Recent postglacial range expansion drives the rapid diversification of a songbird lineage in the genus *Junco*

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Pleistocene glacial cycles are thought to have played a major role in the diversification of temperate and boreal species of North American birds. Given that coalescence times between sister taxa typically range from 0.1 to 2.0 Myr, it has been assumed that diversification occurred as populations were isolated in refugia over long periods of time, probably spanning one to several full glacial cycles. In contrast, the rapid postglacial range expansions and recolonization of northern latitudes following glacial maxima have received less attention as potential promoters of speciation. Here we report a case of extremely rapid diversification in the songbird genus *Junco* as a result of a single continent-wide range expansion within the last 10 000 years. Molecular data from 264 juncos sampled throughout their range reveal that as the yellow-eyed junco (*Junco phaeonotus*) of Mesoamerica expanded northward following the last glacial maximum, it speciated into the dark-eyed junco (*Junco hyemalis*), which subsequently diversified itself into at least five markedly distinct and geographically structured morphotypes in the USA and Canada. Patterns of low genetic structure and diversity in mitochondrial DNA and amplified fragment length polymorphism loci found in dark-eyed juncos relative to Mesoamerican yellow-eyed juncos provide support for the hypothesis of an expansion from the south, followed by rapid diversification in the north. These results underscore the role of postglacial expansions in promoting diversification and speciation through a mechanism that represents an alternative to traditional modes of Pleistocene speciation.

**Keywords:** speciation; postglacial expansion; phylogeography; Holocene; *Junco*

1. INTRODUCTION

Range expansions and colonization of new areas following glacial periods have resulted in some of the most remarkable radiations known in vertebrates (Schluter 2000; Coyne & Orr 2004). In North America, isolation of populations in refugia during Pleistocene glacial cycles is thought to have been largely responsible for the most recent speciation events in birds (Johnson & Cicero 2004; Weir & Schluter 2004), though the overall importance of the Pleistocene relative to older periods remains a topic of considerable debate (Klicka & Zink 1997; Avise & Walker 1998; Zink et al. 2004).

Bird populations underwent rapid continent-wide expansions following glacial maxima as ice sheets receded and climatic amelioration allowed the recolonization of northern latitudes, a process documented for a number of bird species as well as numerous other animal and plant taxa since the last glacial maximum (LGM) 18 000 years ago (Taberlet et al. 1998; Lessa et al. 2003; Hewitt 2004). In birds, intraspecific tests of this ‘postglacial expansion hypothesis’ have documented patterns of low genetic diversity and structure in temperate and boreal populations relative to southern temperate and subtropical populations, demonstrating that the lack of genetic structure is due to shared ancestral polymorphism rather than gene flow (Milá et al. 2006; Ruegg et al. 2006).

Given that genetic distances between sister avian taxa generally correspond to divergence times ranging from 0.1 to 2 Myr (Klicka & Zink 1997; Johnson & Cicero 2004; Weir & Schluter 2007), it has been traditionally assumed that speciation took place in isolated refugia over one to several full glacial cycles (Mengel 1964; Hubbard 1973; Zink & Klicka 2006). The role of postglacial expansions themselves in driving speciation has received much less attention. Since continent-wide range expansions would subject advancing populations to a wide variety of unoccupied habitats with varying selective regimes, relatively short periods of isolation as new areas are colonized could potentially suffice to drive diversification in comparatively short periods of time. Considering that avian postglacial expansions are as short as a few 1000 years (Milá et al. 2006), and that this scenario does not invoke the need for long-term isolation in refugia, the postglacial expansion hypothesis poses an alternative to traditional modes of Pleistocene speciation.

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2. MATERIAL AND METHODS

(a) Taxonomy of the study group

The genus Junco is currently composed of three species—the dark-eyed junco J. hyemalis, the yellow-eyed junco J. phaeonotus and the volcano junco Junco vulcani—although the actual number of species comprised in the dark-eyed junco complex remains a matter of debate (Nolan et al. 2002). The complex comprises at least five well-differentiated, largely allopatric morphotypes that differ prominently in plumage, beak colour and morphology (Miller 1941; Nolan et al. 2002). Formerly considered species (slate-coloured junco J. hyemalis, white-winged junco Junco aikeni, Oregon junco Junco oreganus, grey-headed junco J. phaeonotus and the Guadalupe island junco J. insularis), these five forms were recently lumped to form the dark-eyed junco (J. hyemalis; American Ornithologists’ Union 1973), though their assignment as subspecific ‘groups’ was intended to reflect the marked phenotypic differentiation between them, their allopatric breeding distributions and the stability of hybrid zones that exist between some groups (Nolan et al. 2002). In a recent monograph on the complex, Nolan et al. (2002) assert that with further investigation, the group is likely to be split again into multiple species. Indeed, a recent study on speciation times in birds has already considered two of the dark-eyed junco groups (J. oreganus and J. caniceps) as species based on evidence for lack of interbreeding when found in sympatry at some localities (Johnson & Cicero 2004). The yellow-eyed junco (J. phaeonotus) has been taxonomically stable and is composed of four different subspecies (phaeonotus, paliatus, fulvescens and alticola; Sullivan 1999). Finally, the volcano junco (J. vulcani) of southern Central America is considered a distant relative of other juncos and is included as an out-group for comparison. Given the unresolved status of Junco taxonomy, the number of species comprised by the genus ranges from a minimum of three to as many as seven. For consistency, we follow current...
nomenclature which considers the genus to be composed of three species (dark-eyed, yellow-eyed and volcano juncos) and examine individuals from six dark-eyed junco morphotypes (slate-coloured \textit{Junco hyemalis} hyemalis, white-winged \textit{Junco hyemalis} aikeni, Oregon \textit{Junco hyemalis} oreganus, pink-sided \textit{Junco hyemalis} mearnsi, grey-headed \textit{Junco hyemalis} caniceps and red-backed \textit{Junco hyemalis} dorsalis), referred to here collectively as the ‘dark-eyed junco complex’, and from three of the four described subspecies of the yellow-eyed junco (\textit{phaeonotus}, palliatus and alticola).

(b) Sampling and mtDNA sequencing

Individuals were captured in the field using mist nets, and blood and/or feather samples were collected for genetic analysis. Three digital images of each individual were taken as photographic vouchers. Sampling localities, preceded by sampling and mtDNA sequencing

elapsing between the origin of a new lineage and the next diversification interval (NDI), defined as the average time between initial and current population sizes and time to the most recent common ancestor (TMRCA). We assumed uniform priors and set the two populations and time to the most recent common ancestor and $N_t$; where $N_t$ is the resulting number of species (Coyne & Orr 2004). We calculated NDIs using $N_t$, 2 and 5, and the time divergence values obtained from Mdv using the three mutation rates described above. An $N_t$ of 5 would correspond to the yellow-eyed junco and a minimum number of dark-eyed forms (grey-headed, Oregon, slate-coloured and white-winged), and an $N_t$ of 2 would make our diversification rate estimates even faster.

We also estimated diversification time with a coalescence-based model that generates non-equilibrium estimates of divergence time independent of gene migration (Nielsen & Wakeley 2001). We used Markov chain Monte Carlo simulations with the program MDIV (Nielsen & Wakeley 2001), which generates maximum likelihood estimates of substitutions per site Myr$^{-1}$; Lambert et al. 2002) or geese (0.21 substitutions per site Myr$^{-1}$; Quinn 1992), would make our diversification rate estimates even faster.

We ran four Markov chains of 4 000 000 cycles with different random seeds, each preceded by a 'burn-in' period of 500 000 cycles. Estimates of $T$ and TMRCA were converted to years using $t=(T/2\mu)$; and $t$MRA= TMRCA $\theta/2\mu k$; where $T$ and $\theta$ are generated by the program; $\mu$ is the marker-specific mutation rate; and $k$ is the length of the sequence. We assumed a generation time of 1 year (Nolan et al. 2002) and used the three mutation rates mentioned above.

A third estimate of diversification time was obtained from the distribution of pairwise nucleotide differences among individuals (Rogers & Harpending 1992) of pooled dark-eyed junco samples. To estimate the time since the beginning of an expansion, we used $\tau = 2\mu i$; where $\mu$ is the time elapsed between initial and current population sizes and $\mu = 2\mu k$; where $\mu$ is the mutation rate and $k$ is the length of the sequence (Rogers & Harpending 1992).

We used estimates of divergence time to calculate the net diversification interval (NDI), defined as the average time elapsing between the origin of a new lineage and the next branching of that lineage (assuming no extinction). NDI is defined as $t/\ln N_t$; where $t$ is the time to a single common ancestor and $N_t$ is the resulting number of species (Coyne & Orr 2004).

### Table 1. Genetic diversity in the mtDNA CR and population expansion in Junco. (**p < 0.0001; *p < 0.01; n.s.: p > 0.05; n.a.: not applicable as only one haplotype was found.)

<table>
<thead>
<tr>
<th>taxon</th>
<th>$n$</th>
<th>haplotypes (number)</th>
<th>$h^a$</th>
<th>$p^b$</th>
<th>$F_i^c$</th>
</tr>
</thead>
<tbody>
<tr>
<td>dark-eyed junco (Junco hyemalis)</td>
<td>102</td>
<td>A(39), B(3), H(2), M(3), N(2), Q(1)</td>
<td>0.2722 ± 0.0584</td>
<td>0.0008 ± 0.0009</td>
<td>−12.219***</td>
</tr>
<tr>
<td>Oregon junco (J. h. oreganus)</td>
<td>50</td>
<td>A(25), O(1), P(1), R(1)</td>
<td>0.3886 ± 0.1003</td>
<td>0.0012 ± 0.0013</td>
<td>−3.832***</td>
</tr>
<tr>
<td>pink-sided junco (J. h. meanasi)</td>
<td>5</td>
<td>A(5)</td>
<td>0.0000 ± 0.0000</td>
<td>0.0000 ± 0.0000</td>
<td>n.a.</td>
</tr>
<tr>
<td>slate-coloured junco (J. h. hyemalis)</td>
<td>28</td>
<td>A(6), O(1), P(1), R(1)</td>
<td>0.2063 ± 0.1005</td>
<td>0.0006 ± 0.0008</td>
<td>−3.266***</td>
</tr>
<tr>
<td>white-winged junco (J. h. aikeni)</td>
<td>6</td>
<td>A(6)</td>
<td>0.0000 ± 0.0000</td>
<td>0.0000 ± 0.0000</td>
<td>n.a.</td>
</tr>
<tr>
<td>grey-headed junco (J. h. caniceps)</td>
<td>7</td>
<td>A(6), I(1)</td>
<td>0.2857 ± 0.1964</td>
<td>0.0008 ± 0.0011</td>
<td>−0.095 n.s.</td>
</tr>
<tr>
<td>red-backed junco (J. h. dorsalis)</td>
<td>6</td>
<td>A(6)</td>
<td>0.0000 ± 0.0000</td>
<td>0.0000 ± 0.0000</td>
<td>n.a.</td>
</tr>
<tr>
<td>yellow-eyed junco (J. ph. phaeonotus)</td>
<td>64</td>
<td>A(60), B(1), H(2), F(1)</td>
<td>0.1215 ± 0.0554</td>
<td>0.0004 ± 0.0006</td>
<td>−4.045***</td>
</tr>
<tr>
<td>northern Mexico yellow-eyed junco</td>
<td>6</td>
<td>A(6), B(1), H(2), F(1)</td>
<td>0.6312 ± 0.0330</td>
<td>0.0028 ± 0.0021</td>
<td>−0.850 n.s.</td>
</tr>
<tr>
<td>southern Mexico/Guatemala yellow-eyed junco</td>
<td>96</td>
<td>A(29), B(15), D(1), E(32), G(19)</td>
<td>0.7417 ± 0.0163</td>
<td>0.0040 ± 0.0027</td>
<td>1.497 n.s.</td>
</tr>
<tr>
<td>volcano junco (J. vulcani)</td>
<td>2</td>
<td>S(2)</td>
<td>0.0000 ± 0.0000</td>
<td>0.0000 ± 0.0000</td>
<td>n.a.</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>$a$</th>
<th>Haplotype diversity.</th>
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<td>$b$</td>
<td>Nucleotide diversity.</td>
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<tr>
<td>$c$</td>
<td>Fu’s (14) test of neutrality.</td>
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### 3. RESULTS

#### (a) mtDNA sequence and population expansion analysis

We examined mtDNA CR sequence from 102 individuals of the dark-eyed junco complex, 160 yellow-eyed and 2 volcano juncos. Remarkably, most individuals from all dark-eyed junco morphotypes and most Mexican yellow-eyed juncos share a single mtDNA CR haplotype (A in figure 1c), suggesting a very recent burst of phenotypic diversification. The high frequency of haplotype A and its close relationship to multiple low-frequency haplotypes suggests a sudden and recent population expansion (Avise 2000). Specifically, populations making up the dark-eyed junco complex show low levels of haplotype and nucleotide diversity ($h=0.2722 ± 0.0584$, $\pi=0.0008 ± 0.0009$), a high frequency of ancestral haplotype A, and a large negative $F_i$ value ($F_i=-12.219$, $p<0.0001$; table 1), which are also evidence of a sudden expansion in effective population size. In contrast, yellow-eyed juncos in Mexico and Guatemala show a higher genetic diversity ($h=0.6312 ± 0.0330$, $\pi=0.0028 ± 0.0021$), a lower frequency of haplotype A and a non-significant $F_i$ value ($F_i=-0.085$, $p=0.490$).

A closer examination of patterns of genetic diversity within the yellow-eyed junco reveals an expansion in northern Mexico populations as evidenced by a significant $F_i$ value and low genetic diversity values (due to a high frequency of haplotype A; table 1). Mismatch distributions further suggest a history of expansion in the dark-eyed junco complex and northern Mexican (sites 7–10 in figure 1a) yellow-eyed juncos, in contrast to southern Mexican (sites 4–6) yellow-eyed juncos (see figure S1 in the electronic supplementary material). Indeed, the $F_i$ value between the dark-eyed junco complex and northern Mexico yellow-eyed juncos...
juncos (\(F_{st} = 0.003, p = 0.418\)) was much lower than that between the dark-eyed junco complex and southern Mexico yellow-eyed juncos (\(F_{st} = 0.272, p < 0.001\), table 2). These results suggest that yellow-eyed juncos from southern Mexico expanded through northern Mexico, rapidly diversifying into the various dark-eyed morphotypes after they arrived in temperate North America.

(b) AFLP analysis

A Bayesian analysis of population structure among all individuals using 75 AFLP markers revealed marked genetic similarity and an absence of structure among most dark-eyed junco morphotypes. The optimal number of populations in the assignment probability analysis using STRUCTURE was \(K = 4\) (figure 1b), with the four clusters corresponding broadly to Guatemala (yellow), Mexico (green), the white-winged junco population in the Black Hills and some pink-sided juncos from the nearby Bighorn Mountains (blue) and all remaining dark-eyed junco forms (red).

Also evident in the STRUCTURE results is the gradual pattern of differentiation between yellow-eyed and dark-eyed populations. When individuals are assigned to one of two clusters (\(K = 2\), figure 1b), each one corresponds roughly to yellow-eyed juncos (green) and dark-eyed juncos (red), with average assignment probabilities changing gradually with latitude. Interestingly, red-backed junco individuals (sites 12 and 13 in figure 1a) show similar assignment probabilities to the two clusters as predicted by their intermediate phenotype. For the optimal \(K = 4\) (figure 1b), yellow-eyed individuals from Arizona (site 11) show a higher average assignment probability to the dark-eyed cluster (red colour) than those in southern Mexico (site 5), which show a higher assignment probability to the Guatemalan cluster (yellow colour). This pattern is reflected in the \(F_{st}\) analysis, with values between dark-eyed and northern yellow-eyed juncos being lower than between dark-eyed and southern yellow-eyed juncos (table 2).

(c) Divergence times and diversification rates

The average genetic distance in mtDNA CR between the dark-eyed junco complex and yellow-eyed juncos was 0.019% when corrected for intraspecific polymorphism (Nei 1987). Applying a molecular clock, this value corresponds to divergence times ranging between 1300 and 3800 years BP using mutation rates of 15% Myr\(^{-1}\) and 5% Myr\(^{-1}\), respectively. The non-equilibrium estimates of time divergence between populations obtained with \(N_{st}\) were 2548–7620 years BP, and TMRCA, or the time when genes last shared a common ancestor ranged between 26 764 and 80 028 years. Diversification time obtained from the distribution of pairwise differences among individuals provided comparable time estimates of 4046–11 976 years BP to the time of the population expansion, depending on mutation rate. Using a generation time of 2 years instead of 1 year, which might apply to small passerines with relatively high mortality rates, would double the time divergence estimates above. Finally, NDIs ranged from 0.0109 to 0.0016 Myr, depending on the mutation rate and the number of new taxa (\(N_t\)) considered to have been produced (figure 2).

4. DISCUSSION

Results from the mtDNA analyses provide strong support for a rapid postglacial expansion of the yellow-eyed junco from Mexico into temperate North America, and for a subsequent rapid burst of diversification that gave rise to at least five distinct morphotypes of the dark-eyed junco as expanding populations reached temperate latitudes. An alternative explanation for the genetic pattern found among dark-eyed junco morphotypes is the occurrence of a selective sweep by an adaptive mtDNA haplotype, which could have spread across previously differentiated morphotypes by crossing hybrid zones. The ubiquity of haplotype A in yellow-eyed junco populations (with whom dark-eyed juncos are not known to hybridize), the limited amount of gene flow evident in southern populations (e.g. haplotypes D and E are restricted to central Mexico, and G is restricted to Guatemala, see table 1) and the gradual latitudinal increase in the frequency of ancestral haplotype A, all strongly suggest that the predominance of haplotype A in northern populations reflects shared ancestral polymorphism resulting from a rapid population expansion, and not gene flow (Milà et al. 2006).

However, in order to confidently reject the selective sweep hypothesis, a congruent pattern of low genetic structure and diversity in dark-eyed juncos must be confirmed with unlinked nuclear markers. This is because factors such as bottlenecks and population expansions

| Table 2. Differentiation between dark-eyed and yellow-eyed juncos based on mtDNA CR sequence data (\(F_{st}\)) and AFLP loci (\(F_{st}\) and Weir and Cockerman’s \(\theta\)). Pairwise comparisons of all dark-eyed junco populations combined (DEJU) and yellow-eyed junco populations (northern sites, NYEJU; and southern sites, SYEJU). (**p < 0.001; n.s.: p > 0.05.) |
|-----------------|-----------------|-----------------|
|                | \(F_{st}\)      | \(F_{st}\)      | \(\theta\)      |
| DEJU versus NYEJU | 0.003 n.s.    | 0.129***        | 0.129           |
| (Mex only)      | 0.272***       | 0.200***        | 0.199           |
| DEJU versus SYEJU | 0.193***      | 0.202***        | 0.202           |

Figure 2. Estimates of NDIs in the yellow-eyed and dark-eyed juncos based on mtDNA CR sequence, using three mutation rates (0.15, 0.10 and 0.05 substitutions per site Myr\(^{-1}\)) and three values for the number of diversified taxa (\(N_t\), 2 (filled diamonds), 3 (filled squares) and 5 (filled triangles)).
should affect the entire genome equally, whereas selective sweeps should only be detected in the locus under selection (and tightly linked loci; Galtier et al. 2000). The lack of clear structure in AFLP loci within the dark-eyed junco complex despite marked phenotypic differentiation and considerable geographical distances separating them is congruent with the mtDNA results and supports the hypothesis of rapid diversification following a recent expansion. The differentiation of the white-winged junco population was driven largely by the presence of three nearly diagnostic loci and could be due to founder events and the subsequent fixation of rare alleles in a population of small effective size, although the influence of natural selection cannot be ruled out. The fact that some pink-sided juncos from the nearby Bighorn Mountains of Wyoming and even some Oregon juncos cluster with the white-winged juncos suggests that the alleles involved appeared (or became fixed) in the small Black Hills population and spread west through gene flow across hybrid zones.

Several phenotypic characteristics of juncos are consistent with a history of diversification through a northward expansion from southern forms. The red-backed and grey-headed juncos of Arizona and the southern Rocky Mountains, in particular, are phenotypically intermediate between yellow-eyed and dark-eyed juncos. For example, the loss of the yellow iris in the red-backed junco (otherwise remarkably similar to its yellow-eyed neighbour), and the loss of the bicoloured beak in the grey-headed junco just to the north (figure 1c), appear to represent successive steps in the gradual evolution of dark-eyed forms, which subsequently and rapidly acquired their diverse plumage patterns (often with a prominent increase of eumelanins and phaeomelans). Recent divergence with fast plumage evolution (since the LGM) has been recently documented in Icterus orioles (Baker et al. 2003; Kondo et al. 2004), redpolls (Seutin et al. 1995), bluethroats (Questiaux et al. 1998; Zink et al. 2003), yellow wagtails (Odeén & Björklund 2003) and yellow-rumped warblers (Milá et al. 2007). However, given the higher number and marked distinctiveness of plumage morphs and the short amount of time involved, the dark-eyed junco complex represents an exceptional case of fast plumage diversification.

Large-scale range expansions into formerly glaciated areas following glacial maxima have been reported for numerous animal and plant taxa during the Pleistocene (Hewitt 2000) and speciation during this period is thought to have been driven in part by isolation in glacial refugia (Weir & Schluter 2004). Previous studies on avian speciation rates have shown that coalescence times to the closest common ancestor of extant species pairs are typically in the range of 0.1–2.0 Myr (Avise & Walker 1998; Lovette & Bermingham 1999; Johnson & Cicero 2004; Weir & Schluter 2007) and often pre-date the Pleistocene (Klicka & Zink 1999). In a recent molecular study of 39 sister-species pairs of birds (Johnson & Cicero 2004), only two pairs showed splits younger than 50 000 years (Spizella brevirostris/Spizella tawerner, two weakly differentiated taxa, and Junco oreganus/J. caniceps, two of the taxa in the dark-eyed junco complex examined here). In contrast, our molecular data indicate that diversification of dark-eyed juncos took place within the time span of a single postglacial expansion within the last 10 000 years, as ancestral yellow-eyed junco populations expanded their range through northern Mexico and into temperate North America following the LGM.

The occurrence of hybridization along contact zones between some forms in the dark-eyed junco complex (except for, at least, caniceps/hyemalis, caniceps/aikeni, and insularis), suggests that reproductive isolation between some morphotypes is not yet complete. However, the marked phenotypic differentiation between forms, their largely allopatric distribution, and the fact that most hybrid zones are of limited width and apparently stationary over at least a century (Miller 1941; Nolan et al. 2002), all suggest that dark-eyed junco forms are on distinct evolutionary trajectories and may represent a case of speciation in action. The rate of diversification presented here, even if only two species are considered, is among the fastest observed in vertebrates (Coyne & Orr 2004) and is similar to that reported for the cichlid fish species flock of Lake Nabagabo in East Africa, where five species evolved in less than 4000 years, which is thought to represent the fastest radiation within cichlids (NDI = 0.004 Myr; Coyne & Orr 2004). Because the Junco diversification is so recent, the probability of extinction of new taxa is low, which could account for the unusually low NDI values obtained. Potentially, similarly fast diversification bouts could have taken place in older lineages, yet because only a fraction of the original number of species has survived, speciation rates might be underestimated. However, given that none of the previously studied avian groups show similar recent bouts of diversification, and the fact that several bird taxa show similar signatures of postglacial population expansion over North America yet lack a comparable amount of phenotypic diversification (Ball et al. 1988; Zink & Dittman 1993; Milot et al. 2000; Kimura et al. 2002; Ruegg & Smith 2002; Veit et al. 2005; Milá et al. 2006), the rapid diversification in Junco appears to be exceptional.

Selection-driven evolutionary change can be especially fast in peripheral isolates such as those found at the leading edge of an expansion (Garcia-Ramos 1997; Gavrilets et al. 2000), and given the marked differences in plumage characters, sexual selection may have acted as the mechanism of divergence (Fisher 1930; Lande 1981; Barraclough et al. 1995). Indeed, a recently established Oregon junco population in southern California has evolved marked differences in a sexually selected trait (amount of white on outer tail feathers) after only several generations (Yeh 2004). The relative roles of female choice and male–male competition in the phenotypic divergence of juncos is unclear, although recent research on the slate-coloured junco suggests that both might be involved (McGlothlin et al. 2005). Our results underscore the role of postglacial expansions in driving diversification and speciation, and suggest that the colonization of new areas following glacial periods can lead to exceptionally rapid rates of evolution.

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