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Late Quaternary range dynamics in the Common Grackle *Quiscalus quiscula*

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Climate variability is one of the most important forces affecting the distributional range dynamics of species and consequentially plays a significant role in shaping biogeographic patterns. This study aims to infer the role of climate in the recent evolutionary history of the Common Grackle *Quiscalus quiscula*. Studies of other migratory North American birds have shown that their populations were isolated in two or three refugia in southern North America during the Last Glacial Maximum (LGM). In contrast, preliminary genetic work suggests that Common Grackles may have occupied a single refugium during that time. They subsequently became widespread and northern populations evolved highly migratory behaviour. We used an ecological niche modelling approach that involved the use of three general climate models for the past (the LGM, approximately 22,000 years before present) and for present environmental conditions to identify climatically stable areas. Extrapolations to the past showed contraction to a large continuous refugium located in the southern part of North America, and projection to the present showed expansion that covers much of eastern and middle North America. The most important bioclimatic variable for model predictions was annual mean temperature, which explained 74% of the variation in the model. Results suggest that the Common Grackle has expanded its distributional range by more than 300% after the LGM.

Key words: climate change, ecological niche modelling, range shift, historical biogeography

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The distribution of species has been greatly influenced by changes in global climate. Notably, in the northern hemisphere, glacial cycles have major effects on the geographic distributions of species and therefore on their genetic diversity (Hewitt 1996, 1999). During the late Quaternary, the distributions of many species in temperate regions in the Nearctic and Western Palearctic were fragmented which caused a reconfiguration of patterns of genetic diversity in isolated geographical areas. These areas were climatically favourable and have been described as refugia (Stewart *et al.* 2010). To identify these refugia in temperate regions and to understand their consequences, the effect of past climate change on the geographic patterns of genetic diversity of various species have been studied. Evidence suggests that refugia permitted the persistence of isolated populations during unfavourable conditions, allowed allopatric differentiation and later acted as centres of range expansion (Bennett & Provan 2008, Schmitt & Varga 2012).

Birds are good model organisms for examining how past climates have affected current diversity and distributions; most species breeding in the northern hemisphere migrate south in winter and a large amount of occurrence data is available (www.ebird.org) to researchers. North American species such as the Hairy

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Adult male 'bronzed' form of Common Grackle *Quiscalus quiscula versicolor* (photo Sharon Dorsey, Massapequa Preserve, Nassau County, New York, USA, February 2019).

Woodpecker *Picoides villosus*, Barred Owl *Strix varia*, Red-shouldered Hawk *Buteo lineatus* and Red-bellied Woodpecker *Melanerpes carolinus*, have been studied in terms of their historical biogeography using both ecological niche modelling and phylogeography (Klicka *et al.* 2011, Barrowclough *et al.* 2011, 2018, 2019, Wauchope *et al.* 2017). Range expansion and the development of migration patterns in two Holarctic breeding scolopacids, Dunlin *Calidris alpina* and Red Knot *C. canutus* have also been examined (Wenink *et al.* 1996, Buehler *et al.* 2006). Hence, expansion-contraction patterns of North American and Eurasian bird species have been well documented. Nevertheless, uncertainties remain in our understanding of how past climates have resulted in the current distribution, migratory status and population differentiation observed in many common species today. The Common Grackle *Quiscalus quiscula* provides a particularly useful system to examine these questions due to their ubiquity, population differentiation and historic interest as a model species.

Common Grackles are large (28–34 cm) New World blackbirds (Icteridae) with iridescent plumage. East of the Rocky Mountains, their breeding range extends from British Columbia east to Nova Scotia and Newfoundland and south along the Atlantic Coast to the Florida Keys (Coues 1894, Bent 1958, Peterson 1980, Starzomski 2015). From the south-eastern Gulf Coast, their range continues into Texas and New Mexico, and north to Colorado, Utah, Nevada, Idaho and Montana. Common Grackles are permanent residents in much of their range, but northern birds migrate, often in huge flocks, to overwinter in the south-eastern United States (see Figure 1). The species has declined over the last several decades but is still abundant, with an estimated current population of 69,000,000 individuals (Bird Life International 2018). The literature suggests that the species increased in number and expanded its range after the mass clearing of forests in North America for agriculture (Peer & Bollinger 1997). They prefer wet areas of open and cultivated country and are comfort-

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able in suburban yards and parks. Nests can be found in loose colonies or singly in low shrubs, shade trees, tall conifer stands and sometimes in eaves or holes in abandoned human structures. The breeding season begins around mid-March in southern portions of the range and late-March to mid-April in northern regions (Baicich & Harrison 1997).

The Common Grackle is considered a single polymorphic species (Dickinson & Christidis 2014). Three forms (subspecies) are recognized: Bronzed Grackle *Q. q. versicolor*, Purple Grackle *Q. q. stonei* and Florida Grackle *Q. q. quiscula* (Figure 3). The Florida form is a year-round resident throughout its range (Peer & Bollinger 1997). *Versicolor* and *stonei* meet along a line running along the Eastern Continental Divide of the Appalachian Mountains. From Louisiana to Connecticut they hybridize and produce offspring with a mix of colour characteristics referred to as 'Ridgway's Grackle' (Chapman 1924; see Figure 4). Chapman (1935) proposed that differentiation in Common Grackles was accomplished when an ancestral form (most likely the Florida Grackle) was separated into isolated populations in southern refugia after the last ice age. This was prescient of Chapman; subsequent studies have shown that several avian taxa became morphologically dissimilar by this process (Rand 1948, Mengel 1964, Lira-Noriega & Manthey 2013). However, this hypothesis has not been tested in the Common Grackle.

In addition to morphometric studies of this species conducted since Chapman's work, Powell *et al.* (2008) used mtDNA to infer relationships at the species level in *Quiscalus*. The Common Crackle was the model species

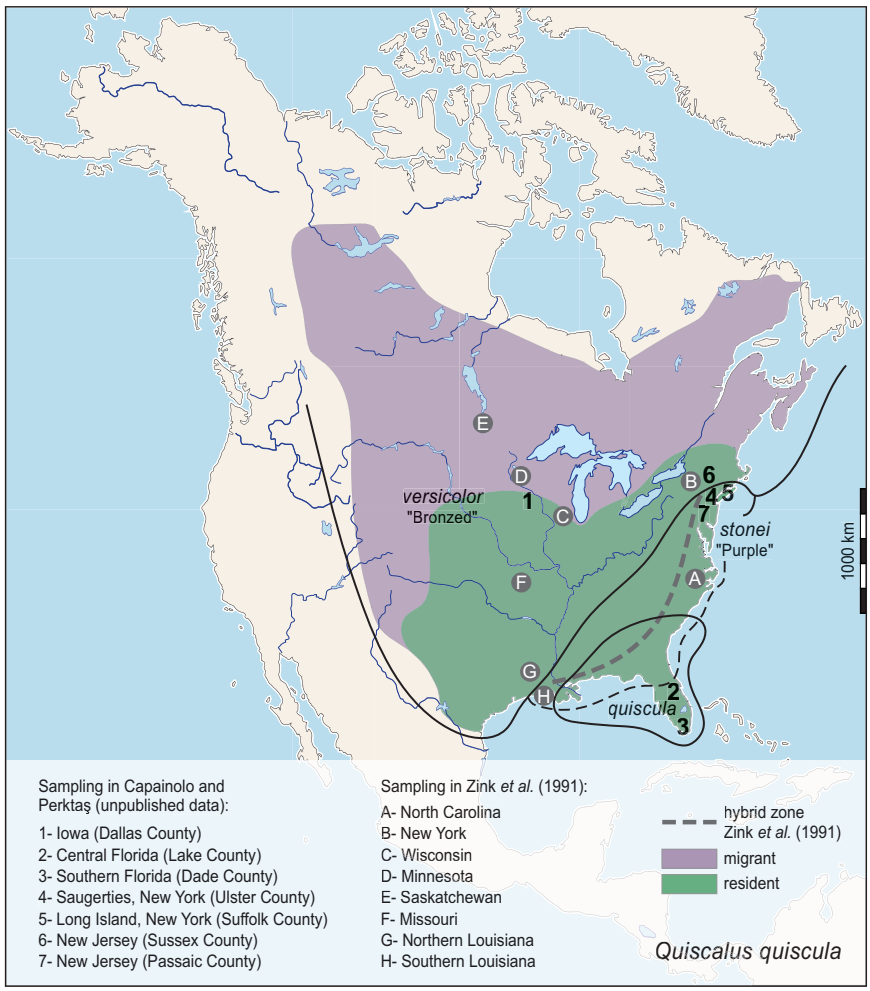


Figure 1. Distribution range of the Common Grackle in North America. Approximate boundaries of three subspecies are indicated based on Bent (1958) and Jaramillo & Burke (1999). Line and black dots show hybrid zones and sampling sites respectively in Zink *et al.* (1991). Numbers indicate our specimen collection sites that cover one region missing in Zink *et al.* (1991).

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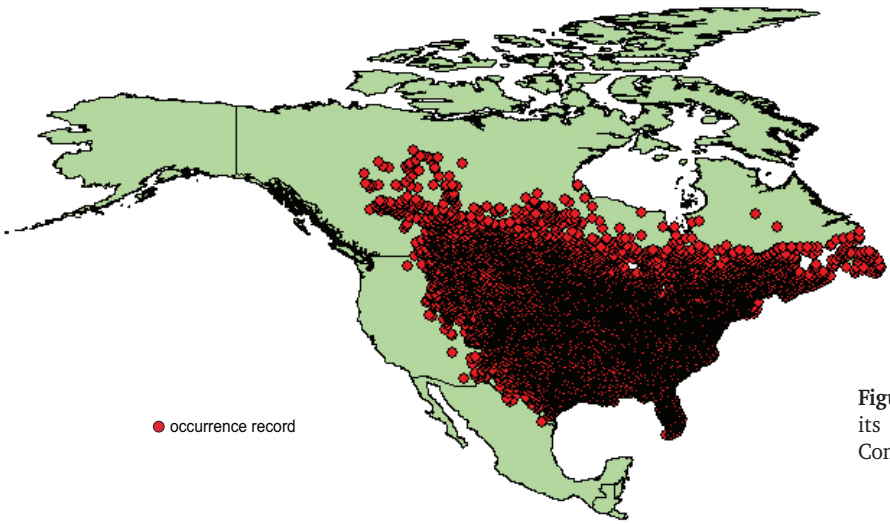


Figure 2. Species occurrence data and its distribution in the range of the Common Grackle.

used for assessing variation, population structure and evolution by Zink *et al.* (1991). Genetic work has focused on a small number of loci or an analysis of family and generic relationships, not species level systematics (Lanyon & Omland 1999, Powell *et al.* 2008, Remsen *et al.* 2016). Our preliminary mtDNA analysis (Capainolo & Perktaş unpubl. data) revealed no concordant pattern between morphology and genetic variation, although the Common Grackle shows substantial morphological variation within its range. This means subspecies are not geographically isolated from one another due to lack of isolating mechanisms such as geographical barriers or rapid population expansion. We tested this hypothesis, and our preliminary mtDNA data showed no structure in the current distribution range. In cases where morphological discontinuity is due to high gene flow, rapid adaptation and/or rapid population expansion, discordance may



Figure 3. Dorsal view of three subspecies of Common Grackle. Breeding males left to right: Bronzed Grackle *Q. q. versicolor*, Purple Grackle *Q. q. stonei*, Florida Grackle *Q. q. quiscula* (photo Peter Capainolo).



Figure 4. Dorsal view of parental and hybrid forms of Common Grackle. Breeding males left to right: Bronzed Grackle *Q. q. versicolor*, Purple Grackle *Q. q. stonei* and hybrid 'Ridgway's Grackle' (photo Peter Capainolo).

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be expected between patterns inferred from morphological variation and those inferred using neutral genetic markers (e.g. mtDNA). Various studies have proposed such patterns for Common Crossbill *Loxia curvirostra* (Questiau *et al.* 1999), Song Sparrow *Melospiza melodia* (Zink & Ditmann 1993) and for the Australian Magpie *Gymnorhina tibicen* (Toon *et al.* 2003). In this study we return to Chapman's original hypothesis and examine the distributional range dynamics of the Common Grackle during the late Quaternary. Using an ecological niche modelling approach, we tested whether this species followed an expansion-contraction pattern in its biogeographic history.

METHODS

Species occurrence data were obtained from eBird (www.ebird.org; Figure 2). Only breeding records between April and July of 2000–2019 were included ($n > 4$ million). We considered sampling bias and spatial autocorrelation (Brown 2014) for occurrence records and filtered all records by eye for particularly unusual, unlikely or spurious sightings. These types of artefacts were removed from the dataset. Occurrence records were spatially filtered within 25 km distances to remove duplicates. In total, 9804 occurrence records were obtained for ecological niche modelling after filtering. Bioclimatic data from WorldClim (Hijmans *et al.* 2005, www.worldclim.org) were obtained for the Present and LGM (approximately 22,000 years before present) for three global climate models (CCSM4, MIROC-ESM and MPI-ESM-P) at a spatial resolution of 2.5 arc-minutes. Bioclimatic data included 19 bioclimatic variables derived from monthly temperature and precipitation values. Since Common Grackles are widespread and migratory in North America, all these variables were masked to include only –170° to 13°W and –50° to 84°N. The following analyses were conducted for ecological niche modelling: (1) we checked the correlation among the variables and made two different climatic data sets based on different correlation coefficients (0.8 and 0.9) among bioclimatic variables, (2) applying a 200-km buffer zone, we described the M-area based on breeding dispersal distance of Common Grackles, (3) we used the kuenm package (Cobos *et al.* 2019) in R v. 3.5.0 (R Core Team 2018) with the maximum entropy machine learning algorithm in MaxEnt v. 3.4.0 (Phillips *et al.* 2006, Elith *et al.* 2009) to model ecological niches of the Common Grackle for bioclimatic conditions of the two time frames.

We ran MaxEnt with different regularization multipliers (0.1, 0.2, 0.5, 1, 2, 5, 8, 10) and five different feature types, linear (L), quadratic (Q), product (P), threshold (T) and hinge (H), with 29 combinations of these feature types for model calibration, and produced different candidate models for each regularization multipliers and feature type combinations. Using the R package 'kuenm', we evaluated all possible candidate models and selected the best one using the Akaike Information Criterion corrected for small sample sizes (AIC_c; Hurvich & Tsai 1989), performed significance tests using partial ROC (Peterson *et al.* 2008), and evaluated performance using a 5% training presence threshold to evaluate omission (Peterson *et al.* 2011) for two different climatic data sets. We chose the best calibration based on these three different statistics (AIC_c, ROC and omission rate) and ran MaxEnt to produce the final models with ten replicates and bootstrap run type. Model outputs were converted to binary predictions using 10% training presence threshold (Perktaş *et al.* 2017) and we visualised the models in ArcGIS v. 10.2.2.

RESULTS

A total of 464 candidate models, with parameters reflecting all combinations of 8 regularization multiplier settings, 29 feature class combinations and 2 distinct sets of environmental variables, were evaluated. Results showed that the best performing model (among 180 statistically important models) was using a linear feature type with 0.1 regularization multiplier based on statistical significance (Partial ROC), omission rates (OR) and the AIC_c. The average training AUC for the replicate runs was 0.638 and the standard deviation was 0.001. Since AUC was larger than 0.6, model predictions were better than random predictions, that is, the model was significant for distributional predictions for the Common Grackle. In addition, the small SDs for the mean AUCs suggested that the model performance was robust to variation in the selection of the occurrence records for training. The final models showed that BIO1 (Annual Mean Temperature) is the most important variable for ecological niche modelling predictions for the Common Grackle as follows: BIO1 (Annual Mean Temperature) 74.4%, BIO2 (Mean Diurnal Range) 8.6%, BIO4 (Temperature Seasonality) 7.4%, BIO12 (Annual Precipitation) 4.4%, BIO8 (Mean Temperature of Wettest Quarter) 3.2% and BIO15 (Precipitation Seasonality) 2.1%.

Under the LGM bioclimatic conditions, areas of relatively high suitability were predicted across southern

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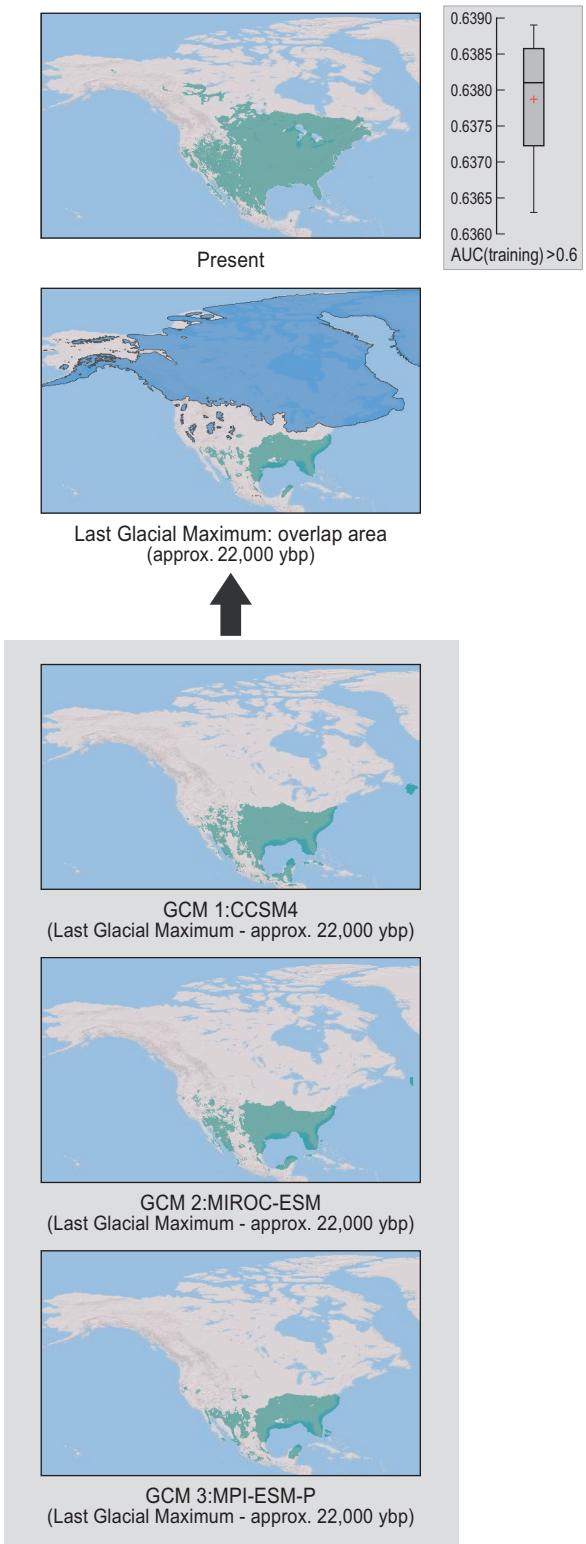


Figure 5. Ecological niche modelling of the Common Grackle during the late Quaternary. The boxplot shows mean AUC value and its standard deviation.

North America (including the Florida peninsula). Three predictions under three Global Climate Models (GCM) simulations were largely similar in this respect and showed substantial contraction (Figure 5). Under present bioclimatic conditions, areas of relatively high suitability were predicted across most of the known distribution of the Common Grackle. However, the model overpredicted the patchy distributions in both northwest and southwest parts of North America (Figure 6). This is most likely to be an effect of recent climate change. The distribution area of Common Grackles during the LGM accounted for about 22% of its present distribution, meaning an expansion of its distribution area by more than 300% after the LGM.

DISCUSSION

This study is an example of ecological niche modelling to test the glacial refugia hypothesis (see Brito 2005, Perktaş *et al.* 2011, Ülker *et al.* 2018, Barrowclough 2019) in a widespread, common bird species. There is clear evidence of a large refugium (small patchy areas to the west may be due to artefacts in the analysis) located in the southern part of the North American continent. Our results suggest that the Common Grackle responded to climate change through late Quaternary glacial-interglacial cycles. This pattern has also been found for other temperate bird species in North America (Avise & Zink 1988, Ball *et al.* 1988, Zink 1991, Zink 1996, Zink *et al.* 2002, 2008, Pulgarín-R & Burg 2012, Williford *et al.* 2014, 2016, Barrowclough *et al.* 2019).

Our ecological niche modelling prediction for the present distribution of the Common Grackle was largely concordant with its known distribution. This is an important assumption for the confidence of ecological niche modelling results (Nogués-Bravo 2009). It demonstrates the species-climate equilibrium of the ecological niche of the Common Grackle based on bioclimatic data. Therefore, it is plausible to say that the Common Grackle-climate equilibrium is valid.

A noteworthy part of this study is that we found one large contiguous refugium for this species, rather than separated refugia during the LGM. Separated refugia have been a common biogeographic pattern for widespread North American migratory birds such as the Swainson's Thrush *Catharus ustulatus*, Chipping Sparrow *Spizella passerina* and Yellow-throated Warbler *Setophaga dominica* (Ruegg *et al.* 2006, Mila *et al.* 2006, McKay 2009). These species appear to have survived through the Quaternary glaciations in eastern

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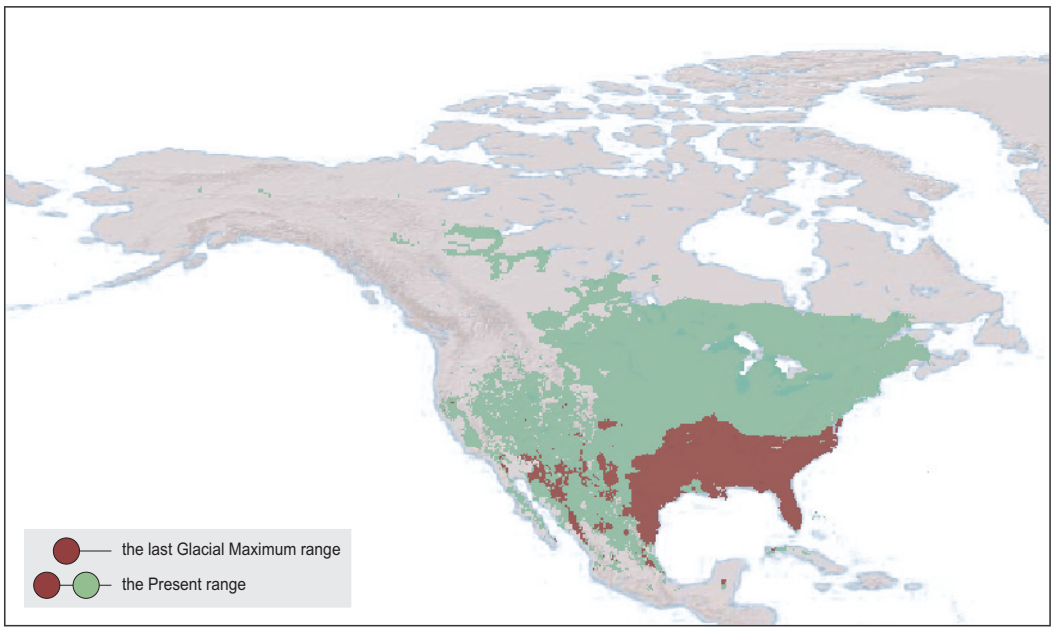


Figure 6. Range shift of Common Grackle from the LGM to the Present. The projections show 10 percentile training presence logistic threshold results. Predicted species range is in green.

and western refugia (Colbeck *et al.* 2008, see also Zink 1996).

However, Common Grackles have substantial amounts of morphological variation within the species, particularly in colours of the head, back and breast. This suggests that morphological diversification within the Common Grackle occurred within a short time period following a fast expansion event after the LGM. This is because the rate of morphological differentiation exceeds the rate of change of neutral genetic loci (Zink 1991, Zink & Dittmann 1993). This happens quickly if the species experiences recent and rapid demographic expansion in its distribution range (see Perktaş & Elverici 2019). This situation seems likely for the Common Grackle because our preliminary mitochondrial DNA analysis (Capainolo & Perktaş unpubl. data) shows that genetic diversity is relatively high in populations located in Florida and lower in northern regions. Zink *et al.* (1991) also indicated recent demographic expansion for the Common Grackle based on mitochondrial DNA data and restriction fragment analysis. Thus, it is plausible that mitochondrial phylogeography, in terms of demographic history of this taxon, matches the ecological niche modelling results in this study, but this remains to be tested with samples from additional locations and more DNA markers for the Common Grackle in the future.

A combination of several bioclimatic variables was important in the ecological niche modelling for the species, but one of them, annual mean temperature, was the most important. The model predictions were tested based on four different statistics (i.e. omission rate, AICc, AUC and partial ROC), and predictions were better than random. Therefore, we suggest that migratory behaviour in this temperature sensitive species evolved after its last expansion event, that is, after its demographic expansion following the LGM (see Zink 2011). A similar pattern is seen in the Chipping Sparrow. Mila *et al.* (2006) suggested that migratory behaviour in this species evolved from a sedentary ancestor located in the southern part of its distribution range. Although this suggestion was criticized by Zink (2011), we found a similar pattern for Common Grackle. Our results indicate that an ancestral form from the resident range of the Common Grackle colonized its present distribution range.

Morphological variation within the Common Grackle also supports this suggestion, because body size variation in this species shows clinal variation, which is a sign of natural selection and adaptation after the LGM (Huntington 1952, Rand 1961, Ashton 2002). In addition, different colour morphs usually indicate different subspecies within the species. The boundaries of these subspecies look arbitrary in terms of patterns of

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morphological differences and genetics; only the nominate form, *Q. q. quscula*, looks valid as a subspecies due to its size, distribution and resident behaviour in southern regions of North America (Bent 1958, Jaramillo & Burke 1999). This evidence, together with low mtDNA variation in the north and high variation in the south (Capainolo & Perktaş unpubl. data), supports our preliminary hypothesis, that the Common Grackle extended its range from a southern sedentary ancestor into northern regions that at present precipitate migratory behaviour due to cold winters. Therefore, Common Grackles had shallow mtDNA diversification with large areas of genetically homogeneous populations (see Zink *et al.* 1991, Capainolo & Perktaş unpubl. data), showed rapid range expansion from a single big glacial refugium and follow a simplified example of a refugia ('R') type species (Recuero & Garcia-Paris 2011).

In this study, we focused on late Quaternary range dynamics of the Common Grackle, and our work suggests that past climate change initiated a rapid northward expansion of the ancestral form. This work leads to the predictions that populations of Common Grackle are expected to show (1) low genetic variability, such as minimal levels of mtDNA divergence and (2) signs of a recent demographic expansion and rapid morphological diversification, particularly after the LGM. The Common Grackle, largely ignored as a species of interest regarding North American biogeography but representative of a widespread and ecologically important taxon, is certainly worth further investigation.

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SAMENVATTING

De areaalgrenzen van vogels veranderen geregeld in de loop van de tijd, onder andere onder invloed van klimaatverandering. In dit onderzoek wordt geprobeerd de rol van klimaatverandering in de verspreidingsgeschiedenis van de Glanstroepiaal *Quiscalus quiscula*, een algemene soort uit de familie van de Noord-Amerikaanse Icteridae, te achterhalen. Veel Noord-Amerikaanse vogelsoorten hebben zich op de piek van de laatste IJstijd (zo'n 22.000 jaar geleden) tot twee of drie zuidelijke gebieden (refugia) teruggetrokken. Op grond van ongepubliceerd genetisch onderzoek is het waarschijnlijk dat de Glanstroepiaal destijds maar één refugium heeft gehad en zich daarna over een groot deel van Noord-Amerika heeft verspreid (waarbij de noordelijke populaties zich tot trekvogel hebben ontwikkeld). Met behulp van 'ecological niche modelling' is op basis van drie klimaatmodellen en uitgaande van de huidige situatie de verspreiding tot aan de piek van de laatste IJstijd gereconstrueerd. Uit het onderzoek blijkt dat dat de soort zich in het verleden inderdaad heeft teruggetrokken tot één groot doorlopend gebied in het zuiden van Noord-Amerika en dat zij zich daarna over een groot deel van het midden en oosten van het continent heeft verspreid. De jaarlijkse gemiddelde temperatuur bleek de belangrijkste variabele in de modelberekeningen. Deze variabele verklaarde 74% van de variatie in het model. Na de piek van de laatste IJstijd heeft de Glanstroepiaal, parallel aan de opwarming van de aarde, zijn verspreidingsgebied met waarschijnlijk meer dan 300% kunnen uitbreiden.

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