
Explosive speciation in the New World *Dendroica* warblers

I. J. Lovette^{1,2*} and E. Bermingham¹

¹Smithsonian Tropical Research Institute, Unit 0948, APO AA 34002-0948, USA

²Department of Biology, University of Pennsylvania, Philadelphia, PA 19104, USA

The 27 species of *Dendroica* wood-warblers represent North America's most spectacular avian adaptive radiation. *Dendroica* species exhibit high levels of local sympatry and differ in plumage and song, but the group contrasts with other well-known avian adaptive radiations such as the Hawaiian honeycreepers and Galapagos finches in that *Dendroica* species have differentiated modestly in morphometric traits related to foraging. Instead, sympatric *Dendroica* tend to partition resources behaviourally and they have become a widely cited example of competitive exclusion. We explored the temporal structure of *Dendroica* diversification via a phylogeny based on 3639 nucleotides of protein-coding mitochondrial DNA (mtDNA). The taxa sampled included 60 individuals representing 24 *Dendroica* species and a variety of other paruline warbler and outgroup species. Mitochondrial divergences among *Dendroica* species were generally large (mean pairwise interspecific distances, 10.0%) and many species were rooted in a basal polytomy. The prevalence of long terminal branches indicates that these species have evolved efficient isolating mechanisms that have prevented mtDNA introgression despite the many opportunities for hybridization resulting from local sympatry. Comparisons with a null model of random bifurcation–extinction demonstrate that cladogenesis in *Dendroica* has been clustered non-randomly with respect to time, with a significant burst of speciation occurring early in the history of the genus, possibly as long ago as the Late Miocene or Early Pliocene periods. Although this non-random clustering of speciation is consistent with the pattern expected of an adaptive radiation, the age of the *Dendroica* radiation suggests it is an 'ancient species flock' in which most extant species represent lineages that have long been evolutionarily independent.

Keywords: speciation; adaptive radiation; sexual selection; phylogeny; mitochondrial DNA; *Dendroica*

1. INTRODUCTION

Adaptive radiations occur when an evolutionary lineage differentiates into a suite of closely related species which differ in their use of ecological resources (Huxley 1942; Schluter 1996; Givnish 1997). Adaptive radiations are commonly defined by bursts of rapid speciation which may follow the evolution of key innovations or dispersal into novel or unoccupied habitats (Simpson 1953). The relative timing of such speciation clusters has implications for the historical interpretation of present-day interspecific differentiation in adaptive radiations. Geological and molecular evidence suggests that some extant radiations are the result of recent periods of speciation: the explosive diversification of the highly speciose Lake Victoria cichlids, for example, probably occurred within the past 10 000–20 000 years (Meyer *et al.* 1990; Johnson *et al.* 1996) and, similarly, recent speciation events have been inferred for some other adaptive radiations (Hodges & Arnold 1994; Schluter 1996; Baldwin & Sanderson 1998). In these recent radiations, the causes of differentiation and speciation may be linked to existing environmental or ecological factors (Schluter 1996). These causal factors may be less obvious in radiations which have

resulted from more ancient periods of speciation followed by high lineage survival. In the resulting 'ancient species flocks' (Johns & Avise 1998), the taxa produced in an earlier explosive radiation have had a long period of subsequent evolutionary independence. Distinguishing between these historical extremes requires information about the temporal pattern of speciation in groups that have undergone adaptive radiation.

The *Dendroica* wood-warblers of North America have long been cited as an exemplary continental adaptive radiation (e.g. MacArthur 1958; Mayr 1963, p. 70; Morse 1989). Unlike many avian groups in which allied species are separated by geographical barriers or distributional disjunctions, the *Dendroica* warblers are frequently found in local sympatry, particularly in the forests of north-eastern North America where eight or more species may co-occur with overlapping or abutting territories. These high levels of sympatry are particularly notable because the *Dendroica* lack the conspicuous morphometric differentiation seen in island passerine radiations such as the Galapagos finches or Hawaiian honeycreepers, in which sympatric species differ greatly in characters such as bill size and shape (Lack 1971, pp. 129–132; Grant & Grant 1986). This unusual combination of general morphometric conservatism coupled with high local diversity has made *Dendroica* a model group for the

* Author for correspondence (ilovette@sas.upenn.edu).

investigation of behavioural differentiation and competitive exclusion, a field pioneered by R. MacArthur and refined by many later workers (MacArthur 1958; reviewed in Morse 1989). Behavioural differences among *Dendroica* species are often pronounced, for example sympatric *Dendroica* species usually differ significantly in their use of foraging strata and feeding behaviours (MacArthur 1958; Robinson & Holmes 1982; Sabo & Holmes 1983; Morse 1989).

The evolution of adaptive differences such as the behavioural differentiation seen among sympatric *Dendroica* must have a historical component, but little is known about the timing or topology of speciation in this group. Price *et al.* (1998) used putative mitochondrial DNA (mtDNA) divergences to infer that the radiation had occurred relatively recently, but their inferences were erroneous because some sequences included in their analyses were probably slowly evolving nuclear homologues of the mtDNA cytochrome *b* gene (H. L. Gibbs and T. Price, personal communication). To provide a historical framework for the study of the *Dendroica* radiation, we constructed an mtDNA phylogeny including most extant *Dendroica* species. We used this phylogeny to explore the pattern of cladogenesis that has produced North America's most diverse avian adaptive radiation.

2. METHODS

With 27 species, *Dendroica* is the most speciose of the 25 genera of New World paruline warblers and is the most diverse genus of passerine birds in North America (American Ornithologists' Union 1998). Most *Dendroica* species breed exclusively in North America and winter to the south, but six are resident endemics of the West Indies and two species have breeding distributions that extend into Central America. Several early studies found little allozyme variation among *Dendroica* species (Barrowclough & Corbin 1978; Avise *et al.* 1980), but more recent mtDNA-based studies have identified a much greater degree of phylogenetic variation in several smaller taxonomic subsets of the *Dendroica* radiation (Bermingham *et al.* 1992; Klein & Brown 1994; Lovette *et al.* 1998). As noted above, a previous mtDNA-based study that included 14 paruline warbler taxa (Price *et al.* 1998) was flawed due to the presence of many slowly evolving, nuclear-encoded sequences in a data set that was presumed to reflect differentiation in the rapidly evolving, mitochondrial-encoded cytochrome *b* gene (H. L. Gibbs and T. Price, personal communication).

(a) Taxonomic sampling and laboratory techniques

We analysed samples representing 24 out of the 27 *Dendroica* species, several monotypic warbler genera often considered to be closely allied to *Dendroica* (*Setophaga ruticilla*, *Catharopiza bishopi* and *Mniotilta varia*), several representative warbler taxa considered more distantly related to *Dendroica* (*Basileuterus culicivorus* and *Seiurus aurocapillus*) and two passerine outgroup taxa (*Coereba flaveola* and *Vireo latimeri*). Almost all species were represented by sequences from two or more individuals. The three *Dendroica* species not represented in our data set are the endangered *Dendroica kirtlandi* and *Dendroica chrysoparia* and the Cayman Islands' endemic *Dendroica vitellina*. Although most *Dendroica* species are monotypic, we partially characterized intraspecific variation within several widespread taxa by sequencing individuals representing different geographical subspecies. All samples

consisted of DNAs extracted from muscle tissue. Information on the collection locations and tissue, DNA and voucher numbers is available from the authors.

We obtained 3639 nucleotides of protein-coding mtDNA sequence from each sample (60 individuals in total). These sequences included the entire coding region of the cytochrome *b* (1143 bp), NADH dehydrogenase subunit II (1041 bp), ATP-synthase 8 (ATPase 8), and ATP-synthase 6 (684 bp) genes and a portion (613 bp) of the cytochrome oxidase subunit I gene. Sequences were obtained via gene-specific polymerase chain reaction (PCR) amplification followed by dideoxy terminator cycle sequencing reactions and electrophoresis in an Applied Biosystems 373 or 377 automated sequencer. We have recently described laboratory techniques identical to those used here (Lovette *et al.* 1998); information on the primer sequences and PCR conditions is available from the authors. Several lines of evidence indicate that our sequences were of mitochondrial origin, including identical sequences obtained from purified mtDNA and whole-genome extractions, a high transition:transversion ratio, an absence of unexpected stop codons and the congruency between four independently amplified and sequenced gene regions that together span more than 10 kb of the ca. 17 kb mtDNA genome.

(b) Phylogenetic reconstruction

We conducted all analyses using the full 3639 bp concatenated sequence obtained from each individual because fully linked mitochondrial genes constitute a single phylogenetic marker and because the five genes that we sequenced in whole or in part have similar nucleotide frequencies. Distance estimates and phylogenetic reconstructions were generated using PAUP* (Swofford 1999). It was apparent from preliminary phylogenetic analyses that no analytical approach (including parsimony) would satisfactorily resolve the basal relationships of the majority of *Dendroica* lineages. We therefore used a maximum-likelihood (ML) method to estimate the distances between nodes and pairwise distances among species. Using the matrix of ML distances, we generated an initial neighbour-joining (NJ) tree which included all 48 *Dendroica* individuals and a variety of other warbler and outgroup taxa. Additional reconstructions that included only a single randomly chosen representative of each *Dendroica* species were estimated via ML using the quartet puzzling search algorithm for 1000 puzzling steps. In all ML reconstructions, the gamma parameter was set to 0.12 with eight rate categories and the transition:transversion ratio set to 6. These values reflect estimates generated from ML searches on 15-taxon random subsets of the intractably large warbler data set, in which the parameters were estimated as part of the search process. Restricting the ML analyses to one representative per species is unlikely to have biased the resulting species-level reconstructions because most intraspecific replicates had almost identical sequences and in all cases all conspecific replicates were much more similar to one another than they were to sequences from other taxa.

(c) Speciation rates

We used the method of Wollenberg *et al.* (1996) to test for a non-random pattern of diversification among extant *Dendroica* lineages. This analysis is based on a null distribution of nodal placement in a tree of *n* terminal taxa, in which the distribution of distances between the base of the tree and interior nodes is simulated under the assumption that bifurcations and extinctions occur randomly from time 0 at the base of the tree to

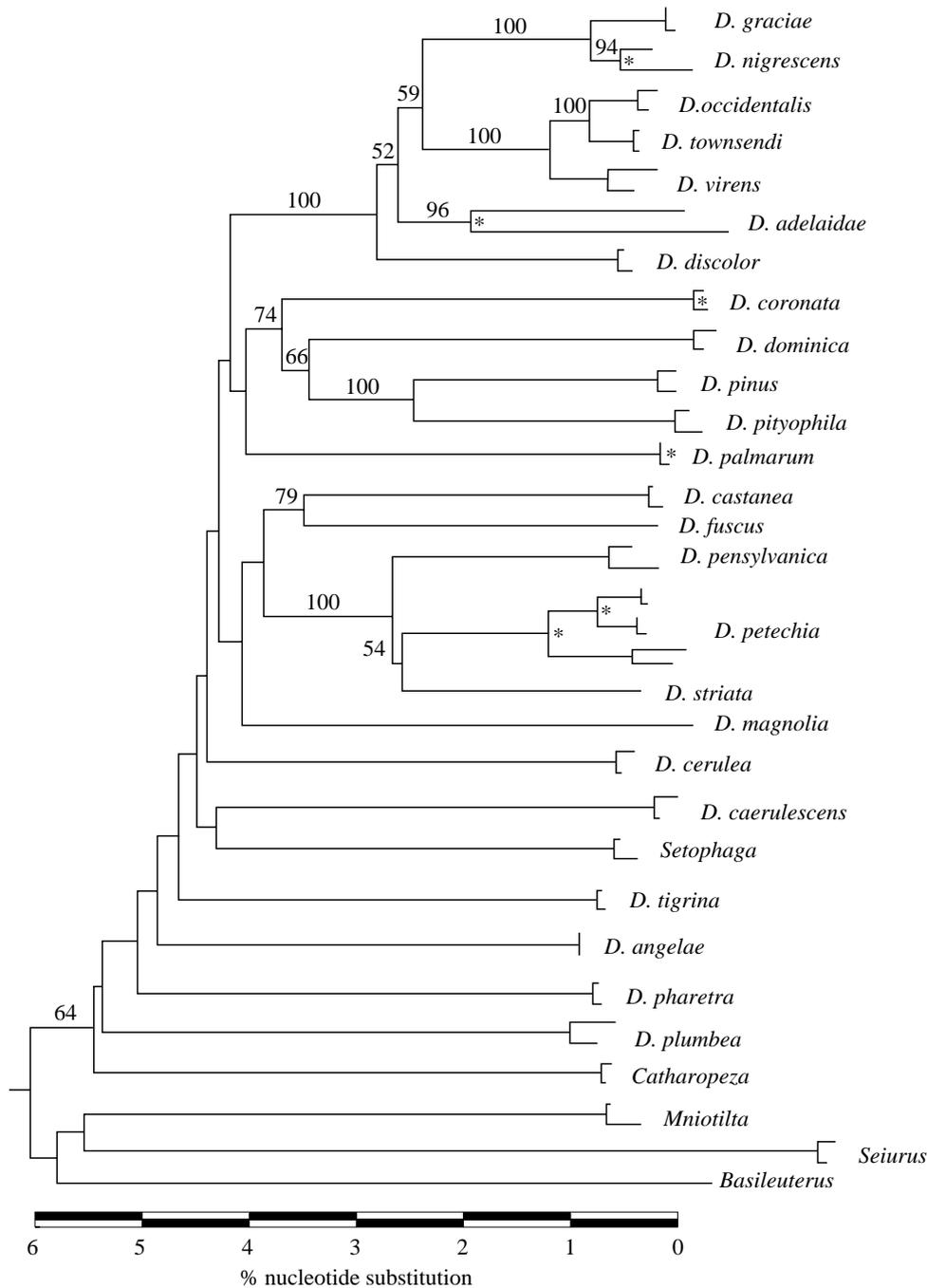


Figure 1. Phylogenetic relationships among 24 *Dendroica* species and five other paruline warbler genera. The tree shown is a neighbour-joining reconstruction based on Hasegawa *et al.* (1985) gamma distances. Numbers above internal branches indicate all bootstrap proportions greater than 50. Bootstrap proportions for species-specific branches are indicated only for the two taxa where they were less than 100. Starred nodes link representatives of different conspecific subspecies. The tree was rooted to the outgroup taxa *Coereba flaveola* and *Vireo latimeri* (neither are shown). The scale bar at the bottom indicates the percentage nucleotide substitution along branches (approximately half of the pairwise percentage divergence between termini).

time t at the n extant termini. Differences between empirical and null patterns of diversification are explored via comparisons of cumulative frequency distributions of base–node distances. When the empirical frequency distribution falls to the left of the null distribution, lineage diversification deep in the tree is greater than expected by chance, whereas when the empirical results fall to the right, speciation events are clustered more recently than expected. Differences between empirical and null distributions are explored statistically via a Kolmogorov–Smirnov goodness-of-fit test. As this method of assessing the structure of phylogenetic diversification requires empirical trees with contemporaneous tips, we used ML under the assumption of a molecular clock to generate a clock-like tree representing the mtDNA-defined ‘*Dendroica* radiation’ (all sampled *Dendroica* species, *Setophaga* and *Catharopeza*).

3. RESULTS

To explore the historical pattern of diversification in the *Dendroica* adaptive radiation, we first reconstructed phylogenetic relationships between 25 *Dendroica* species and related taxa and then examined the temporal structure of speciation events among them.

An NJ reconstruction based on ML distances is presented in figure 1. In the reconstructed phylogeny, the 25 *Dendroica* species group with the monotypic genera *Setophaga* and *Catharopeza*; warbler taxa falling outside of this group include the representative *Basileuterus* and *Seiurus* species along with *Mniotilta varia*, a monotypic genus once thought to be closely allied to *Dendroica* (Parkes 1978). Mitochondrial DNA-based reconstructions

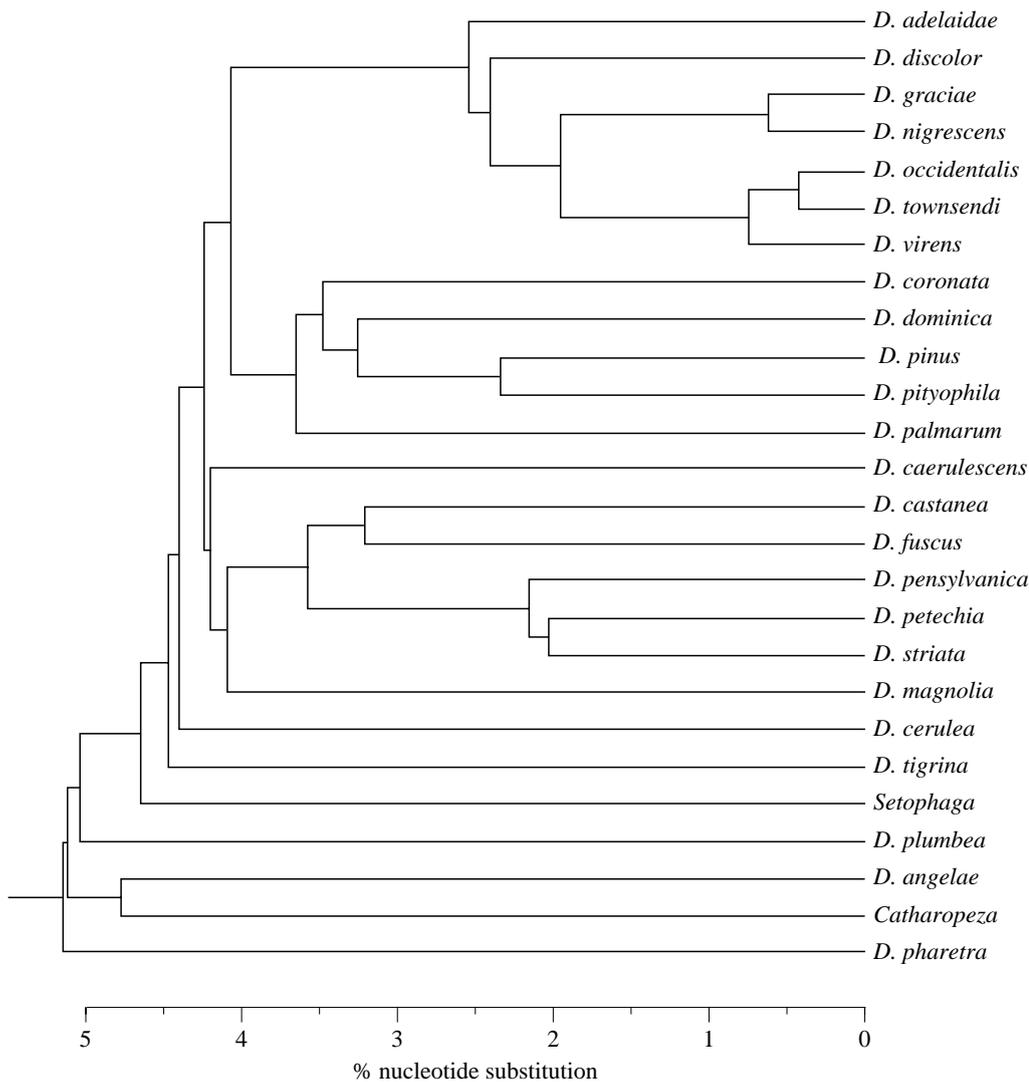


Figure 2. ML tree for single representatives of each 'Dendroica radiation' species reconstructed under the assumption of a fixed-rate molecular clock. The scale bar at the bottom indicates the percentage nucleotide substitution along branches. The tree is rooted to *Seiurus aurocapillus* (not shown).

which included representatives of all 24 extant paruline warbler genera (I. J. Lovette and E. Bermingham, unpublished data) similarly support this *Dendroica*–*Setophaga*–*Catharopeza* grouping, which we collectively refer to hereafter as the 'Dendroica radiation'.

Within this *Dendroica* radiation, many species-specific lineages had long terminal branches that clustered into a conspicuous basal polytomy (figure 1). Low bootstrap proportions in the NJ tree (figure 1) indicate that support for a hierarchical topology among these short basal internodes is low; most branch lengths do not differ significantly from zero in the ML reconstructions. Hierarchical structure is more prevalent among the lineages that cluster at shallower levels of divergence. Several groups of more closely allied *Dendroica* species are defined by a long basal branch with high bootstrap support, including the apparent sister species *Dendroica pinus* and *Dendroica pityophila*, a large group composed of *Dendroica adelaidae*, *Dendroica graciae*, *Dendroica nigrescens*, *Dendroica occidentalis*, *Dendroica townsendi*, *Dendroica virens* and *Dendroica discolor* and a group composed of *Dendroica petechia*, *Dendroica striata* and *Dendroica pennsylvanica*.

Although our sampling strategy was not designed to characterize intraspecific genetic variation, whenever possible we sequenced representatives of different

Dendroica subspecies. The resulting estimates of intra-specific diversity are notably low in comparison with the large genetic distances separating most *Dendroica* species. We found large intraspecific variation in only one species, *D. adelaidae* (pairwise interpopulation divergence 4.8%), a resident taxon with a disjunct geographical distribution on three Caribbean islands where each island population probably warrants species status (Lovette *et al.* 1998). The mitochondrial distances between other *Dendroica* subspecies were modest. For example, *D. petechia* has the broadest breeding distribution of any *Dendroica* species and has been subdivided into three geographical clades based on plumage and genetic characters (Browning 1994; Klein & Brown 1994; American Ornithologists' Union 1998), but the mtDNA divergence among representatives of these three groups was 0.9–2.4%. The mitochondrial differentiation between geographical races of other species was even lower (*Dendroica coronata coronata* versus *Dendroica coronata auduboni* 0.2%, *Dendroica nigrescens nigrescens* versus *Dendroica nigrescens halseii* 1.0%, *Dendroica palmarum palmarum* versus *Dendroica palmarum hypochrysea* 0.1% and *Dendroica pinus pinus* versus *Dendroica pinus achrustera* 0.4%). Furthermore, we found a maximum of 0.7% (mean = 0.3%) divergence in the 20 instances in which we sequenced multiple individuals representing the

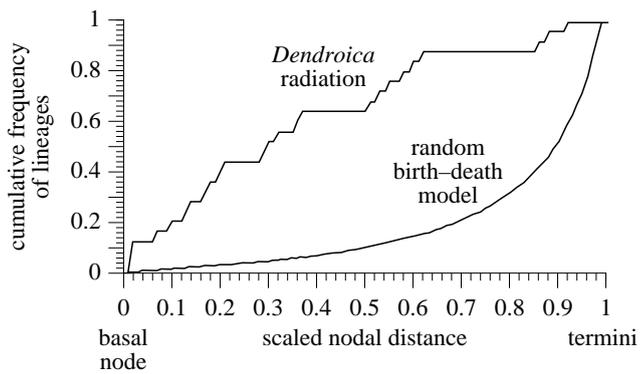


Figure 3. Cumulative distribution function for the warbler radiation depicted in figure 2. The taxa represented include the 24 *Dendroica* species, *Catharopeza bishopi* and *Setophaga ruticilla*. The curve at the right indicates the corresponding distribution generated under the assumption of random cladogenesis and extinction (Wollenberg *et al.* 1996).

same subspecies or where subspecific status was not determined.

The structure of the *Dendroica* tree shown in figure 1 suggests that phylogenetic diversity in *Dendroica* has accumulated non-randomly, with a pulse of speciation occurring soon after the origin of the clade and relatively few speciation events occurring since. A similar pattern was obtained in the ML reconstruction where a molecular clock was enforced (figure 2). Comparisons between empirical and null distributions of nodal distances (figure 3) support this assessment: in these comparisons, the empirical cumulative frequency distribution falls significantly to the left of the null distribution ($n=24$, $D=0.71$ and $p=0.0001$), indicating that bifurcations are clustered near the root of the tree. We tested whether this observed pattern of early speciation was robust to incomplete taxonomic sampling by assuming that the three non-sampled *Dendroica* species were involved in recent bifurcations equal in depth to that of the most recent observed node (*D. occidentalis* versus *D. townsendi*). This represents a conservative assumption because the three missing taxa probably span a range of divergence, from highly (*D. kirtlandi*) to weakly (*D. vittelina*) differentiated (Mayr & Short 1970). This simulation of complete taxonomic sampling caused the nodal frequency distribution to shift slightly to the right, but because the nodes were significantly clustered deep in the tree even in this simulated data set ($n=27$, $D=0.62$ and $p=0.0001$), the pattern of early cladogenesis cannot be attributed to taxonomic sampling biases.

4. DISCUSSION

The most striking pattern in the *Dendroica* phylogeny is the depth and clustering of the many bifurcations that occurred early in the history of the radiation. As shown in figure 1, almost half of the species-specific lineages are rooted in a basal polytomy that lacks a well-supported hierarchical structure. Comparisons with the random birth-death model indicate that this early burst of speciation produced a significantly large number of surviving lineages. Similar periods of rapid diversification involving fewer descendant lineages are apparent in one or two

clades at an intermediate level of divergence. The distribution of nodes thus suggests that *Dendroica* speciation has not occurred randomly with respect to time. This pattern is also apparent in a histogram of pairwise genetic divergences (figure 4), in which the majority of comparisons fall between 7 and 10% divergence, a level of differentiation that corresponds to the initial burst of cladogenesis deep in the tree. A smaller group of interspecific differences falls between 4 and 6% and reflects cladogenesis within the three lineages in which speciation occurred more recently (figure 1). Intraspecific differences form a third non-overlapping cluster below 2.5% pairwise distance.

Under the assumption that mitochondrial divergence accumulates in a clock-like manner, we can use the matrix of pairwise distances to estimate roughly when periods of rapid cladogenesis occurred. A consensus figure of 2% divergence per million years (Myr) has been derived from the few available avian mtDNA rate calibrations, including the single rate calibration for a passerine bird (Fleischer *et al.* 1998). This consensus rate has been widely employed in studies that use avian mtDNA divergence values to test biogeographic hypotheses (e.g. Bermingham *et al.* 1992; Klicka & Zink 1997; Avise & Walker 1998). Although it must always be used with caution owing to stochastic variation and to possible taxonomic and methodological biases (Lovette *et al.* 1999), a straightforward application of the 2% per Myr rate suggests that the initial burst of *Dendroica* differentiation occurred surprisingly early, at 4.5–7 Myr before present (BP). Similarly, the intermediate cluster of bifurcations at 4.5% divergence corresponds to an estimated date range of 2.3–3.5 Myr BP. Even if the 2% Myr⁻¹ calibration is a several-fold underestimate of the rate of mitochondrial evolution in *Dendroica*, the age of the *Dendroica* radiation contrasts with other avian groups for which genetic data suggest comparatively recent diversification, including the Hawaiian honeycreepers (Tarr & Fleischer 1995) and Galapagos finches (Sato *et al.* 1999).

Mengel (1964) and Price *et al.* (1998) suggested that new habitats appearing in response to cooling at the end of the Pliocene period drove the *Dendroica* adaptive radiation. It instead appears that the *Dendroica* radiation underwent an initial explosive burst of speciation somewhat earlier than that, possibly as early as the Late Miocene or Early Pliocene periods. In North America, an abrupt rise in temperature and aridity occurred near the Miocene–Pliocene boundary, resulting in a reduction and fragmentation of forest habitats (Webb *et al.* 1995). These environmental changes are associated with significant faunal turnover, including a well-characterized extinction event in North American ungulates (e.g. Cerling *et al.* 1997). By the Middle Pliocene period, however, the continent-wide distribution of forest habitats approximated present-day conditions (Barron *et al.* 1995). This sequence of palaeoenvironmental changes suggests that the many deep *Dendroica* lineages may have initially differentiated allopatrically in the forest refugia of the Early Pliocene period, followed by ecological reinforcement of adaptive differentiation during secondary contact in the expanded forests of the Middle Pliocene era.

In our reconstructions, the only nodes that are good candidates for Late Pliocene or Pleistocene speciation are those involving two groups of closely

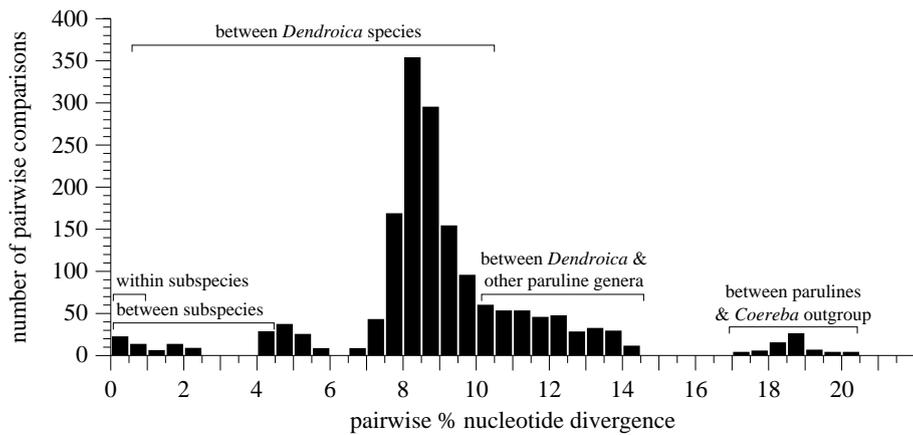


Figure 4. Distribution of pairwise mitochondrial sequence divergence among New World paruline warblers. The distances are based on the rate-variable metric of Hasegawa *et al.* (1985). The histogram includes pairwise distances between all individuals represented in figure 1 and the outgroup taxon *Coereba flaveola*. Brackets indicate the range of divergence values among samples at five taxonomic levels.

related taxa: (i) *D. townsendi*, *D. occidentalis* and *D. virens*, and (ii) *D. nigrescens* and *D. graciae* (figure 1). Out of these five species, all but *D. graciae* are members of a super-species complex (Mayr & Short 1970; American Ornithologists' Union 1998) that was central to Mengel's (1964) influential model of vicariance-based speciation in North American birds in which speciation events were linked to successive waves of Pleistocene glaciation. Although the topology of the mtDNA tree does not match Mengel's (1964) explicit prediction (Bermingham *et al.* 1992), interspecific distances within these shallow clades (range 0.9–1.7%) are consistent with speciation in the Middle Pleistocene era under the assumption of a 2% Myr⁻¹ rate of divergence.

The unexpected mitochondrial similarity of *D. nigrescens* and *D. graciae*, two phenotypically dissimilar species traditionally placed in separate superspecies complexes (Mayr & Short 1970), raises the issue of hybridization and mitochondrial introgression across *Dendroica* species boundaries. The frequency of interspecific introgression is important because hybridization with subsequent introgression is one of only two historical processes that can cause incongruencies between mitochondrial 'gene trees' and organismal 'species trees'. The other potential cause of historical incongruency—incomplete fixation of polymorphism in ancestral lineages—will less probably confound mtDNA-based reconstructions because the maternal transmission and concomitant small effective population size of the mtDNA genome renders it robust against lineage sorting incongruencies (Neigel & Avise 1986; Moore 1995). A relatively recent mitochondrial introgression event between *D. nigrescens* and *D. graciae* seems plausible because these species differ by only 1.5% sequence divergence and they occur in partial sympatry, yet they are phenotypically dissimilar and morphological criteria suggest that *D. graciae* is closely allied to a third taxon, *D. adelaidae* (American Ornithologists' Union 1998).

This single example of possible introgression is an exception to a more general pattern of long, species-specific terminal branches. These long termini show that mitochondrial gene flow between *Dendroica* species has been exceedingly rare: if introgression had been more frequent, more examples of species that share similar mtDNA would be expected. Because many *Dendroica* species are sympatric during the breeding season, they

have had ample opportunity for hybridization. The prevalence of deep branches in the mitochondrial tree is therefore an indirect but powerful indication that these species have evolved efficient isolating mechanisms. The rarity of mtDNA introgression amongst *Dendroica* species is therefore consistent with 'Parkes' Paradox' (Gill 1998), the observation that known hybridizations among paruline warbler genera exceed those among congeneric species, a trend that Parkes (1978) attributed to rapid selection for isolating mechanisms among closely related taxa. Although *Dendroica* species show only modest differentiation in morphometric characters, they are much more variable in plumage traits (Burt 1986) and in the songs of breeding-season males (Spector 1992; Van Buskirk 1997). These plumage and song differences have probably arisen via sexual selection (Shutler & Weatherhead 1990) and are the probable cues involved in species recognition.

MacArthur's (1958) study of the foraging behaviour of five sympatric *Dendroica* species rapidly became a textbook example of competitive exclusion and later workers using more sophisticated methods of data collection and analysis extended his work and confirmed that *Dendroica* species differ behaviourally such that sympatric species use different resources (Morse 1989). Although the non-random temporal clustering of cladogenesis in the *Dendroica* phylogeny is consistent with the explosive pattern expected of an adaptive radiation (Simpson 1953), the mitochondrial evidence further suggests that the *Dendroica* radiation is an ancient species flock (*sensu* Johns & Avise 1998), in which most extant species represent lineages that have been evolutionarily independent for several million years. The five sympatric species studied by MacArthur (1958), for example, differ by 7.7–11.1% pairwise sequence divergence.

Given the age of most *Dendroica* species, their differentiation in sexually selected plumage and song characters and in seemingly adaptive traits such as foraging behaviour and microhabitat use could have origins associated with the group's initial diversification. If so, these differences should show evidence of phylogenetic effects, but in this case any such effects would be difficult to detect using comparative methods owing to the lack of topological structure in the mtDNA-based reconstruction (figure 1). An alternative scenario is also possible given the age of the radiation: because most *Dendroica* species have been

evolutionarily independent for several million years, they have probably occurred in local assemblages with widely varying species compositions, particularly during the climatically variable Pleistocene period. Hence, adaptive differences in behavioural traits like those quantified by MacArthur (1958) may have arisen long after the period of explosive speciation that occurred early in the group's history.

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