. Analyses of the product estimator of SAS were less consistent, and the only statistically significant predictor of SAS was maximum PET. Precipitation effect sizes were all negative (figure 1*d*; note the sign of the product estimator of SAS is reversed from the difference estimator, in that high values indicate reduced SAS), which is qualitatively consistent with results from the analysis of the difference estimator. However, the effects of

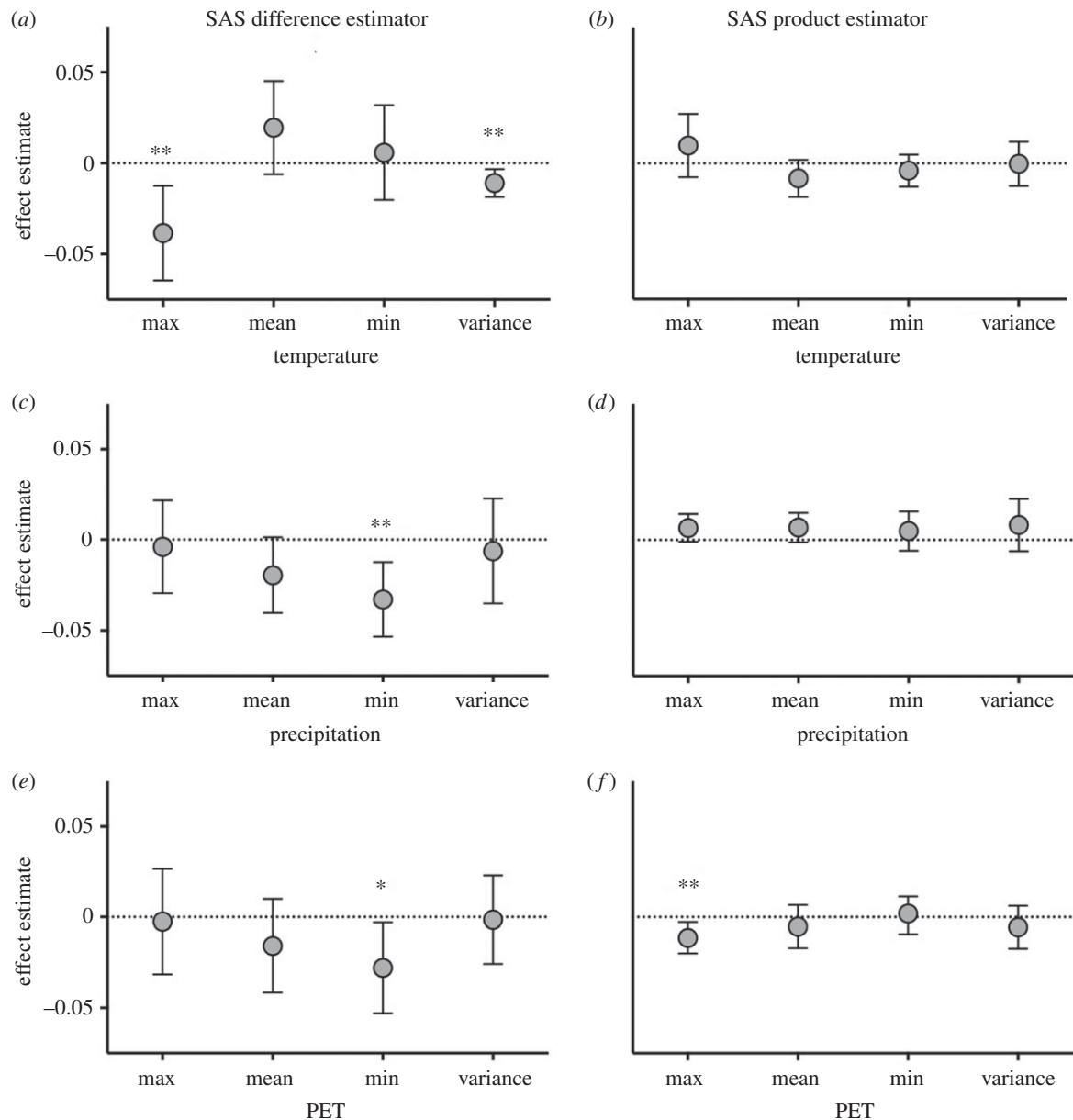


Figure 1. Microclimatic predictors of SAS. Effect sizes are the fixed effect estimates (with 95% CIs) for the relationship between within-study variation in the microclimatic variable and the strength of SAS, measured as either the difference estimator (*a,c,e*) or the product estimator (*b,d,f*). Microclimatic variables were standardized to unit variance within each study, making effects comparable across all models that treat the same SAS estimator. Negative values of the effect size in analyses of the SAS difference estimator indicate a reduction in SAS with an increase in the independent variable, while positive values of the effect size in the analysis of the SAS product estimator indicate reduced SAS with an increase in the independent variable. Asterisks indicate statistical significance at the 0.05 (*) and 0.01 (**) levels.

temperature (figure 1*b*) and PET (figure 1*f*) were partly reversed when using the product estimator as our measure of SAS. Increases in mean temperature and PET, as well as minimum temperature and maximum PET, were associated with increased levels of SAS (figure 1*f*). Thus, our results suggest that environmental extremes influence the expression of SAS, particularly when measured as the difference between male and female selection, with some indication that specific environmental drivers of variation in SAS are complex and depend on the estimator used.

Analysis of among-study geographical variation indicates the strength of SAS decreases with latitude, when SAS is taken as the difference estimator ($F_{1,639} = 17.01$, $p < 0.0001$, figure 2*a*); this effect is reduced and not significant in the analysis of the product estimator ($F_{1,602} = 1.42$, $p = 0.24$; figure 2*b*). This is consistent with the prediction that SAS

should become increased in stable environments and should become reduced under conditions of environmental change [16], as latitude is often correlated with both the degree of seasonality and climatic stability on a global scale [35,36].

Across species' ranges, we found evidence of reduced SAS at large absolute distance from the range centre in the analysis of the difference estimator of SAS ($F_{1,621} = 7.13$, $p = 0.008$; figure 3*a*). This effect was not statistically significant in the analysis of the product estimator ($F_{1,584} \approx 0$, $p = 0.95$; figure 3*b*) or in the analysis of relative distance from the range centre (difference estimator $F_{1,621} = 0.16$, $p = 0.69$; product estimator $F_{1,584} = 2.4$, $p = 0.12$, although see electronic supplementary material, table S3). Intriguingly, the mean (absolute value of male and female average) strength of selection was also highest at the centre of the range, although the

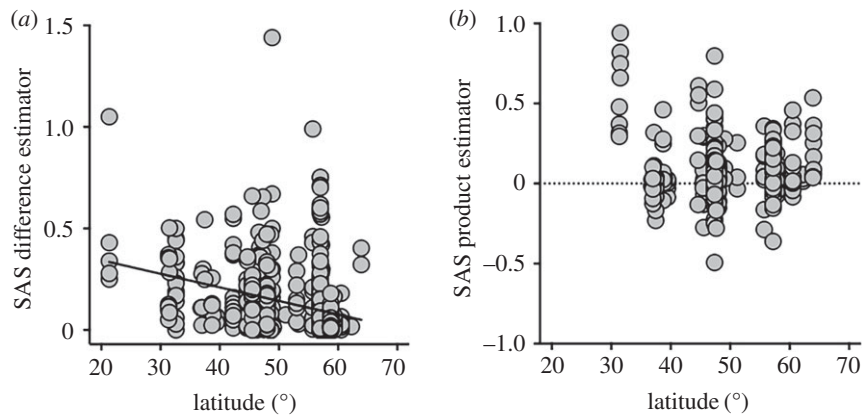


Figure 2. Relationship between latitude and SAS. A significant relationship between latitude and SAS was observed using (a) the difference estimator of SAS although not for (b) the product estimator. Analyses were performed using mixed models with random intercepts among studies and over-dispersed Poisson (a) or Gaussian (b) error, although raw values are plotted here. For details of the statistical models, see main text.

effect was weak (estimate: -0.00009 , $F_{1,625} = 4.25$, $p = 0.04$). This association is exactly opposite of expectations of existing theoretical models, in which sexually concordant selection is expected to be strongest at the range margins as gene flow swamps local adaptation. Refitting the model with the difference estimator of SAS and absolute distance to range centre, but including the average strength of selection as a covariate, indicated a weaker negative effect of position in the species' range on SAS ($F_{1,621} = 2.05$, $p = 0.15$). In the light of these results and in order to disentangle the drivers of geographical variation in SAS, we used a model selection approach and re-fit (using Laplace maximum likelihood to make likelihoods comparable across models) three candidate models: a global model with range position and mean strength of selection as a covariate (AIC = 507), a model with only range position as a predictor (AIC = 522.6) and a model with only mean strength of selection as a predictor (AIC = 526.3). This analysis provides strong support ($\Delta\text{AIC} = 15.6$) for both range position and mean strength of selection as joint predictors of SAS and indicates that the relationship between SAS and range position is not a spurious effect of covariation with mean strength of selection.

4. Discussion

We have used a newly compiled dataset of temporally and spatially replicated estimates of sex-specific selection to quantify how climatic and biogeographic factors influence SAS. We found that the strength of SAS is partly explained by local microclimatic factors, such as means and variance in temperature, precipitation and evaporative potential. Although this is broadly consistent with theoretical predictions, variation in the strength and direction of effects across analyses suggest that the relationship between environmental variables and sex-specific selection is complex, which is perhaps unsurprising given that the physiological and ecological responses to microclimate likely varies across species [37]. At a broader (across-study) scale, we find evidence that the strength of SAS is lower at high latitudes, consistent with theoretical predictions under the assumption that environments at high latitudes are less stable, a point which we discuss below. Finally, we test the prediction [21] that geographical position in the species' range may influence the strength of SAS. Consistent with this prediction, we find

evidence that SAS is reduced in populations far from the centre of the range, although we also find that the average (across the sexes) strength of selection is weakly reduced in these populations, contrary to the assumptions of the theory.

In their analysis of the environmental drivers of phenotypic selection, ignoring sex effects, Siepelski *et al.* [24] found precipitation to be the strongest predictor of selection across a wide range of taxa and studies. In contrast, we found no such evidence of a single salient predictor of the strength of SAS. Instead, we find that all three microclimatic factors that we investigated (temperature, precipitation and evaporative potential) play some role in generating variation in the strength of SAS (figure 1). Our results suggest that different environmental factors can contribute to generating sex-specific optima for shared traits, with some idiosyncratic effects that may in part be due to differential responses across taxa that differ in ecology, natural history details, and especially physiological response to microclimatic variation [37]. Although Siepelski *et al.* [24] found only limited evidence of a role for temperature as a driver of phenotypic selection, it is possible that temperature variation could have sex-specific effects on selection in some taxa, for example in ectotherms whose fitness is strongly influenced by ambient temperature [37]. Consistent with this, empirical evidence in some taxa suggest temperature can play a mediating role in sexual selection [38,39]. These results are perhaps less puzzling than the findings of a single major environmental driver of selection reported by Siepelski *et al.* [24]; our finding of multiple environmental drivers is broadly consistent with emerging theory linking environmental variation and SAS [15,16,40] and that sex-specific selection and sexual conflict are often influenced by complex environmental effects [41–43].

We found that the difference estimator of SAS was more strongly and consistently associated with environmental variables across analyses than was the product estimator. Although it is difficult to directly assess the reason for this, it is noteworthy that these two estimators of SAS represent different, but related, biological phenomenon. Our finding of consistent environmental drivers of the difference estimator of SAS suggests that selection on sexual dimorphism varies widely in response to local environmental conditions. Although in many cases this may result from sex differences in the magnitude, but not sign, of univariate selection, it is noteworthy that any such differences are expected to lead

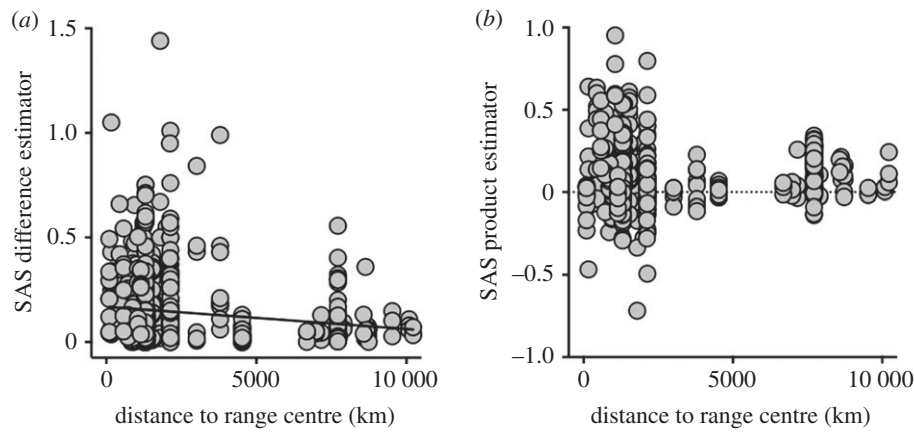


Figure 3. Relationship between SAS and position in the species' range. A significant relationship between SAS and distance from the species' range centre to the study population was observed using (a) the difference estimator of SAS although not for (b) the product estimator. Analyses were performed using mixed models with random intercepts among studies and over-dispersed Poisson (a) or Gaussian (b) error, although raw values are plotted here. For details of the statistical models and estimation of position in the species' range, see main text.

to sex differences in the direction of multivariate selection. Concomitantly, our finding of weaker associations between these same variables and the product estimator of SAS, which is very sensitive to sex differences in the sign of selection, indicates that environmental variables rarely reverse the sign of (sex-specific) selection. This latter point is consistent with past work, ignoring sex, that indicates the sign of selection can be stable in wild populations [44].

We found a striking relationship between latitude and the strength of SAS. Although latitude should reflect a broad range of biotic and abiotic factors, one key factor is environmental stability, which is generally lower at higher latitudes on both short (e.g. seasonal variation within years) and longer time scales (e.g. geologic time) [35,36]. On long time scales, latitudinal position may reflect geological age of an ecological niche, as glaciation cycles continually create and erase adaptive optima, creating a situation where species at northern latitudes enjoy only a transient period of stable suitable habitat [45]. Given that latitude might often reflect such a gradient of both short and long-term environmental stability, our finding of a negative relationship between latitude and the strength of SAS (figure 2) is consistent with the general theoretical expectation that sexual antagonism should become reduced under conditions of high environmental variation [15,16]. Note also that such a latitude effect is not a statistical artefact of our finding of a relationship between environmental variance and SAS, as our analyses treated environmental variation within individual studies. The possibility that, to some extent, SAS varies predictably over such broad geographical scales is consistent with recent theoretical work [15,16,21] and suggests exciting scope for future empirical work linking biogeography, sex-specific selection and the evolution of sexual dimorphism. For example, although we found a negative relationship between latitude, our database included no estimates from the tropics [24].

We found some evidence that the strength of SAS was reduced in populations located far from the centre of the species' geographical range, which is consistent with two-sex extensions [21] of models of the evolution of a species' range. This result suggests that sexual antagonism plays a more important role in adaptation at the range centre compared to the range margins across a wide range of organisms. However, our simultaneous finding of a negative relationship between

distance from the range centre and the average strength of selection adds some complications for interpretation. Theoretical models of the evolution of a species' range, particularly that of Kirkpatrick & Barton [23] and its derivatives [21], make the opposite prediction: (sexually concordant) selection should be stronger at the edge of a species' range than at the centre. These models assume a simple linear gradient in the optimum phenotype radiating from the range centre and (often) a corresponding gradient in density, creating a situation where gene flow from the range centre to the margin prevents marginal populations from reaching their phenotypic optima. Thus, these models predict stronger directional selection in marginal populations, opposite to what we found in this study, although our estimate of this relationship was weak. Many factors could account for this discrepancy, such as a complex or nonlinear spatial change in the optimum, range limits imposed by factors other than niche limits (such as dispersal limitation; [46]), density-dependent selection or violations of the assumption of a declining population density gradient from the range centre [47] that yields the strongest effects in these models [21]; our approach illustrates that existing selection databases could be used to explicitly test predictions and assumptions of theoretical models of species' range evolution at much broader scales. Regardless, our finding of increased SAS at the range centre suggests scope for the idea that sexual antagonism interacts with local adaptation across species' ranges.

Despite an increasing number of laboratory studies that suggest environmental factors, such as harshness and variability, may often mediate the expression of sexual conflict [9,17,41,42], the contribution of sex-specific evolution to the dynamics of local adaptation in the wild has received limited attention (see also [48]). Our work examining patterns of variation in SAS in natural populations indicates that climatic factors and biogeography also influence local sex-specific selection in the wild in predictable ways, suggesting that sexual antagonism plays a general role in the process of local adaptation. Our work also suggests that the traditionally separated research fields of local adaptation, biogeography and range limit evolution and sexual conflict require theory and data that explicitly incorporate all three processes, and transcend the small spatial scales at which sexual conflict is often studied.

Data accessibility. Data and code are provided in the electronic supplementary material.

Authors' contributions. All authors contributed to the design of the study; S.D., A.R. and D.G. collected and prepared data, performed analyses and prepared figures; S.D. wrote the first draft of the manuscript; all authors revised the manuscript.

Competing interests. We declare we have no competing interests.

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