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## Latitudinal clines in sexual selection, sexual size dimorphism and sex-specific genetic dispersal during a poleward range expansion

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## Abstract

1. Range expansions can be shaped by sex differences in behaviours and other phenotypic traits affecting dispersal and reproduction.
2. Here, we investigate sex differences in morphology, behaviour and genomic population differentiation along a climate-mediated range expansion in the common bluetail damselfly (*Ischnura elegans*) in northern Europe.
3. We sampled 65 sites along a 583-km gradient spanning the *I. elegans* range in Sweden and quantified latitudinal gradients in site relative abundance, sex ratio and sex-specific shifts in body size and mating status (a measure of sexual selection). Using single nucleotide polymorphism (SNP) data for 426 individuals from 25 sites, we further investigated sex-specific landscape and climatic effects on neutral genetic connectivity and migration patterns.
4. We found evidence for sex differences associated with the *I. elegans* range expansion, namely (a) increased male body size with latitude, but no latitudinal effect on female body size, resulting in reduced sexual dimorphism towards the range limit, (b) a steeper decline in male genetic similarity with increasing geographic distance than in females, (c) male-biased genetic migration propensity and (d) a latitudinal cline in migration distance (increasing migratory distances towards the range margin), which was stronger in males. Cooler mean annual temperatures towards the range limit were associated with increased resistance to gene flow in both sexes. Sex ratios became increasingly male biased towards the range limit, and there was evidence for a changed sexual selection regime shifting from favouring larger males in the south to favouring smaller males in the north.
5. Our findings suggest sex-specific spatial phenotype sorting at the range limit, where larger males disperse more under higher landscape resistance associated with cooler climates. The combination of latitudinal gradients in sex-biased dispersal, increasing male body size and (reduced) sexual size dimorphism should have emergent consequences for sexual selection dynamics and the mating system at the expanding range front. Our study illustrates the importance of considering sex differences in the study of range expansions driven by ongoing climate change.

## KEYWORDS

climate change, insect, *Ischnura elegans*, landscape genetics, range expansion, sexual selection, sexual size dimorphism, temperature

## 1 | INTRODUCTION

There is increasing interest in both the evolution of sex differences and the process of local adaptation during range expansion and colonisation of novel environments, and these previously separated research fields are becoming increasingly integrated (Connallon, 2015; Connallon et al., 2018). Individuals that colonise new areas are often genetically or phenotypically different from their source populations due to evolutionary consequences of demographic expansion, directional gene flow, spatial sorting and/or genetic drift (Excoffier et al., 2009; Hill et al., 1999; Miller & Inouye, 2013). Colonisers may also undergo in situ selection for traits conferring increased local adaptation to novel environments (Duckworth & Badyaev, 2007; Hill et al., 1999; Kelehear & Shine, 2020). As a result of sex differences in behaviour, morphology or physiology, range expansion speed and dynamics can be shaped by sexual size dimorphism, sex-specific dispersal, gene flow and sex differences in natural or sexual selection, resulting in sex-specific local adaptation (Aguilée et al., 2013, 2016; Clarke et al., 2019). In addition, intralocus sexual conflict can also vary across a species range, being relaxed at range limits or in harsh environments where selection becomes concordant between males and females (Connallon, 2015; De Lisle et al., 2018).

Several hypotheses have been put forward to explain the evolution and adaptive significance of sex-biased dispersal (Beirincx et al., 2006). For example, resource defence by males might favour female-biased dispersal (Nagy et al., 2007), whereas scramble male competition for females might favour male-biased dispersal (Höner et al., 2007; Spritzer et al., 2005). Inbreeding avoidance may favour dispersal in either sex (Pusey, 1987). Sex-biased dispersal may create spatial clines in sex ratios and may reduce reproductive output at species' range limits when the more dispersive and gamete-limited sex is over-represented (Miller & Inouye, 2013; Miller et al., 2011). For example, female-biased dispersal might initially accelerate range expansions due to female demographic dominance and greater contribution to population growth (Harts et al., 2014), at least until the negative effects of male limitation exceed the benefit of greater female dispersal (Miller & Inouye, 2013).

In insects, morphological variation along environmental gradients has been shown to affect dispersal capacity and thermoregulation (Harris et al., 2013; Hassall & Thompson, 2008; Lancaster et al., 2015; Tüzün et al., 2017; Yadav et al., 2019), which is especially evident in areas of range expansion (Hill et al., 1999; Thomas et al., 2001; Simmons & Thomas, 2004; reviewed in Hill et al., 2011; Lancaster et al., 2016). Spatial sorting of dispersal-enhancing traits during range expansion in combination with sex differences in dispersal and sex-specific selective regimes that vary across a species range (Connallon, 2015; De Lisle et al., 2018) can therefore

contribute to shape latitudinal clines in phenotypic traits of both sexes.

Sex-specific variance in reproductive rates combined with novel environmental conditions at the range limit can further affect the rate and dynamics of range expansions (Kot et al., 1996; Miller et al., 2011). Individuals at the leading edge of a range expansion often differ in phenotypic traits from those closer to the centre of the historic range (Krause et al., 2016). For example, spatial sorting of individuals with dispersal-enhancing traits during range expansion will lead to an accumulation of dispersive genotypes at the leading edge of a species dispersal zone (Krause et al., 2016; Phillips et al., 2006; Shine et al., 2011; Travis & Dytham, 2002). Conversely, unfavourable or novel environmental conditions at the range limit can reduce the body condition of individuals in these edge populations, slowing down the rate of range expansion (Hardie & Hutchings, 2010; Swaegers et al., 2015; Therry et al., 2014). Sexual dimorphism in phenotypic traits can also change across a species range as well as by selection on traits that enhance dispersal of one sex (Hill et al., 1999; Teder & Tammaru, 2005), differences in sexually antagonistic selection across the range (Connallon, 2015; De Lisle et al., 2018) or by sex differences in phenotypic plasticity and different environmental conditions across the range (Stillwell et al., 2010; Svensson et al., 2018).

Landscape genetic relationships can reveal sex differences in dispersal behaviour, although sex differences have seldom been analysed using this approach (Amos et al., 2014; Coulon et al., 2004; Harrisson et al., 2014; Tucker et al., 2017). When analysing sexes together, the landscape genetic responses (i.e. determined by the best supported resistance parameters) of one sex may mask the influence of landscape features on the other sex (Tucker et al., 2017) and ecological differences between the sexes might then not be revealed (Amos et al., 2014; Coulon et al., 2004; Harrisson et al., 2013, 2014). Failing to account for sex-specific landscape genetic responses may also obscure climatic or landscape effects on genetic connectivity, and potentially alter predictions about species movement and persistence (Tucker et al., 2017). This is particularly relevant for range expanding organisms where declining habitat suitability or shifting thermal regimes could have differential effects on each sex (Miller & Inouye, 2013).

Here, we investigate sex differences in dispersal and evidence for sexual selection on males during the range expansion of the common bluetail damselfly (*Ischnura elegans*) along its latitudinal gradient towards the northern range limit in southern Sweden. The range of this damselfly species is currently extending northwards in Europe, and in the United Kingdom it has extended by >140 km in the last 50 years (Hickling et al., 2005). Our previous research identified several important ecological factors, phenotypic traits and genomic signatures associated with the ongoing range

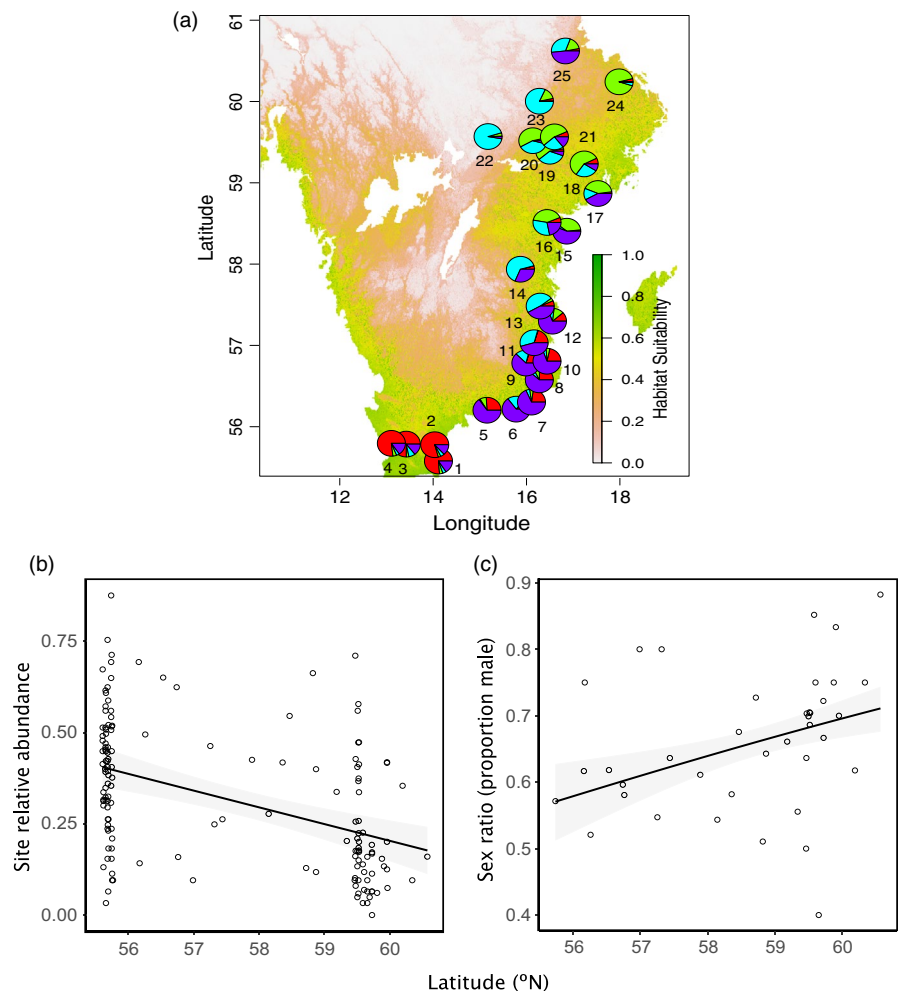
expansion of *I. elegans* in Sweden. We documented increased cold tolerance and increased cold tolerance plasticity over the expansion gradient (in contrast to heat tolerance mechanisms that were largely conserved across latitudes) (Lancaster et al., 2015). We also documented molecular signatures of local adaptation associated with this recent range expansion, including genes that exhibit significant spatial associations with summer temperature, wind speed and rainfall (Dudaniec et al., 2018). Moreover, some of these genes were annotated to thermal response, visual and cellular response functions in *I. elegans* (Dudaniec et al., 2018), and overlapped with the loci exhibiting latitudinal clines in gene expression in response to thermal stress (Lancaster et al., 2016). We expand on these findings by investigating sex-specific shifts in body size towards the range limit of *I. elegans*, and ask whether sexual selection, measured via male copulation status, is associated with body size shifts. We further compare male and female patterns of genetic migration across the range expansion gradient, and investigate sex differences in the effect of landscape and climatic variables on genetic dispersal. Our study reveals several interactions between sex-biased phenotypic variation, sexual selection, genetic dispersal and migration that suggest an important, yet rarely appreciated, role for sex-specific eco-evolutionary processes in the success of species' range expansions.

## 2 | MATERIALS AND METHODS

### 2.1 | Field sampling and study design

*Ischnura elegans* (Coenagrionidae: Odonata) has a widespread distribution throughout Europe and Asia. Its north-western range extends to the southern coastal areas of Scandinavia and the north of the United Kingdom (Dijkstra & Lewington, 2006). Adult *I. elegans* thrive in disturbed areas (Hofmann & Mason, 2005) and prefer open and light waterbodies with abundant reed growth to more natural, shady areas with overhanging canopy (Dijkstra & Lewington, 2006). Our study area spans a latitudinal gradient of approximately five degrees of latitude in Sweden (latitudinal range: 55.53° to 60.58°), extending 583 km. In the summer months of July–August in 2013, 65 sites were surveyed for *I. elegans* following a paired gradient sampling design of both coastal and inland localities that spanned the southern core region to the northern range limit (Figure 1a). Adult *I. elegans* were caught near reed beds and in the vegetation along shores using sweep nets within 10 m of the water bodies (ponds, lakes and coastal inlets). Sampling was conducted only under conditions suitable for *I. elegans* flight (i.e. temperatures above 13°C, low wind, not raining), and during times when damselflies are actively flying (i.e. between 9:00 and 16:00 hours), following Svensson and

**FIGURE 1** (a) Sample sites and genetic structure of *I. elegans* across southern Sweden, reproduced from Dudaniec et al. (2018). The proportion of each colour within each pie chart indicates the mean assignment probability of individuals to a genetic cluster in that population, displayed for 426 individuals across 25 populations (site names from Table S3). Data are shown over habitat suitability, which declines with latitude (Lancaster et al., 2015); (b) Site relative abundance (number of individuals caught per minute) as a function of latitude, with values back-transformed for visualisation; (c) Sex ratio (proportion of males at a site) as a function of latitude. For (b), the marginal effect of the focal variable is depicted after accounting for multiple sampling of sites and day of year. Shading represents 95% CI



Abbott (2005). Average temperature conditions for fieldwork did not differ across the sampling gradient (Lancaster et al., 2015).

Searching was performed by two to three people simultaneously and catching time was totalled for all searchers as the total minutes spent searching at a site. Site relative abundance was calculated from capture rates as the total number of *I. elegans* caught at a site divided by the number of minutes spent searching (i.e. 'number of captured individuals per minute'), which has been used previously as a density index (Gómez-Llano et al., 2020; Svensson & Abbott, 2005). The date, time of day and time spent searching were recorded for each site. Sex and age category (mature or teneral adult) information were recorded for each damselfly that we collected. Teneral (i.e. newly emerged) individuals were identified as having brownish soft wings or an immature colour morph in the case of females; these individuals are unable to have yet dispersed, and thus were not included in genetic migration analyses. Copulation status of all individuals (0: not in copula; 1: in copula) at the time of capture was recorded for all individuals, as pairs of *I. elegans* are often found in the 'mating wheel' formation. Data on morphology were collected for 44 of the 65 sites ( $n = 1,097$  individuals) and these sites covered the sampled latitudinal gradient (Table S1). Images were obtained after field sampling by scanning live individuals which were immobilised and placed dorso-ventrally on a portable scanner (CanoScan 400; Canon, Tokyo, Japan). We only scanned mature adults for morphological analyses. Finally, all damselflies were preserved in 90% ethanol for DNA preservation. All procedures were conducted in accordance with Swedish law and also in accordance with the ethical requirements of Lund University in Sweden.

## 2.2 | Effect of latitude on relative abundance

To test for latitude shifts in site relative abundance, we carried out a linear mixed-effects model on relative abundance ( $n = 65$  sites) between sites using the `lmer` function in the `R` packages `LME4` (Bates et al., 2014) and `LMERTEST` (Kuznetsova et al., 2017), which estimates significance of mixed effects using the Satterthwaite approximation. We included latitude as a fixed effect, and sampling site and day of year (categorical) as random factors, to statistically control for the potential influence of seasonal variation, daily weather variability across sampling days, and to account for some sites being sampled on multiple days. However, the inclusion of sampling date did not alter model Akaike information criterion (AIC), suggesting that any variation in weather conditions on day of sampling (see methods) had very limited effects on our relative abundance estimates. Site relative abundance was ( $\log(n + 1)$ ) transformed to meet model assumptions.

## 2.3 | Sex ratio and morphometric analysis

Of the 65 total sites, individual information on damselflies was obtained from 44 sites (Table S1), comprising 700 females (of which 469 were measured for body size) and 1,355 males (628 were measured

for body size). At all sites with  $>3$  individuals captured ( $n = 38$  sites), sex ratio at each of these sites was calculated as the proportion of all individuals that were male, and analysed as a function of latitude in a binomial generalised linear model (GLM), weighted by the total number of individuals captured at each site. From the scanned images of live individuals, we used the program ImageJ (Schneider et al., 2012) to quantify five body size variables (mm): total length, wing length, abdomen length, thorax width and S4 width (width of abdomen segment no. 4, counted from the thorax). If the dorsal side of an individual was not entirely visible, the image was excluded from analysis. Due to correlation among our morphological measurements, we conducted a principal component analysis, incorporating all five body size measurements. This PCA was conducted using the `prcomp()` function within the `STATS R` package for the males and females combined. The first axis of this PCA captured the majority of the variance (66%) (Table S2). We compared morphological changes along the range expansion axis separately for all five morphological traits, as well as for PC1, using linear mixed models (LMM) and generalised linear mixed models (GLMMs) using the `LME4`, `LMERTEST` (Bates et al., 2014) and `MCMCglmm` (Bartoń, 2014) `R` packages. In these mixed-effects models, latitude and sex were assigned as fixed effects and site was included as a random effect. A LMM with a Gaussian error distribution was used to test the interaction effect of sex  $\times$  latitude on each morphological variable and PC1 with site included as a random effect.

## 2.4 | Quantifying sexual selection on male body size through copulation status

To measure sexual selection on body size across the *I. elegans* range expansion, we analysed male copulation status (i.e. whether a male was found in copula or not) as a function of latitude and body size, using a similar cross-sectional sexual selection approach as Gosden and Svensson (2008). We filtered the data to only include reproductively mature individuals (males with mature wings,  $n = 450$  and females exhibiting sexually mature morphs,  $n = 197$ ). We then removed sites that contained fewer than three mature females so that there would be sufficient opportunity to detect any spatial variation in sexual selection, which reduced the number of sites analysed to 24 sites (Table S1). The effect of male body size and latitude on male copulation status was tested using a GLMM with a binomial error structure in `R`. The response variable was an individual's copulation status (0 = non-copulating, 1 = copulating). Fixed effects were latitude, body length and latitude  $\times$  body length interactions. Due to the fixed effect variables having different distributions, we scaled them by setting the mean to 0 and expressing the variance in units of standard deviation. Site was included as a random effect. We further tested for direct effects of latitude on male versus female copulation status, to see how the opportunity for sexual selection might increase or decrease with latitude. This was similarly run using a binomial GLMM, but including both males and females, with (scaled) latitude, sex, and

their interaction as fixed effects, and site as a random effect. For all depicted relationships, plots depict marginal effects of fixed effects and were created using the *GGEFFECTS* (Lüdtke, 2018) and *GGPLOT2* (Wickham, 2016) packages for R, with shading representing 95% confidence intervals for fitted values.

## 2.5 | DNA sequencing and SNP characterisation

DNA was extracted and quantified from 425 *I. elegans* (209 males and 217 females, Table S3) across 25 sites evenly distributed across the latitudinal gradient (10–20 individuals per site, mean  $17.04 \pm 0.72$ ) as described in Dudaniec et al. (2018) and supplementary Text S1. Paired-end RAD libraries were prepared according to Etter et al. (2011) and sequenced on an Illumina HiSeq 2500 at the Beijing Genomics Institute (BGI), Hongkong. Sequencing reads were aligned to a de novo draft *I. elegans* genome (Chauhan et al., in press; available on Dryad: <https://doi.org/10.5061/dryad.8s449qb>) using *BOWTIE2* v.2.2.5 (Langmead & Salzberg, 2012) as described in Dudaniec et al. (2018). Raw reads were filtered using *STACKS* (Catchen et al., 2013) as described in Dudaniec et al. (2018) and Text S1, with 13,612 SNPs retained. To minimise the inclusion of closely linked SNPs, we filtered one SNP per RAD tag, resulting in 3,809 SNPs. As described in Dudaniec et al. (2018) this dataset was further filtered for putative loci under selection using both *BAYESCAN* (Foll & Gaggiotti, 2008) and *OUTFLANK* (Foll & Gaggiotti, 2008; Whitlock & Lotterhos, 2015), which were removed from the dataset ( $n = 255$  SNPs), resulting in a final dataset of 3,554 putatively neutral SNPs for connectivity and neutral diversity analysis (see Dudaniec et al., 2018).

## 2.6 | Genetic diversity and isolation by distance

Observed heterozygosity was calculated for each site ( $n = 25$ ) using the R package *ADEGENET* (Jombart, 2008) and allelic richness was calculated for each site using the R package *POPGENREPORT* (Adamack & Gruber, 2014). We ran linear regression models in R to test for changes in allelic richness and observed heterozygosity with latitude. Genetic distance was calculated between the 25 sites using Nei's pairwise  $F_{ST}$  (Nei, 1977) using the R package *ADEGENET* (Jombart, 2008) and Hedrick's pairwise  $G'_{ST}$  (Hedrick, 2005) was calculated using the R package *MMOD* (Winter, 2012). Hedrick's  $G'_{ST}$ , a standardised version of  $G_{ST}$ , has been recommended as an appropriate measure of genetic differentiation as it takes into account different levels of within-population genetic diversity and is thus effective when comparing sampling sites across large areas (Heller & Siegmund, 2009). Geographic distance (km) between sites was calculated using the R package *GEOSPHERE* (Hijmans et al., 2015). Mantel tests were conducted in the R package *ECODIST* (Goslee & Urban, 2007) to test for patterns of isolation by distance (IBD). Spatial autocorrelation analysis was conducted to test for fine-scale genetic structure in *GENALEX* v 6.5 (Peakall & Smouse, 2006) using a distance class of 50 km. To examine for

genetic indicators of sex-biased dispersal, IBD and spatial autocorrelation analyses were repeated for males and females separately (Banks & Peakall, 2012). Due to a smaller per site sample sizes when separating males and females, and to minimise effects of low sample size of genetic distance calculations, we only included sites that had at least eight individuals of each sex genotyped. This resulted in 17 sites for males and 18 sites for females that were well-distributed across the sampling gradient (Table S3).

## 2.7 | Detection of migrants

Bayesian assignment tests are useful when detecting ongoing migration events that may have directional movement across the range (Ramakrishnan et al., 2010). To identify first generation migrants between the 25 sampling sites we used Paetkau et al.'s (2004) frequency-based assignment tests and resampling method in *GeneClass2* (Piry et al., 2004). *GeneClass2* computes the probabilities that each individual belongs to each reference population, or is a resident in the population (i.e. not a first-generation migrant). Notably, detection of migrants from more distant generations is challenged by unsampled source sites and ongoing genetic admixture. The test statistic  $L_h/L_{max}$  was used, where  $L_h$  is the likelihood of drawing a genotype from the same site it was sampled and  $L_{max}$  is the greatest likelihood of drawing the genotype from any of the sampled sites. These methods generate critical values for rejecting the null hypothesis that an individual originated from the site where it was sampled. We simulated 1,000 individuals and set the alpha for type 1 error at 0.01. The results of *GeneClass2* were examined using binomial GLMs in R to measure the proportion of individuals migrating ( $p < 0.05$ ), and their directional pattern of migration (north or south, based on latitudinal direction) along the range expansion gradient (i.e. for the total dataset, and males and females). The sex ratio of migrants per site was analysed as a function of latitude. For this we used a binomial GLM where each site is a replicate and the response variable is the proportion of migrants that were male, weighted by the total number of migrants. Latitude was included as a fixed effect and the total number of individuals genotyped at a site was included as a fixed covariate to control for sampling effort.

To examine drivers of migration distance, we calculated distance between all sites (in km) using the *GEODIST* package for R and the Haversine formula to calculate circular distances from coordinates (Padgham & Sumner, 2020). We then modelled individual migration distance (km) of individuals detected as migrants as a function of sex, latitude of site where individuals were detected, direction of movement, and all interaction terms, using a linear mixed model with a random effect included to control for sample site. AIC was used to select the best set of these predictors, with the lowest score representing the best-selected model and  $\Delta i$ , which is the difference between the AIC of model  $i$  and the most supported model with the lowest AIC (minimum value) (Akaike, 1998; Bozdoğan, 1987). Burnham and Anderson (2003)



recommend that when  $\Delta_i \leq 2$  the model has substantial support, with limited to no support above this value, therefore, we only discuss AIC models with  $\Delta_i \leq 2$ . To evaluate whether differences in dispersal distances from south to north along the expansion gradient might reflect bias in the geographic spacing of study sites, we selected the sites with detected migrants and evaluated whether the geographic distance (km) between adjacent sites was correlated with the latitudinal order of the site.

## 2.8 | Temperature and land cover data

The effect of landscape and climatic variables on neutral genetic connectivity was tested using two raster datasets for (a) mean annual temperature and (b) land cover. Mean annual temperature (BIO1) was obtained from the WorldClim Version 1.4 database (Hijmans et al., 2005) at a cell resolution of 1 km using a WGS84 projection system and showed a change of 3°C along the sampling gradient. Mean annual temperature was chosen due to its well-known effects on the distribution, physiology, growth and reproduction in ectothermic insects (e.g. Evangelista et al., 2011; Lancaster et al., 2015; Sánchez-Guillén et al., 2016; Zhu et al., 2012). A previous model for *I. elegans* found mean annual temperature to be the best predictor of habitat suitability, with 62.1% of the variation explained (Lancaster et al., 2015).

Land cover data were obtained for our study area from the Corine Land Cover database (Büttner & Eiselt, 2013) which contained 44 land cover variables that we collapsed into seven categories considered relevant to the dispersal of *I. elegans* (Table S4). *Ischnura elegans* prefers open areas with sparse canopy (Dijkstra & Lewington, 2006); and studies on other *Ischnura* species found evidence for greater population genetic differentiation in urban than rural areas (Sato et al., 2008). The seven categories, in order of low to high resistance, were: (1) inland wetlands and waterbodies, (2) marine wetlands and waterbodies, (3) agriculture, (4) scrubland (e.g. grasslands and heathland), (5) forests (three types: broad-leaved, coniferous and mixed), (6) open, non-vegetated areas (e.g. beaches and glaciers) and (7) developed areas (including urban, industrial and mining areas) (Figure S1, described in Table S4). Category 2, marine wetlands and waterbodies, was limited to 500 m beyond the coastline as *I. elegans* can inhabit both freshwater and coastal, brackish environments, but only close to the shore, with larger expanses of water representing a barrier (Dijkstra & Lewington, 2006). Land cover data were processed using the R package RASTER (Hijmans et al., 2016), at a 100 m cell resolution using the ETRS89 projection system.

Generally, we predicted that lakes, rivers and agricultural land use would offer lower resistance to dispersal than developed (i.e. urban or industrial) and forested areas (temperate coniferous) (Figure S1). Categorical variables were represented in one resistance surface and ranked from least to most resistant based on expert opinion and findings from the published literature (Dijkstra & Lewington, 2006; Dudaniec et al., 2018; Sato et al., 2008; Swaegers et al., 2015; Wellenreuther et al., 2011).

## 2.9 | Landscape resistance surfaces and modelling

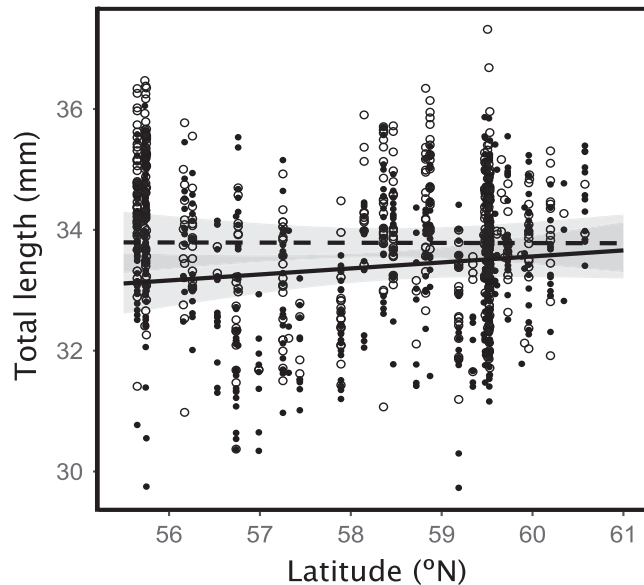
To evaluate climatic and landscape effects on genetic distance in *I. elegans*, we applied a resistance approach based on circuit theory (McRae & Beier, 2007) combined with multimodal inference using linear regression and log-likelihood to evaluate multiple competing, linear and nonlinear resistance models as described previously (Dudaniec et al., 2013, 2016; Yadav et al., 2019; Text S2). Different resistance surfaces were created by varying slope ( $\gamma$ ) and intercept ( $\alpha$ ) parameters (Text S2; Figure S2). The effect of temperature on resistance was assumed to be negative (as temperature decreases, resistance increases, Figure S2a) and that the effect of land cover was assumed to be positive (as land cover rank increases, resistance increases, Figure S2b) in accordance with prior knowledge of the species (Dudaniec et al., 2018; Keller et al., 2012; Sato et al., 2008; Wellenreuther et al., 2011). The combination of our chosen slope ( $\gamma$ ) and intercept ( $\alpha$ ) parameters produced 29 resistance surfaces each for mean annual temperature and land cover (Figure S2), calculated using the program CIRCUITScape (McRae & Beier, 2007), which uses electrical circuit theory to model pairwise resistance among sampling localities (Shah & McRae, 2008). Each resistance matrix was treated as a predictor of genetic distance between sites. All resistance surfaces were evaluated against the null model of isolation by geographic distance (i.e. when  $\alpha = 0$ , all cells were assigned a value of one). The R packages RESISTANCEGA (Peterman, 2014) and M<sub>U</sub>MI<sub>N</sub> (Bartoń, 2014) were used to conduct AIC model selection and multimodal inference to determine which resistance surface(s) best explained genetic distance (i.e. had the best relative support of each parameter combination of  $\alpha$  and  $\gamma$ ). We modelled resistance first for mean annual temperature, with the a priori assumption that temperature was a dominating driver of landscape genetic relationships, and then tested for an additional effect of land cover in a separate model. The most supported model parameters from each analysis were compared to assess the relative effects of temperature and land cover on genetic distance, with any effects of land cover interpreted as being additional to, or correlative with temperature. Notably, Marrotte and Bowman (2017) conducted a simulation analysis that found little to no effect of spatial autocorrelation and isolation by distance on resistance-distance estimates. Sex-specific landscape genetic responses were further examined by analysing male and female genetic distances separately each for temperature and land cover effects.

## 3 | RESULTS

### 3.1 | Abundance changes across the latitudinal gradient and morphological variation

There was a decline in *I. elegans* site relative abundance with increasing latitude, in a model accounting for random effects of site and capture date (effect of latitude on log(abundance) =  $-0.06 \pm 0.01$ ,

$t = -4.04$ ,  $p < 0.001$ ,  $n = 151$  daily observations at 65 locales, Figure 1b), with most higher latitude sites towards the range limit having less than 0.5 individuals captured per minute. The sex ratio was male biased at most sites (Table S1), but we also find an association between sex ratio and latitude, with more male-biased sex ratios in the north, towards the range limit (effect of latitude on proportion male, tested using a binomial GLM =  $0.12 \pm 0.04$ ,  $z = 3.37$ ,  $p = 0.0007$ , Figure 1c). Wing length showed no detectable association with latitude in a GLMM model including a random effect to control for site (estimate =  $0.05 \pm 0.04$ ,  $t = 1.05$ ,  $p = 0.30$ ,  $n = 1,097$ ) and there was no interaction between sex and latitude for wing length

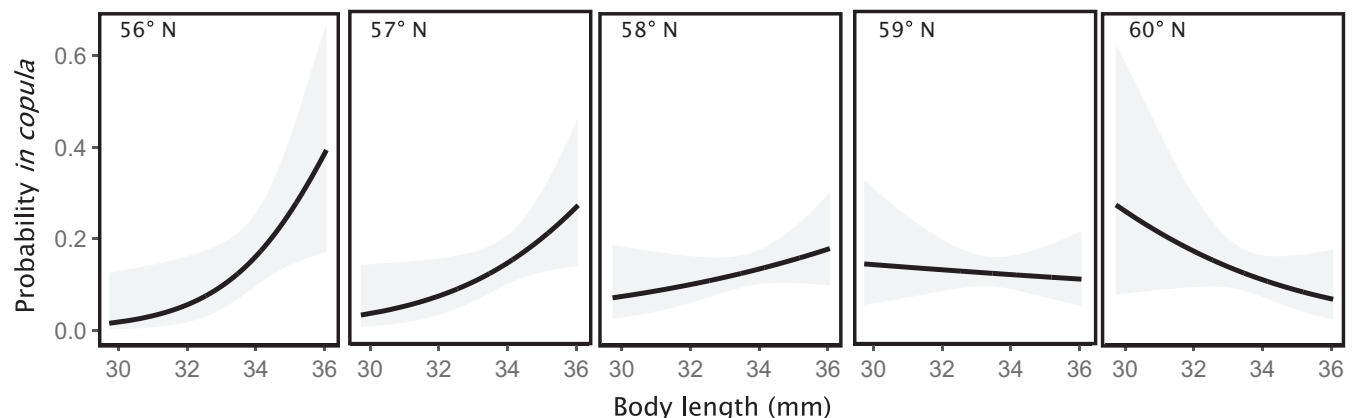


**FIGURE 2** Latitudinal differences in males and females are shown for total body length (sex  $\times$  latitude interaction:  $p = 0.006$ ). Males exhibit a steeper latitudinal gradient, resulting in convergence in total length (mm). Female points were jittered slightly to avoid overlap with male points. Males = solid line, solid points, females = broken line, open points. Shading represents 95% CI

(estimate =  $0.04 \pm 0.03$ ,  $t = 1.35$ ,  $p = 0.18$ ). Likewise, we found no evidence for a relationship between thorax width and latitude, either as a main effect (estimate =  $0.0001 \pm 0.009$ ,  $t = 0.013$ ,  $p = 0.99$ ,  $n = 1,092$ ) or in interaction with sex (Figure S3). However, we did find evidence for a sex  $\times$  latitude interaction for both total body length (estimate =  $0.10$ ,  $t = 2.78$ ,  $p = 0.006$ ,  $n = 1,096$ ; Figure 2), and abdomen length (estimate =  $0.081$ ,  $t = 2.71$ ,  $p = 0.006$ , Figure S3). The sex  $\times$  latitude interaction for these two body size traits revealed that male body size increased with latitude and converged with female body size at the range limit (Figure 2), resulting in reduced sexual dimorphism closer to the range limit. Notably, Pearson correlations ( $r$ ) of all morphological variables showed high ( $>0.9$ ) correlation between total length and abdomen length (males and females, both  $r = 0.98$ ). If we instead used PC1 as a composite measure of body size (derived from the first axis of PCA incorporating the five body size variables) we found no detectable main effect of latitude (estimate =  $-0.04$ ,  $t = -0.40$ ,  $p = 0.70$ ,  $n = 1,091$ ), but again a sex  $\times$  latitude interaction (estimate =  $-0.10$ ,  $t = 3.05$ ,  $p = 0.02$ ,  $n = 1,091$ , Figure S3).

### 3.2 | Effect of latitude and body size on copulation status

We found a total of 58 males in copula, 392 non-copulating males, 59 females in copula and 138 non-copulating females from 24 sites (Table S1). Over all sites combined, females were much more likely to be captured in copula than males (effect of sex on copulation status in a binomial GLMM accounting for site =  $-1.09 \pm 0.23$ ,  $t = -4.77$ ,  $p < 0.0001$ ), and this did not vary with latitude (sex  $\times$  latitude: estimate =  $0.14 \pm 0.21$ ,  $z = 0.86$ ,  $p > 0.4$ ). Looking at size-associated variation in copulation rates with latitude separately within each sex, however, we found evidence for an interaction between male body length and latitude in affecting male mating status (effect of male body size by latitude on copulation success in a GLMM accounting

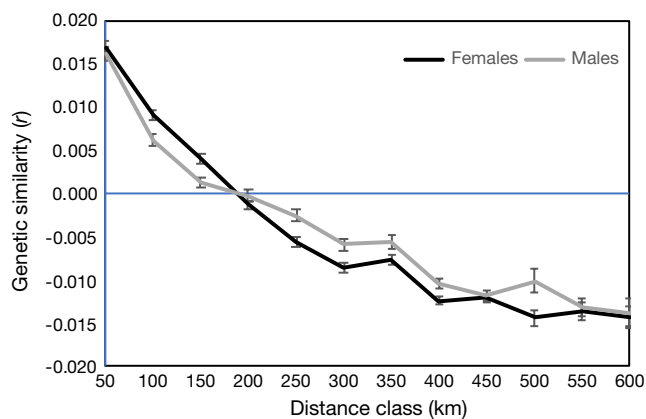


**FIGURE 3** The probability of being in copula in relation to male body size along the latitudinal gradient ( $n = 56$  males captured at 24 sites). The continuous interaction surface represented by latitude  $\times$  body size on copulation status (after accounting for random effect of site) here has been sliced at five latitudinal locations to depict the overall shape of the surface and the change in the sign of apparent sexual selection from south to north. Shading represents 95% CI. As can be seen in this graph, the sexual selection regime changed from favouring large males in the south to favouring small males in the north

for site =  $-0.39 \pm 0.16$ ;  $z = -2.48$ ,  $p = 0.01$ ). Smaller males had a lower probability of being in copula towards the core of the sampled range, but their copulation probability increased with latitude, and copulation status became comparable across all body length classes at the range limit (Figure 3). Conversely, the proportion of females captured in copula did not vary according to female body size, latitude or the interaction between these variables (effect of body size in a binomial GLMM accounting for site =  $0.20 \pm 0.14$ ,  $z = 1.42$ ,  $p = 0.16$ ; effect of latitude =  $-0.02 \pm 0.14$ ,  $z = -0.18$ ,  $p = 0.86$ , interaction effect =  $-0.17 \pm 0.14$ ,  $z = -1.26$ ,  $p = 0.21$ ).

### 3.3 | Genetic differentiation and isolation by distance

Pairwise  $F_{ST}$  ranged from 0.01 to 0.04 and pairwise  $G'_{ST}$  ranged from  $-0.002$  to  $0.098$  across all sites ( $n = 25$ ). We found no change in allelic richness ( $\text{Adj } R^2 = -0.02$ ,  $p = 0.45$ ) or observed heterozygosity ( $\text{Adj } R^2 = 0.04$ ,  $p = 0.172$ ) across the latitudinal gradient when analysing all 25 sites. There was a significant isolation by distance (IBD) relationship for both genetic distance measures when analysing the total dataset ( $F_{ST}$ :  $r = 0.47$ ,  $p = 0.001$ , Figure S4a;  $G'_{ST}$ :  $r = 0.5$ ,  $p = 0.001$ , Figure S4b) and for males ( $F_{ST}$ :  $r = 0.46$ ,  $p = 0.002$ , Figure S5a;  $G'_{ST}$ :  $r = 0.51$ ,  $p = 0.001$ , Figure S5b) and females separately ( $F_{ST}$ :  $r = 0.52$ ,  $p = 0.001$ , Figure S6a;  $G'_{ST}$ :  $r = 0.5$ ,  $p = 0.001$ , Figure S6b). Spatial autocorrelation analysis of all individuals using distance classes of 50 km showed genetic similarity of individuals up to 200 km ( $\omega = 163.01$ ,  $p = 0.001$ ; Figure S7). When analysing males and females separately, weaker spatial autocorrelation in males was evident from the faster decline in genetic similarity among females up to a distance class of 200 km, where males and females intersected (Figure 4). Female genetic differentiation then remained stronger than males beyond this distance class, up to 600 km,

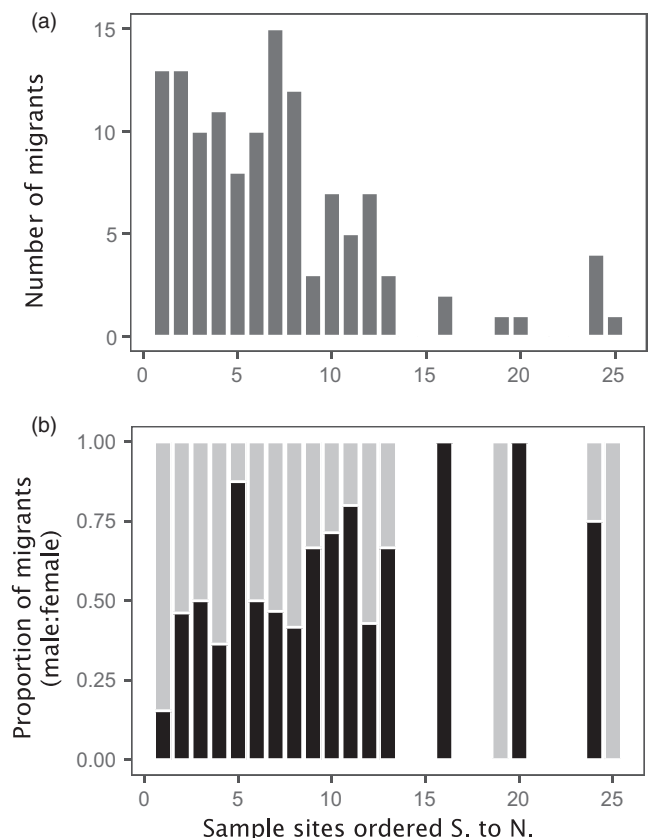


**FIGURE 4** Spatial autocorrelation of genetic similarity ( $r$ ) and geographic distance class (km) with 50 km intervals along the *I. elegans* latitudinal gradient, shown for males (grey line;  $n = 164$ ) and females (black line;  $n = 184$ ). Error bars represent the upper and lower 95% confidence intervals from the null model of no spatial structure, determined by 999 permutations

further indicating that males show less spatial genetic structure, at both shorter and longer distance classes.

### 3.4 | Detection of migrants

Across all sites, GeneClass2 identified 126 putative first-generation migrants (i.e. with a probability below 0.05) out of the 426 individuals analysed (29.6%). Notably these estimates (i.e. of the probability that a multi-locus genotype of an individual is encountered in a given population) are influenced by incomplete sampling of source populations and therefore should be regarded as relative estimates (Piry et al., 2004). The proportion of individuals that was identified as migrants declined with latitude (estimate =  $-1.06$ ,  $z = -8.952$ ,  $p < 0.0001$ ,  $n = 426$ , Figure 5a; Figures S8 and S9), and this decline persisted when analysing only males (estimate =  $-0.88$ ,  $z = -6.081$ ;  $p < 0.0001$ ;  $n = 209$ ) and only females (estimate =  $-1.30$ ;  $z = -6.44$ ;  $p < 0.0001$ ;  $n = 217$ , Figure 5b) separately. The majority of migrants were identified among the more southern sites 1–13 (Figure 1a) at latitudes between  $55$  and  $58^\circ\text{N}$  (Figure 5a). Migration patterns were overall consistent between males and females, with 29.2% of males and 30.0% of females migrating (effect of sex on migration status in a binomial GLMM, after accounting for effects of site =  $0.03 \pm 0.04$ ,  $t = 0.76$ ,  $p = 0.45$ ,  $n = 426$ ). The relative distance between sites that



**FIGURE 5** Latitudinal changes in the, (a) total number of genetic migrants identified, and (b) the proportion of male (black bars) and female (grey bars) genetic migrants. Sample sites of *I. elegans* are ordered from South to North



received migrants ( $n = 18$ ) was independent of latitude (Kendall's tau = 0.25,  $p = 0.18$ ). However, the spatial patterns of migration differed between males and females, with the sex ratio (proportion of males) among migrants increasing with latitude (Latitude: estimate = 0.54;  $z = 2.10$ ,  $p = 0.036$ ; Figure 5b).

Consistent with the ongoing range shift, the predominant direction of genetic migration was northwards, with more migrants being genetically assigned to sites south of their sampled location ( $n = 71$ ) compared to north of their sampled location ( $n = 55$ ), indicating northward and southward genetic dispersal respectively (Figures S8 and S9). More males than females showed a pattern of northward genetic migration, but this was not statistically significant (40/63 male migrants moved north, while 32/63 female migrants moved north;  $\chi^2 = 2.61$ ,  $p = 0.10$ , Figure 5b). Using Euclidean distance (km) between sites, an average movement of 60 km north compared to 28.4 km south was evident (Figure S9). When excluding a single identified migrant with a very large northward migration distance (~360 km to site 20, Figure S9) compared to other migrants, the average movement distance decreased to 44 km north, which may be a better estimate of average movement distance. Among identified migrants, the best model explaining migration distance included effects of sex, latitude and sex  $\times$  latitude (effect of sex [male] =  $-17.30 \pm 6.52$ ,  $t = -2.65$ ,  $p = 0.009$ ; effect of latitude =  $0.21 \pm 0.09$ ,  $t = 2.28$ ,  $p = 0.03$ ; effect of sex  $\times$  latitude =  $0.31 \pm 0.11$ ,  $t = 2.65$ ,  $p = 0.009$ ). In general, females dispersed further than males and all individuals dispersed further at the range limit; however, the slope of migration distance with latitude was greater for males, resulting in much longer

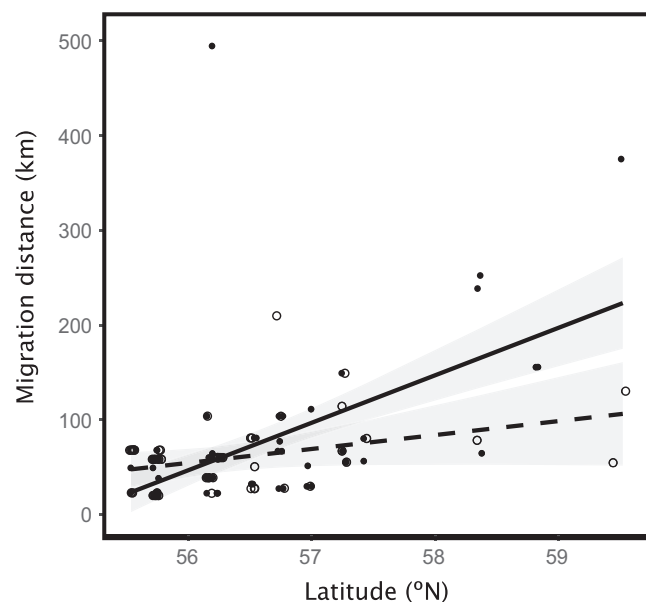
male than female migration distances near the range limit (Figure 6). Migration direction did not correlate with migration distance. These data suggest that range expansion in *I. elegans* is shaped by male bias in both migration distance and direction (Figures 5 and 6), and could explain all of: the male-biased sex ratio towards the range limit (Figure 1c), the increased body size of males towards the range limit (Figure 2) and the latitudinal cline observed in sexual selection on males (Figure 3).

### 3.5 | Effect of mean annual temperature and land cover on genetic connectivity

Lower mean annual temperatures were associated with higher resistance to gene flow in *I. elegans* using either  $F_{ST}$  or  $G'_{ST}$  as response variable when analysing the total dataset. For  $F_{ST}$ , the parameter values that gave the lowest AIC scores were those with  $\gamma = 1$ ,  $\alpha = 1,000$ , which indicates that resistance decreases linearly with temperature, with a maximum resistance 1,000 times greater than

**TABLE 1** Landscape genetic resistance models for mean annual temperature are shown for the best-supported parameter combinations that describe the shape ( $\gamma$ ) and maximum value ( $\alpha$ ) of resistance that explain genetic distance, where  $\gamma = 1$  is a linear relationship (see Figure S2). Landscape genetic results are shown for all individuals ( $n = 426$ ), for males ( $n = 164$ ) and females ( $n = 184$ ) for both  $F_{ST}$  and  $G'_{ST}$  genetic distance measures. The log-likelihood value (LLV), the AIC statistic (AIC), change in AIC between models ( $\Delta AIC < 2$  only) and the weight ( $w$ ) of each model are shown

		Resistance parameters		LLV	AIC	$\Delta AIC$	w
		$\alpha$	$\gamma$			< 2	
All							
Fst	1,000	1	1,357.18	-2,706.23	0.00	0.57	
	100	1	1,356.81	-2,705.48	0.75	0.39	
G'st	1,000	1	975.01	-1,942.04	0.00	0.58	
	100	1	974.71	-1,941.28	0.76	0.40	
Males							
Fst	1,000	1	594.42	-1,180.54	0.00	0.25	
	100	1	594.32	-1,180.34	0.20	0.23	
	100	2	594.07	-1,179.84	0.69	0.18	
	10	2	593.54	-1,178.77	1.76	0.10	
G'st	1,000	1	422.07	-835.84	0.00	0.29	
	100	1	422.07	-835.54	0.30	0.25	
	100	2	422.07	-835.22	0.62	0.21	
Females							
Fst	100	2	700.22	-1,392.16	0.00	0.45	
	1,000	1	699.95	-1,391.63	0.53	0.35	
	100	1	699.36	-1,390.44	1.72	0.19	
G'st	1,000	1	504.44	-1,000.60	0.00	0.51	
	100	1	503.93	-999.59	1.01	0.31	



**FIGURE 6** Latitudinal differences in males and females are shown for genetic migration distance (i.e. distance between genetically assigned source site and the site of sampling: sex  $\times$  latitude interaction =  $p = 0.009$ ). Males exhibit a steeper latitudinal gradient resulting in increased migration distance towards the northern range limit (i.e. 59–61°). Female points were jittered slightly to avoid overlap with male points. Males = solid line, solid points, females = broken line, open points. Shading represents 95% CI

the null model of zero resistance (Table 1, Table S5, Figures S5 and S6). However, using multi-model inference, the models containing  $\alpha$  values of 1,000 and 100 and  $\gamma = 1$  shared similar AIC values with an  $\Delta\text{AIC} = 0.75$ , therefore support for each model could not be distinguished (Table S5). The analysis using  $G'_{ST}$  selected the same two models ( $\gamma = 1$ ,  $\alpha = 1,000$ , and  $\gamma = 1$ ,  $\alpha = 100$ ; Table S5). Therefore, genetic connectivity decreases towards the range limit due to increasing resistance associated with cooler mean annual temperatures (Figure S10).

When analysed separately, males ( $n = 164$ ) and females ( $n = 184$ ) showed a similar pattern of high landscape resistance towards the cooler north with support for a linear ( $\gamma = 1$ ) or slightly nonlinear ( $\gamma = 2$ ) decrease in resistance as temperature increases in the south for both  $F_{ST}$  and  $G'_{ST}$  (Table 1, Tables S6 and S7). In the second analysis using land cover data only, there was no effect of land cover on genetic connectivity for models applying  $F_{ST}$  or  $G'_{ST}$  in either the total dataset (Table S8), males or females (Tables S9 and S10), with the best-selected model being the null isolation by distance model in all cases (Text S3).

## 4 | DISCUSSION

Here, we present data on how sexual size dimorphism, apparent sexual selection on male body size and sex differences in genetic migration and dispersal vary along a latitudinal gradient of the damselfly *I. elegans*. We found that males increased in size towards the range limit, resulting in reduced sexual size dimorphism in the north (Figure 2), that was opposed by apparent sexual selection, measured via copulation status (Figure 3). We further found evidence for an increased proportion of males among migrants, a male-biased latitudinal cline in migration distance and a more male-biased sex ratio towards the range limit (Figures 1c, 5b and 6). Furthermore, compared to females, genetic differentiation among males declined more rapidly with increasing geographic distance than in females (Figure 4). Despite evidence for sex-biased dispersal (Figures 4 and 5), the sexes showed similar landscape genetic relationships, with high resistance to gene flow associated with cooler northern temperatures and no effect of land cover (Table 1). Overall our results suggest that males are likely to colonise novel areas ahead of females during the ongoing range expansion of *I. elegans* in northern Europe. These results contribute empirical insights into sex differences in local adaptation (Svensson et al., 2018) and reveal how the rate of range expansion and local adaptation can be strongly shaped by sex differences (Aguilée et al., 2013, 2016).

### 4.1 | Latitudinal cline in sexual size dimorphism

We found that increasing male body size with latitude resulted in body size convergence between males and females and reduced sexual size dimorphism towards the range limit (Figure 2). Interestingly, this increase in male body size towards the range limit was opposed by apparent sexual selection: in the south large males were more

likely to be in copula, a pattern that reversed in sign near the range limit (Figures 4 and 5). We therefore conclude that apparent sexual selection is unlikely to explain the increase in male body size with latitude. Instead, the increase in male body size is more likely a result of shifts in natural selection due to abiotic factors (e.g. climate), sex-differences in temperature-dependent growth rates or different dispersal processes during range expansion (e.g. spatial sorting of differently sized phenotypes, especially pronounced in higher-dispersing males) (Krause et al., 2016). Some previous studies suggest that selection for dispersal-enhancing traits is more important than environmental selection in explaining latitudinal body size clines (Hassall et al., 2014; Hassall & Thompson, 2008). However, it is also well known that lower temperatures increase both development time and adult size in many insects (Angilletta, 2009; Kingsolver & Huey, 2008). The lack of change in female body size with latitude may reflect stronger temperature-dependent thermal plasticity trade-offs in females than males in this species. We have observed female trade-offs between large size beneficial for dispersal and fecundity and smaller size for avoidance of male harassment, and our previous work suggests that these female trade-offs were not ameliorated at the range edge (Lancaster et al., 2017; Svensson et al., 2020). Alternatively, the lack of female body size cline may reflect weaker spatial sorting process on body size in females than males, due to lower dispersal rates and migration distances in females at the range edge.

### 4.2 | Shift in the direction of sexual selection on body size along the gradient

Smaller males were not disadvantaged in terms of their probability to copulate near the range limit, in comparison to at the range core (Figure 3). Thus, sexual selection on male body size changed in sign, from favouring larger males in the south to instead favouring smaller males in the north near the range limit (Figure 3). Interestingly, the sex ratio was more male biased near the range limit (Figure 1c), and the frequency of males among genetic migrants was also higher at the range limit (Figure 5b). Previous work in southern Sweden revealed that sexual selection on *I. elegans* male body size fluctuates rapidly between generations and over small spatial and temporal scales (Gosden & Svensson, 2008). These fluctuating selective regimes are partly driven by intraspecific interactions, resulting in density- and possibly also frequency-dependent sexual selection (Gosden & Svensson, 2008). Moreover, range expansion has previously been associated with shifting patterns of both frequency-dependent and frequency-independent selection on female morphs in this system (Lancaster et al., 2017; Svensson et al., 2020; Wood et al., 2019).

Coenagrionid damselflies are mainly characterised by male-male scramble competition over females, and female choice is of relatively little importance in this family, compared to other taxa (Gómez-Llano et al., 2020; Janicke et al., 2016). Under increased male-male competition, frequency-dependent selection on male body size could intensify (Serrano-Meneses et al., 2008), with a possible

frequency-dependent fitness benefit for smaller males when average male size is larger, such as near the range limit. Concomitantly, sexual selection on large body size may also be relaxed at the range limit if most males have reached their sexual selection peaks where natural selection for larger size caused by abiotic factors counteracts sexual selection. These findings suggest that sexual selection, natural selection and spatial sorting can have different effects on male body size and might oppose each other during range expansion.

### 4.3 | The role of sexual antagonism in latitudinal clines

Recent theoretical work (Connallon, 2015) and a large meta-analysis across many taxa (De Lisle et al., 2018) suggest that sexually antagonistic selection is stronger at the centre of a species range and under more benign environmental conditions, compared to at the edge of a species range where conditions are harsher. This might be due to both sexes experiencing concordant natural selection towards the same optimum under harsher environments when becoming displaced from their adaptive peaks, which we expect to happen at the edge of a species range or in other novel environments (De Lisle et al., 2018; Svensson et al., 2018). Our findings in *I. elegans* of reduced sexual size dimorphism at the edge of this species range (Figure 2, Figure S3) is therefore broadly consistent with these previous findings and recent theory (Connallon, 2015). Our previous work on *I. elegans* has already suggested that selection on female colour morphs in this species change in sign and direction (i.e. switching from negative to positive frequency dependence) at expanding, poleward range margins (Lancaster et al., 2017; Wood et al., 2019). Such phenomena imply that shifts in social and sexual interactions may facilitate range shifts, if such social changes make populations better adapted to novel environmental conditions.

### 4.4 | Sex-specific genetic dispersal and migration

We provide several lines of evidence supporting male-biased dispersal and migration in *I. elegans* during range expansion. Although there were no detectable differences in isolation by geographic distance (Figure S6) or thermal resistance relationships (Tables S6 and S7) between males and females across the range expansion, we observed differences in spatial autocorrelation (Figure 4), with genetic similarity declining more rapidly in males than in females up to distances of 200 km. In contrast, at larger distance classes there were indications of female site fidelity, as revealed by decreasing genetic similarity among females than in males (i.e. greater gene flow among males at larger distances; Figure 4). Furthermore, genetic migration estimates pointed to (a) a higher proportion of male migrants with increasing latitude towards the range limit (Figure 5b), (b) steeper latitudinal clines in migration distance in males versus females (Figure 6, Figure S9) and (c) a tendency for males to drive

a northward directionality of migration (Figure 6, Figure S8). These patterns were observed in spite of a decrease in the total number of detected migrants among the northernmost sites (Figure 5a). Male-biased migration during the *I. elegans* range expansion may therefore partly explain more male-biased sex ratios in the north, near the range limit. Notably, both male- and female-biased dispersal is present in odonates, depending on the species (Beirincx et al., 2006; Chaput-Bardy et al., 2010; Conrad et al., 1999; Corbet, 1999). The evidence for male-biased migration we present, combined with our finding of increasing male body size and reduced sexual size dimorphism near the range limit, is consistent with selection for dispersal-enhancing traits in males during this ongoing range expansion. Taken together, this might suggest that the documented increase in male body size has largely been driven by natural selection for dispersal or to adapt to abiotic conditions near the range limit, while sexual selection apparently opposes this latitudinal change.

### 4.5 | Genetic diversity and landscape resistance

Genetic diversity is expected to decline along a range expansion axis due to founder effects and population bottlenecks, which potentially reduce the capacity of populations to adapt to novel environments (Reed & Frankham, 2003; Song et al., 2013). However, we found that overall genetic diversity (heterozygosity and allelic richness) did not change with latitude, consistent with an increase or maintenance of genetic diversity at the expanding edge (Leydet et al., 2018; Song et al., 2013). These findings and our previous study (Dudaniec et al., 2018) suggest that genetic diversity does not limit rapid local adaptation in *I. elegans* during its ongoing range expansion, and instead may introduce novel genetic variation. Although genetic diversity did not decline across the *I. elegans* range expansion gradient, abundance decreased (Figure 1b). Reduced habitat suitability at the Swedish range limit in *I. elegans* (found by Lancaster et al., 2015; Figure 1a), combined with increased landscape resistance and lower numbers of migrants overall, is likely to affect local *I. elegans* abundance and other species at or near their range limits (Bennie et al., 2013; Eckert et al., 2008).

The rather weak isolation-by-distance (Figure S4) and spatial autocorrelation (Figure 4, Figure S7) relationships we found in *I. elegans* indicate that geographic distance only weakly explains genetic dispersal, which is in contrast to mean annual temperature, which strongly correlated with genetic connectivity. This finding and a lack of a land cover effect on gene flow (Figure S1, Tables S8–S10) is consistent with our previous findings that show a dominant role of temperature in driving the *I. elegans* range expansion (Lancaster et al., 2015), and in other insects (Buckley et al., 2012; Swaegers et al., 2013; Watts et al., 2010). Although possibly limited by low resolution of climatic and spatial data, sex-specific landscape genetic responses indicated similar resistance relationships with temperature in both sexes (Table 1). This suggests that temperature is not a key driver of male-biased dispersal, which may instead be affected by social or ecological factors.

## 5 | CONCLUSIONS

Here, we have used an integrative approach combining phenotypic data, quantification of sexual selection on male body size and genetic analyses to characterise the ecological, demographic and genetic factors shaping climate change-mediated range expansion in *I. elegans*. We find evidence for male-biased dispersal reduced sexual size dimorphism and a shift in the direction of sexual selection towards the range limit, with larger males being favoured in the south and smaller males in the north. Our findings might reflect sex differences in phenotypic plasticity during range expansion possibly in combination with changing sex-specific natural selection on body size along the latitudinal cline and spatial change in the frequencies of different dispersal phenotypes. In addition, we found that low temperature was associated with reduced gene flow in *I. elegans*, suggesting that all three of: abiotic environmental gradients, sex differences in spatial sorting processes and/or thermal physiology, and social interactions, such as frequency-dependent and sexual selection, shape the success of range expanding colonisers in this system.

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## AUTHORS' CONTRIBUTIONS

R.Y.D., L.T.L., E.I.S. and B.H. conceived and designed the study; R.Y.D., L.T.L. and E.I.S. collected the field data; R.Y.D. conducted the molecular laboratory work and bioinformatics; A.R.C., L.T.L., R.Y.D. and C.J.Y. conducted the genetic analysis; R.Y.D., L.T.L. and A.R.C. wrote the manuscript with editing from all authors.

## DATA AVAILABILITY STATEMENT

SNP datasets, data for morphology, copula, sex ratio, GeneClass output and R code for generating resistance surfaces are provided on Dryad at the <https://doi.org/10.5061/dryad.w9ghx3fp7> (Dudaniec et al., 2021).

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## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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