

BUILDING A REGIONAL SPECIES POOL: DIVERSIFICATION OF THE *ENALLAGMA* DAMSELFLIES IN EASTERN NORTH AMERICA

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Abstract. We use a phylogeny of the North American *Enallagma* damselflies, derived from molecular and morphological data, to examine how the patterns of local and regional assemblage structure developed in this taxon across eastern North America. The two primary clades in the genus have nearly identical numbers of extant species, but the centers of diversity and the diversification rates for the two clades are quite different. One clade has its center of diversity in New England and radiated very recently from three species to give the current 18. Although most of this radiation involved the creation of new species in the ancestral fish-lake habitat, at least two independent lineages invaded and adapted to a new habitat: ponds and lakes lacking fish but supporting large numbers of large predatory dragonflies. The other clade, with greatest diversity in the southeastern United States, contains species that inhabit only water bodies that support fish populations. This “southeastern” clade diversified at a much slower and more steady pace within the fish-lake habitat than the “New England” clade, but four speciation events in this clade appear to have occurred at the same time as the northern radiation. Combined with our current understanding of local community structure in fish and fishless lakes, these results indicate that most of the species in this regional assemblage were created by speciation mechanisms other than filling empty niches, which have resulted in many locally coexisting species that are very similar in their ecological characteristics. Damselflies in eastern North American ponds and lakes appear to exemplify features of both a regulated component of the littoral food web (i.e., a functional group) and an assemblage whose local community composition is influenced by nonadaptive macroevolutionary processes that have operated on a much larger regional scale.

Key words: biogeography; community assembly; damselflies; diversification; *Enallagma*; *Odonata*; phylogeny; speciation.

INTRODUCTION

Understanding how pattern and structure in natural assemblages of organisms are generated remains a perplexing problem for community ecology. At a given local site, community dynamics can be simultaneously influenced by complex interactions among many abiotic (e.g., temperature, humidity, inorganic nutrients availabilities) and biotic (e.g., species that are resources, predators, parasites, diseases, mutualists) agents. On a regional scale, different assemblages of species may develop at different sites, because different abiotic conditions provide different templates on which community structure must develop (e.g., Connell 1961, Paine 1966, 1974, Lubchenco 1978, 1980, Menge 1995) or key species are unable to colonize particular sites (Tonn and Magnuson 1978, Rahel 1984, McPeck 1990a, Werner and McPeck 1994). Finally, when comparisons are made across biogeographic regions, pattern in community structure may be influenced as much by differences in the regional species pools as by differences in underlying environmental factors (Mooney

1977, Schluter 1986, Ricklefs 1987, 1989, Lawton 1984, Cornell and Lawton 1992, Ricklefs and Schluter 1993, Brown 1995). Therefore, understanding community structure across these disparate scales (i.e., local, regional, biogeographic) requires that we study how processes operating at these various scales interact.

Conceptually, ecologists have generally approached these issues by assuming a paradigm in which a defined regional pool of species exists, and each member of the pool can potentially colonize every local site within a biogeographic region (e.g., Diamond 1975, Post and Pimm 1983, Robinson and Dickerson 1987, Robinson and Edgemon 1988, Drake 1991, Wilson 1992, Drake et al. 1993, Lawler and Morin 1993, Grover 1994, Lockwood et al. 1997). The abiotic environment and species interactions determine which species can and cannot exist at each local site; some set of species from the regional pool can coexist at a given site, and the rest are driven locally extinct. For example, under the “keystone predator hypothesis,” one or a few prey species competitively exclude all others in the pool from sites where the keystone predator is absent, but many species in the pool coexist at other sites with the keystone predator because predation prevents competitive

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exclusion (Paine 1966, 1974, Menge et al. 1994). Patterns in local community structure result from variation in ecological conditions across sites and potentially from the order of colonization of species into local sites (e.g., Robinson and Dickinson 1987, Robinson and Edgemon 1988, Drake 1990, 1991, Wilson 1992, Drake et al. 1993).

This has been a very useful paradigm for stimulating thought and experimentation into these issues, but it begs the critical question of where the regional species pool comes from in the first place. Ultimately, the species pool is determined by the speciation and extinction processes operating within component taxa and by migration of taxa into the region from other biogeographic areas. However, the operation of these macroevolutionary and biogeographic processes may depend on the same ecological features of systems that influence local patterns of community structure (Eldredge 1989, Allmon 1992, McPeck 1996, Stanley 1998). For example, consider the consequences of different, but general, modes of speciation. In many taxa, speciation appears to be the by-product of lineages filling different ecological niches (e.g., "adaptive" radiations) (Rosenzweig 1978, 1995, Pimm 1979, Feder et al. 1988, 1990, Schluter and MacPhail 1992, Schluter 1993, Rice and Hostert 1993, Schluter and Nagel 1995, Losos et al. 1998). When speciation is driven by such adaptive processes, the per lineage speciation rate should decrease with increasing species richness, and these new species should deterministically persist in at least the community type in which they arose. Moreover, new species enter the regional species pool precisely because of their abilities to invade and persist in a subset of the available local communities.

In contrast, speciation can also result from many nonadaptive processes as well (i.e., speciation resulting from processes where adaptive niche diversification is not the driving force generating reproductive isolation). For example, it has been estimated that 70–80% of all angiosperm species are the result of speciation via polyploidy (Goldblatt 1980, Lewis 1980, Masterson 1994, and see review by Barrett 1989). In animals, nonadaptive speciation may result from chromosomal rearrangements (King 1993), sexual selection (Lande 1981, 1982, Lande and Kirkpatrick 1988, West-Eberhard 1983, Kaneshiro 1983, 1988, 1989, Seger 1985, Kaneshiro and Boake 1987, Turner and Burrows 1995, Seehausen et al. 1997, Payne and Krakauer 1997), diversification in specific mate recognition systems (Patterson 1978, 1993), or many other reasons (e.g., Vrba 1980, Taylor 1988), all of which proceed without the need for ecological diversification. Under these nonadaptive speciation modes, per lineage speciation rates may be largely independent of species richness and result in no substantial niche diversification of daughter lineages. As a result, new species will be introduced to the regional species pool without regard to the number of available empty niches in local communities,

and if the rate of introduction of new species is greater than the rate of extinction, local communities may always contain many more species than could coexist deterministically (e.g., Hubbell 1979, 1997, *in press*, Hubbell and Foster 1986). These considerations suggest that local and regional patterns of community structure may be influenced as much by the idiosyncrasies of diversification within particular taxa as by present-day ecological interactions (Ricklefs 1987, 1989, Brown and Nicoletto 1991, Cornell and Lawton 1992, Cornell 1985a, b, Ricklefs and Schluter 1993, Brown 1995).

Consequently, if we are to understand the assembly of natural communities, we must integrate this broader macroevolutionary perspective of how the regional and biogeographic pool of species are formed into studies of community structure. A number of workers are beginning to address these issues. Losos et al. (1998) have shown that *Anolis* lizards have independently and repeatedly diversified on different Caribbean islands to fill up to six niches on each island; the regional species pool was created by ecological diversification establishing local diversity and community structure on each island. Schluter, McPhail and coworkers (1992, Schluter 1993, 1996, Schluter and Nagel 1995) have identified analogous mechanisms of repeated local diversification into two niches as brackish water sticklebacks (*Gasterosteus* spp.) invaded fresh water lakes on Vancouver Island following the last glacial retreat. Benkman (1993) has shown that the diversity of Red Crossbills (*Loxia* spp.) in northwestern North America can be explained by their differential abilities to utilize various conifer species as resources. Radtkey et al. (1997) used biogeographic and phylogenetic patterns to understand how species interactions have shaped the evolution of body size in whiptail lizards (*Cnemidophorus*) on the mainland and on islands in the Gulf of California.

All of these studies identify adaptation to local ecological conditions (i.e., evolving to fill local niches) as playing a significant role in generating new species and shaping local community structure. However, they all also demonstrate that niche filling cannot entirely explain patterns of local and regional community structure. For example, some lakes on Vancouver Island contain two stickleback morphs, one utilizing the limnetic zone of the lake and the other the benthic zone, while other lakes in the region contain only one stickleback morph that is intermediate in phenotype to the two coexisting morphs in other lakes and that utilizes both the limnetic and benthic zones of their lakes (Schluter and McPhail 1992). Presumably both limnetic and benthic niches are available in these "one morph" lakes, but two stickleback morphs have not evolved in them (Schluter and McPhail 1992). Likewise, many Caribbean islands are missing one or more of the six *Anolis* morphs, and surprisingly a number of islands have two species of the same morph that are presum-

ably filling the same niche and that resulted from one speciation event on the island (Losos et al. 1998). Radtkey et al. (1997) also discuss a number of adaptive and nonadaptive explanations for why body size patterns are not consistent with hypothesized patterns in some populations of whiptails. Taken together, the results of these studies suggest that many other evolutionary and biogeographic processes besides adapting and diversifying in response to local ecological conditions may influence the development of local and regional species pools.

We are addressing these issues in ecological and evolutionary studies of the North American *Enallagma* damselflies (Odonata: Coenagrionidae). With 38 species, *Enallagma* is one of the most diverse genera of aquatic insects in North America (Bridges 1991, Tsuda 1991, Westfall and May 1996). This group diversified in North America, and now species can be found throughout the continent (Westfall and May 1996). Larvae of *Enallagma* species are a substantial component of food webs in the littoral zones of more permanent ponds, lakes, and streams across the continent (Johnson and Crowley 1980, Pierce et al. 1985, McPeck 1989, 1990a, b, 1998, Blois-Heulin et al. 1990). Also, adaptation has played a significant role in their diversification (McPeck 1995a, b, 1997, 1999, McPeck et al. 1996). Finally, as many as 12 species can be found coexisting in one water body (Johnson and Crowley 1980, McPeck 1989, 1990a, 1998; M. A. McPeck, unpublished data). In this paper we use a phylogenetic hypothesis of the North American *Enallagma* derived from molecular and morphological data to reconstruct the development of the local and regional *Enallagma* assemblages of eastern North American waters. Speciation and extinction rates appear to have been quite different in different parts of North America for this clade, and both adaptive and nonadaptive mechanisms appear to have influenced their diversification. We consider the consequences of these inferred mechanisms in light of our current understanding of the ecology of the group to interpret how local and regional patterns of community structure developed over evolutionary time and to generate new hypotheses to guide future tests of these conjectures.

BACKGROUND

Thirty-eight species of *Enallagma* are distributed across North America and the Caribbean islands (Westfall and May 1996). May (M. L. May, personal communication) has proposed synapomorphies that unite these species as a monophyletic group. Three of these species, which have wide distributions on North America, are also found on other continents: *E. civile* is also found in northern South America, *E. boreale* is also in eastern Asia, and *E. cyathigerum* has a circumpolar distribution. Two to three other *Enallagma* species found in eastern Asia are also probably members of this clade. These Asian species appear to be closely

allied to *E. boreale* (M. L. May, personal communication, and M. A. McPeck, personal observations), a lineage that recently invaded Asia from North America.

Enallagma species diversity is high in eastern North America and declines as one moves west across the continent (Fig. 1). Two centers of diversity exist: one from New Jersey to Maine, and the other in the southeastern United States. The northeastern center of diversity is dominated by the "bluet" species within the genus (i.e., species having adults that are generally pale blue in base color). The southeastern diversity center is dominated by the group of "yellow-orange" species.

Previous ecological studies have shown that the *Enallagma* species in eastern North America segregate as larvae between water bodies that do and do not support fish populations (Johnson and Crowley 1980, Pierce et al. 1985, McPeck 1990a, b, Blois-Heulin et al. 1990). One group of *Enallagma* species coexists with fish, the top predators in lakes containing fish, but fish predation excludes the remaining *Enallagma* species from these water bodies (Pierce et al. 1985, McPeck 1990a). The species that are excluded from fish lakes are found in water bodies lacking fish, where large dragonflies (*Anax*, *Aeshna*, and *Tramea* species) are the top predators; these dragonflies, like the *Enallagma* species with which they coexist, are restricted to fishless waters by fish predation (Crowder and Cooper 1982, Morin 1984, Werner and McPeck 1994). However, dragonfly predation excludes the species that coexist with fish from fishless lakes (McPeck 1990a). (Hereafter, we will refer to fishless ponds and lakes as dragonfly lakes, to emphasize the important role that dragonfly predation plays in structuring that assemblage.) Because ponds, marshes, and lakes that have and lack fish are generally interspersed, *Enallagma* assemblages have a checkerboard distribution across the landscape on a local scale (e.g., on the order of tens of square kilometers) (Johnson and Crowley 1980, McPeck 1989, 1990a, 1998).

The only discrepancy we have found from this pattern in larval distributions is in lakes dominated by salmonid fishes. For example, *E. boreale* and *E. cyathigerum* coexist with trout in high-altitude ponds in the White Mountains of New Hampshire (M. A. McPeck, unpublished data). *E. boreale* is also found in high-altitude trout ponds in British Columbia (Anholt 1990). These two *Enallagma* species are typical of fish-free, dragonfly lakes at lower elevations in eastern North America and are never found as larvae in water bodies with other fish species (e.g., centrarchids) in our experience (McPeck 1989, 1990a, 1998). Our experience in these ponds also suggests that trout are ineffective littoral predators, since the entire littoral invertebrate fauna in these ponds is nearly identical to those of completely fish-free ponds and lakes in the same area (including large dragonflies in abundance). Therefore, references to "fish" below refer to nonsalmonid fish species (e.g., see McPeck 1990a), and

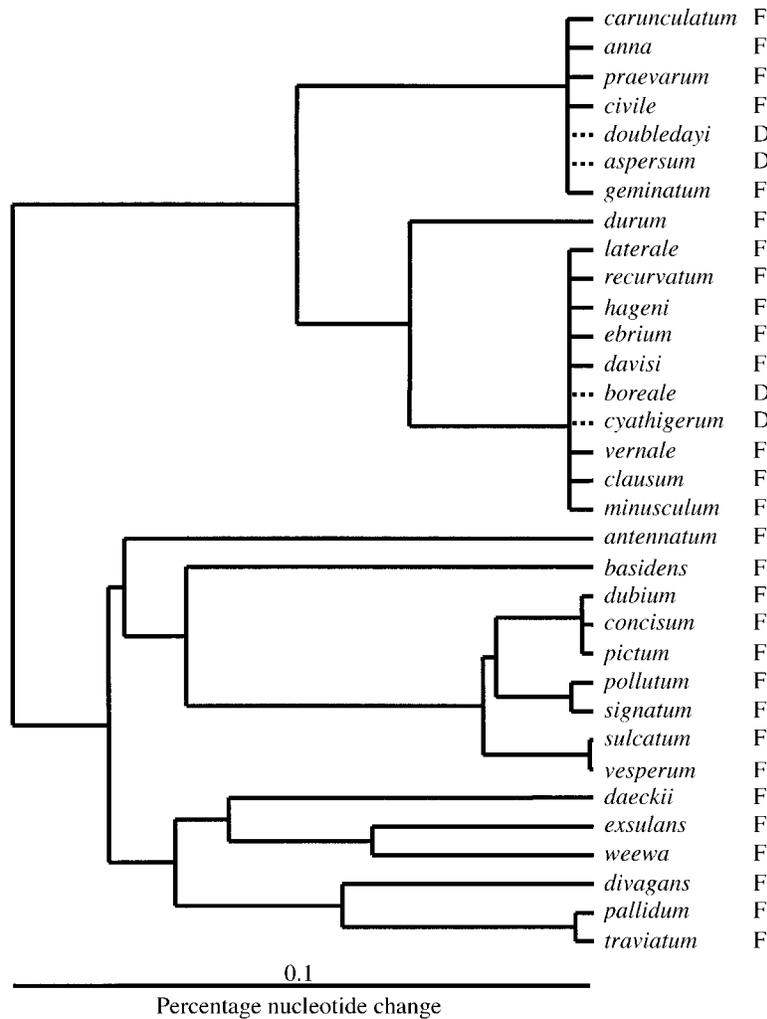


FIG. 2. Phylogenetic hypothesis derived from 51 morphological characters and 842 base pairs of mtDNA sequences (J. M. Brown et al., *unpublished manuscript*) and presenting branch length estimates assuming a molecular clock derived from the HKY model of nucleotide substitutions (see *Tempo and mode of diversification* for details). Dragonfly-lake species are identified by a "D" following their names and dashed lines for branches leading to them, and fish-lake species are identified by an "F" following their names. The habitat affinities of *E. anna*, *E. praevarum*, and *E. clausum* are currently not known to us. The remaining 26 species are found as larvae in fish lakes.

Carolina, Virginia, Delaware, New Jersey, Kentucky, Ohio, Michigan, New York, Connecticut, Massachusetts, Rhode Island, New Hampshire, Vermont, Maine, Ontario, Quebec) has confirmed that this disparity in diversity (4–5 times more species in fish lakes than in dragonfly lakes) is a common feature at local, regional, and biogeographic scales across eastern North America (M. A. McPeck, *unpublished data*). Overall, within the clade, the larval habitat affinities of 30 species are known, with 26 in fish lakes and four in dragonfly lakes (Fig. 2).

TEMPO AND MODE OF DIVERSIFICATION

J. M. Brown et al. (*unpublished manuscript*) presents the resulting phylogenetic hypotheses derived for 35 of the 38 North American *Enallagma* species from a

cladistic analysis of 51 larval and adult morphological characters and DNA sequences for 842 base pairs spanning the cytochrome oxidase I and II mitochondrial genes plus the intervening tRNA. These analyses used the combined morphological and DNA data sets, and five other coenagrionid damselflies (*Ischnura posita*, *Ischnura ramburii*, *Argia violacea*, *Telebasis byersi*, and *Coenagrion resolutum*) were included in the analyses as outgroups. Eighteen most parsimonious trees were identified from the combined morphological and DNA data set.

For the present study we utilized the 842 base pairs of mtDNA sequence data to estimate branch lengths for phylogenetic hypotheses derived for the 33 species for which we have DNA sequence data in the above analysis. We estimated branch lengths using the SPOT

program, version 1.0 (Rambaut and Grassley 1996) assuming the HKY model of nucleotide evolution. The HKY model is a maximum likelihood algorithm which assumes different rates for transitions and transversions and allows unequal nucleotide base frequencies (Hasegawa et al. 1985, Swofford et al. 1996). Because all the species included in this analysis are extant, we further assumed that rates of nucleotide substitutions occurred according to a molecular clock; this assumption constrains the sum of branch lengths from every tip species to the basal split in the phylogeny to be the same for all extant species. We have made this assumption so that we can estimate the pattern of change in the number of lineages over time (e.g., see Kubo and Iwasa 1995). We repeated this analysis for each of the 18 most parsimonious trees, and all 18 analyses gave quantitatively nearly identical results.

Fig. 2 presents the resulting phylogenetic hypothesis and associated branch lengths. A number of lineages in the genus have speciated very recently, and two have undergone radiations to create many species in a very short time period. Because of the almost complete lack of resolution in the *carunculatum-geminatum* and the *lateral-minusculum* clades, we were unable to calculate standard confidence analyses (e.g., bootstrapping [Swofford et al. 1996]) on the full tree. We did perform repeated bootstrap analyses including only three randomly chosen haplotypes from each of these two clades. These two clades were present in all bootstrapped trees (i.e., bootstrap values of 100). Most branches in the other primary clade *antennatum-traviatum* were also strongly supported, and most of the rest with low bootstrap values had unique synapomorphies uniting species (J. M. Brown et al., unpublished manuscript).

If the typical value for divergence rate of mitochondrial genes (2.3% sequence divergence per 10^6 yr [Brower 1994, Funk et al. 1995]) is assumed, the basal split within the genus dates to $9-10 \times 10^6$ years ago. Using this rate also gives estimates of 52 000–380 000 years ago for the very recent events within the genus, but this range of dates probably greatly overestimates times since the radiation. Mitochondrial haplotypes within the recently arisen extant species represent sampling from the ancestral species via lineage sorting of mitochondrial haplotypes and not differentiation of haplotypes in species following speciation events (J. M. Brown et al., unpublished manuscript). Lineage sorting of haplotypes occurs when the daughter species resulting from a speciation event acquire different mitochondrial haplotypes that were already present in the ancestral species; the mutation events that gave rise to the distinct mitochondrial haplotypes in the descendants predate the speciation events. Because phylogenetic analyses using DNA sequence data are really estimating the phylogeny of the haplotypes and species phylogenies are only inferred from these “gene trees,” the timing of branching events using DNA sequence

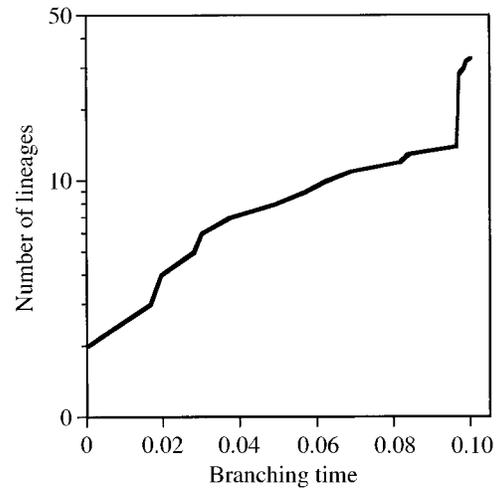


FIG. 3. The accumulation of lineages over evolutionary time (note log scale on the vertical axis). The data are derived from the phylogeny presented in Fig. 2 by counting the number of lineages at each time point. Branching time is measured in units of percentage nucleotide change as illustrated in Fig. 2.

data actually date the times of mutation events creating the haplotypes (Harrison 1991). Consequently, dates derived for these recent splits greatly overestimate the timing of speciation events because of lineage sorting in the recent radiation and should be taken as absolute maximum values. We are currently examining other molecular techniques in order to date the timing of this radiation more accurately.

The pattern of increase in the number of lineages over time can provide important insights into the processes of diversification and in particular speciation (Kubo and Iwasa 1995, Nee et al. 1995). Kubo and Iwasa (1995) have shown that major discontinuities like the one seen at the relative branching time of 0.096 in Fig. 3 are characteristic of a very rapid burst of speciation. This relationship derived for the North American *Enallagma* provides further support for a radiation having occurred very recently (Fig. 2).

ASSEMBLAGE STRUCTURE BETWEEN HABITATS

Reconstruction of habitat affinity on the hypothesized phylogeny shows that fish lakes were the ancestral habitat for North American *Enallagma* (Fig. 2). Only four extant species are found as larvae in dragonfly lakes, and all four are members of recently radiated clades. These four species resulted from a minimum of two, and more probably three, independent invasions of the dragonfly-lake habitat by fish-lake progenitors that occurred in association with or closely following the radiation of these clades (see also McPeck 1995a, McPeck et al. 1996). *E. boreale* and *E. cyathigerum* are indistinguishable in ecologically important behavioral and morphological characters: e.g., when larvae of these two species were included

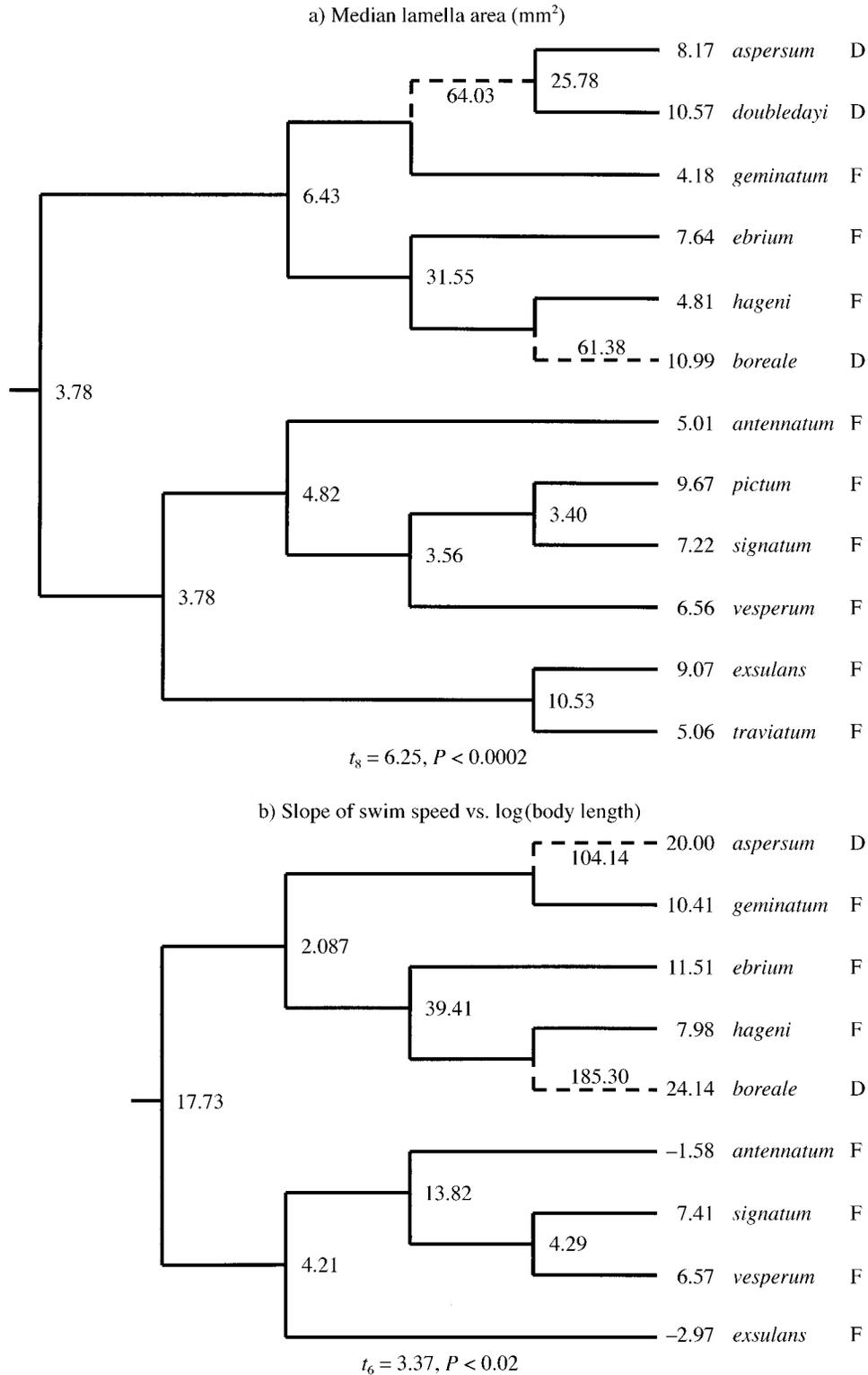


FIG. 4. Results of evolutionary contrast analyses for (a) the lateral surface area of the median caudal lamella of final instar larvae of 11 *Enallagma* species, and the (b) slope of swimming speed and \log_e (body size) across a wide range of instars for nine *Enallagma* species. The numbers at the tips of external branches on the phylogeny are means of 10–40 individuals for each species. Numbers associated with branches of the phylogeny are standardized evolutionary contrast values for those branches. “D” identifies dragonfly-lake species, and “F” identifies fish-lake species. Two independent habitat shifts from the fish-lake habitat to the dragonfly-lake habitat are hypothesized to have occurred along the two dashed branches.

in previous studies as one operational taxonomic unit, phenotypic variation among these individuals was similar to variation among individuals of one species (McPeck 1990b, 1995a). Therefore, *E. boreale* and *E. cyathigerum* are probably directly descended from one progenitor that shifted habitats.

In contrast, *E. aspersum* and *E. doubledayi* are very different in many characters. For example, adult males of *E. aspersum* have abdomens that are mostly black with blue markings on the dorsal surfaces of a few segments, much like *E. geminatum*. Males of *E. doubledayi* have the typical bluet color pattern of pale blue abdomens with black dorsal marking like all other species in the *carunculatum*–*minusculum* clade except *E. aspersum* and *E. geminatum* (Westfall and May 1996). The larvae of these two species are also strikingly different in many features. These differences suggest that *E. aspersum* and *E. doubledayi* are descended from two different progenitors that independently invaded the dragonfly-lake habitat.

Previous analyses suggested that rapid evolution in characters that enhance swimming performance were associated with these shifts from fish lakes to dragonfly lakes (McPeck 1995a, b, McPeck et al. 1996). These analyses used a phylogeny derived from a subset of the morphological data used by J. M. Brown et al. (*unpublished manuscript*) and no molecular data, and used the number of character state changes in this morphological data set as estimates of branch lengths. Here we reanalyze two variables identified in these previous analyses to have been critical for the adaptation of lineages to dragonfly lakes following habitat shifts, the lateral surface area of the median caudal lamellae and the ontogenetic relationship between swim speed and body size, using the new phylogenetic hypothesis for the genus, branch lengths estimated from nucleotide substitution rates (Fig. 2), and data from more species than previous analyses. Swimming speed is a critical feature of avoiding dragonfly predators, and the lateral surface area of the caudal lamellae generate thrust for swimming (McPeck 1990b, McPeck et al. 1996).

Evolutionary contrasts partition character change into orthogonal estimates of rates of character evolution across a phylogeny (Felsenstein 1973, 1985, 1988, Martins and Garland 1991, McPeck 1995b). We utilized McPeck's (1995b) modification of the method to isolate change in characters along single branches on which we hypothesize habitat shifts to have occurred (Fig. 4:

to construct a more conservative test, we assume here that *E. aspersum* and *E. doubledayi* are derived from a common ancestor after the habitat shift), in order to compare rates of character evolution within lake types to rates associated with habitat shifts (a graphical windows program written in Java is available from M. A. McPeck on request for performing these comparative analyses). The lateral surface area of the median lamella greatly increases along branches on which habitat shifts are hypothesized to have occurred, and this morphological feature shows much greater rates of evolution associated with invading the dragonfly-lake habitat than with evolution within the two lake types ($t_8 = 6.25$, $P < 0.0002$; Fig. 4a). Likewise, the slope of the relationship between swimming speed and body length shows much greater rates of evolution along branches on which shifts into dragonfly lakes are hypothesized to have occurred ($t_6 = 3.37$, $P < 0.02$, contrast values were natural-logtransformed for this test to equalize variances between the two classes; Fig. 4b). Because larvae of all species swim at similar rates when they are very small, the increase in the slope of this relationship associated with habitat shifts into the dragonfly-lake habitat is indicative of the fact that larvae of dragonfly-lake species are much faster swimmers than fish-lake species over much of the larval period (see also McPeck et al. 1996).

More recent studies have also shown that adaptation at the biochemical level to fuel greater swimming speeds also occurred (McPeck 1999). Specifically, this adaptation occurred in the activity of arginine kinase, the enzyme in insects that replenishes the pool of ATP during strenuous exertion to fuel muscle contractions (Blethan and Kaplan 1968, Morrison 1973). Three dragonfly-lake species were shown to have significantly higher activities of arginine kinase per unit of tissue mass than eleven fish-lake species from across the genus, and evolutionary contrasts analyses (like those presented in Fig. 4) demonstrated that these differences resulted from adaptation associated with invading dragonfly lakes (McPeck 1999).

BIOGEOGRAPHIC ASSEMBLAGE STRUCTURE

Species in the two primary clades in the genus tend to be found in different parts of North America. New England has the greatest concentration of species in the *carunculatum*–*minusculum* clade, whereas most species in the *antennatum*–*triviatum* clade are found in

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Contrast values were partitioned as follows: for median lamella area (a) *aspersum*–*doubledayi*, ancestor of *aspersum*–ancestor of *geminatum*, *geminatum*–ancestor of *ebrium*, *boreale*–ancestor of *boreale*, *hageni*–*ebrium*, *exsulans*–*triviatum*, *signatum*–*vesperum*, *antennatum*–ancestor of *signatum*, ancestor of *antennatum*–ancestor of *exsulans*, and finally the basal pair of branches; for the slope of swimming speed vs. body length (b) *aspersum*–ancestor of *geminatum*, *geminatum*–ancestor of *ebrium*, *boreale*–ancestor of *boreale*, *hageni*–*ebrium*, *signatum*–*vesperum*, *antennatum*–ancestor of *signatum*, *exsulans*–ancestor of *antennatum*, and finally the basal pair of branches. Because we are interested in interpreting standardized contrasts as rates (McPeck 1995b) without regard to the direction of character change (except for change along the dashed branches), the absolute values of all standardized contrast values are used for analyses.

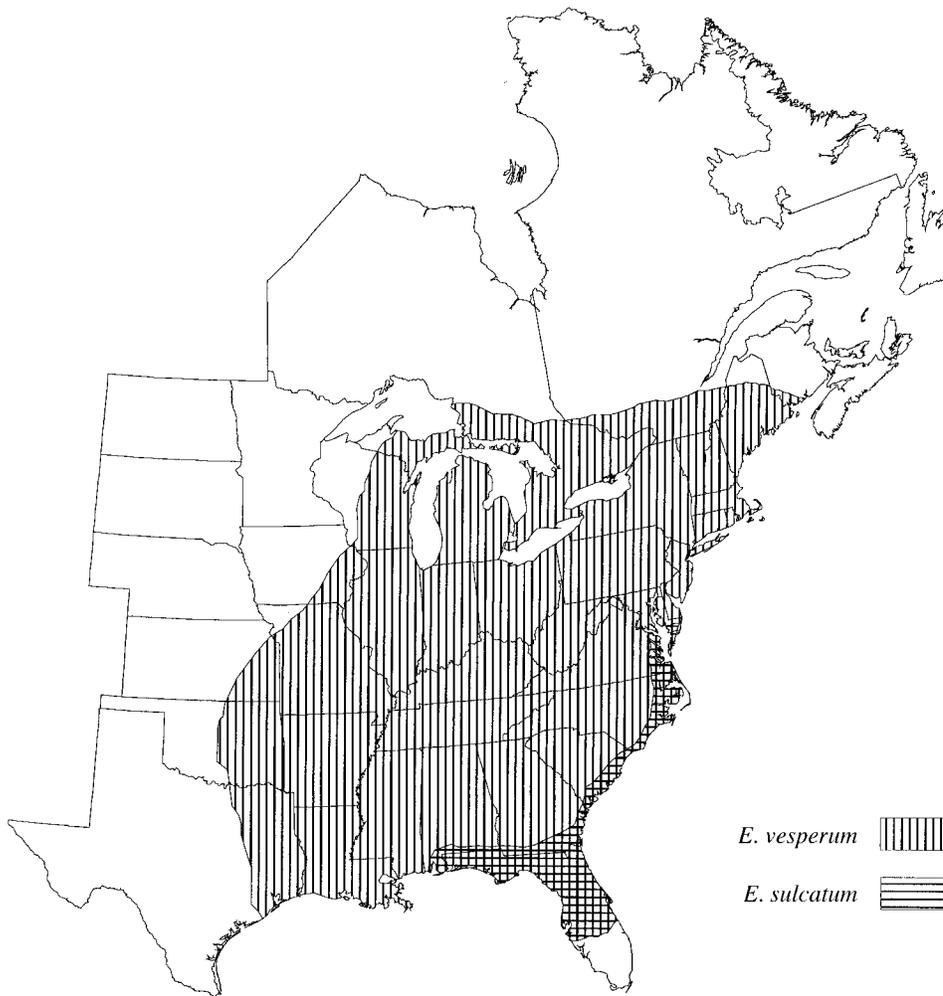


FIG. 5. Distributions of *E. vesperum* and *E. sulcatum*. These two species were the result of a very recent speciation event (Fig. 2).

the southeastern USA. However, the two clades contain species that have very similar geographic ranges. The geographic information presented below is compiled from many sources (Walker 1953, Kormondy 1958, Garrison 1984, Dunkel 1990, 1992, Carpenter 1991, Donnelly 1992, Glotzhofer 1995, Tennessen et al. 1995, May and Carle 1996, Miller and Gustafson 1996, Westfall and May 1996, Brunelle 1997, Mauffery 1997, Paulson 1997).

Three of the four recent speciation events in the *antennatum-traviatum* clade involve species with similar distributional patterns. Fig. 5 presents the distributions for *E. vesperum* and *E. sulcatum*, which are sister species resulting from a very recent speciation event (Fig. 2). *E. vesperum* has a wide distribution covering much of eastern North America, whereas *E. sulcatum* is confined to the southeastern coastal plain from Alabama to Virginia (Fig. 5). The species pairs *E. signatum*–*E. pollutum* and *E. traviatum*–*E. pallidum* (Fig. 2) display similar distribution patterns within each pair, with the

first species listed in the pair having a wide distribution and the second being restricted to the southeastern coastal plain. This distribution pattern suggests either classical allopatric speciation or speciation via the isolation of peripheral populations to the coastal plain during the radiation in these lineages (Mayr 1947, 1963, 1982, García-Ramos and Kirkpatrick 1997), with secondary invasion of the coastal plain by the wide-ranging species after reproductive isolation was established. In the *dubium*–*pictum* triplet, *E. dubium* and *E. concisum* have distributions similar to *E. sulcatum* (Fig. 5), but *E. pictum* is distributed only along the coastal plain from the Pine Barrens of New Jersey to Cape Cod in Massachusetts (Westfall and May 1996). Again, an allopatric mode of speciation is indicated for the split creating *E. pictum*, but the precise mode generating the other two in the triplet is unclear.

The other species in the *antennatum-traviatum* clade that did not recently speciate have distributions as follows: *E. daeckii* and *E. weewa* have distributions re-

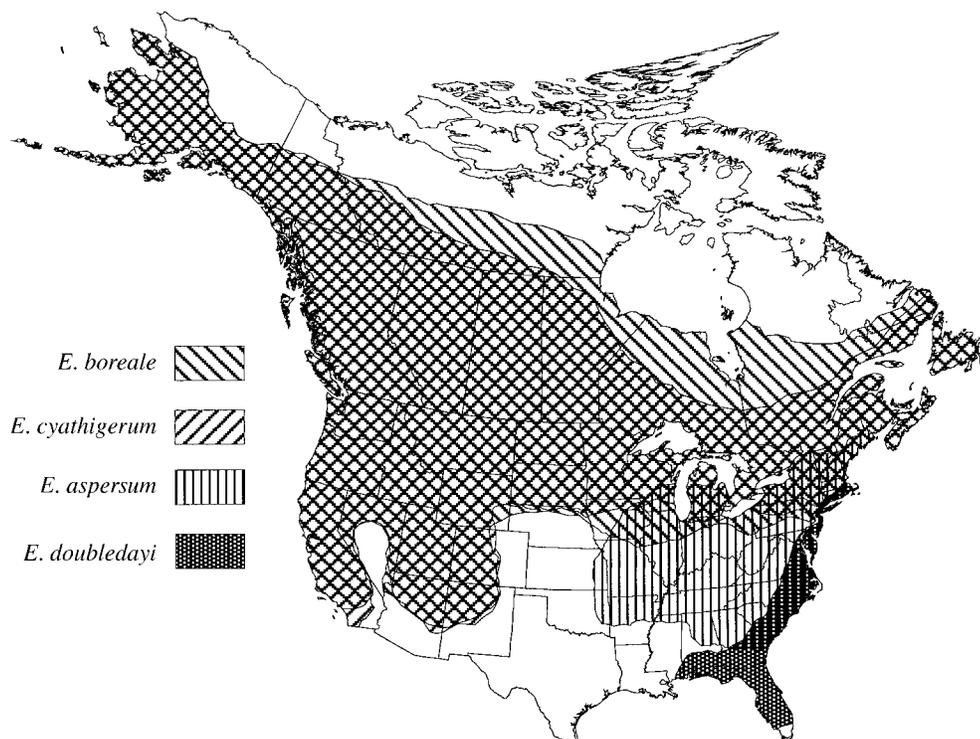


FIG. 6. Distributions of the four *Enallagma* species known to inhabit dragonfly lakes.

stricted to the southeastern coastal plain, with *E. daeckii* being found as far north as Massachusetts. The rest have wide-ranging distributions analogous to *E. vesperum*, except *E. antennatum* which does not extend south of the line of states from Virginia to Colorado. Interestingly, *E. basidens* appears to have greatly expanded its range northward out of Texas during this century, until now it can be found from the Great Lakes to northern California (Glotzhober 1995, Westfall and May 1996).

In contrast, there is little geographic pattern to the distributions among species in the other primary clade. In the *carunculatum*–*geminatum* clade (Fig. 2), *E. civile* and *E. carunculatum* have widespread distributions across the continent, *E. anna* and *E. praevarum* are found primarily west of the Rocky Mountains, *E. aspersum* and *E. geminatum* have similar distributions across eastern North America (Fig. 6 for *E. aspersum*), and *E. doubledayi* is found in the coastal plain and piedmont regions from Massachusetts to Mississippi (Fig. 6). The species in the *laterale*–*minusculum* clade display a similar variation of distribution types: *E. boreale*, *E. cyathigerum*, *E. hageni*, and *E. ebrium* are widespread across the continent (e.g., Figs. 6 and 7), *E. vernale* has a smaller eastern distribution stretching from New England and Quebec to Michigan, *E. clausum* is a western species, *E. davisii* is found on the southeastern coastal plain (Fig. 7), and *E. minusculum*, *E. laterale* and *E. recurvatum* are found on the coastal plain from New Jersey north (Fig. 7). The radiation

that generated these two subclades did not leave a clear geographic signal like that in the species pairs of the other primary clade, although distribution patterns repeated across the phylogeny suggest that particular geographic areas (e.g., the coastal plains of the southeast and New England) have promoted isolation of populations from the rest of the continent.

DISCUSSION

A substantial fraction of extant species in the North American *Enallagma* clade are the result of a very recent radiation (Figs. 2 and 3), but we can presently only infer the causes of that radiation. This is an area of North America that has been periodically glaciated during the Pleistocene (Davis and Jacobson 1985, Muller and Calkin 1993, Martini 1997). It seems likely that the radiation occurred in response to one of these recent glacial cycles, since the explosive portion of the radiation creating 17 species from two progenitors occurred in the subclade that now has its center of diversity in New England. The similarity in levels of sequence divergence for the recent splits in the *antennatum*–*triviatum* clade to those in the *carunculatum*–*minusculum* clade also suggests that the speciation events in the southeastern US occurred at the same time as the explosive radiation in the other clade.

Based on our molecular data, we estimate a maximum date for this radiation at somewhere between 52 000 and 380 000 years ago. These figures probably overestimate the true date. Haplotypes for species in the radiating clades do not branch together on the clad-

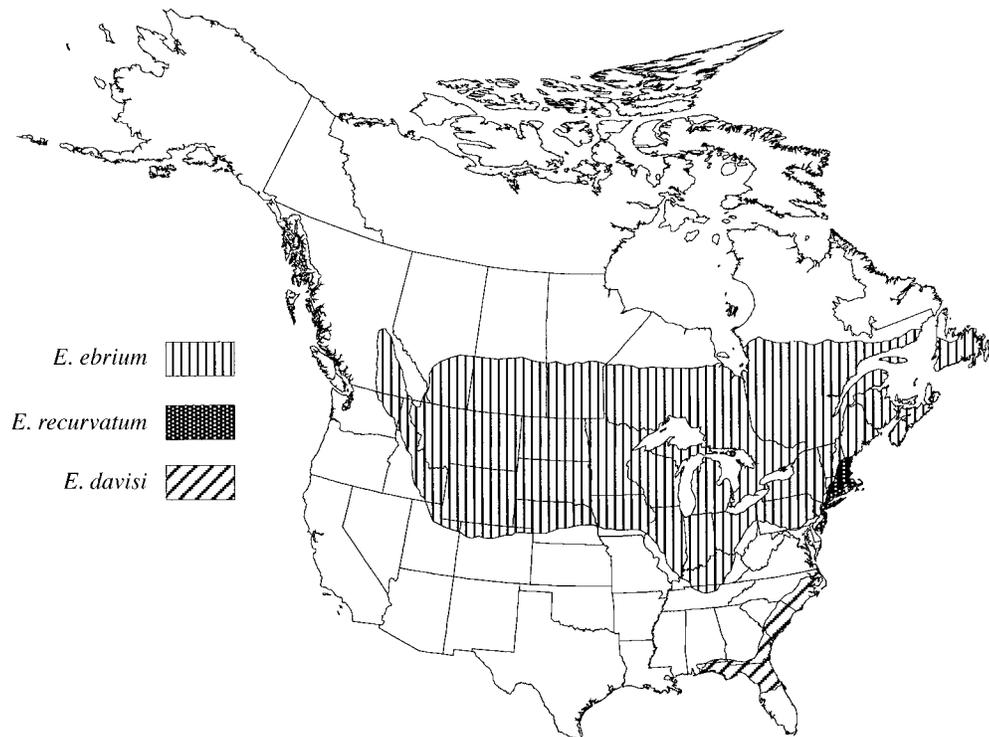


FIG. 7. Distributions of three *Enallagma* species in the *laterale*–*minusculum* clade that inhabit fish lakes. All other fish-lake species in this clade except *E. clausum* have distributions that are similar to these three species (see *Biogeographic assemblage structure* for specifics).

ogram of gene sequences (i.e., there was substantial lineage sorting of haplotypes into species during the radiation), suggesting that the mitochondrial haplotypes present in species today arose before the radiation that gave rise to the extant *Enallagma* fauna (J. M. Brown et al., *unpublished manuscript*). It seems logical that the radiation occurred following the last glacial cycle 15 000 years ago, since this glacial advance would have denuded much of northern North America, and particularly New England (see below) for hundreds of years. At present, this is only conjecture, but it can be tested by developing a more precise date using molecular data from more rapidly evolving loci. If true, the glacial advance may have caused the extinction of some number of *Enallagma* species in northern North America, with only the three progenitors of extant lineages in the *carunculatum*–*minusculum* clade surviving in the glacial refuge lakes that existed on the continental shelf at the time (Hocutt and Wiley 1986, Billington and Hebert 1988, Bernatchez and Dodson 1990, 1991, Todd and Hatcher 1993, Stemberger 1995).

The radiation of the *carunculatum*–*minusculum* clade probably occurred as the two progenitor species recolonized the ponds and lakes that formed as the glaciers retreated. It is, first, interesting to note that *E. durum*, the one surviving lineage that did not radiate during this episode, is now a coastal plain species, and is the only *Enallagma* associated with brackish estu-

aries (Westfall and May 1996). If this species had a similar habitat affinity during the radiation period, this affinity would have maintained the species on the borders of the ice sheet on the coast and also prevented it from recolonizing inland lakes during the glacier's retreat. This may explain why this lineage did not rapidly speciate like the other two in the clade.

Adaptation played a role in the radiation of the two other lineages within the clade. Evolutionary reconstruction of habitat affinities using parsimony criteria indicates that these two progenitor species coexisted with fish. Outgroup analysis provides the same conclusion; all species in the *antennatum*–*triviatum* clade, the outgroup for the *carunculatum*–*minusculum* clade, coexist with fish. While most of the species resulting from the radiation also coexist with fish, four appear to have descended from at least two and possibly three independent invasions of the dragonfly-lake environment (Fig. 2), and a large amount of adaptive evolution was associated with these habitat shifts (Fig. 4, and McPeck 1995a, 1997, 1999, McPeck et al. 1996). Experiments have shown that *Enallagma* adults are unable to discriminate between fish and dragonfly waters (McPeck 1989), but dispersal among lakes is currently rare because adults are very philopatric to the water bodies from which they emerge (McPeck 1989). However, females of fish-lake *Enallagma* do sometimes oviposit in dragonfly lakes (M. A. McPeck, *personal ob-*

servations). As these two *Enallagma* progenitors colonized the ponds and lakes that formed as the glaciers retreated, eggs were deposited in some ponds and lakes where dragonflies were the top predators. Most of these founder populations in this inhospitable habitat would have been driven extinct, as they continually are today (M. A. McPeck, *personal observation*). However, at least two of these founder populations adapted to this new selective environment before being driven extinct, thus permitting their persistence (Gomulkiewicz and Holt 1995). Both philopatry to the natal lake and adaptation to a new environment would have contributed to reproductive isolation between these new lineages and their progenitors.

The mechanisms giving rise to the rest of the species during the radiation are uncertain. The remaining species were the product of speciation events occurring within the fish lake habitat. The recent speciation events giving the species pairs in the *antennatum*–*triviatum* clade were probably the result of non-adaptive differentiation of peripheral isolate populations on the coastal plain (Figs. 5–7), given that the wide-ranging species in each pair is now sympatric with the coastal plain endemic, and in many cases the widespread species are as or more abundant in coastal plain lakes than the coastal plain endemic species: e.g., in coastal plain lakes of New Jersey and Massachusetts, *E. vesperum*, a widely distributed species, is generally 10–30 times more abundant than *E. pictum*, a coastal plain endemic (M. A. McPeck, *unpublished data*). Such speciation is also evident in other aquatic taxa inhabiting this part of North America (Hocutt and Wiley 1986, Avise 1992).

The geographic distributions of species in the *carunculatum*–*geminatum* clade provide no clues as to the geographic affinities of the clade; *E. anna* and *E. praevarum* are both found in the western half of the continent, *E. aspersum*, *E. doubledayi* and *E. geminatum* are eastern species, and *E. civile* and *E. carunculatum* have distributions from coast to coast.

In contrast, species distributions in the *laterale*–*minusculum* clade indicate that the clade radiated in northeastern North America, and probably specifically in New England. Only *E. clausum* is found exclusively in western North America (Garrison 1984). *E. boreale* and *E. cyathigerum*, the two dragonfly-lake species, are distributed across the entire continent (Fig. 6); the range of *E. boreale* extends into Siberia, and *E. cyathigerum* has a circumpolar distribution. The remaining seven fish-lake species have primarily eastern distributions. *E. hageni* and *E. ebrium* have similar distributions extending from New England and the maritime provinces of Canada to the Rocky Mountains (Fig. 7). *E. vernale* has a smaller distribution ranging from Quebec and New England to Michigan. *E. recurvatum*, *E. laterale*, and *E. minusculum* are all found only on the coastal plain north from New Jersey, and *E. davisii* is found on the southeastern coastal plain. Geographic isolation can account for separation of the coastal plain

species from the interior continental species, but such geographic isolation cannot account for the differentiation of the northeastern coastal plain species or of the interior species from one another. These seven species also have very similar larval morphologies, and all of these species found within a given region coexist in local lakes (M. A. McPeck, *unpublished data*). The only substantial differences between the species are in the morphologies of the male abdominal appendages used to grasp females during tandem pairing (M. A. McPeck, *unpublished manuscript*). These are the appendages used by females to identify the species of potential mating partners, and thus are part of the proximate mechanism generating reproductive isolation among species (Paulson 1974, Robertson and Paterson 1982).

Also, available evidence suggests that locally coexisting *Enallagma* species in fish lakes are not ecologically diversified to any degree. Larvae of all *Enallagma* species within a fish lake are found in the same microhabitats; 5–7 species can usually be taken with one 15 cm diameter stovepipe sample (McPeck 1990a, 1998) or one dipnet sweep through a littoral weedbed (Johnson and Crowley 1980, and M. A. McPeck, *personal observation*). Also, larvae of coexisting fish-lake species from across the entire genus are behaviorally very similar (Pierce et al. 1985, McPeck 1990b), and display similar growth and mortality rates in both natural populations and controlled field experiments (McPeck 1990a, 1998).

In fact, the assemblage of *Enallagma* species in fish lakes appears to be organized in similar fashion to that proposed by Hubbell (1979, 1997; *in press*; Hubbell and Foster 1986) for tropical forest trees. Hubbell has argued that tropical forest trees are ecologically quite similar, and thus the total number of trees, regardless of species, in a given area is the regulated parameter in tropical forest communities, and not the abundances of individual species. Consequently, the relative abundances of individual species fluctuate randomly under this total abundance constraint (Hubbell 1979, 1997; *in press*; Hubbell and Foster 1986). In addition to the lack of clear ecological differences among fish-lake *Enallagma* species, almost all species in the local fauna can be found at every lake within a local area. Relative abundances of species differ dramatically among lakes (McPeck 1990a, 1998, and M. A. McPeck, *unpublished data*), but these differences do not appear to covary with physical or biotic gradients among lakes. We hypothesize that, like tropical tree assemblages, these among-lake differences in relative abundances are the result of largely random processes operating among ecologically similar species. This does not imply that *Enallagma* abundances are not regulated within a lake; field experiments have shown that both fish predation and resource competition impose strong, negative density dependence on *Enallagma* abundances in fish lakes (McPeck 1990a, 1998). But because species are eco-

logically so similar, the parameter that is probably regulated in a lake is the total absolute abundance of all *Enallagma* larvae, regardless of species, and not the absolute abundance of each individual species. Analogous statements can be made for the *Enallagma* species within the dragonfly-lake habitat (McPeck 1990a, 1998).

The lack of ecological differentiation among extant species also implies that the radiation within the fish-lake habitat was not driven by species filling unique ecological niches (i.e., not an adaptive radiation). If this radiation followed our usual notions about how such events are caused, new *Enallagma* species would have been created by their filling vacant ecological niches as they colonized the lakes formed by the retreating glaciers (e.g., Erwin et al. 1987, Schluter and McPhail 1992, Schluter and Nagel 1995, Erwin and Pan 1996, Schluter 1996, Losos et al. 1998). However, the lack of ecological differentiation among extant species forces us to reject such a mechanism. It also seems unlikely that the splitting of the coastal plain and continental interior species was the result of adaptation to different ecological conditions in these two areas, since most of the continental interior species also thrive on the coastal plain (Dunkle 1990, 1992, Carpenter 1991, Westfall and May 1996; M. A. McPeck, *unpublished data*).

An alternative to these adaptive scenarios is the possibility that this radiation was driven by differentiation of the specific mate recognition system in the small populations that formed as the glaciers retreated and not any adaptive differentiation. *Enallagma* females choose males based on the sizes and shapes of the clasper appendages (i.e., cerci) used by males to hold females while in tandem and prior to mating; females refuse to mate with males having the wrong shaped appendages (Paulson 1974, Robertson and Paterson 1982). Lande (Lande 1981, 1982, Lande and Kirkpatrick 1988; see also West-Eberhard 1983, Seger 1985, Turner and Burrows 1995, Payne and Krakauer 1997) proposed a series of models in which genetic drift in female choice could lead to population differentiation in mate recognition and thus speciation via sexual selection. Paterson's (1978, 1993) specific mate recognition hypothesis posits similar predictions. Such evolutionary processes could have occurred in the populations formed immediately following the glacial retreat. In these populations, there may have been relaxed pressures for strong mate discrimination because few if any other species were present. Also, population sizes may have remained small for many generations as the populations built up. Small population size would have permitted genetic drift in female preferences for male cerci morphology, which in turn would have imposed selection for corresponding changes in cerci size and shape (Lande 1981, 1982). Because the evolutionary impetus for change is genetic drift in female choice, populations in different lakes would have differentiated

randomly. Analyses of the evolution of cerci morphology for all 38 North American *Enallagma* show little phylogenetic signal in how this structure has evolved, and its evolution is most consistent with a punctuational model in which all change occurs at the time of speciation (M. A. McPeck, *unpublished manuscript*). Moreover, because reproductive isolation would have been generated directly by differentiation in female mating preferences, the resulting sibling species would not necessarily be ecologically differentiated at all. Obviously, these hypotheses must be rigorously tested, but this scenario is completely consistent with all available ecological, phenotypic, and biogeographic data, and thus deserves serious scrutiny. We are currently testing these hypotheses.

If this nonadaptive scenario is true, the great disparity in species richness between fish and dragonfly lakes must then be examined from both ecological and macroevolutionary perspectives. The simplest explanation for the disparity in species richness between the two lake types is that the *Enallagma* clade has only recently invaded the dragonfly-lake habitat and insufficient time for significant diversification has elapsed. However, this explanation is overly simplistic and ignores more dynamical explanations based on extinction and speciation rates relative to the number of available niches in each lake type. The discontinuity in the number of lineages over time, as seen in Fig. 3 for the *Enallagma* clade, is characteristic of a rapid burst of speciation, but patterns and rates of extinction do not leave such characteristic signals in the data that can be extracted from phylogenies (Kubo and Iwasa 1995, Nee et al. 1995). Without an adequate fossil record, which does not exist for the *Enallagma*, we cannot conclude that the extant lineages in dragonfly lakes are the first successful invaders. *Enallagma* lineages may have inhabited this niche throughout the history of the clade, but these lineages may have been extirpated during the event that triggered the most recent radiation (e.g., mass extinction followed by a radiation of the two lineages recolonizing the area [cf. Erwin et al. 1987, Erwin and Pan 1996]).

Also, the background extinction rate (sensu Raup 1991) may be intrinsically higher for the dragonfly-lake habitat. The bodies of water in which dragonflies are the top predators are generally smaller and shallower than lakes supporting fish populations (Tonn and Magnuson 1982, Rahel 1984), and are probably much more prone to drying during severe droughts (e.g., Stahle et al. 1998, M. A. McPeck, *personal observation*). Because *Enallagma* larvae are generally univoltine and thus require 10–11 mo to complete the aquatic larval phase of their life cycle, a drought that caused the drying of all dragonfly ponds and lakes in a region for only one year could cause the extinction of species occupying this environment. (It is tempting to speculate that this may be why dragonfly-lake species are missing from the southern plains states of the USA [Fig. 6].)

If extinction rate is higher in the dragonfly-lake habitat than in fish lakes, and if nonadaptive speciation rates are comparable in the two environments because the mechanisms are similar, the macroevolutionary equilibrium number of species should be higher for fish lakes.

Combining the ecological, phylogenetic and biogeographic data available for *Enallagma* provides a complex picture for the development of the species assemblages inhabiting eastern North America waters and suggests many new hypotheses to consider about the development of local and regional community structure in natural assemblages. Assemblages in ponds and lakes in the northeastern United States and Canada were the result of a recent radiation from two progenitor species that greatly diversified in their ancestral fish-lake habitat without ecologically differentiating to any substantial degree and that invaded or recolonized the dragonfly-lake habitat by evolving new adaptations to cope with a new top predator. In contrast, assemblages in southeastern US waters resulted from a more gradual buildup of species within the fish-lake habitat and the apparent migration of dragonfly-lake species in the radiating clade southward. This difference between the two major clades in the genus offers an exciting opportunity to test whether the rate of diversification and the degree of ecological differentiation are correlated.

Also, if the radiation within the fish-lake habitat was the result of nonadaptive speciation processes, the extant assemblage may consist of many ecologically similar species which are all currently contesting only one available niche; this hypothesis is consistent with all currently available data. Competitive exclusion is a very slow process when species are ecologically very similar (Shmida and Ellner 1984, Shmida and Wilson 1985, Hubbell and Foster 1986); the extant assemblage of species may have been and continues to be losing species at an exceedingly slow rate that is imperceptible over the time spans that humans have catalogued species compositions (roughly 100 yr for this group). Moreover, mixing due to migration of species may have resulted in local assemblages across eastern North America that are well above the expected ecological equilibrium of one species per niche. These hypotheses can be tested (1) by comparing the relative abundances of species across lakes within a biogeographic region to the theoretical distribution expected for a system in which all species are ecologically equivalent (Hubbell 1997, Hubbell, *in press*), and (2) by experimentally transplanting species between lakes where they have high and low relative abundances and comparing their performances. We are currently conducting such studies.

Tests of such hypotheses in many different taxa at many trophic levels within communities will be critical if we are to develop more realistic models of community assembly and faunal buildup than currently ex-

ist. Speciation can occur by myriad adaptive and nonadaptive processes (Mayr 1942, 1947, 1963, Simpson 1944, Stebbins 1950, 1971, Dobzhansky 1970, White 1978, Grant 1981, Otte and Endler 1989, King 1993), and these different speciation modes can have profound consequences for the structure of local communities and regional species pools. Ecologists must begin to consider more explicitly the ecological implications of the evolutionary processes that gave rise to the species we study today and that shaped the abilities of these species to perform in the ecological interactions we currently examine.

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