ORIGINAL ARTICLE

Revenant clades in historical biogeography: the geology of New Zealand predisposes endemic clades to root age shifts

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ABSTRACT

Aim Our aim was to elucidate the effect of mass extinctions on inferred crown ages of terrestrial clades endemic to ancient islands. We thereby assessed the potential for mass extinction events, such as the Zealandian marine incursion episode in the Oligocene, to skew the interpretation of the evolutionary history of clades of various sizes.

Location Simulation study focusing on New Zealand.

Methods Clades of various sizes were simulated under a birth–death model with variable parameters for diversification, invoking a prolonged extinction event, using the R package TreeSim. We measured the scaled root shift *J* between actual (i.e. first cladogenetic event) and inferred (i.e. most recent common ancestor of extant taxa) clade divergence times in simulated phylogenies incurred by extinction processes.

Results A pulse of extinction followed by a prolonged period of low cladogenetic potential – modelled after the geological history of Zealandia in the Oligocene – produced large root shifts in clades of all sizes. Small clades with high net diversification rates were especially prone to belying pre-Oligocene history. In simulations invoking mass extinctions wherein a pre-extinction root was retained, phylogenies of extant taxa were characterized by anti-sigmoidal log lineage-through-time plots that mimicked an upturn in diversification rate after the extinction period.

Main conclusions Non-selective mass extinctions can engender large discrepancies in actual and inferred root ages, particularly in small, old clades. The evolutionary histories of lineages that survive mass extinctions are difficult to distinguish from scenarios of rapid radiation. This outcome challenges previous interpretations of post-Oligocene crown ages for clades endemic to New Zealand as sufficient evidence for rejecting a pre-Oligocene evolutionary history. As a corollary, our results suggest that the extant size of a particular clade is the foremost indicator of its potential for historical biogeographical inference. We therefore review the hypothesis of the total submersion of Zealandia, highlighting empirical cases of lineages with demonstrable pre-Oligocene history that refute the hypothesis of total submersion.

Keywords

Diversification, molecular dating, neoendemic, Oligocene drowning, palaeoendemic, rapid radiation, relict, Southwest Pacific, Zealandia.

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INTRODUCTION

New Zealand lies at the fulcrum of one of the most engaging disputes in the discipline of historical biogeography. Presently and principally composed of two large islands (North Island and South Island), New Zealand is part of an extensive submarine plateau of continental origin, called Zealandia, which includes several smaller islands, such as New Caledonia and

Chatham Island (Neall & Trewick, 2008). Zealandia separated from the supercontinent Gondwana c. 85–90 Ma and its constituent islands have been isolated from nearby continental margins (e.g. Australia) for a period in excess of 55 Myr (reviewed by Neall & Trewick, 2008; but see Schellart et al., 2006 on the subsequent completion of geological separation). Accordingly, the biota of New Zealand can be divided into two categories: palaeoendemic lineages of putatively Gondwanan character (Nelson, 1975; Cooper et al., 2001; Ericson et al., 2002; Stöckler et al., 2002) and neoendemics that colonized islands by long-distance dispersal (McGlone, 2005; Waters & Craw, 2006; McDowall, 2008). Owing to its inclusion among the remnants of Gondwana, New Zealand has historically figured prominently in studies of circum-Antarctic biogeography (e.g. Nelson & Platnick, 1981; Sanmartín & Ronquist, 2004).

The nature of the dispute over the biota of New Zealand stems from the geology of Zealandia in the Oligocene, a period of substantial marine incursion (Cooper & Cooper, 1995; Landis et al., 2008) during which New Zealand's surface was greatly reduced in size (Cooper & Millener, 1993). More recently, the hypothesis of the complete submersion of New Zealand during the Oligocene has taken hold (McGlone, 2005; Waters & Craw, 2006; Trewick et al., 2007; Landis et al., 2008; Crisp et al., 2011). The implication of this hypothesis is that New Zealand is a de facto oceanic island, despite being composed of continental crust (Trewick et al., 2007); the biota of New Zealand thus consists exclusively of neoendemics that colonized the island and radiated in the last 22 Myr (Landis et al., 2008). The 'Oligocene drowning' hypothesis draws upon (1) geological evidence of plate-thinning and subsidence, with a concomitant absence of late Oligocene terrestrial deposits (Landis et al., 2008), and (2) the abundance of molecular phylogenetic studies that indicate post-Oligocene divergence dates of many endemic lineages once thought to represent palaeoendemics.

The geological evidence that is frequently cited in favour of total marine inundation is in fact far from conclusive. Waters & Craw (2006) argued that there is 'no direct evidence for continuously emergent land through the middle Tertiary', but conceded that 'resolution of rock ages is too low to allow conclusive definition of times of complete submergence, or… an emergent archipelago' (Waters & Craw, 2006, p. 352); that is, the geology does not favour either hypothesis. Similarly, Trewick et al. (2007) strongly favoured the hypothesis of complete submergence, which implies that the entire biota cannot pre-date 22–25 Ma. But they nevertheless hedged this bet: 'Of course an emergent New Zealand archipelago does not preclude Zealandia having had a Gondwanan (vicariant) biota prior to submergence in the Oligocene, or the possibility that some lineages survived' (Trewick et al., 2007, p. 4). Finally, Landis et al. (2008) reviewed geological evidence for marine incursion and corroborated major aspects observed by Waters & Craw (2006): there is 'no geological evidence to indicate that land areas were continuously present' and 'the New Zealand subcontinent was largely, or entirely, submerged' (Landis et al., 2008, p. 173).

To our knowledge, no geological work has unequivocally claimed complete and unambiguous inundation of New Zealand.

The purpose of the aforementioned series of studies, which favour an inundation scenario (complete or otherwise), has been to question previous assumptions of the Gondwanan origin of New Zealand endemic lineages. This critique has proved to be largely valid for many New Zealand clades and species, which in fact appear to represent post-Cretaceous radiations of colonists. For example, many of the endemic New Zealand lineages once thought to have been of Gondwanan origin were subsequently demonstrated to be too young to be attributed to vicariance. These include the southern beech (Nothofagus; Swenson et al., 2001; Cook & Crisp, 2005), the galaxiid fishes (Burridge et al., 2012), the kauri (Agathis; Knapp et al., 2007; Biffin et al., 2010) and the moas (Phillips et al., 2010), among others. In other cases, outright transoceanic dispersals to New Zealand in the post-Oligocene account for several neoendemic radiations, especially among plant taxa (e.g. Spalik et al., 2010).

Furthermore, ancient lineages with few species, termed relicts, are disfavoured for biogeographical inference because they cannot falsify the continuous persistence of a landmass through time in the absence of a detailed fossil record (Crisp et al., 2011). For example, the two extant species of Sphenodon (the tuataras) are endemic to New Zealand and are the only surviving representatives of the sister lineage to the squamates, but they do not inform New Zealand's biogeography, insofar as the divergence of the two species is very recent and their fossil record in New Zealand does not pre-date the Oligocene. As a consequence, it is not feasible to falsify alternative biogeographical scenarios, such as the dispersal of the tuatara to New Zealand after the Oligocene with subsequent extinctions everywhere else. Another relictual taxon endemic to New Zealand is the frog genus Leiopelma (four extant species), which diverged from its sister lineage in the Late Triassic (Roelants et al., 2007).

The standard accepted for refutation of pre-Oligocene evolutionary history has typically been to test whether the crown root, or diversification, age (typically with a confidence interval) of an endemic New Zealand lineage coincides with or pre-dates the Oligocene drowning. If a specific divergence is too young, both pre-Oligocene history and, as a corollary, a vicariant origin for a clade can be rejected (Crisp et al., 2011). The assumption inherent to this framework is that the inferred root age is equal to the actual root age of the endemic clade. This assumption in turn hinges upon the supposition that extinction does not affect the estimation of the root age. This is because Slowinski & Guyer (1989) showed that the probability of a lineage surviving to time t is given by

$$P(t) = (\lambda - \mu)[(\lambda - \mu e^{-(\lambda-\mu)t})^{-1}],$$

where λ and μ are the probabilities of cladogenesis and extinction. A corollary of this equation is that when the net diversification rate $(\lambda - \mu)$ is low, a given lineage has a

higher probability of going extinct as time increases. In the absence of extrinsic perturbations to the net diversification rate (e.g. mass extinctions), the observable root age (i.e. the most recent common ancestor, MRCA, of extant taxa) is invariably equal to the actual root age if and only if μ is equal to zero. A non-zero value of μ in a birth–death model is expected to engender a gap between observed and actual node ages, especially for old clades (see Appendix S1: Fig. S1 in Supporting Information).

Neither of these conditions – the absence of extrinsic perturbations or non-zero μ – applies in the case of New Zealand. Analysis of diversification rates in New Caledonia, a Zealandian island that emerged 34 Ma (Grandcolas *et al.*, 2008), has suggested that density-dependent models of clado-genesis (i.e. decreasing net diversification rates over time) are suitable for describing the pattern of many endemic radiations (Espeland & Murienne, 2011; but for alternative interpretations of diversification rate deceleration, see Rabosky & Lovette, 2008; Rabosky, 2009; Cusimano & Renner, 2011; Pennell *et al.*, 2012). In spite of New Zealand's comparatively greater size, a period of decreasing net diversification rate is expected in the 35–80 Ma period, during which New Zealand could plausibly have reached carrying capacity for many old lineages, and in the 24 Ma–present period, when New Zealand's geology and biota took the forms observed today. Furthermore, a marine incursion of any size is anticipated to cause extrinsic extinction (unrelated to μ). If New Zealand were reduced to an emergent archipelago for the duration of the Oligocene, the effect on the endemic terrestrial biota could best be described as a prolonged mass extinction event.

We therefore investigated the effects of a simulated period of extinction, comparable in profile to the geological history of New Zealand (Fig. 1a), on the root ages of simulated endemic terrestrial clades. A cardinal element of this modelling is that a vicariant origin of the simulated clade is not invoked; the simulation conditions could equally well apply to a taxon that dispersed to a geologically dynamic landmass prior to the mass extinction event. Thus only a 'pre-Oligocene' history is stipulated. We were specifically interested in how extinction affects the inferable root age of clades of various sizes, because the diversity of clades on islands is extrinsically constrained by landmass availability.

Recent theoretical work has demonstrated that mass extinctions can cause shifts in the root age of virtual clades (Yedid *et al.*, 2012), although under those simulated conditions the majority of clades retained an inferable root age approximately equal to their actual root age even under strong episodes of extinction. Here, we show that the Oligocene bottleneck is predisposed to causing significant root shifts in small clades (10–100 extant species), even when no background extinction (μ) occurs. This may bias interpretation of diversification age towards the rejection of pre-Oligocene history when this hypothesis is true. Consistent with previous reports (Crisp & Cook, 2009), we observe that the evolutionary signature of clades surviving a simulated
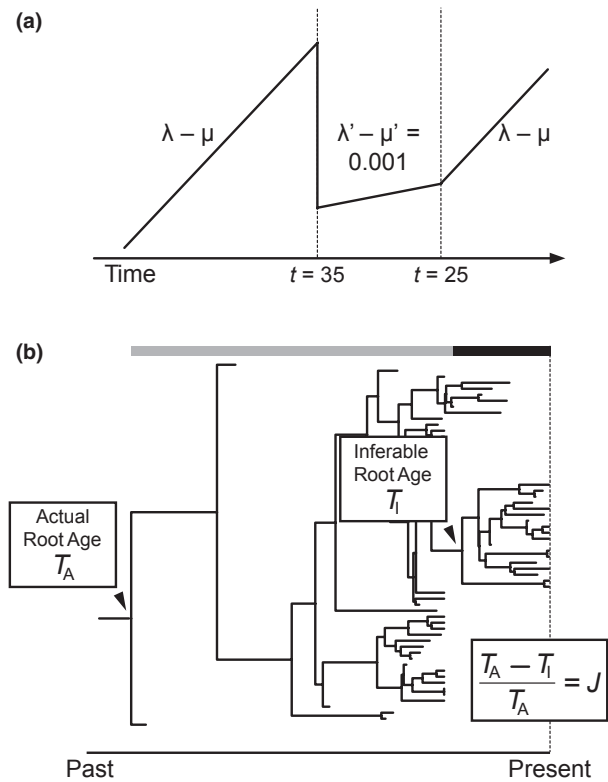

Figure 1 (a) Schematic of the New Zealand-like evolutionary history stipulated for simulations: an initial net diversification rate equal to $\lambda - \mu$; a 90% cull of species at time $t = 35$; a period of low cladogenetic potential from $t = 35$ to $t = 25$ ($\lambda' - \mu' = 0.001$); and a post-extinction recovery with net diversification rate equal to $\lambda - \mu$. (b) Schematic of a hypothetical phylogeny including extinct tips, indicating actual root age (T_A), inferable root age (T_I), and the definition of J. The shaded bar above the phylogeny indicates a visual representation of J, as the proportion of T_A (entire bar) that cannot be inferred from the extant tips alone (in grey). The black portion of the bar indicates T_I.

inundation event may be indistinguishable from a scenario of recent increase in net diversification rate.

MATERIALS AND METHODS

Phylogenies were simulated under a birth–death model using the R package TreeSim 1.6 (Stadler, 2011). To incorporate geological dynamism, the multi-phase function sim.rateshift.taxa was used to simulate clades with the following numbers of extant taxa: 10, 25, 50 and 100. Simulations commenced with diversification rate $\lambda - \mu$, such that $\mu/\lambda = 0.5$. Actual root ages were not constrained.

Following the terminology of Yedid *et al.* (2012), we refer to instantaneous culls of diversity as 'pulses' and to prolonged periods of low cladogenetic potential as 'presses'. Extinctions were induced as an initial pulse (a non-selective cull of 90% of terminals) occurring at time $t = 35$, followed by a press (a period when $\lambda' = \lambda/10$ and $\mu' = \lambda' - 0.001$) occurring at time $t = 25$ to $t = 35$, and then by post-extinction recovery

with the pre-extinction parameters (diversification rate: λ – μ; extinction fraction: μ/λ = 0.5). The general form of the simulated evolutionary history is depicted in Fig. 1a. We tested three values of λ (with associated values of μ, λ′ and μ′): 0.10, 0.30 and 0.50.

We measured the proportion J of the evolutionary history of a given clade (commencing from the actual root, or the first cladogenetic event) that is not represented by the MRCA of the extant taxa:

$$J = (T_A - T_I)(T_A)^{-1},$$

where T_A is the actual root age and T_I is the inferable root age (the MRCA of the extant terminals) (Fig. 1b). Manipulation of simulated trees and calculation of J made use of the R package PHYTOOLS 0.1-9 (Revell, 2012). We incorporated no sampling failure among extant taxa. Five hundred simulations were conducted for each combination of clade size and diversification parameters.

RESULTS

Sensitivity of *J* to extinction is inversely proportional to clade size

Under all parameters tested for λ and μ, smaller extant clades were prone to high values of J subsequent to imposed extinction (Fig. 2). Owing to the stochasticity of the simulations, values for J had large variance, but a general trend of decreasing J with increasing clade size was observed under all stipulated parameters (Appendix S1: Fig. S2).

Clades simulated under high net diversification rates (and thus higher values of μ) underwent greater losses of evolutionary history (high J) than those under low net diversification rates. This is because clades evolving slowly after the press of extinction (λ = 0.1, μ = 0.05) had more extant lin-

eages at time $t = 25$ than clades evolving more rapidly. For clades with more than 25 extant taxa evolving at the slowest diversification rate imposed here, J clustered close to 0 owing to the comparatively larger number of species surviving the mass extinction (Fig. 2 & Appendix S1: Fig. S2).

Clades undergoing a press of extinction incur large *J*, regardless of μ

To dissociate lineage turnover (the effect of a high extinction fraction, μ/λ) from the press of extinction, we additionally simulated 500 phylogenies of 100 extant taxa under a pure birth model (λ = 0.3, μ = 0) subjected to the press of extinction. Of 500 simulations conducted, only 1.8% of cases ($n = 9$ phylogenies) retained a pre-extinction press root ($T_I > 35$) (Appendix S1: Fig. S3). An inferred root age less than $t = 25$ (i.e. indistinguishable from a post-extinction radiation) was obtained for 97.6% of simulations ($n = 488$ phylogenies).

DISCUSSION

Prolonged mass extinctions cause observed clade age to belie ancient evolutionary history

A cardinal outcome of a previous study (Yedid *et al.*, 2012) was that lineages subject to mass extinction events could undergo root age shifts. In that study, however, the majority of lineages undergoing simulated mass extinction retained the actual root (generating an approximately exponential distribution with a mean close to the root age; 1B, 1C of Yedid *et al.*, 2012), probably owing to the size of simulated clades. By contrast, endemics observed on real islands often have much lower limits on clade size than their continental counterparts; the largest New Zealand endemic clades well sampled in a molecular phylogeny presently do not exceed 50
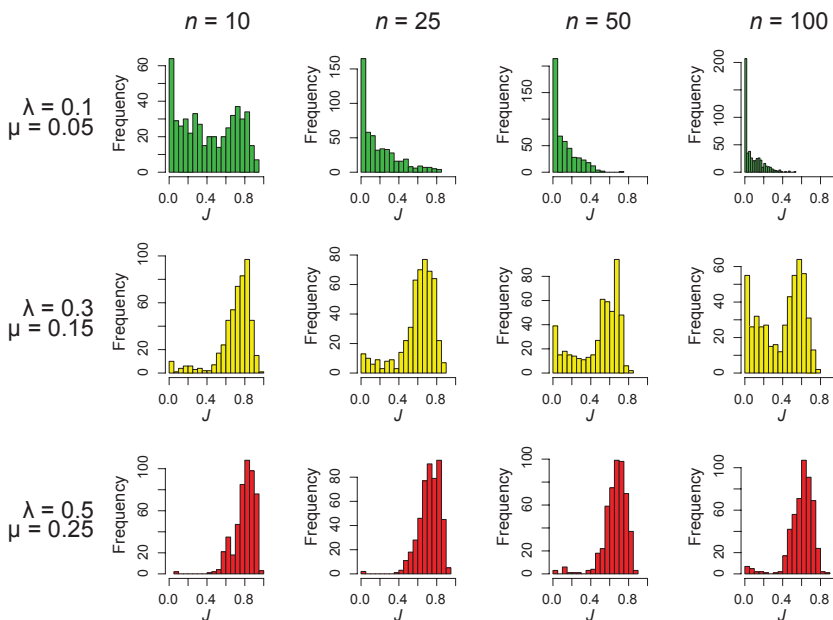

Figure 2 Distribution of J obtained for simulated clades of various sizes and under various diversification parameters.

species (Nielsen *et al.*, 2011). Thus, in the present study, we tested the effects of mass extinction events on the inferable evolutionary history of simulated endemic clades with 100 or fewer species.

The results of our simulations show that clades with a pre-extinction root age simulated under a birth–death model are highly prone to losses of observable evolutionary history (large values of J) (Fig. 2). Small clades ($n < 25$ extant taxa) can lose significant spans of evolutionary history even in the absence of mass extinction events, given non-zero μ (Appendix S1: Fig. S1). Only if a large number of lineages survives the imposed extinction episode can the gap between the actual and the inferred root age be reliably closed. In our simulations, this corresponded to the cases where $\lambda = 0.1$, which stipulates a larger number of species surviving at time $t = 25$ than in simulations with greater λ.

In our simulations, we constrained λ and μ such that net diversification rates were fixed within and outwith the extinction period (Fig. 1). Empirically, λ and μ are difficult to measure in the absence of a highly detailed fossil record approaching the completeness of taxa such as Bivalvia or Gastropoda – a quality attributable to few terrestrial New Zealand taxa. Furthermore, estimating λ and μ from the observed net diversification rate curve is feasible only if specific conditions are met, such as birth–death parameters holding constant over time (Nee *et al.*, 1995; but see Rabosky, 2010). For New Zealand, this condition is violated both by the finite size and the carrying capacity of Indo-Pacific

islands (Espeland & Murienne, 2011) and by the marine incursion event during the Oligocene.

Even in the absence of intrinsic or background extinction (μ), simulating a prolonged period of extinction comparable to the Oligocene bottleneck drastically shifts the root age towards the present (Fig. S3). This suggests that the geological history of New Zealand is uniquely prone to engendering phylogenies wherein endemic clades appear to be younger than they actually are (regardless of μ). Therefore, an observed clade diversification age post-dating the Oligocene does not have to constitute an actual case of post-Oligocene colonization, leading to a false rejection of the hypothesis of pre-Oligocene history.

Rapidly radiating lineages may represent palaeoendemic survivors of bottlenecks

It was previously demonstrated that a severe pulse of extinction often engenders an observed lineage-through-time plot of anti-sigmoidal shape, which is indistinguishable from a recent upturn in speciation rate (Crisp & Cook, 2009). We corroborate this effect for a pulse of extinction followed by a prolonged press of low cladogenetic potential. Alarmingly, we observe that the lineage-through-time plot corresponding to a press of mass extinction for clades of 10–100 taxa does not leave a signature during the extinction period that is distinguishable from either a single pulse of extinction (see Crisp & Cook, 2009) or an upturn in net diversification rate,
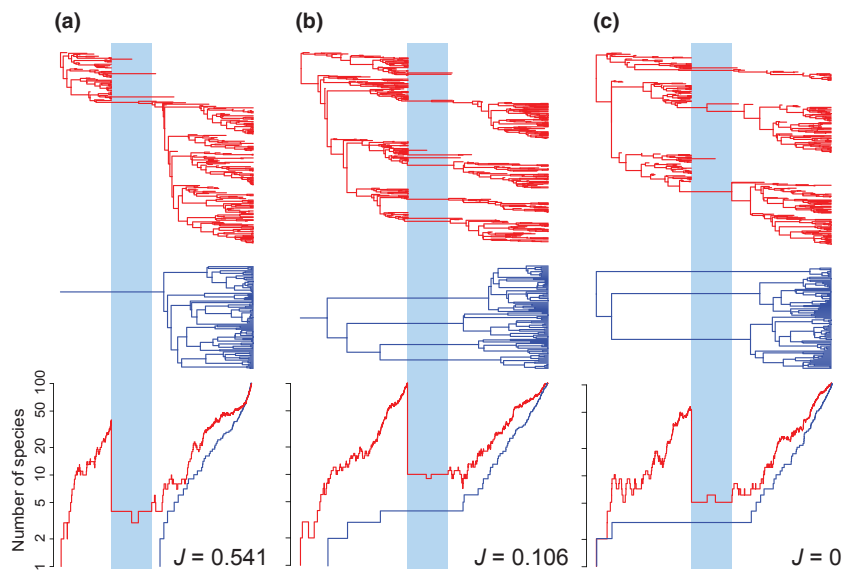

Figure 3 Complete (red) and extant-only (blue) topologies and log lineage-through-time (LTT) plots of three sampled phylogenies with 100 extant taxa, simulated under a birth–death process ($\lambda = 0.3$, $\mu = 0.15$) and subjected to an extinction press ($\lambda' = 0.03$, $\mu' = 0.029$), as in Fig. 2. The blue bar indicates the duration of the extinction press. (a) Exemplar of a phylogeny with a pre-extinction origin and a post-extinction root, corresponding to a revenant clade. The observed phylogeny and log LTT plot are indistinguishable from a birth–death process. (b) Exemplar of a phylogeny with a pre-extinction origin and a pre-extinction root closer to the actual root. The observed phylogeny and log LTT plot record a characteristic post-extinction upturn in net diversification rate. (c) A rare example of a phylogeny (4.8% of simulated trees) wherein the actual and inferable root ages are the same. As in (b), the observed phylogeny and log LTT plot show an apparent post-extinction upturn in net diversification rate.

when a pre-extinction root is retained (Fig. 3). Observed lineage-through-time plots of clades surviving an Oligocene-like history portray a signature of rapid radiations in the recovery period. These results call for an attendant reassessment of putative post-Oligocene radiations in New Zealand, which may represent survivors of the bottleneck event if the time of origin pre-dates the Oligocene.

As an example, Nielsen *et al.* (2011) estimated that the New Zealand clade of Diplodactylidae, one of the most fully sampled vertebrate radiations on the island, diversified *c.* 24.4 Ma. The authors contended that this age, spanning the Oligocene bottleneck, refutes the hypothesis of complete inundation. This argument is reinforced by the age estimate of the split between the New Zealand and Australian geckos: 40.2 Ma [confidence interval (CI): 28.9–53.5 Ma] (Nielsen *et al.*, 2011). The gecko lineage could therefore be interpreted to have persisted in Zealandia for some time prior to surviving the Oligocene marine incursion and to have diversified in its wake.

It is imperative to note that rapid radiation is not inconsistent with surviving a mass extinction event. It is anticipated that a mass extinction will empty ecological niches occupied by pre-existing competitors, permitting radiations of surviving lineages. In this manner, an ancient endemic lineage surviving the Oligocene bottleneck could (1) go extinct, either by chance or by failure to compete successfully with newly arriving colonists, (2) survive to the present as a relict, or as an otherwise minor element of the biota, or (3) give rise to a spectacular radiation of apparent recent age, once released from constraints on diversification (Jablonski, 2001).

We therefore submit that pre-Oligocene evolutionary history can be rejected only if both the diversification and the origin (divergence from the sister clade) of a New Zealand clade post-date the end of the Oligocene (Fig. 4). Implementation of this criterion including stem age in the evaluation of biogeographical hypotheses was most recently exemplified in a study of Sulawesi (Stelbrink *et al.*, 2012). In this respect, a pre-Oligocene persistence cannot be rejected for a post-Oligocene diversification subtended by a branch persisting through the Oligocene bottleneck, which we term a 'revenant clade' – a possible survivor of the marine incursion that subsequently diversifies. A revenant clade is distinguished from a relict (such as the tuatara) by a large number of extant species and/or by rapid diversification after an extinction event. But, however spectacular the post-Oligocene radiation or decline, the revenant and the relict have the same implication for biogeographical hypothesis testing: they cannot falsify a pre-Oligocene history (Fig. 4).
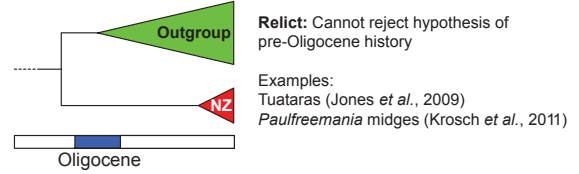
Large clades of small-sized taxa may be better suited to falsifying pre-Oligocene persistence

The idea that New Zealand is a Darwinian landmass (*sensu* Gillespie & Roderick, 2002) holds tremendous appeal and prima facie is surprisingly plausible. Like many oceanic islands, New Zealand lacks key terrestrial vertebrate lineages
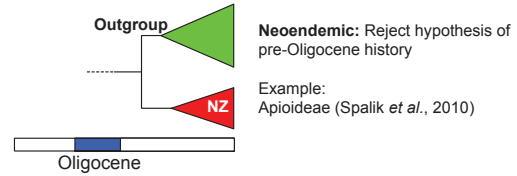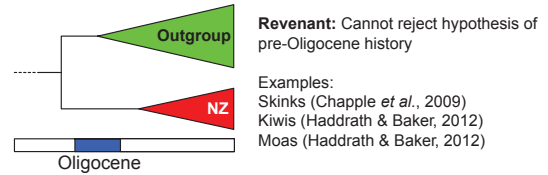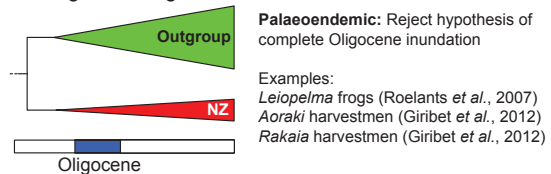

Figure 4 Summary of empirical phylogenetic patterns and their implications for inferring the pre-Oligocene history in New Zealand.

that are indicative of continental biotic origin. These include non-volant mammals (but see Worthy *et al.*, 2006, for a ghost non-volant mammal lineage through the middle Miocene), terrestrial turtles (but see Worthy *et al.*, 2011, for New Zealand's fossil turtles from the early Miocene) and snakes, among others. Apropos, the flightless and/or giant birds of New Zealand, such as the moa and kiwi, have been viewed as colonists of vacant niche space typically occupied by mammals, in a manner comparable to their counterparts on oceanic islands of volcanic origin (Trewick *et al.*, 2007; Bunce *et al.*, 2009; but see Tennyson *et al.*, 2010). The occurrence of lineages such as *Leiopelma* frogs and tuataras in New Zealand has been regarded as an anomaly, attributable to the relictual nature of these lineages (Trewick *et al.*, 2007; Crisp *et al.*, 2011). Certainly from the perspective of some vertebrate biogeographers, the biota of New Zealand might appear to be composed entirely of neoendemic radiations younger than 22 Ma.

The opposite is generally the case from the perspective of invertebrate biogeographers (reviewed by Giribet & Boyer, 2010). New Zealand's invertebrate fauna includes several extant lineages that are invariably associated with continental biotas [e.g. velvet worms (Onychophora), Allwood *et al.*, 2010; mite harvestmen (Cyphophthalmi), Boyer *et al.*, 2007; Giribet *et al.*, 2012;]. Such invertebrates are often small, cryptic and remarkably diverse; almost all display type-locality

endemism (Boyer *et al.*, 2007). The theoretical expectation is that the larger the number of ingroup lineages surviving a bottleneck, the better the prospects of recovering deep evolutionary history (small *J*) (Fig. 2). As a consequence, small-sized and species-rich invertebrate clades may be better suited than larger vertebrates for inferring deep evolutionary events on islands with a turbulent geological history, insofar as multiple small-sized lineages may persist on small islands of an emergent archipelago without exhausting ecological resources. Our results suggest that falsifying pre-Oligocene evolutionary history is best pursued by inferring origin and diversification times for key taxa that are diverse and could plausibly survive the reduction of New Zealand to an emergent archipelago.

Does the Oligocene drowning hold water?

To test empirically the prediction that clade size is positively correlated with divergence time for taxa with pre-Oligocene history, we plotted the recorded diversity and estimated divergence times of New Zealand clades for which pre-Oligocene origin has been documented. As a corollary, we also tested the previous claims that geckos and skinks have diversified rapidly and filled numerous ecological niches in New Zealand (Chapple *et al.*, 2009; Nielsen *et al.*, 2011).

We observed a positive relationship between the diversification ages of New Zealand clades with pre-Oligocene origins and extant clade sizes (Spearman rank correlation coefficient $\rho = 0.730$; Fig. 5), which accords with the predictions of the modelling and disfavours an explanation based on erroneous dating or random pattern. Consistent with previous characterizations of the squamate rapid radiations, we observe that both clades are outliers in this trend, being much more
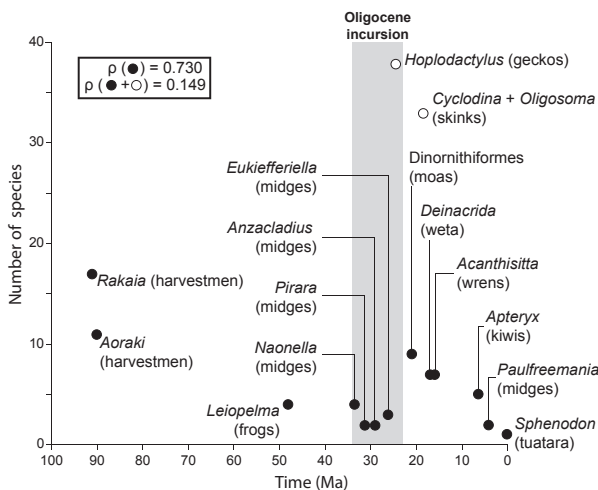

Figure 5 Diversity and diversification dates of New Zealand clades whose dates of origin pre-date the Oligocene. Boxed: Spearman rank correlation coefficient ρ for taxa without demonstrable evidence of rapid radiation (black icons only) and all taxa (black and white icons). Grey shading indicates a period of Oligocene marine incursion. Taxon divergence dates and literature references are provided in Appendix S2.

diverse than expected based on clade age. The next most diverse pair of clades, the harvestmen genera *Aoraki* and *Rakaia*, is not demonstrably diverse with respect to morphology, behaviour or ecology, in contrast to the squamates (Boyer *et al.*, 2007; Giribet *et al.*, 2012). However, we add the caveat that the linear relationship between extant clade size and inferable clade age is contingent upon the assumption of near-constant net diversification rates, which can be empirically violated by bursts of speciation or extinction, or by intrinsic differences between lineages (Rabosky *et al.*, 2012). Such violations of the trend are expected to be the case for the rapidly radiating New Zealand squamates (Fig. 5).

In the course of the literature survey, we encountered eight cases of endemic New Zealand clades with crown ages coincident with or preceding the Oligocene. These cases are characterized by extensive taxon sampling in multi-locus phylogenies and reliable dating using fossil taxa for calibrations. The sum of the biogeographical literature therefore falsifies the hypothesis of the total submersion of New Zealand, as multiple lineages have demonstrably persisted on this island through the Oligocene. These eight cases are as follows (Fig. 5).

(1) Frogs of the genus *Leiopelma* diversified *c.* 48 Ma (Roelants *et al.*, 2007). A recent and densely sampled amphibian phylogeny including all four extant *Leiopelma* species indicates that the two species sampled in the topology of Roelants *et al.* (2007) span the MRCA of *Leiopelma* (Pyron & Wiens, 2010). Although a Gondwanan origin of this relictual genus is not demonstrable (owing to divergence from its North American sister genus before 200 Ma), *Leiopelma* does falsify the hypothesis of complete Oligocene inundation.

(2)–(3) The mite harvestmen non-sister genera *Aoraki* (11 species) and *Rakaia* (17 species) are inferred to date back to 90 Ma (CI: 75–108 Ma) and 91 Ma (CI: 72–108 Ma), respectively (Giribet *et al.*, 2012). All mite harvestman families are endemic to particular geographical terrains, and their distributions and divergence times closely accord with vicariant patterns elsewhere (Boyer *et al.*, 2007; Giribet *et al.*, 2012). In addition, all New Zealand mite harvestman are distributed in close geographical correspondence to the microplates of New Zealand, suggesting an ancient evolutionary history (Boyer & Giribet, 2009). Beyond refuting the hypothesis of complete Oligocene inundation (the confidence intervals greatly pre-date the Tertiary, much more so the Oligocene), *Aoraki* and *Rakaia* represent the only known cases at present for which divergence dates are unambiguously consistent with Gondwanan vicariance.

(4)–(7) Another quartet of cases constitutes non-sister genera of chironomid midges (Krosch *et al.*, 2011). *Anzacladius* (two species), *Eukiefferiella* (New Zealand clade; three species), *Naonella* (*sensu lato*, including *Tonnoirocladius*; four species) and *Pirara* (two species) are estimated to have diversified *c.* 29, 26, 33 and 31 Ma, respectively (Krosch *et al.*, 2011). The origins of all four pre-date the Oligocene (*c.* 40 Ma).

(8) The diplodactylid gecko clade of New Zealand, discussed above, diversified *c.* 24.4 Ma (Nielsen *et al.*, 2011). This diversity of the gecko (and also skink; Chapple *et al.*, 2009) clades has previously been attributed to rapid radiation into empty ecological niche space after the extinction period (Nielsen *et al.*, 2011). As with the chironomid midges, the origins of both squamate clades pre-date the Oligocene (*c.* 40 Ma), suggesting that these geckos exemplify revenants.

Thus, the characterization of New Zealand's biota as 'Darwinian' or 'oceanic' is contingent upon a biogeographer's point of view and fraught with exceptions. It is better characterized as an amalgam of old and young elements (*sensu* Fleming, 1979), as are the biotas of mostly all fragment islands that are geologically dynamic (e.g. constituents of the Indo-Malay Archipelago; Stelbrink *et al.*, 2012). Attempting to salvage the Oligocene drowning argument by claiming that a preponderance of post-Oligocene radiations in the composition of New Zealand's biota favours its characterization as a 'young' or 'oceanic' biota (despite multiple glaring exceptions) is inherently tautological. Older lineages are theoretically and empirically more likely to go extinct over time than younger lineages, or to appear younger owing to extinction events (Slowinski & Guyer, 1989; Nee *et al.*, 1995; Jablonski, 2001). Post-Oligocene diversifications taken without regard for stem ages therefore constitute negative evidence when testing biogeographical hypotheses. Furthermore, even the biotas of the largest and most stable terranes – the tropics of large continents – include numerous non-Gondwanan radiations of neoendemics, many precipitated by intercontinental dispersal (e.g. McKenna & Farrell, 2006; Jønsson *et al.*, 2011). To call the biota of such regions 'Darwinian' blurs the definition and utility of this label.

CONCLUSIONS

Prolonged mass extinctions engender large disparities between the actual and inferable ages of simulated clades. The period of mass extinction in New Zealand wrought by marine incursion in the Oligocene is anticipated to have this effect on endemic lineages, particularly on small clades. A pre-Oligocene lineage that survives a mass extinction and diversifies in the post-Oligocene can resemble a neoendemic rapid radiation of a colonizing ancestor, leading to false rejection of the hypothesis of pre-Oligocene history. Multiple published cases of ancient lineages with pre-Oligocene history refute the hypothesis of complete inundation of New Zealand. As palaeontological and phylogenetic data accumulate, it is anticipated that more pre-Oligocene lineages will be discovered in New Zealand, particularly if the onychophoran and earthworm clades can be reliably calibrated using fossils (Allwood *et al.*, 2010; Buckley *et al.*, 2011), and as more ghost vertebrate lineages continue to be unearthed (Worthy *et al.*, 2006, 2011). Our results illustrate the necessity of considering times of origin when evaluating competing biogeographical hypotheses.

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SUPPORTING INFORMATION

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

Appendix S1 Supplementary figures (Figs S1–S3).
Appendix S2 Empirical divergence dates and literature references for Fig. 5.

BIOSKETCHES

Prashant P. Sharma has a PhD in biology from Harvard University and is a postdoctoral researcher in the Wheeler Lab at the American Museum of Natural History. He is interested in the effects of geological processes on the phylogenies of endemic clades. A particular focus of his research is the invertebrate fauna of the Indo-Pacific.

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