Ecological Diversification and Community Structure in the Old World Leaf Warblers (Genus Phylloscopus): A Phylogenetic Perspective

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ECOLOGICAL DIVERSIFICATION AND COMMUNITY STRUCTURE IN THE OLD WORLD LEAF WARBLERS (GENUS *PHYLLOSCOPUS*): A PHYLOGENETIC PERSPECTIVE

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Abstract.—I investigated the historical basis for variation in regional species diversity. I used a molecular phylogenetic analysis within a single genus of birds (the Old World leaf warblers, genus *Phylloscopus*) in conjunction with ecological studies in Europe, the Himalayas, and Japan to evaluate the importance of historical events in shaping the present constellation of morphology and behavior in the three different regions. The relatively depauperate assemblages have different histories. In Japan, there was invasion of several lineages, which have more closely related species elsewhere in Asia, whereas in Europe there was also limited in situ speciation. Much of the structure of peripheral communities is attributable to invasions from species-rich Asia, with little in situ morphological diversification. Within the *Phylloscopus* there are several phylogenetic clades with nonoverlapping size distributions. Major ecological and morphological shifts occurred early in the history of diversification within the group, and rarely since.

Key words.—Community structure, comparative method, ecological invasions, habitat selection, molecular phylogeny, regional diversity, speciation.

The number of species in a community depends on features local to the community (e.g., resource abundance, competition, and predation), the region in which the community is embedded (a species' pool able to disperse into the community), and history (rates of speciation, time the community has been present). The balance between a regional process (colonization) and local process (extinction) in determining local diversity is exemplified in the equilibrium theory of island biogeography (MacArthur and Wilson 1967), but similar processes should apply to continents. For example, comparisons of the number of species in matched habitats on different continents find consistent effects of habitat type indicating the importance of local processes (Schluter 1986), but also consistent differences between regions in species diversity across habitats (Ricklefs 1987). The causes for regional differences may vary, depending on differences in age, rates of speciation and immigration, and history of extinction (Schluter and Ricklefs 1993). The focus here is on evaluating the importance of these historical and regional processes as they affect local diversity of three *Phylloscopus* warbler communities in Europe, Kashmir, and Japan.

Warbler communities in different parts of Asia often consist entirely of members of the genus *Phylloscopus*. Thus, importance of history in affecting structure of these assemblages can be assessed by examining the history of this single genus. A molecular phylogeny will be used to investigate historical and regional processes of colonization, in situ speciation, and time, in the buildup of the communities. More generally, rates and patterns of adaptive diversification in different regions can be related to special local conditions, and explanations sought for the absence of particular species (Losos 1992). Some attempt has been made to evaluate the importance of regional influences on speciation rates and the generation of species diversity in the New World Warblers (Mengel 1967; Greenberg 1979; Bermingham et al. 1992), but this has been hampered by the lack of a good phylogeny for the group.

I compare the breeding *Phylloscopus* assemblages of Finland, Kashmir (Himalayas), and Japan to ask the following: (1) To what extent are the assemblages similar in species diversity and morphology? (2) How long have the communities been present in each location? (3) How much in situ speciation has there been? (4) How much species exchange between the three communities has there been? (5) How have rates and patterns of morphological evolution varied within and between communities?

MATERIALS AND METHODS

The *Phylloscopus* warblers are a largely temperate genus of arboreal insectivorous warblers, breeding throughout Eurasia and wintering in Africa and South Asia. More than 30 species have been described (Ticehurst 1938; Williamson 1974), of which 20 are included in the present study (Table 1). The *Phylloscopus* reach their highest local and regional diversity in the Himalaya, where up to nine species may breed at a single locality (Martens 1980). *Phylloscopus* of East Asia overwinter in southeast Asia (Williamson 1974; Ticehurst 1938); whereas species breeding in the western Himalaya overwinter in India (Ali and Ripley 1983). A relatively distinct *Phylloscopus* assemblage of four species occurs in Europe, which overwinters in Africa and the Mediterranean (Williamson 1974). In addition, there are several nonmigratory tropical species in southeast Asia (Williamson 1974; Higuchi and Kawaji 1989) and Africa (Sibley and Monroe 1990). I concentrate here on comparing breeding assemblages in mainland Japan (three species), Kashmir (eight species) and Finland (three species).

Phylogeny

I obtained DNA sequences for a contiguous portion of the cytochrome *b* gene of 910 bases for 23 specific and subspecific *Phylloscopus* taxa, and for single species from three related genera, *Regulus*, *Sylvia*, and *Cettia*, using the poly-

TABLE 1. Mean morphology (and standard errors) for *Phylloscopus* species. See text for discussion.

	Sample	Tarsus (mm)	Beak length (mm)	Beak width (mm)	Beak depth (mm)
pulcher	5	18.3 (0.3)	5.4 (0.48)	2.3 (0.04)	1.9 (0.04)
proregulus	5	16.4 (0.4)	4.7 (0.15)	2.4 (0.05)	1.9 (0.04)
inornatus	5	17.5 (0.3)	5.3 (0.20)	2.0 (0.05)	1.9 (0.04)
tytleri	5	17.5 (0.1)	7.3 (0.28)	2.2 (0.04)	2.1 (0.04)
affinis	5	19.0 (0.3)	5.7 (0.30)	2.1 (0.04)	1.9 (0.04)
griseolus	2	19.2 (2.5)	6.8 (0.36)	2.4 (0.10)	2.4 (0.08)
collybita abietanus	5	19.1 (0.8)	6.0 (0.24)	2.3 (0.06)	2.1 (0.05)
trochilus	5	19.2 (1.2)	6.4 (0.30)	2.5 (0.05)	2.3 (0.05)
magnirostris	4	18.7 (0.2)	6.7 (0.64)	3.0 (0.07)	2.8 (0.07)
tenellipes	5	19.0 (0.5)	6.3 (0.36)	2.9 (0.05)	2.9 (0.04)
borealis xanth.	5	18.7 (1.2)	7.4 (0.28)	2.9 (0.03)	2.9 (0.03)
trochiloides ludlowi	5	19.1 (0.2)	6.3 (0.32)	2.9 (0.05)	2.5 (0.03)
occipitalis	5	17.3 (1.2)	7.5 (0.39)	2.8 (0.06)	2.8 (0.04)
trivirgatus	5	18.9 (0.2)	5.9 (0.12)	2.7 (0.04)	2.8 (0.06)
coronatus	4	17.0 (0.5)	7.3 (0.69)	3.1 (0.09)	2.9 (0.06)
ijimae (Miyake)	5	18.0 (0.5)	7.4 (0.32)	3.0 (0.03)	3.0 (0.06)
cebuensis	5	18.0 (0.3)	7.2 (0.27)	3.1 (0.03)	3.1 (0.02)
sibilatrix	5	18.2 (0.8)	6.0 (0.24)	2.4 (0.03)	2.5 (0.03)
bonelli	5	18.4 (0.2)	6.3 (0.60)	2.5 (0.04)	2.5 (0.05)

merase chain reaction (White et al. 1989) and universal primers for amplification and sequencing (Kocher et al. 1989). The cytochrome *b* gene has proven to be a useful source of phylogenetic information for reconstructing evolutionary relationships among closely related species (Kocher et al. 1989). In a previous study that focused on the phylogeny of eight sympatric species in a breeding assemblage in Kashmir, these sequence data were shown to resolve major groups within the *Phylloscopus* (Richman and Price 1992).

Tissues for preparation of DNA for the following species, with collecting localities (Fig. 1) in parentheses, were provided by J. Tiainen, University of Helsinki: *Phylloscopus bonelli* (N. Turkey), *Phylloscopus collybita abietanus* (Nurmijarvi, S. Finland), *Phylloscopus trochilus* (Nurmijarvi, S. Finland), *Phylloscopus trochiloides viridanus* (Soderskar, S. Finland) and *Phylloscopus sibilatrix* (Lammi, S. Finland). *Sylvia melanocephalus* material was provided by P. Bertholdt, Max Planck Institute, West Germany. *Regulus satrapa* ma-
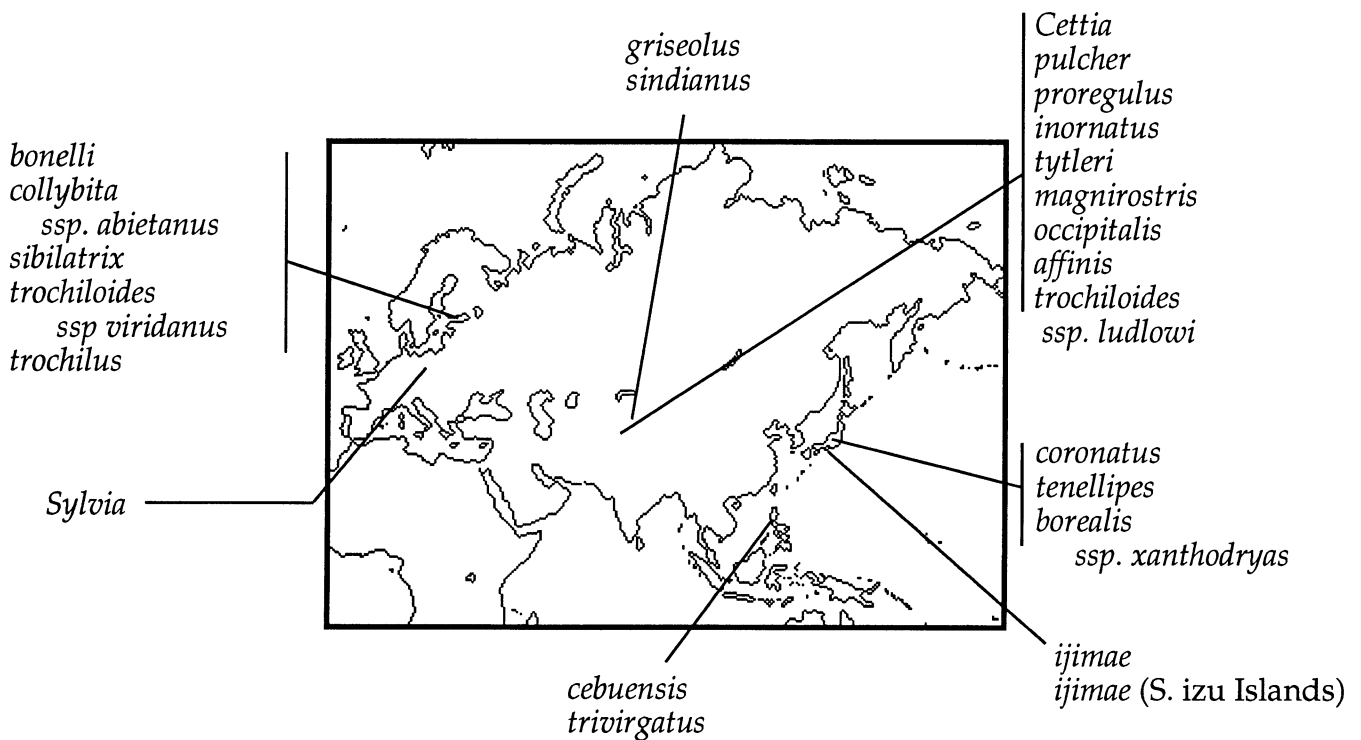

FIG. 1. Collecting localities for 24 sylviid taxa discussed in the text. See text for names of site localities. Not shown: *Phylloscopus borealis kennecotti* collected in Alaska by T. Price, and *Regulus satrapa*, collected by C. Wood in Washington State.
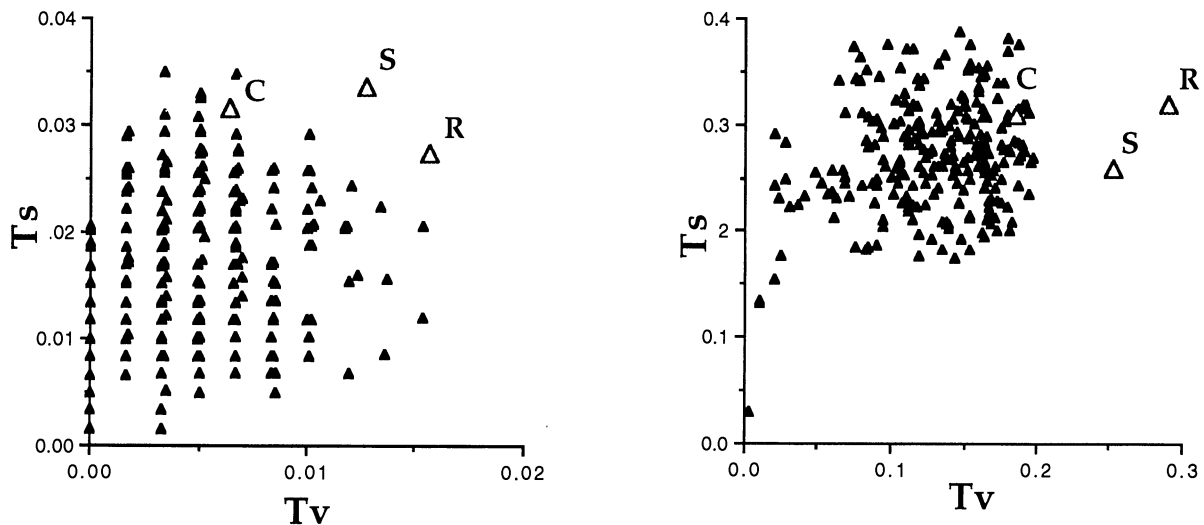
FIG. 2. Pairwise transition (Ts) distance versus transversion distance (Tv) for (A) third-position sites and (B) first- and second-position sites for *Phylloscopus* taxa included in phylogenetic analyses. The average distance between *Phylloscopus* taxa and each of three outgroup species is indicated by a hollow triangle; C, *Cettia*; S, *Sylvia*; R, *Regulus*.

terial was provided by C. Wood, Burke Museum of Natural History. Tissues of *Phylloscopus cebuensis* and *Phylloscopus trivirgatus* (both collected on Luzon Island, Philippines) were provided by L. Heaney, National Museum. Tissues for *Phylloscopus affinis*, *Phylloscopus griseolus*, *Phylloscopus sindianus*, *Phylloscopus magnirostris*, *Phylloscopus trochiloides ludlowi*, *Phylloscopus occipitalis*, *Phylloscopus tytleri*, *Phylloscopus pulcher*, *Phylloscopus proregulus*, *Phylloscopus inornatus*, and *Cettia fortipes* were collected by myself in May and June 1988 near Pahalgam, Kashmir state, northern India. Japanese species collected by H. Higuchi and myself in May and June 1989 were *Phylloscopus borealis xanthodryas* and *Phylloscopus coronatus* (Chichibu Prefecture, Honshu), *Phylloscopus ijimae* (Miyakejima Island, Tokyo Prefecture, Honshu), and *Phylloscopus tenellipes* (Mt. Fuji, Chichibu Prefecture, Honshu). Samples of putative *P. ijimae* (Higuchi and Kawaji 1989) from S. Izu Islands, Japan were provided by H. Higuchi, Wild Bird Society of Japan. *Phylloscopus borealis kennecotti* was collected in Alaska by T. D. Price in June, 1989.

Mitochondrial sequences containing a portion of the cytochrome *b* gene were obtained by the use of the polymerase chain reaction (PCR). DNA sources consisted of frozen or alcohol preserved muscle tissue, or dried blood. DNA from muscle was extracted as described in Kocher et al. (1989). DNA from dried blood was extracted as described in Kawasaki (1990). Methods used for amplification and sequencing are described in Richman and Price (1992). Intraspecific variation was found to have no effect on analysis of phylogenetic relationships of specific taxa in the *Phylloscopus* (Richman and Price 1992), and here I used single sequences for all species, with the exception of inclusion of subspecific taxa for *P. borealis*, *P. trochiloides*, and *P. ijimae*. Sequences obtained are deposited in GenBank (accession numbers L77120-77145).

Phylogeny Estimation.—Analysis of DNA sequence data was performed using both parsimony and distance methods. For parsimony analysis, I used the software package PAUP

3.1 (Swofford 1989). A combination of transversion parsimony and weighted parsimony analyses were used. Most observed differences were at third-position sites, and the number of observed transitions among species of *Phylloscopus* at third-position sites is similar to that observed for more distant intergeneric comparisons, indicating rapid saturation for transitional changes within the genus, whereas the number of the more slowly accumulating transversional changes is not similarly affected (Fig. 2). Nevertheless, for some closely related taxa, the accumulation of transitions at third-site positions did not approach saturation. For these portions of the phylogeny, a weighted parsimony analysis including third-site positions was performed, with transversions weighted 3 to 1 relative to transitions.

Distance analyses were performed using the program NEIGHBOR in PHYLIP (Felsenstein 1990), in which the entry order of each taxon was varied over several trials. Because transitional changes are largely saturated, the distance measure used considered only transversion differences. Distances were corrected for multiple substitutions (Kimura 1980). Again, for several comparisons among closely related taxa, transitions did not approach saturation, but inclusion of transitions did not affect the topology obtained in these instances.

Bootstrap resampling was performed for both methods. Bootstrapping of the parsimony tree was performed in PAUP (Swofford 1989). Bootstrapping of the distance tree was performed using PHYLIP. One hundred resampled data sets were generated using BOOTSEQ, these were then converted to matrices of pairwise distances, each matrix was analyzed using NEIGHBOR and then the consensus of the 100 trees obtained using CONSENSE. For subspecific comparisons, and for comparisons between specific taxa differentiated by few transversional differences (Richman and Price 1992), bootstrap values were obtained using distances calculated using the Kimura 2 parameter model (Kimura 1980), which includes transitions as well as transversions.

Habitat Associations and Altitudinal Distributions

Data on the ecology of species in Finland and Kashmir were taken from Tiainen et al. (1983) and Price (1991), respectively. I collected data for Japan in June 1989 in Chichibu Prefecture, Honshu. I visited several locations along an altitudinal gradient and recorded the number of singing males at each location. To do this, I walked slowly along a 1-km route through suitable habitats.

Morphological Measurements

Morphological measurements of wing, beak, and tarsus were made on museum specimens and private collections. Five males of each species were measured for tarsus length, beak length anterior to the nares, and beak width and depth measured at the same point as beak length. In a study of the Kashmir species, Price (1991) extracted three principal components from the correlation matrix of six morphological measurements (wing-length and weight in addition to the four measurements above), using the species' means of the Ln-transformed data. Included in the analysis were the eight Kashmir *Phylloscopus* plus *R. regulus*, which is the other arboreal warblerlike species. There were strong correlates with ecological variables: PC1 (body size) correlated with prey size, PC2 (a tarsus length to beak size ratio) with habitat choice, and PC3 (beak shape) with feeding method. Recalculating the principal components using only the three beak and one tarsus measure gave the same results and interpretations (unpubl.). Because ecological measurements are not available from Finland or Japan, scores on these three principal-component axes provide the best available measure of adaptive differentiation between the species. Accordingly, to compare morphological attributes among all species, I projected species' means on to the components of morphological variation obtained from the Kashmir assemblage. To assess the effect of sample and measurement error, I performed additional analyses using data provided by J. Tiainen (unpubl.), which did not include all species considered here. To the extent the two data sets could be compared, conclusions were unaltered from those presented here.

Analysis.—I assess change on the tree through the use of Felsenstein's (1985) method of independent contrasts. This method estimates the amount of evolution that has occurred between sister nodes (or species) on the tree, scaling by the standard deviation of change expected under a Brownian motion model. The method is directly related to ancestral reconstruction by the use of squared change parsimony (Maddison 1991). Large contrast values indicate rapid or large evolutionary change at a particular point in the phylogeny. The sensitivity of these analyses of evolutionary change to errors in phylogeny was assessed by application of the contrast method to trees derived from bootstrapped data sets. To assess whether observed patterns of change within the tree differed from that expected by chance, the contrast procedure was repeated for the same 100 bootstrap topologies, but the identity of species (and their trait values) to tips were randomly assigned without replacement.

RESULTS

The number of species that occur in a region and the number found in particular habitats are associated. In Japan and Finland, two species occur largely or exclusively in coniferous habitat and one species in deciduous habitat (Tiainen et al. 1983, Richman, pers. obs.), whereas in Kashmir three species occur in conifer and four species occur in deciduous habitat (Price 1991). For each of the three sites, *Phylloscopus* warblers are the only arboreal warblers present. Two conclusions are evident. First, regional diversity has failed to converge across the three regions. Second, the dependency of local on regional diversity implies that an understanding of the region in which the assemblage is embedded is needed to understand fully local diversity.

Phylogeny

The parsimony (Fig. 3) and distance (Fig. 4) methods find similar trees, although the parsimony tree is less resolved. Unresolved aspects of the parsimony tree correspond to less well-supported aspects of the distance tree, as assessed by bootstrap resampling, particularly at the base of the phylogeny. In particular, the placement of the clade including *P. pulcher*, *P. proregulus*, and *P. inornatus* differs between the two trees, but the position of this group is poorly known for either tree. The placement of *trochiloides* taxa is ambiguous in the parsimony tree, but the grouping according to the distance method is consistent with previous taxonomic treatments (see below).

The phylogenetic analyses using molecular data identify several major clades, which have been previously described by taxonomists (Ticehurst 1938; Williamson 1974), who used characteristics such as color patterns and rictal bristles to classify the group. The classification of the *Phylloscopus* and points of disagreement between the schemes of the taxonomists and the molecular phylogeny are discussed in the Appendix.

Morphological Variation

Species that are closely related tend to be similar to each other in morphology (Fig. 5). For example, the smallest, and the largest species, as measured by PC1 form monophyletic groups. Species of intermediate body size (as measured by PC1) also tend to be closely related, although they are not monophyletic in phylogenetic analyses (Figs. 3, 4), and also differ from both the smaller and larger species along the other morphological axes. They tend to have relatively long tarsi and small beaks (PC2), and relatively long, narrow beaks (PC3).

The analysis of evolutionary change in morphology (Fig. 6) shows that the greatest change in overall size (Fig. 6, PC1, contrast 3) occurs deep in the tree, at the split between the clade of large warblers and the others. Size changes elsewhere in the phylogeny are usually quite small by comparison. Large changes at the base of the tree are also inferred for beak shape (Fig. 6, PC3, contrast 1) and in morphology associated with habitat selection (PC2, contrast 4). Variation within each clade for morphology is associated with habitat selection (Fig. 6, PC2, contrasts 4, 5, 8, 9, 15, 17, 18).

Large contrast values for each of the three principal components occur at the base of the phylogeny. The sensitivity of these results to uncertainty in the phylogenetic reconstructions was assessed by examining frequency of occurrence of

Regulus

Sylvia

Cettia

inornatus

proregulus

pulcher

affinis

griseolus

tytleri

collybita

sindianus

trochilus

sibilatrix

bonelli

magnirostris

tenellipes

borealis kennecotti

borealis xanthodryas

trochiloides ludlowi

trochiloides viridanus

occipitalis

trivirgatus

coronatus

ijimae

ijimae (S.izu islands)

cebuensis

Bootstrap values: 79, 58, 42, 37, 55, 100, 44, 100, 100, 98, 54, 80, 100, 68, 35, 100, 76, 78, 92, 80, 96
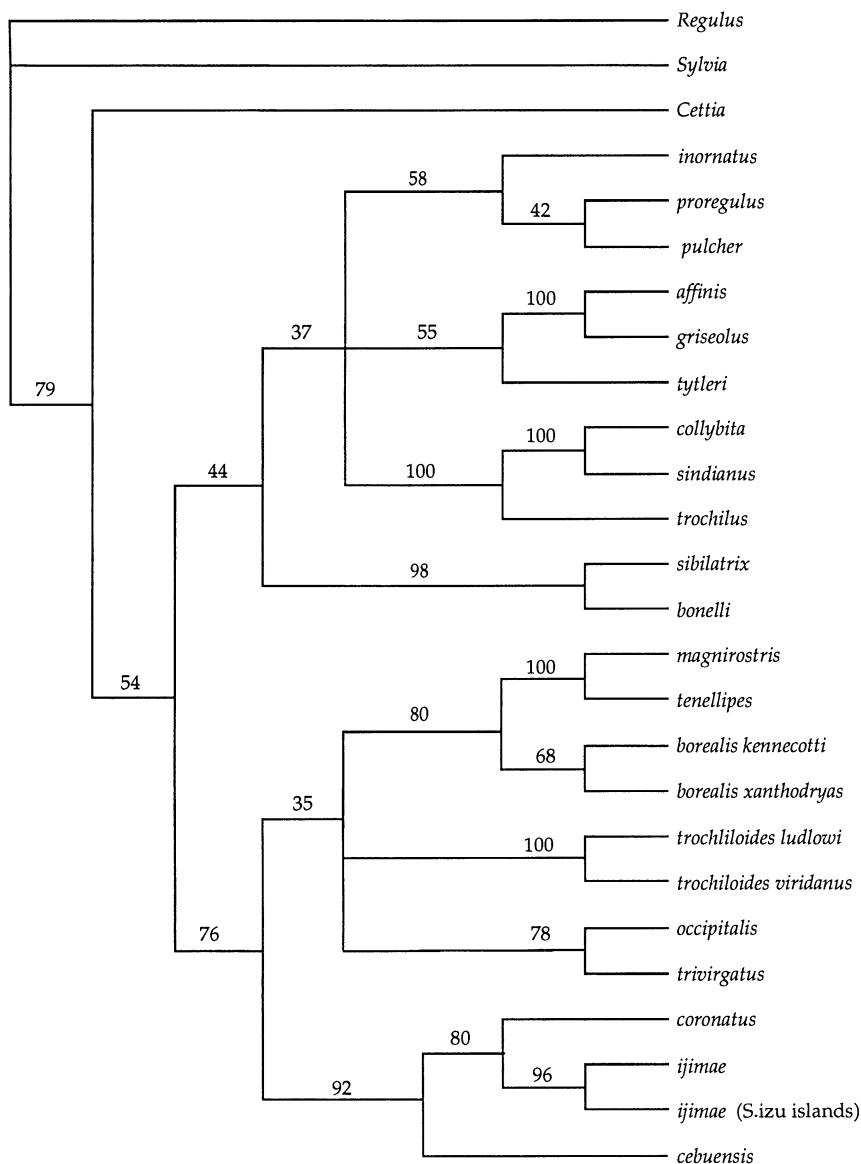
FIG. 3. Strict consensus tree for six most-parsimonious trees of length 404 found using PAUP 3.1. Only transversion differences were considered, with the exception of the clade consisting of *Phylloscopus magnirostris, tenellipes*, and *borealis* spp. For the latter group, weighted parsimony was used, with transversions weighted three to one relative to transitions. A heuristic search method was used, with 10 replicates of stepwise random addition of taxa with global rearrangements (SPR branch swapping option). Frequencies of occurrence of different groups in 100 bootstrap replicates are indicated at internal nodes. Bootstrap frequencies for the clade consisting of *P. magnirostris, tenellipes*, and *borealis* were obtained using weighted parsimony as described above.

these patterns in trees constructed from resampled data sets. I arbitrarily defined the base of the tree to include contrasts between internal nodes above which there are at least seven species in total. For example, there are four such contrast comparisons in Figure 6, of a total of 18. The largest or second largest contrast value in PC1 occurred for contrasts at the base of the tree in 99 of 100 replicates (mean rank, 1.5; SD, 0.3). Similarly, the largest or second largest value for PC3 occurred at the base of the tree in 92 replicates (mean rank, 1.7; SD, 1.1). These results can be compared with those obtained for trees in which *Phylloscopus* species were randomly assigned to tips. In 100 such trees the largest or second largest values of PC1 and PC3 never occurred at the base.

The results for PC2 differ somewhat, in that large contrast values occur higher in the tree, as well as at the base (see above). Thus, in bootstrap replicates the inference of a large change at the base is not as robust to resampling. Nevertheless, the largest value of PC2 occurs at the base in 18 bootstrap replicates, whereas this observation did not occur among the random trees. The inference that large changes occurred early is robust to error in the phylogeny and is not expected to occur purely by chance.

Geographical Comparisons

Japan.—The Japanese assemblage is composed of three *Phylloscopus* species that belong to the large body-size clade.
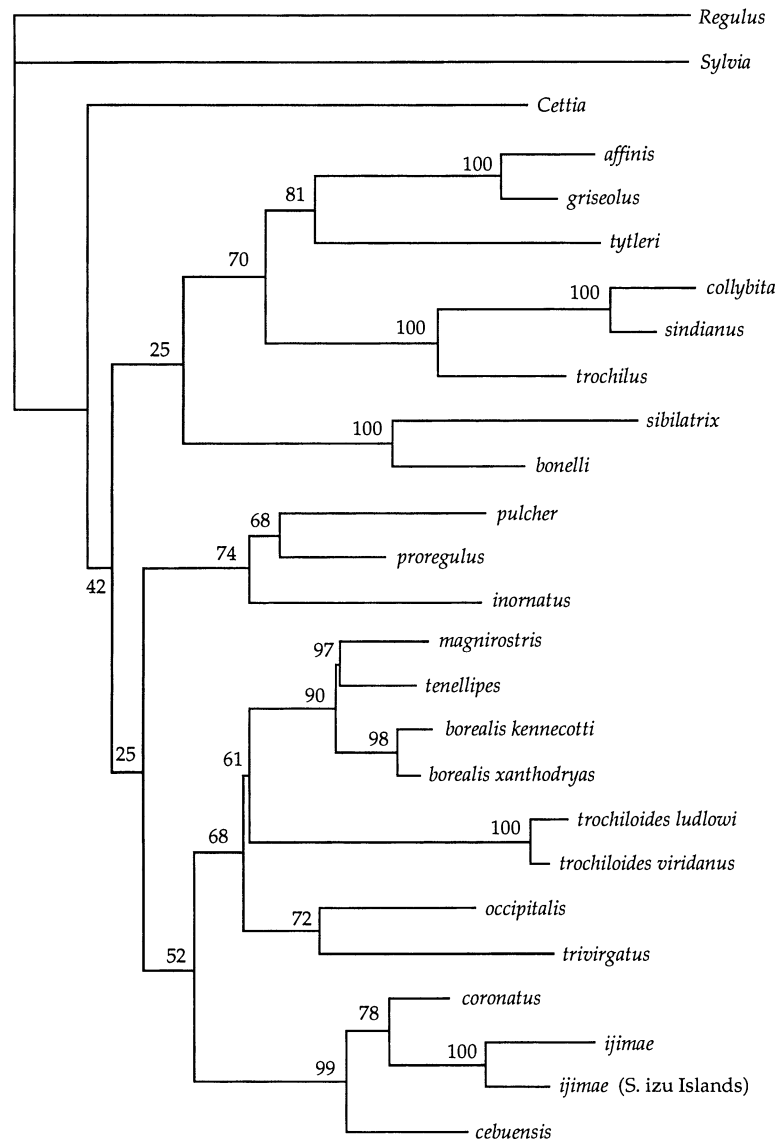
FIG. 4. Neighbor-joining tree using the Kimura (1980) transversion distance between taxa. Frequencies of occurrence of different groups in 1000 bootstrap replicates are indicated at internal nodes. Bootstrap frequencies for the clade consisting of *Phylloscopus magnirostris*, *tenellipes*, and *borealis* were obtained using the Kimura (1980) two parameter distance measure, which considers both transversions and transitions.

The Japanese species are not most closely related to each other, indicating the build-up diversity in this assemblage has been by repeated invasion and not in situ diversification. This hypothesis was evaluated using the more fully resolved distance tree. Inferred dispersal events for the preferred phylogeny, and three alternative scenarios that occurred in bootstrap resampling are presented in Figure 7. A total of three dispersal events are indicated in light of the preferred phylogeny (Fig. 7). Only two dispersal events are required under an alternative arrangement in which *coronatus* is the sister taxon to (*borealis magnirostris*, and *tenellipes*). However, this alternative is observed in only 4% of bootstrap data sets.

Europe.—The four European species are divided into two closely related pairs of intermediate size species ([*P. bonelli*, *sibilatrix*], [*P. collybita*, *trochilus*]) that are themselves not sister taxa (Figs. 3, 4). Although these species do occur as a monophyletic group in 15% of bootstrap replicates, such that it is not possible to rule out in situ origin of all European species, short branch lengths separating (*P. bonelli*, *sibilatrix*) from the initial diversification within the *Phylloscopus* (Fig. 4), indicate that the evolutionary history of the *Phylloscopus* in Europe is of similar age to that of the group in Asia.

Kashmir.—All three major body-size clades are represented in the Kashmir assemblage. In particular, the clade of small-bodied species absent from other regions is represented in Kashmir by three species. In addition, there are also three species of the large-bodied clade, and two species of intermediate size. Whereas the small-bodied species appear to have originated in Asia and failed to disperse to other regions, the intermediate-sized species are descended from what are exclusively European species suggesting that the presence of this clade in Asia is the result of a secondary invasion.
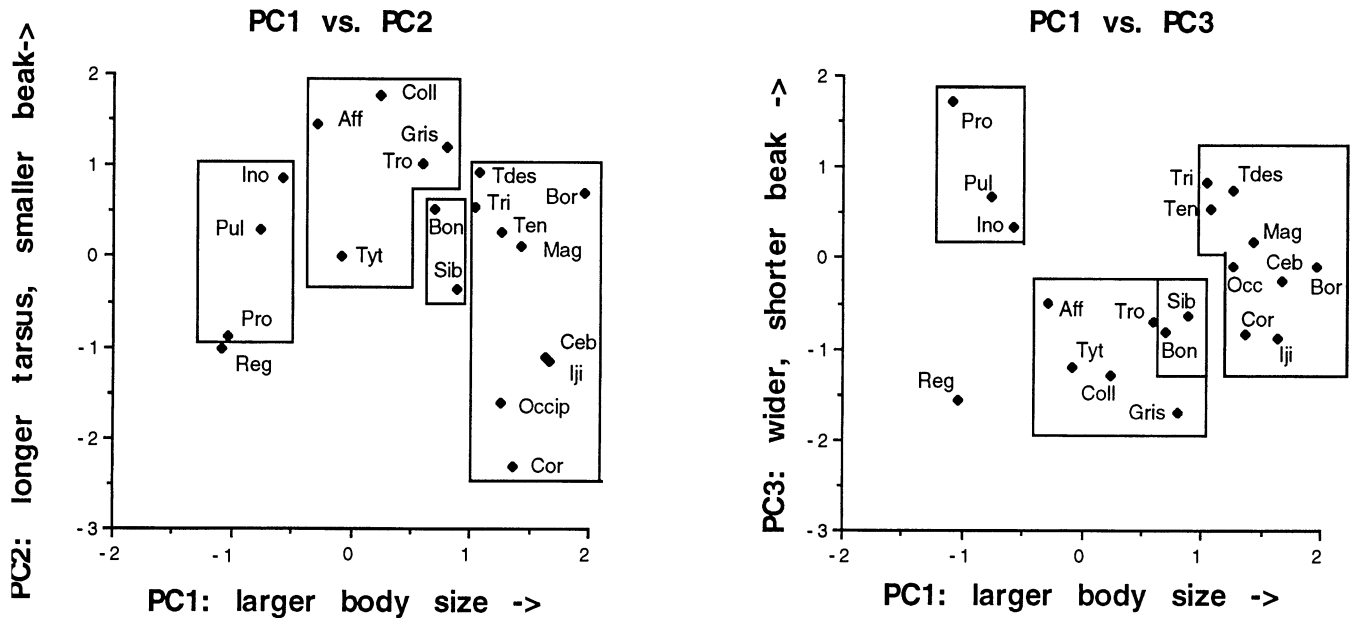
FIG. 5. Mean morphology for 18 taxa projected onto principal-component axes shown by Price (1991) to be significant predictors of habitat selection and prey size in a sympatric assemblage of *Phylloscopus* warblers in Kashmir. Key to species abbreviations: reg: *Regulus satrapa*, pro: *proregulus*, ino: *inornatus*, pul: *pulcher*, tri: *trivirgatus*, ten: *tenellipes*, tdes: *trochiloides ludlowi*, mag: *magnirostris*, ceb: *cebuensis*, occ: *occipitalis*, cor: *coronatus*, iji: *ijimae*, bor: *borealis*, aff: *affinis*, tro: *trochilus*, coll: *collybita*, tyt: *tytleri*, gris: *griseolus*, bon: *bonelli*, sib: *sibilatrix*. Left, PC1 versus PC2. Right, PC1 versus PC3.

DISCUSSION

Large morphological and ecological shifts have occurred rarely within the Phylloscopus, and it is therefore possible to identify the origin of major themes of ecological diversification within the genus. Body size (PC1) and beak shape (PC3) evolved rapidly and early in the history of the group. Large- and small-bodied species co-occur in mature forest habitats in Asia, whereas intermediate size species occur in edge and more open habitats (*P. affinis, griseolus, tytleri, trochilus*, some subspecies of *collybita*). The magnitude of shifts in PC1 and PC3 early in diversification are matched by only one other comparison, between the sister taxa *P. affinis* and *griseolus* (Fig. 6, contrast 12), which emphasizes both how unusual the shifts are, and how they arise in association with the exploitation of a new adaptive zone. *Phylloscopus griseolus* has evolved a unique foraging behavior in this genus, as it climbs on tree trunks (Ali and Ripley 1983). Large- and small-bodied species form monophyletic clades, indicating there has been no dramatic transitions between these ecological zones throughout subsequent diversification. The most evolutionarily labile trait is PC2, a measure of tarsus to beak size ratio (Price 1991). This has changed in association with repeated shifts in altitudinal distribution (Richman and Price 1992) and also in association with invasions on to islands. Thus, although there have been rapid shifts in species' habitat use and related morphology, with several examples of sister taxa occupying either coniferous or broadleaf habitats (Richman and Price 1992), the phylogeny suggests a conservative evolution of habitat use with respect to vegetation height and/or structure.

The Japanese assemblage is probably the product of repeated invasions from species-rich Asia; each of the three

species is most closely related to a different form or lineage composed of mostly central Asian taxa. There is pronounced altitudinal and habitat segregation among the three Japanese species, and in parallel among their Asian relatives; species found at similar elevation are also similar in morphology. This resemblance is in part due to the recent spread of ancestral taxa. For example *P. magnirostris* (Kashmir) and *P. tenellipes* (Japan) are sister taxa and are both found at intermediate elevation. However, the similarity between communities is not entirely accounted for by close sister relationships between ecological analogues. *Phylloscopus occipitalis* (Kashmir) and *P. coronatus* (Japan) both occur at the bottom of the gradient, and are very similar in morphology, but the phylogenetic analyses indicate these taxa have been separate for a long time, whether the relative age of taxa is determined by the order of branching in the phylogeny (Figs. 3, 4) or pairwise distances (Richman and Price 1992). These observations can be used to deduce the sequence of the evolution of ecological segregation over time; the oldest taxa are found at the bottom of the gradient, the next oldest species pair appears at the top of the gradient, with the youngest species found at intermediate elevation. This sequence is consistent with the inference that community diversity has been built up by three successive waves of invasion, presumably from mainland Asia to Japan, rather than by parallel diversifications within each region.

Patterns of morphological and ecological diversification within Europe have been quite different from Asia. First, despite evidence that European species are composed of two quite distantly related clades, all the European species are similar in body size and beak shape (although Gaston [1974] noted that *P. sibilatrix* does have unusual wing and tail mor-
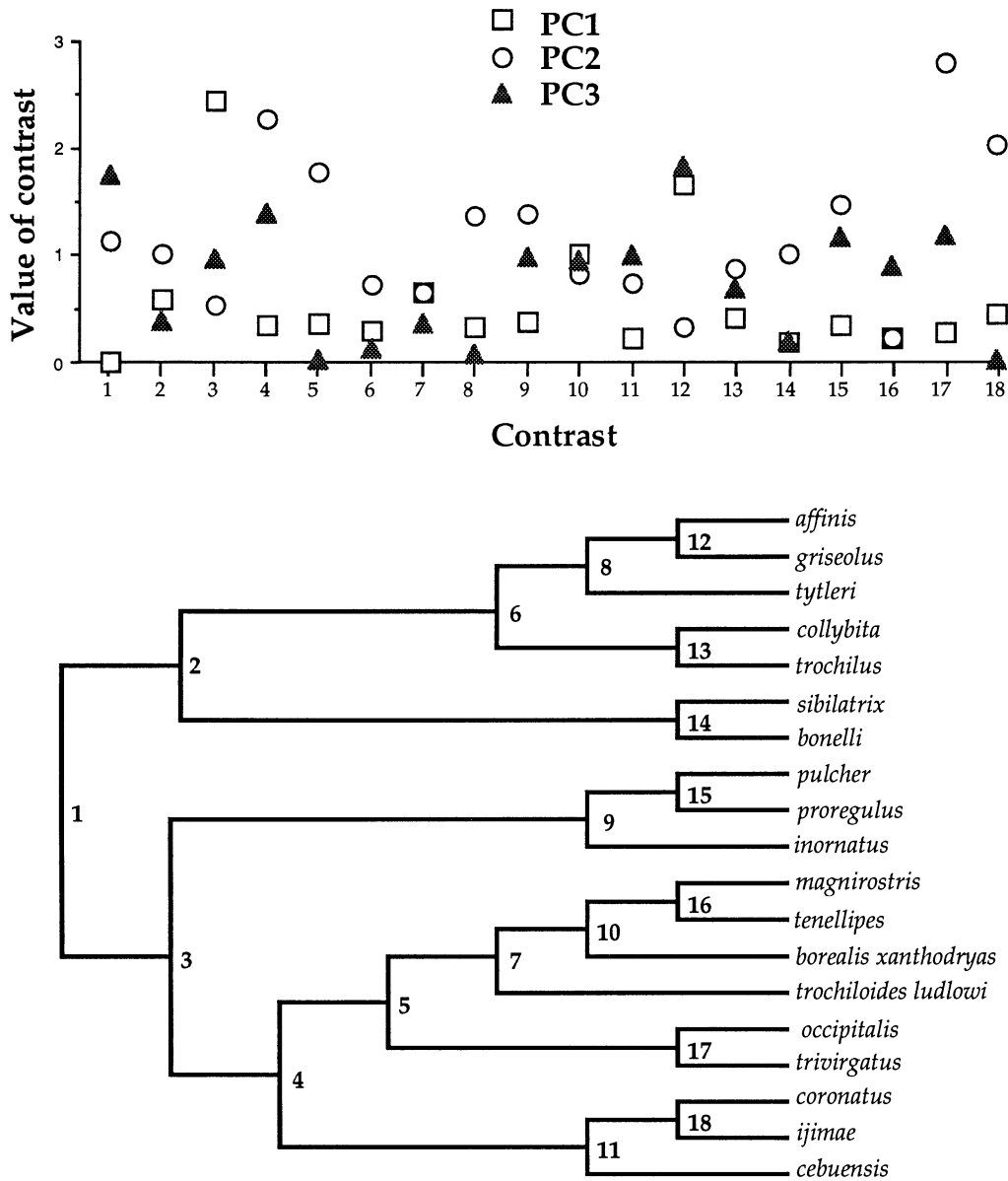
FIG. 6. Results of an analysis of evolutionary change in morphology using Felsenstein's method of independent contrasts (Felsenstein 1985). The position of each contrast on the phylogenetic tree is shown below, the numbers at internal nodes corresponding to the plot of contrast values shown at the top of the figure: PC1 (□), PC2 (○) and PC3 (△). The method requires a fully resolved phylogeny, consequently only the neighbor joining tree was used for this analysis.

phology). Second, habitat segregation among the sister species *P. trochilus* and *P. collybita* is weak (Cody 1978; Tiainen et al. 1983; Saether 1983) and may be currently evolving: in Norway these species are interspecifically territorial (Saether 1983), whereas in Finland they show different habitat preferences (Tiainen et al. 1983). Thus, in situ speciation in the European assemblage has not led to evolution of strong habitat selection among sympatric species, nor to size divergence among species co-occurring in the same habitats, as is found in Asia.

The peripheral communities of Europe and Japan are of independent origin, both derived from multiple invasions from species-rich Asia, but by different lineages. Although this would seem an ideal opportunity to detect convergence in morphology and behavior in matched habitats, this has not occurred. Although there has been limited speciation and diversification in Europe, these species retain similar morphology, which is correlated with phylogeny, as well as failing to show marked habitat selection found in other regions. The Japanese assemblage has persisted largely unchanged from Asiatic species from which they are derived. The reasons for the different evolutionary trajectories in Europe and Japan are unclear. Although it is possible that the presence of other species may have limited morphological diversification of *Phylloscopus* species in Europe (Saether 1982), another explanation must be sought for apparent evolutionary stasis in Japan, where no similar ecological analogues are present.

3 dispersal events:
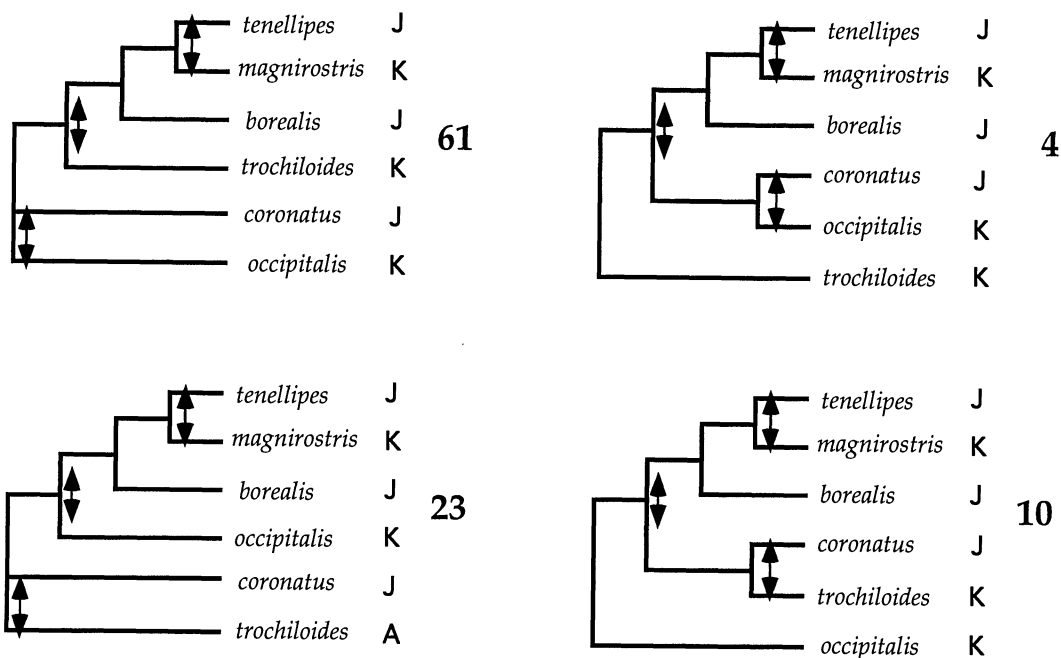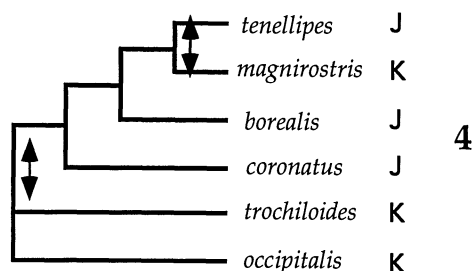

2 dispersal events:

FIG. 7. Inferred number of dispersal events for the Japanese assemblage, for the preferred phylogeny, and alternative scenarios identified in bootstrapping of the distance tree. The number to right of each topology indicates the relative support for the topology in bootstrap analysis. Additional alternative topologies consistent with three dispersal events which occurred in two or fewer in 100 bootstrap replicates are not shown.

Despite the importance of dispersal events in contributing to buildup of diversity in peripheral communities, and observation of recent range expansions in some species (Williamson 1974), the distributions of other species appear to be relatively stable over time. Conspicuous by their absence from peripheral communities are the small-bodied Asiatic species (occurring only in mainland Asia), which account for the most part for the "missing" species in other regions. Given the presence of frequent vagrants in Europe and in the Japan Sea (Williamson 1974), their absence seems unlikely to be due to an inability to disperse to these regions. I conclude that these communities are stable in the sense that other species not present are capable of dispersing but do not invade and suggest the following explanation as a regional effect causing nonconvergence in species diversity. In the absence of evidence that suitable breeding habitats are lacking, particularly in Japan where three large species are close relatives of Asian species which co-occur in the same habitats as the small bodied species in the Himalaya, the absence of nearby suitable wintering grounds in Japan and Europe may have selected against the dispersal of the small *Phylloscopus* species. In the Himalayas the small species are short-distance altitudinal migrants (Marchetti et al. 1995), but equivalent short distances in Japan and Europe would result in experiencing a very harsh winter.

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APPENDIX

Systematics of the Phylloscopus

Ticehurst (1938) was the first to treat the genus, using morphological characters such as length of nasal bristles and beak characters. More recently Williamson (1974) identified major groups within the Phylloscopus using plumage characters that he believed "provided a more natural classification of the genus." The scheme according to Williamson is listed below. A point of disagreement between these authors is the placement of P. sibilatrix, which Ticehurst classified as a member of the crowned and greenish warblers, whereas Williamson placed this species with other species of largely European distribution.

The results of the molecular analyses agree well with a major division within the group identified by Ticehurst (1938) he designated the subgenus Acanthopneuste, consisting of Williamson's (1974) Arctic and greenish and crowned warblers (see below). Within this larger group, Williamson's Arctic and greenish warblers are also monophyletic according to the distance tree. The crowned warblers are not monophyletic according to either of the molecular phylogenetic analyses, falling into two well-supported groups. The Asiatic warblers represented in this study by P. inornatus, P. pulcher, and P. proregulus also form a monophyletic group, as do the dusky warblers P. affinis and P. griseolus. The European warblers P. trochilus and P. collybita occur as sister taxa, as does the pair P. bonelli and P. sibilatrix, but these species pairs are apparently only distantly related. Finally, a significant difference from Williamson's scheme is the grouping of P. tytleri with the dusky warblers. Williamson placed P. tytleri among the greenish warblers, a grouping that did not occur in any of the 100 bootstrap replicates for the distance method.

Classification of the Phylloscopus presented by Williamson (1974). An asterisk indicates species for which molecular sequence data are available. The placement of the tropical resident species P. trivirgatus and P. cebuensis were not considered by Williamson (1974) crowned leaf warblers:—*occipitalis, *coronatus, *ijimae, reguloides, davisoni, cantator, ricketti.

Arctic and greenish leaf warblers:—*borealis, *trochiloides, nitidus, plumbeitarsus, *tenellipes, *magnirostris, *tytler.

Asiatic leaf warblers:—*inornatus, *pulcher, *proregulus, maculipennis, subviridis.

Dusky leaf warblers:—*affinis, fuscatus, schwarzi, *griseolus, armandii, fuligiventer.

European leaf warblers:—*collybita, neglectus, *trochilus, *bonelli, *sibilatrix, *sindianus.