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A multilocus phylogeny of a major New World avian radiation: The Vireonidae

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ABSTRACT

The family Vireonidae represents one of the most widespread and well-known New World avian radiations, but a robust species-level phylogeny of the group is lacking. Here, we infer a phylogeny of Vireonidae using multilocus data obtained from 221 individuals from 46 of 52 vireonid species (representing all four genera) and five "core Corvoidea" outgroups. Our results show Vireonidae to be monophyletic, consistent with a single colonization of the New World by an Asian ancestor. *Cyclarhis* and *Vireolanius* are monophyletic genera that diverged early from the rest of Vireonidae. *Hylophilus* is polyphyletic, represented by three distinct clades concordant with differences in morphology, habitat, and voice. The poorly known South American species *Hylophilus sclateri* is embedded within the genus *Vireo*. *Vireo*, in turn, consists of several well-supported intrageneric clades. Overall, tropical vireonid species show much higher levels of intraspecific genetic structure than temperate species and several currently recognized species are probably comprised of multiple cryptic species.

1. Introduction

The vireos, shrike-vireos, greenlets, and peppershrikes comprising the avian family Vireonidae represent one of the most widespread and well-known radiations of birds in the Western Hemisphere. Vireonids are small- to medium-sized passerines that exhibit a morphologically conserved body structure, generally possessing a rather thick bill with a short hook. Some 52 species of vireonids breed across the Americas in habitats ranging from shrublands to primary forest (Brewer and Orenstein, 2010). Four genera are presently recognized, with *Cyclarhis* (*C.*), *Vireolanius* (*Vl.*), and *Hylophilus* (*H.*) restricted to the Neotropics and *Vireo* (*V.*) occurring in both temperate and tropical areas.

The systematic placement of Vireonidae within Passeriformes has been controversial for many years (reviewed in Brewer and Orenstein, 2010). Recently a series of molecular phylogenetic studies unequivocally placed Vireonidae within the "core Corvoidea" clade of passerines (Barker et al., 2004; Cibois et al., 2002; Reddy and Cracraft, 2007; Sibley et al., 1988). The alliances of vireonids within the largely Old World core Corvoidea were unclear until recent work discovered Vireonidae to be allied with two south Asian genera, the *Pteruthius* shrike-babblers and the enigmatic *Erpornis zantholeuca* (Barker et al., 2004; Cibois et al., 2002; Reddy and Cracraft, 2007). As such, an Old World origin of Vireonidae implies at least one colonization of the New World (Cicero and Johnson, 2001; Johnson et al., 1988; Reddy and Cracraft, 2007).

Knowledge of relationships within Vireonidae remains incomplete due to taxonomically limited sampling in vireonid phylogenetic studies to date (Cicero and Johnson, 2001; Johnson et al., 1988; Murray et al., 1994; Sibley and Ahlquist, 1982). Other molecular studies of vireonid relationships used denser sampling but either limited their scope of inquiry to species complexes of interest (Cicero and Johnson, 1998; Johnson and Zink, 1985; Johnson, 1995) or examined phylogeographic variation within single species (Cicero and Johnson, 1992; Zink et al., 2010).

Here, we use one mitochondrial locus and three *Z*-linked nuclear loci to infer the first comprehensive phylogenetic hypothesis of the Vireonidae. We employ maximum likelihood and Bayesian inference and a combination of single-gene, concatenation, and species-tree approaches. We combine nearly complete species-level sampling with geographically dense sampling of multiple individuals across the distributions of widespread or polytypic species to explore broad patterns of phylogeography and uncover cryptic diversity. With our novel phylogenetic hypothesis in hand, we (1) assess the monophyly of Vireonidae, (2) place a lower bound on the number of New World colonization events within the family, (3) discuss new taxonomic implications, and (4)

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identify vireonid clades where sampling of additional loci and localities may be productive in further resolving relationships. Our study provides a comprehensive phylogenetic basis for future comparative studies of the ecology, behavior, and biogeography of this important group.

2. Methods

2.1. Taxon sampling and lab protocols

We obtained sequences from 221 individuals from 46 of the 52 currently recognized species within Vireonidae (Brewer and Orenstein, 2010) and five outgroup species (Table S1). Many species were represented by multiple samples that spanned intraspecific biogeographic (e.g. *cis*- and *trans*-Andean) and/or subspecific (e.g. *V. gilvus gilvus* and *V. g. swainsonii*) boundaries (Table S1). We were unable to obtain samples from several island or localized endemics, specifically *V. caribaeus, V. gundlachii, V. gracilirostris, V. nelsoni, V. masteri*, and *H. amaurocephalus*. We used *Cyanocitta stelleri*, *Pteruthius xanothochlorus*, *Pteruthius rufiventer*, *Pteruthius melanotis*, and *Erpornis zantholeuca* as outgroups (Barker et al., 2004; Cibois et al., 2002; Reddy and Cracraft, 2007). All sequences were newly generated for this study with the exception of three ND2 samples we downloaded from GenBank (*Erpornis zanthogaster*, one *V. leucophrys*, and one *V. atricapilla*; Table S1).

We extracted total genomic DNA using a DNeasy tissue extraction kit (Qiagen, Valencia, CA) following the manufacturer's protocol. We sequenced the mitochondrial gene ND2 (1041 base pairs (bp)) using methods previously described (Bryson et al., 2013; Smith and Klicka, 2013). For a subset of specimens ($n = 34$, including one outgroup sample), we also sequenced three *Z*-linked nuclear introns, including 968 bp of aconitase 1 (ACO1), 454 bp of receptor tyrosine kinase MUSK (MUSK), and 624 bp of spindlin 1 (SPIN1). We chose *Z*-linked loci because non-recombining Z-linked genes have a lower effective population size than autosomal loci and should thus more closely reflect the true species tree. We used previously published primers for ACO1 and MUSK (Kimball et al., 2009). For SPIN1, we designed two new primers: VireoSPINf 5′-GGCATCACTAATTCGAGACGAAGC-3′ and VireoSPINr 5′-AAGCCATCTAGACTGTGTTGTCT-3′. Sequences were amplified in 12.5 μL reactions under the following conditions: denaturation at 94 °C, followed by 35 cycles of 94 °C for 30 s, 56 °C (MUSK), 60 °C (ACO1), or 62 °C (SPIN1) for 45 s, and 72 °C for 1 min. This was followed by a 10 min extension at 72 °C. PCR products were sent to the High Throughput Genomics Center (University of Washington, Seattle, WA) for sequencing. We edited and manually aligned forward and reverse sequences for each individual using Sequencher v5.0 (Gene Codes Corporation, Ann Arbor, MI). Heterozygous sites in nuclear loci were coded with the appropriate IUPAC ambiguity code.

2.2. Phylogenetic analyses

We determined the best-fit models of evolution for each locus with jModeltest v2.1.4. (Posada, 2008) using the Akaike Information Criterion (AIC; Burnham and Anderson, 2002). We evaluated partitioning schemes of the ND2 gene using Bayes factors (Nylander et al., 2004), and partitioned the ND2 gene into three partitions (codon positions 1, 2, and 3) in final analyses. We then used Bayesian inference and maximum likelihood phylogenetic methods to estimate phylogenetic trees for the mitochondrial DNA (mtDNA) data set. We conducted Bayesian inference analyses with MrBayes v3.2.1 (Ronquist et al., 2012) using three heated and one cold Markov chain that sampled trees and parameters every 1000 generations for 10 million generations. Adjusting the heated chain temperature from the default value of 0.2 to 0.02 resulted in higher harmonic mean log likelihoods and better convergence and mixing. We applied a 25% burn-in after checking for convergence and stationarity using TRACER v1.5 (Rambaut and Drummond, 2007). We used the remaining trees to calculate posterior probabilities in a 50% majority-rule consensus tree. We conducted maximum likelihood analyses using RAxML v7.2.6 (Stamatakis, 2006) under a GTRGAMMA model, and used 1000 nonparametric rapid bootstrap replicates to assess nodal support.

We estimated phylogenetic trees for a subset of samples ($n = 34$) using a relaxed Bayesian molecular clock framework implemented in BEAST v1.7.4 (Drummond et al., 2012). We analyzed two groupings of the data: (1) combined *Z*-linked genes, and (2) concatenated ND2 and *Z*-linked genes. We conducted independent analyses on each data set for 40 million generations, sampling trees and parameters every 1000 generations. Substitution and clock models were unlinked for each gene in both analyses. We used lognormal relaxed clock priors for each gene and a Yule process speciation tree prior. We displayed results in TRACER to confirm acceptable mixing and likelihood stationarity and adequate effective sample sizes (ESS) above 200 for all estimated parameters. We summarized the parameter values of the samples from the posterior distribution on the maximum clade credibility tree, after discarding the first 4 million generations (10%) as burn-in using TreeAnnotator v1.7.4 (Drummond et al., 2012).

We also estimated a species tree for the same subset of 34 samples in *BEAST v1.7.4 using all four loci (Drummond et al., 2012). We used models of sequence evolution described above for each locus, respectively, unlinked all clock and substitution models, and constrained the three non-recombining *Z*-linked loci to a single tree topology. We selected Yule process speciation tree priors, lognormal relaxed clock priors, and ran the analysis for 1 billion generations, sampling trees and parameters every 100,000 generations. We confirmed acceptable mixing and likelihood stationarity and adequate ESS above 200 for all estimated parameters. We summarized the parameter values of the samples from the posterior distribution on the maximum clade credibility tree, after discarding the first 100 million generations (10%) as burn-in using TreeAnnotator v1.7.4 (Drummond et al., 2012).

3. Results

The ND2 alignment contained 550 parsimony-informative sites. The *Z*-linked genes contained less variation than ND2 (parsimony-informative sites, ACO1: 100/968 bp; MUSK: 63/454 bp; SPIN1: 72/624 bp). A GTR + I + G model of sequence evolution was selected for each codon partition of ND2, and GTR (MUSK, SPIN1) and GTR + G (ACO1) were selected for the *Z*-linked genes. Preliminary analyses of the four-gene concatenated data set in BEAST resulted in over-parameterization and subsequent low ESS values for several important parameters, including the posterior, prior, and likelihood, so the simpler HKY + I + G model was specified for the ND2 codon partitions, which resulted in ESS values > 200. Sequences were deposited in GenBank (Table S1).

In the full ND2 tree (Fig. 1), 33 of 51 (65%) interspecific nodes and 94 of 181 (52%) intraspecific nodes were strongly supported (>0.95 posterior probability and >70% bootstrap). No strongly supported topological conflicts occurred between the Bayesian and maximum likelihood ND2 trees. Among interspecific nodes, four received >70% bootstrap support but <0.95 posterior probability, and three received >0.95% posterior probability but <70% bootstrap support (Fig. 1).

The *Z*-linked and four-gene concatenated trees are presented in Fig. 2; a pruned ND2 cladogram with node support values from the full ND2 phylogeny is shown for comparison purposes. The

Z-linked and four-gene trees and the pruned ND2 tree had similar overall node support, though node support values in the ND2 cladogram were inferred from the full ND2 dataset, and thus are not directly comparable with node support values in the other trees. The ND2, *Z*-linked, and four-gene concatenated trees (Fig. 2) were concordant with each other with two notable exceptions. First, the ND2 tree differed from the *Z*-linked and four-gene concatenated trees in the phylogenetic placement of *Cyclarhis*. Whereas ND2 placed *Cyclarhis* sister to the rest of Vireonidae, the *Z*-linked and four-gene concatenated trees recovered *Cyclarhis* as sister to a clade of *Hylophilus*. Second, the intrageneric relationships of *Cyclarhis* differed among analyses. ND2 and the four-gene concatenated tree found *C. nigrirostris* to be embedded within *C. gujanensis*, whereas the *Z*-linked tree supported a monophyletic *C. gujanensis*

Fig. 1. (a–c) Phylogeny of Vireonidae based on Bayesian (tree shown) and maximum likelihood analyses of mitochondrial ND2 sequence data. Black circles at nodes indicate ⩾0.95 posterior probability and ⩾70% bootstrap support. Numbers at nodes indicate posterior probability (left of slash) and bootstrap support (right of slash) for clades with moderate or mixed support. Poorly supported nodes (<0.5 posterior probability and <50% bootstrap support) are collapsed into polytomies. Tip labels (*C.* = *Cyclarhis*, *Vl.* = *Vireolanius*, *H.* = *Hylophilus*, *V.* = *Vireo*) include the three-letter country abbreviation or two-letter state/province abbreviation and museum/sample number (see Table S1). Bolded tip labels indicate samples also included in the *Z*-linked, four-gene concatenated, and species trees (Figs. 2 and S1).

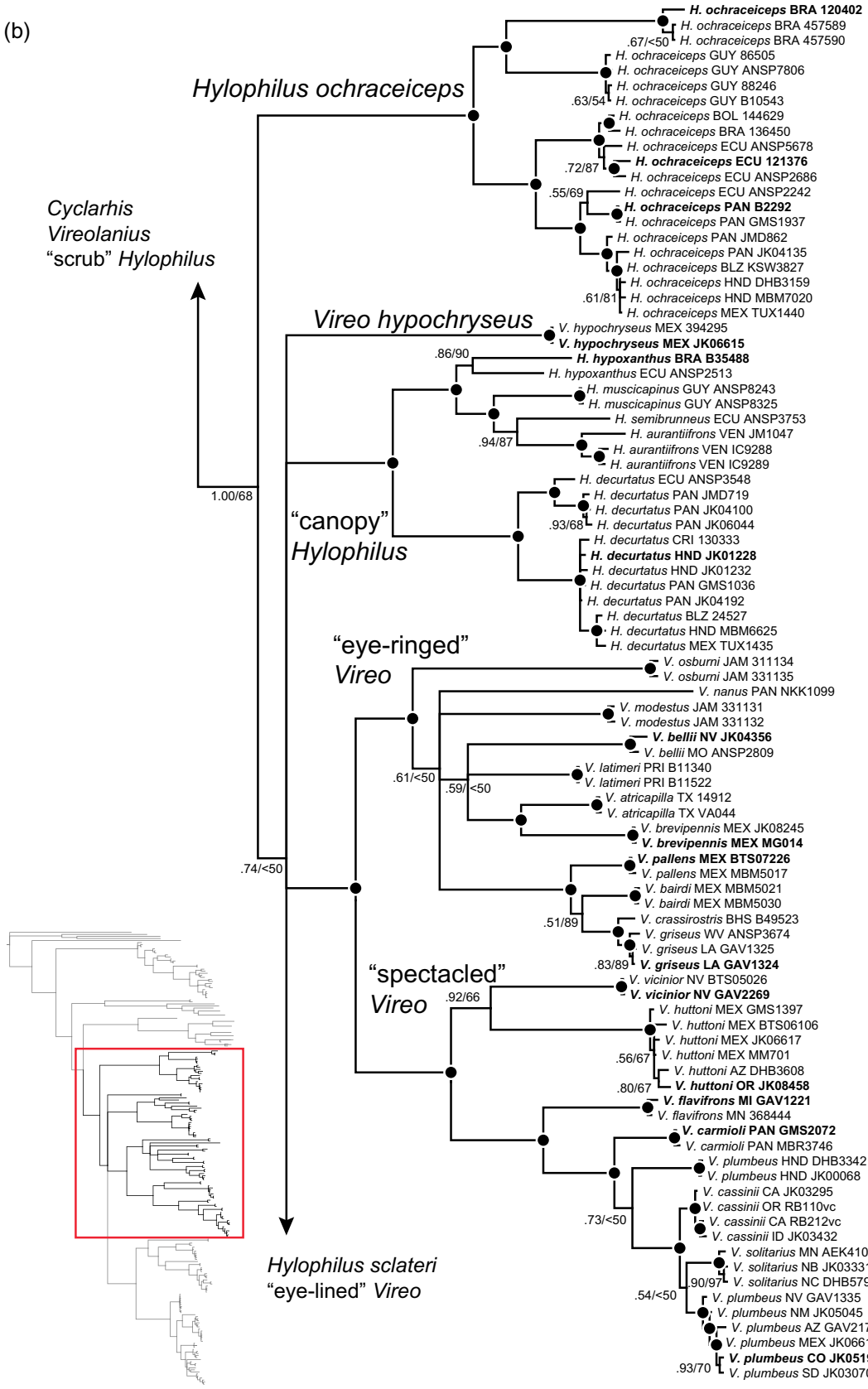

Fig. 1 (*continued*)

(Fig. 2). The *BEAST species tree (Fig. S1) contained no strongly supported conflicts with either the *Z*-linked or concatenated trees. The co-estimated gene trees from the *BEAST analysis are supplied in Files S1 and S2.

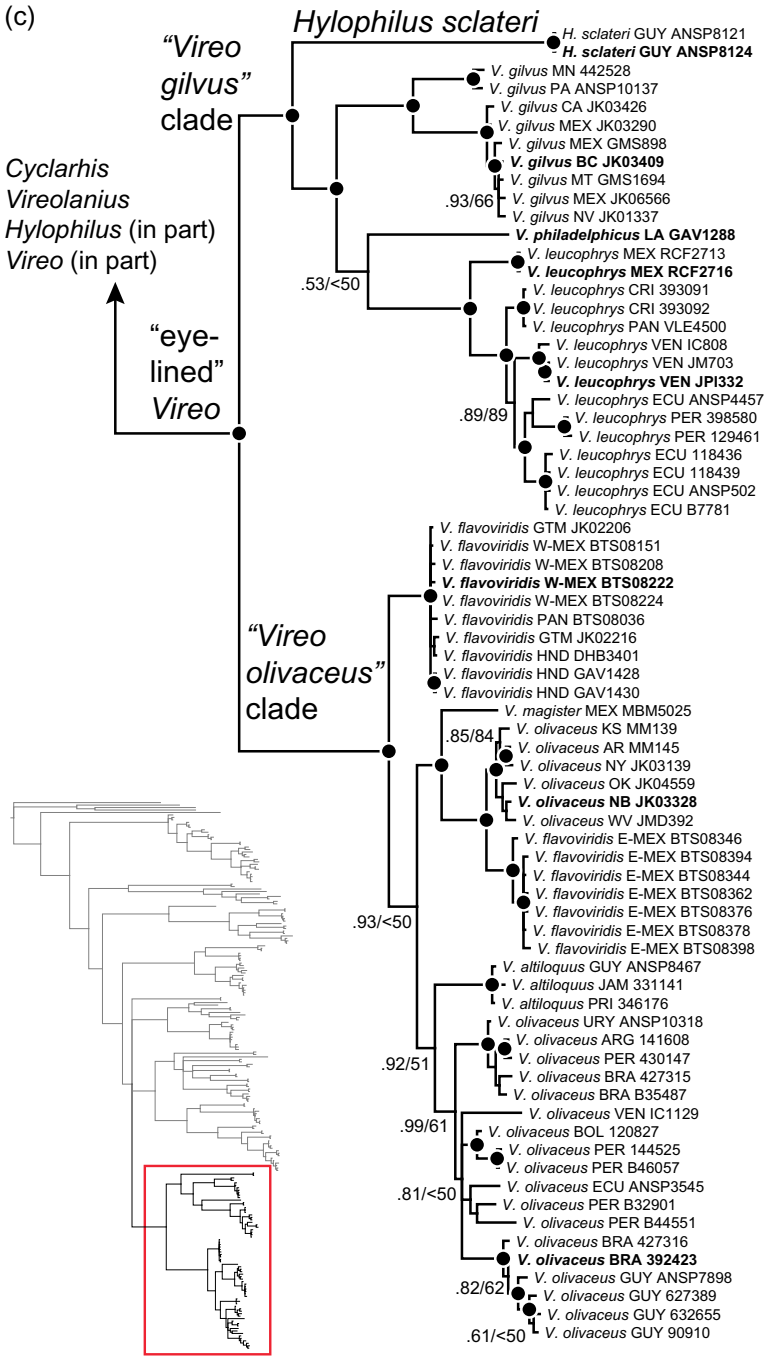

Fig. 1 (*continued*)

4. Discussion

4.1. Monophyly of Vireonidae

All datasets resolve a monophyletic Vireonidae (Fig. 2, Fig. S1), a hypothesis that had remained incompletely tested until this study because previously published phylogenies that included *Erpornis* and *Pteruthius* (the closest known relatives of Vireonidae) did not include all major vireonid lineages (Barker et al., 2004; Reddy and Cracraft, 2007). The topology we resolved at the base of our ND2 tree (Fig. 1) is concordant with that of Reddy and Cracraft (2007), who found *Erpornis* sister to Vireonidae and *Pteruthius* sister to both of these. Our results are thus consistent with the hypothesis of a single colonization of the New World from an Asian ancestor (Cicero and Johnson, 2001; Johnson et al., 1988; Reddy and Cracraft, 2007).

4.2. Basal groups

The mitochondrial and *Z*-linked trees conflict in their placement of basal groups (Fig. 2). The ND2 tree supports *Cyclarhis* as sister to *Vireolanius* and the rest of Vireonidae (Fig. 1), but the *Z*-linked and four-gene concatenated trees (Fig. 2) find *Cyclarhis* and the "scrub" *Hylophilus* clade sister to the rest of Vireonidae (including *Vireolanius*). The species tree exhibits the latter topology but with moderate posterior support (Fig. S1).

All analyses resolve both *Cyclarhis* and *Vireolanius* to be monophyletic genera but disagree on intrageneric relationships of

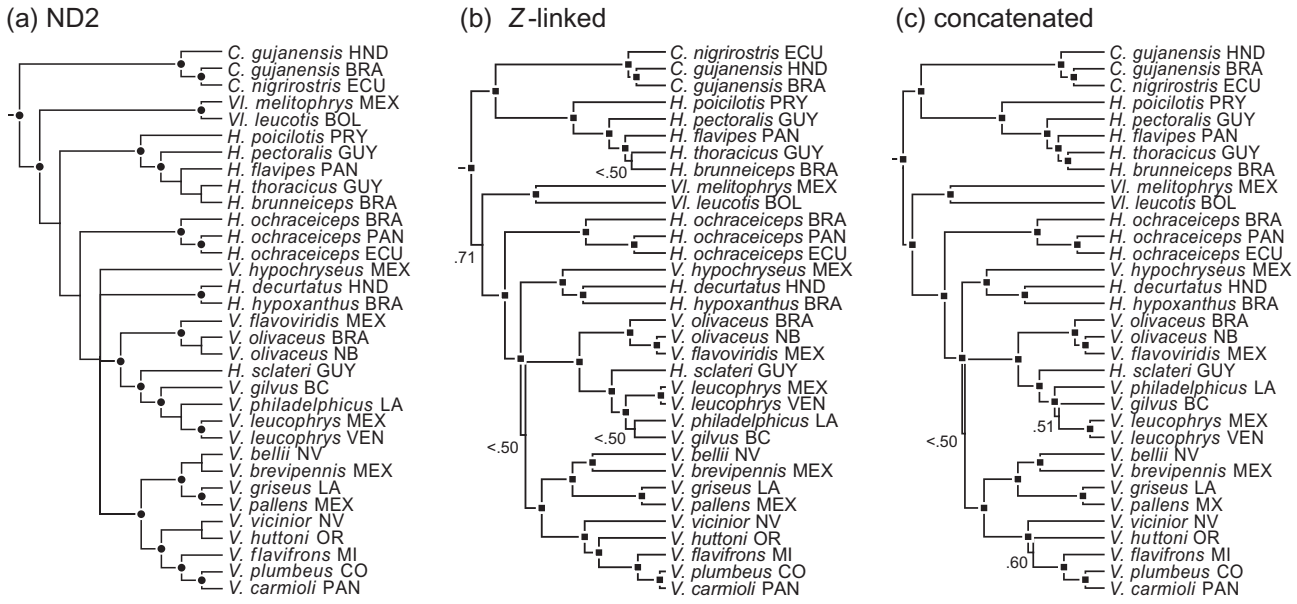

Fig. 2. Comparison of trees inferred using a subset of vireonid samples and different sequence alignments. (a) Mitochondrial ND2 sequence data (pruned cladogram summarizing topology and node support from full tree (Fig. 1)), (b) three *Z*-linked nuclear loci, and (c) concatenated ND2 and *Z*-linked data. Black circles at nodes indicate ⩾0.95 posterior probability support and ⩾70% bootstrap support (a), black squares at nodes indicate ⩾0.95 posterior probability support (b and c), and numbers at nodes (b and c) represent posterior probability support. The *BEAST species tree (Fig. S1) of the same subset of samples contained no strongly supported conflicts with the concatenated (c) or Z-linked (b) trees. Tip labels (*C. = Cyclarhis*, *Vl. = Vireolanius*, *H. = Hylophilus*, *V. = Vireo*) include the three-letter country abbreviation or two-letter state/province abbreviation (see Table S1). These same 33 taxa are labeled in bold on the full ND2 tree (Fig. 1). Outgroups are not shown.

Cyclarhis (Figs. 1, 2 and S1). ND2 and the four-gene concatenated tree find *C. nigrirostris* embedded within *C. gujanensis*, whereas *Z*-linked supports a monophyletic *C. gujanensis* (Fig. 2). The species tree exhibits weak support for a polyphyletic *C. gujanensis* (Fig. S1). Regardless, high levels of phylogeographic structuring (Fig. 1) and up to 4.9% uncorrected sequence divergences within *C. gujanensis* suggest that future studies of this taxon with additional loci and morphological and/or ecological data may uncover cryptic species (but see Tubaro and Segura (1995) for evidence of little correspondence between voice and subspecific boundaries in *C. gujanensis*).

4.3. Hylophilus

All of our trees reject the monophyly of *Hylophilus* (Figs. 1, 2 and S1), and we are not the first to note strong phylogenetic divergence within the genus. Johnson et al. (1988) rejected the monophyly of *Hylophilus* in their early electrophoretic study, but their limited taxon sampling precludes detailed comparisons with our study. Ridgely and Tudor (1989) subdivided *Hylophilus* into three groups based on concordant differences in eye color, habitat type, and voice, which our results mostly corroborate with exceptions discussed below.

Our results show a strongly supported monophyletic clade of "scrub" *Hylophilus* containing *H. poicilotis, H. olivaceus, H. pectoralis, H. flavipes, H. semicinereus, H. brunneiceps*, and *H. thoracicus* (Figs. 1, 2 and S1). This group corresponds to clade "B" *sensu* Ridgely and Tudor (1989) but with the notable addition of *H. brunneiceps*, which Ridgely and Tudor had placed with the "canopy" greenlets (their group "A"). Our placement of *H. brunneiceps* with the "scrub" greenlets (Fig. 1) corroborates Zimmer and Hilty (1997), who clarified that the rather poorly known *H. brunneiceps* has a pale iris, a simple song, and scrubby habitat preferences similar to the rest of the "scrub" *Hylophilus*.

Our trees also indicate a well-supported clade of "canopy" *Hylophilus* containing *H. hypoxanthus, H. muscicapinus, H. semibrunneus, H. aurantiifrons*, and *H. decurtatus* (Fig. 1). This canopy-dwelling clade, with dark irises and complex songs, nearly corresponds to group "A" of Ridgely and Tudor (1989) but excludes *Hylophilus sclateri*, which we discuss below. The *Z*-linked, four-gene concatenated, and species tree analyses place the taxonomically enigmatic *V. hypochryseus* sister to these "canopy" *Hylophilus*, but the ND2 tree is poorly resolved with regard to that relationship (Figs. 2 and S1).

Our trees resolve a monophyletic *H. ochraceiceps* and place it sister to a clade containing *Vireo*, *H. sclateri*, and "canopy" *Hylophilus* with strong support (Figs. 1, 2 and S1). Ridgely and Tudor (1989) highlighted the understory-dwelling *H. ochraceiceps* as a divergent group within *Hylophilus* (placing it in a monotypic group "C"), and our results also suggest that *H. ochraceiceps* is highly divergent from other vireonids. Indeed, "scrub" *Hylophilus*, "canopy" *Hylophilus*, and the understory-dwelling *H. ochraceiceps* represent deeply divergent, monophyletic clades that warrant splitting into three separate genera (Slager and Klicka, in preparation) based on molecular polyphyly (Figs. 1, 2 and S1) as well as strong and concordant differences in behavior, voice, and habitat.

H. ochraceiceps exhibits deep and strongly supported phylogeographic structure (Fig. 1). Indeed, others have suggested that *H. ochraceiceps* may contain cryptic species (Brewer and Orenstein, 2010; Milá et al., 2012; Tavares et al., 2011). In our analysis (Fig. 1), the most basal split is between dark-eyed, eastern Amazonian *H. ochraceiceps* and all other populations (4.6% average uncorrected pairwise ND2 distance). Within eastern Amazonia, another deep divergence (Fig. 1; 5.1% average uncorrected pairwise ND2 distance) exists between samples of *H. o. luteifrons* and *H. o. lutescens/rubrifrons*, which occur north and south of the Amazon River in the Guiana and Parà endemic bird areas, respectively (Brewer and Orenstein, 2010; Cracraft, 1985). Sister to the eastern Amazonian clade are two monophyletic sister clades (separated by 2.5% average uncorrected pairwise ND2 distance) containing western Amazonian birds and all *trans*-Andean samples, respectively (Fig. 1). Although our geographic sampling is not sufficient for a full taxonomic revision of *H. ochraceiceps*, it seems likely that the

dark-eyed birds, at a minimum, represent separate phylogenetic species and that a thorough phylogeographic study of *H. ochraceiceps* may reveal additional species-level taxa.

4.4. "Eye-ringed" vireos

Both mtDNA and nuclear datasets strongly support a sister relationship between an "eye-ringed" *Vireo* clade and a "spectacled" *Vireo* clade, and these two clades are themselves monophyletic (Figs. 1, 2 and S1). The deep split between these two clades is illustrative of the high intraspecific molecular distances within *Vireo* (as currently circumscribed) relative to genetic distances among other avian congeners, possibly warranting a generic split (Avise et al., 1982). Earlier taxonomists erected the genus *Lanivireo* (type species *V. solitarius*) for some members of the "spectacled" clade and *Vireosylva* (type species *V. olivaceus*) for the "eye-lined" clade (Ridgway, 1904). Pending additional resolution at key nodes, it may be appropriate to eventually resurrect these genera for these clades to reflect this diversity. In that case, the genus *Vireo* (type species *V. griseus* (= *V. noveboracensis*)) would be restricted to the "eye-ringed" clade (Ridgway, 1904).

The "eye-ringed" clade we recovered contains mostly thicket-dwelling *Vireo* species, including the *V. griseus* complex (Fig. 1). Many species in this clade occur in and around the Caribbean, and several are island endemics; most species have prominent wing bars and pale or yellowish lores. The clade generally lacks well-supported relationships but contains *Vireo osburni, V. nanus, V. bairdi, V. pallens, V. crassirostris, V. griseus, V. modestus, V. bellii, V. latimeri, V. atricapilla, V. brevipennis*, and *V. atricapilla* (Fig. 1).

The enigmatic, large, and distinctively plumaged *V. osburni* of Jamaica falls within the "eye-ringed" clade with strong support (Fig. 1). Although first described as the monotypic genus *Laletes* and later lumped with *Cyclarhis*, more recent authors have grouped it with other members of our "eye-ringed" clade (Bond, 1934; Hamilton, 1962). We found weak support for its basal position in the "eye-ringed" clade (Fig. 1), consistent with earlier hypotheses that this island endemic is in a late-stage taxon cycle (Ricklefs, 1970) and that the "eye-ringed" clade independently colonized Jamaica twice (Hamilton, 1962). Although perhaps less shrub-loving than some members of the clade, *V. osburni* overlaps more in foraging height with the "eye-ringed" *V. modestus* than it does with the "eye-lined" *V. altiloquus* where the three are syntopic (Cruz, 1980); it has been suggested that the size difference between *V. osburni* and *V. modestus* may be sufficient to prevent competitive exclusion (Hamilton, 1962).

The "eye-ringed" clade (Fig. 1) also includes four species that breed away from the Caribbean. One of these, *V. griseus*, is a migratory North American breeder that winters primarily in and around the Caribbean. It is embedded within a monophyletic group with the morphologically and behaviorally similar *V. crassirostris*, *V. pallens*, and *V. bairdi*, all of which are sedentary Caribbean species (Fig. 1). The phylogenetic position of *V. griseus* is thus consistent with a tropical-origin scenario for the evolution of migration, in which migration out of the Caribbean evolved in the lineage leading to *V. griseus*, with *V. griseus* returning to or near this Caribbean ancestral area during the non-breeding season (Cox, 1985).

The remaining three continental members of the "eye-ringed" clade occupy shrubby habitats outside the Caribbean, spending at least part of their annual cycle in southern or western Mexico. Two of these, the range-restricted *V. atricapilla* and *V. brevipennis*, are well-supported sister species in our tree (Fig. 1). Both species are atypically dark-plumaged vireos with a history of taxonomic uncertainty. Hamilton (1962) placed the migratory, shrub-nesting *V. atricapilla* within the more arboreal *V. solitarius* complex on account of plumage similarities, but a preliminary phylogenetic study did not consistently resolve a placement for *V. atricapilla* (Murray et al., 1994). The sedentary Mexican endemic *V. brevipennis* was described as the monotypic genus *Neochloe* (Sclater, 1857) and despite subsequent lumping with *Vireo* it has remained difficult to place taxonomically (Hamilton, 1962; Phillips, 1962). The final continental member of the "eye-ringed" clade is *V. bellii*, a migratory North American breeder that winters along the Pacific coast of Mexico. It has previously been suggested that *V. bellii* shares affinities with the "eye-ringed" clade (Brewer and Orenstein, 2010).

4.5. "Spectacled" vireo clade

Our analyses recover a "spectacled" clade containing spectacled *V. flavifrons* and the spectacled *V. solitarius* complex (= *V. plumbeus* + *V. solitarius* + *V. cassinii*) in addition to the unspectacled *V. vicinior*, *V. huttoni*, and *V. carmioli* (Fig. 1). These species are North and Central American in distribution (with the possible exception of the unsampled and recently discovered South American *V. masteri*; see Section 4.7) and arboreal with the exception of *V. vicinior*, which inhabits juniper and desert scrub habitats. We recover *V. flavifrons*, *V. carmioli*, and the *V. solitarius* complex as a monophyletic group, with *V. flavifrons* sister to *V. carmioli* + the *V. solitarius* complex (Fig. 1). Relationships between this monophyletic group, *V. vicinior*, and *V. huttoni* are less well resolved, with moderate support for a sister relationship between *V. vicinior* and *V. huttoni* (Fig. 1). The placement of *V. vicinior* was also uncertain in an early phylogenetic analysis due to limited species sampling (Murray et al., 1994).

We recovered a topology of the *V. solitarius* complex congruent with that of Cicero and Johnson's (1998) with an important exception (Fig. 1). Our ND2 analysis shows *V. plumbeus* to be polyphyletic, with *V. plumbeus* samples from south of the Isthmus of Tehuantepec falling outside of the monophyletic group containing the rest of the *V. solitarius* complex, including northern *V. plumbeus* (Fig. 1). In our study, a *V. plumbeus* specimen collected in Guerrero, just north of the Isthmus of Tehuantepec, grouped with more northern birds. Our Central American *V. plumbeus* samples had an average uncorrected ND2 distance of 2.6% from other *V. plumbeus* samples, on par with levels of divergence reported between *V. solitarius, V. cassinii*, and northern *V. plumbeus* (Cicero and Johnson, 1998) that led to species recognition for those three taxa. *V. plumbeus* populations on either side of the Isthmus therefore likely represent species-level taxa, with subspecies *V. p. plumbeus* and *V. p. gravis* constituting the northern species and *V. p. notius* and *V. p. montanus* (Phillips, 1991) forming the southern species. Although our *V. plumbeus* sampling south of the Isthmus was limited to Honduras, strong genetic divisions across the Isthmus of Tehuantepec are a common motif in Mexican phylogeography (Barber and Klicka, 2010; Bryson et al., 2011), and at least one checklist authority considers *V. plumbeus* populations south of the Isthmus (= *V. p. notius* and *V. p. montanus*) to represent a single identifiable subspecific form (Clements et al., 2013). Although we stop short of fully endorsing a species split here, such an outcome seems plausible once additional localities and loci are sampled. Our detection of ND2 polyphyly in *V. plumbeus* highlights the importance of range-wide sampling; indeed, limiting one's sampling of *V. plumbeus* to northern populations (e.g. Cicero and Johnson, 1998) would preclude detection of cryptic southern diversity potentially key to interpreting evolutionary history and relationships within this species complex.

4.6. "Eye-lined" vireos

All analyses support the monophyly of an "eye-lined" clade consisting of taxa previously grouped into the *V. gilvus* and *V. olivaceus* superspecies (Hamilton, 1962) plus *H. sclateri* (Figs. 1, 2 and S1). With the exception of the latter, all members of this "eye-lined"

clade have a prominent supercilium. Some members of the clade are highly migratory (*V. gilvus*, some *V. olivaceus*, and *V. philadelphicus*), while many species that breed in Mexico, Central America, and South America are sedentary. Several closely related species pairs (e.g. *V. gilvus* and *V. leucophrys*; *V. olivaceus* and *V. altiloquus*) are sympatric in the tropics during winter.

4.6.1. Vireo gilvus clade

All trees support the monophyly of a clade consisting of *H. sclateri*, *V. philadelphicus*, *V. gilvus*, and *V. leucophrys* (Figs. 2 and S1). *H. sclateri*, a little-studied species from the Guyana Shield region of northern South America (Ridgely et al., 2005; Zyskowski et al., 2011), is unexpectedly recovered as sister to the other members of this clade in ND2, *Z*-linked, concatenated, and species trees (Figs. 2 and S1), and as such should be subsumed within the genus *Vireo*. The morphological resemblance of this species to "scrub" *Hylophilus* (Ridgely and Tudor, 1989) undoubtedly contributed to the present classification of *H. sclateri* within *Hylophilus*. *H. sclateri* was originally described as a *Hylophilus* species on the basis of size and plumage features (Salvin and Godman, 1883), and we are not aware of any published work until now that has questioned its affinities with *Hylophilus*. Strong multilocus support and large genetic distance between *H. sclateri* and other *Hylophilus* firmly place it within the genus *Vireo*; and we recommend the English name Tepui Vireo for the taxon. In hindsight, *H. sclateri* does differ substantially from other *Hylophilus* on the basis of its large size and gray (rather than green) flight feathers and wing coverts (Brewer and Orenstein, 2010; Hellmayr, 1935).

The topological placement of *V. gilvus*, *V. leucophrys*, and *V. philadelphicus* varies between the ND2 and *Z*-linked trees, but all datasets resolve the three species as a monophyletic group (Figs. 2 and S1). Eastern and western North American populations of *V. gilvus* have long been observed to differ in morphology, song, and timing of molt and migration (Brewer and Orenstein, 2010; Gardali and Ballard, 2000; Sibley and Monroe, 1990; Voelker and Rohwer, 1998). Previous molecular work has revealed relatively large genetic distances between the two populations (Hebert et al., 2004; Murray et al., 1994). Our data support the broad subdivision of the species into eastern *V. g. gilvus* and western *V. g. swainsonii* groups (Fig. 1; average ND2 uncorrected sequence divergence 2.6%).

Within *V. leucophrys*, the ND2 tree reveals well-supported phylogeographic structure, with relatively deep divergences among the Mexican, Central American, and Andean populations (Fig. 1). The deepest divergence within *V. leucophrys* occurs between birds from central Mexico and all other populations (average pairwise divergence 1.4%), consistent with the division of the species into northern and southern groups by some authors (e.g. Brewer and Orenstein, 2010).

4.6.2. Vireo olivaceus clade

As sister to the *V. gilvus* clade, all trees recover a monophyletic clade comprised of *V. olivaceus*, *V. flavoviridis*, *V. magister*, and *V. altiloquus* (Figs. 2 and S1). ND2 analyses strongly support the polyphyly of both *V. olivaceus* and *V. flavoviridis*. *V. olivaceus* is split between divergent North and South American lineages (*V. o. olivaceus* and *V. o. chivi* subspecies groups, respectively, *sensu* Cimprich et al. (2000)), whereas *V. flavoviridis* is split between birds breeding in eastern Mexico and western Mexico + Central America (Fig. 1). *V. magister* is strongly supported as sister to a combined clade of North American *V. olivaceus* and eastern Mexican *V. flavoviridis,* while *V. altiloquus* is placed sister to South American *V. olivaceus* with weak support (Fig. 1). The *Z*-linked tree also suggests a polyphyletic *V. olivaceus*, but places western Mexican *V. flavoviridis* sister to North American *V. olivaceus*, rather than sister to the rest of the group as in the ND2 tree (Fig. 2). The species tree exhibits the same topology as *Z*-linked with respect to *V. olivaceus* and *V. flavoviridis*, but with moderate support (Fig. S1).

These results suggest that a previous phylogenetic hypothesis recovering reciprocal monophyly between *V. flavoviridis* and *V. olivaceus*, which relied on a single *V. flavoviridis* from Costa Rica and lacked *V. altiloquus* (Johnson and Zink, 1985), may have been an artifact of incomplete taxon sampling. In part because *V. olivaceus* breeds in disjunct areas of North and South America separated by over 3200 km, its recognition as a single species has long been suspect (reviewed in Johnson and Zink, 1985). Our results suggest that North and South American *V. olivaceus* represent deeply divergent evolutionary lineages concordant with the divide in breeding range, and may represent distinct species. However, the relationships discussed here should be considered preliminary given gene tree conflicts and mixed topological support within the *V. olivaceus* clade (Figs. 2 and S1). Further analyses using more loci are needed to better resolve species relationships within this group and allow a detailed assessment of the biogeography and evolution of migration within the *V. olivaceus* clade.

4.7. Unsampled taxa

The six species for which we were unable to obtain genetic samples can be tentatively placed on our tree given their strong morphological and biogeographic affinities with sampled taxa. *H. amaurocephalus* is considered to form a superspecies with *H. poicilotis* in the "scrub" greenlet clade (Raposo et al., 1998; Willis, 1991). *V. caribeaus* and *V. gundlachii* are thought to have affinities with the "eye-ringed" clade (Brewer and Orenstein, 2010). The island endemic *V. gracilirostris* belongs with the *V. olivaceus* clade (Brewer and Orenstein, 2010). *V. nelsoni* has sometimes been considered conspecific with *V. atricapilla*, which would place it in the "eye-ringed" clade (Brewer and Orenstein, 2010). *V. masteri* is thought to be closely related to *V. carmioli*, which itself falls within the "spectacled" clade (Brewer and Orenstein, 2010; Salaman and Stiles, 1996). If this latter relationship holds true, then *V. masteri* would represent the southernmost colonization of the "spectacled" clade.

4.8. Taxonomic and genetic diversity in tropical and temperate regions

Several species for which we sampled multiple individuals show relatively deep phylogeographic structure. In our analysis (Fig. 1), such divisions occur most often in tropical species (*C. gujanensis, Vl. leucotis, H. decurtatus, H. ochraceiceps,* and *V. leucophrys*) but also in several temperate species (*V. gilvus*, *V. plumbeus, and V. olivaceus*). Geographic sampling gaps preclude us from making strong quantitative conclusions regarding tropical-temperate patterns in intraspecific genetic diversity, but we do observe a trend of higher intraspecific genetic diversity in tropical vireonids. This pattern is consistent with observations of higher intraspecific genetic diversity in the tropics across birds and other vertebrates (Chek et al., 2003). The extent to which this pattern is simply an artifact of regional taxonomic bias or stems from biological reality, such as higher speciation rates in the tropics (Martin and McKay, 2004), remains an active area of research (Araújo and Costa-Pereira, 2013; Martin and Tewksbury, 2008).

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.ympev.2014.07.021.

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