INTRODUCTION

Environmental gradients can generate large-scale variation in morphology, physiology, life history and behaviour. The essence of the correlations between environmental factors and phenotypic traits is captured by ecogeographical rules (Gaston et al., 2008), many of which have been formulated long ago. However, the data to formally statistically test them have become available only recently. Birds play a prominent role in investigating global patterns of trait variation, because they are one of the best-studied taxonomic groups. Accordingly, recent studies have shown predictable patterns of spatial variation in several avian life-history or phenotypic traits, including body size (Olson et al., 2009) and shape (Symonds & Tattersall, 2010), sexual size dimorphism (Friedman & Remeš, 2016), clutch size (Jetz et al., 2008), longevity (Valcu et al., 2014), and plumage coloration (Delhey et al., 2019).

These and other studies highlight how the evolution of avian mating strategies and of sexually selected traits is influenced by environmental conditions (Macías-Ordóñez et al., 2013). A key aspect of the mating behaviour of birds is the occurrence of extra-pair paternity. Most bird species are socially monogamous with biparental care, but individuals can engage in copulations outside the pair bond, which often lead to multiple paternity within a brood (Kempenaers & Schlicht, 2010; Westneat & Stewart, 2003). Extra-pair paternity
(EPP) can substantially affect the variance in reproductive success among males and therefore influence the intensity of sexual selection (Kempenaers & Schlicht, 2010). Several hypotheses have been proposed to explain the observed variation in EPP rates among individuals, populations and species, based for example on a link with breeding synchrony and density (Stutchbury & Morton, 1995; Westneat et al., 1990), life history (Wink & Dyracz, 1999), genetic diversity (Westneat et al., 1990) or pathogen prevalence (Gohil et al., 2013; O’Connor et al., 2018). Because many of the ecological and life-history predictors of EPP vary geographically (summarised in Table S1), the frequency of EPP is also predicted to vary along environmental gradients (reviewed by Brouwer & Griffith, 2019; Macedo et al., 2008). Despite several lines of evidence that the occurrence and frequency of EPP vary consistently across space (Brouwer & Griffith, 2019; Griffith, 2000; Spottiswoode & Møller, 2004), the large-scale spatial variation in EPP has been difficult to describe and we still lack a broad geographical perspective on variation in this trait. Capturing the large-scale variation of complex traits such as EPP requires relatively large sample sizes and wide spatial coverage. Over the last decades, reliable estimates of the frequency of EPP have become available for an increasing number of avian species and for species across a wider geographical range.

Several studies have searched for predictable geographical patterns of variation in EPP rates (Bonier et al., 2014; Brouwer & Griffith, 2019; Lijfeld et al., 2019; Spottiswoode & Møller, 2004). Although they provided clear evidence for the existence of geographical variation in the frequency of EPP, the results of these studies have been contradictory, with the frequency of EPP either positively (Bonier et al., 2014; Spottiswoode & Møller, 2004), negatively (Brouwer & Griffith, 2019), or not correlated with latitude (Lijfeld et al., 2019). While all of them performed carefully designed comparative analyses among populations or species, on curated data sets, we identified several factors that were not considered in these studies and that may explain the different results.

1. Species distribution ranges. Geographical patterns are often dominated by wide-ranging species, firstly because of their broad occurrence (Jetz et al., 2008) and secondly, because they show more variation within their breeding range, due to the greater environmental variation and greater opportunity for local adaptation (Gaston et al., 2008). The species’ contribution to geographical patterns is therefore weighted by the size of their breeding range. Comparative analysis at species level cannot reflect appropriately how geographical patterns emerge because it assumes that all species have an equal contribution.

2. Considering different levels of variation in EPP rates. Spatial variation in phenotypic traits can occur at multiple levels, that is, among individuals, populations, species and species assemblages (Gaston et al., 2008). Previous studies have already proposed that a hierarchical approach is needed to best explain variation in the occurrence of EPP (Griffith et al., 2002), and several studies confirmed that different predictors can explain the frequency of EPP at individual, population and species levels (Brouwer & Griffith, 2019; Brouwer et al., 2017). For example, Brouwer and Griffith (2019) showed that EPP rates vary with latitude, but differently at population and species levels. However, so far, the variation of EPP rates at the assemblage level has not been investigated.

3. Within-range variation and geographical sampling bias. There is increasing evidence that the frequency of EPP depends on the population location (Bonier et al., 2014; Brouwer & Griffith, 2019). This implies that accurate species estimates cannot be obtained by simply averaging population values. Even when measurements are available from multiple populations of a given species, if a particular region within the breeding range has been sampled more intensively, that region will weigh more in the analysis, even though its population characteristics are not necessarily representative of the entire breeding range. With few exceptions (Bonier et al., 2014; Brouwer & Griffith, 2019), intraspecific variation in EPP rates and the sampling bias within the species’ breeding range have largely been disregarded in comparative analyses both at species and population level.

4. Different patterns of geographical variation. The existing hypotheses (Table S1) predict variation in EPP rates along geographical gradients (latitudinal, altitudinal), and between populations with different levels of genetic diversity (e.g., central/marginal, island/mainland). Although it is recognised that these patterns can occur simultaneously, we are only aware of a single study that investigated variation in EPP rates along both latitude and altitude (Bonier et al., 2014). Moreover, EPP rates can exhibit different geographical patterns of variation at different levels (see (2) above).

Here, we explore the geographical variation in the frequency of EPP at the assemblage level, using an approach that explicitly addresses the above-described issues. We then discuss some of the key hypotheses that predict geographical variation in EPP rates. Assemblage-level analysis is a powerful tool to investigate the effect of shared environment on populations from different species, and integrates information about the species’ EPP rates with information about their breeding range (Jetz et al., 2008) (issues 1–2). Assemblage-level analyses have been used previously to describe geographical variation in clutch size (Jetz et al., 2008) and body size (Olson et al., 2009). A known limitation of such analyses is that they use mean values of the phenotypic trait of interest for each species, thereby disregarding differences between populations from different parts of the species’ breeding range (Gaston et al., 2008). We resolved this problem by modelling the variation in EPP rates within the species’ breeding range based on population-level predictors that describe the specific ecological context of each population (issue 3). We used distinct predictors to model EPP rates at the intraspecific and interspecific level, which also allows to assess multiple geographical patterns simultaneously (issue 4). Finally, we verified the generality of the geographical patterns of EPP rate variation identified at the assemblage level by assessing them separately for each zoogeographical realm. Zoogeographical realms are regions with distinct evolutionary histories, defined by the distribution and
phylogenetic relationships of the major land vertebrates (Holt et al., 2013). Thus, each realm can be considered to represent an independent macro-ecological and evolutionary unit of analysis, containing subsets of species which are largely restricted to these regions (Delhey et al., 2019). Zoogeographical realms have previously been used as “evolutionary replicates” both in species- (Friedman & Remeš, 2016) and assemblage-level analyses (Delhey et al., 2019).

Using this approach, we confirm the existence of globally consistent patterns of geographical variation in the frequency of EPP at the within-species level, as well as across bird assemblages.

2 | MATERIALS AND METHODS

2.1 | Definitions

To define extra-pair paternity, we first need to define the social unit. Following Westneat et al. (1990), we define a social bond as “a consistent association” between a female and a male established “before and during egg laying” which involves “coordinated social interactions”. One social unit can then include a single social bond (i.e., socially monogamous species), or multiple social bonds (i.e., cooperative breeding species, Westneat et al., 1990). Note that groups comprised of one breeding pair and offspring from previous breeding attempts which remain on their natal territory as auxiliary non-breeding helpers are considered a pair rather than a group, because the social unit includes a single social bond related to reproduction (i.e., the helpers do not reproduce).

We define extra-pair paternity as the occurrence of paternity outside the social unit (pair or group). Our definition excludes offspring sired by subordinate males in cooperatively breeding species because (1) the breeding females establish social bonds with the subordinate males, (2) mating with a subordinate male does not bear the same costs as mating with a male outside the group, and (3) subordinate males invest in parental care for the group’s offspring, including their own. Our definition also implies that we excluded species where individuals do not form pair bonds, that is, species with female-only care, lekking species and species that reproduce exclusively via brood parasitism. Note that these species can have clutches sired by multiple males, but investigating variation in the frequency of multiple paternity in such systems lies outside the scope of our study.

We use the term extra-pair offspring (EPO) for any offspring sired by males outside the social unit, that is, offspring sired by extra-pair males for socially monogamous species and by extra-group males for cooperatively breeding species. Extra-pair broods (hereafter EPB) are broods or clutches containing at least one extra-pair offspring or extra-pair sired egg.

2.2 | Extra-pair paternity data

We compiled data on EPP rates from original, peer-reviewed publications and dissertations found by searching Web of Science, Google Scholar and the major biological and ornithological journals, and by back-tracing sources cited in published reviews and comparative analyses. We only included studies (1) on free-living populations of unmanipulated individuals, (2) that clearly described the analytical and statistical procedures employed, (3) that used reliable genetic techniques to establish paternity (single-locus: minisatellites, microsatellites or SNPs; multilocus: minisatellites or microsatellites), and (4) that provided the geographical location of the population. If multiple studies of the same population were available, we only included data from nonoverlapping years to avoid redundancy, then added the samples and computed the proportion of EPB and EPO for the population.

For each study, we recorded the number of broods genotyped, the number of EPB, the number of genotyped offspring, the number of EPO, the social unit (pair vs. group), the genotyping technique, the location of the population and the years covered by the study. The compiled data set includes data on the proportion of EPB from 634 populations (386 species) and data on the proportion of EPO from 637 populations (390 species). For 608 populations (375 species) the proportion of both EPB and EPO were available. Overall, the data set includes 663 populations from 401 species of 91 families.

2.3 | Predictors

Our models include two types of predictors: (1) population-level predictors that describe the ecological context in which each population occurs relative to other populations within the species’ breeding range, and (2) species-level predictors, describing the life-history and the breeding biology of the species. Most of the predictors vary and can influence EPP both at the population and the species level. Assigning each of the predictors to one of the two levels was based on data availability, and on previous studies indicating how the predictor influences EPP rates.

2.3.1 | Population-level predictors

Because EPP varies among populations of the same species and because for many species data are only available from few populations, averaging EPP rates measured at the population-level does not produce reliable species estimates (Brouwer & Griffith, 2019). We therefore modelled the proportion of EPO and EPB based on four variables, computed for each population. (a) Relative latitude. This indicates the position of a population relative to the centre of the species’ latitudinal breeding range and the Equator. Thus, positive or negative relative latitudes indicate locations further from, respectively closer to the Equator than the centre of the latitudinal range of the species. A population located at the middle range latitude of the species has a relative latitude of zero. We used relative latitude, because the same absolute latitude can represent the northern extreme of one species’ breeding range, but the southern extreme of another species’ breeding range. Absolute latitude may thus have
opposite effects for the two species. (b) Relative distance to the breeding range boundary. The same absolute distance to the breeding range boundary can describe a population located relatively close to the boundary of a large breeding range and a population in the middle of a small breeding range. We therefore used relative distance to ensure that the values can be interpreted similarly across species. We first measured the absolute distance between the location of each population and the breeding range boundary. We then generated a distribution of distances to the breeding range boundary for 10,000 equally spaced locations covering the entire range, and computed the relative distance of a population to the breeding range boundary as the quantile of the measured distance on this distribution. (c) Seasonality. For each population we computed seasonality as the coefficient of variation (CV) of the average gross primary production on a 1,000 m² surface centred in the population location, for time windows of eight days across the entire year. We obtained data on gross primary production between 2000–2016 at a resolution of 500 m from (Zhang et al., 2017). The index captures both the latitudinal and altitudinal variation of seasonality (Figure S1). (d) Social unit. We recorded the social unit (pair vs. group) from each of the publications from which the EPP data originated. The type of social unit in which breeding occurs is typically a species-level characteristic. However, in rare cases, the social unit varies among populations. For example, the carrion crow (Corvus corone) and the stitchbird (Notiomystis cincta) breed as pairs in some populations, but cooperatively in other populations (see Supporting Information Data). We therefore used the social unit as a population-level rather than a species-level predictor.

By modelling the proportion of EPB and EPO based on population-level predictors, we obtained unbiased EPP predictions across the species’ breeding range, independent of the number of sampled populations.

2.3.2 Species-level predictors

Previous studies have associated variation in EPP across species to variation in life history, ecology or genetic diversity (Kempenaers & Schlicht, 2010). Based on these prior findings, we compiled data on six independent variables for each species, as follows. (e) Generation length (in years), obtained from BirdLife International (2020, downloaded on 04/04/2020). (f) Social bond duration (transitory, short-term, long-term), based on Tobias et al. (2016). (g) Clutch size, compiled from Del Hoyo et al. (1992–2010). (h) Territoriality (nonterritorial, weakly territorial, year-round territorial), based on Tobias et al. (2016). (i) Breeding range size (km²), computed based on the species’ breeding range obtained from BirdLife International (2017). Range size is correlated with and a good proxy for genetic diversity (Fan et al., 2019). (j) Migration distance (km), computed as the median of the distribution of potential migration distances for each species, obtained from Dufour et al. (2020). Note that migration distance estimates the seasonal movements for all species, including those whose breeding and wintering ranges overlap. The partial correlation between life-history predictors varied between ~0.53 (between clutch size and generation length) and 0.62 (between migration distance and breeding range size) (Table S2).

For the analyses considering different realms, we assigned each population location to one of 11 zoogeographical realms according to Holt et al. (2013).

2.4 Data analyses

We used the proportion of broods containing at least one extra-pair offspring (EPB) as a direct measure of the proportion of females which obtain extra-pair fertilizations (Stutchbury & Morton, 1995) and as a good proxy for the probability of paternity loss in a given species (Liker et al., 2015). Note, however, that females that produced broods without EPO might still have performed extra-pair copulations that did not lead to fertilizations (Brommer et al., 2007). For completeness, and because for 29 populations only data on EPO were available, we also replicated all analyses using the proportion of EPO.

We used R version 4.0.3 for all statistical and spatial computations (R Core Team, 2020). We used a hierarchical Bayesian approach and ran model-based analyses with brms version 2.13.0 (Bürkner, 2017), which is a front-end to the probabilistic programming language STAN (S. D. Team, 2018).

Posterior distributions for the predictors were obtained through Markov-chain Monte-Carlo sampling, using five chains of 5000 iterations each, among which 2500 were warm-up iterations. To avoid any divergent transitions, we increased the target average proposal acceptance probability to 0.99 and the maximum tree depth to 20. We used the default priors proposed in brms (Bürkner, 2017) in all models (i.e., uninformative, flat priors for the fixed effects; Student t-distribution with 3 degrees of freedom for the random effects; and a beta-distribution prior for the zero-inflation parameter). All models achieved convergence, with R-hat values of 1 or close to 1 for all predictors (Gelman & Rubin, 1992). We evaluated models using model diagnostic plots (Gabry et al., 2019), that is, we compared observed data with simulated data from the posterior predictive distributions (the distribution of possible unobserved values conditional on the observed values). As model output, we report posterior means, the standard deviation of the posterior distributions and the two-sided 95% credible intervals of the posterior means (95% CI), as well as the probability of direction. The probability of direction (PD) of an effect ranges between 0.5 and 1 and represents the percentage of the posterior distribution which has the sign of the median. PD is comparable to the frequentist p-value (Makowski et al., 2019), whereby PD values of 0.5 and 1 correspond to p-values of 1 and 0, respectively. As a guidance for readers more familiar with the frequentist approach, we also report two-sided Bayesian p-values computed according to Makowski et al. (2019).

We modelled the proportion of EPB and the proportion of EPO using binomial models with a logit-link function. We fitted full models with both population and species-level predictors. We loge
transformed clutch size, generation length, migration distance and breeding range area to normalize their distributions. We added social bond duration, territoriality, genotyping method (multilocus vs. single-locus) and social unit (pair vs. group) as ordered factors in the model and included species identity as random intercept. Note that population-level predictors could not be included as random slopes, because for 295 of the 401 species data were only available from single populations. We therefore modelled within-species variation of EPP under the assumption that the population-level predictors have similar effects across species. All explanatory variables were standardised by centring and dividing by the standard deviation. Because the distribution of the predicted proportions of zero values indicated zero-inflation for both EPO and EPB models (i.e., the models predicted fewer zero values than observed), we updated the models with a zero-inflation component (binomial model with logit function). The diagnostic distribution of the predicted zero-value proportions for the updated model indicated no zero-inflation and the PD values for the zero-inflation parameter was 1 for all models (Table S3–S6). To control for nonindependence due to shared ancestry (between 1 and 8394, median 498, predicted EPP values per breeding range distribution for each of the 401 species in our data set), we therefore modelled within-species variation of EPP under the assumption that the population-level predictors have similar effects across species. All explanatory variables were standardised by centring and dividing by the standard deviation. Because the distribution of the predicted proportions of zero values indicated zero-inflation for both EPO and EPB models (i.e., the models predicted fewer zero values than observed), we updated the models with a zero-inflation component (binomial model with logit function). The diagnostic distribution of the predicted zero-value proportions for the updated model indicated no zero-inflation and the PD values for the zero-inflation parameter was 1 for all models (Table S3–S6). To control for nonindependence due to shared ancestry, we first built a consensus phylogeny using 1,000 trees (sampled from Birdtree.org; Jetz et al., 2012) with Ericsson backbone using the maxCladeCred function in phangorn 2.5.5 (Schliep, 2011). We then used the consensus phylogeny to create a phylogenetic covariance matrix with the function inverseA in the MCMCglmm package (Hadfield, 2010), and included this covariance matrix in the Bayesian models.

We assessed the models’ predictive performance through k-fold cross-validation (Vehtari et al., 2017), whereby the model is fitted on a subset of the data and then used to predict the dependent variable for the complementary subset. To evaluate the predictive accuracy of the model we computed for each of the subsets (1) the Spearman rank correlation between the predicted values (extracted from the posterior distribution) and the observed values, and (2) the root mean-squared logarithmic error (RMSLE) between the predicted and the observed values (Kuhn & Johnson, 2016). RMSLE is a model performance criterion (Hamner & Frasco, 2018); it has the units of the original data and it is used to assess the relative performance of models, whereby lower RMSLE values indicate a better predictive performance of the model (Kuhn & Johnson, 2016). We used k-fold cross-validation to compare the models’ predictive performance (1) among 10 sets of randomly selected populations (stratified random sampling of 20% of the populations of each zoogeographical realm), and (2) between the subset of species represented by multiple populations and the subset of species with only a single population.

We used the R package rangeMapper version 2.0 (Valcu et al., 2012) to generate maps of predicted proportions of EPB and EPO at the assemblage level. We created a rangeMapper project using hexagonal cells (Birch et al., 2007) with a diagonal of 130 km on a pseudocylindrical, equal-area projection (Eckert IV). Based on the models described above (Table S3–S6) we first computed the proportions of EPB and EPO for new locations covering the entire breeding range distribution for each of the 401 species in our data set (between 1 and 8394, median 498, predicted EPP values per species, depending on the size of the breeding range). We then computed assemblage-level EPP frequencies (proportion EPB or EPO) as averages of the species EPB/EPO values for each grid cell. For mapping and statistical analyses, we only included grid cells with at least three species (\(N_{\text{EPB}} = 14,262, N_{\text{EPO}} = 14,323\)). The average number of species per assemblage was 24.9 (SD = 18.1) for the assemblage proportion of EPB and 24.8 (SD = 18.1) for the assemblage proportion of EPO.

We used Gaussian models to assess geographical variation in the assemblage-level EPB and EPO values for the six realms with an assemblage coverage of at least 95% based on data from at least 10 species (Australian, Nearctic, Neotropical, Palearctic, Panamanian, Sino-Japanese). We used the average proportion of EPB or EPO of the assemblage as dependent variable, and included the absolute latitude and altitude (square-root transformed) as predictors. To remove small-scale spatial autocorrelation, we used for each realm 100 subsets of randomly selected assemblages. We used a stratified sampling scheme to cover the entire latitudinal range of the realm and to ensure an accurate proportional representation of the different latitudes of the realm. We randomly sampled 10% of the assemblages from each band of 5 degrees latitude within the realm. We then used the function "brm_multiple" in the brms package (Bürkner, 2017) to fit the assemblage-level models for each of the 100 assemblage subsets. The function then combines the posterior distributions of all 100 models per realm.

3 | RESULTS

3.1 | Variation in the frequency of extra-pair paternity

We compiled a nonredundant data set of EPP rates which covers 4% of the extant species and 47% of the extant avian families (Figure 1 and Supporting Information Data). Across all populations in the data set, the proportion of EPB ranged between 0 and 1, and the proportion of EPO between 0 and 0.77. EPP estimates were available from two or more populations for 106 species. The proportion of EPB and EPO varied among populations within species by up to 69% and 50%, respectively. All 11 zoogeographical realms are represented in our data set (Figure 1a), but only three of the realms include at least 50 species, and only two include more than 10% of their avifauna (Figure 1b). The Nearctic and Palearctic realms are the best represented and – given that multiple populations are studied for many of the species occurring in these realms – they collectively account for 67.9% of the data.

3.2 | Within- and between-species variation in EPP rates

We modelled the proportion of EPB and EPO based on four population-level and six species-level predictors (Figure 2a, Tables
The direction of the effects of the population-level predictors was consistent for both estimates of the frequency of extra-pair paternity. Within a species’ breeding range, populations located at lower latitudes (i.e., closer to the equator) and those further from the breeding range boundary had higher proportions of EPB and EPO. Populations breeding in less seasonal environments also had higher...
proportions of EPO. Pair breeders had higher proportions of EPB and EPO than cooperative breeders.

Among the life-history predictors, generation length showed the largest effect, whereby species with shorter generation length had higher proportions of EPB and EPO. Species with short-term bonds also had higher proportions of EPB and EPO than those maintaining long-term bonds. Species with larger clutches tended to have a higher proportion of EPB, but a lower proportion of EPO, albeit with broad posterior distributions. The effects of all other species-level predictors were small, with low PD values. Species identity explained more than 35% of the total variance.

### 3.3 | Effects of phylogeny

In the above models, the dependent variable contains a phylogenetic signal (Brouwer & Griffith, 2019). Thus, these models could suffer from pseudoreplication. Comparative studies typically solve this problem by including phylogeny in the model. However, using phylogenetic models "by default" in any interspecific comparison is not advisable because it can mask real, biologically relevant effects (Uyeda et al., 2018). Phylogenetic models are necessary for preventing pseudoreplication only when there is a phylogenetic signal in the residuals of the models (Hansen, 2014; Hansen & Bartoszek, 2012; Revell, 2010), as for example under strong phylogenetic constraints (Blomberg & Garland Jr, 2002). This may not be the case for EPP, because even closely-related species can vary substantially in EPP rates (Kingma et al., 2009). We therefore first checked whether there is a phylogenetic signal in the residuals of the EPB and EPO models. We fitted models with the residuals of either the EPB or EPO models as dependent variable and species identity as random factor, controlling for phylogeny. The variance explained by phylogeny (i.e., lambda) was close to zero (EPB: 1.1%, 95% CI [0, 3.9%]; EPO: 0.6%, 95% CI [0, 2.6%]). The models are therefore statistically valid and do not suffer from elevated type I errors.

Closely-related species can have similar EPP rates not only due to phylogenetic constraints, but also if EPP is correlated with other variables which contain a phylogenetic signal (McElreath, 2020). In this case, although accounting for phylogeny is not required for the validity of the model, phylogeny can explain part of the variation in EPP and inform the interpretation of the effects of the other predictors. We therefore updated the models on EPO and EPB with the phylogeny covariance matrix. The variance explained by phylogeny was 31% for the EPB model (Table S5) and 29% for the EPO model (Table S6). The effects of the population-level predictors were virtually unchanged after accounting for phylogeny (Figure 2b, Tables S5–6). However, the effects of generation length and social bond duration strongly decreased and none of the species-level predictors except for clutch size predicted variation in EPP in the models containing phylogeny. Species identity explained less than 20% of the total variance in the models containing phylogeny (Tables S5–6).

The predicted proportions of EPB and EPO for the populations in our data set were highly correlated between models that did and did not include phylogeny (Pearson's $r = 0.999$ for both EPB and EPO). The marginal $R^2$ (the proportion of variance explained by the predictors) of the model without phylogeny was 0.35 for EPB (Table S3) and 0.30 for EPO (Table S4). The marginal $R^2$ values were lower for the model including phylogeny (0.19 for EPB, Table S5; 0.12 for EPO, Table S6).

### 3.4 | Model validation

The predictive accuracy of the models could be affected by (1) nonrandom sampling of populations within the species' breeding range, or of species across zoogeographical realms and (2) potential between-species variation in the effects of the population- and species-level predictors on EPP. We therefore assessed the predictive accuracy of the models using posterior predictive checks and k-fold cross-validation (Hooten & Hobbs, 2015). The diagnostic distribution of the predicted proportions of EPB and EPO contained the observed values for all 11 zoogeographical realms, confirming that the model can generate robust predictions across the realms. The proportion of EPB and EPO of randomly selected subsets of populations (Figure S2), as well as those of species represented by either one or multiple populations (Figure S3) were predicted with similar accuracy from the models fitted on the complementary subsets, indicating that there is no bias caused by the species representation or population location. Finally, the predicted proportion of EPB and EPO for the locations of the populations in the data set were strongly correlated with the observed values for all 11 zoogeographical realms (Table S7), confirming that populations from all realms are modelled accurately. Further evidence for the accuracy of the predictions across species is also provided by the stability of the effects of the population-level predictors in models which controlled for phylogeny compared to those that did not (Section 3.3).

### 3.5 | Large-scale geographical variation in EPP

To investigate the large-scale geographical variation in EPP rates, we first used the models described above (Tables S3–4) to predict the proportions of EPB and EPO for new locations covering the entire breeding range distribution, for each of the 401 species in our data set (see Figure 3 for an example of the well-studied blue tit, Cyanistes caeruleus). We then averaged the predicted EPB and EPO values for each grid cell to obtain average EPB and EPO estimates at assemblage level and mapped them at global scale (Figure 4a,c).

The global map (Figure 4) revealed striking inter-continental variation in the frequency of extra-pair paternity at assemblage level, with a 3-fold difference in the proportion of EPB among zoogeographical realms (Figure 4b) and a 4-fold difference in the proportion of EPO among realms (Figure 4d). The assemblage-level proportion of EPB and EPO were highly correlated across realms (Pearson's $r = 0.85, N = 11$). At the assemblage level, the proportion of EPB...
and the proportion of EPO decreased with absolute latitude in all six realms (Figure 5a, Table S8). The assemblage-level proportion of EPB and EPO increased with altitude in the Nearctic and Australian realms (Table S8). However, we found no consistent pattern of altitudinal variation in the frequency of EPP across all zoogeographical realms.
FIGURE 4 Geographical distribution of the assemblage-level proportions of extra-pair broods (a, b) and extra-pair offspring (c, d). Global distribution of assemblage-level extra-pair paternity estimates (a, c) and assemblage-level proportions for each zoogeographical realm, shown as box plots (b, d).

FIGURE 5 Relationship between latitude and the proportion of extra-pair broods (a) or the proportion of extra-pair offspring (b) at the assemblage level for each of six zoogeographical realms. Presented are regression lines and 95% confidence bands. The colours match the code for realms in Figure 1. For the full model output see Table S8.
4 | DISCUSSION

4.1 | Within-species variation in the frequency of EPP

Previous studies have shown that the frequency of EPP can vary substantially within species (Brouwer & Griffith, 2019), but the underlying causes of this variation remained unclear. Ecological and environmental gradients across a species’ breeding range can cause different selective pressures and populations may thus differ genetically, morphologically, physiologically and in other life-history traits. Such differences have for example been documented between central and marginal populations (central-marginal hypothesis; Eckert et al., 2008; Sexton et al., 2009), high- and low-latitude populations (Ashton, 2002; Bonier et al., 2014; Martin et al., 2019; Rose & Lyon, 2013), and high- and low-altitude populations (Boyle et al., 2016). We modelled the proportion of EPB and EPO using population-level predictors that broadly describe the population's ecological context relative to the species’ breeding range and found that EPP decreases with increasing latitude within the breeding range (Figure 2a, Tables S3–4). This negative correlation was even stronger when the environmental and life-history predictors were not accounted for (Figure S4). This result contradicts an earlier study showing that in Emberizidae (12 species) the proportion of EPB is positively correlated with the latitude of the population (Bonier et al., 2014). However, a recent analysis of 245 socially monogamous species which also accounted for other life-history and ecological predictors found a slight negative association between the proportion of EPO and latitude within noncolonial species (Brouwer & Griffith, 2019).

Using latitude values relative to each species’ breeding range, our study confirms that this within-species pattern holds across species. The proportion of EPO also decreased with seasonality, but the effect size was lower. Populations breeding at higher latitudes and in seasonal environments have higher breeding synchrony, supporting the idea of a trade-off between investing in extra-pair mating versus mate guarding (Westneat et al., 1990). Populations breeding at lower latitudes may, on the other hand, have a higher prevalence of pathogens (O’Connor et al., 2018) with higher virulence (Møller et al., 2009), which could favour EPP as a strategy to increase the diversity of genes with immune function in the offspring (O’Connor et al., 2018).

We also found that populations closer to the breeding range boundary have lower EPP rates than central populations. Theory predicts lower EPP rates when benefits to females are lower or when costs are higher (Petrie & Kempenaers, 1998). In peripheral populations genetic benefits are expected to be lower, because such populations show lower genetic variation (Eckert et al., 2008). In addition or alternatively, peripheral populations often experience suboptimal environmental conditions (Sexton et al., 2009), which might increase the costs related to reduced male investment in parental care (Westneat et al., 1990). Three of the hypotheses summarised in Table S1 could thus contribute to explain this pattern: the male trade-off, the constrained female and the genetic benefits hypothesis.

We predicted that paternity outside the social unit is more frequent when individuals are breeding in pairs as compared to breeding cooperatively, because in the latter (1) a larger proportion of the females can mate with multiple males and, therefore, females may benefit less from engaging in extra-pair copulations; (2) multiple males can better guard the female; and (3) extra-group copulations may translate less often into fertilizations, due to increased sperm competition with males within the group. Our results confirmed this prediction (Figure 2a, Tables S3–4).

4.2 | Between-species variation in the frequency of EPP

EPP varies widely between species, for example along the slow-fast life-history continuum (Wink & Dyracz, 1999). Species with slow life histories have slow development, low reproductive rates, long lifespan, and long-term pair bonds (Kempenaers & Schlicht, 2010; Shultz & Dunbar, 2010). In such species, males may invest more in pair-bond maintenance and less in seeking extra-pair mating opportunities (male trade-off hypothesis; Westneat et al., 1990), and females may engage less in extra-pair copulations to avoid male retaliation through physical aggression, withdrawal of parental care or divorce (constrained female hypothesis; Gowaty, 1996). We found three lines of evidence in support of these hypotheses. (1) Long-lived species had lower proportions of EPB and EPO than short-lived species (Figure 2a, Tables S3–4), a result consistent with previous studies (Arnold & Owens, 2002; Botero & Rubenstein, 2012; Crouch & Mason-Gamer, 2018; Wink & Dyracz, 1999). (2) Species with long-term social pair bonds had lower proportions of EPB and EPO compared to species with short-term social bonds. Similar results were previously reported for Passerine species (Lifjeld et al., 2019). (3) Species with small clutches tended to have lower proportions of EPB. This confirms an earlier study based on a considerably smaller sample size (Arnold & Owens, 2002). Interestingly, species with small clutches tended to have higher proportions of EPO. This effect could be due to the fact that the average number of EPO per brood is smaller than two for 98.6% of species. Thus, as the absolute number of EPO per brood is small and varies relatively little between species, the proportion of EPO necessarily is larger for species with smaller clutch sizes.

We found no support that the other life-history and ecological factors investigated here drive variation in the frequency of EPP among species. Genetic diversity determines the indirect genetic benefits which can be gained by females through EPP and can thus predict EPP rates (Gohli et al., 2013; Petrie et al., 1998). Range size is correlated with, and a good proxy for, genetic diversity (Fan et al., 2019), and a previous study reported a relationship with EPP rates (Crouch & Mason-Gamer, 2018). Although in our study the direction of the effect was consistent with this idea, there is no statistical support for such an effect (Figure 2, Tables S3–4). Three hypotheses have linked variation in the frequency of EPP to migratory behaviour. Firstly, migratory species breed more
synchronously than resident species, which can increase the opportunity for extra-pair copulations, and hence EPP rates (Stutchbury & Morton, 1995). Note however, that the opposite effect has also been postulated, because if males must trade-off pursuing extra-pair copulations and mate guarding or parental care, high breeding synchrony could also lead to decreased levels of EPP (Westneat et al., 1990). Secondly, migratory birds have to find their breeding partners within a short time, hence a higher proportion of females may not be paired with the preferred partner, which could result in increased EPP rates (Macedo et al., 2008). Thirdly, migratory birds are more exposed to pathogens (Gohli et al., 2013), which could result either in lower EPP levels if females try to minimize exposure (Gohli et al., 2013), or higher EPP levels if the offspring benefit from a broad allelic repertoire of genes with immune function (O’Connor et al., 2018). Several previous studies suggested that migration distance is associated with increased EPP rates (Albrecht et al., 2007; Lifjeld et al., 2019; Spottiswoode & Møller, 2004). Although we also used the estimated median migration distance (Dufour et al., 2020) to quantify migratory behaviour, our results do not confirm these earlier studies. However, our results are consistent with those of (Brouwer & Griffith, 2019), who used a binary classification into migratory and resident species as predictor, and found no evidence that migratory behaviour predicts variation in the frequency of EPP.

Finally, it has been proposed that stronger territoriality is associated with higher EPP rates. The reasoning is that in territorial species, females may choose a male based on territory quality or due to site fidelity, rather than based on the assessment of the male’s phenotype, such that a higher proportion of females may not be paired with the preferred partner, which could then result in increased EPP rates (Westneat et al., 1990). We found no support for this hypothesis (Figure 2, Tables S3–4).

In the phylogenetically explicit model, phylogeny explained all the variance in the proportion of EPB and EPO that was explained by the life-history traits in the model without phylogeny (compare Figure 2a,b, and Tables S3–4 and S5–6). This is not surprising, because unlike environmental and ecological factors, these predictors are expected to contain a strong phylogenetic signal. The only life-history variable which predicted the proportion of EPB after accounting for phylogeny was clutch size, which is also the only life-history trait for which latitudinal variation has been clearly demonstrated for all zoogeographical realms (Jetz et al., 2008).

4.3 Variation in EPP frequency at the assemblage level

Our Bayesian models show that the frequency of EPP varies with the species’ life-history and with the population’s position within the species’ breeding range. We used these models to predict, for each species, the proportion of EPB and EPO at new locations covering their entire breeding range. Thus, the predicted proportions of EPB and EPO captured the geographical variation in the frequency of EPP within the breeding range due to position (latitude, distance to breeding range boundary) and environmental factors (seasonality). Subsequently, we computed EPB and EPO estimates at the assemblage level as averages of the population values predicted for each location (Figure 4). The main limitation of assemblage-level analysis is that it uses mean values for each species, and thus disregards within-species variation (Gaston et al., 2008). By accounting for the variation of the frequency of EPP within the species breeding range we resolved this issue and obtained more accurate estimates at the assemblage level.

Using these assemblage-level estimates, we assessed large-scale (global) variation in EPP rates. Ecogeographical rules aim to describe spatial patterns in biological traits occurring at a global scale (Gaston et al., 2008). Yet, conformity to ecogeographical rules can depend on multiple correlated factors (Mainwaring & Street, 2019). Although many traits vary consistently along one or two geographical dimensions such as latitude and altitude (Jetz et al., 2008; Olson et al., 2009; Symonds & Tattersall, 2010), other traits have more complex patterns of geographical variation, with biogeographical regions explaining a large proportion of their variation (Delhey et al., 2019; Friedman & Remeš, 2016; Valcu et al., 2014). In such cases, the patterns of geographical variation must be sought within bioregions rather than at global scale (Delhey et al., 2019; Friedman & Remeš, 2016; Valcu et al., 2014). The global distribution of predicted assemblage-level proportions of EPB and EPO shows that this is also the case for extra-pair paternity (Figure 4a,c). Although large-scale latitudinal gradients can be observed within continents, the most striking variation in the frequency of EPP is among continents. In the northern hemisphere for example, species breeding in North America have much higher average EPP levels than those breeding at similar latitudes in Eurasia (Figure 4). Likewise, species breeding at high latitudes in the southern hemisphere do not mirror the EPP rates of species breeding at similar latitudes in the northern hemisphere. Disregarding this variation may hinder the identification of geographical patterns of variation and could explain why recent studies found no latitudinal variation in the frequency of EPP (Lifjeld et al., 2019).

Our analysis shows broad variation in the frequency of EPP among zoogeographical realms (Figure 4b,d), with the highest levels in the Nearctic realm. Nearctic birds have comparatively short lifespans and experience relatively high adult predation pressure (Valcu et al., 2014). Interestingly, Nearctic birds are also more sexually size dimorphic than birds breeding elsewhere (Friedman & Remeš, 2016), suggesting a higher intensity of sexual selection. Levels of EPP were lowest in the islandic zoogeographical realms (Oceania and Madagascar), which is consistent with the prediction that the intensity of sexual selection is lower on islands due to lower genetic diversity (Frankham, 1997; Griffith, 2000). Alternatively, low EPP levels on islands could also be related to increased longevity (Beauchamp, 2021).

We found a negative association between assemblage-level EPP rates and absolute latitude within each of the six zoogeographical realms analysed (Figure 5; Table S8). Although no similar studies at assemblage level are available for comparison, several comparative analyses have considered this effect at the species level. An early study on 46 passerines suggested that a direct correlation with breeding synchrony could cause a latitudinal increase in the proportion of
EPB, a notion also supported by lower testis size in tropical species as compared to high-latitude species (Stutchbury & Morton, 1995). A later study on 186 species reported a positive relationship between the proportion of EPO and the midpoint latitude of the species breeding range (Spottiswoode & Møller, 2004). The proportion of EPB was also positively correlated with population latitude in 12 Emberizidae species breeding in temperate regions in the Northern Hemisphere, but some species breeding in the tropics did not match this pattern (Bonier et al., 2014). Recently, a study on 131 species of the passerine Passerida found no correlation between the proportion of EPO and the average latitude of the species’ populations (Lifjeld et al., 2019). However, an analysis of 245 socially monogamous species which also accounted for other life-history and ecological predictors, found a slight negative association between the proportion of EPO and the mean latitude of the species (Brouwer & Griffith, 2019). Our results at assemblage level are in accordance with the latter study. We note, however, that all of these studies assessed variation in EPP between species and across zoogeographical realms.

Latitudinal variation in the frequency of EPP has been predicted by multiple hypotheses (Macedo et al., 2008). However, these hypotheses do not all agree on the direction of this variation (Table S1). Synchronous breeding, for example, was proposed to increase the opportunity for extra-pair copulations and allow the comparative assessment of males (Stutchbury & Morton, 1995). Although synchronous breeding can also occur at low latitudes (Cramer et al., 2011), shorter breeding seasons at higher latitudes do generally translate into more synchronous breeding, putatively favouring increased levels of EPP at high latitudes. However, the opposite prediction has also been made, under the assumption that males need to trade-off investment in extra-pair mating and mate guarding (Westneat et al., 1990). Our results are consistent with the latter interpretation of the breeding synchrony hypothesis.

The genetic benefits hypothesis also makes opposing predictions for latitudinal variation of EPP rates. Because genetic diversity is positively correlated with breeding range size (Fan et al., 2019), which in turn increases with latitude (Rapport’s rule), EPP levels are predicted to be higher at high latitudes. However, some studies on birds have shown that genetic diversity is higher at lower latitudes (Chek et al., 2003; Hughes & Hughes, 2007), which predicts higher EPP levels at lower latitudes, a pattern supported by our results (Figure 5).

Pathogen-mediated selection on EPP could also have opposing effects on EPP levels. Because pathogen richness (O’Connor et al., 2018) and virulence (Møller et al., 2009) are higher at lower latitudes, species breeding at low latitudes could have either higher EPP levels if females pursue extra-pair copulations to increase their offspring’s repertoire of immune genes (O’Connor et al., 2018), or lower EPP levels if females avoid extra-pair copulations to minimize exposure to pathogens (Gohli et al., 2013). Our results are consistent with the former prediction.

Last, but not least, the life-history hypothesis predicts high frequencies of EPP in species with fast life histories (Wink & Dyracz, 1999), which occur more frequently at high latitudes (reviewed by Hille & Cooper, 2015). Although we found multiple lines of evidence that species with fast life histories have higher frequencies of EPP (Figure 2), the assemblage-level proportion of EPB and EPO were both negatively associated with latitude (Figure 5). The “pace-of-life” is a complex of traits which, despite their general covariation, can display distinct patterns of geographical variation. For example, basal metabolic rate (Wiersma et al., 2007) and clutch size (Jetz et al., 2008) increase with latitude. However, latitudinal variation in adult survival rate – the strongest predictor of species-level variation in EPP (Figure 2) – is still debated (Gill & Haggerty, 2012; Karl et al., 1990; Peach et al., 2001; Scholer et al., 2020), with a recent analysis showing that it varies primarily among biogeographical regions (Valcu et al., 2014). This further supports the idea that variation in EPP rates between zoogeographical realms is explained by the different life histories of the species breeding there (Figure 4). Although previous studies showed that latitude is correlated with and explains variation in the pace-of-life, comparisons were often made across zoogeographical realms, which could explain differences between populations in the absence of a latitudinal trend (Ricklefs, 1997; Tieleman et al., 2006; Wikelski et al., 2003). We argue that comparisons of life-history traits across zoogeographical realms should be interpreted with caution.

The negative association between the frequency of EPP and absolute latitude was consistent across realms (Figure 5). Zoogeographical realms are not only geographically distinct, but also have independent evolutionary histories (Holt et al., 2013) and lineage diversification rates (Jetz et al., 2012), and can therefore be considered independent “evolutionary replicates” (Delhey et al., 2019; Friedman & Remes, 2016). Our results thus show a robust association between assemblage-level EPP and latitude, consistent across realms, despite different evolutionary processes that might have shaped avian life histories in response to specific environmental and ecological conditions in each zoogeographical realm.

Several of the mechanisms proposed to explain latitudinal variation in EPP rates can be extended to altitude (Table S1). Until now, evidence for altitudinal variation in EPP rates is only available within species. A study on Emberizidae showed that the proportion of EPB is negatively correlated with the altitude of the population (Bonier et al., 2014). Although the negative correlation between the population-level frequency of EPP and seasonality (Figure 2) is consistent with the prediction that EPP rates are lower at higher altitudes, there was no support for an altitudinal decline in the assemblage-level EPP rates. The assemblage-level proportions of EPB and EPO did not vary with altitude in most zoogeographical realms, and increased with altitude in the Nearctic and Australian realms (Table S8). It has recently been proposed that high-altitude birds exhibit a combination of life-history traits which are typically associated with either high- or low-latitude breeding birds and thus have a distinct pace-of-life (Boyle et al., 2016; Hille & Cooper, 2015). Our results support this idea, and suggest that the altitudinal and the latitudinal variation in the frequency of EPP are driven by different trade-offs among life-history traits. Overall, there was no support for a consistent pattern of altitudinal variation in assemblage-level EPP rates across zoogeographical realms. A more extensive sampling
across species and populations could help uncover altitudinal patterns of EPP variation in the future.

4.4 | Limitations of the study

Although this is a correlational study which does not allow inference of causality or rigorous hypothesis testing, the results provide useful indications of factors underlying geographical variation in the frequency of EPP and point to further experimental research. As in any comparative analysis, the quality of the output is contingent upon the quantity and quality of the data. While the results presented here are based on the largest nonredundant curated EPP data set compiled to date, the data cover only 4% of the extant species and 47% of the extant avian families (Figure 1 and Supporting Information Data). Our analytical approach accounted for uneven sampling effort, genotyping technique, geographical sampling within the species breeding range, geographical sampling among zoogeographical realms and phylogenetic representation of the populations in the data set. However, due to the limited number of species represented in the data set, the influence of these factors on the results cannot be completely excluded. Despite the fact that we could identify clear geographical patterns of variation in EPP, a large proportion of variation remains unexplained (Table S8), which could be due to random variation in EPP levels within or between species, or to unaccounted ecological, environmental or life-history factors.

5 | CONCLUSIONS

This study shows that the frequency of EPP covaries with multiple predictors with strong geographical signatures. The frequency of EPP is the product of influences of multiple environmental, ecological and life-history factors and therefore follows a complex pattern of geographical variation. Taken together, our results support the hierarchical explanation for variation in EPP proposed by (Griffith et al., 2002): (1) variation in the frequency of EPP within the breeding range is mostly driven by the population’s breeding synchrony and genetic diversity; (2) differences in EPP rates among species are explained by their life-histories, in particular by longevity; (3) assemblage-level EPP variation occurs primarily among zoogeographical realms (possibly due to differences in life-history and genetic variation among realms), and along latitude within each realm (possibly due to latitudinal variation in breeding synchrony or genetic diversity). In the future, we expect that an increasing availability of EPP estimates will allow a more detailed and accurate description of the geographical variation in the occurrence and frequency of EPP. Until then, the results of our study can guide and inspire further experimental work to test the hypotheses which are given support here.

ACKNOWLEDGEMENTS

We thank Katja Temnow and Anne Rutten for collection of preliminary data, and Wolfgang Forstmeier and Kaspar Delhey for comments on an earlier version of the manuscript. The comments of four anonymous reviewers have helped improve the manuscript. Ginger Bolen, Susan Urbanek Linville, Valérie Ducret, Jörn Theuerkauf,Graeme Buchanan, Matthew Evans, Joanna Rutkowska, Lucyna Halupka and EstebanBotero Delgadillo have kindly provided additional information on their published studies.

AUTHOR CONTRIBUTIONS

Mihai Valcu and Bart Kempenaers conceived the study, Cristina-Maria Valcu and Mihai Valcu collected the data, Mihai Valcu and Cristina-Maria Valcu analysed the data. Cristina-Maria Valcu and Bart Kempenaers wrote the manuscript with input from Mihai Valcu.

DATA AVAILABILITY STATEMENT

Data and scripts have been made available at https://osf.io/rhgez/.

ORCID

Cristina-Maria Valcu  https://orcid.org/0000-0002-3336-6979
Mihai Valcu  https://orcid.org/0000-0002-6907-7802
Bart Kempenaers  https://orcid.org/0000-0002-7505-5458

REFERENCES

Albrecht, T., Schnitzer, J., Kreisinger, J., Exnerová, A., Bryja, J., & Munclinger, P. (2007). Extrapair paternity and the opportunity for sexual selection in long-distance migratory passerines. Behavioral Ecology, 18(2), 477–486. https://doi.org/10.1093/beheco/arm001.
Arnold, K. E., & Owens, I. P. (2002). Extra-pair paternity and egg dumping in birds: life history, parental care and the risk of retaliation. Proceedings of the Royal Society of London B: Biological Sciences, 269(1497), 1263–1269.
Ashton, K. G. (2002). Patterns of within-species body size variation of birds: strong evidence for Bergmann’s rule. Global Ecology and Biogeography, 11(6), 505–523. https://doi.org/10.1046/j.1466-822X.2002.00313.x.
Beauchamp, G. (2021). Do avian species survive better on islands? Biology Letters, 17(1), 20200643. https://doi.org/10.1098/rsbl.2020.0643.
Birch, C. P., Oom, S. P., & Beecham, J. A. (2007). Rectangular and hexagonal grids used for observation, experiment and simulation in ecology. Ecological Modelling, 206(3–4), 347–359. https://doi.org/10.1016/j.ecolmodel.2007.03.041.
BirdLife International (2017). BirdLife International and handbook of the birds of the world (2017) Bird species distribution maps of the world. Retrieved from http://datazone.birdlife.org/species.
BirdLife International (2020). BirdLife International and handbook of the birds of the world (2020) Bird species distribution maps of the world. Retrieved from http://datazone.birdlife.org/species.
Blomberg, S. P., & Garland, T. Jr (2002). Tempo and mode in evolution: phylogenetic inertia, adaptation and comparative methods. Journal of Evolutionary Biology, 15(6), 899–910. https://doi.org/10.1046/j.1420-9101.2002.00472.x.
Bonier, F., Eikenaar, C., Martin, P. R., & Moore, I. T. J. T. A. N. (2014). Extrapair paternity rates vary with latitude and elevation in Emberizid sparrows. American Naturalist, 183(1), 54–61. https://doi.org/10.1086/674130.
Botero, C. A., & Rubenstein, D. R. (2012). Fluctuating environments, sexual selection and the evolution of flexible mate choice in birds. PLoS One, 7(2), e32311. https://doi.org/10.1371/journal.pone.0032311.
