



Phylogenetic divergence of island biotas: Molecular dates, extinction, and “relict” lineages

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Abstract

Island formation is a key driver of biological evolution, and several studies have used geological ages of islands to calibrate rates of DNA change. However, many islands are home to “relict” lineages whose divergence apparently pre-dates island age. The geologically dynamic New Zealand (NZ) archipelago sits upon the ancient, largely submerged continent Zealandia, and the origin and age of its distinctive biota have long been contentious. While some researchers have interpreted NZ’s biota as equivalent to that of a post-Oligocene island, a recent review of genetic studies identified a sizeable proportion of pre-Oligocene “relict” lineages, concluding that much of the biota survived an incomplete drowning event. Here, we assemble comparable genetic divergence data sets for two recently formed South Pacific archipelagos (Lord Howe; Chatham Islands) and demonstrate similarly substantial proportions of relict lineages. Similar to the NZ biota, our island reviews provide surprisingly little evidence for major genetic divergence “pulses” associated with island emergence. The dominance of Quaternary divergence estimates in all three biotas may highlight the importance of rapid biological turnover and new arrivals in response to recent climatic and/or geological disturbance and change. We provide a schematic model to help account for discrepancies between expected versus observed divergence-date distributions for island biotas, incorporating the effects of both molecular dating error and lineage extinction. We conclude that oceanic islands can represent both evolutionary “cradles” and “museums” and that the presence of apparently archaic island lineages does not preclude dispersal origins.

KEYWORDS

colonization, dispersal, molecular clock, New Zealand, Oligocene drowning, vicariance

1 | INTRODUCTION

Geological and genetic analyses have together shaped important advances in our understanding of evolutionary history, with many studies identifying strong links between biological and earth-history processes (Craw, Upton, Burridge, Wallis, & Waters, 2016; Kornfield & Smith, 2000; Mendelson & Shaw, 2005; Meredith et al., 2011; Riddle, Hafner, Alexander, & Jaeger, 2000). In particular, geologically based calibrations of molecular evolution provide an important method for

formulating and testing evolutionary hypotheses, and for understanding timeframes of biodiversification (Ayala, Rzhetsky, & Ayala, 1998; Donoghue & Benton, 2007; Kumar, 2005; Rambaut & Bromham, 1998).

Island formation is a key driver of biological evolution (Cole et al., 2019; Shaw & Gillespie, 2016; Warren et al., 2015), and island ages have been successfully used to calibrate biological evolution (Fleischer, McIntosh, & Tarr, 1998; Mendelson & Shaw, 2005). Although some biogeographers have criticised the use of island ages to assess rates of DNA change (e.g., Heads, 2011), molecular

approaches remain crucial to assessing the timing and dynamics of island-colonization events (Emerson, 2002; Gillespie & Roderick, 2002). Notable examples have focussed on oceanic archipelagos such as the Hawaiian (Percy et al., 2008), Macaronesian (Juan, Emerson, Oromí, & Hewitt, 2000) and Galápagos (Parent, Caccone, & Petren, 2008) island groups.

Newly formed volcanic islands are rapidly colonized by dispersing biological lineages (Barber, Moosa, & Palumbi, 2002; Gillespie & Roderick, 2002; MacArthur & Wilson, 1967). In some cases, colonization is rapid enough to generate near-linear relationships between genetically determined lineage divergence and geologically determined island age (e.g., Fleischer et al., 1998; Mendelson & Shaw, 2005; Percy et al., 2008; Shaw & Gillespie, 2016). Additionally, the evolution of phylogenetic “progression” patterns (Shaw & Gillespie, 2016; Wagner & Funk, 1995) implies that the first colonizing lineages often have an evolutionary advantage relative to late-arriving taxa (Carlquist, 1966; Emerson & Gillespie, 2008; Waters, Fraser, & Hewitt, 2013).

Despite the clear links between island formation and evolutionary diversification (see above), several studies have detected island-endemic lineages whose divergence apparently pre-dates the geologically estimated age of the island(s) they inhabit (Buckley & Leschen, 2013). For instance, Hawaiian *Drosophila* apparently diverged from their closest extant relatives up to 40 million years ago (mya) (Beverley & Wilson, 1985; Lewin, 1985; Obbard et al., 2012), well before the accepted geological formation of the modern archipelago (5 Ma; Fleischer et al., 1998), perhaps a reflection of now “extinct” islands within this Pacific region. Additionally, Caccone, Gibbs, Ketmaier, Suatoni, and Powell (1999) inferred that Galápagos tortoises diverged from mainland South American taxa prior to the formation of the oldest existing Galápagos island. While such findings might be seen as anomalous (i.e., “exceptions that prove the rule”), “old” divergence times have also been reported for Galápagos marine iguanas and lava lizards (see Parent et al., 2008). Archaic island lineages have similarly been reported in the South Pacific (e.g., Buckley, Attanayake, & Bradler, 2008) and in the Indian Ocean (Shapiro et al., 2002).

The geologically dynamic archipelago of New Zealand (NZ) (Figure 1) represents an outstanding system for understanding biological evolution, and in particular the role of earth history in driving evolutionary divergence (Craw et al., 2016). The “Zealandia” landmass broke away from Gondwana 80 mya, but subsequently subsided and was largely (or completely) drowned during the Oligocene 25–23 mya (Fleming, 1979; Landis et al., 2008; Waters & Craw, 2006). There has been ongoing debate about the extent to which this region's biota is descended from ancient “Gondwanan” continental lineages (Baker, Huynen, Haddrath, Millar, & Lambert, 2005; Daugherty, Gibbs, & Hitchmough, 1993; Fleming, 1979; Gleeson, Rowell, Tait, Briscoe, & Higgins, 1998; Haddrath & Baker, 2001), versus the extent to which drowning and subsequent colonization predominate (Knapp, Mudaliar, Havell, Wagstaff, & Lockhart, 2007; Knapp et al., 2005; McGlone, 2005; Pole, 1994; Trewick, Paterson, & Campbell, 2007; Waters & Craw, 2006). Indeed, some studies

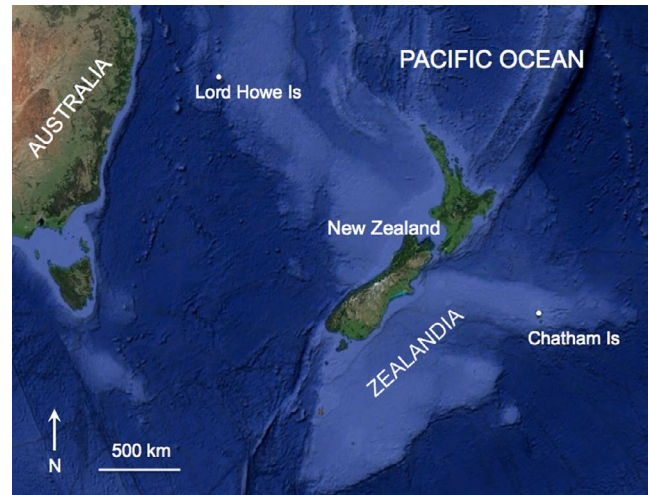


FIGURE 1 Map illustrating the location of Lord Howe Island and the Chatham Islands

have suggested that NZ's biota might be equivalent to that of a post-Oligocene oceanic island (Daugherty et al., 1993; Trewick et al., 2007).

The finding of diverse biological lineages in NZ's Miocene fossil record has often been interpreted as evidence for the persistence of Zealandia's biota throughout the Oligocene (Kaufuss, Brown, Henderson, Szwedo, & Lee, 2018; Kaufuss et al., 2015; Worthy, Tennyson, & Scofield, 2011; Worthy, Tennyson, Scofield, & Hand, 2013). Worthy et al. (2013), for instance, noted that “all the key elements” of NZ's modern terrestrial biota were in place only 4 mya after the maximum Oligocene inundation and concluded that these data likely supported vicariant origins for these Miocene lineages. Alternatively, in the light of the rapid colonization of geologically young archipelagos (e.g., Fleischer et al., 1998; Johnson, Adler, & Cherry, 2000; Shaw & Gillespie, 2016), and the advantages likely conferred to early colonizers (Waters et al., 2013), it could be argued that such patterns are merely consistent with a rapid island-colonization scenario. Indeed, distinctive biotic assemblages are often detected on recent oceanic islands (Heenan, Mitchell, De Lange, Keeling, & Paterson, 2010; Paulay, 1994). Additionally, while the presence of phylogenetic “relicts” in the NZ biota (e.g., *Sphenodon*; *Leiopelma*) has been interpreted as a signature of Gondwanan history (Fleming, 1979), such isolated, divergent lineages can be produced by either vicariance or dispersal (see island examples above), with extinction playing a key role in obscuring their biogeographic ancestry (Paulay, 1994; Waters & Craw, 2006).

Most recently, Wallis and Jorge (2018) reviewed molecular evidence for the origins of NZ's biota, noting that a sizeable proportion of NZ lineages had divergence-time estimates pre-dating Oligocene drowning (Figure 2a). These authors also noted a continuous range of divergence timings, with no apparent “pulses” of lineage arrival, and interpreted these data as sufficient evidence to “put the idea [of Oligocene inundation] to rest”.

Here, we review genetic evidence for island lineage divergence timing and ask the question whether the data for NZ lineages (whose

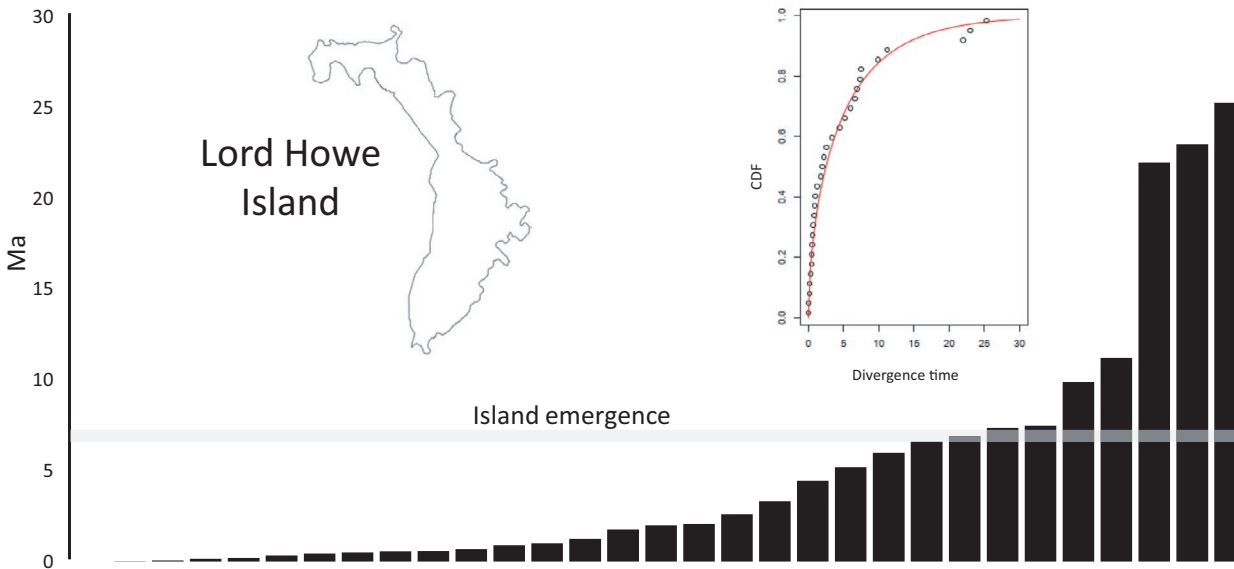
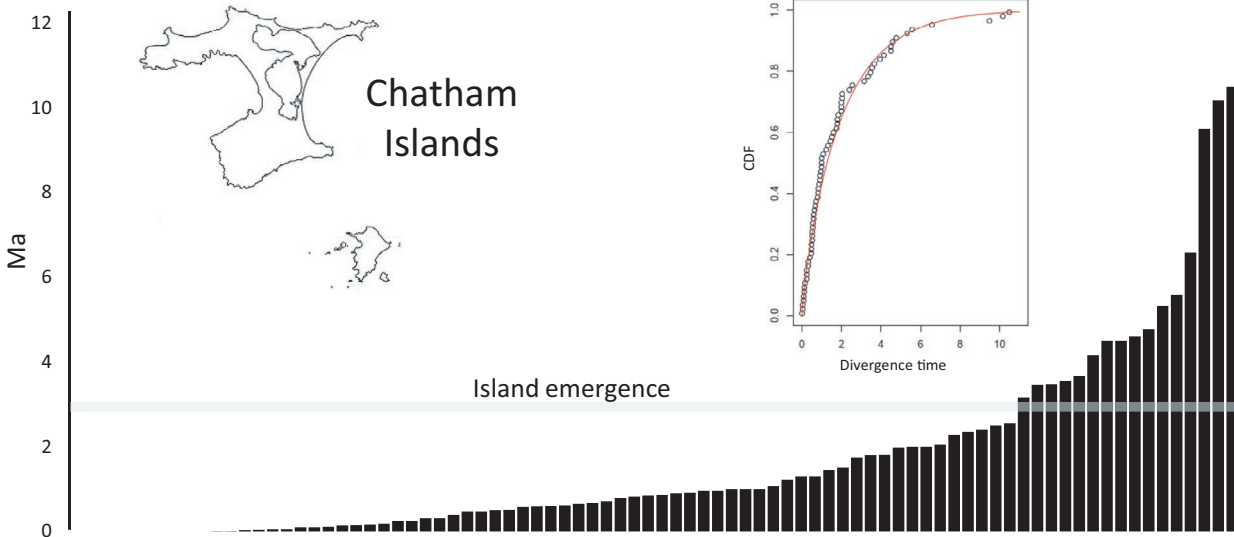
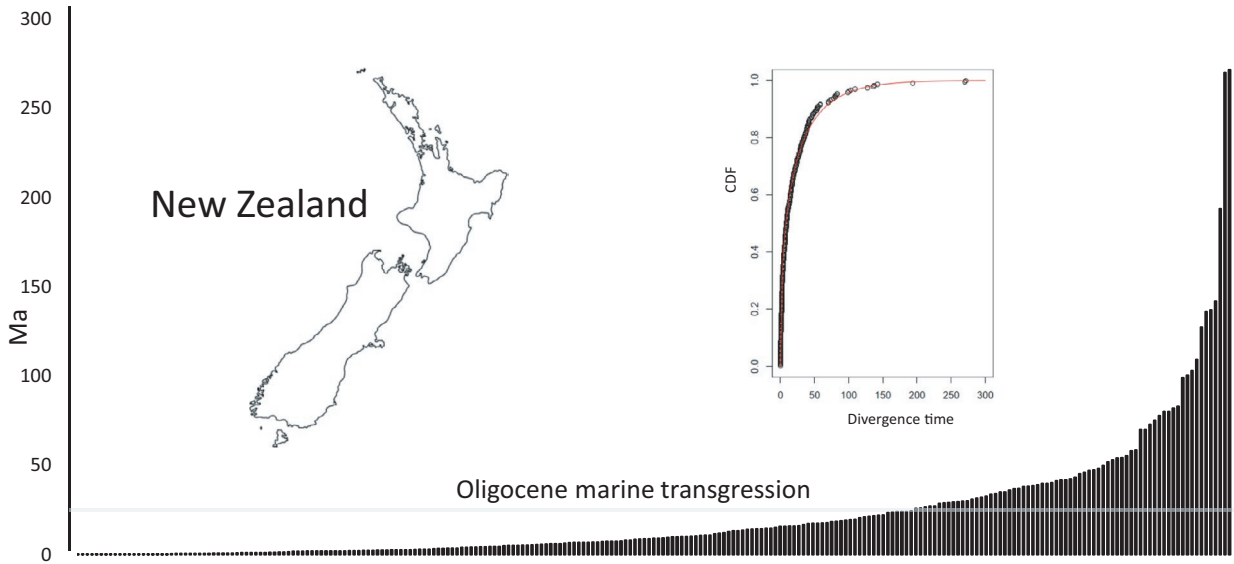


FIGURE 2 Univariate plot of genetic divergences between island lineages and their closest relatives, ordered by depth of divergence time for (a) New Zealand (modified from Wallis & Jorge, 2018), (b) Chatham Islands and (c) Lord Howe Island. Grey shaded lines indicate the marine transgression or the formation of islands. Inset: Empirical and theoretical cumulative distribution functions, indicating fits of divergence times to an exponential distribution

origins are often controversial) differ appreciably from data sets for other oceanic islands (Lord Howe Island and the Chatham Islands) for which geological origins and timing are not contentious.

2 | METHODS

Lord Howe is a small archipelago (ca. 15 km²) situated some 600 km east of the Australian mainland (Figure 1). This island group was formed by volcanic activity ca. 6.9–6.4 mya (McDougall, Embleton, & Stone, 1981). Similarly, the Chatham Islands are a small island group situated approximately 700 km east of NZ's main islands (Figure 1). The Chatham Islands archipelago consists of ten islands, including two substantial landmasses (Chatham Island and Pitt Island) and eight smaller islands, sitting upon the largely submerged continent of Zealandia (Mortimer et al., 2017). Stratigraphic evidence suggests that the Chatham Islands were completely submerged during the late Miocene/early Pliocene (ca. 6 mya), before re-emerging due to tectonic activity <3 mya (Campbell, 2008; Campbell, Adams, & Mortimer, 2008; Campbell et al., 2009; Landis et al., 2008). We selected these island groups as they are geographically isolated, geologically well studied and well dated (here, we assume current geological interpretations are correct), and their biotas are genetically well studied, having relatively unambiguous phylogeographic relationships in the context of nearby mainland assemblages.

We searched the literature for published papers, conference proceedings, and unpublished PhD theses that used genetic data to explore the relationship between taxa from Lord Howe and the Chatham Islands and their respective sister lineages on other landmasses. Studies that focused on invasive species, or on taxa that were likely introduced anthropogenically, were excluded from our analysis. We collated information from these publications on the estimated divergence date of Lord Howe and Chatham Islands lineages from their sister lineages. We followed Wallis and Jorge (2018) in using the stem age divergence, rather than the crown radiation divergence, as in the majority of cases only a single lineage was sampled from each Island. Where different divergence dates were estimated using different genes (e.g., Heenan et al., 2010), we calculated an average divergence date across the genes (Table S1). For publications that did not include any molecular dating (but calculated the genetic divergence between lineages from Lord Howe/Chatham Islands and their sister taxa), we employed a “standard” rate of divergence based on the gene sequenced (e.g., 3.54%/million years for insect COI (Papadopoulou, Anastasiou, & Vogler, 2010; see Tables S1 and S2). Several studies using molecular data did not directly estimate genetic distance between island taxa and their closest mainland relatives. For these studies, we downloaded sequences from GenBank

and used MEGAX (Kumar, Stecher, Li, Knyaz, & Tamura, 2018) to determine the most appropriate nucleotide substitution model and estimate the genetic divergence between lineages.

To assess whether there was an excess of divergence times directly after the emergence of these islands, we followed the protocols of Wallis and Jorge (2018). Specifically, we produced a univariate plot of ranked divergence times between Island lineages and their closest relatives and looked for the predicted “pulse” of divergence times directly after Island emergence. We then fitted an exponential distribution to divergence times using the FITDIST function of the FITDISTRPLUS (Delignette-Muller, Pouillot, Denis, & Dutang, 2014) package in R (R Core Team, 2017) to test for goodness of fit to an exponential distribution. Taxa for which no genetic differentiation was detected between island and mainland samples were excluded from the goodness of fit test, as these data may skew the distributions (Wallis & Jorge, 2018). It was hypothesized that there would be an excess of arrival times directly after the re-emergence of the Chatham Islands (ca. 3 mya; Campbell, 2008; Campbell et al., 2008; Campbell et al., 2009; Landis et al., 2008), resulting in a poor fit around this period. Likewise, it was hypothesized that an excess of arrival times would be evident directly after the formation of Lord Howe Island (ca. 6.9–6.4 mya; McDougall et al., 1981), resulting in a poor fit around this period.

3 | RESULTS

3.1 | Chatham Islands divergences

We identified 84 genetic splits between Chatham Islands taxa and their sister taxa on other landmasses (primarily NZ; Table S1). The focal taxa included marine species, freshwater and terrestrial invertebrates, together with birds, plants and reptile lineages (Table S2). Divergence-date estimates for these Chathams lineages ranged from 0 to 10.5 mya (median age 0.85 mya). Seventeen taxa (20%) yielded divergence-date estimates pre-dating the geological formation of the current Chatham Islands, including plant (Heenan et al., 2010; Himmelreich, 2009), bird (Garcia-R, Gibb, & Trewick, 2014), lizard (Liggins, Chapple, Daugherty, & Ritchie, 2008) and invertebrate (e.g., Buckley & Leschen, 2013; McGaughran, Hogg, Stevens, Lindsay Chadderton, & Winterbourn, 2006) lineages (Table S1). The univariate distribution plot of divergence times for Chatham Islands taxa showed a similar pattern to that observed from NZ assemblages, with an exponential increase of lineages with time (Figure 2b). The cumulative distribution function (CDF) plot showed a close fit between the empirical and theoretical distribution (Figure 2b), with no clear evidence for an arrival “pulse” associated with island emergence ca. 3 mya.

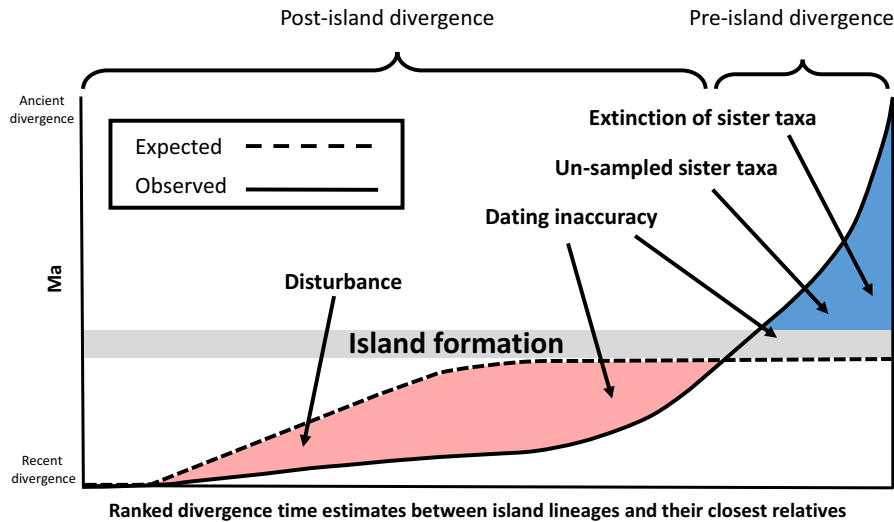


FIGURE 3 Schematic illustration of the expected versus observed divergence timings for island biotas. The expectations of rapid community assembly (with priority effects expected to decrease the success of later arrivals; e.g., Diamond, 1975; Shaw & Gillespie, 2016) following island emergence (grey shading) are illustrated by a dashed line, whereas observed distributions of divergence-time estimates are indicated by a solid line. Discrepancies between observed versus expected distributions of divergence dates are shown in red (divergence estimates postdating island formation) and blue (divergence estimates pre-dating island formation). The latter may potentially be explained by a combination of molecular calibration error, incomplete sampling and extinction of sister taxa; the former may potentially be explained by calibration error and/or lineage turnover (e.g., driven by disturbance; Rawlence et al., 2019)

3.2 | Lord Howe Island divergences

We identified 31 genetic splits between Lord Howe taxa and their sister taxa on other landmasses (primarily Australia; Table S2). These data points were derived from diverse lineages including marine taxa, freshwater and terrestrial invertebrates, birds, plants and reptiles (Table S2). Divergence dates ranged from 0 to 25 mya (median age 2.4 mya). Eight taxa (26%) exhibited divergence-date estimates pre-dating the geological formation of Lord Howe Island, including plants (e.g., Thomas, Bruhl, Ford, & Weston, 2014; Wagstaff et al., 2010), invertebrates (e.g., Buckley et al., 2008; Lo et al., 2016) and a lizard (Chapple, Ritchie, & Daugherty, 2009) lineage. The univariate distribution plot of divergence times for Lord Howe Island taxa suggests an exponential increase of lineages with time, a strikingly similar pattern to that observed for NZ and Chatham Islands taxa (Figure 2c). Additionally, a CDF plot again showed a close fit between the empirical and theoretical distribution, with no apparent “pulse” of arrivals clearly associated with the emergence of Lord Howe *ca.* 6.9–6.4 mya (Figure 2c).

4 | DISCUSSION

Although the sizes of the NZ, the Chathams and Lord Howe island data sets are substantially different (likely reflecting contrasts in island size, age, and the attention their biotas have received), they yielded similar patterns of lineage divergence timing. Specifically, more than 20% of lineages sampled from the Chathams and Lord Howe apparently pre-date the formation of these islands,

comparable to the substantial proportion of NZ lineages apparently pre-dating its Oligocene inundation. The apparent dominance of Quaternary divergence-time estimates in all three biotas apparently highlights the importance of rapid biological turnover (e.g., extinctions and/or new arrivals) in response to recent climatic, geological and/or ecological disturbance (i.e., colonizing lineages that substantially postdate island formation (e.g., Rawlence, Scofield, McGlone, & Knapp, 2019; Figure 3).

In explaining their NZ data set, Wallis and Jorge (2018) noted a surprisingly smooth gradation of divergence-time estimates (Figure 2a) and argued that these data represent the gradual, ongoing accumulation of lineages, in contrast to the “pulsed” divergence estimates that might be expected under a sudden, rapid colonization scenario (Johnson et al., 2000). At face value, these data certainly seem to contrast with our understanding of archipelagos elsewhere for which divergence times have been strongly linked to island emergence dates (Fleischer et al., 1998; Mendelson & Shaw, 2005), and where early colonizing lineages are suggested to reduce the success of late-arriving lineages (Shaw & Gillespie, 2016; Waters et al., 2013). As noted above, the major “pulse” of NZ lineage arrival seems to be recent, likely associated with Quaternary climate cycles and geological uplift.

Similar to the NZ findings of Wallis and Jorge (2018), the current study reveals smooth, relatively continuous divergence-age distributions for two oceanic island biotas—assemblages that were unequivocally established by trans-oceanic dispersal (Figure 2b,c). Below, we discuss potential reasons for the apparent absence of older lineage divergence “pulses” associated with early land emergence, and the presence of numerous island lineages that apparently pre-date island formation.

4.1 | Molecular dating uncertainty

Molecular dating often involves substantial uncertainty, especially when divergences are ancient, sequence data are limited (e.g., short sequences of mtDNA), prone to saturation and lacking reliable calibration points (e.g., see Bromham, 2019). Notably, the apparent inability of even complex DNA sequence-evolution models to accurately capture substitution processes (e.g., saturation; rate heterogeneity; time dependency) can be particularly problematic for branch-length estimation of deeply divergent lineages when using rapidly evolving mitochondrial sequences (Phillips, 2009; Phillips et al., 2013). Such limitations have potential to confound divergence-time estimation, perhaps making it difficult to detect predicted “pulses” of colonization associated with island formation.

In some cases, uncertainty can be reduced to an extent by the availability of more extensive (e.g., genomic) data, and the existence of detailed, phylogenetically informative fossil records (e.g., Cole et al., 2019), but these attributes represent a relatively small proportion of current data sets. While some studies have attempted to overcome the limitations of fossil records by assuming ancient vicariance when temporally calibrating particular phylogenetic nodes (Bauzà-Ribot et al., 2012; Giribet, Vogt, González, Sharma, & Kury, 2010), such biogeographic assumptions carry a risk of circularity.

Molecular divergence-date estimates, even those derived from relatively well-calibrated phylogenies, typically have wide credibility intervals (Burrige, McDowall, Craw, Wilson, & Waters, 2012; McCulloch, Wallis, & Waters, 2016). Given such substantial uncertainty, the “optimal” (mean) node-age estimate seems unlikely to accurately reflect the *actual* divergence timing. As a case in point, wide divergence-time estimates previously obtained for NZ-endemic stonefly clades (relative to Australian and/or South American sister clades) highlight this issue of uncertainty (mean age; 95% credibility distributions): NZ Notonemouridae (38 mya; 18–48 mya); NZ Gripopterygidae clade (42; 25–49); *Austroperla* (37; 17–50); *Zelandobius* (35; 20–44); NZ *Notonemoura* (31; 19–38); *Spaniocerca* (25; 17–36); *Stenoperla* (16; 11–20); *Halticaperla* (27; 11–47) (McCulloch et al., 2016). Together, these eight NZ plecopteran clades (seven of which are included in Wallis and Jorge's (2018) list of “pre-drowning” NZ lineages) exhibit broadly similar divergence-timeframes (approximately 10–50 mya), but lack precision. While the optimal node-age estimates for most of these splits pre-date NZ's Oligocene drowning (mean 31 mya; range 16–42 mya), in our view it seems unlikely that members of this diverse stonefly assemblage (which typically require high-relief, cool-temperate conditions) simultaneously colonized a low-relief, sinking Zealandia landmass around 30 mya. By contrast, it seems more plausible that these eight lineages colonized a rapidly emerging (post-Oligocene), high-relief NZ landscape approximately 20 mya, seemingly consistent with the “younger end” of credibility intervals listed above. More broadly, we suggest that it may be unrealistic to expect to recover clear temporal signatures of even near-simultaneous colonization events when the dates are ancient and sequence data are approaching saturation. Crucially, the substantial uncertainty associated with these molecular date estimates seems

likely to at least partly obscure the phylogenetic record of near-simultaneous but ancient island-colonization events (Figure 3).

4.2 | Effects of sister-lineage extinction

The finding of old lineages on young islands is not a rare phenomenon in biogeography (Paulay, 1994). Indeed, archipelagos around the world are home to lineages whose estimated divergence dates are substantially older than the islands they inhabit (Beverley & Wilson, 1985; Buckley et al., 2008; Caccone et al., 1999; Lewin, 1985; Obbard et al., 2012; Parent et al., 2008). While some biogeographers have seemingly proposed that such “relict” island lineages have persisted in situ throughout inundation events (e.g., vicariant origins proposed for Galápagos biota: Grehan, 2001), a simpler explanation is that their closest sister relatives have gone extinct (or have yet to be sampled). Incomplete sampling is likely to be particularly relevant as a confounding issue for dating of invertebrate lineages which typically receive relatively little attention and thus are often poorly sampled. Additionally, lineage extinction is particularly likely to affect archipelagic systems, as a result of the sinking of previous islands within an island cluster (e.g., Lewin, 1985).

In the current study, we show that NZ, the Chatham Islands and Lord Howe Island all house substantial numbers (>20%) of ancient lineages that are estimated to pre-date landmass formation/inundation. Assuming these “old” divergence dates are accurate, these patterns seem most easily explained by sister-lineage extinction (Figure 3). Certainly, in the case of the Chatham Islands and Lord Howe, there seem to be no plausible alternatives to extinction or incomplete sampling as explanations. For the biota of NZ, which has been emergent since at least the late Oligocene, the issue of sister-lineage extinction is likely to be particularly important. We note that slight variation in the proportions of relict taxa may be associated with time of emergence, with Lord Howe (6.4–6.9 mya; 26% relict lineages) housing more relicts than the younger Chatham Islands (3 mya; 20%). Indeed, in some cases (e.g., NZ) the evidence of lineage extinction is overwhelming, and provides a clear explanation for ancient divergence dates. For instance, the ancient reptilian order Rhynchocephalia has a vast and widespread fossil record stretching back to the Triassic, but is now restricted to NZ (Tuatara; *Sphenodon*). As noted by Waters and Craw (2006), the only certainty regarding this lineage is that it has gone extinct from other landmasses; current fossil data seem to shed little light on when these extinctions occurred. A similar case exists for the divergent NZ-endemic frog family Leiopelmatidae (Worthy et al., 2013) for which neither extant nor extinct sister lineages have been recorded from any other Southern Hemisphere landmass.

5 | CONCLUSION

Recent reviews have concluded that NZ's biota is dominated by numerous recent arrivals, but also with a small yet substantial proportion of persisting ancient vicariant lineages (Giribet & Boyer, 2010;

Wallis & Jorge, 2018). Our study, by contrast, suggests that the genetic composition of NZ's biota (in terms of lineage divergence-time relative to inundation history) may not be substantially different to that of an oceanic island. Specifically, our findings suggest that the composition of NZ's biota, with around 30% of endemic lineages pre-dating Oligocene drowning, is comparable to that of Lord Howe and the Chatham Islands, where similar proportions of "relict" (pre-emergence) lineages have been detected. Indeed, phylogenetic relict lineages seem likely to be a shared feature of many (if not all) island biotas, attesting to the ongoing effects of lineage extinction throughout the globe. While estimates of arrival timing can be confounded by phylogenetic calibration issues, we suggest that extinction may be a crucial factor in some islands being interpretable as both evolutionary "cradles" and "museums" (McKenna & Farrell, 2006). Overall, we provide a schematic model to explain the discrepancies detected between expected versus observed divergence-date distributions for island biotas incorporating the effects of both molecular dating error and lineages extinction (Figure 3).

While the findings of the present study certainly do not reject the possibility of Oligocene land persistence in the NZ region, we suggest that they leave open the possibility of total Oligocene inundation (Landis et al., 2008; Pole, 1994). In the light of the apparent compositional (divergence-time distribution) similarities between NZ and nearby oceanic island assemblages, it seems premature to "put the idea to rest" (Wallis & Jorge, 2018).

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CONFLICT OF INTEREST

The authors have no competing interests.

AUTHOR CONTRIBUTIONS

J.W. and G.M. conceptualised and contributed equally to the study.

DATA AVAILABILITY STATEMENT

This study represents a synthesis of publicly available data.

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