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ARTICLE



Direct long-distance dispersal shapes a New World amphitropical disjunction in the dispersal-limited dung moss *Tetraplodon* (Bryopsida: Splachnaceae)

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ABSTRACT

Aim Many intercontinental disjunctions, especially among spore-producing plants, are shaped by long-distance dispersal (LDD) via wind currents. Amphitropical disjunctions are most commonly explained through LDD, but other vectors and dispersal scenarios must also be considered. To interpret the New World amphitropical disjunction in the dung-moss genus *Tetraplodon*, we compared stepwise migration along the Andes, direct LDD and ancient vicariance.

Location Global, specifically high-latitude and high-elevation localities, with a focus on the New World.

Methods Phylogenetic relationships were inferred from four loci sampled from 124 populations representing the global range of *Tetraplodon*, and analysed using maximum-likelihood and Bayesian optimality criteria, with divergence dates estimated in BEAST.

Results The monophyletic *T. mnioides* complex diversified between the early Miocene and early-to-mid Pliocene into three well-supported clades, each with a unique geographical distribution: Laurasian, primarily high-elevation tropical, and amphitropical. Populations from southernmost South American were reconstructed as a monophyletic lineage that diverged from high-latitude Northern Hemisphere populations around 8.63 Ma [95% highest posterior density (HPD) 3.07–10.11 Ma].

Main conclusions Direct LDD has resulted in the American amphitropical disjunction in *Tetraplodon*. A lack of modern or historical wind connectivity between polar regions and the poor resistance of *Tetraplodon* spores to the conditions associated with wind-dispersal suggest that bird-mediated LDD provides the best explanation for the establishment of amphitropicality.

Keywords

Amphitropical, bipolar, bryophyte, disjunctions, long-distance dispersal, migratory shorebird, New World, *Tetraplodon*.

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INTRODUCTION

Intercontinental disjunctions are common among land plants and may be shaped by vicariance (Raven & Axelrod, 1974), dispersal (Nathan, 2006) or a combination of both processes (Cook & Crisp, 2005). Molecular tools and dating approaches have provided increasing support for the significance of dispersal in shaping modern disjunctions (de Queiroz, 2005; Heinrichs *et al.*, 2009). In both the Northern and Southern Hemispheres, wind serves as an important vector

for long-distance dispersal (LDD; Muñoz *et al.*, 2004; Wilkinson *et al.*, 2012). Disjunctions between antipodal high latitudes (i.e. amphitropical disjunctions), and in some cases low-latitude, high-elevation localities, have also been largely shaped by LDD, according to inferences based on molecular phylogenetic topologies (see Wen & Ickert-Bond, 2009, for review) and dating (Gussarova *et al.*, 2008; Popp *et al.*, 2011; Fernández-Mendoza & Printzen, 2013). An absence of wind connectivity across the equator due to the Intertropical Convergence Zone (Hyeong *et al.*, 2005) has led to the proposal

of alternative vectors to wind, such as migratory birds (Popp *et al.*, 2011), or complex dispersal scenarios involving stepwise migration along tropical highland bridges (Raven, 1963; Fernández-Mendoza & Printzen, 2013).

Du Rietz (1940) noted that amphitropicality is most common among bryophytes and lichens. Current estimates include at least 66 species of moss (Norris *et al.*, 1999; Ochyra & Buck, 2003; Ochyra & Bednarek-Ochyra, 2008), 24 species of liverwort (Schuster, 1983; Streimann, 1998; Norris *et al.*, 1999; Bednarek-Ochyra *et al.*, 2000) and 160 species of lichen (representing 41.4% of the lichen flora) from Antarctica and South Georgia (Øvstedal & Lewis Smith, 2001) as being disjunct across the tropics. Despite the frequency of this extreme pattern in bryophytes and lichens, relatively few studies have applied molecular phylogenetic tools to assess the processes that underlie the amphitropical distribution in bryophytes (Kreier *et al.*, 2010; Piñeiro *et al.*, 2012) and lichens (Myllys *et al.*, 2003; Wirtz *et al.*, 2008), with only a single study – on the lichen *Cetraria aculeata* – employing molecular dating approaches (Fernández-Mendoza & Printzen, 2013).

Unlike the vast majority of bryophytes, approximately half of the species in the dung-moss family Splachnaceae rely on insects (entomochory) rather than wind (anemochory) to disperse their spores (Koponen, 1990). The fly-mediated spore-dispersal syndrome includes deep purple or brightly coloured capsules, the emission of volatile compounds that mimic carrion or faeces, the production of sticky spores, and coprophily (Koponen, 1990). Flies, seeking fresh decaying organic matter on which to feed, reproduce or lay their eggs, are attracted to the capsules through olfactory and visual cues and may inadvertently pick up spores during their visit. The spores of entomochorous species rapidly germinate after they fall off the fly onto fresh dung. Although entomochorous species are well adapted to efficient dispersal locally and perhaps regionally via insect vectors (Marino, 1988a,b), their sticky spores may severely limit their ability to be dispersed by wind currents (Cameron & Wyatt, 1986). Because the spores are thin-walled, they are vulnerable to desiccation, freezing and UV radiation, and are thus unlikely to survive dispersal via high atmospheric winds (van Zanten, 1978).

Among entomochorous Splachnaceae, *Tetraplodon* Bruch & Schimp. (Fig. 1) displays the broadest geographical range and most extreme disjunctions. Its distribution spans Laurasia, with disjunct populations in Central Africa, Borneo, Papua New Guinea and, within the New World, in the northern Andes, south-eastern Brazil and southernmost South America. The populations from southernmost South America are accommodated under the putative endemic *Tetraplodon fuegianus* Besch., whereas those from south-eastern Brazil are treated as *Tetraplodon itatiaiae* Müll. Hal. All other tropical high-elevation populations are considered to belong to the widespread *Tetraplodon mnioides* (Hedw.) Bruch & Schimp. or *Tetraplodon urceolatus* (Hedw.) Bruch & Schimp. The identification of South American putative endemics is based on geography, with no known diagnostic

morphological traits. The broad phenotypic variation in *T. mnioides* (Steere, 1977) and the uncertain status of *T. urceolatus* (Frivoll, 1978) have confounded taxonomy within the genus, limiting evolutionary inferences within the group. In the absence of robust unambiguous morphological species, phylogenetic delimitation of lineages is necessary to reconstruct the phylogeographical history leading to the origin of the southernmost populations, and thus the New World disjunctions.

Several processes may have contributed to the amphitropical disjunctions observed within *Tetraplodon*. If vicariance resulting from the breakup of Pangaea shaped the disjunctions, the ages of lineages are expected to correlate with geological events, but only disjunctions above the generic level have to date been associated with ancient tectonic events (Mao *et al.*, 2012). If divergence times post-date continental movements, the New World amphitropical disjunction may result from either stepwise migration (i.e. a series of dependent dispersal events along the Andes) or direct LDD across the tropics (Nathan, 2006; Popp *et al.*, 2011). If stepwise dispersal has occurred from north to south via the Andes, we would expect northern Andean populations to mark intermediate dispersal events, and share a unique common ancestor with southern South American populations.

The detection of historical stepwise migration relies on the presence of species in the fossil record or extant flora of low-latitude intermediate regions. Without intermediate populations, it may not be possible to discriminate between stepwise and direct dispersal events. Fernández-Mendoza & Printzen (2013) suggested that stepwise migration along the Andes played a role in the trans-tropical range expansion of the lichen *Cetraria aculeata*. Gussarova *et al.* (2008) inferred stepping-stone migration across Malaysia as the process leading to amphitropical distributions in *Euphrasia*. Few studies addressing amphitropical disjunctions have focused on species with intermediate low-latitude populations, thus precluding differentiation between stepwise migration and direct LDD (Myllys *et al.*, 2003; Escudero *et al.*, 2010; Popp *et al.*, 2011), focusing rather on the rejection of ancient vicariance in favour of LDD *sensu lato*. Although the role of LDD *sensu lato* is being increasingly recognized as shaping amphitropical disjunctions at the infraspecific and infrageneric levels (see Wen & Ickert-Bond, 2009, for review), more studies are needed to disentangle stepwise and direct LDD. The New World distribution of *Tetraplodon*, with intermediate low-latitude, high-elevation populations in the northern Andes, suggests that stepwise migration may have played a role in the establishment of the New World amphitropical disjunction. *Tetraplodon* offers an opportunity to discriminate between the relative importance of stepwise and direct dispersal in establishing amphitropical disjunctions in mosses, a group of plants with many bipolar disjunct species but for which the phylogeographical history has never been reconstructed within an explicit time-calibrated evolutionary scenario.

Based on variation in four discrete loci, we seek (1) to define phylogenetic lineages within *Tetraplodon* and their



Figure 1 *Tetraplodon* (left centre) grows on dung, most commonly of carnivores, or on decaying carcasses, typically in open environments. Sporophytes (right) are a deep red–purple colour and produce sticky masses of bright yellow–green spores.

geographical ranges and (2) to estimate maximum divergence dates for major lineages and the New World amphitropical disjunction, in order (3) to assess the roles of stepwise and direct dispersal events, as well as ancient vicariance, in the origin of the New World amphitropical disjunction in *Tetraplodon*.

MATERIALS AND METHODS

Sampling, PCR amplification and sequencing

The samples we used represent the complete taxonomic and geographical ranges of *Tetraplodon* as well as an undescribed cleistocarpous taxon known only from Bhutan, included based on preliminary results suggesting affinities with *Tetraplodon*, and the genus *Voitia* Hornsch., which may be the sister genus to *Tetraplodon* (Goffinet *et al.*, 2004). Total genomic DNA was extracted from 128 accessions with Nucleospin Plant II Kit (Macherey–Nagel, Bethlehem, PA, USA) following the manufacturer's guidelines or using a modified CTAB protocol (Goffinet *et al.*, 1998). Three species of *Tayloria* subgenus *Orthodon* (R. Br.) Broth., and *Neomeesia paludella* (Besch.) Deguchi from the sister family Meesiaceae, were chosen as outgroups following Goffinet *et al.* (2004).

Three chloroplast loci (*atpB–rbcL*, *rps4* and *trnG*) and one nuclear locus (ITS2) were targeted based on amplification success and informativeness at infraspecific and infrageneric levels (Stech & Quandt, 2010). Loci were sequenced on an ABI3100 Genetic Analyzer (Applied Biosystems, Grand Island, NY, USA), and manually edited in SEQUENCHER 4.8 (Gene Codes Corporation, Ann Arbor, MI, USA). All sequences were deposited in GenBank (see Appendix S1 in Supporting Information). Sequences were aligned with

CLUSTAL W2 (<http://www.ebi.ac.uk/>) and manually edited in MESQUITE 2.75 (Maddison & Maddison, 2011). Regions of ambiguous alignment for *trnG*, ITS2 and *atpB–rbcL* were identified and removed using the GBLOCKS server 0.91b, with settings allowing for smaller final blocks, gap positions within the final blocks, and less strict flanking positions (Castresana, 2000). Indels in the sequenced *atpB–rbcL* intergenic spacer were coded in SEQSTATE 1.4.1 according to simple indel coding (SIC; Simmons & Ochoterena, 2000) after excluding ambiguous regions.

Phylogenetic analyses

Models of nucleotide evolution for each locus (Table 1) were chosen with jMODELTEST 2.1.3 (Posada, 2008) under the Bayesian information criterion (BIC) and corrected Akaike information criterion (AIC_c), with likelihood scores calculated from base trees optimized by maximum likelihood (ML) using the nearest-neighbour interchange search algorithm. The model of evolution for SIC indels followed Lewis (2001), implemented in GARLI 2.0 (Zwickl, 2006) as the standard variable model for ML analyses, and in MRBAYES 3.2.1 (Ronquist & Huelsenbeck, 2003) as the standard discrete model with no transition-rate asymmetry across sites for Bayesian analyses. Indels were included only in single-locus *atpB–rbcL* analyses, with *atpB–rbcL* also analysed independently of coded indels.

Maximum-likelihood and bootstrap replicate analyses were performed in GARLI 2.0 (Zwickl, 2006). One hundred replicate searches were completed for each locus, with 2000 bootstrap replicates. Best trees with 50% majority-rule consensus bootstrap scores from each locus were visually inspected to identify conflicts in topology and bootstrap support values

Table 1 Sample size (*n*), total number of characters (chars) included in analyses, proportion of parsimony informative characters (PI chars), and model of molecular evolution used for each locus based on both corrected Akaike information criterion and Bayesian information criterion. Concatenated data sets were partitioned and modelled according to locus for final analyses. Samples represent the complete taxonomic and geographical ranges of *Tetraplodon*.

Locus	<i>n</i>	Chars (bp)	PI chars (%)	Model
<i>atpB-rbcL</i>	122	616	16	GTR + Γ
<i>rps4</i>	124	694	12	GTR + Γ
<i>trnG</i>	128	550	12	HKY + Γ
ITS2	113	417	14	HKY + Γ

between loci. No conflicts with higher than 70% bootstrap support were identified and loci were concatenated to form a 2277-bp final data set, excluding *atpB-rbcL* indels. The *atpB-rbcL* locus was analysed separately including coded indels to explore the phylogenetic significance of indels. Consistency indices based on *atpB-rbcL*, including coded indels, were calculated in PAUP* 4.0a129 (Swofford, 2003) under both ACC-TRAN and DELTRAN parsimony optimization methods, based on the ML tree inferred from *atpB-rbcL* to identify non-homoplasious characters. The concatenated data set was partitioned by locus, with parameter estimates unlinked between partitions, and analysed as described above. Bootstrap values were mapped onto the best ML topology in the SUMTREES program, part of the DENDROPY-3.7.1 Python library (Sukumaran & Holder, 2010).

Bayesian analyses and calculation of clade posterior probabilities were carried out in MRBAYES 3.2.1 (Ronquist & Huelsenbeck, 2003). Three chains were run independently twice for each of the four loci, and for *atpB-rbcL* with SIC indels, for 10^6 generations, discarding the first 10% of trees as burn-in. The 50% majority-rule consensus trees were visually inspected to identify conflicts in topology and posterior probabilities between loci. No conflicts with posterior probability greater than 0.95 were identified. The concatenated data set was partitioned by locus and run with three chains twice for 10^6 generations each, with parameter estimates unlinked between partitions. The effective sample sizes for all estimated parameters for all runs were visually checked in TRACER 1.5 (Rambaut & Drummond, 2007) to verify convergence of each analysis. Support values were compared across

optimality criteria by mapping the ML bootstrap support values onto the 50% majority-rule consensus Bayesian topology in SUMTREES (Fig. 2).

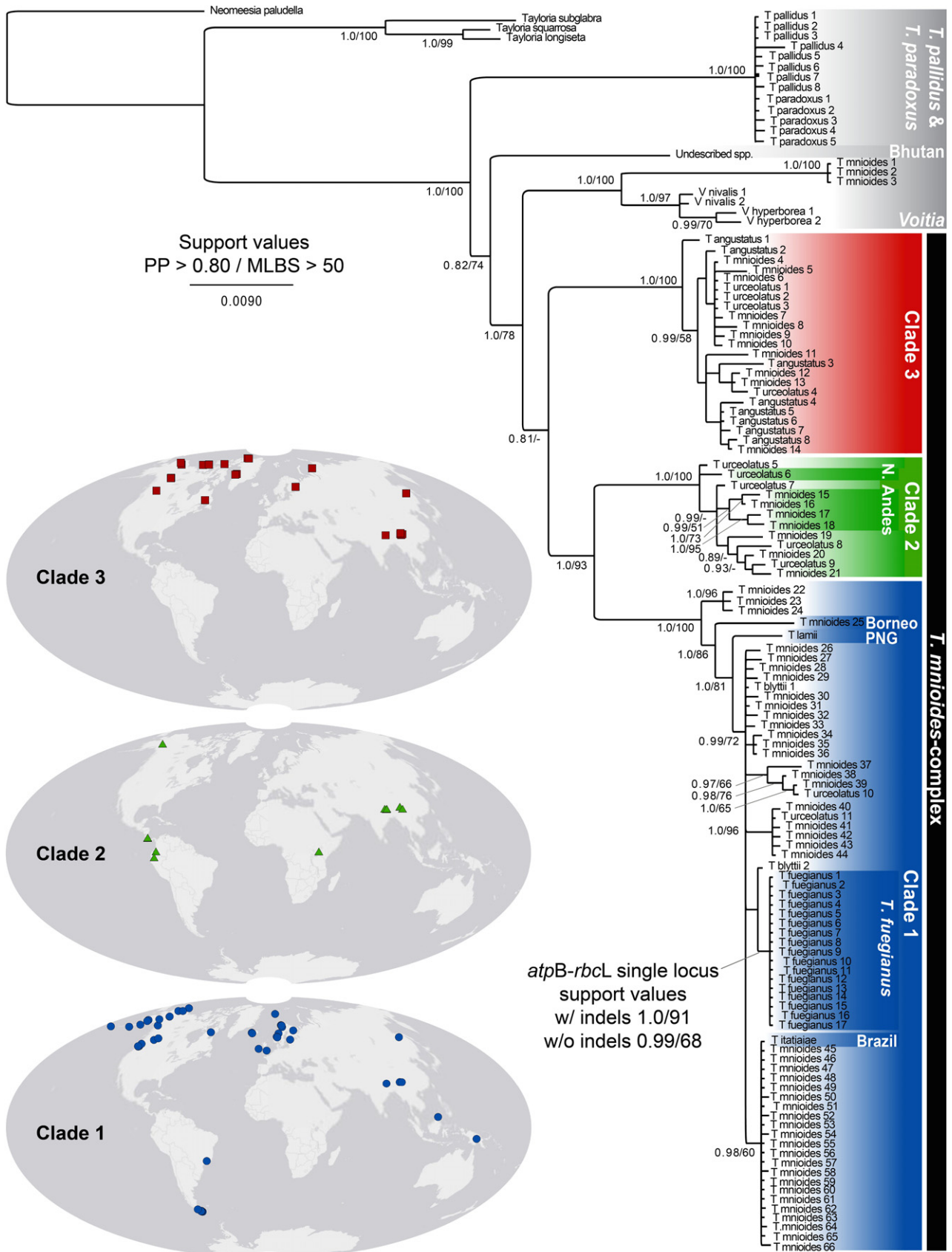
Molecular dating

BEAST 1.7.5 (Drummond *et al.*, 2012) was used to estimate divergence dates for *Tetraplodon* lineages based on chloroplast loci, excluding SIC indels. A lack of fossils or geological events that would be appropriate for use as calibration points within the Splachnaceae or Splachnales necessitates the use of a defined rate of substitution to tease apart substitution rates and time along branches. A mean chloroplast nucleotide substitution rate of 5×10^{-4} substitutions per site per million years has been used in previous molecular dating studies in mosses (Shaw *et al.*, 2010; Pokorný *et al.*, 2011) when fossil-based calibration was not possible or for testing alternative dating schemes. This rate is based on estimates derived from tracheophyte chloroplast coding regions (Sander-son, 2002), and it is well documented that substitution rates vary, sometimes dramatically, across lineages (Sander-son, 2002). Villarreal & Renner (2012) recovered the same rate *de novo* for hornwort *rbcL* sequences in a fossil-calibrated divergence dating analysis, suggesting that this rate may characterize a broader range of groups than simply tracheophytes. Furthermore, non-coding genomic regions typically undergo faster rates of substitution than coding regions. We expect the published estimate of chloroplast substitution rates based on tracheophyte exons and the *rbcL* region in hornworts to be much slower than the actual, and as yet unknown, rate of substitution in non-coding regions in *Tetraplodon*. Analyses using this rate are thus anticipated to inflate divergence-time estimates and will be used here to identify hypotheses for estimates of maximum divergence dates.

For all BEAST analyses, clock and tree models were linked across partitions, and models of substitution (Table 1) were unlinked across loci. Strict and uncorrelated log-normal relaxed clocks (Drummond *et al.*, 2006) were both tested, with two speciation tree models: Yule and birth–death process (Gernhard, 2008). A normal distribution with a mean of 5×10^{-4} substitutions per site per million years, and a standard deviation of 1×10^{-4} (20% of the mean rate; Huttunen *et al.*, 2008) was set as the prior distribution of the substitution rate.

All analyses were run twice with three chains for 50,000,000 generations each. Parameter values were sampled

Figure 2 Bayesian consensus tree, showing posterior probabilities (PP) and maximum-likelihood bootstrap support values (MLBS) from a concatenated data set comprising the loci *atpB-rbcL*, *trnG*, *rps4* and ITS2, representing the complete taxonomic range and global distribution of *Tetraplodon*. Support values are shown for nodes with values greater than 0.80 for PP and 50% for MLBS. Support values from *atpB-rbcL* single-locus analyses with and without coded indels included are also given for the *T. fuegianus* clade. Clades 1–3 are referred to as the *T. mnioides* complex. All Southern Hemisphere and tropical high-elevation accessions are highlighted and labelled (abbreviations: PNG, Papua New Guinea; N. Andes, northern Andes). The maps show the distinct global distributions for each clade in the *T. mnioides* complex, based on the sampling. Accession data can be found in Appendix S1 in Supporting Information.



every thousand generations, with the first 10% of trees discarded as burn-in. All analyses were run without data (data-free), sampling only from the prior, and posterior marginal densities were compared in TRACER 1.5 with those of analyses that included data, in order to determine the influence of the priors on posterior estimates. The effective sample sizes of all estimated parameters were checked in TRACER 1.5 to ensure values were greater than 200. Tree and log files from duplicate runs were combined using LOGCOMBINER 1.7.5 (Drummond *et al.*, 2012) for converged runs; all duplicate runs converged. Bayes factors (Kass & Raftery, 1995) were calculated in TRACER 1.5 based on log-likelihood scores, to compare the fit of the different combinations of clock and tree models (Table 2). The sampled trees were summarized in TREEANNOTATOR 1.7.5 (Drummond *et al.*, 2012) and viewed in FIGTREE 1.3.1 (available at: <http://tree.bio.ed.ac.uk/software/figtree/>).

RESULTS

Three well-supported clades form what will be referred to as the *T. mnioides* complex (Fig. 2), and together include nearly all accessions that fall under the morphological or geographical species concepts of *T. mnioides*, *T. angustatus*, *T. urceolatus*, *T. blyttii*, *T. itatiaiae*, *T. lamii* and *T. fuegianus*. Each of the three clades in the *T. mnioides* complex has a different geographical distribution, with areas of sympatry in Alaska (clades 1–3), the Himalayas (clades 1–3) and northern Europe (clades 1 and 3) (Fig. 2). Clade 3 is strictly Laurasian, spanning northern high-latitude localities and southwards to the Rocky Mountains and Himalayas (Fig. 2). Clade 2 is primarily tropical high-elevation, with localities in the northern Andes, East Africa and the Himalayas, except for one sample collected near Denali, Alaska. Clade 1 is characterized globally by an amphitropical distribution, with low-latitude, high-elevation localities in Southeast Asia (Mount Kinabalu, Borneo, and Mount Giluwe, Papua New Guinea) and south-eastern Brazil. All populations sampled from narrow endemic taxa (i.e. *T. blyttii*, *T. fuegianus* and *T. itatiaiae*) belong to clade 1.

Tetraplodon fuegianus is reconstructed as a unique lineage nested within a well-supported amphitropical clade (Fig. 2: Clade 1). Single-locus analyses revealed that support for the

monophyly of *T. fuegianus* is based on three non-homoplasious (consistency index of 1.0) apomorphic transversions (A to C) and two indels (single-A deletions) in the *atpB-rbcL* intergenic spacer. Support for its monophyly, however, is low based on the concatenated data set (posterior probability, PP 0.51; maximum-likelihood bootstrap, MLBS 28%), suggesting that homoplasious characters may be present in the other loci, and based on MLBS of the *atpB-rbcL* data set without indels (PP 0.99; MLBS 69%), a difference in support values probably associated with the reliance of this relationship on three non-homoplasious apomorphic transversions. The unambiguous placement of *T. fuegianus* within the amphitropical Clade 1, and its closer relationship to Northern Hemisphere populations than those from the northern Andes, which are resolved with high support in Clade 2, is robustly supported (Fig. 2). *Tetraplodon itatiaiae* is resolved within the amphitropical Clade 1, distinct from the *T. fuegianus* lineage (Fig. 2).

Accessions of *T. pallidus* and *T. paradoxus* are not differentiated from one another but form a robust clade sister to all other ingroup exemplars. *Voitia* is nested within *Tetraplodon* and sister to three interior Alaskan populations phenotypically aligned with the morphological species concept for *T. mnioides* (*T. mnioides* 1–3; Fig. 2, Appendix S1). Accessions sister to *Voitia* were resampled, extracted and sequenced in order to confirm this result. Soft incongruence in the topologies of both trees (Figs 2 & 3) reflect the unresolved placement of the *Voitia* lineage and the undescribed cleistocarpous taxon from Bhutan. *Tetraplodon*, *Voitia* and the sample from Bhutan compose a maximally supported monophyletic group. All major lineages are resolved with high support, although their relationships relative to each other remain ambiguous.

A relaxed clock with Yule speciation prior was the model that best fitted the data (Table 2). The lineages of the *T. mnioides* complex, along with the *Voitia* lineage, diverged from the ancestor to *T. paradoxus* and *T. pallidus* between the mid-Miocene and the early Oligocene, 11.2–33.4 million years ago (Ma) (average 26.6 Ma). The three major lineages of the *T. mnioides* complex (clades 1–3) began to diversify within largely overlapping time periods between the early Miocene and the early-to-mid Pliocene, with mean estimates of 12.6 Ma (95% highest posterior density, HPD, 4.7–17.7 Ma) for Clade 1, 7.9 Ma (95% HPD 3.6–13.8 Ma) for Clade 2, and 10.1 Ma (95% HPD 4.7–17.7 Ma) for Clade 3. The clade comprising *T. fuegianus* is estimated to have diverged from Laurasian populations between the late Miocene to Pliocene, with a mean estimate of 8.63 Ma (95% HPD 3.07–10.11 Ma) and to have diversified between the late Miocene and the late Pleistocene, with a mean estimate of 5.2 Ma (95% HPD 1.4–7.0 Ma) (Fig. 3).

Table 2 Bayes factors (\log_{10}) calculated from log-likelihood scores in TRACER 1.5 were used to compare the fit of different clock (strict; relaxed) and tree (Yule; birth–death, BD) model combinations employed in BEAST 1.7.5 for the estimation of divergence times. The combination of a relaxed molecular clock with a Yule speciation prior provided the best fit to the concatenated data set (*atpB-rbcL*, *trnG* and *rps4*) representing the complete taxonomic and geographical range of *Tetraplodon*.

Model	Strict BD	Strict Yule	Relaxed BD
Relaxed Yule	6.384	18.87	1.945
Strict BD	—	12.486	–4.439
Strict Yule	—	—	–16.925

DISCUSSION

Phylogenetic inferences from discrete loci reveal that the *Tetraplodon mnioides* complex comprises three robustly

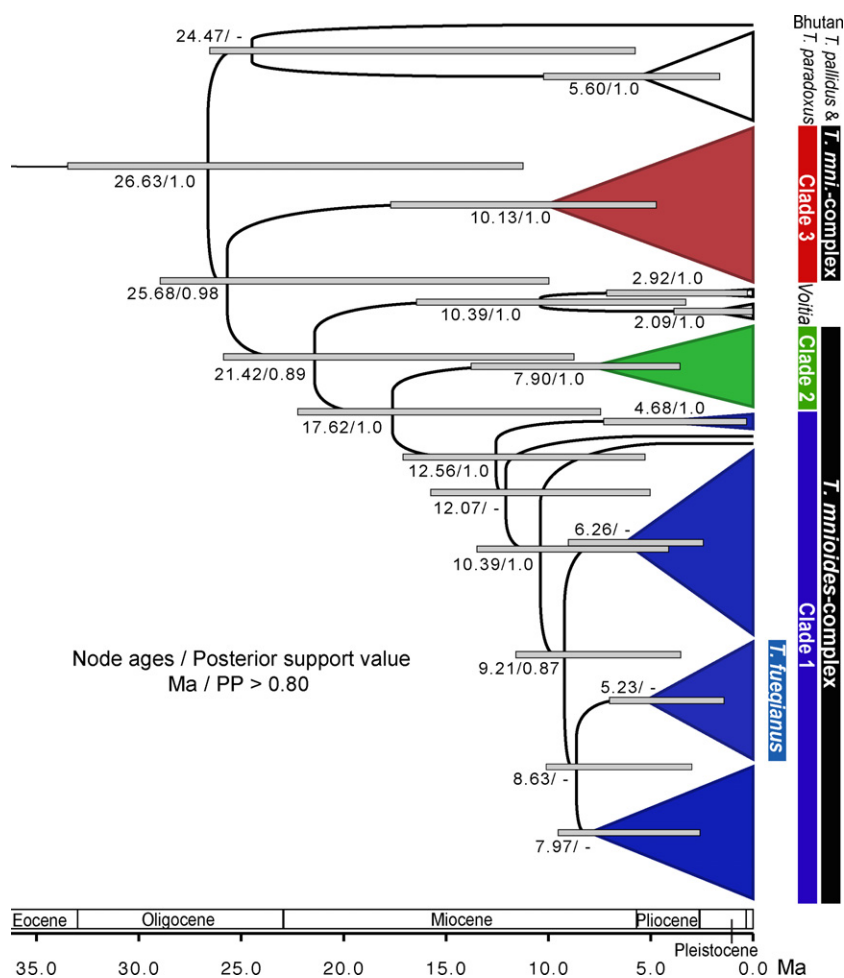


Figure 3 Chronogram showing mean divergence-date estimates of *Tetraplodon* in millions of years and posterior probabilities (node age/PP) for major lineages as estimated in BEAST 1.7.5 from a concatenated data set (*atpB-rbcL*, *trnG* and *rps4*) with a relaxed clock and Yule speciation prior with a fixed mean rate of substitution of 5×10^{-4} substitutions per site per million years. Samples represent the complete taxonomic and geographical ranges of *Tetraplodon*. Posterior support values are shown for nodes with values greater than 0.80. Node bars indicate 95% highest posterior density intervals around mean estimates. Labels used to identify clades correspond to those used in Fig. 1.

supported clades (Fig. 2) encompassing most of the diversity within the genus. These lineages display broad geographical distributions (Fig. 2): exclusively Laurasian (clade 3), low-latitude high-elevation with occurrences in Alaska and the Himalayas (clade 2), and Laurasian with disjunctions into southern South America, Brazil, Mount Kinabalu in Borneo and Mount Giluwe in the Southern Highlands of Papua New Guinea (amphitropical; clade 1 in Fig. 2). All three clades are sympatric in Alaska and in the Himalayas. Northern Andean and southern South American *T. fuegianus* populations are resolved within distinct lineages, with each being more closely related to phylogenetically distinct but sympatric Northern Hemisphere high-latitude populations than they are to each other. The Brazilian *T. itatiaiae* is a member of the amphitropical clade 1, is closely aligned with Laurasian *T. mnioides* populations, and does not share a unique common ancestor with populations of *T. fuegianus*. The clades in the *T. mnioides* complex do not match taxa under the morphological species concept (Lawton, 1971; Nyholm, 1975; Frisvoll, 1978; Chien & He, 1999; Marino, 2009), an incongruence which is unsurprising given the broad phenotypic variation in *T. mnioides* (Steere, 1977), *T. angustatus* (Frisvoll, 1978) and *T. urceolatus* (Frisvoll, 1978). Our phylogenetic results highlight the variability in specific traits used

to distinguish species of *Tetraplodon* and the need for a critical taxonomic revision of this group.

The resolution of northern Andean and southernmost South American *T. fuegianus* populations in distinct clades (Fig. 2) is inconsistent with the hypothesis of stepwise migration along the Andes for the origin of the New World amphitropical disjunction observed in clade 1. Support for the monophyly of *T. fuegianus* from the *atpB-rbcL* locus, and the resolution of *T. itatiaiae*, with Laurasian populations based on posterior support from the concatenated data set, suggests that independent and direct dispersal events have led to the establishment of Brazilian and southernmost South American populations. A larger sampling of the rare southeast Brazilian populations should be included in future work to further test the phylogenetic affinities of *T. itatiaiae* relative to *T. fuegianus* and Laurasian populations.

An estimated Oligocene origin and Miocene diversification of *Tetraplodon* are incongruent with Late Jurassic to Early Cretaceous Pangaean tectonic events (160–138 Ma; Scotese, 2001; Rogers & Santosh, 2003; Smith *et al.*, 2004) accounting for intercontinental disjunctions within the genus. Divergence-time estimates suggest that the clades in the *T. mnioides* complex arose between the Oligocene and the mid-Miocene, or as late as the early Pliocene for clade 1, and

diversified in the mid-Miocene to late Pliocene. Southernmost South American populations diverged from Laurasian populations 8.63 Ma (95% HPD 3.07–10.11 Ma), consistent with estimates for the origin of amphitropical disjunctions in seed plants (Wen & Ickert-Bond, 2009). Divergence times, based on a conservative absolute rate, thus strongly support direct LDD as the mechanism behind the amphitropical disjunctions in clade 1.

Bipolar LDD events must be explained in the absence of a continuous wind path given the presence of the Intertropical Convergence Zone during the diversification of the clades of the *T. mniooides* complex (Hyeong *et al.*, 2005). In this case, the vulnerability of *Tetraplodon* spores to the extreme conditions associated with high-altitude wind currents (van Zanten, 1978) must also be considered. Bird-mediated dispersal provides the most likely scenario for direct LDD across the tropics (Popp *et al.*, 2011). Birds can disperse diaspores internally (endozoochory) or externally (ectozoochory). Endozoochory requires that birds consume and then retain diaspores throughout their migration and that diaspores remain viable. Spores of the liverwort *Riella* were found to be viable following a 30-minute passage through the gut of domesticated mallard ducks (*Anas platyrhynchos*; Proctor, 1961), and viable spores and vegetative fragments have been recovered from the dung of slugs (*Arión vulgaris*, *Arión rufus* and *Limax cinereoniger*; Boch *et al.*, 2013) and spectacled flying fox (*Pteropus conspicillatus*; Parsons *et al.*, 2007). These studies suggest that bryophytes may be resistant to ingestion, although studies on seed plants have shown that resistance varies according to both vector and plant (Traveset *et al.*, 2001) and that viability decreases in general with increasing time inside a bird (van Leeuwen *et al.*, 2012). Although bird-mediated endozoochory is a more effective means of dispersal than ectozoochory in terms both of number and of diversity for seeds (Brochet *et al.*, 2010; Costa *et al.*, 2014) and aquatic invertebrates (Sánchez *et al.*, 2012), the relative significance of these two modes of zoochory has not been estimated for sporic plants. Migratory shorebirds of the order Charadriiformes are the most likely candidate vectors, as a number of species occupy and provide a direct path between the suitable but disjunct habitats of amphitropical bryophyte species (Pyle, 2008). Vegetative fragments of mosses have been recovered from the plumage of transtropical migrant birds (order Charadriiformes), demonstrating that suitable vectors do pick up diaspores (Lewis *et al.*, 2014). Vegetative diaspores of mosses and fungi have been also recovered from the coats and hooves of roe deer (*Capreolus capreolus*), wild boar (*Sus scrofa*) (Heinken *et al.*, 2001), domesticated sheep (Pauliuk *et al.*, 2011) and the feet of albatrosses (Bailey & James, 1979), suggesting that they are able to adhere to animals' bodies despite a lack of features to facilitate adhesion.

Effective dispersal ultimately depends on establishment in a suitable habitat and substrate, growth and reproduction. Although *Tetraplodon* is specialized for substrates associated

with carnivores and carrion, it may not be strictly confined to growth on these substrates (Koponen, 1990), and may be most commonly associated with dung and carrion as a result of fly-mediated dispersal (Cameron & Wyatt, 1986) or its ability to withstand high nutrient concentrations better than other mosses (Fischer, 1936; Koponen, 1990). LDD events may lead to the establishment of sexual populations if the individuals are monoecious, as in the case of the angiosperm genus *Empetrum* (Popp *et al.*, 2011) or *T. mniooides* (Lawton, 1971), and self-compatible, a trait which has been assumed but not yet tested in *Tetraplodon*. Bird-mediated LDD events followed by establishment are assumed to be extremely rare events, but the large size of migrating bird populations and a period of 12.6 Myr since clade 1 began diversifying, may have provided sufficient opportunities for effective LDD in *Tetraplodon* (Nathan, 2006; Gillespie *et al.*, 2012).

CONCLUSIONS

The analysis of discrete loci resolved well-supported lineages within *Tetraplodon*. Three major lineages diversified between the early Miocene and early-to-mid Pliocene and contain the majority of the diversity within the genus, each displaying a different but overlapping geographical distribution. Southernmost South American populations were reconstructed as a monophyletic lineage that diverged from high-latitude Northern Hemisphere populations around 8.63 Ma. The recovery of northern Andean and southernmost South American *T. fuegianus* in distinct clades supports the establishment of southernmost South American populations via direct dispersal rather than stepwise migration along the Andes. Divergence-date estimates and phylogenetic inferences support direct LDD as the mechanism behind the amphitropical disjunction in *Tetraplodon*. Given a lack of wind connectivity between the Northern and the Southern Hemisphere, we propose that migratory birds of the order Charadriiformes are the most likely dispersal vectors.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Specimen data.

BIOSKETCHES

Lily R. Lewis is a PhD candidate in the Department of Ecology and Evolutionary Biology at the University of Connecticut. Her dissertation research focuses on the phylogenetics and population genetics of *Tetraplodon* with an emphasis on the southern South American *T. fuegianus* and the inclusion of bryophyte diversity in conservation and ecotourism in Southern Chile.

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