



## Research

**Cite this article:** Iversen LL, Svensson EI, Christensen ST, Bergsten J, Sand-Jensen K. 2019 Sexual conflict and intrasexual polymorphism promote assortative mating and halt population differentiation. *Proc. R. Soc. B* **286**: 20190251.  
<http://dx.doi.org/10.1098/rspb.2019.0251>

Received: 29 January 2019  
 Accepted: 27 February 2019

**Subject Category:**  
 Evolution

**Subject Areas:**  
 evolution, ecology

**Keywords:**  
 coevolution, sexual antagonism,  
 sympatric speciation, population variation,  
 spatial structure

**Author for correspondence:**  
 Lars Lønsmann Iversen  
 e-mail: [lliversen@bio.ku.dk](mailto:lliversen@bio.ku.dk)

Electronic supplementary material is available online at <https://dx.doi.org/10.6084/m9.figshare.c.4430081>.

# Sexual conflict and intrasexual polymorphism promote assortative mating and halt population differentiation

Lars Lønsmann Iversen<sup>1,2</sup>, Erik I. Svensson<sup>3</sup>, Søren Thromsholdt Christensen<sup>1</sup>, Johannes Bergsten<sup>4</sup> and Kaj Sand-Jensen<sup>1</sup>

<sup>1</sup>Department of Biology, Freshwater Biology, University of Copenhagen, Copenhagen 2100, Denmark

<sup>2</sup>Center for Biodiversity Outcomes, Arizona State University, Tempe, AZ, USA

<sup>3</sup>Evolutionary Ecology Unit, Department of Biology, Lund University, Lund 223 62, Sweden

<sup>4</sup>Department of Zoology, Swedish Museum of Natural History, Box 50007, 104 05 Stockholm, Sweden

LLI, 0000-0001-5640-458X; EIS, 0000-0001-9006-016X

Sexual conflict is thought to be an important evolutionary force in driving phenotypic diversification, population divergence, and speciation. However, empirical evidence is inconsistent with the generality that sexual conflict enhances population divergence. Here, we demonstrate an alternative evolutionary outcome in which sexual conflict plays a conservative role in maintaining male and female polymorphisms locally, rather than promoting population divergence. In diving beetles, female polymorphisms have evolved in response to male mating harassment and sexual conflict. We present the first empirical evidence that this female polymorphism is associated with (i) two distinct and sympatric male morphological mating clusters (morphs) and (ii) assortative mating between male and female morphs. Changes in mating traits in one sex led to a predictable change in the other sex which leads to predictable within-population evolutionary dynamics in male and female morph frequencies. Our results reveal that sexual conflict can lead to assortative mating between male offence and female defence traits, if a stable male and female mating polymorphisms are maintained. Stable male and female mating polymorphisms are an alternative outcome to an accelerating coevolutionary arms race driven by sexual conflict. Such stable polymorphisms challenge the common view of sexual conflict as an engine of rapid speciation via exaggerated coevolution between sexes.

## 1. Introduction

Theory suggests that sexual conflict can promote rapid evolutionary diversification and speciation [1,2]. The antagonistic selection that characterizes sexual conflict distinguishes it from conventional sexual selection in which mate choice is largely seen as a benign outcome of mutualistic male–female mating interactions [3]. Under sexual conflict, the fitness of one sex comes at the expense of the other sex, which can lead to an escalating coevolutionary chase between males and females over mating rates [2,4–6]. Although a few empirical studies support this idea [7–9], other studies have failed to demonstrate a pronounced role of sexual conflict as a driver of population differentiation and reproductive isolation [10–12]. This conflicting empirical evidence has led to questioning of the generality of sexual conflict as a driver of population differentiation and a promoter of reproductive isolation [10–13].

However, an alternative body of theory and some limited empirical evidence point to an alternative possible outcome. Sexual conflict could, instead of causing population differentiation, produce selective regimes in which the expected coevolutionary arms race between sexes is halted and stable polymorphic equilibria are instead expected [14,15]. Under this alternative

scenario, negative frequency-dependent sexual conflict acts as a conservative pullback force that prevents population divergence by maintaining rare male and female morphs in local populations rather than resulting in evolutionary escalation [13,16]. Sexual conflict can thus maintain stable polymorphic populations in which selective male mating harassment prevents any female phenotype from going to fixation [16]. If such male and female sexually antagonistic traits are heritable, frequency-dependent sexual conflict could maintain stable genetic clusters ('morphs') [17,18]. Therefore, although sexual conflict can lead to rapid population divergence and promote speciation under some conditions [4,19], the alternative outcome might instead be the formation of male and female genetic clusters and subsequently, sympatric local coexistence of discrete mating morphs [14,19]. To distinguish between these alternative outcomes of sexual conflict, more empirical studies are needed, particularly in natural populations and under realistic ecological conditions in the field.

Here, we undertake a comprehensive biogeographic and comparative investigation of sexual conflict traits across 29 natural populations of the diving beetle species *Graphoderus zonatus* (see Methods, figure 1). Diving beetles (Coleoptera: Dytiscidae) are one of the few known cases in which the coevolution of male and female traits has been shown to be sexually antagonistic [4,20,21] (see Methods). Sexual conflict over mating in these beetles arises when males try to force copulation with females by attaching themselves using protarsal suction discs (electronic supplementary material, figure S1). Females in some populations of *G. zonatus* (and other species of diving beetles) have evolved counter-defences against male mating harassment in the form of structured elytra surfaces that reduce male attachment and disc adhesion [21] (figure 1). To counter this female defence trait, male beetles have adaptive suction discs that they use in mating [20]. The size and density of these male suction discs are correlated to female elytra structures across species, presumably to optimize disc adhesive power to a given female type [20]. In addition to this correlation across species, a similar correlation among male and female traits has also been demonstrated at the intraspecific level across populations of *G. zonatus* [22].

The concordance between this macroevolutionary correlation (between species) and a similar microevolutionary correlation (within species) of male suction discs and female elytra structural traits presents an excellent opportunity for direct tests of the evolutionary dynamics of sexual conflict within *G. zonatus* populations. Based on previous theoretical models [17,18] of these diving beetles, it was suggested that assortative mating between males and females with respect to sexually antagonistic traits in combination with frequency-dependent selection could maintain polymorphisms and result in stable equilibria. However, to date, no empirical study has demonstrated either the existence of male discrete morphs or assortative mating between any such male and female morphs. Here, we present the first empirical evidence for both the prediction of the existence of discrete male morphs and assortative mating between male and female morphs. We document and quantify a discrete male polymorphism based on a set of quantitative morphological traits in male mating structures (male suction cups). We then connect this male polymorphism to the female morphs, by demonstrating assortative mating between male and female morphs and a

geographical co-occurrence between the different proportions of these discrete male and female morphological mating clusters. Finally, we connect these results to long-term evolutionary dynamics in morph frequencies across a series of natural populations across a large biogeographic area in Sweden. If polymorphism in *G. zonatus* populations is maintained by sexual conflict, we thus predicted that males should form distinctive functional 'morphs' which should be correlated to female morphs reflecting functional pairs of male mating and female defence traits [14,20]. We further predicted that pairs of female and male traits are connected via assortative mating. In combination with negative frequency-dependent selection, which is likely to be present in this system based on previous theoretical work [17,18], we predicted that our populations should approach 0.5/0.5 morph frequencies across our study period [17,23].

## 2. Methods

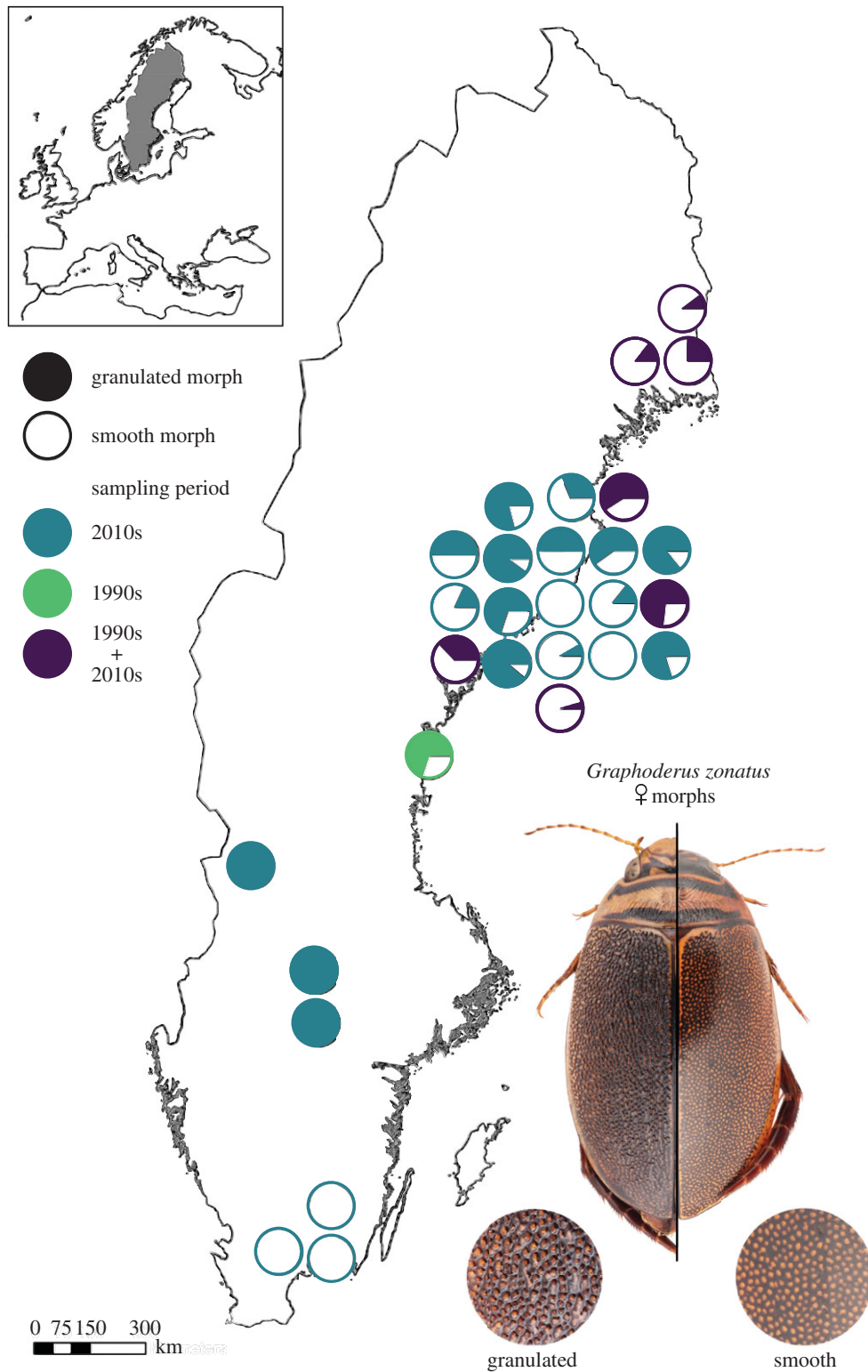
### (a) Sexually antagonistic phenotypes in diving beetles

As far as it is known, mating interactions in diving beetles are not preceded by courtship, instead initial contact between sexes sparks a precopulatory struggle [20,24]. A set of external morphological adaptations in each sex meet physically during this struggle and have been shown to evolve in a coevolutionary fashion [20], and to act antagonistically [4,21]. On the male's end, the three most basal protarsal segments are expanded and form a unit like a 'painter's pallet' (electronic supplementary material, figure S1), that are ventrally equipped with adhesive discs of varying sizes and numbers depending on species [24]. Adhesive tarsal setae are common in beetles and not restricted to males [25], but these elaborate male palettes with large symmetrical adhesive discs, are unique to the subfamily Dytiscinae to which *G. zonatus* belong. Upon initial contact, these palettes are placed dorsally on the female, either on the pronotum or anterior half of the elytra, where a variety of structured modifications in females have evolved, especially in Dytiscinae [24,26]. In *G. zonatus*, there are two distinct morphs with no intermediates. One female morph has an entirely granulate elytra and a wrinkled pronotum, while the second morph is smooth and male-like [22] (figure 1). The species is polymorphic throughout its northern and eastern distribution range [22,27].

### (b) Data collection

We examined male and female traits of *G. zonatus* across 29 lakes, sampled during the spring and/or late summer of 2015, 2016, and 2017 (electronic supplementary material, table S1). The 29 sites cover a 10.78 degree latitudinal gradient from southern to northern Sweden. The study sites are all oligotrophic lakes in watersheds dominated by conifer forest. Such lakes are stable in time and it is reasonable to assume that the study sites have been occupied by *G. zonatus* populations for long periods of time (relative to the one year lifespan of the species). The study sites include six sites that were chosen *a priori* based on previous studies of this species [27–29] and were known to harbour monomorphic female populations, and 23 sites with polymorphic female populations (figure 1).

During fieldwork, diving beetles were collected by sweeping the submerged vegetation with a standard 250 mm wide dipnet. Female morphs were recorded, classified, and counted in the field, whereas males were preserved in 6% formaldehyde and brought to the laboratory for fine-scale trait measurements. Assortative mating was evaluated by linking male front tarsal discs to the female elytra morph in all pairs found mating. In 2017, we collected a total of 51 mating pairs. These were observed and collected



**Figure 1.** Female polymorphism in *Graphoderus zonatus*. Spatial distribution of female polymorphism in the 29 populations investigated in the study. Pie charts correspond to accumulated observed proportions of females with granulated (closed circles) or smooth (open circles) elytra surfaces. (Online version in colour.)

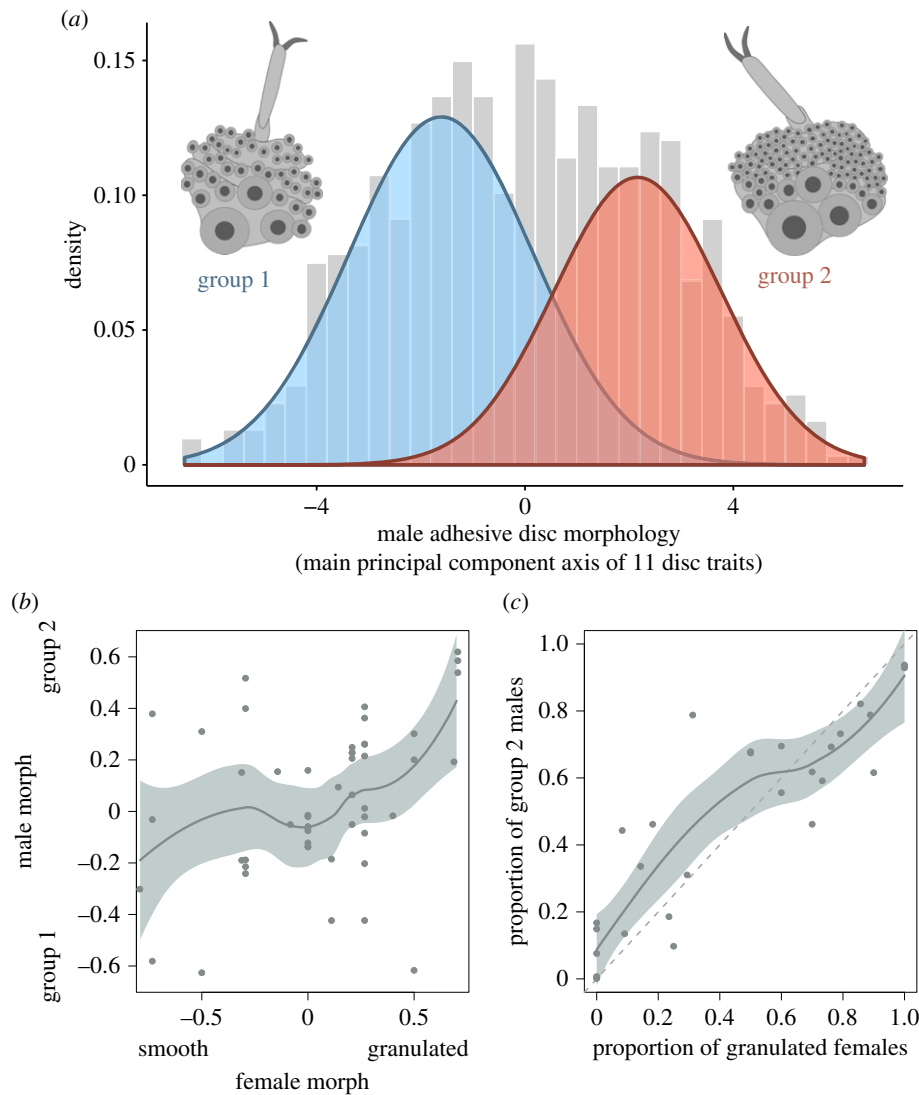
by gently searching through the submerged riparian vegetation and by walking night transects illuminating active mating pairs with a flashlight. Temporal changes in morph frequencies were documented by revisiting seven sites from which male and female trait data were collected in 1993–1996 [22] (electronic supplementary material, table S1).

### (c) Male sexual traits

The morphology of male protarsal discs in diving beetles correlates with the female elytra structure at the intraspecific level [22,30,31].

It has been shown experimentally that disc adhesive force on rough elytra structures is much lower than on smooth surfaces, and that adhesive capacity to specific elytra morphs varies between males [21]. The biomechanical link between male disc morphology and structured female elytra has been modelled as a bi-directional transformation of male discs where the three largest discs increase in size and the smaller discs decrease in size and increase in total number [20,22].

Following [20,22], we measured 11 traits describing the size and density of male protarsal discs that *a priori* are expected to reflect adaptations to different female elytra structures. These are



**Figure 2.** Correlation between male and female sexual traits in *Graphoderus zonatus*. (a) Two separated morphological clusters of males based on variation in male protarsal discs (the inserts depict examples from each group). (b) Relationship between male and female morph clusters in pairs caught in copulation. The axes represent trait deviation from random mating scenarios and the significant positive relationship between male and female traits ( $t = 2.67$ , d.f. = 49,  $p$ -value < 0.01) suggest the presence of assortative mating. (c) Positive relationship between the proportion of females with granulated elytra and males with group 2 disc-trait in the 29 sampled populations ( $t = 9.91$ , d.f. = 27,  $p < 0.001$ ). The dotted line depicts a saturated morph correlation. The solid line in (b) and (c) shows a locally fitted regression line and the 95% confidence interval of the central tendency of the line. (Online version in colour.)

as listed (see also electronic supplementary material, table S2): the width of the protarsus, number of protarsal discs on each of the three protarsal segments, and the diameter of the three largest suction cups (electronic supplementary material, figure S1). From these measurements, the abundance of protarsal discs was calculated (total number of discs counted), as well as the relative size of the largest protarsal disc (width of largest disc divided by protarsal width), the relative size of the mean of the three largest discs (mean width of the three largest discs divided by protarsal width), and the relative density of the protarsal disc (total number of discs divided by protarsal width). All measurements were done under a stereomicroscope, at a magnification of  $40\times$  to  $60\times$ .

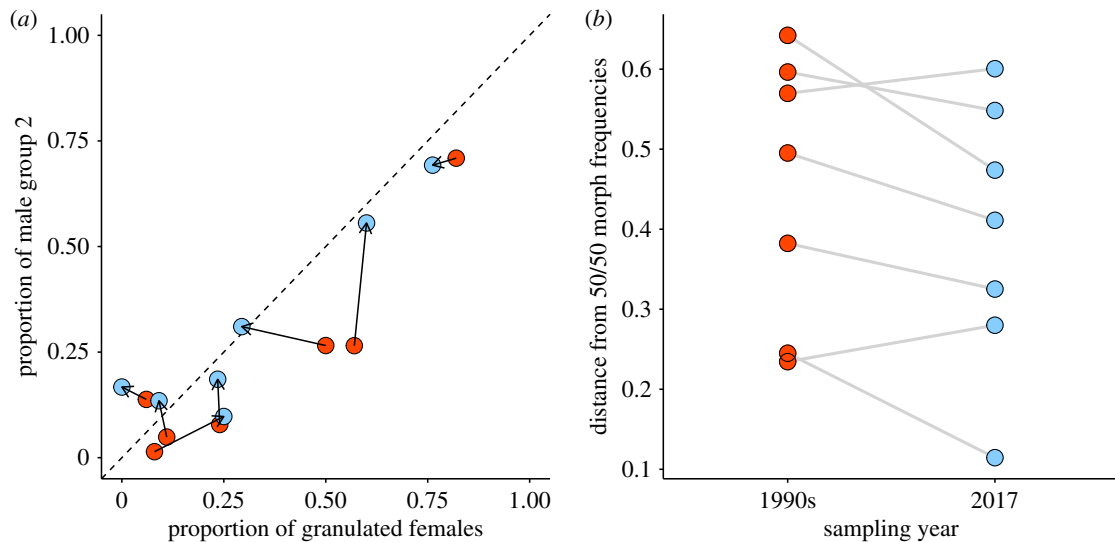
#### (d) Defining and quantifying male trait clusters

We performed an explorative parametric search for clusters in the 11 male traits following two steps. First, we condensed the shared information of the 11 traits via a principal component analysis. From  $z$ -scores, we identified a trait axis reflecting male diving beetle tarsal morphology adapted to smooth female elytra surfaces (low density and quantity of equally sized discs) or granulated female elytra (high disc density and quantity and few large discs) (see electronic supplementary material, figure S2 and table

S2). Second, we fitted expectation–maximization (EM) algorithms [32] for univariate normal mixtures given male individual placements on the principal component axis. We did not provide prior information on the different components in the mixture fittings and all mixture models were fitted by the standard random sampling procedure given by [33]. The number of components  $k$  (underlying groupings) supported by the data were evaluated via parametric bootstrapping of the likelihood ratio test statistic values. We progressively compared  $k = k_0$  versus  $k = k_0 + 1$  for  $k_0 = 1, 2, \dots$ , terminating after the bootstrapped  $p$ -value for one of these tests exceeded a significance level (pre-specified as  $p < 0.05$ ) [33]. Both the full dataset and data for the polymorphic female populations alone suggested two components in the mixture models (electronic supplementary material, figure S3).

#### (e) Associations between male and female traits

For each male, we calculated the probability of belonging to one of the two male clusters identified by the normal mixture models (figure 2). The proportion of males in group 2 (sum of probabilities divided by the number of individuals) and the proportion of granulate females were estimated for each of the 29 sites (electronic supplementary material, table S1). Using the most recent



**Figure 3.** Evolutionary dynamics of male and female morph frequencies in *Graphoderus zonatus* polymorphism. (a) Change in the proportion of male and female morphs from 1990s (red) to 2017 (blue) in seven populations. The dotted line depicts a saturated morph correlation. (b) Distance from observed proportions of male and female morphs to the 0.5/0.5 equilibrium point in the 1990s (red) and 2017 (blue). The average distance to the predicted equilibrium point decreased during the study period ( $|t| = 1.99$ , d.f. = 6,  $p < 0.05$ ), consistent with equal fitness of all morphs, frequency-dependent sexual conflict selection, and assortative mating maintaining both male and female morphs locally.

survey, the association between proportions of male and female traits was evaluated by the Pearson's product moment correlation coefficient (significance test derived from a Student's  $t$ -distribution).

Assortative mating between male and female traits was evaluated from data for 51 mating pairs collected in 2017. For each pair, the observed male and female traits were compared to trait values expected in a random mating scenario. Using site-level proportions of granulate females and group 2 males (electronic supplementary material, table S1) as probabilities of observing a given trait cluster by chance, we subtracted these probabilities from the observed trait values. A relationship between male and female traits following this subtraction would indicate trait association in mating pairs stronger than what would be expected by chance.

Association between male and female traits across the 29 sites (excluding 1990s data in revisited sites) and the 51 mating pairs was evaluated by a Pearson's product moment correlation coefficient (significance test derived from a Student's  $t$ -distribution). Trait associations were graphically visualized by a local second order polynomial regression line fitted via weighted least squares and a smoothing span of 0.75 (figure 2*b,c*).

### (f) Morph frequency dynamics in populations

The expected evolutionary dynamics given correlated sexual traits and assortative mating has received extensive theoretical attention [14,17,18]. From the first to the second sampling event (from 1993–1996 to 2017, 21–24 generations), we expect *a priori* that the seven populations maintained polymorphisms [14]. Furthermore, given the presence of assortative mating and the promiscuous mating system of *G. zonatus*, populations should predominantly move towards stable 0.5/0.5 morph frequencies [17,18]. Using a one-sided  $t$ -test for repeated measurements, we tested if these population dynamics were detectable across the seven sites. The alternative hypothesis being that the Euclidian distance to a central 0.5/0.5 morph frequency point decreased from the 1990s to 2017.

All analyses were conducted in R version 3.1.0 or later (www.R-project.org). We used the R software platform and core packages (v.3.1.0 or later), with the addition of FactoMineR [34] and mixtools [33] for our analyses.

## 3. Results

We quantified morphological mating traits of protarsal discs of 768 males from 29 populations (electronic supplementary material, table S1). The main variability in the 11 disc-traits that we measured was positively correlated to traits associated with, (i) a higher density of discs in total, and (ii) the size of the three largest discs (electronic supplementary material, figures S1 and S2 and table S2). The observed distribution of trait morphology in males along this gradient showed significant evidence of bimodal clustering explained by two separated normal distributions ( $p < 0.001$ , figure 2*a*, electronic supplementary material, figure S3). These two normal distributions correspond to two groups of male disc types with morphological structures known to be associated with smooth female elytra surfaces (low density of discs and small size of the three largest discs, group 1 in figure 2*a*) or structured elytra surfaces (high density of discs and greater size of the three largest discs, group 2 in figure 2*a*) [20,21]. These two male clusters coexist sympatrically in all populations that have polymorphic females (electronic supplementary material, table S1). Hence, these data strongly suggest that females have two morphs and that males are polymorphic in *G. zonatus*, which has been suggested [21] but not demonstrated previously.

We further found that male and female trait morphs in polymorphic populations exhibited strong assortative mating (figure 2*b*). The likelihood of observing a granulated female copulating with a male from the group 2 cluster was significantly higher than expected by chance ( $|t| = 2.67$ , d.f. = 49,  $p$ -value  $< 0.01$ ). Correlation between trait clusters was detected across all 29 study sites (figure 2*c*). The proportion of females of the granulated morph increased with the proportion of males in the group 2 cluster ( $|t| = 9.91$ , d.f. = 27,  $p < 0.001$ ). The evolutionary dynamics of morph frequency change, across 21–23 annual generations, produced morph dynamics expected with assortative mating between sexual antagonistic traits [17,18]. All seven populations maintained male and female polymorphisms from the 1990s to 2017 (figure 3*a*). The mean population change

in morph frequencies moved towards a stable 50/50 morph equilibrium that is predicted by theory [17,18] for the male and female morph types ( $|t| = 1.99$ , d.f. = 6,  $p < 0.05$ ; figure 3b).

#### 4. Discussion

This study presents the first empirical support for previous predictions [17,18] of the dynamics of sexual conflict in polymorphic diving beetles, namely (i) the existence of discrete male mating clusters ('morphs') and (ii) assortative mating between such male morphs and female elytral morphs. These results point to a conservative role of sexual conflict in maintaining male and female mating polymorphisms through a dynamic balance between negative frequency-dependent selection and assortative mating within local populations, rather than sexual conflict as a promoter of population divergence. Although we did not directly measure the strength of negative frequency-dependent selection in the present study, our results are certainly consistent with either negative frequency dependence or some other unknown stabilizing force in maintaining the polymorphism in at least some populations in Sweden (figure 1) and for almost two decades (figure 3). We acknowledge that the results in the present study cannot in themselves and alone decisively exclude any other such stabilizing force that could maintain this polymorphism in multiple populations in northern Sweden. However, we consider such alternatives to negative frequency-dependent selection driven by sexual conflict (such as overdominant selection) rather unlikely, in light of previous research in these and other diving beetles that strongly point to a key role for sexual conflict in this system [17,20,23].

Given the strong assortative mating between male and female morphs that we demonstrate in this study, the stabilizing force of negative frequency-dependent selection through sexual conflict is needed to maintain the observed polymorphism [17,18] (figure 3). Hence, assortative mating needs to be opposed by negative frequency-dependent sexual conflict to maintain these polymorphisms. The evolutionary dynamics that we observed in this study is likely to reflect the balance between these two opposing forces (figures 2 and 3). If negative frequency-dependent selection was not operating in this system, the positive mating assortment we have documented here would be expected to lead to sexual selection against rare morphs, causing their loss in some populations [17,18,35]. The fact that some populations are monomorphic or heavily skewed towards one set of morph pairs (figures 1 and 2c) indicates that strong assortment might have led to the loss of rare morphs through sexual selection or, alternatively, by genetic drift in populations where the stabilizing force of negative frequency-dependent sexual conflict was not strong enough or was temporarily relaxed [9,23,36]. A previous study on the molecular population differentiation in *G. zonatus* revealed that neutral differentiation between Swedish populations was quite high ( $F_{st}$ : ranging from 0.19 to 0.21) suggesting that genetic drift plays at least some role in this system and that local populations are finite in size [23]. Moreover, population differentiation in morph frequencies was not significantly different from neutral molecular differentiation, consistent with stochastic factors and genetic drift also partly influencing morph frequency variation between populations [23].

Deviations from balanced morph frequencies (figures 2c and 3) are also expected given that sexual conflict is likely to interact with local abiotic and biotic factors and other selection pressures that are unrelated to the internal mating dynamics between males and females and the resulting sexual conflict [3]. Selection on secondary sexual traits often fluctuates in strength and direction in response to spatial and temporal environmental heterogeneity driven by both abiotic and biotic factors, such as population density [37]. In diving beetles, natural selection driven by environmental factors could also operate on these mating traits, either jointly or in opposition to sexual conflict, resulting in local and regional gradients in morph frequencies [38,39]. If this is the case, measurements of various fitness components in the *G. zonatus* female morphs would be expected to vary both across environmental and morph frequency gradients. Future reciprocal transplant experiments would be a fruitful research avenue in this system to investigate the relative importance of local adaptation to different environmental conditions of the different morphs of *G. zonatus* and how such differential sensitivity to local environmental conditions could influence local sexual conflict dynamics and affect both male and female fitness components [40].

Environment gradients could thus potentially influence the dynamics of sexual conflict itself, independently of morph types, by relaxing or strengthening assortative mating and negative frequency-dependent selection [41,42]. The results of such interactions between local environmental conditions and sexual conflict would be heterogeneous deviations from balanced morph frequencies, resulting in some populations becoming monomorphic under certain environmental conditions (figures 1 and 2c) [23]. Sexual conflict could either become strengthened or relaxed at a species' northern or southern distribution range margins, where population densities might differ from the central part of the species range. In the present study, the observed gradient from monomorphic populations in southern Sweden to polymorphic populations in the north (figure 1) suggests that the sexual antagonism might depend on climatic factors, with more intense sexual conflict under cooler conditions (figure 1). If this is the case, we would expect future local losses of the polymorphism in the north and an increasing number of monomorphic populations at higher latitudes as a consequence of increasing annual temperatures in the future.

The existence of two distinct mating clusters which exhibit assortative mating could theoretically lead to sympatric speciation by sexual conflict in polymorphic populations [14]. However, this would presumably require long periods with stable environmental conditions promoting sexual conflict combined with low levels of genetic recombination and random genetic drift [15]. Moreover, sympatric speciation by sexual conflict might be less likely than the formation of male and female mating clusters and the subsequent maintenance of sexual polymorphisms by negative frequency-dependent selection [13,17,18].

The connection between male grasping and female anti-grasping phenotypes described in this study resembles cases in which sexually antagonistic coevolution has been shown to drive rapid evolutionary divergence (e.g. in water striders [43,44], bedbugs [45], and seed beetles [46]). In these cases, male and female traits continue to evolve in an exaggerated manner creating sexual arms races [4]. In contrast, sexual conflict in diving beetles is driven by a repeated gain and loss of

female elytral granulations as a response to the grasping ability of males [20,26]. These more or less evenly matched traits within species are equivalent to the morphs described in this study. It remains to be shown how and when speciation can originate within the polymorphic populations of *G. zonatus*.

Our findings contrast the previous understanding that sexual conflict causes population divergence and rapid speciation [1,2,47]. The observed stable polymorphism created by paired male and female sexual traits in *G. zonatus* show that sexual conflicts can halt divergence in natural populations. These findings expand our knowledge of the potential outcome of mating conflicts between sexes, as well as their evolutionary trajectories.

**Data accessibility.** Original data underlying this manuscript can be accessed from the electronic supplementary material, table S1 and the Dryad Digital Repository: <https://doi.org/10.5061/dryad>.

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