Different timing of the adaptive radiations of North American and Asian warblers

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The timing of speciation events among warblers (small insectivorous woodland birds) in the Himalayas of India and in the White Mountains of New Hampshire, USA, is compared. Sequence divergence in the mitochondrial cytochrome *b* gene for 13 New World species in six genera averages 2.6%, which according to standard calibrations places most of the diversification in the early Pleistocene. In contrast, eight Himalayan species in the single genus *Phylloscopus* differ by an average of 10.7% in the same gene sequence. The New Hampshire warblers appear to have undergone a relatively recent burst of speciation and morphological evolution, but there is a detectable slowing of speciation rates (or increase in extinction rates) within the community towards the present. Other North American passerine groups that have been studied show no signs of explosive diversification in the Pleistocene. In these groups, pairs of sister species are often older than the entire warbler radiation. Boreal forest migrated south from very high latitudes towards the end of the Pliocene and this apparently created conditions ripe for explosive diversification among the warblers, but not for many other groups.

Keywords: adaptive radiation; cytochrome *b*; *Dendroica*; *Phylloscopus*; phylogeny; warblers

1. INTRODUCTION

The most spectacular adaptive radiations occur when a species colonizes a relatively complex but unexploited environment (Simpson 1953; Schluter 1996). Multiple ecological opportunities result in the rapid diversification of a single lineage into different species, each of which is adapted to exploit a different part of the resource spectrum. Adaptive radiations such as these require not only the presence of an empty habitat, but also limitations on the number of different species that can colonize that environment from elsewhere. Multiple colonists result in less *in situ* adaptive radiation. In the extreme case, each species in a community is derived from a separate colonization event, and there is no adaptive radiation.

In groups with relatively poor dispersal, notably fish in lakes and lizards on islands, adaptive radiation is the frequent result of the appearance of a new lake or island (Schluter & MacPhail 1993; Schluter 1996; Losos *et al.* 1998). In groups with much better dispersal, such as land birds on continents, adaptive radiations occur over a much larger spatial scale. Here we compare continental adaptive radiations of warblers of the north temperate regions. These species are small insectivorous birds and form a large component of woodland bird communities. Richman (1996) used a phylogenetic study to infer that among Asian warblers of the genus *Phylloscopus*, most adaptive diversification took place in the Himalayas. Communities of *Phylloscopus* warblers that are several thousand kilometres distant (in Europe and in Japan)

seem to be largely structured by repeated invasions from central Asia with little (Europe) or no (Japan) *in situ* diversification. In fact, warbler communities of the north temperate forests are largely accounted for by just three adaptive radiations: the genus *Sylvia* in Europe (Blondel *et al.* 1996), the *Phylloscopus* in Asia (Richman 1996), and the Paruline warblers of North America (Morse 1989).

Although three adaptive radiations are relatively few, it is not clear why there should have been even this many, given the dispersal ability of these species, many of which are long-distance migrants, spending the winter in or near the tropics. One possibility is that the three radiations occurred more or less simultaneously in relatively southern refugia, with little potential for dispersal between them. In this paper we test this by comparing the timing of the adaptive radiations of the *Phylloscopus* and North American Paruline warblers on the basis of mitochondrial DNA divergence. We find that the North American warblers have speciated very recently. Their adaptive radiation appears to have originated in the late Pliocene or early Pleistocene. Diversification of most of the group occurred long after all species of extant *Phylloscopus* warblers had formed. Even though the *Phylloscopus* have successfully spread across the whole of Eurasia, barriers to successful dispersal into North America operated on time-scales longer than a complete *in situ* adaptive radiation there.

2. METHODS

The New World warblers are only distantly related to the *Phylloscopus* warblers (Sibley & Ahlquist 1990). Nevertheless, the

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timing of speciation events within the two groups can be compared by using the same DNA sequences, given the assumption that molecular evolution proceeds at the same rate in the two groups.

(a) *Choice of species*

We set out to compare species' radiations by considering communities of sympatric species in localities where species diversity is high. We studied the entire complement of warblers breeding in restricted localities (White Mountain national forest, New Hampshire, in North America, and Kashmir, India, in Asia). These species form only a proportion of all the species in each group (about 30% of the temperate breeding North American Parulines (based on Curson *et al.* 1994) and about 25% of the temperate Asian breeding *Phylloscopus* (based on Baker 1997)). There are also tropical species in both groups that we did not study. We restricted our study to sympatric assemblages because this gives a clear criterion for which species should be included. Nevertheless, because most of the *Phylloscopus* species have been sequenced (Helbig *et al.* 1995, 1996; Richman 1996; Price *et al.* 1997), we are able to generalize our results to a comparison of the New World warblers with *Phylloscopus* communities breeding across the whole of Eurasia.

We use sequences of the mitochondrial DNA cytochrome *b* gene (ca. 1070 bases) from 14 species of North American warblers and nine species of Asian warblers in our comparisons. We also include three species of the ecologically similar kinglets (*Regulus*), two from New Hampshire and one from Kashmir.

(b) *Sequencing*

Sequencing methods used for the *Phylloscopus* are described in Richman & Price (1992) and Price *et al.* (1997). To sequence the New World warblers, we extracted DNA from blood samples collected from between one and three breeding individuals from a variety of locations in eastern Canada (samples from *Regulus satrapa*, *Dendroica virens* and *Vermivora ruficapilla* were obtained from autumn migrants captured at Kalamazoo, Michigan, USA). The mtDNA cytochrome *b* fragment was amplified as described previously in Richman & Price (1992). Annealing temperatures for each set of amplifications varied between 48 and 55 °C. Gel-purified products were cycle-sequenced using the above primers and additional internal primers, all of which had been end-labelled with ³³P. We obtained sequences initially from a single individual for each species. We sequenced an additional one or two individuals for five of the species: *Dendroica virens*, *Seiurus aurocapillus*, *Wilsonia canadensis*, *Setophaga ruticilla* and *Vermivora ruficapilla*. In all cases, the sequence from the additional samples was similar to the initial sequence, with either zero or one bases different. One individual of each species was chosen to use in all analyses.

(c) *Phylogeny estimation*

We combined all species into a single analysis, but results are similar when the New and Old World groups are analysed separately. We estimated phylogenetic relationships using neighbour-joining based on distances estimated according to the Hasegawa *et al.* (1985) substitution model, implemented in the program LINTRE (Takezaki *et al.* 1995). The substitution model takes into account unequal base frequencies and uses an empirically determined transition/transversion ratio. We assumed that rate variation across sites follows a gamma distribution with parameter $\alpha=1.0$. We calculated a linearized (constant-rate tree) using the algorithm of Takezaki *et al.* (1995).

As we are comparing quite distantly related taxa, it is plausible that inferred differences in timing are an artefact of rate variation in molecular evolution across taxa. We tested for deviations from a molecular clock using the method of Takezaki *et al.* (1995), also implemented in LINTRE. The test compares the distances between groups of paired taxa that should be identical under the null hypothesis of no rate variation, and requires a rooted tree in order to identify pairs. To root the tree we used published sequence data from the shrike *Lanius ludovicianus* (Helmbychowski & Cracraft 1993), which according to the phylogeny of Sibley & Ahlquist (1990) is a close outgroup. We also rooted the tree of New World warblers and *Phylloscopus* using *Regulus*. *Regulus* is actually an ingroup (Sibley & Ahlquist 1990; this paper) and therefore provides a strong test for deviations from a molecular clock. Results were similar to those using the shrike, and are not presented here. Our main conclusions on relative timings of adaptive radiation were identical when we used alternative maximum-likelihood methods (Felsenstein 1996).

(d) *Signature of adaptive radiation*

If an adaptive radiation occurs, speciation events should be clustered in time (Simpson 1953). To test for this we asked if speciation rates predicted from terminal branch lengths are consistent with speciation rates deeper in the tree. We used two test statistics derived from the coalescent theory for samples of neutral alleles (Uyenoyama 1997): $R_{SD} = S/(D - 1/nD)$, $R_{ST} = S a_n / T$, where S is the sum of terminal branch lengths, D is the distance from root to tip, $a_n = \sum_{i=1}^{n-1} (1/i)$, n is the number of species, and T is the total branch length in the phylogeny. Although both statistics assume a molecular clock, the calculation of R_{SD} requires the construction of a clock-like tree (to measure the depth of the tree), whereas R_{ST} can be calculated from a tree in which tips are not all contemporaneous. Large values of either statistic imply relatively long terminal branches.

We calculated R_{SD} and R_{ST} by modifying the program NEIGHBOR in PHYLIP (Felsenstein 1996). We generated a linearized tree using UPGMA, based on the Kimura two-parameter distance metric with a 20:1 transition:transversion ratio. To obtain distributions for these statistics under the null hypothesis of no change in speciation rate, we used TREEEVOLVE, written by N. Grassly (version 1.02, distributed by the author, Oxford University, 1997). TREEEVOLVE simulates the evolution of DNA sequences along a phylogeny generated using the coalescent theory for neutral alleles. We simulated sequence evolution according to the same Kimura two-parameter model, with a transition:transversion ratio of 20:1, and other relevant parameters set to their default values. We used simulated data sets of 20 and 10 taxa. Because the distribution with 20 taxa had the slightly higher variance (i.e. is more conservative), that distribution is presented here. We repeated the analysis using LINTRE and the algorithms for tree building as described in the phylogeny reconstruction section above, but were only able to calculate R_{ST} on the nonlinearized tree for this test, because of difficulties of rooting trees in the simulated data sets. The analysis using LINTRE gave a similar result to that presented here.

(e) *Comparisons of rates of speciation*

If probabilities of speciation and extinction do not vary across lineages, a set of contemporaneous lineages examined at any one point in time in a reconstructed phylogeny will leave descendants in which the numbers are distributed among those lineages according to a broken-stick distribution (Rambaut *et al.* 1997; Nee *et al.* 1996). Using this distribution as the basis for the

Figure 1. Estimated phylogenetic relationships among New World and Old World warblers (see § 2). (a) Unrooted neighbour-joining tree, based on Hasegawa *et al.* (1985) gamma distances. Bootstrap values higher than 50, based on 100 replicates, are indicated. (b) Linearized (constant-rate) version of the same tree, rooted using the shrike *Lanius ludovicianus*. Abbreviated genus names are P., *Phylloscopus*; R., *Regulus*; D., *Dendroica*. Species indicated by genus names are *Cettia fortipes*, *Setophaga ruticilla*, *Seiurus aurocapillus*, *Vermivora ruficapilla*, *Wilsonia canadensis*, *Geothlypis trichas* and *Mniotilta varia*. Lineages highlighted by arrows leave significantly more present-day species than other contemporaneous lineages (circles, $p < 0.01$; squares, $p < 0.0001$).

null hypothesis, any lineage at its point of bifurcation can be compared with other contemporaneous lineages to ask if it has given rise to significantly more daughter species than expected (Rambaut *et al.* 1997; Nee *et al.* 1996). We used the program END-EPI (Rambaut *et al.* 1997) to identify lineages leading to high numbers of species.

The chief difficulty with this method is that the point in the tree at which speciation rates become elevated is not identified (Purvis *et al.* 1995). A highly speciose clade can create a result whereby lineages that are deeply ancestral to the clade have high numbers of present-day species relative to their contemporaries. To search for multiple points of accelerated speciation we worked down from the tip of the tree and identified the first lineage with significantly higher numbers of descendants than expected. All descendants above that lineage were then collapsed to a single species and the more ancestral lineages retested for accelerated speciation. This test is very conservative because even under a constant rate of speciation we expect a lineage to often leave more than one descendant. Therefore, ancestral lineages that leave more descendants after the collapsing procedure can be taken as additional points of accelerated speciation.

(f) Morphology

Adaptive radiations are defined both by ecological diversification and by the accompanying morphological differentiation (Schluter 1996). As a measure of morphological diversification

within each group, we measured six traits (wing, tail and beak length, beak depth, beak width and tarsus length) from museum specimens. We measured ten males collected close to each community, and calculated species means (methods as in Richman 1996). We calculated euclidean distances (square root of summed squared differences) between log-transformed species' means as a measure of morphological differentiation.

3. RESULTS

The phylogeny presented in figure 1 suggests much more recent divergence among the North American warblers than among *Phylloscopus* and *Regulus* species. This result does not seem to be attributable to rate variation in molecular evolution: the null hypothesis of a molecular clock is not rejected ($\chi^2_{25} = 23.027$, $p > 0.5$). Additional evidence for the recent speciation of the New World warblers comes from limited DNA–DNA hybridization data (for three *Phylloscopus* species, three *Regulus* species, two *Dendroica* species and two *Vermivora* species (Sibley & Ahlquist 1990; their figures 380, 381 and 384)), which indicate relative divergence times very similar to those obtained from the mtDNA sequences.

A linearized version of the mtDNA tree, calculated using the algorithm in Takezaki *et al.* (1995) is shown in figure 1b. Tests using this linearized tree and the program

Figure 2. Two statistics for tree-shape (Uyenoyama 1997) compared against simulated null distributions. Indicated values are for the New World (including all *Dendroica*, but excluding *Setophaga*) and *Phylloscopus* clades. In both clades the statistic lies in the extreme tail of the distribution ($p < 0.01$ for the New World, $p < 0.05$ for the Old World), indicating overly long terminal branches.

END-EPI clearly show that the New World warblers have undergone a burst of speciation much later in time than the Old World warblers (figure 1). The p -value for the lineage leading to the New World warblers is $p = 0.004$, and that leading to all the New World warblers after the branch to *Setophaga* is $p = 0.000003$, suggesting most of the effect is due to high speciation rates after *Setophaga* split from the rest. This interpretation is supported when the *Dendroica* are collapsed to a single species. The lineage leading to the New World warblers as a whole is now not significant ($p = 0.1$), whereas the lineage leading to the New World warblers after the *Setophaga* split remains significant ($p = 0.002$). Within the New World warblers there is a second burst of speciation. The lineage leading to the *Dendroica* shows increased rates of speciation with respect to the other New World lineages (using END-EPI, $p = 0.004$).

Both the Old World warblers and the New World warblers show evidence of long terminal branch lengths with respect to internal branches (figure 2). This is most evident in the New World (figure 2). Speciation events among the species that make up these communities were clustered in time, as expected during an adaptive radiation. An alternative model based on a constant probability of turnover of species within each community may not lead to shorter terminal branches than those observed (because sympatry can only be formed between reproductively isolated pairs, and reproductive isolation may take a substantial time to achieve (Avise & Walker 1998)), but it should then result in longer internal branches.

In figure 3 we compare morphological and sequence differences for the three separate radiations we have identified (the *Phylloscopus*, six genera of New World warblers

Figure 3. Plot of genetic divergence (uncorrected % base difference) versus morphological differentiation (euclidean distance of six morphological measurements). Three groups are distinguished. The first (open circles) contains five species of *Dendroica* (*D. castanea*, *D. striata*, *D. magnolia*, *D. coronata*, *D. virens*); the second (filled squares) contains the six genera representing the first adaptive radiation in the New World (see figure 1, not including *Setophaga*, and including a single randomly chosen *Dendroica* (*D. coronata*)); and the third (open squares) contains the eight *Phylloscopus* species. Summary statistics (mean $\pm$ s.d.) are for the groups in the figure. Molecules: *Dendroica*, $2.4 \pm 0.5\%$; New World genera, $2.3 \pm 0.5\%$; *Phylloscopus*, $10.7 \pm 1.2\%$. Morphology: *Dendroica*, $0.25 \pm 0.09 \log_e(\text{mm})$; New World genera, $0.42 \pm 0.13 \log_e(\text{mm})$; *Phylloscopus*, $0.39 \pm 0.2 \log_e(\text{mm})$.

(excluding *Setophaga*) and the *Dendroica*). Molecular distances are about four times higher among the *Phylloscopus* than among the New World warblers, but levels of morphological divergence are similar. When *Setophaga* is excluded, the average level of sequence divergence among the New World warblers is $2.6\% \pm 0.07\%$ s.d. (range 0.3% (between *Dendroica magnolia* and *D. tigrina*) to 4.3% (between *D. striata* and *Mniotilta varia*)). Several calibrations indicate a rate of mtDNA sequence divergence of about 2% per million years (summarized in Klicka & Zink 1997; see also Fleischer *et al.* 1998), which places most of the adaptive radiation in the New World within the Pleistocene. The calibration of Sibley & Ahlquist (1990) similarly places the radiation in the Pleistocene for the New World species they studied.

The results from the New World warblers are contrasted with results from other North American groups in figure 4 (based on data in Klicka & Zink 1997; Avise & Walker 1998). The figure shows that many pairs of sister species, or even subspecies, are more distantly diverged than most of the North American warblers we studied. All of these pairs are largely allopatric, and some meet in hybrid zones.

4. DISCUSSION

If *Setophaga ruticilla* is excluded, sequence differences among the warblers of the New Hampshire community are on average 24% the differences among the warblers of a Himalayan community. We interpret this to mean

Figure 4. (a) Estimated mtDNA sequence divergence between pairs of North American species (filled bars) and major phylogeographic groups within some North American species (open bars) (modified from Avise & Walker 1998). (b) Pairwise comparisons between eight *Dendroica* species (filled bars) and single representatives of six North American warbler genera (open bars; compared groups are as in figure 3).

that these New World warblers are much younger than their Old World counterparts. This interpretation requires first that molecular distances are an accurate representation of relative times of divergence, and second that the community of warblers we studied in the Old World is representative of all Old World communities. Because the difference between the New and Old World is so large, it is unlikely to be explained by changes in rates of molecular evolution, and our tests were unable to detect such rate changes. Several independent calibrations of a molecular clock across different groups of birds have placed absolute divergence times between 1.6% and 2% per million years (Klicka & Zink 1997; Fleischer *et al.* 1998). Thus, there is little evidence for the sort of differences in rates of molecular evolution that would be needed to explain the discrepancy between the New and Old World warblers.

We conclude that the New World warblers are relatively young. They are young by comparison with all the Old World warbler communities that have been studied. Communities of *Phylloscopus* warblers from Europe, Japan and Siberia contain species that are as divergent in DNA sequence as the species in the Himalayan community (Richman 1996; Price *et al.* 1997). In addition, some superspecies groups within the *Phylloscopus* often have greater levels of sequence divergence among their component members than many New World warblers (Helbig *et al.* 1995, 1996).

None of the North American groups studied to date show evidence for the recent burst of speciation which is inferred to have occurred among the warblers of New Hampshire. Many ecologically similar sister taxa in other

North American groups are thought to be old (Zink & Slowinski 1995; Klicka & Zink 1997; figure 4), being similar to the *Phylloscopus* in this respect. They include one genus of New World warbler not studied here (*Oporornis*) in which a pair of species differ by 7.3% (Klicka & Zink 1997), more than three times as large as the average genetic distances between six of the New World warbler genera we studied. The absence of much recent evolution in many New World groups and in the *Phylloscopus* contrasts with the New World warblers. Not only has there been a great deal of speciation, but there has also been much morphological and ecological diversification. The most remarkable differentiation is seen in the ovenbird (*Seiurus aurocapillus*), a thrush-like ground dwelling form, with many habits distinct from those foliage gleaning warblers that are its close relatives.

The standard calibration of rates of molecular divergence (2% per million years) puts the adaptive radiation of six genera of New World warblers around the end of the Pliocene/beginning of the Pleistocene (usually placed at 1.8 million years (Ma) before present (BP)). This finding supports a proposal by Mengel (1964), who used reconstructions of the vegetation at the beginning of the Pleistocene to argue that the coniferous forests of the north were colonized by ancestral forms from the broad-leaf forests in the south-east. It seems that there were fewer ancestors than Mengel postulated, with perhaps only *Setophaga ruticilla* among the species we studied representing an independent invasion. The second part of Mengel's theory was that repeated episodes of glaciation created the allopatric conditions ripe for repeated episodes of speciation. A subsequent test of this proposition for a single group of *Dendroica* warblers has found mixed support (Bermingham *et al.* 1992).

Both the New and Old World warblers contain species which are largely long-distance migrants, overwintering in the tropics of America and Asia. Here we suggest one possible scenario to explain (i) why the *Phylloscopus* failed to exploit an apparently empty habitat even though all the species were present in Asia, and (ii) why other North American groups did not experience similar adaptive radiations. The middle Pliocene (3 Ma BP) was very hot and boreal forests occurred as far as 80° north (Matthews & Ovenden 1990; Dowsett *et al.* 1992). Old World warblers migrating out of wintering grounds in Asia may have exploited these forests. The first well-documented glaciation in the association with impending ice ages was at about 2.4 Ma BP (Shackleton 1993). As the forests moved south in response to cooling, the lengthening migration route out of tropical Asia would make it increasingly difficult for the Old World warblers to occupy these forests, and could thus favour exploitation by a colonist from the southern part of North America. The vegetation history in North America for the end of Pliocene, especially in the east, is not well known, but the cooling was accompanied by a dry period (Groot 1991; Behrensmeyer *et al.* 1992). In northern California pollen records indicate a severe drought and an absence of forest (Thompson 1991). Thus the exploitation of northerly forest may have required crossing a sufficiently difficult barrier that only one or a few species readily colonized, creating the conditions ripe for an adaptive radiation.

In Asia, speciation among the *Phylloscopus* warblers occurred well before the Pleistocene (according to the molecular clock calibration, before *ca.* 5 Ma BP). It is likely that the Himalayas and other southerly areas formed refuges for these species during ice ages (Price *et al.* 1997). The uplift of the Himalayas occurred on a time-scale such that most contemporary habitats were established by about 6 Ma BP (Shroder 1993). During periods of drought and glaciation, these habitats have persisted in the Himalayas, although they migrated altitudinally (Behrensmeyer *et al.* 1992, p. 487). Present-day north Asia communities have been formed by multiple recolonization events from these southern refuges (Price *et al.* 1997). Species track habitat and possibly climate, and move to lower altitudes at higher latitudes (Price *et al.* 1997). Effects of dispersal on Asian community structure can also be seen in areas containing species different from the Himalayas. For example, the three Japanese species all share ecologically similar relatives in the Himalayas, and the Japanese community appears to have been formed long ago by three separate invasions from central Asia with no *in situ* radiation (Richman 1996). Presumably colonization along an east–west route is generally easier than along the north–south route, because climate is more similar in an east–west direction; a point made by Diamond (1997) in his discussions of human history.

The New World warblers differ from the *Phylloscopus* in that they are generally dimorphic in plumage coloration (among the New World species studied here, only the ovenbird is monomorphic (Curson *et al.* 1994)). All of the *Phylloscopus* are monomorphic and generally dull. Although the pattern of species diversification in the New World fits an adaptive radiation, sexual selection may also have played a role in speciation. In particular, the *Dendroica* warblers are young, sexually dimorphic in colour pattern and extremely similar ecologically (MacArthur 1958; Morse 1989). Lack (1971, p.132) described the North American *Dendroica* as ‘a more complex case of ecological interdigitation than any found in European passerine species’. It may be that adaptive radiations are accompanied by strong sexual as well as natural selection, with sexual selection producing ecologically similar species. Under this idea, part of the explanation for the ecological differences between the New and Old World warblers lies in their different ages, and it is plausible that some species would eventually be lost from the New World communities as a result of ecological interactions.

We conclude that the timings of the adaptive radiations in the New World and Old World differ. We attribute the differences to patterns of climate change and the geography of the two continents. If these conclusions are confirmed and extended to other groups, it may be possible to use molecular phylogenies of adaptive radiations to aid in the reconstruction of past environments, and in the dating of environmental upheavals.

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As this paper exceeds the maximum length normally permitted, the authors have agreed to contribute to production costs.