Evolutionary biology

Reproductive niche conservatism in the isolated New Zealand flora over 23 million years

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The temporal stability of plant reproductive features on islands has rarely been tested. Using flowers, fruits/cones and seeds from a well-dated (23 Ma) Miocene Lagerstätte in New Zealand, we show that across 23 families and 30 genera of forest angiosperms and conifers, reproductive features have remained constant for more than 20 Myr. Insect-, wind- and bird-pollinated flowers and wind- and bird-dispersed diaspores all indicate remarkable reproductive niche conservatism, despite widespread environmental and biotic change. In the past 10 Myr, declining temperatures and the absence of low-latitude refugia caused regional extinction of thermophiles, while orogenetic processes steepened temperature, precipitation and nutrient gradients, limiting forest niches. Despite these changes, the palaeontological record provides empirical support for evidence from phylogeographical studies of strong niche conservatism within lineages and biomes.

1. Introduction

Niche conservatism is a significant constraint on adaptive evolution in organisms and has been advanced as a major influence on speciation and trait development [1]. Integration of phylogenetics with environmental modelling has identified ecological conservatism within both lineages [2] and biomes [3]. Evidence for niche conservatism comes from similarities between closely related taxa within bioclimatic zones and their shared physiological and morphological traits.

Niche conservatism is the retention of ecological traits over evolutionary time [4]. This is usually inferred by mapping traits onto phylogenies and/or using ancestral state reconstructions to test adaptive shift hypotheses [5]. However, although this approach is informative, it lacks independent evidence for trait consistency or lability over time.

A recent review of niche conservatism suggested that it may break down over long time scales [6]; a meta-analysis of Holocene speciation and distributional shifts showed conservatism was less dominant across older lineages. Nevertheless, although traits like small leaf size persisted in multiple shrub lineages over 5 Myr of transition from forest to chaparral in California [5], the rates at which trait conservatism declines within lineages are largely unknown [6].

Here, we examine features associated with floral structure, pollination and dispersal syndromes in New Zealand, representing an isolated island forest biome with over 20 Myr of environmental change as temperatures declined, mountains arose and environmental gradients steepened [7]. We compare...
Table 1. Plant families and genera with macrofossil material at Foulden Maar based on reproductive structures (flower, fruit and seed), supporting evidence for identification to extant relatives (Adapted from [10,11]), and reproductive syndrome data [12–16]. Voucher specimens of the fossils are housed at the University of Otago Geology Museum (OU). U, unisexual; H, hermaphrodite; P, pollination and D, dispersal. AU=Australia, NC=New Caledonia, NG=New Guinea, AS=South-east Asia, OT=Old World tropics, PT=Pantropical.

<table>
<thead>
<tr>
<th>taxon</th>
<th>reproductive organs preserved at Foulden Maar</th>
<th>other evidence for occurrence</th>
<th>modern relatives</th>
<th>diagnostic features shared with modern relatives</th>
<th>reproductive syndromes</th>
</tr>
</thead>
<tbody>
<tr>
<td>Alseuosmiaceae (Alseuosmia)</td>
<td>flower</td>
<td>—</td>
<td>Alseuosmia*</td>
<td>corolla long funnelform, five lobed. Stamens 5, inserted near throat (exserted in dry flowers)</td>
<td>bell flower (H): bird, moth (P)</td>
</tr>
<tr>
<td>Arellaceae (Pseudopanax)</td>
<td>umbels of flowers and fruits</td>
<td>leaves, pollen</td>
<td>Pseudopanax*</td>
<td>umbellate; petals 5; styles shortly connate; fruit ± fleshy, five locular</td>
<td>dish bowl (U): small insect (P)/ avichory (D)</td>
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<tr>
<td>Atherospermataceae (Laurasia)</td>
<td>fruits</td>
<td>leaves, pollen</td>
<td>Laurasia*</td>
<td>achenes with long, plumose styles, enclosed in enlarged receptacle</td>
<td>(U/H) anemochory (P/D)</td>
</tr>
<tr>
<td>Bignoniaceae</td>
<td>winged seeds</td>
<td>—</td>
<td>?Tecomanthe*, ?Deplanchea (AU, NC, NG, AS)</td>
<td>seed wing transparent, very thin; embryo tear-drop shaped</td>
<td>(H) anemochory (D)</td>
</tr>
<tr>
<td>Cassuinaceae (Casuanina)</td>
<td>fruits</td>
<td>pollen</td>
<td>Casuarina (AU, NC, Alcosuautina (AU), Gymnostoma (AU, NC, NG, AS)</td>
<td>fruit woody, oval, cone like; carpels numerous, one seeded</td>
<td>(U) anemochory (D)</td>
</tr>
<tr>
<td>Cunoniaceae (Weinmannia)</td>
<td>flowers with in situ pollen; fruit</td>
<td>leaves, pollen</td>
<td>Weinmannia*</td>
<td>sepals 4–5, united basally, imbicate; petals 4–5; stamens 8–10; ovary two locular; capsules two valved, septicidally dehiscent</td>
<td>brush (H): small insect (P)/ avichory (D)</td>
</tr>
<tr>
<td>Elaeocarpaceae (Elaeocarpus and Sloanea)</td>
<td>flowers; fruits (Sloanea only)</td>
<td>leaves</td>
<td>Elaeocarpus*, Sloanea (PT)</td>
<td>petals 4–5; stamens numerous; anthers linear, ± awned, opening by terminal pores or slits; fruits 3–5 cm, two to five valved, smooth to spinose hairy</td>
<td>bell flowers (H): small insect (P)/ avichory (D)</td>
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<tr>
<td>Euphorbiaceae (Malloranga)</td>
<td>flowers with in situ pollen; fruits; seeds</td>
<td>leaves</td>
<td>Mallotus, Macaranga (PT)</td>
<td>flowers 2–3 mm diam.; stamens numerous; capsules three locular, one seeded, hairy; seeds globular</td>
<td>brush (U): wind (P)/avichory (D)</td>
</tr>
<tr>
<td>Fabaceae subfam. Caesalpinioidae</td>
<td>fruits; ?seeds</td>
<td>pollen</td>
<td>Caesalpinioideae legumes (PT)</td>
<td>fruit a legume, mostly dry, dehiscent or indehiscent</td>
<td>(H): hydrochoery, zoochoory or ballistochory (D)</td>
</tr>
<tr>
<td>Lauraceae (Beilschmiedia, Cryptocarya, Litsea)</td>
<td>flowers; fruits; seeds</td>
<td>leaves</td>
<td>Beilschmiedia*, Cryptocarya (OT), Litsea*</td>
<td>flowers small, one to clustered, occasionally involucrate; calyx tube short, sometimes, lobes or teeth 4–6; fruit a one-seeded berry, pome or drupe</td>
<td>dish bowl (H): small insect (P)/ avichory (D)</td>
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<tr>
<td>Loasaceae</td>
<td>flower with in situ pollen</td>
<td>pollen; flowers</td>
<td>Alepis*, ?Trileptea</td>
<td>perianth of four reflexed petaloid tepals; stamens 4; stigma 1</td>
<td>bell flowers, explosive pollen (H): birds, bees, wasps (P)/avichory (D)</td>
</tr>
<tr>
<td>Meliaceae (Dysoxylum and others)</td>
<td>flower with in situ pollen; fruits</td>
<td>leaves, pollen</td>
<td>Dysoxylum*</td>
<td>sepals and petals 4–5; staminal tube cylindrical, toothed at mouth; anthers 8–10, included in tube; disk tubular; capsule loculicidally dehiscent; seeds</td>
<td>dish bowl (H): small insect (P)/ avichory (D)</td>
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<tr>
<td>Menispermaceae (Hyperpa)</td>
<td>endocarps</td>
<td>leaves</td>
<td>Hyperpa (AU, NC, NG)</td>
<td>endocarp bony, curved, rugulose with radial transverse ridges; condyle with two lateral externally apurate cavities</td>
<td>dish bowl (H): small insect (P)/ avichory (D)</td>
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</table>

(Continued.)
<table>
<thead>
<tr>
<th>taxon</th>
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<th>reproductive syndromes</th>
</tr>
</thead>
<tbody>
<tr>
<td>Monimiaceae (&lt;i&gt;Hedycarya&lt;/i&gt;) [17]</td>
<td>flowers with in situ pollen; fruits</td>
<td>leaves</td>
<td>&lt;i&gt;Hedycarya&lt;/i&gt;*</td>
<td>dioecious, flowers cup shaped, male perianth 5–10 partite; spreading; stamens numerous, anthers flat, ± sessile; drupes several on receptacle</td>
<td>dish bowl (U): small insect (P); avichory (D)</td>
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<tr>
<td>Moraceae (?&lt;i&gt;Streblus&lt;/i&gt;) [18]</td>
<td>possible infructescence</td>
<td>pollen</td>
<td>&lt;i&gt;Streblus&lt;/i&gt;*</td>
<td>unisexual flowers in spikes with distinctive flattened scales; fruit a one-seeded drupe</td>
<td>brush (U): wind (P); avichory (D)</td>
</tr>
<tr>
<td>Myrtaceae (&lt;i&gt;Metrosideros&lt;/i&gt; and &lt;i&gt;Syzygium&lt;/i&gt;) [18]</td>
<td>fruits; seeds</td>
<td>leaves; pollen</td>
<td>&lt;i&gt;Metrosideros&lt;/i&gt;<em>; &lt;i&gt;Syzygium&lt;/i&gt;</em></td>
<td>receptacle adnate to inferior ovary; fruit a one-seeded ‘berry’ (Syzygium) or many-seeded loculicidal capsule (Metrosideros)</td>
<td>inflorescence (H): bird, insect (P); avichory (D)</td>
</tr>
<tr>
<td>Onagraceae (&lt;i&gt;Fuchsia&lt;/i&gt;) [24]</td>
<td>flower and anther mass with in situ pollen</td>
<td>pollen</td>
<td>&lt;i&gt;Fuchsia&lt;/i&gt;*</td>
<td>floral tube tubular; sepals 4; petals minute or 0; stamens 8, in two whorls, exserted; anthers dorsifixed</td>
<td>bell (H/U): bird (P); avichory (D)</td>
</tr>
<tr>
<td>Picrodendraceae (?&lt;i&gt;Scagea&lt;/i&gt;) [17,18]</td>
<td>male flowers with in situ pollen; female flowers; fruits</td>
<td>pollen; ?leaves</td>
<td>&lt;i&gt;Scagea&lt;/i&gt; (NC)</td>
<td>staminate flower tepals concave, three outer and three inner; stamens (4–)6; pistillode usually present</td>
<td>dish bowl (U): small insect (P)</td>
</tr>
<tr>
<td>Picrodendraceae (?&lt;i&gt;Whyanbeelia&lt;/i&gt;) [17,18]</td>
<td>male flowers in situ pollen; female flowers; fruits</td>
<td>pollen; ?leaves</td>
<td>&lt;i&gt;Whyanbeelia&lt;/i&gt; (AU)</td>
<td>male flowers short pedicellate, tepals 1–1.5 mm, stamens 50–55; female flowers long pedicellate, tepals 3–4 mm, styles 3–4 mm; disk glands prominent; fruits globose, ± 20 mm, mericarps separating at maturity</td>
<td>dish bowl (U): small insect (P); avichory (D)</td>
</tr>
<tr>
<td>Pittosporaceae (&lt;i&gt;Pittosporum&lt;/i&gt;) [18]</td>
<td>fruit</td>
<td>–</td>
<td>&lt;i&gt;Pittosporum&lt;/i&gt;*</td>
<td>fruit a two- to three-segmented loculicidal capsule, segments rounded, spreading</td>
<td>bell (H): bees (P); avichory (D)</td>
</tr>
<tr>
<td>Podocarpaceae (&lt;i&gt;Podocarpus&lt;/i&gt;) [18,25]</td>
<td>cone with seeds</td>
<td>leaves; pollen</td>
<td>&lt;i&gt;Podocarpus&lt;/i&gt;*</td>
<td>receptacle fleshy; epimatium connate with inverted ovule, concrescent with integument; seed nut-like</td>
<td>wind (U); avichory (D)</td>
</tr>
<tr>
<td>Proteaceae (?&lt;i&gt;Stenocarpus&lt;/i&gt; or &lt;i&gt;Alloxylon&lt;/i&gt;) [18]</td>
<td>winged seed</td>
<td>leaves; pollen</td>
<td>&lt;i&gt;Stenocarpus&lt;/i&gt; (AU, NC, NG), &lt;i&gt;Alloxylon&lt;/i&gt; (AU, NG)</td>
<td>Seeds flat, with a narrow, oblong, terminal wing and large seed body</td>
<td>bell (H): bird (P); anemochory (D)</td>
</tr>
<tr>
<td>Rubiaceae (&lt;i&gt;Goprosma&lt;/i&gt;) [18]</td>
<td>infructescence</td>
<td>pollen</td>
<td>&lt;i&gt;Goprosma&lt;/i&gt;*</td>
<td>fruits ± globose drupes, sessile, sometimes in decussate pairs along infructescence stalk</td>
<td>brush (H): wind (P); avichory (D)</td>
</tr>
<tr>
<td>Rutaceae (?&lt;i&gt;Melicope&lt;/i&gt;, ?&lt;i&gt;Fouldenia&lt;/i&gt;, ?&lt;i&gt;Neoschmidia&lt;/i&gt;) [17]</td>
<td>flowers with in situ pollen; bud; ?seeds</td>
<td>leaves, possible pollen</td>
<td>&lt;i&gt;Melicope&lt;/i&gt;*; &lt;i&gt;Neoschmidia&lt;/i&gt; (NC); affinities of &lt;i&gt;Fouldenia&lt;/i&gt; uncertain</td>
<td>Melicope: flowers 4-merous, petals with infolded apices; Neoschmidia: flowers actinomorphic, petals 5, thick, one nerved, ovate-elliptic stamens 10, anthers glabrous</td>
<td>dish bowl (H/U): small insect (P); avichory (D)</td>
</tr>
<tr>
<td>Sapotaceae (&lt;i&gt;Planchnella&lt;/i&gt;) [17]</td>
<td>flower bud with in situ pollen</td>
<td>?leaves, pollen</td>
<td>&lt;i&gt;Planchnella&lt;/i&gt;*</td>
<td>Flower buds ovoid-elliptical, pedicellate, densely hairy with prominent hair bases</td>
<td>bell (H): bees (P); avichory (D)</td>
</tr>
</tbody>
</table>

*Present in modern New Zealand; †recently extinct.
the characteristics of flowers, fruits, cones and seeds from a highly diverse, well-dated Lagerstätte in southern New Zealand with extant relatives [8].

2. Material and methods

Fossils were recovered from a finely laminated biogenic lake deposit that accumulated in Foulden Maar, a small, deep volcanic crater [9]. Fossils include diatom frustules, insects, fish and plant remains. The flora comprises numerous leaf compressions with cuticle, fruits, seeds, wood, pollen and rare flowers. All material is held in the Geology Museum, University of Otago. The site is dated 23 Ma from radiometric ages from maar-associated basalts [9].

The comparison between well-preserved fossil and extant genera used well-defined diagnostic characters for assigning the fossils to modern equivalents. These features have been taken from the appropriate taxonomic authorities and are listed as follows:

- (a) Fossil and (b) living Cunoniaceae (Weinmannia) flowers (generalist insect pollination).
- (c) Fossil and (d) living Alseuosmiaceae (Alseuosmia) flowers (bird pollination).
- (e) Fossil and (f) living Elaeocarpaceae (Elaeocarpus) flowers (generalist insect pollination).
- (g) Fossil (tribe Elytrantheae) and (h) living Loranthaceae (Alepis) flowers (specialist insect pollination).
- (i) Fossil and (j) living Atherospermataceae (Laurelia) achene (wind dispersal).
- (k) Fossil and (l) living Araliaceae (Pseudopanax) berries (small bird dispersal).
- (m) Fossil and (n) living Lauraceae (Beilschmiedia) berries (large bird dispersal).
- (o) Fossil and (p) living Meliaceae (Dysoxylum) capsules (arillate seed dispersal).

Scale bars: a, b, i, j = 2 mm, c–h, k, l = 5 mm, m–p = 10 mm. (Online version in colour.)

Figure 1. Comparison of fossil and modern New Zealand flowers, fruits and seeds. (a) Fossil and (b) living Cunoniaceae (Weinmannia) flowers (generalist insect pollination). (c) Fossil and (d) living Alseuosmiaceae (Alseuosmia) flowers (bird pollination). (e) Fossil and (f) living Elaeocarpaceae (Elaeocarpus) flowers (generalist insect pollination). (g) Fossil (tribe Elytrantheae) and (h) living Loranthaceae (Alepis) flowers (specialist insect pollination). (i) Fossil and (j) living Atherospermataceae (Laurelia) achene (wind dispersal). (k) Fossil and (l) living Araliaceae (Pseudopanax) berries (small bird dispersal). (m) Fossil and (n) living Lauraceae (Beilschmiedia) berries (large bird dispersal). (o) Fossil and (p) living Meliaceae (Dysoxylum) capsules (arillate seed dispersal). Scale bars: a, b, i, j = 2 mm, c–h, k, l = 5 mm, m–p = 10 mm. (Online version in colour.)
in table 1. Many of these assignments have already undergone critical appraisal in other publications (e.g. *Fuchsia, Laurelia, Litsea*). Once identified, using non-reproductive characters where possible, the pollination and dispersal features of the fossils were compared with data for extant-related New Zealand taxa [12–14,26–29] and lists of floral [15] and diaspore [16] reproductive syndrome characteristics.

3. Results

Floral reproductive parts from 12 mainly thermophilic families are present at the site; in most cases, the identity of these reproductive structures is supported further by fossil leaves and/or pollen. The flowers, from 2 to 20 mm diameter, were probably insect pollinated (Cunoniaceae, Elaeocarpaceae, Lauraceae [22], Loranthaceae [17], Meliaceae, Monimiaceae (*Hedyca* [17], Picrodendraceae, Rutaceae, Sapotaceae [17]), but some, such as *Fuchsia* (Onagraceae) [24] and *Alseomusia* (*Alseuosmia*) [17] show bird-pollination syndromes, while *Malloranga* (Euphorbiaceae) [21] was wind pollinated (table 1).

Nineteen families at the site have fossilized diaspores, ranging from 3 to 50 mm in diameter. Many show animal (bird) dispersal features. These include fleshy fruit/cone (e.g. Araliaceae (*Pseudopanax*) [18], Lauraceae [22], Menispermaceae (*Hystryna*) [23], Moraceae, Myrtaceae (*Syzygium*), Podocarpaceae (*Podocarpus*) [25], Rubiaceae) and arils (e.g. Meliaceae (*Dysosylum*) [18], Elaeocarpaceae (*Slovakia*), Euphorbiaceae (*Malloranga* [21], Pittosporaceae, Picrodendraceae). The remainder are either wind dispersed (*Atherospermataceae* (*Laurelia*) [19], Bignoniaceae, Casuarinaceae, Cunoniaceae, Proteaceae, Meliaceae), or display no specialized mode of dispersal (Fabaceae, Myrtaceae (*Metrosideros*), Rutaceae).

Many of these reproductive features show remarkable similarity in appearance with those of extant New Zealand relatives (table 1). For example, strong pollination syndrome conservatism is seen both for generalist insect-pollinated flowers such as *Weinmannia* (figure 1a,b) and *Elaeocarpus* (figure 1c,f), specialist Loranthaceae: *Elytranthe* (figure 1g,h) and bird-pollinated *Alseomusia* (figure 1c,l) and *Fuchsia*. Similarly, conservatism is apparent in the hairy achenes of *Laurelia* (figure 1i,j), small bird-dispersed epigynous berries of *Pseudopanax* (figure 1k,l), large bird-dispersed drupes of *Beilschmiedia* (figure 1m,n) and capsules of *Dysosylum* (figure 1o,p), which contain large, arillate seeds. While preservation limits detailed measurements of many parameters, most of the fossil flowers and diaspores appear remarkably similar to extant relatives (figure 1).

4. Discussion

Empirical evidence for reproductive niche conservatism is extremely rare because of the dearth of appropriate sites and fossil material. Foulden Maar is one of the best global pre-Quaternary Lagerstätten examples for such an investigation because it is dated precisely and contains extremely well-preserved fruits and flowers with petals, anthers and often *in situ* pollen, reproductive organs that are rare globally [30]. Additionally, although all species at Foulden are extinct, most have living relatives in New Zealand, Australia, New Caledonia or South America, allowing explicit comparisons. This contrasts with diverse Eocene-aged Lagerstätten such as Messel and Eckfeld in Germany [31,32] and Laguna del Hunco, Patagonia [33], which contain fossils phylogenetically more distant from possible living relatives.

Using diagnostic criteria, we show that across 23 families and 30 genera of New Zealand forest plants, including insect-, wind- and bird-pollinated flowers and wind- and bird-dispersed propagules, features have remained relatively constant for more than 20 Myr. This demonstrates remarkable reproductive niche conservatism during a period of widespread environmental change in New Zealand. It is therefore unlikely that these persistent reproductive features were sustained by habitat or environmental filtering. During the Late Cenozoic, New Zealand underwent declining temperatures, renewed tectonic activity and significant reconfiguration of terrestrial habitats with associated cyclical temperature and sea-level changes through the Pleistocene glaciations [7]. However, these processes appear to have eliminated plant taxa primarily on the basis of temperature tolerance [7], rather than reproductive syndromes [28].

Changes in pollinator assemblages have caused significant shifts in floral features since the Miocene in other regions. A notable example is the transition from insect to hummingbird pollination in South America where *Iochroma* (Solanaceae) corolla length increased up to sixfold in strongly bird-pollinated species [34]. By contrast, New Zealand’s pollinator assemblage appears to have remained stable, with low diversity of generalist bird pollinators since the Miocene [35,36].

In the New Zealand flora, reproductive conservatism has occurred in lineages with contrasting levels and temporal shifts in richness. For example, Lauraceae and Proteaceae (both over 10 taxa) were highly diverse during the Cenozoic [8,22], but currently have few species (under 3), whereas Rubiaceae and Pittosporaceae remain species rich (both over 20).

Our results indicate that many lineages seem to be highly constrained for reproductive syndromes, this conservatism occurring across all major floral and dispersal types and through periods of substantial environmental change. We find no evidence to support within lineage simplification of floral structures in forest trees and shrubs in New Zealand [28], unless this had occurred by the mid-Cenozoic.

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References


