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Shared geographic histories and dispersal contribute to congruent phylogenies between amphipods and their microsporidian parasites at regional and global scales

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Abstract

In parasites that strongly rely on a host for dispersal, geographic barriers that act on the host will simultaneously influence parasite distribution as well. If their association persists over macroevolutionary time it may result in congruent phylogenetic and phylogeographic patterns due to shared geographic histories. Here, we investigated the level of congruent evolutionary history at a regional and global scale in a highly specialised parasite taxon infecting hosts with limited dispersal abilities: the microsporidians *Dictyocoela* spp. and their amphipod hosts. *Dictyocoela* can be transmitted both vertically and horizontally and is the most common microsporidian genus occurring in amphipods in Eurasia. However, little is known about its distribution elsewhere. We started by conducting molecular screening to detect microsporidian parasites in endemic amphipod species in New Zealand; based on phylogenetic analyses, we identified nine species-level microsporidian taxa including six belonging to *Dictyocoela*. With a distance-based cophylogenetic analysis at the regional scale, we identified overall congruent phylogenies between *Paracalliope*, the most common New Zealand freshwater amphipod taxon, and their *Dictyocoela* parasites. Also, hosts and parasites showed similar phylogeographic patterns suggesting shared biogeographic histories. Similarly, at a global scale, phylogenies of amphipod hosts and their *Dictyocoela* parasites showed broadly congruent phylogenies. The observed patterns may have resulted from covicariance and/or codispersal, suggesting that the intimate association between amphipods and *Dictyocoela* may have persisted over macroevolutionary time. We highlight that shared biogeographic histories could play a role in the codiversification of hosts and parasites at a macroevolutionary scale.

KEYWORDS
codiversification, cophylogeny, cophylogeography, microsporidia, vertical transmission

1 | INTRODUCTION

Cophylogenetic analyses can be used to infer the evolutionary history of associations between two interacting taxa (Page, 2003). Congruent phylogenetic patterns at a macroevolutionary scale may arise due to adaptive processes, but also mainly due to other processes such as shared biogeographic histories (Clayton, Bush, & Johnson, 2015; Weckstein, 2004). Concomitant occurrence of speciation (= cospeciation) of two interacting taxa can promote congruent phylogenies (but see de Vienne, Giraud, & Shykoff, 2007 for cases of preferential host-shifts). For instance, in host-parasite associations, speciation in the host lineage can directly cause speciation of its parasites and result in cospeciation. However, phylogenies of hosts and parasites are seldom perfectly congruent due to other

events that disrupt cophylogenetic patterns such as host shift, duplication, or extinctions (Page, 2003; de Vienne et al., 2013). In fact, according to an extensive review of cophylogenetic studies, host-shift speciation seems to be the dominant mechanism in parasite diversification (de Vienne et al., 2013). Although data are scarce, some systems show congruent phylogenies of host and parasite including the classical example of pocket gophers and their chewing lice (Hafner et al., 1994). In this example, a combination of several factors such as the solitary life-style of the host species, allopatric species distributions of hosts, and limited dispersal abilities of parasites were suggested as contributing factors which may have lowered the chances of host-shift, resulting in congruent host-parasite phylogenies (Clayton & Johnson, 2003; Nieberding, Jousselin, & Desdevises, 2010; de Vienne et al., 2013).

Dispersal is a fundamental biological process that acts on multiple evolutionary scales (Nathan, 2001). From the parasite's perspective, there are broadly two kinds of dispersal: host-dependent and host-independent. By their nature, parasites spend at least a part of their life within or on hosts and therefore rely on the host for dispersal to various degrees depending on lifecycle characteristics and transmission type (Blouin, Yowell, Courtney, & Dame, 1995; Clayton et al., 2015). Many parasites have multiple hosts, as well as a free-living stage during which independent dispersal could occur. On the other hand, parasites that spend their whole lifespan within/on hosts probably rely on the host for dispersal (e.g., chewing lice on birds; Clayton et al., 2015). In such cases, host dispersal is crucial for parasite dispersal, potentially leading to congruent evolutionary histories. Similarly, vertically transmitted microparasites are likely to follow the evolutionary trajectories of their hosts (Althoff, Segraves, & Johnson, 2014), and it is thus unsurprising that clear cases of co-speciation typically involve parasites that have vertical transmission (de Vienne et al., 2013).

In a system where a parasite is highly reliant on its host for dispersal over the long term, these shared biogeographic histories alone may be sufficient to explain congruent phylogenies (Althoff et al., 2014), without requiring any adaptive explanation. Vicariance or dispersal events that impact host evolutionary history can simultaneously affect the parasites' evolutionary history. Therefore, the degree of host-parasite associations and dispersal capabilities of hosts and parasites can influence cophylogenetic patterns. Although some studies have underscored the role of host dispersal ability (Moon, Chown, & Fraser, 2019; Norte et al., 2020), parasite dispersal ability (Engelbrecht, Matthee, Du Toit, & Matthee, 2016; Sweet & Johnson, 2018), and geographic barriers (Larose & Schwander, 2016; Weckstein, 2004) in parasite diversification, studies linking life history traits of hosts and parasites and their respective biogeographical patterns to the outcome of their co-evolutionary association are still scarce (Nieberding et al., 2010).

Microsporidian parasites, which can be transmitted effectively both vertically and horizontally, are common in amphipod hosts (Bojko & Ovcharenko, 2019; Lipsitch, Nowak, Ebert, & May, 1995). Among more than 30 named species and many other unnamed taxa that were found in amphipod hosts, *Dictyocoela* is the most common genus with about 10 known species (Bojko & Ovcharenko, 2019; Dimova et al., 2018; Grabner, 2017; Grabner et al., 2015; Kuzmenkova, Sherbakov, & Smith, 2008; Quiles et al., 2019; Slothouber Galbreath, Smith, Terry, Becnel, & Dunn, 2004; Williams, Hamilton, Jones, & Bass, 2018; see Table 1 in Appendix S1). However, the known diversity of *Dictyocoela* seems to be restricted both geographically and in terms of host range. Geographically, all known microsporidians in amphipods are from the Northern Hemisphere, including southern Europe, the Ponto-Caspian area, Lake Baikal (Asia) and southeastern USA (Bacela-Spychalska et al., 2018; Dimova et al., 2018; Quiles et al., 2019; Slothouber Galbreath et al., 2004; Väinölä et al., 2008). In terms of host range, gammarids are the best-studied amphipod hosts for microsporidians, although some *Dictyocoela* species were found parasitizing species of Talitridae, Melitidae, and Hyalellidae (Terry et al., 2004).

Given the limited knowledge on their distribution and diversity, the antiquity and strength of associations between *Dictyocoela* species and their hosts remain poorly understood. A recent study revealed some degree of host specificity and overlapping geographical distributions between microsporidian parasites and their amphipod hosts, suggesting their ancient associations (Quiles et al., 2019). In a pilot study conducted across a few locations on New Zealand's South Island, we detected microsporidian species similar to *Dictyocoela* in several endemic amphipod species. The presence of *Dictyocoela* in New Zealand amphipods provides an opportunity to ask questions regarding the evolutionary history of their association and codiversification patterns. How diverse and widely distributed are *Dictyocoela* and other microsporidian parasites in New Zealand amphipods? What are the phylogenetic relationships between *Dictyocoela* in New Zealand and from other parts of the world? Can we observe congruent phylogenies in the amphipod-*Dictyocoela* system? What are the underlying ecological and geological factors influencing the degree of congruence between their phylogenies? Can we infer the duration and intimacy of associations between *Dictyocoela* parasites and their amphipods hosts?

Some ecological and geographical factors make our study system highly suitable for investigating patterns of codiversification and the potential underlying roles of dispersal and geographic barriers. Amphipod dispersal abilities are highly limited due to the lack of planktonic larval stages (Kristjánsson & Svavarsson, 2007; Myers, 1993). Therefore, it is believed that vicariance may have played important roles in amphipod diversification and their biogeographical patterns reflect historical events (Copilaş-Ciocianu, Borko, & Fišer, 2020; Hou & Sket, 2016). New Zealand's geographic history is relatively well known, and is reflected in the unique fauna and the phylogenetic structure of a diverse range of organisms. New Zealand separated from Australia around 82 Mya (Kamp, 1986), with some lineages of archaic vicariant origin (McGlone, 2005; Stevens, 1980). Also, several relatively recent geological events such as the formation of the Southern Alps, shifting climatic conditions and sea-levels, and volcanic eruptions have strongly influenced the current phylogeographic structure of many extant taxa (Trewick, Wallis, & Morgan-Richards, 2011). The role of vicariance, for

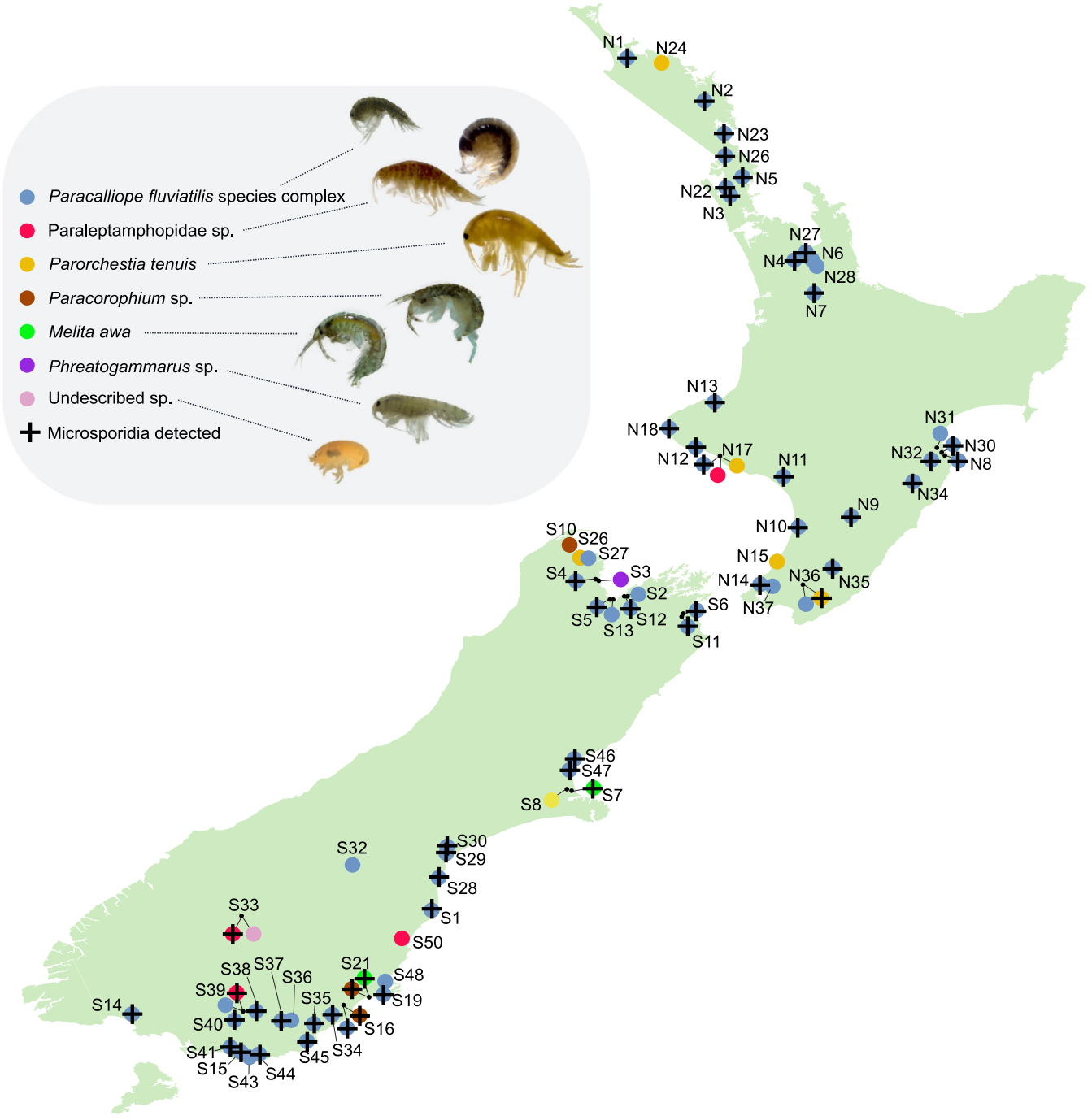

FIGURE 1 Map of New Zealand showing the 69 sampling sites with circles. Seven different families of amphipods are marked with circles of different colours. The sites where microsporidians were detected are marked with +. Site codes correspond to those in Table 1 in Appendix S1 [Colour figure can be viewed at wileyonlinelibrary.com]

example, has been demonstrated in New Zealand's endemic freshwater (*Paracalliope* species complex) and estuarine (*Paracorophium*) amphipods (Hogg, Stevens, Schnabel, & Ann Chapman, 2006; Knox, Hogg, & Pilditch, 2011; Sutherland, Hogg, & Waas, 2009). These studies uncovered highly divergent lineages within taxa, probably due to prolonged isolation and the presence of several cryptic species.

We conducted a regional scale cophylogenetic analysis focusing on *Paracalliope-Dictyocoela* associations in New Zealand. *Paracalliope* is the most common and widely distributed amphipod taxon and its phylogeographic structure largely reflects historical events (Hogg et al., 2006; Sutherland et al., 2009). We compared phylogenetic and phylogeographic structures between *Paracalliope* and their *Dictyocoela* parasites to assess the degree to which patterns overlap and the prevalence of shared co-differentiation/evolutionary histories. We then extended the cophylogenetic analyses to a global scale. The comparison of phylogenies and geographic patterns can provide interesting insights into the duration and the

intimacy of host-parasite associations (Clayton et al., 2015; Garrick, Sabree, Jahnes, & Oliver, 2017). The highly limited dispersal abilities of amphipods have resulted in largely different diversity patterns between the Northern and the Southern Hemispheres (Barnard, 1974; Lowry & Myers, 2017). Accordingly, the presence of *Dictyocoela* in amphipods in both hemispheres can be explained by either an ancient origin or recent dispersal of parasites. Considering patterns of codiversification within a geographic and ecological context, we infer their intimate and ancient associations.

To answer the questions posed above, we conducted nationwide molecular screening on diverse New Zealand amphipods for the presence of microsporidians, covering phylogenetically diverse amphipods (from population to family level). Specifically, we aimed at (a) quantifying the diversity, distribution, and prevalence of microsporidians in New Zealand, and for the first time in the Southern Hemisphere; (b) elucidating the phylogenetic positions of newly discovered microsporidian species within the phylum, and the phylogenetic relationships among *Dictyocoela* species; (c) assessing the degree of congruence between host and parasite phylogenies and phylogeographic structures at both local and global scales; (d) inferring the intimacy and the duration of the association between *Dictyocoela* and their amphipod hosts; and (e) discussing the role of dispersal and geological barriers in explaining codiversification.

2 | MATERIALS AND METHODS

2.1 | Collection of specimens

Amphipods were collected from 69 sites throughout both the South and North Islands of New Zealand between August 2017 and April 2019 (Figures 1, and Table 2 in Appendix S1). Specimens were collected with fine-mesh hand nets (<0.2 mm) and then preserved in 96% ethanol on site. Our main target taxon was the *Paracalliope* species complex, the most common and widely distributed freshwater amphipod species in New Zealand. *Paracalliope* spp. were obtained from 59 locations. At 63 locations, only one amphipod species was found and collected, while at six locations (S16, S21, S33, S39, N17, N36), two or more species were collected. Most of the specimens were found around weed beds in slow-flowing lowland streams and rivers. Some rare amphipod species were found from mountain streams and estuaries.

2.2 | Identification of amphipods

Initial identification of collected specimens was done based on gross morphology (Chapman, Lewis, & Winterbourn, 2011; Fenwick, 2001). Morphologically similar amphipods may be genetically distant due to the presence of cryptic species and/or morphological conservatism (Fišer, Robinson, & Malard, 2018; Murphy, Adams, & Austin, 2009). Therefore, genomic DNA was obtained from several appendages per individual for further genetic identification. Mitochondrial COI and nuclear 28S regions were sequenced for each morphospecies per location (see Table 1 in Appendix S2 for PCR conditions). The sequences obtained were deposited in GenBank (Accession ID: MT465134-MT465172, MT466574-MT466580). Based on both morphological and genetic data, amphipod specimens collected in this study were ascribed to seven families: Paracalliopidae (*Paracalliope* species complex), Paraleptamphopidae (*Paraleptamphopus* sp.), Phreatogammaridae (*Phreatogammarus* sp.), Corophiidae (*Paracorophium excavatum*), Melitidae (*Melita awa*), Talitridae (*Parorchestia tenuis*), and one undescribed family that belongs to the suborder Senticaudata.

2.3 | DNA extraction from pooled specimens

In order to maximize detectability while lowering the cost and time needed for molecular screening for microsporidians, we used pooled host specimens instead of individual specimens for DNA extraction, for amphipod species with small body sizes (<4 mm). This approach allowed us to detect microsporidians even in a host population with low prevalence, with relatively low effort. We used the same number of host individuals for each location when we had enough specimens to compare relative prevalence: 12 pooled samples of four individuals for each location (= 48 individuals) were used for DNA extraction for most populations (Table 2 in Appendix S1). For each pooled sample, the whole bodies of 4 individual amphipods were washed with distilled water, cut into small pieces and pooled into a tube. Then, 400 μl of Chelex solution and 3 μl of proteinase K were added to each tube, which was then incubated at 55°C overnight. The next day, tubes were incubated at 90°C for 8 min and then run in a centrifuge for 10 min at 20,000 x*g* . For *Parorchestia tenuis* which have large body size (>10 mm), pereonites 5 to 7 were dissected (which include gonads) and used for DNA extractions without pooling specimens.

2.4 | Detection of microsporidia by PCR

A partial small subunit ribosomal DNA (*SSU* rDNA) sequence was amplified to detect microsporidian infections. Either a primer pair of 18F (CACCAGGTTGATTCTGCC) and 1492R (GGTTACCTTGTTACGACTT), or V1f (CACCAGGTTGATTCTGCCTGAC) and MC3R (GATAACGA CGGGCGGTGTGTACAA) were used to amplify 1,248 bp and 1,163 bp, respectively (Ovcharenko et al., 2010; Vossbrinck & Debrunner-Vossbrinck, 2005; Weiss & Vossbrinck, 1999; Zhu et al., 1993). For PCR reactions, 12.3 μl of distilled water, 4 μl of reaction buffer, 0.8 μl of each forward and reverse primers, 0.1 μl of MyTaq (Bioline), and 2 μl of DNA were used. For each set of PCR reactions, both negative and positive controls were included with water and DNA obtained from initial screening, respectively. PCR conditions for the primer pair of 18F and 1492R were the following: 94°C initial denaturation for 3 min, 35 cycles of 94°C for 30 s, 50°C for 60 s, 72°C for 60 s, final extension for 10 min at 72°C. For the primer pair of V1f and MC3R, a touchdown

PCR was conducted under the following conditions: initial denaturation at 94°C for 3 min, seven cycles of denaturation at 94°C for 30 s, annealing at 62°C for 30 s (decreasing 1°C/cycle) and extension at 65°C for 80 s, 25 cycles of denaturation at 94°C for 30, annealing at 55°C for 30 s and extension at 65°C for 80 s, with a final extension at 65°C for 5 min. Then, 2 μl of PCR product from each PCR reaction was run on a 1.5% agarose gel. For a subset of samples, representing each species-level taxon, a primer pair of HG4f (GCGGCTTAATTTGACTCAAC) and 580R (GGTCCGTGTTTCAAGACGG) was additionally used to obtain a full SSU, ITS, and LSU sequence (a total length of ~1,760 bp) with the same PCR conditions as for V1f/MC3R (Bacela-Spychalska et al., 2018; Gatehouse & Malone, 1998; Weiss, Zhu, Cali, Tanowitz, & Wittner, 1994).

2.5 | PCR from individual specimens and sequencing

Because we used pooled samples, the risk of contamination due to multiple microsporidian strains of one species or several species in one sample was expected to be higher than when non-pooled samples were used. Therefore, we extracted and sequenced DNA from individual specimens from populations with high infection rates (Table 2 in Appendix S1). When no microsporidians were detected from eight individual samples, or when no amphipod specimens were available after the initial screening, PCR products were directly obtained from pooled samples assuming low prevalence (= single microsporidian species per tube). PCR products were purified with MEGAquick-spin Total Fragment DNA Purification Kit (iNtRON biotechnology) according to the manufacturer's instructions. Purified PCR products were sent to either Genetic Analysis Services at the University of Otago, New Zealand or Macrogen, Korea, for Sanger sequencing. Raw nucleotide sequences were trimmed with the trim function in Geneious prime 2019.0.4 (https://www.geneious.com) with the default settings, and then ambiguous sites were carefully examined and corrected by eye. Some multipeaks were identified only in two short hypervariable regions within SSU. This could be due to multiple infections or intragenomic variation among rRNA copies (Ironside 2013). In our case, the pooling method may have increased the chance of contamination by including more than one infected individual in the same tube. However, this was not probably a major factor because sequences with multiple peaks were evenly distributed among both individual and pooled samples. For these sequences, the International Union of Pure and Applied Chemistry (IUPAC code) was used to avoid possible errors in delineating strains or species (Alperi, Figueras, Inza, & Martínez-Murcia, 2008).

2.6 | Species delimitation

Haplotypes were identified by using the package pegas (Paradis, 2010) in R version 3.5.2 (R Core Team, 2013). Haplotypes that diverged by <1% were grouped into a putative species, following the criteria of Terry et al. (2004). A tree-based (mPTP) method and a distance-based (ABGD) species delimitation method, along with morphological assessment, confirmed the validity of the "1% rule" (Bacela-Spychalska et al., 2018). A formal description of these species would require an integrative approach with morphological, ecological, and phylogenetic data (Stentiford, Feist, Stone, Bateman, & Dunn, 2013). Therefore, our newly discovered microsporidian putative "species" will remain as candidates until full description. In this study, we assigned them provisional names for convenience (Table 3 in Appendix S1).

2.7 | Phylogenetic and cophylogenetic analyses

Six phylogenetic trees were assembled for four different purposes: (a) to place newly found putative species within the phylum Microsporidia; (b) to resolve the phylogenetic relationships among all dictyocoelan species, as most of our sequences belong to this genus; (c) to be used in cophylogenetic analysis between *Dictyocoela* and their *Paracalliope* hosts at a regional scale; and (d) to be used in cophylogenetic analysis between *Dictyocoela* and their amphipod hosts at a global scale. The following procedures were applied to all data sets: all sequences were aligned in Geneious prime with the MAFFT algorithm (Katoh & Standley, 2013) using consistency-based iterative refinement methods (E-INS-i or G-INS-i). Ambiguous sites were then eliminated in Gblocks with the least restrictive setting (Castresana, 2000). The best-fitting model of nucleotide evolution for each data set was determined based on the corrected Aikake information criterion (AICc) using jModelTest v2.1.6 (Darriba, Taboada, Doallo, & Posada, 2012), which was conducted through the CIPRES Science Gateway v3.3 (Miller, Pfeiffer, & Schwartz, 2010). For all analyses of microsporidians, the general time reversible (GTR) model of nucleotide substitution along with Gamma distributed rate variation across sites (G) and the proportion of invariable sites (I) were used for Bayesian tree inference in MrBayes 3.2.7 (Ronquist et al., 2012). For the host phylogeny based on 28S sequences, GTR + G was used for tree reconstruction. For all data sets, two independent runs, consisting of four chains each, were simultaneously conducted for 2,000,000 generations with a sampling frequency of 1,000. A stop rule was applied to terminate the MCMC generations as soon as the standard deviation of split frequencies fell below 0.01. The initial 25% of samples were discarded. Maximum likelihood trees were reconstructed in RAxML with GTRGAMMA + I as a model of nucleotide evolution. A rapid bootstrap analysis was conducted with 1,000 replicates. The resulting trees were visualized in FigTree v1.4.4. No major differences between Bayesian and ML tree were found for all the data sets (see Appendix S2 for the ML trees).

2.7.1 | Phylogeny of the phylum Microsporidia

A full SSU, a full ITS, and partial LSU sequences of representative species from the major clades of microsporidians (clade 1–5; Vossbrinck,

Debrunner-Vossbrinck, & Weiss, 2014) and several sequences that are similar to our sequences (>88%), based on a BLAST search, were obtained from GenBank (Table 4 in Appendix S1). Two species that belong to the 'expanded Microsporidia', *Nucleophaga amoebae* (JQ288099), *Paramicrosporidium saccamoebae* (JQ796369), and one aphelid species, *Amoeboaphelidium protococcarum* (JX507298), were used as outgroups (Bass et al., 2018). An alignment of 1,115 bp of 93 sequences was used for tree reconstruction after eliminating ambiguous sites in Gblocks as described above.

2.7.2 | Phylogeny of the genus *Dictyocoela*

Representative sequences of each dictyocoelan species were included for the analysis. A full SSU, a full ITS, and partial LSU sequences were used to resolve deeper relationships within the genus (Bacela-Spychalska et al., 2018). Ten dictyocoelan species (*D. duebenum*, *D. muelleri*, *D. roeselum*, *D. berillonum*, *D. dipoereiae*, *D. gammarellum*, *D. cavimanum*, *D. deshyesum*, *D.* sp. N1, and *D.* sp. N4) known from Eurasia and the USA were included along with our seven newly identified, species-level taxa (see results) of the *Unikaryon-Dictyocoela* group. *Glugea anomala* (AF044391), *Pleistophora mulleri* (FN434084), *Spraguea lophii* (AF104086), *Nosema granulosis* (AJ011833), and *Enterocytozoon bieneusi* (L07123) were included as outgroups.

2.7.3 | Cophylogeny on a regional scale: *Dictyocoela* and *Paracalliope*

A fine-scale tree (population-species level) was made for all haplotypes belonging to the dictyocoelan species (*Dictyocoela* sp. NZ1-3) discovered from *Paracalliope* species complex to test for congruent phylogeny between parasite and host species. The two sequences of *Dictyocoela* sp. NZ4, obtained from *Paracorophium excavatum* and *Melita awa*, were used as outgroups. For host phylogeny, nuclear 28S sequences obtained from each *Paracalliope* population were included in the ingroup. Three sequences with the highest similarity in GenBank were used as outgroups, based on the BLAST search. Several methods are available for cophylogenetic analyses. A tanglegram is commonly used to visually represent congruence between two phylogenies (Page, 2003; but see de Vienne, 2019 for criticism). Therefore, a tanglegram was drawn manually on a vector graphics editor, Affinity Designer (https://affinity.serif.com/). Additionally, overall congruence between parasites and hosts was quantified using Procrustean Approach to Cophylogeny (PACo), one of the commonly used distance based global-fit methods for cophylogenetic analysis (Balbuena, Míguez-Lozano, & Blasco-Costa, 2013). PACo computes a goodness-of-fit statistic from the residual sum of squares of the Procrustean fit as a measure of congruence between parasite and host phylogenies, with its significance established by randomization of the host-parasite association matrix. It also allows for the assessment of the contribution of each individual host-parasite association to the overall global fit. PACo provided several advantages for our study. First, this method does not require fully resolved trees and allows multiple parasite-host associations for analysis. Second, PACo is especially appropriate for study systems where one phylogeny is expected to depend upon another. Assuming inherently high dependence of *Dictyocoela* upon their hosts (i.e., the former being an obligate intracellular parasite), we hypothesized that the phylogeny of *Dictyocoela* should mirror that of its *Paracalliope* hosts, by showing a significant degree of congruence with amphipod phylogeny. Three data matrices were used as input: two phylogenetic trees of hosts and parasites, and a binary matrix of parasite-host associations. The two trees were transformed into matrices of patristic distances, and then the parasite matrix was rotated and scaled to fit the host matrix by Procrustean superimposition. A residual sum of squares was obtained as a global goodness-of-fit statistic; its significance was established by assigning hosts randomly to parasites in the parasite-host matrix with 100,000 permutations. The sum of squared residuals and the upper 95% confidence intervals of each parasite-host link were obtained using a jackknife method, and used to assess the contribution of each link to the overall goodness-of fit. A significance level of 0.05 was applied for all the analyses.

2.7.4 | Cophylogeny at a global scale: *Dictyocoela* and amphipods

To evaluate the level of cophylogenetic congruence at a global scale between *Dictyocoela* and their respective amphipod hosts, the distance-based PACo was again used. Only one sequence per species of *Dictyocoela* was included for tree inference, because including multiple sequences of the same species could overestimate the degree of phylogenetic congruence (Refrégier et al., 2008). For amphipod hosts, we inferred a genus-level phylogenetic tree, since the family Gammaridae was not recovered as a monophyletic group in Copilaş-Ciocianu et al. (2020). We used 18S, 28S, and COI sequences available in GenBank and obtained in this study (Table 5 in Appendix S1). Most of the *Dictyocoela* were found from freshwater amphipods; because freshwater amphipods evolved independently multiple times from marine groups (Lowry & Myers, 2017), most freshwater amphipod families are distantly related and comprise a small portion of the diversity across all amphipods. However, unresolved trees would not affect our inferences since PACo estimates overall congruence of the two phylogenies based on the patristic distances which measure the amount of genetic divergence accounting for the divergence time among taxa (Balbuena et al., 2013). Using these two trees, PACo analysis was conducted as described above.

3 | RESULTS

3.1 | Microsporidians are widespread in diverse New Zealand amphipods

Microsporidians were widely distributed in freshwater and estuarine amphipods in New Zealand (Figure 1). Also, a putative

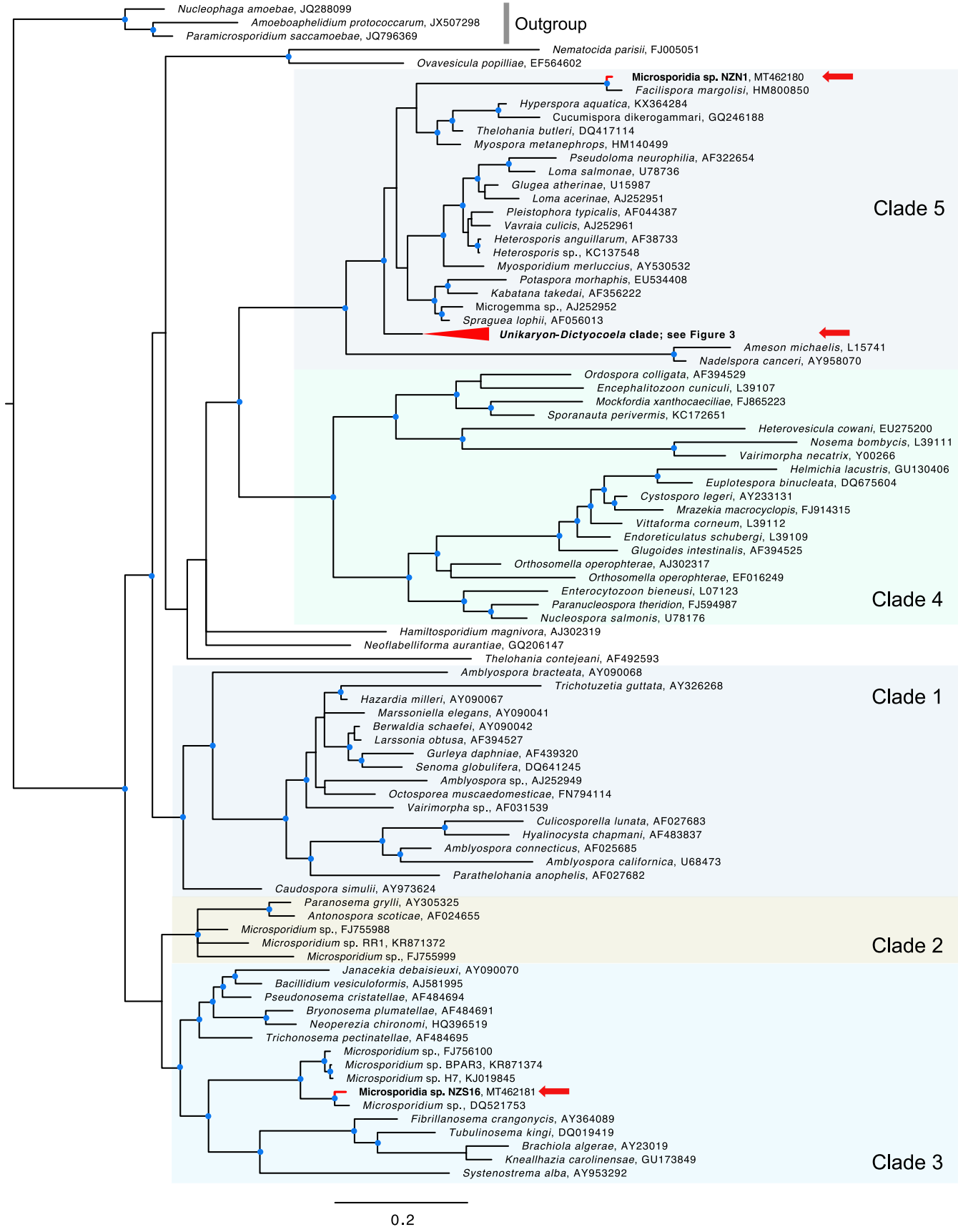

FIGURE 2 Bayesian tree showing phylogenetic positions of microsporidians obtained from this study within the phylum Microsporidia. Nodes with posterior probability higher than 0.9 are shown with blue circles. Major clades defined from Vossbrinck et al. (2014) are marked. All our newly discovered sequences (red arrows) belong to either Clade 3 or 5 [Colour figure can be viewed at wileyonlinelibrary.com]

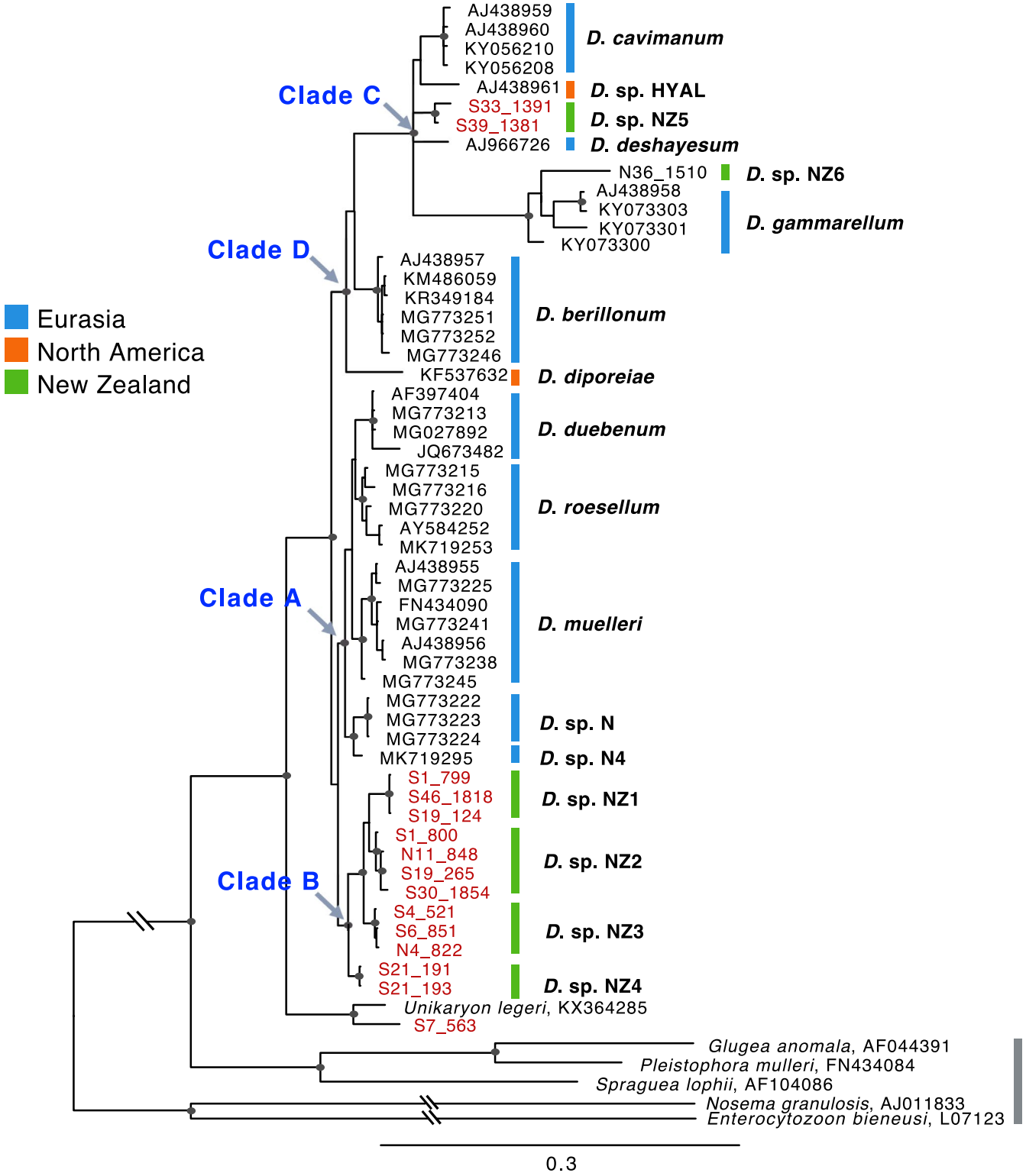

FIGURE 3 Bayesian tree of the relationships among species within *Dictyocoela*. Each coloured bar represents a species and their region of origin is shown with different colours. Well-supported major groups are marked (Clade AD) [Colour figure can be viewed at wileyonlinelibrary.com]

microsporidian species was detected from a freshwater-terrestrial amphipod species (*Parorchestia tenuis*). Among 69 locations, microsporidians were detected from 51 sites (73.9%). Because we used pooled samples, the actual prevalence in a population could not be estimated. Relative prevalence varied from low (1/12 pooled samples) to high (12/12 pooled samples) among populations and sites (Table 2 in Appendix S1). Among seven identified host taxa, five harboured microsporidians: *Paracalliope*,

Paraleptamphopus, *Paraorchestia*, *Paracorophium*, and *Melita*. A total of 46 of 59 *Paracalliope*, two of four *Paraleptamphopus*, one of six *Parorchestia*, two of three *Paracorophium*, and two of two *Melita* populations were positive for microsporidian infections. In total, 169 of 724 pooled samples (23.3%) tested positive for microsporidians.

3.2 | Placing species-level taxa within the phylum

A total of 71 SSU sequences was obtained from the 51 sampled locations. In total, 31 haplotypes were identified from 71 sequences, which were delimitated as nine species-level taxa. A BLAST search against GenBank showed that 28 of these haplotypes were genetically similar to sequences of the genus *Dictyocoela* (86%–94% uncorrected sequence similarity). Of the remaining three haplotypes, one was 96.4% identical to the sequence of *Unikayon legeri* (KX364285), a hyperparasitic species infecting the digenean trematode *Meiogymnophallus minutus*, which is a parasite of cockles (Stentiford et al., 2017). The Bayesian tree of the phylum shows the phylogenetic positions of the newly identified species (Figure 2). *Dictyocoela* and *Unikaryon* are closely related, forming a monophyletic clade (PP = 1). Two haplotypes were located outside of the *Unikaryon-Dictyocoela* clade (Figure 2). One of these two haplotypes (GenBank ID: MT462181) was obtained from both *Paracalliope* and *Paracorophium* in Lake Waihola (S16), and is similar to sequences obtained from other amphipods forming a monophyletic clade (Figure 2). The other haplotype (GenBank ID: MT462180) found from a divergent lineage of *Paracalliope* in Kaingaroa (N1) was 91.27% identical to *Facilispora margolish* (HM800849) previously reported from a parasitic copepod in the northeast Pacific Ocean (Jones, Prosperi-Porta, & Kim, 2012).

3.3 | Six new molecular species identified within *Dictyocoela*

Figure 3 shows phylogenetic relationships among the dictyocoelan species obtained globally, including six species-level taxa (*Dictyocoela* sp. NZ1-6) obtained in this study. Several well-supported clades were identified. Clade A (PP = 0.97) contains all the dictyocoelan species obtained from gammarids in Eurasia, except for *D. berillonum*. Clade B (PP = 0.98) includes all the dictyocoelan species obtained from *Paracalliope*, *Paracorophium*, and *Melita* (*Dictyocoela* sp. NZ1-4), all obtained from this study. Clade A and B were grouped together, but their sister relationship was weakly supported (PP = 0.74). Clade C includes all the microsporidian species from talitrids from Europe, New Zealand, and the USA. *Dictyocoela* sp. NZ5 from Paraleptamphopidae was the exception, being the only species in this clade not found from the superfamily Talitroidea. In addition to Clade C, *D. berillonum* and *D. diporeiae* were clustered together forming a highly supported Clade D (PP = 1).

3.4 | Host specificity of New Zealand microsporidian species

Dictyocoela sp. NZ1-3 were exclusively detected from *Paracalliope* amphipod hosts despite their large geographic ranges, suggesting strong host fidelity. Some evidence for host specificity was observed at several sites with co-occurring species. Two or three amphipod species of different families were sampled from six locations (see Figure 1). In four of six of these locations, a microsporidian species was detected from only one species. However, some evidence of horizontal transmission among distantly related hosts was observed in two locations. Specifically, *Paracorophium excavatum* and *Melita* sp., in Kaikorai estuary, harboured dictyocoelan sequences that were genetically very similar to each other (*Dictyocoela* sp. NZ4; >99.4% similarity). Similarly, *Paracorophium excavatum* and *Paracalliope* sp. shared the same microsporidian species (Microsporidia sp. NZS16; 100% identical sequences) in Lake Waihola.

3.5 | Cophylogeny at a regional scale

Figure 4 shows a tanglegram of associations between *Dictyocoela* and their hosts from the *Paracalliope* species complex (see also Figure S3). Based on 28S sequences, host populations were largely divided into two groups showing geographic structure: Northern and Central (NC) and Southern (S) (Figure 4b). Interestingly, the Southern group was further divided into two main subgroups (SA and SB) and a divergent lineage (S30), with *Dictyocoela* haplotype (rather than geography) being a strong predictor of host genotypic groups, i.e., host populations of subgroups SA and SB harboured different haplotypes of *Dictyocoela*. *Dictyocoela* sp. NZ3 was found throughout the country but some haplotypes of this species were associated only with the SA, SB, or NC groups (Figure 3). Within *Dictyocoela* sp. NZ2, six of eight haplotypes were found in group C. Also, this species included a widespread haplotype that was found throughout the country. The rare species, *Dictyocoela* sp. NZ1, was only found at a few locations in the South Island. Overall, some congruent patterns between parasite and host phylogenies were observed from visual inspection. In addition, we tested for a significant congruent pattern between parasite and host phylogenies using PACo including all the three species of *Dictyocoela* (*Dictyocoela* sp. NZ1-3) found in New Zealand. We rejected the null hypothesis of random association ($m^2 = 0.8683122$, $p = .01559$), in favour of the alternative hypothesis that overall *Dictyocoela* phylogeny is constrained by that of their amphipod hosts.

3.6 | Cophylogeny at a global scale

Figure 5 shows the tanglegram between the genus *Dictyocoela* and their amphipod hosts. PACo analysis provided evidence for rejection of the null hypothesis that host phylogeny does not predict the parasite ordination ($m^2 = 1.93561$, $p < .0001$). Therefore, we opted for

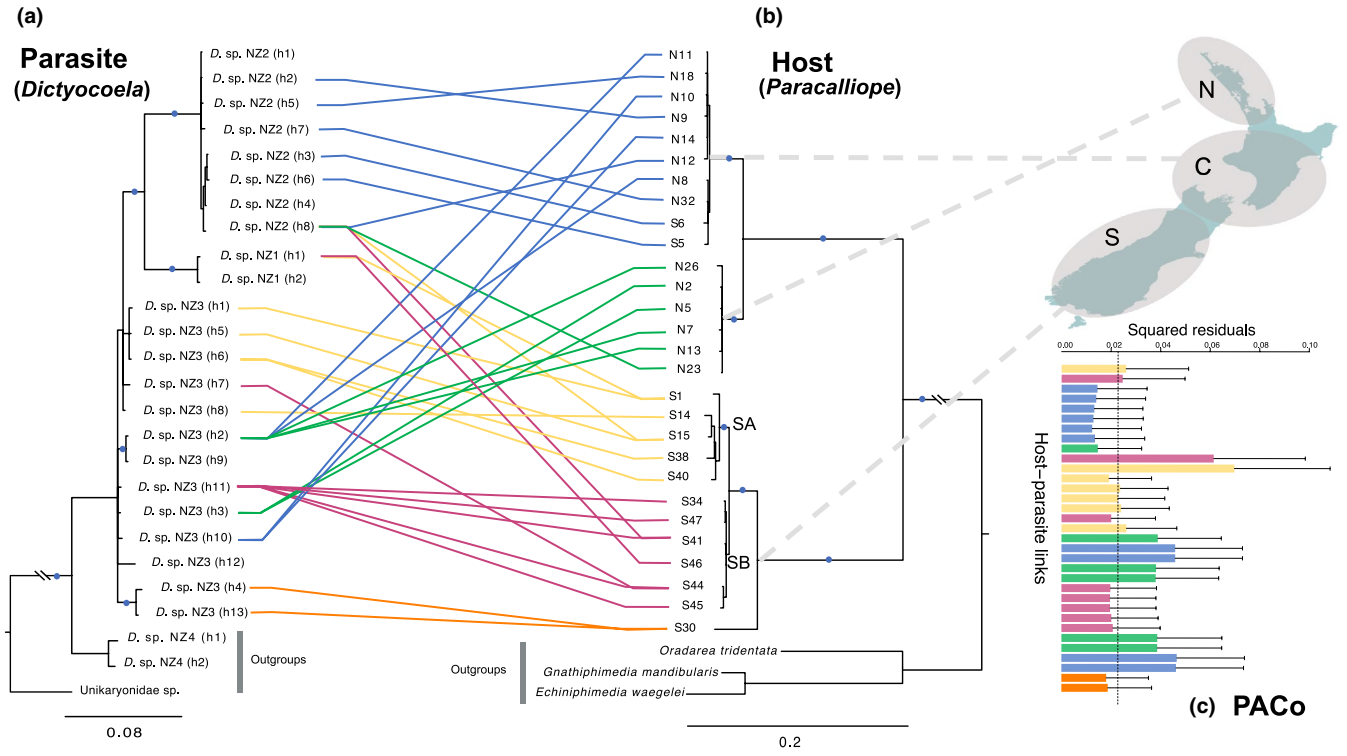

FIGURE 4 Tanglegram illustrating associations between parasites (*Dictyocoela*) and their hosts (*Paracalliope*). Lines between the two trees represent individual parasite-host links. Colours of the lines and bars are marked based on the host group (see below). (a) Bayesian tree of the 26 haplotypes of SSU rDNA sequences obtained from *D.* sp. NZ1-3. (b) Bayesian tree (28S rDNA sequences) showing the relationships among *Paracalliope* populations. Four main groups are defined (N, C, SA and SB). The map shows geographic distributions of the host groups (upper right). (c) Residual bars of each parasite-host link are shown. The dotted line shows the median residual value and error bars show the upper 95% confidence intervals (see Figure S3 for identity of each parasite-host link) [Colour figure can be viewed at wileyonlinelibrary.com]

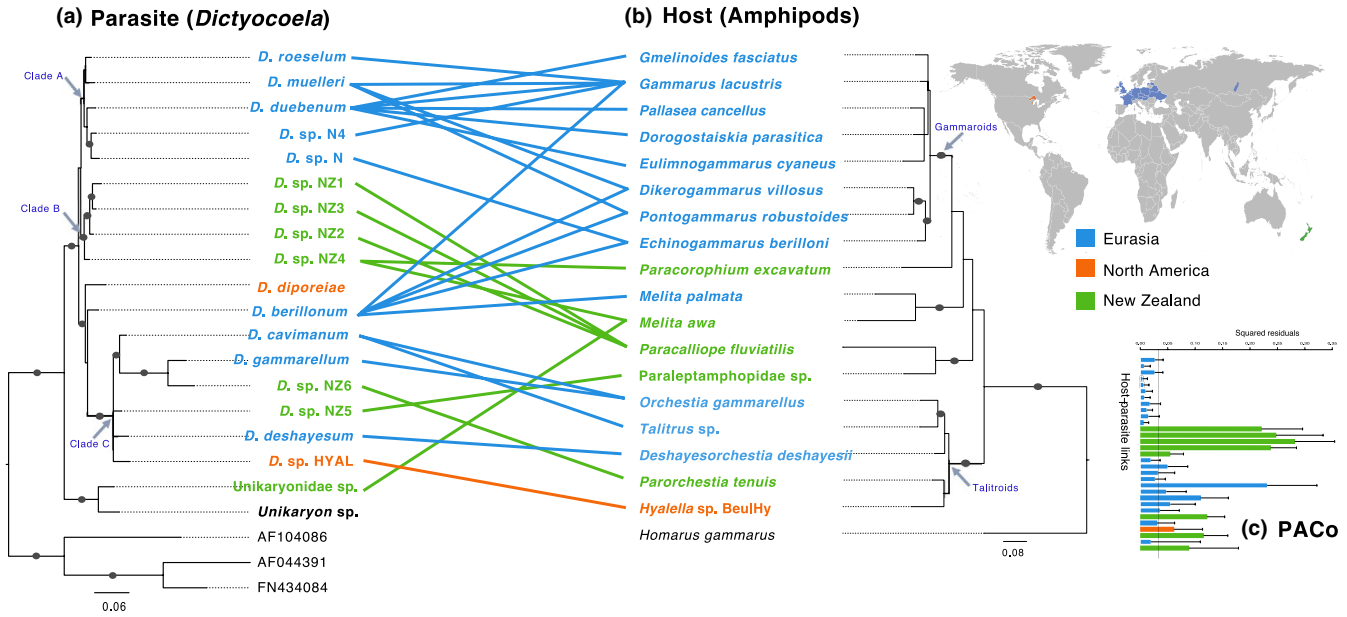

FIGURE 5 Tanglegram showing associations between the parasites (*Dictyocoela*) and their amphipod hosts. The same colour code from Figure 3 was used. (a) The species level Bayesian tree of the genus *Dictyocoela* based on the SSU and LSU sequences. (b) The genus level Bayesian tree of all the amphipods which harbor *Dictyocoela* based on the concatenated data set (18S, 28S and COI sequences). (c) Residual bars of each parasite-host link are shown. The dotted line shows the median residual value and error bars show the upper 95% confidence intervals (see Figure S4 for identity of each parasite-host link) [Colour figure can be viewed at wileyonlinelibrary.com]

our alternative hypothesis that the host-parasite associations show some degree of phylogenetic congruence. Several host-parasite association patterns were observed. First, clade A of *Dictyocoela* was found only in gammarid hosts, with the respective squared residuals of each of their individual links contributing the most to the congruence of the two phylogenies (Figure S4) and could potentially represent codivergence links. Second, Clade B was found only in New Zealand amphipods but in genetically distantly related families (Paracalliopidae, Corophiidae, and Melitidae). Squared residuals associated with these links contributed the least to the level of congruence of the phylogenies. Third, all the species from clade C, except for *Dictyocoela* sp. NZ5, were found in talitroid hosts distributed across different continents. Generally, the host-parasite links of clade C seem to represent incongruent coevolutionary links given the high associated residuals (Figure 5c; see also Figure S4).

4 | DISCUSSION

Our study uncovered the diversity of microsporidian parasites in amphipods in New Zealand and, for the first time, across the Southern Hemisphere. We also investigated patterns of codiversification by comparing phylogenies between *Dictyocoela* microsporidians and their amphipod hosts at both local and global scales, providing new insights into processes that may have shaped their current diversity and distribution. In addition, we inferred the duration and intimacy of amphipod-*Dictyocoela* associations in the context of codiversification history, dispersal limitation, and historical geological events.

It is important to note that we are not explicitly testing coevolutionary diversification, or linking coevolution with codiversification, as we are not assessing reciprocal natural selection pressures or the resulting microevolutionary changes between host and parasite (Althoff et al., 2014; de Vienne et al., 2013). Coevolutionary diversification is the process by which coevolution between two or more taxa increases net diversification in at least one of them (Althoff et al., 2014). Instead, we hypothesise a pattern of codiversification (correlated diversification between interacting lineages; Clayton et al., 2015) as inferred from the level cophylogenetic and cophylogeographic congruence. We discuss some ecological traits (mode of parasite transmission, dispersal abilities of host and parasite, the presence of genetically similar taxa within the same area) as well as shared biogeographic histories (e.g., covicariance and codispersal) to explain phylogenetic congruence at macroevolutionary scales.

4.1 | Phylogenetic and phylogeographic congruence between *Paracalliope-Dictyocoela* suggests their shared phylogeographic history

Considering the overall congruent phylogenetic and geographic patterns, and the known geological history of New Zealand, we infer that the phylogeographic pattern of *Dictyocoela* may in part reflect the colonization history of *Paracalliope*. Based on the sequence divergence among *Paracalliope* lineages within New Zealand, it was estimated that dispersal of *Paracalliope* from Australia to New Zealand occurred during the Miocene (~17 Mya) (Sutherland et al., 2009). During the Pliocene (~5 Mya), New Zealand was divided into several large and small islands due to rising sea levels. The S group may have been isolated from the NC groups since that time. During the Pleistocene (3-1 Mya), the sea level decreased, and land emerged in the southern North Island (Trewick et al., 2011), and *Paracalliope* may have (re)colonized the newly available area like other invertebrates. The North and South Islands were connected until about 500 Kya (Fleming, 1979; Lewis, Carter, & Davey, 1994), which may explain why the populations of the southern North Island and the northern South Island are genetically homogeneous. Meanwhile, the presence of the two main host subgroups in the South Island (SA and SB) may have resulted from different colonization events. (Re)colonizations may have occurred due to sea-level changes and occasional flooding and tsunami events in lowland streams, which are common events in the South Island (Scrimgeour & Winterbourn, 1989). When (re) colonization occurred, the associated parasite haplotypes may have codispersed with their hosts into the new habitat. Based on their high abundance in the host populations, overlapping geographic regions, host fidelity, and associated population structures, we infer that dictyocoelan parasites were present in the most recent common ancestor of *Paracalliope* and have been maintaining their relationship mainly by vertical transmission.

4.2 | Codiversification between *Dictyocoela* and their amphipod hosts

The presence of *Dictyocoela* in several ancient lineages of major amphipod families could explain their present-day occurrence in numerous extant amphipod taxa. Gammarids in Europe, Ponto-Caspian, and Lake Baikal are genetically closely related and are believed to have originated from their the most recent common continental ancestors (Barnard & Barnard, 1983; Macdonald, Yampolsky, & Duffy, 2005; Väinölä et al., 2008). This may explain why similar microsporidians were found in diverse gammarid hosts across those regions, despite geographic distances (Ironside & Wilkinson, 2018). On the other hand, frequent horizontal transmission among genetically similar hosts were assumed based on the common presence of *Dictyocoela*, and their lack of clear host specificity among some gammarids in Eurasia (Ironside & Wilkinson, 2018; Quiles et al., 2019). On the other hand, the New Zealand amphipod fauna has low species-level diversity but a broad taxonomic range, with 24 described species from 10 genera and eight families (Chapman et al., 2011). It seems that dictyocoelan species can switch relatively easily between con-familiar species but overcoming the barrier between species of different families is much more difficult. Interestingly, although strong host fidelity of *Dictyocoela* in *Paracalliope* and overall family-level host specificity were observed in New Zealand, host-switching

events among genetically distantly related hosts were also inferred (see 3.6). The strongly supported monophyly of clade B (Figures 4 and 5) suggests that host-shift speciation contributed to the diversity of *Dictyocoela* in New Zealand.

4.3 | Inferring the evolutionary history of amphipod-*Dictyocoela* associations

Our findings significantly expand the known geographic and host range of *Dictyocoela*. Because *Dictyocoela* is highly specialized in amphipod hosts, its present-day global distribution could be explained either by an ancient origin followed by prolonged association with the host, or perhaps by more recent, host-independent dispersal events. Given the life history characteristics of microsporidians and the strong association between *Dictyocoela* and their amphipod hosts, we suggest three possible scenarios to explain the transoceanic distribution of *Dictyocoela* (Figure 6).

4.3.1 | Vicariance

An ancient origin of *Dictyocoela* predating the split of the supercontinent Pangaea would be the most parsimonious scenario for the occurrence of *Dictyocoela* species in most freshwater amphipod species whose dispersal abilities are significantly limited (Figure 6). In the absence of effective indirect means of transfer, *Dictyocoela* must have been vertically transmitted or horizontally transmitted between other species in the same habitat. It is believed that the breakup of Pangaea and the formation of Laurasia and Gondwana supercontinents played an important role in the diversification of many amphipod groups, although this hypothesis still remains to be tested (Copilaş-Ciocianu et al., 2020). Given that the northern and southern amphipod fauna are largely different (Barnard, 1974; Lowry & Myers, 2013), the origin of *Dictyocoela* could potentially date back to the split of Pangaea (~180 Mya), before the major diversification of amphipods and/or when they were separated into different lands.

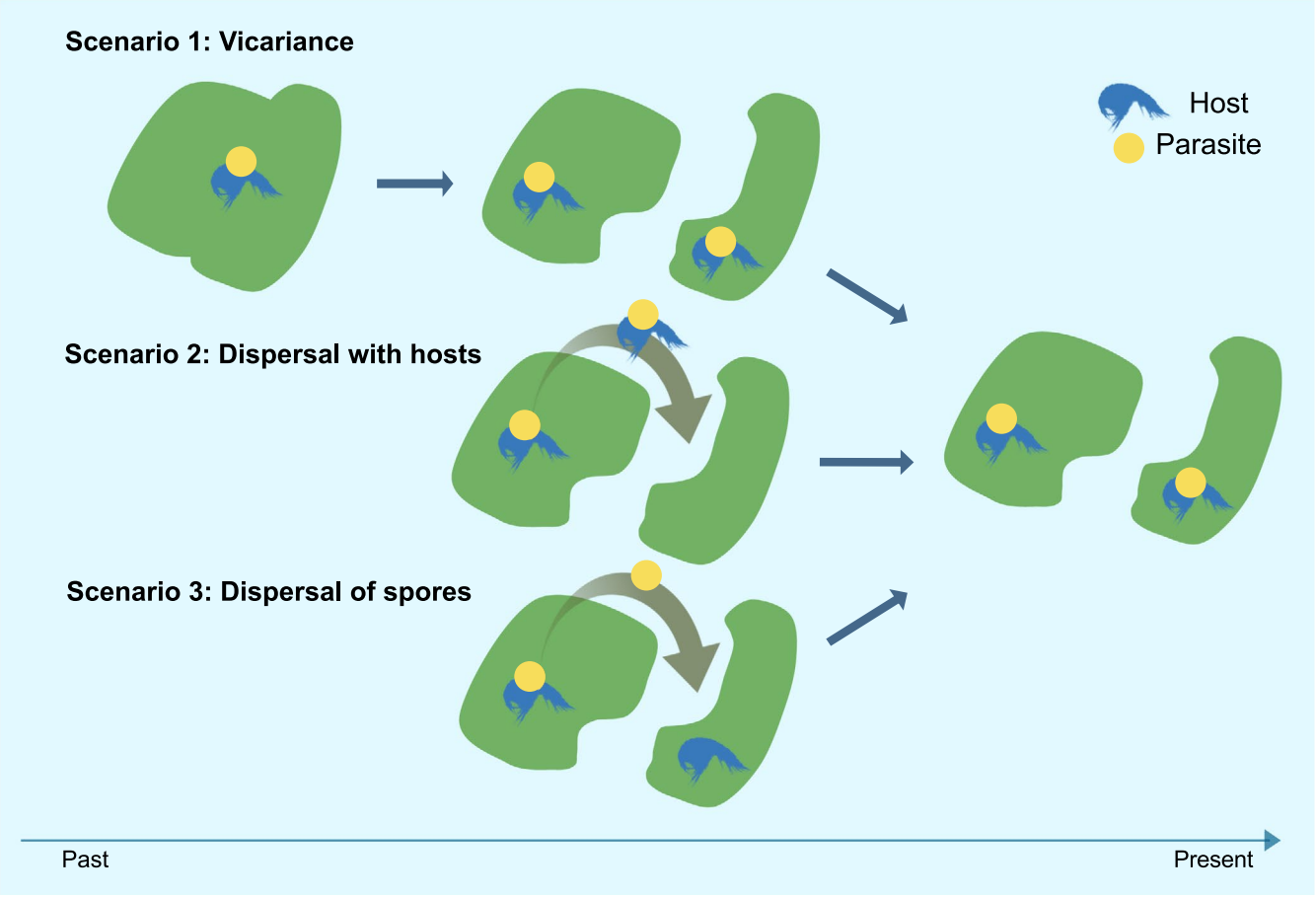

FIGURE 6 Three possible scenarios to explain transoceanic (inter-continental) distribution of parasites. Scenario 1. Vicariance. Split of parasite lineages in different continents may be due to vicariance events. Scenario 2. Host-dependent long-distance dispersal (LDD). Parasites that are highly dependent on hosts may have traveled with them, if hosts were capable of LDD. Scenario 3. Host-independent parasite LDD. Spores may have dispersed via water, air, driftwood, or birds, to other remote area. In all cases, current host-parasite associations are not necessarily assumed. Accordingly, the amphipod host and the parasite in the figure represent hypothetical species [Colour figure can be viewed at wileyonlinelibrary.com]

4.3.2 | Host dependent long distance dispersal: Dispersal with hosts

Long distance dispersal (LDD) of parasites within or on their hosts (Figure 6) could play an important role for parasite dispersal, as shown in ticks on their penguin hosts and tick-borne bacterial pathogens in birds (Moon et al., 2019; Norte et al., 2020). This scenario can explain especially the global distribution of talitroid hosts and their associated *Dictyocoela* parasites. Talitridae is the only family that includes terrestrial species that can disperse by several means (Fenwick & Webber, 2008; Friend & Richardson, 1986; Wildish, 2012). Interestingly, all *Dictyocoela* species detected from talitrids belong to Clade C, suggesting codiversification (Figure 5). Also, talitrids and their *Dictyocoela* parasites are distributed globally, consistent with a codispersal scenario.

4.3.3 | Host independent parasite LDD: Dispersal of spores

Dictyocoela may have traveled long distances independently as spores. If this is the case, then the origin of *Dictyocoela* does not necessarily need to be ancient. Microsporidians produce spores that are resistant to the external environment, but little is known about their dispersal potential over long distance. Spores may be able to travel in the air and water and explain the wide distributions of opportunistic microsporidians such as *Encephalitozoon* and *Enterocytozoon* (Stentiford et al., 2016). However, this mode is more plausible for generalists and is incompatible with the host specificity observed in *Dictyocoela* in amphipod hosts on remote islands and seen in this study. Nevertheless, because we know very little about the dispersal ability of spores, and the lack of occurrence data of microsporidians in amphipods over large areas, we cannot rule out the possibility of this scenario.

Distinguishing among these scenarios requires more evidence. First, targeted screening of microsporidians of marine and additional freshwater amphipods covering a larger geographic area would provide valuable information for inferring historic host-parasite associations. Second, only with time calibrated phylogenies can we possibly discern between a vicariant origin versus other more recent origin of *Dictyocoela* in New Zealand. Third, assessing the dispersal abilities of microsporidian spores could support the LDD by spore scenario.

4.4 | Host-parasite associations across scales: From mode of transmission to macroevolutionary patterns

Vertical and horizontal transmission occur within a short time frame and across small geographic scales. Although vertical transmission is often expected to produce congruent patterns with hosts on larger scales (Althoff et al., 2014), the impact of vertical transmission on macroevolutionary patterns has rarely been shown by empirical data. Biological interactions can affect the distribution of species, but this is a scale-dependent process and its role over large scale patterns remains controversial (Araújo & Rozenfeld, 2014; McGill, 2010). A mathematical model predicts that parasites can co-occur with their hosts across geographical scales according to their dependency on the hosts (Araújo & Rozenfeld, 2014). Our study provides empirical evidence that vertically transmitted parasites show similar phylogenetic and geographic patterns with their hosts across spatial scales. However, this does not undermine the role of horizontal transmission (which could lead to host-shift speciation) in parasite diversification. A large body of evidence suggests that host-shift speciation is a common process even for specialized symbionts or vertically transmitted parasites (Bailly-Bechet et al., 2017; Doña et al., 2017; de Vienne et al., 2013). Microsporidians show similar patterns. Despite apparent vertical transmission, frequent host-switching events have been inferred in studies of microsporidians in Eurasia (Ironside & Wilkinson, 2018; Quiles et al., 2019). In New Zealand, even though tight host-parasite associations were inferred based on the congruent spatial-genetic structure in *Paracalliope*, horizontal transmission (or host-shift) among species of different families was also inferred. Therefore, it seems that host-switching may be common from local to regional scales. When comparing Europe and New Zealand, it seems that geological barriers that simultaneously acted on both *Dictyocoela* and their amphipod hosts, coupled with vertical transmission as the main transmission mode, could in part explain their congruent phylogeographies.

In summary, evidence of both vertical and horizontal transmission can be seen at small scales, and both modes may have played pivotal and far-arching roles; however, parasite distribution at larger scales could be mainly explained by host distribution and geographical processes. Our study underscores that considering multiple processes operating at different scales is necessary to explain parasite distribution and its connection to host associations.

In conclusion, our study confirmed the worldwide distribution of *Dictyocoela* in many different lineages of aquatic amphipods. Based on their strong reliance on the host for dispersal as an intracellular parasite as well as the limited dispersal capabilities of amphipod hosts, we inferred their intimate association that may have persisted over macroevolutionary time, by comparing phylogenetic and phylogeographic patterns. Both vertical and horizontal transmission may have played substantial roles in the evolution of the parasites. However, at a macroevolutionary scale, host range and geological processes can primarily explain parasite distribution. Our study highlights that considering multiple processes operating at different scales is necessary to explain codiversification of hosts and their parasites. Also, our study shows that uncovering parasite diversity in new host taxa and geographic regions can provide novel insights into the evolutionary history of host-parasite associations. Further studies of diverse host-parasite systems with varying ecological traits and known biogeographic histories will be important to further investigate patterns of codiversification and underlying mechanisms.

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AUTHOR CONTRIBUTIONS

E.P. and R.P. conceived the study. E.P. conducted field sampling, generated and analysed the data, and wrote the manuscript. E.P., F.J., and R.P. interpreted and discussed the results. F.J., and R.P. provided critical feedback on the manuscript. All the authors read and approved the final version of the manuscript.

DATA ACCESSIBILITY

All the sequences generated in this study are deposited in GenBank (Accession ID: MT462166-MT462196, MT465134-MT465172, MT466574-MT466580). The alignment files used for this study are available on Dryad at https://doi.org/10.5061/dryad.83bk3j9pb

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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