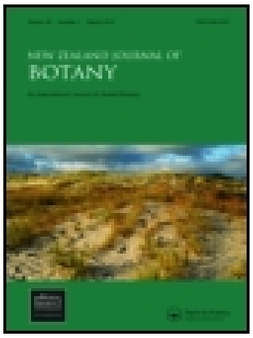

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Evolution of the New Zealand vascular flora: regional and provincial patterns of richness, radiation, and endemism

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Abstract Analysis of species richness, radiation, and endemism in 171 list-regions and 19 botanical provinces of the New Zealand botanical region indicates that the Late Cenozoic radiation of the New Zealand vascular flora has produced divergent phylogenetic trends in regional and provincial floras. Floristic richness at all taxonomic levels is strongly determined by land area. After accounting for area, most exceptionally species-rich list-regions occur immediately east of the South Island main divide, on calcareous substrates in West Nelson, or on several central North Island ranges. Depauperate floras are predominantly in the south on Auckland and Campbell Islands, and four Central Otago and two Southland ranges or basins. Family and genus richness decrease with latitude, but it appears that there has been compensatory radiation from a few herbaceous families in southern island and upland floras, so that species richness shows no latitudinal trend. We present a measure of aggregate regional endemism that is comparable between list-regions and provinces of different floristic richness. Offshore island groups are the most insular floras, with exceptionally high endemism across different taxonomic ranks; northern island floras have high degrees of family and genus endemism and high phylogenetic diversity, while the subantarctic island floras have high species endemism and high radiation. In contrast, mainland botanical provinces all show average levels of regional endemism after correcting for species richness. With the exception of gymnosperms, the most New Zealand-endemic plant groups have the most narrow regional distributions. We discuss latitudinal patterns of endemism among plant groups in terms of dispersal and adaptation. Land protection measures will achieve different phylogenetic outcomes in different landscapes across the New Zealand botanical region.

Keywords New Zealand; species richness; biogeography; endemism; radiation

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INTRODUCTION

Discussion of the biogeography and evolution of the New Zealand vascular flora has focused on regional patterns of endemism and substantial disjunctions in species ranges. There are strong claims for endemic-rich latitudinal centres in northern North Island, northern South Island, and southern South Island, with depauperate zones in southern North Island and the waist of the South Island (Cockayne 1928; Burrows 1965; Wardle 1963, 1991; Druce 1984; McGlone 1985; McGlone et al. 2001). Reported patterns of species disjunctions more or less reinforce this predominant pattern (McGlone 1985; Wardle 1988; Rogers 1989; Heads 1997, 1998). However, when the zones are analysed in detail, their degree of endemism and disjunction vary in terms of boundary position (Rogers 1989; Williams & Courtney 1998; Connor 2002). Biogeographic hypotheses for these patterns have emphasised just one or permutations of tectonics, glaciation, and plant dispersal. Cockayne (1926), Willet (1950), Wardle (1963), and Burrows (1965) suggested that plants tended to become concentrated in refugia due to the disruption of glacial ice and harsh climates. Climo (1975) was first to make extensive use of tectonism to explain biogeographic distributions of, in particular, snails. Panbiogeographic explanations have emphasised tectonic movement of geological terranes (Craw

1989; Heads 1989, 1998; Craw et al. 1999). Further work has debated the biogeographic origins of both the New Zealand flora and the patterns of endemism and disjunction within New Zealand (Raven 1973; Wardle 1978; Pole 1994; Burrows 1998; Lee et al. 2001; McGlone et al. 2001). Lee et al. (2001) characterised the Cenozoic evolution of the flora as a filtering out of characteristically Australian lineages, with compensatory radiation of an upland flora. McGlone et al. (2001) favoured Pleistocene extinctions, speciation, and dispersal and repeated glaciation to explain endemic and disjunct patterns. Using the alpine flora, they have shown that less endemic plant groups have the widest distributions within New Zealand. Trewick & Wallis (2001) have used invertebrate phylogeography and genetic distance to show that patterns of endemism are not consistent with ancient vicariant processes, preferring instead the explanation of disparate responses to late Cenozoic mountain building and glacial dislocation.

There are several ways to gauge the biodiversity value of floras, including species richness, richness adjusted for area, the relative abundance of species, the number of rare or endemic species, species richness at higher taxonomic rank, and phylogenetic diversity. New Zealand's insular biota shows marked variations in the ratio of species to higher taxonomic ranks (Fenner et al. 1997), with particularly striking contrasts between the offshore islands and the mainland, and between coastal or lowland regions and those in the uplands (Rogers & Overton 2000). Fenner et al. (1997) promoted the measurement of phylogenetic diversity (i.e., the distribution of species among higher taxonomic ranks) for assessing priorities and allocating resources for conservation, on the basis that if species are spread across numerous genera and families, a flora is likely to contain more genetic and character diversity than one where species are concentrated in few genera. Polasky et al. (2001) suggested that taxon diversity may be a good surrogate for phylogenetic diversity, but Rodrigues & Gaston (2002) cautioned against this generalisation if the phylogenetic tree is highly unbalanced (highly ramified branches as opposed to monophylic branches in different areas). Since detailed phylogenies for all New Zealand plant lineages will not be available in the foreseeable future, we judge that taxon richness and the ratio of species to higher taxonomic ranks (i.e., taxonomic structure) are both useful current measures of phylogenetic diversity.

Knowledge of regional species pools and taxonomic structure contributes to conservation policy as surrogate measures of ecosystem diversity, phylogenetic diversity, biotic and ecological distinctiveness, and spatial heterogeneity. Assessment of New Zealand biodiversity is advancing on all of these fronts. Recent advances in spatial modelling techniques to quantify and map environmental pattern and distinctiveness (Overton & Leathwick 2001; Leathwick et al. 2003) will need validation against databases of biological richness. Investigations of taxonomic richness and endemism at regional scales (e.g., Wardle 1988; McGlone et al. 2001) are continuing to generate hypotheses regarding ecological and evolutionary processes operating at large geographic scales, which exert control over regional species pools (Rosenzweig 1995; Karlson & Cornell 2002). Understanding of the origins of the New Zealand biota is also being advanced by studies of the fossil record (e.g., Pole 1994; Lee et al. 2001) and elucidation of taxonomic and evolutionary relationships through molecular studies (e.g., Wagstaff & Wardle 1999; Trewick & Wallis 2001). For the flora, molecular work is especially useful since Tertiary and Quaternary records are incomplete and generally biased to woody plants (Wardle 1991).

The debate on New Zealand plant biogeography needs to be advanced beyond numbers of endemic and disjunct species in large, latitudinally defined zones, not least because endemism is a function of sampling area and floristic richness. Divergent patterns of richness, endemism, and radiation have been used previously to extend the concept of regionalism in the flora of southern New Zealand (Rogers & Overton 2000). We now seek to typify gamma-scale biodiversity across the New Zealand botanical region, at regional and provincial scales, by examining measures of richness, endemism, and radiation at various taxonomic ranks and across gradients of land area, species richness, and latitude. We introduce a new measure of endemism that goes beyond that of the simple number of species confined to an area, by compiling measures of the relative ranges of the entire floras of different regions. We focus particularly on the question of whether the Late Cenozoic radiation of the New Zealand flora produced divergent patterns of richness, radiation, and endemism, particularly between the offshore islands and the mainland, with their different potentials for gene pool mixing. Moreover, we ask whether the least New Zealand endemic plant groups show the most widespread distributions within New Zealand, reflecting less environmental specialisation. We assess the relevance of our findings to biodiversity conservation policies for New Zealand.

METHODS

Data collection

Following the methods of Rogers & Overton (2000), we used 173 mostly unpublished vascular plant lists (Table 1) to compile a database of species by list-region for New Zealand, with species' taxonomy standardised against Druce's (1993) list of 2470 New Zealand species. Taxonomic revision of the New Zealand vascular flora has continued since 1993, especially for grass genera which are published in Edgar & Connor (2000). However, many putative taxa included in Druce (1993) have subsequently been formally validated in taxonomic revisions. Overall, we judge the taxonomic changes to be numerically insufficient to significantly influence our analyses of regional or generic patterns of taxonomic richness, radiation, and endemism. While the database provides the most comprehensive coverage of the New Zealand botanical region that has been possible to date (Fig. 1), we acknowledge that it remains incomplete. In particular, species lists from several mainland provinces are concentrated in upland areas, principally because, 1) extensive tracts of native vegetation remain only there, 2) relict vegetation elsewhere is of such small scale as to not provide an ecologically representative flora, and 3) absence of floristic lists of a comprehensive and authoritative nature. The bias toward upland zones may be most acute for Waikato and Canterbury (e.g., in the latter we have no lists representing the extensive northern hills and downlands, the Canterbury Plains Ecological District, the southern Kirkliston Mountains, the Hunter Hills, or the Waitaki River catchment). From the published reports of the Protected Natural Areas Programme (Kelly & Park 1986) we include only those plant lists we believe to be ecologically comprehensive because some lists are based on plot samples only. Of the major off-shore islands of the New Zealand archipelago, our database includes plant lists for the Kermadec, Three Kings, Chatham, Auckland, Campbell, Antipodes, and Snares island groups. The Bounty Islands are devoid of vascular plants and Macquarie Islands are administered by Australia. The large west Nelson and Fiordland provinces are comprehensively represented by list-regions for nine geological substrate-defined areas and four Ecological Districts (McEwen 1987), respectively.

Data analysis

The dataset of 90 011 entries comprised 2249 species, 418 genera, and 135 plant families. Fourteen plant groups were recognised (after Druce 1993; see Table 5). Species richness of list-regions ranged from 9 (White Island) to 842 (Richmond, Gordon, and Bryant Ranges). Two geographical scales of resolution were used to examine patterns of species and taxonomic richness and endemism. Fine-resolution analyses use 171 list-regions (White Island (List 445: 9 species) and the Snares (List 491: 18 species) were excluded from list-region analyses for statistical distortion reasons). For coarse-resolution analyses, each of the 173 list-regions was allotted to 1 of 20 botanical provinces (after Wardle 1991, fig. 6.1 left). These provinces include two that are additional to the 18 of Wardle (1991); they distinguish the upland zones of the axial ranges and mountains of the North and South Islands. However, since our dataset contained no species lists for the Westland botanical province (Westland National Park was included in the South Island axial range province), coarse-resolution analysis is restricted to 19 botanical provinces.

Species richness in relation to area

Differences in the size of floras may be due to differences in land area, environmental heterogeneity, and evolutionary history. Globally, the faunal richness of the earth's continents is closely correlated with their land areas. However, the combined species richness of the continents is much higher than is predicted from this species to area relationship. This is attributed to the biogeographic isolation of the individual continents, which has led to evolution of distinct faunas (Vitousek et al. 1997, fig. 4). After accounting for the effect of area, it has also been shown that the species richness of some faunal groups decreases with distance from the equator (e.g., Lyons & Willig 2002). To seek evidence for such patterns of floristic richness within the New Zealand botanical region, we plotted family, genus, and species richness against log area across the 171 list-regions and the 19 botanical provinces. Using the regression equations, we compared the predicted maximum number of species for the total New Zealand land area with the actual number from this dataset. We highlighted list-regions and botanical provinces falling outside the 95% confidence limits of the regression relationships in order to identify those with higher or lower than expected richness that might be accounted for by environment or evolutionary history. Finally, to look for latitudinal trends in richness at different taxonomic levels, the residuals from the family, genus, and species richness with area equations were regressed against latitude for the 171 list-regions.

Table 1 Species richness, species/area relationships, endemism, and aggregate regional endemism (see Methods) for 171 list-regions and 19 botanical provinces (after Wardle 1991) in New Zealand. For botanical provinces, average values from the list-regions within each are shown. Values for Richness are number of families (F), number of genera (G), number of species (S), and direction (dir.) and rank of the percentage deviance (dev.) (most positive +82 to most negative –76) from the richness predicted by the species-area regression. Values for Regional endemism are the number of species restricted to that list, the number shared with one additional list, the number shared with two additional lists, their sum, the rank order of that sum (from joint lowest = 1 to joint highest = 128), and the rank order of composite species endemism (see Methods (lowest = 1 to highest = 171)). List no., list-region number from dataset used in the present study.

List no.	List-region	Reference (see Appendix 1)	(F, G, S Richness [dir, dev])	Regional endemism Range restricted species (1, 2, 3, sum, rank sum), and rank aggregate endemism	NZ endemism (%[rank])
2	Central North Island andesitic volcanoes	Druce 1992a	101, 246, 644 [+48]	0 ,3 ,2 ,5 ,123 [145]	71[71]
19	Aorangi Range	Druce 1992b	96, 223, 495 [+37]	0 ,0 ,3 ,3 ,98 [102]	69[55]
24	Northwest Nelson coast	Druce 1992c	95, 216, 391 [+79]	1 ,1 ,1 ,3 ,98 [96]	62[19]
28	Mount Stokes	Druce 1992d	50, 93, 172 [–29]	0 ,2 ,1 ,3 ,98 [36]	80[138]
29	Moa Park, Abel Tasman National Park	Druce 1992e	52, 107, 192 [+57]	0 ,0 ,0 ,0 ,36 [18]	77[114]
46	Pukeamaru Scenic Reserve, Raukumara Range	Druce 1992f	83, 175, 297 [–22]	0 ,0 ,1 ,1 ,62 [46]	73[85]
51	Mount Tauhara	Druce 1992g	55, 107, 185 [–5]	0 ,0 ,0 ,0 ,36 [10]	74[92]
52	Paeroa Range	Druce 1992h	70, 141, 239 [–23]	0 ,0 ,1 ,1 ,62 [33]	65[35]
55	Mt Tunurangi, Ahimanawa Range	Druce 1992i	39, 60, 94 [–82]	0 ,0 ,0 ,0 ,36 [1]	78[118]
59	White Cliffs area, north Taranaki	Druce & Ogle 1992a	92, 180, 305 [–2]	0 ,1 ,1 ,2 ,82 [57]	67[46]
60	Puketoi Range	Druce 1992j	57, 96, 152 [–68]	0 ,0 ,1 ,1 ,62 [4]	78[122]
62	Upper Kaingaroa Plains	Druce 1992k	63, 146, 288 [–49]	0 ,0 ,1 ,1 ,62 [65]	65[36]
76	Maungaharuru Range	Druce 1992l	96, 230, 545 [+49]	1 ,1 ,1 ,3 ,98 [115]	73[87]
77	Kaimanawa Mountains including upper Moawhango	Druce 1992m	86, 208, 571 [+27]	0 ,4 ,1 ,5 ,123 [139]	76[112]
81	Wairarapa Taipos	Druce 1992n	93, 214, 446 [+17]	1 ,0 ,1 ,2 ,82 [91]	66[41]
82	Hicks Bay, East Cape	Druce 1992o	93, 195, 298 [+13]	0 ,1 ,0 ,1 ,62 [62]	65[33]
87	Rainbow Mountain (Mt Maungakakaramea)	Druce & Ogle 1992b	57, 118, 190 [+8]	0 ,0 ,1 ,1 ,62 [25]	61[15]
90	Mount Egmont	Druce 1992p	116, 270, 666 [+75]	5 ,0 ,1 ,6 ,133 [149]	68[51]
93	Waitaanga Plateau and Waitaanga State Forest	Druce 1992q	68, 129, 217 [–67]	0 ,0 ,0 ,0 ,36 [11]	72[82]
104	Mt St Patrick, St James Range, north Canterbury	Druce & Simpson 1992	54, 135, 335 [+44]	0 ,1 ,4 ,5 ,123 [99]	84[159]
106	Black Birch Range	Druce 1992r	59, 133, 283 [–27]	0 ,0 ,1 ,1 ,62 [69]	80[136]
107	Ben More, Chalk Range	Druce 1992s	93, 216, 565 [+66]	2 ,8 ,7 ,17 ,163 [158]	74[95]
108	Kauaeranga Valley	Druce 1992t	113, 247, 504 [+73]	0 ,3 ,3 ,6 ,133 [130]	64[24]
110	Red Hills, Wairau Valley	Druce 1992u	57, 123, 255 [+20]	0 ,5 ,1 ,6 ,133 [71]	76[113]
111	Inland Kaikoura Range	Druce 1992v	65, 159, 446 [+1]	4 ,5 ,8 ,17 ,163 [159]	83[154]
116	Maungaraki Range	Druce 1992w	77, 152, 286 [–64]	0 ,1 ,0 ,1 ,62 [49]	72[78]
118	South Wellington Coast	Druce 1992x	109, 263, 577 [+83]	0 ,5 ,6 ,11 ,153 [146]	65[34]
119	Northern Ruahine Range	Druce 1992y	100, 236, 645 [+69]	0 ,1 ,1 ,2 ,82 [135]	76[111]
119.1	Central Ruahine Range	Druce 1992y	94, 221, 603 [+58]	1 ,1 ,0 ,2 ,82 [123]	77[115]
119.2	Southern Ruahine Range	Druce 1992y	93, 202, 448 [+36]	1 ,0 ,0 ,1 ,62 [74]	74[96]
122	Hills south-west of Cape Campbell	Druce 1992z	69, 144, 220 [–58]	3 ,1 ,1 ,5 ,123 [83]	62[22]
125	Lakes Wairarapa & Onoke	Druce 1992aa	65, 119, 196 [+81]	1 ,0 ,1 ,2 ,82 [58]	51[2]
133	Upper Wairau – Branch River	Druce 1992ab	83, 211, 711 [+65]	5 ,5 ,11 ,21 ,164 [167]	81[142]

Table 1 (*continued*)

List no.	List-region	Reference (see Appendix 1)	(F, G, S Richness [dir, dev])	Regional endemism Range restricted species (1, 2, 3, sum, rank sum), and rank aggregate endemism	NZ endemism (%[rank])
134.1	Tararua Range	Druce 1992ac	100, 245, 640 [+56]	5 ,0 ,2 ,7 ,139 [143]	72[80]
134.2	Rimutaka Range	Druce 1992ac	102, 229, 545 [+51]	0 ,1 ,2 ,3 ,98 [111]	69[52]
134.3	Western Wellington Hills	Druce 1992ac	88, 182, 356 [–39]	0 ,0 ,0 ,0 ,36 [48]	65[37]
142	Kaihoka Lake, NW Nelson	Druce 1992ad	69, 131, 199 [+82]	0 ,0 ,0 ,0 ,36 [17]	62[23]
150	Wither Hills	Druce 1992ae	56, 106, 179 [–75]	0 ,0 ,0 ,0 ,36 [20]	64[28]
152	Waewaepa Range	Druce 1992af	56, 97, 168 [–59]	0 ,0 ,0 ,0 ,36 [2]	74[97]
153	Oringi Clearing and Dannevirke area	Druce 1992ag	72, 138, 251 [+4]	0 ,0 ,0 ,0 ,36 [34]	74[93]
160	Lake Tennyson, Mount Princess	Druce 1992ah	60, 137, 352 [+31]	0 ,3 ,3 ,6 ,133 [113]	84[162]
161	Central Hawke's Bay	Druce 1992ai	94, 199, 371 [–60]	1 ,2 ,2 ,5 ,123 [106]	66[43]
164	Lower Turakina Valley	Druce 1992aj	76, 132, 217 [–48]	0 ,0 ,0 ,0 ,36 [13]	72[77]
171	Mataroa	Druce 1992ak	67, 123, 226 [+54]	0 ,0 ,0 ,0 ,36 [21]	74[91]
175	Lewis Pass	Druce 1992al	76, 175, 450 [+33]	1 ,0 ,2 ,3 ,98 [98]	80[137]
178	Herangi Range	Druce 1992am	87, 180, 335 [–34]	0 ,0 ,0 ,0 ,36 [47]	70[65]
179	Pirongia Mountain	Druce 1992an	89, 187, 403 [+15]	0 ,0 ,1 ,1 ,62 [75]	66[38]
185	Spenser Mountains	Druce 1992ao	57, 141, 367 [–8]	0 ,0 ,1 ,1 ,62 [86]	86[169]
190	Surville Cliffs	Druce et al. 1992a	62, 108, 149 [+76]	1 ,7 ,6 ,14 ,156 [94]	58[9]
200	Richmond, Gordon, Bryant Ranges	Druce 1992ap	113, 278, 842 [+74]	10 ,15 ,10 ,35 ,169 [171]	75[102]
208	Denniston and Stockton Plateaux	Druce 1992aq	56, 124, 232 [–61]	3 ,1 ,2 ,6 ,133 [89]	75[101]
215	Mt Burnett	Druce 1992ar	57, 116, 200 [+70]	1 ,1 ,1 ,3 ,98 [45]	76[109]
219	Kaimai Range	Druce et al. 1992d	94, 215, 462 [+21]	0 ,1 ,1 ,2 ,82 [95]	68[49]
236	Waimarino Stream and Erua	Druce & Ogle 1992c	66, 113, 183 [+80]	0 ,1 ,0 ,1 ,62 [23]	72[79]
242	Haldon Hills	Druce et al. 1992b	69, 138, 235 [–66]	1 ,1 ,0 ,2 ,82 [56]	69[54]
254	Upper Saxton	Druce 1992as	47, 116, 289 [–42]	0 ,0 ,4 ,4 ,108 [97]	86[168]
257	Mountains west of Upper Glenroy	Druce 1992at	58, 132, 341 [+5]	0 ,1 ,0 ,1 ,62 [82]	84[161]
269	Rangitoto Range	Druce et al. 1992c	50, 92, 159 [–80]	0 ,0 ,0 ,0 ,36 [3]	70[69]
274	Editor Hill-Lookout Peak	Druce & Burke 1992	47, 92, 163 [+84]	0 ,2 ,1 ,3 ,98 [19]	75[103]
286	Aniseed and Puhipuhi Valleys, Marlborough	Druce 1992au	74, 139, 252 [+26]	1 ,2 ,2 ,5 ,123 [68]	79[125]
288	Ngakawau Gorge	Druce 1992av	68, 127, 214 [+19]	0 ,1 ,0 ,1 ,62 [35]	69[58]
290	Cape Foulwind	Druce 1992aw	51, 77, 99 [–83]	0 ,1 ,0 ,1 ,62 [9]	62[18]
299	Upper Hope Valley, south Nelson	Druce 1992ax	53, 107, 181 [–16]	0 ,0 ,0 ,0 ,36 [29]	73[86]
310	Ahipara Gumfields-Tauroa Peninsula	Druce 1992ay	97, 202, 354 [+14]	3 ,2 ,4 ,9 ,144 [118]	61[17]
323	Omaui Peninsula	Rance & Druce 1992	72, 142, 247 [+12]	0 ,4 ,1 ,5 ,123 [67]	69[59]
325	Tawarau State Forest	Ogle & Druce 1992	82, 169, 323 [+35]	0 ,0 ,1 ,1 ,62 [42]	68[50]
331	Hauhungaroa Range	Druce 1992az	89, 205, 437 [–11]	0 ,1 ,0 ,1 ,62 [79]	69[61]
332	Raukumara Range	Druce 1992ba	98, 222, 514 [+0]	3 ,3 ,2 ,8 ,141 [124]	77[117]
333	Kaweka Range	Druce 1992bb	95, 232, 616 [+53]	0 ,0 ,2 ,2 ,82 [131]	75[99]
334	NW Nelson – Mafic and Ultramafic Rocks	Druce 1992bc	59, 111, 214 [–26]	1 ,4 ,1 ,6 ,133 [78]	81[143]
335	NW Nelson Eastern Granites	Druce 1992bd	67, 145, 338 [–28]	2 ,1 ,1 ,4 ,108 [93]	78[124]

Table 1 (*continued*)

List no.	List-region	Reference (see Appendix 1)	(F, G, S Richness [dir, dev])	Regional endemism Range restricted species (1, 2, 3, sum, rank sum), and rank aggregate endemism	NZ endemism (%[rank])
336	NW Nelson non-calcareous sedimentary rocks	Druce 1992be	81, 203, 612 [+46]	5 ,6 ,5 ,16 ,161 [163]	82[146]
337	NW Nelson eastern sedimentary rocks	Druce 1992bf	83, 203, 582 [+78]	2 ,6 ,3 ,11 ,153 [154]	84[160]
338	NW Nelson Tertiary calcareous sedimentary rocks	Druce 1992bg	78, 187, 578 [+72]	8 ,3 ,3 ,14 ,156 [164]	83[155]
339	NW Nelson indurated limestones	Druce 1992bh	58, 132, 371 [+9]	0 ,4 ,3 ,7 ,139 [125]	88[170]
340	NW Nelson western granites	Druce 1992bi	76, 189, 554 [+25]	4 ,2 ,3 ,9 ,144 [153]	80[133]
341	NW Nelson eastern sedimentary rocks (non-calcareous)	Druce 1992bj	57, 137, 341 [–18]	2 ,2 ,3 ,7 ,139 [119]	86[167]
342	NW Nelson Central sedimentary & volcanic rocks	Druce 1992bk	77, 193, 633 [+60]	4 ,7 ,4 ,15 ,159 [165]	83[157]
343	Margins of Lake Wakatipu	Druce et al. 1992e	71, 147, 309 [–14]	0 ,0 ,2 ,2 ,82 [63]	75[108]
344	Kawarau and Cromwell Gorges	Druce et al. 1992e	56, 111, 208 [–65]	0 ,1 ,1 ,2 ,82 [51]	80[129]
345	Eyre Mountains	Druce et al. 1992e	81, 200, 707 [+61]	6 ,6 ,4 ,16 ,161 [166]	82[151]
346	Thomson Mountains	Druce et al. 1992e	68, 164, 454 [+18]	0 ,3 ,2 ,5 ,123 [120]	80[132]
347	Livingstone Mountains	Druce et al. 1992e	64, 160, 407 [–19]	1 ,0 ,1 ,2 ,82 [105]	80[130]
348	Forbes Mountains	Druce et al. 1992e	63, 157, 408 [+6]	0 ,0 ,0 ,0 ,36 [81]	80[139]
349	Richardson Mountains	Druce et al. 1992e	71, 171, 527 [+22]	0 ,0 ,2 ,2 ,82 [121]	80[131]
350	Harris Mountains	Druce et al. 1992e	62, 149, 429 [–15]	1 ,0 ,1 ,2 ,82 [117]	85[165]
351	Mt Alta, Buchanan Peaks – Lake Wanaka area	Druce et al. 1992e	75, 169, 430 [+42]	0 ,1 ,2 ,3 ,98 [112]	80[134]
352	Crown Range	Druce et al. 1992e	44, 111, 294 [–45]	2 ,1 ,1 ,4 ,108 [107]	85[166]
355	Hector Mountains	Druce et al. 1992e	71, 169, 503 [+40]	1 ,0 ,1 ,2 ,82 [137]	83[156]
356	Nevis Valley	Druce et al. 1992e	50, 117, 281 [–21]	0 ,3 ,1 ,4 ,108 [80]	80[140]
357	Garvie Mountains	Druce et al. 1992e	77, 189, 591 [+59]	0 ,4 ,6 ,10 ,149 [152]	83[158]
358	Old Woman and Carrick Ranges	Druce et al. 1992e	60, 143, 361 [–31]	0 ,1 ,1 ,2 ,82 [109]	82[148]
359	Umbrella Mountains	Druce et al. 1992e	81, 194, 544 [+45]	0 ,3 ,2 ,5 ,123 [134]	80[128]
360	Old Man Range	Druce et al. 1992e	68, 156, 397 [+10]	1 ,2 ,1 ,4 ,108 [133]	81[141]
361	Pisa Range	Druce et al. 1992e	71, 165, 436 [–6]	2 ,2 ,2 ,6 ,133 [141]	84[163]
362	Dunstan and Cairnmuir mountains	Druce et al. 1992e	70, 155, 394 [–35]	2 ,1 ,1 ,4 ,108 [127]	82[152]
363	Central Otago intermontane lowlands (Upper Clutha Valley to Strath Taieri)	Druce et al. 1992e	52, 108, 205 [–77]	1 ,3 ,1 ,5 ,123 [84]	74[94]
364	Rough Ridge	Druce et al. 1992e	41, 96, 186 [–81]	0 ,0 ,0 ,0 ,36 [43]	82[149]
365	Lammermoor and Lammerlaw Ranges	Druce et al. 1992e	52, 115, 240 [–72]	0 ,0 ,0 ,0 ,36 [53]	80[126]
366	Rock and Pillar Range	Druce et al. 1992e	49, 110, 221 [–74]	0 ,0 ,0 ,0 ,36 [50]	80[135]
401	d'Urville Island	Ogle 1983	97, 222, 433 [+32]	0 ,4 ,3 ,7 ,139 [103]	64[26]
402	Rotorua Lakes Ecological District	Ecroyd et al. 1990	102, 243, 571 [+34]	0 ,5 ,4 ,9 ,144 [138]	62[21]
405	Otago Peninsula	Johnson 1991	84, 196, 361 [+16]	1 ,2 ,0 ,3 ,98 [90]	64[25]
411	Stewart Island	Wilson 1987	91, 224, 569 [+28]	19 ,8 ,8 ,35 ,169 [169]	72[75]
412	Banks Ecological District	Wilson 1992	96, 232, 520 [+23]	7 ,3 ,1 ,11 ,153 [148]	68[48]
413	Waitakere Range	Gardner 1982	113, 250, 509 [+55]	4 ,1 ,3 ,8 ,141 [144]	61[16]
414	Farewell Spit	Bulfin 1982	51, 106, 148 [–69]	0 ,1 ,0 ,1 ,62 [27]	52[3]
415	Victoria Forest Park	Wilson 1985	78, 190, 497 [–4]	0 ,0 ,0 ,0 ,36 [108]	81[144]

Table 1 (*continued*)

List no.	List-region	Reference (see Appendix 1)	(F, G, S Richness [dir, dev])	Regional endemism Range restricted species (1, 2, 3, sum, rank sum), and rank aggregate endemism	NZ endemism (%[rank])
416	Old Man Range, Canterbury	Molloy 1984	56, 127, 281 [–30]	2 ,1 ,0 ,3 ,98 [77]	81[145]
417	Rangitoto Island	Gardner 1987	81, 151, 210 [–38]	0 ,0 ,1 ,1 ,62 [41]	58[10]
419	Mount Aspiring National Park	Mark 1977	79, 191, 518 [–7]	0 ,3 ,1 ,4 ,108 [132]	82[153]
420	Waima Forest	Bellingham 1985o	76, 144, 253 [–44]	0 ,0 ,1 ,1 ,62 [38]	73[85]
421	Te Urewera National Park	Shaw 1990	105, 254, 635 [+43]	0 ,1 ,1 ,2 ,82 [126]	71[73]
422	Mt Cook/Aoraki National Park	Wilson 1976	65, 159, 462 [+3]	1 ,2 ,2 ,5 ,123 [128]	82[150]
423	Karamea District	Wardle & Buxton 1985	95, 220, 523 [+29]	2 ,3 ,1 ,6 ,133 [129]	73[89]
424	Waimakariri Basin	Burrows 1962	94, 239, 746 [+63]	3 ,4 ,8 ,15 ,159 [168]	80[127]
425	Fanal Island	Wright 1980; Cameron & Wright 1990	65, 111, 141 [+71]	0 ,2 ,1 ,3 ,98 [44]	57[8]
427	Houtu Forest	Bellingham 1985b	66, 107, 167 [–43]	0 ,0 ,0 ,0 ,36 [5]	71[72]
428	Maungataniwha Forest	Bellingham 1985g	59, 95, 160 [–73]	0 ,0 ,0 ,0 ,36 [6]	69[64]
429	Three Kings Islands	Oliver 1948; Cameron et al. 1987	65, 108, 141 [–46]	7 ,0 ,0 ,7 ,139 [88]	60[14]
430	Pukenui Forest	Bellingham 1985j	73, 120, 199 [–17]	0 ,0 ,0 ,0 ,36 [16]	69[62]
431	Kaihu Forest	Bellingham 1985c	67, 125, 217 [–52]	0 ,0 ,0 ,0 ,36 [22]	69[57]
432	Opua Forest	Bellingham 1985i	65, 113, 176 [–37]	0 ,0 ,0 ,0 ,36 [14]	66[45]
433	Tangihua Forest	Bellingham 1985n	78, 143, 234 [–40]	0 ,0 ,0 ,0 ,36 [26]	70[66]
434	Herekino Forest	Bellingham 1985a	74, 139, 226 [–50]	0 ,0 ,2 ,2 ,82 [40]	72[74]
435	Warawara Forest	Bellingham 1985q	92, 182, 331 [–10]	1 ,0 ,2 ,3 ,98 [66]	66[39]
436	Puketi Forest	Bellingham 1985k	88, 190, 348 [–1]	2 ,0 ,1 ,3 ,98 [85]	66[44]
437	Raetea Forest	Bellingham 1985l	75, 137, 230 [–57]	0 ,0 ,0 ,0 ,36 [24]	72[76]
438	Omahuta Forest	Bellingham 1985h	81, 149, 243 [–51]	0 ,0 ,1 ,1 ,62 [39]	66[42]
439	Mataraua Forest	Bellingham 1985f	65, 119, 192 [–70]	0 ,0 ,0 ,0 ,36 [12]	69[60]
440	Marlborough Forest	Bellingham 1985e	75, 141, 240 [–41]	0 ,0 ,0 ,0 ,36 [32]	69[53]
441	Mangahakia Forest	Bellingham 1985d	71, 130, 205 [–55]	0 ,0 ,0 ,0 ,36 [15]	73[83]
442	Waipoua Forest	Bellingham 1985p	99, 209, 395 [+30]	1 ,2 ,2 ,5 ,123 [104]	65[31]
443	Russell Forest	Bellingham 1985m	84, 166, 295 [–36]	0 ,0 ,1 ,1 ,62 [52]	65[32]
446	Westland National Park	Wardle 1975	94, 236, 597 [+47]	0, 1, 3, 4, 108 [136]	75[100]
447	Little Barrier Island	Hamilton & Atkinson 1961	100, 203, 352 [+52]	1, 1, 0, 2, 82 [92]	64[27]
448	Auckland Islands	Johnson & Campbell 1975	45, 92, 178 [–78]	6, 19, 13, 38, 170 [156]	69[56]
450	Great Barrier Island	Bartlett & Gardner 1983; Wright & Cameron 1986; Cameron et al. 2002	114, 264, 561 [+68]	3, 4, 8, 15, 159 [162]	59[11]
451	Northern Horowhenua	Duguid 1990	104, 236, 494 [+24]	0, 2, 2, 4, 108 [114]	62[20]
452	Cuvier	Beever et al. 1969;	Wright 1981	75, 121, 165 [+64]	0, 0, 0, 0, 36 [31]
453	Opotiki – East Cape	Heginbotham & Esler 1985	113, 233, 485 [–20]	1, 2, 1, 4, 108 [116]	65[30]
459	Waitutu Ecological District	Mark et al. 1988	54, 94, 146 [–79]	0, 0, 0, 0, 36 [8]	73[88]
460	Upukeroa Ecological District and wetlands of the Te Anau Basin	Rance 1991a	48, 91, 150 [–84]	0, 0, 0, 0, 36 [7]	70[67]
461	Longwood Ecological District	Rance 1997a	74, 162, 346 [–33]	0, 2, 0, 2, 82 [70]	74[90]

Table 1 (*continued*)

List no.	List-region	Reference (see Appendix 1)	(F, G, S Richness [dir, dev])	Regional endemism Range restricted species (1, 2, 3, sum, rank sum), and rank aggregate endemism	NZ endemism (%[rank])
462	Hokonui Ecological District	Rance 1997b	75, 169, 340 [–25]	2, 1, 0, 3, 98 [72]	75[107]
468	Matemateaonga Ecological District	Ravine 1996	92, 186, 375 [–63]	1, 0, 1, 2, 82 [61]	67[47]
475	Subalpine Blue Mountains	Rance 1991b	51, 104, 185 [–47]	0, 0, 0, 0, 36 [28]	78[119]
477	Mararoa Valley, Southland	Johnson & Lee 1993	66, 142, 301 [+38]	0, 0, 0, 0, 36 [55]	75[105]
478	Alpine Takitimu Mountains, Southland	Rance 1997c	45, 105, 215 [–32]	0, 1, 0, 1, 62 [59]	85[164]
479	Campbell Island	Given & Meurk 1977	42, 73, 126 [–85]	2, 21, 12, 35, 169 [142]	72[81]
480	Chatham Islands	de Lange et al. 1999	80, 186, 399 [–24]	28, 8, 6, 42, 171 [170]	55[5]
481	Moawhango Ecological District	Rogers 1993	98, 245, 739 [+67]	0, 7, 3, 10, 149 [161]	75[106]
482	Taumaranui Ecological District	Bibby et al. 2000	90, 179, 380 [–53]	0, 1, 0, 1, 62 [64]	70[68]
484	Te Anau E. D.	Rance 2001	91, 238, 725 [+62]	2, 3, 5, 10, 149 [160]	78[121]
485	Darran E. D.	Rance 2001	87, 225, 602 [+39]	1, 1, 3, 5, 123 [140]	76[110]
486	Doubtful E. D.	Rance 2001	88, 211, 580 [+7]	3, 1, 6, 10, 149 [150]	78[120]
487	Preservation E. D.	Rance 2001	87, 214, 528 [–3]	3, 2, 5, 10, 149 [147]	74[98]
488	Kermadecs	Sykes 1977; Sykes & West 1996	52, 87, 114 [–76]	19, 6, 2, 27, 166 [157]	42[1]
489	Poor Knights Islands	de Lange & Cameron 1999	83, 151, 232 [+77]	1, 3, 2, 6, 133 [87]	56[7]
490	Antipodes Islands	Rance 2003	28, 45, 62 [–86]	0, 2, 11, 13, 154 [54]	55[4]
492	Southland Plains Ecological District	Walls & Rance 2003	88, 186, 368 [–54]	1, 1, 4, 6, 133 [101]	66[40]
493	South Westland	Wardle 1979	93, 215, 526 [+2]	0, 2, 1, 3, 98 [122]	75[104]
494	Te Moehau, Coromandel	Gardner & Smith-Dodsworth 1984; McCraith 2002	75, 155, 303 [–9]	1, 0, 0, 1, 62 [60]	71[70]
495	Mt Somers, Canterbury	Druce & Molloy 1992a	67, 156, 398 [+50]	0, 0, 0, 0, 36 [76]	78[123]
496	Winterslow Range, Canterbury	Druce & Molloy 1992b	39, 85, 161 [–71]	0, 0, 0, 0, 36 [37]	89[171]
497	Maungatautari Mountain Scenic Reserve	Clarkson 2002	81, 147, 248 [–13]	0, 0, 1, 1, 62 [30]	69[63]
498	Poutu Peninsula, Kaipara Harbour	Cameron et al. 2001	81, 159, 251 [–62]	1, 1, 3, 5, 123 [73]	60[13]
499	North Cape	Cameron & Jones 1996	92, 192, 314 [+41]	5, 12, 10, 27, 166 [155]	55[6]
500	Two Thumb Range	Druce & Molloy 1992c	76, 176, 503 [+11]	3, 5, 3, 11, 153 [151]	82[147]
501	Valleys of upper Waitaki River	Macmillan 1979; Woolmore 2003	59, 130, 331 [–56]	0, 2, 5, 7, 139 [110]	77[116]
502	Hunua Ranges, Auckland	Gardner & Dakin 1989	105, 213, 412 [–12]	1, 0, 4, 5, 123 [100]	64[29]

Table 1 (*continued*)

List no.	Botanical province	Reference (see Appendix 1)	(F, G, S Richness [dir, dev])	Regional endemism Range restricted species (1, 2, 3, sum, rank sum), and rank aggregate endemism	NZ endemism (%[rank])
1	Northland		116, 282, 654 [–3]	35, 43, 33, 111, 15 [10]	62[3]
2	Auckland		124, 309, 817 [5]	16, 40, 42, 98, 14 [9]	64[4]
3	Volcanic plateau		123, 323, 1024 [3]	1, 26, 43, 70, 11 [11]	71[9]
4	Gisborne		122, 306, 864 [–4]	2, 7, 31, 40, 4 [7]	69[8]
5	Taranaki		117, 284, 761 [–6]	6, 4, 5, 15, 2 [5]	68[7]
6	Southern North Island		121, 322, 1024 [2]	7, 23, 21, 51, 7 [13]	72[11]
7	Crests of North Island axial ranges		118, 305, 1017 [–2]	11, 20, 35, 66, 10 [14]	75[12]
8	Sounds-east Nelson		101, 242, 526 [9]	0, 7, 7, 14, 1 [2]	67[5]
9	West Nelson		116, 311, 1165 [7]	79, 51, 42, 172, 19 [19]	77[14]
11	Fiordland		97, 263, 890 [–5]	15, 17, 33, 65, 9 [8]	77[13]
12	Marlborough		119, 315, 1186 [8]	51, 53, 51, 155, 17 [18]	78[17]
13	Canterbury		110, 302, 1148 [6]	18, 48, 55, 121, 16 [16]	78[16]
14	Otago		101, 284, 1085 [–1]	48, 67, 51, 166, 18 [17]	79[18]
15	Southland		101, 265, 923 [4]	4, 35, 45, 84, 12 [12]	78[15]
16	South Island axial mountains		103, 275, 1052 [1]	6, 34, 55, 95, 13 [15]	80[19]
17	Rakiura (Stewart Island)		92, 225, 573 [–7]	20, 17, 14, 51, 7 [6]	72[10]
18	Kermadec Islands		52, 87, 114 [10]	19, 8, 3, 30, 3 [1]	42[1]
19	Chatham Islands		80, 186, 399 [–8]	28, 13, 6, 47, 5 [4]	55[2]
20	Subantarctic islands		49, 104, 213 [–9]	33, 17, 7, 57, 8 [3]	68[6]

Taxonomic richness (radiation)

Given the highly skewed distribution of species across genera in our typically island flora (Fenner et al. 1997), there has been wide differential success of lineages in diversifying in response to late Cenozoic environmental change. Further, a flora with species distributed across numerous genera and families is likely to contain more genetic and character diversity than one in which the same number of species is concentrated in fewer genera or families (Fenner et al. 1997). Therefore, the distribution of species among higher taxa or ranks is a measure of phylogenetic diversity. However, larger floras have a higher probability of containing genera and families that are more speciose, due to greater opportunities for local speciation or colonisation, and this will influence mean genus and family size (Fenner et al. 1997). To compare regional floras of different sizes on an equable basis, we used a process of rarefaction, which simulates a fixed number of species by random sampling of individuals from each flora. In each list-region, we repeatedly selected at random, without replacement, a fixed number of species equal to the size of the smallest of the 171 list-region floras (i.e., 62 species; Antipodes Islands). For botanical provinces, we repeatedly selected 114 species at random, equating to the size of the smallest, Kermadec Islands, flora. Each flora was sampled 2000 times, and each time the number of plant groups, families, and genera in the sample was recorded. The average across the 2000 samples was taken for each flora. Then, to identify floras with exceptionally high or low radiation, species-per-family and species-per-genus ratios were calculated from the rarefaction averages and regressed against the species richness of list-regions and botanical provinces. Regions falling outside the confidence limits of the regressions were identified. Residual variation in species-per-genus and species-per-family ratios from the regression on species richness were ranked and tabulated. To identify latitudinal trends in radiation, we regressed species-per-family and species-per-genus ratios on the latitude of the 171 list-regions. Finally, to determine whether radiation may have compensated for a loss of families and genera at higher latitudes in the late Cenozoic (Lee et al. 2001), we regressed species-per-genus ratios against the residuals of regressions of family and genus-richness on land area, which we

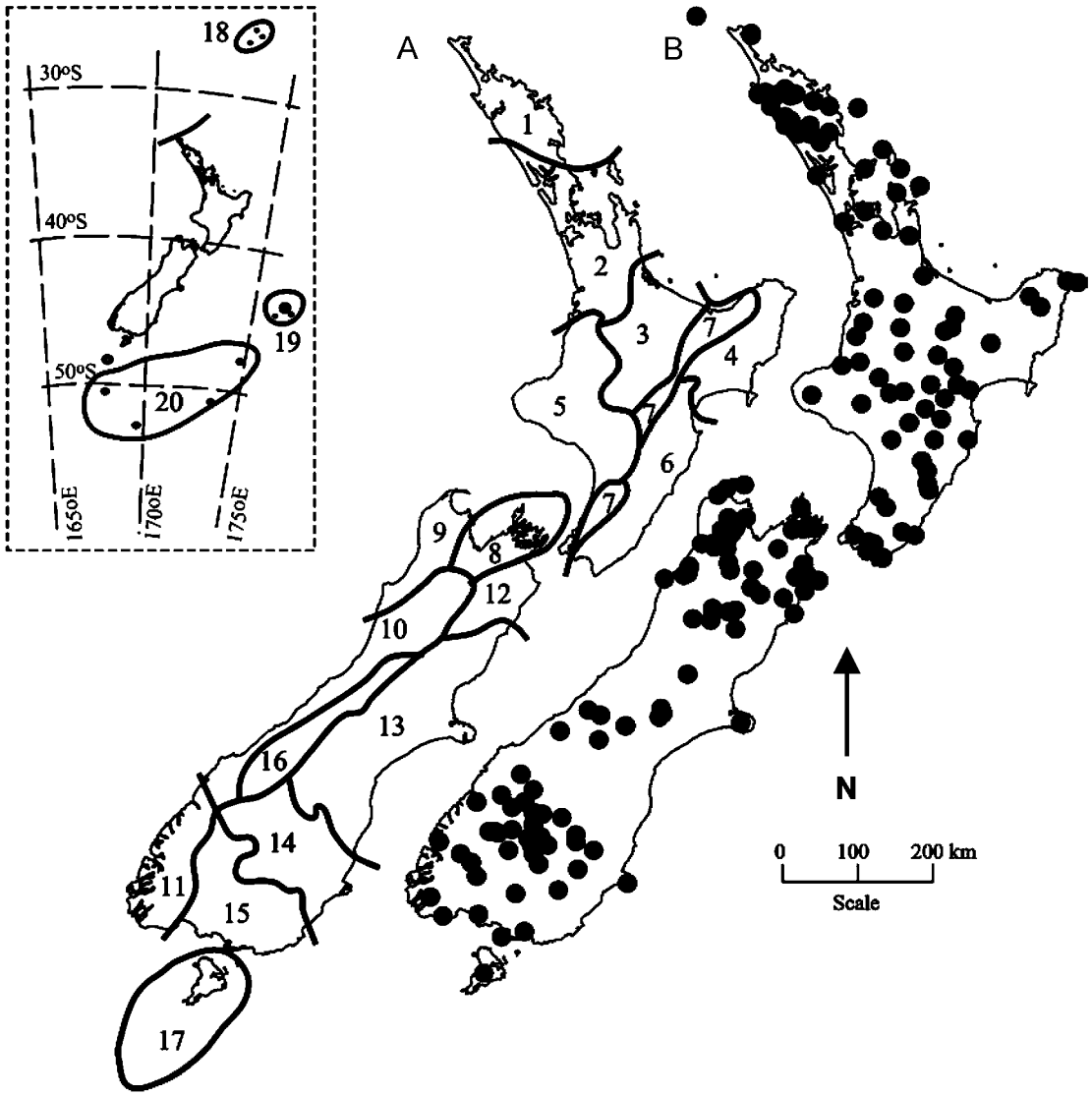

Fig. 1 **A**, Twenty coarse-scale botanical provinces (after Wardle 1991, fig. 6.1 left) and **B**, 171 fine-scale list-regions (centroids only), used to analyse patterns of taxonomic richness, endemism, and radiation in New Zealand. 1, Northland; 2, Auckland; 3, Volcanic Plateau; 4, Gisborne; 5, Taranaki; 6, southern North Island; 7, North Island axial ranges; 8, Sounds-east Nelson; 9, West Nelson; 10, Westland; 11, Fiordland; 12, Marlborough; 13, Canterbury; 14, Otago; 15, Southland; 16, South Island axial mountains; 17, Rakiura; 18, Kermadec Islands; 19, Chatham Islands; 20, Subantarctic islands.

calculated above. A negative relationship between radiation and family and genus-richness would be evidence for compensatory radiation.

Endemism

Regional endemism may result from radiation in compact landscapes with steep environmental gradients, from isolation-driven evolution, from the survival of relict species from previous, more widespread environments, or from recent immigration. Regional endemism confers floristic distinctiveness, and is an important criterion for determining optimum design for conservation units. We compiled three indices of endemism for list-regions and botanical provinces, namely 1) traditional range-restricted endemism, which focuses only on those species that

have smallest ranges, 2) aggregate regional endemism, and 3) average aggregate regional endemism (Table 1). For range-restricted endemism (Index 1), we computed the number of species restricted to each list, the number shared with one additional list, the number shared with two additional lists, and their sum (we set an arbitrary limit of two additional list-regions). The aggregate regional endemism indices (2 and 3) are more comprehensive measures of endemism, because they take account of the distributional ranges of all families, genera, and species in each list-region and botanical province (i.e., aggregate endemism across the full list). For Index 2, the inverse of the number of list-regions containing each species was calculated and summed for all the species in each list. Since larger floras will tend to contain more endemics, neither range-restricted endemism nor aggregate regional endemism may be validly compared between floras of different size. We therefore derived Index 3 (average aggregate regional endemism, which may be validly compared between floras of different size) by dividing aggregate regional endemism by the number of taxonomic entities in that list.

We used regression to compare the indices of traditional range-restricted endemism (Index 1) and aggregate regional endemism of species (Index 2) across the 171 list-regions and 19 botanical provinces. Next, to examine the relationship between regional endemism of species and New Zealand endemism across list-regions and botanical provinces, we regressed the average aggregate regional endemism of species (Index 3) on the percentage of species that are New Zealand endemics. We then sought evidence for latitudinal trends in regional endemism at different taxonomic levels (i.e., average aggregate regional endemism of families, genera, and species) across list-regions and botanical provinces. Finally, we examined relationships between average aggregate regional endemism and floristic richness at the three different taxonomic levels.

In the alpine flora, McGlone et al. (2001) found that the New Zealand plant groups that were least endemic had the widest distribution within New Zealand. To determine whether this relationship holds for most of the flora, we calculated the third index of regional endemism as a surrogate for distributional restrictedness, for each of the 14 plant groups recognised in the study. This index, average aggregate regional endemism of species, was derived as for list-regions and botanical provinces, by summing the inverse of the number of list-regions each species of a plant group occurred in, and taking the average across those species. We then regressed the average aggregate regional endemism of species on the percentage of species that are New Zealand endemics, across the 14 plant groups, to test whether distributional range and New Zealand endemism are related. To examine the relationship between distributional range (regional endemism), New Zealand endemism, and the size of the plant group, we then regressed both the percentage of New Zealand endemics and average aggregate regional endemism of species within each plant group on plant group species richness. Next, to compare latitudinal trends in the regional endemism of different plant groups, the average aggregate regional endemism of each plant group in turn was regressed on latitude across the 19 botanical provinces.

Taxonomic richness (radiation) and endemism

To provide a synthesis of the geographic patterns in the evolution of the New Zealand flora, we plotted the relationship between radiation and endemism across the 171 list-regions. For each list-region, we plotted the residual variation from the significant linear relationship of species-per-genus ratio (i.e., radiation, calculated using rarefaction) on species richness against the deviation from the mean average aggregate regional endemism, with axes intercepts set at zero.

RESULTS

Species richness

Family richness and genus richness are significantly related to list-region area ($R^2 = 0.17$, $R^2 = 0.34$, respectively, both $P < 0.001$). Most of the list-regions that are exceptionally family-rich are also exceptionally genus-rich (Table 2; residual family versus genus richness correlation $R^2 = 0.88$, $P < 0.001$). They are confined to northern and central New Zealand and are concentrated around Auckland and Cook Strait (Table 2). Family- and genus-poor list-regions relative to area are uplands of the central North Island without alpine zones, two Marlborough ranges, Cape Foulwind, several ranges and lowlands of Central Otago, three Southland districts, and the subantarctic islands.

There is also a strong positive relationship between list-region species richness and area (Fig. 2A). A small number of mainland list-regions are exceptionally species-rich relative to their areal extent, which are concentrated in central North Island, Cook

Table 2 List-regions that are family-, genus-, and species-rich or family-, genus-, and species-poor in relation to land area in New Zealand (i.e., outside 95% confidence intervals for the regression), arranged latitudinally from north to south.

No.	List-region	Family	Genus	Species
	Rich			
499	North Cape	X	X	
489	Poor Knights Islands	X		
442	Waipoua Forest	X		
447	Little Barrier Island	X	X	
450	Great Barrier Island	X	X	X
413	Waitakere Range	X	X	
108	Kauaeranga Valley	X	X	X
82	Hicks Bay, East Cape	X		
90	Mount Egmont	X	X	X
481	Moawhango Ecological District			X
119	Northern Ruahine Range			X
24	Northwest Nelson coast	X	X	X
337	NW Nelson eastern sedimentary rocks		X	
338	NW Nelson Tertiary calcareous sedimentary rocks			X
200	Richmond, Gordon, Bryant Ranges		X	X
118	South Wellington Coast	X	X	X
133	Upper Wairau – Branch River		X	
107	Ben More, Chalk Range			X
424	Waimakariri Basin			X
345	Eyre Mountains			X
484	Te Anau E. D.			X
	Poor			
488	Kermadecs		X	X
428	Maungataniwha Forest		X	
269	Rangitoto Range	X	X	X
55	Ahimanawa Range	X	X	
150	Wither Hills		X	X
290	Cape Foulwind		X	X
254	Upper Saxton	X		
496	Winterslow Range, Canterbury	X	X	
352	Crown Range	X		
363	Central Otago intermontane lowlands	X	X	X
364	Rough Ridge	X	X	X
366	Rock and Pillar Range	X	X	X
460	Upukeroa Ecological District	X	X	X
365	Lammermoor and Lammerlaw Ranges	X	X	X
478	Alpine Takitimu Mountains, Southland	X		
459	Waitutu Ecological District		X	X
490	Antipodes Islands	X	X	
479	Campbell Island	X	X	X
448	Auckland Islands	X	X	X

Strait, the west Nelson-Marlborough mountains, along with Waimakariri Basin, Eyre Mountains, and Te Anau E. D. (Table 2; Fig. 2B). Great Barrier is the only species-rich offshore island relative to land area; indeed, Auckland and Campbell Islands are species-poor, along with four Central Otago ranges and basins, two Southland regions, the Wither Hills, the Rangitoto Range, and the Kermadecs. Residuals from the regression of species richness on area are significantly correlated with those of family and genus richness across the 171 list-regions (residual species versus family richness $R^2 = 0.43$; residual species versus genus richness $R^2 = 0.71$, both $P < 0.001$), indicating that exceptionally species-rich list-regions tend also to be genus- and family-rich, relative to their areal extent.

Species richness and land area are also positively related across the 19 botanical provinces, and all 19 provinces fall within the 95% confidence limits of this relationship (Fig. 2C). Relative to land area, Southland botanical province has a richer flora than neighbouring Fiordland, and Northland is less species-rich than Auckland (indicated by the percentage deviance from richness expected on the basis of land area; Table 1). The previously recognised endemic-rich provinces of west Nelson and Marlborough are comparatively species-rich, but so is reputedly endemic-poor Canterbury and the Marlborough Sounds-east Nelson province.

Regression of the residual variation in family, genus, and species richness on area against latitude revealed that family and genus richness decrease significantly southward ($R^2 = 0.26$, $R^2 = 0.13$, respectively, both $P < 0.001$) but that species-richness does not ($R^2 = 0.012$, $P = 0.09$). The only outlier list-region in the two significant latitudinal relationships is the South Wellington Coast, which is exceptionally genus-rich relative to both its land area and its latitude.

Extrapolation from the regression relationship for list-regions between species richness and area predicted 733 species for the entire New Zealand land area compared with the actual 2249 from this dataset (Fig. 2A). A wide disparity between predicted and realised maximum floras for botanical provinces is also evident (Fig. 2C). Accordingly, there is strong evidence for regional and provincial endemism or insularity in the evolution of the flora, which we discuss in more detail below.

Taxonomic richness (radiation)

In the raw data, species-per-family and species-per-genus ratios in the 171 list-regions were strongly positively correlated with species richness (Fig. 3A,C).

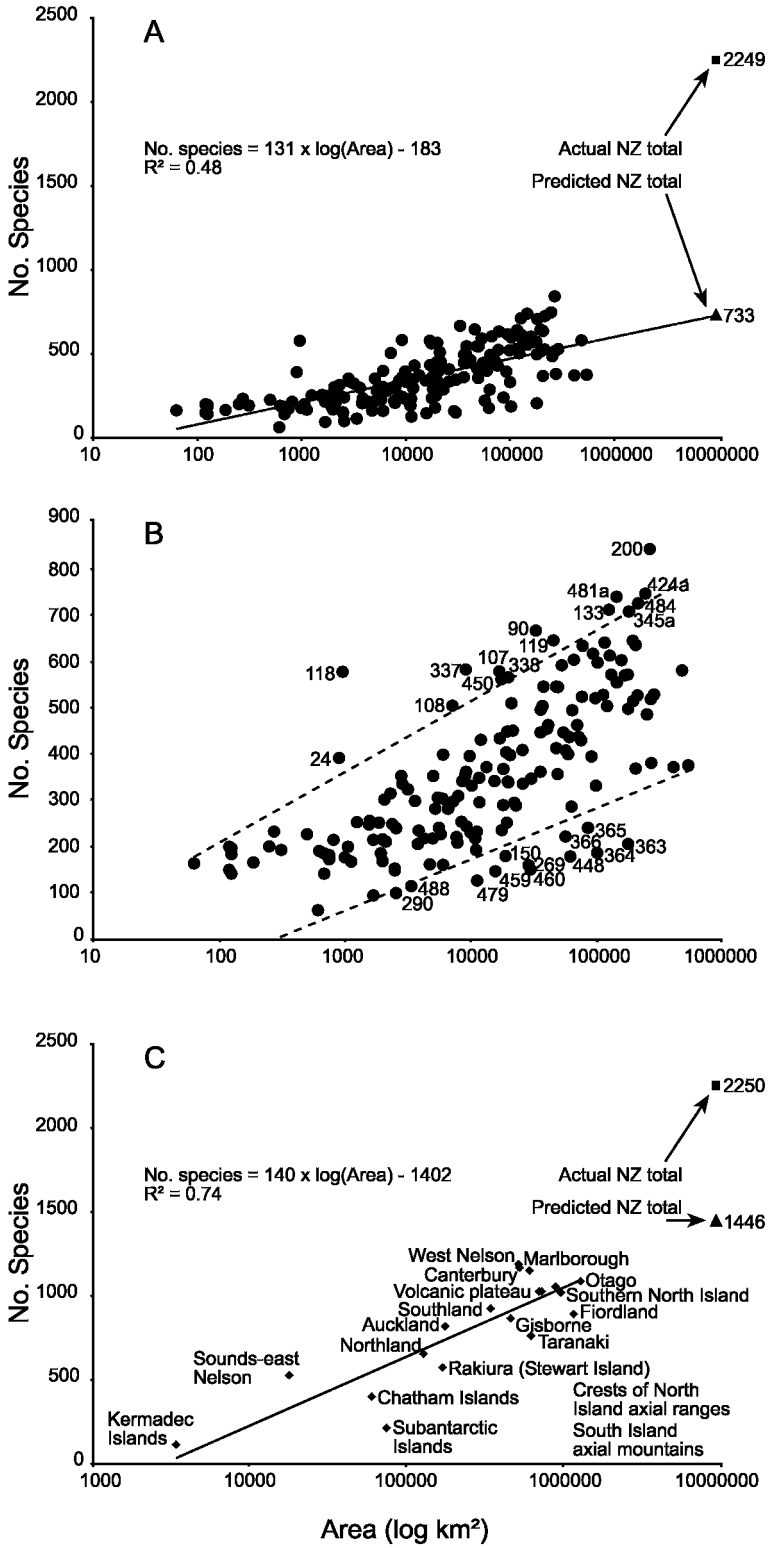

Fig. 2 Species richness-log area relationships across 171 list-regions (White Island and Snares excl.) (**A**, **B**) and 19 botanical provinces (Westland excl., after Wardle 1991) (**C**), with extrapolation of that relationship to the total New Zealand land area. List-regions greater than the 95% confidence limits of the linear regression (dashed lines) are numbered (see Table 1 for number codes of list-regions).

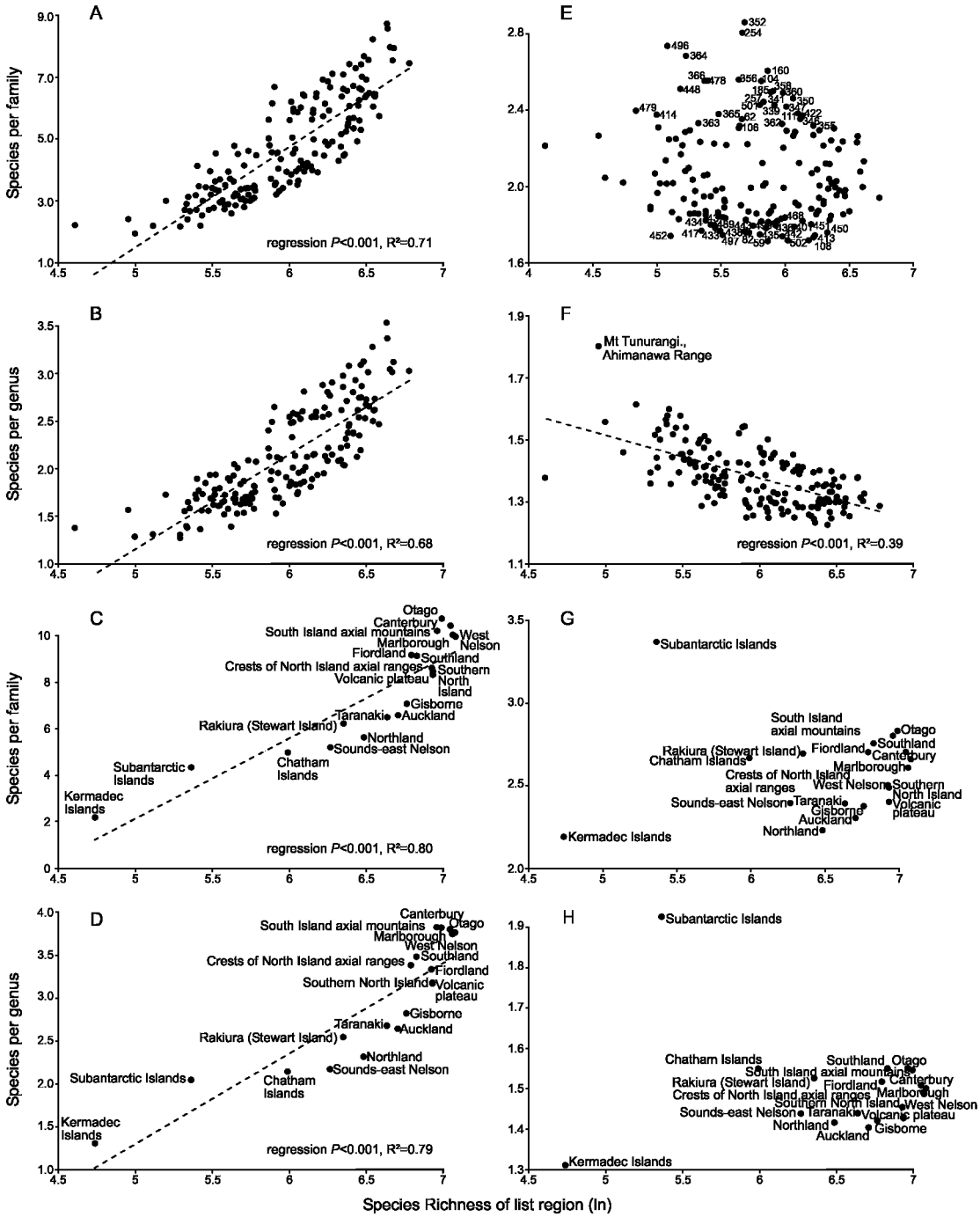

Fig. 3 Radiation: relationships between the ratios of species to higher taxonomic ranks and species-richness of 171 list-regions and 19 botanical provinces (after Wardle 1991), using raw data (**A–D**), and rarefied data (**E–H**, see Methods). Significant linear relationships (dashed lines on A–D, F) are denoted. On rarefaction figures, list-regions that have species-per-family relationships greater than 1 standard deviation above or below the mean are numbered (E; see Table 1 for number codes of list-regions), and on (F) the only list with a species-per-genus ratio outside the 95% confidence limits of the least squares linear regression is labelled.

This reflects an increasing influence of disproportionately speciose genera and families on the average radiation indices in list-regions with larger floras (cf. Fenner et al. 1997). However, rarefaction (i.e., random selections from each flora), which allows unbiased comparison between regions, showed no significant trend in species-per-family ratios with the species richness of list-regions, but the species-per-genus ratio significantly decreased (Fig. 3B,D). The latter suggests that smaller floras have been sourced from relatively few, well-dispersed genera, and that larger floras tend to have a higher representation of species-poor genera. List-regions that have exceptionally large species-per-genus ratios relative to their species richness, or unusually large species-per-family ratios relative to the average, have floras sourced from large, well-dispersed and radiated families and genera. They fall into distinct geographical zones (Table 3): 1) east of the main divide in west and Central Otago, Mt Cook National Park, and throughout Marlborough, 2) two geological substrates of west Nelson, and 3) the subantarctic islands. There are comparatively few North Island list-regions which have exceptionally high species-per-genus or species-per-family ratios (i.e., Mt Turunangi, Rangitoto Range, the Upper Kaingaroa Plains, and Maungataniwha Forest). List-regions with exceptionally low ratios of species to higher taxonomic groups are concentrated in the upper half of the North Island and its offshore islands, with three additional southern outliers of D'Urville Island, the Cape Campbell hills, and the Antipodes Islands (Table 3).

In the 19 botanical provinces, the ratios of species to higher taxonomic ranks in the raw data were again positively correlated with species richness (Fig. 3C,D), indicating the disproportionate influence of large or radiated families and genera in the larger floras. There were no significant relationships between ratios of species to higher taxonomic ranks and floristic richness when the data were put on a comparable basis using rarefaction (Fig. 3G,H). However, the Kermadec Islands is an outlier with a combination of extremely low species richness and taxonomic richness ratios, quite unlike any other botanical province in New Zealand (Fig. 3G,H). When this outlier is removed, the species-to-genus ratio decreases significantly with species-richness across the 19 botanical provinces ($R^2 = 0.42$, $P < 0.01$), as it does across the 171 list-regions.

Residual species-per-family and species-per-genus ratios (calculated using rarefaction, and then adjusted for the size of the flora) both increase significantly with latitude, with a stronger latitudinal increase in the species-per-family ratio (species-per-family $R^2 = 0.38$, $P < 0.001$; species-per-genus $R^2 = 0.26$, $P < 0.001$, respectively). Residual species-per-genus ratios were strongly negatively correlated with area-adjusted (i.e., residual) richness of families and genera across the 171 list-regions ($R^2 = 0.65$, $P < 0.01$; $R^2 = 0.28$, $P < 0.01$, respectively). This indicates that radiation has occurred most markedly in the most family and genus poor list-regions, a result consistent with the phenomenon of compensatory radiation.

Endemism

Large proportions of species but small proportions of genera and families are restricted to one, two, or three list-regions (Table 4). Only one family (Bignoniaceae: *Tecomanthe speciosa*) is a list-region endemic, restricted to the Three Kings Islands. Four families (Avicenniaceae, represented only by *Avicennia marina*, Loxsomataceae, represented by *Loxsoma cunninghamii*, Colchicaceae, represented by *Iphigenia novae-zelandiae*, and Hypoxidaceae, represented by *Hypoxis hookeri*) occur in two list-regions, while three families (Cucurbitaceae, represented by *Sicyos australis*, Sapotaceae, represented by *Planchonella costata*, and Thismiaceae, represented by *Thismia rodwayi*) occur in three list-regions.

The Chatham islands is the list-region with the greatest number of range restricted species (42; endemism index 1, Table 1), followed by the Auckland Islands (38) and Campbell and Stewart islands and the Richmond, Gordon, and Bryant Ranges list-regions (each with 35 range-restricted species). The Richmond, Gordon, and Bryant Ranges (in Marlborough) have the highest total aggregate regional endemism (endemism index 2) of species in the 171 list-regions (Table 1). Others of high rank are Chatham and Stewart islands, Waimakariri Basin, upper Wairau-Branch River, Eyre Mountains, and the west Nelson central sedimentary and volcanic rocks. The botanical provinces of highest rank are west Nelson, Marlborough, Otago, Canterbury, and the South Island axial ranges, the latter two straddling the reputedly endemic-poor waist of the South Island. However, this endemism index is a total, and so, like range-restricted endemism, is dependent upon the size of the flora. We cannot validly compare it between list-regions of different richness.

Measures of regional endemism at the level of species, i.e., range-restricted endemism (Index 1) and total aggregate regional endemism (Index 2) are

Table 3 List-regions with relatively high and low ratios of species-per-genus and species-per-family in relation to the total number of species in the list. The table shows percentage and rank of positive and negative deviation from the expected (from lowest deviation = 1 to highest deviation = highest rank), estimated by least squares regression of (a) genus radiation on ln species richness (species-per-genus), and (b) average family radiation (rarefaction data for species-per-family; no significant trend with species richness was detected). List-regions shown for Species-per-genus radiation are those with values outside the 50% confidence interval (* denotes value outside the 95% C.I.). Lists shown for Species-per-family radiation are those more than 1 standard deviation distant from mean radiation.

List-region		% deviation [rank]	
No.	Radiation > average	(a) Species per genus	(b) Species per family
55	Mt Tunurangi, Ahimanawa Range	18.4[17*]	
352	Crown Range	11.1[16]	38.7[30]
254	Upper Saxton	10.7[15]	36.1[29]
274	Editor Hill-Lookout Peak	9.7[14]	
160	Lake Tennyson, Mount Princess	9.7[13]	26.4[26]
356	Nevis Valley	9.0[12]	24.2[25]
448	Auckland Islands	9.0[11]	21.8[21]
479	Campbell Island	8.5[10]	16.2[11]
496	Winterslow Range, Canterbury	8.2[9]	32.7[28]
350	Harris Mountains	7.9[8]	19.4[17]
269	Rangitoto Range	7.2[7]	
501	Valleys of upper Waitaki River	7.1[6]	17.7[13]
339	NW Nelson indurated limestones	6.9[5]	17.7[14]
364	Rough Ridge	6.8[4]	30.2[27]
428	Maungataniwha Forest	6.2[3]	
478	Alpine Takitimu Mountains, Southland	6.0[2]	23.9[23]
28	Mount Stokes	6.0[1]	
366	Rock and Pillar Range		23.9[24]
104	Mt St Patrick, St James Range, north Canterbury		23.8[22]
185	Spenser Mountains		21.2[20]
358	Old Woman and Carrick Ranges		21.0[19]
360	Old Man Range		20.8[18]
257	Mountains west of upper Glenroy		18.5[16]
341	NW Nelson eastern sedimentary rocks		18.5[16]
347	Livingstone Mountains		17.3[12]
111	Inland Kaikoura Range		15.6[10]
365	Lammermoor and Lammerlaw Ranges		15.4[9]
414	Farewell Spit		15.3[8]
422	Mt Cook/Aoraki National Park		15.0[7]
346	Thomson Mountains		14.2[6]

List-region		% deviation [rank]	
No.	Radiation < average	(a) Species per genus	(b) Species per family
490	Antipodes Islands	–12.2[18]	
82	Hicks Bay, East Cape	–10.0[17]	–14.7[14]
438	Rangitoto Island	–9.9[16]	–14.3[10]
499	North Cape	–9.2[15]	–13.0[6]
310	Ahipara Gumfields-Tauroa Peninsula	–8.8[14]	
437	Poor Knights Islands	–8.6[13]	–12.8[3]
425	Fanal Island	–7.8[12]	
122	Hills south-west of Cape Campbell	–7.6[11]	
59	White Cliffs area, north Taranaki	–7.6[10]	–14.8[15]
447	Little Barrier Island	–7.4[9]	–16.9[24]
401	d'Urville Island	–7.1[8]	–13.2[7]
442	Waipoua Forest	–7.1[7]	–15.7[20]
413	Waitakere Range	–7.0[6]	–15.4[18]
452	Cuvier Island	–6.8[5]	–15.6[19]
46	Pukeamaru Scenic Reserve, Raukumara Range	–6.8[4]	
436	Puketi Forest	–6.6[3]	–13.6[8]
417	Omahuta Forest	–6.4[2]	–14.3[10]
498	Poutu Peninsula, Kaipara Harbour	–6.3[1]	
502	Hunua Ranges, Auckland		–16.7[23]
453	Opotiki – East Cape		–16.7[22]
108	Kauaeranga Valley		–15.9[21]
497	Maungatautari Mountain Scenic Reserve		–15.4[17]
435	Warawara Forest		–15.2[16]
450	Great Barrier Island		–14.7[13]
443	Russell Forest		–14.4[12]
433	Tangihua Forest		–13.6[9]
468	Matemateaonga Ecological District		–12.9[5]
489	Raetea Forest		–12.8[3]
434	Herekino Forest		–12.7[2]
451	Northern Horowhenua		–12.6[1]

Table 3 (*continued*)

List-region No.	Radiation > average	%deviation [rank] (a) Species per genus	(b) Species per family
62	Upper Kaingaroa Plains		14.1[5]
363	Central Otago intermontane lowlands (Upper Clutha to Strath Taieri)		13.1[4]
362	Dunstan and Cairnmuir mountains		12.9[3]
355	Hector mountains		12.5[2]
106	Black Birch Range		12.4[1]

Table 4 Numbers of species and higher taxonomic ranks confined to fewer than 4 of the 171 list-regions used to analyse endemism in New Zealand.

Taxonomic rank	Total in database	1 region	2 regions	3 regions
Species	2249	235 (10%)	159 (7%)	109 (5%)
Genus	418	15 (4%)	9 (2%)	12 (3%)
Family	135	1 (1%)	1 (1%)	0 (0%)

significantly correlated across the 171 list-regions and 19 botanical provinces (Fig. 4). However, there is considerable scatter for the list-region relationship, particularly in smaller and/or more species-poor list-regions (Fig. 4A). Seven outlier list-regions (Chatham, Auckland, Campbell, Kermadec, and Antipodes offshore islands, Surville Cliffs and North Cape; labelled on Fig. 4A) have substantially greater numbers of range-restricted species than their corresponding total aggregate regional endemism would suggest. This indicates that although several unique species are present, many species that occur in these list-regions are relatively widely dispersed on the New Zealand mainland.

Average aggregate regional endemism allows comparisons of intrinsic regional endemism between list-regions irrespective of their floristic richness. The Kermadec, Campbell, Auckland, Chatham, and Antipodes Islands stand out as having the highest ranks for average aggregate regional endemism in the 171 list-regions (Table 1; on average, the species they support occur in between 4 and 9 list-regions). A second group consists of the Three Kings Islands, the northern mainland extremities of North Cape and the Surville Cliffs, and Stewart Island (on average, their species occur in 12 to 13 of New Zealand's list-regions). A third group of high-endemism list-regions consists of the Inland Kaikoura Range, West Nelson Tertiary calcareous sedimentary rocks, the Richmond, Gordon, and Bryant Ranges, the Central Otago intermontane lowlands, the west Nelson central sedimentary and volcanic rocks, Upper Wairau-Branch River, and Denniston and Stockton Plateaux of the greater New Zealand mainland, and the Poor Knights and Great Barrier islands (on average, their species occur in 16 to 20 list-regions).

We show that average aggregate regional endemism of species (Index 3) is not related to the percentage of species that are New Zealand endemics, across either the 171 list-regions or the 19 botanical provinces (Fig. 5A). However, several islands show exceptionally high average aggregate regional endemism of species at both list-region and botanical province scales (Fig. 5A,B). The Kermadec Islands show the highest average aggregate regional endemism of species, but exceptionally low New Zealand species endemism, while North Cape, Surville Cliffs, and the Three Kings Islands also have relatively high average aggregate regional endemism of species but comparatively low New Zealand endemism. These lists contrast with the subantarctic, Stewart, and Chatham Islands, which have high measures of both New Zealand and average regional endemism of species (Fig. 5B).

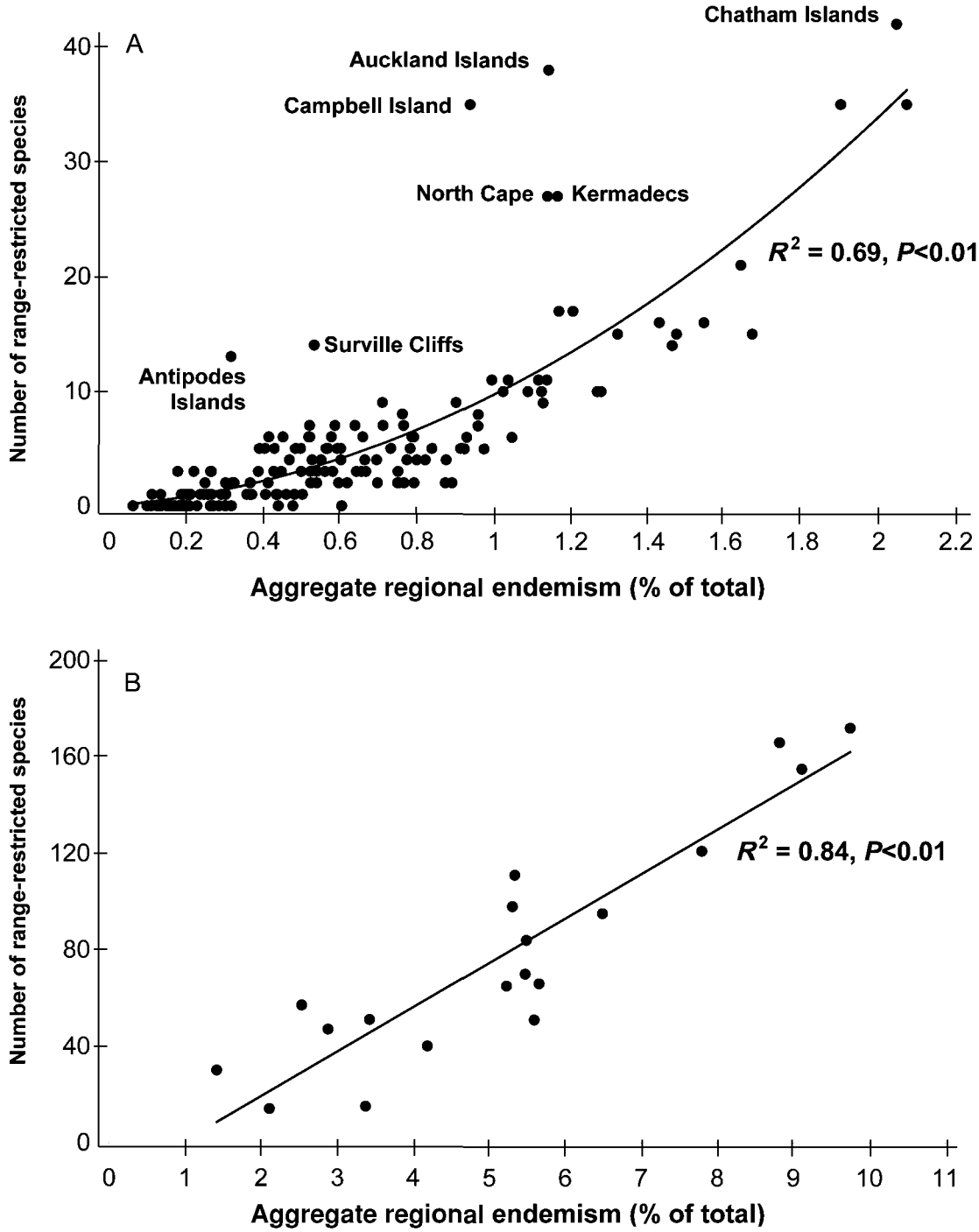

Fig. 4 Regional endemism indices: significant relationships between the sum of range-restricted species (the sum of the number of species restricted to that list-region, plus the number shared with one additional list-region, plus the number shared with two additional list-regions) and aggregate regional endemism (% of the total across all lists) **A**, for 171 list-regions throughout New Zealand (text refers to the seven labelled outliers), and **B**, for the 19 botanical provinces (no outliers identified).

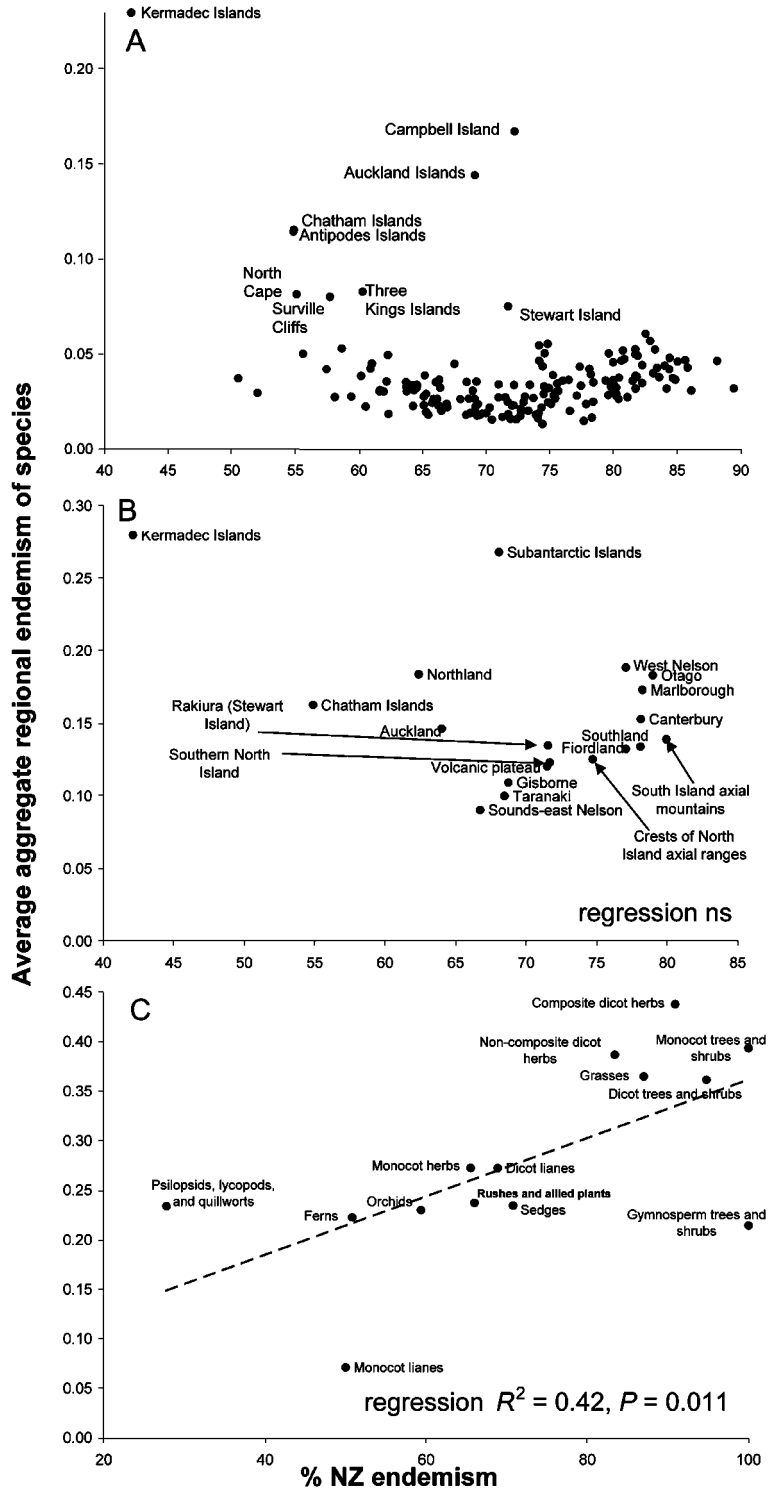

Fig. 5 Regional endemism versus New Zealand endemism: relationships between average aggregate regional endemism of species (see Methods) and the degree of New Zealand endemism for 171 list-regions (**A**), 19 botanical provinces (after Wardle 1991) (**B**), and 14 plant groups (**C**). Numbered list-regions in A have average aggregate regional endemism of species greater than 1 standard deviation above or below the mean for all lists.

New Zealand endemism for list-regions varies widely from 42% to 88% (Table 1). The most New Zealand endemic list-regions are concentrated in the western mountains of Nelson, Marlborough, and Otago (Table 1). List regions with the lowest New Zealand endemism are concentrated in the northern offshore islands, along with North Cape, Surville Cliffs, Chatham Islands, and Antipodes Islands. The South Island axial mountains, Otago, Marlborough, and Canterbury are the most New Zealand endemic provinces. The Kermadecs have extreme endemic character, their New Zealand isolation and tropical affinity reflected in the highest average aggregate endemism and the lowest New Zealand endemism.

Average aggregate regional endemism of families decreases significantly with increasing latitude across the 171 list-regions (Fig. 6A), but genus or species endemism do not (Fig. 6B,C). The Three Kings Islands is the only list-region with exceptionally high average aggregate regional endemism of families. In the absence of a significant relationship with latitude, many offshore islands and a few mainland list-regions have above average aggregate regional endemism of genera or species (Fig. 6B,C).

At the coarser scale of 19 botanical provinces, average aggregate regional endemism of both families and genera are negatively correlated with latitude (Fig. 6D–F) (furthermore, just one substantial outlier, the subantarctic islands, offsets a significant decrease in species endemism with latitude). Average aggregate regional endemism of families is highest in northern provinces such as Auckland and Northland (Fig. 6D; note, however, that in the low-latitude Kermadec Islands this is comparatively low), and lowest in the subantarctic islands. Marlborough Sounds-east Nelson and the Chatham Islands botanical provinces also have low composite family endemism relative to their mid-latitude positions. The Kermadec and subantarctic islands provinces have comparatively high average aggregate regional endemism of genera, whereas in Taranaki and Marlborough Sounds-east Nelson this is comparatively low (Fig. 6E). In the absence of a significant relationship between average aggregate regional endemism of species and latitude, the subantarctic islands stand out as having exceptionally high species regional endemism (Fig. 6F). Because of the relatively high average aggregate regional endemism of all taxonomic ranks on islands

Table 5 Summary of the degree of New Zealand endemism and average aggregate regional endemism within New Zealand for 14 plant groups. Shown are the number of species within each plant group, their percentage New Zealand endemism, their average composite species endemism, and the summary of linear regressions of average aggregate regional endemism in 19 botanical provinces against latitude. Shown for the regression are whether they are +ve or –ve, the percentage of variation in endemism explained by latitude, and asterisks representing Bonferroni-corrected probabilities that the regression is non-significant: *, $P < 0.05$; **, $P < 0.01$.

			Aggregate regional endemism		
				Relationship with latitude	
Plant group	Number of species	% New Zealand endemism	Average	Direction	% variation explained
Non-composite dicot herbs	663	83	0.24	+	51.5**
Dicot trees and shrubs	479	95	0.22	–	10.4
Composite dicot herbs	253	91	0.28	+	50.3**
Grasses	200	87	0.23	+	13.7
Ferns	181	51	0.15	–	45.0**
Sedges	178	71	0.13	–	0.8
Orchids	91	59	0.16	–	34.4*
Monocot herbs	58	66	0.14	+	37.9*
Rushes and allied plants	50	66	0.14	+	27.0
Dicot lianes	45	69	0.18	–	41.0*
Gymnosperm trees and shrubs	23	100	0.10	–	48.3**
Psilopsids, lycopods, and quillworts	18	28	0.15	–	19.0
Monocot trees and shrubs	8	100	0.29	–	31.1*
Monocot lianes	2	50	0.01	–	49.2**
Total	2249	81	0.21	+	1.2

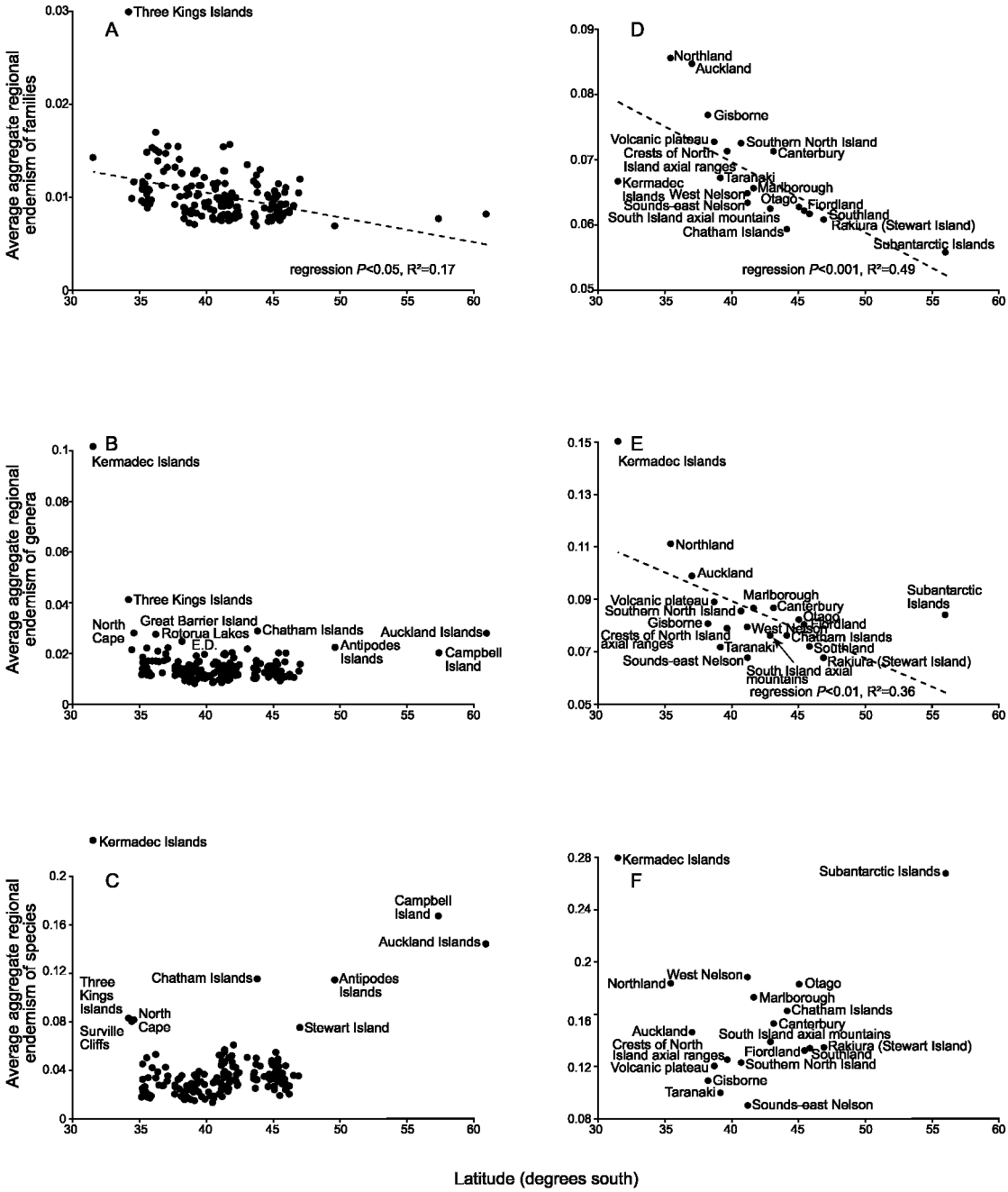

Fig. 6 Relationships between average aggregate regional endemism of families, genera, and species (see Methods) and latitude for 171 list-regions (**A–C**) and 19 botanical provinces (after Wardle 1991) (**D–F**). Significant trends are indicated by dashed lines. List-regions labelled are those falling outside the 95% confidence interval limits of the regression (Fig. 4A), or (where there is no significant trend) those with values deviating from the mean by >1 standard deviation (Fig. 4B,C).

relative to the mainland, we also looked for centres of exceptionally high or low endemism within the mainland only, but none was evident.

There were no significant relationships between average aggregate regional endemism of families, genera, and species and the species richness of the list-regions or provinces.

We next examined New Zealand endemism across the 14 plant groups (i.e., the percentage of species that are New Zealand endemics) and the average aggregate regional endemism of species (our Index 3 of regional endemism). Average aggregate regional endemism of species increases with percentage New Zealand endemism across these plant groups ($R^2 = 0.42$, $P < 0.011$; Fig. 5C; Table 5). Dicot and monocot trees and shrubs, composite and non-composite herbs, and grasses have high values for both of these measures of endemism. Gymnosperms have 100% New Zealand endemism but are more widespread than the relationship predicts (i.e., they have low average aggregate regional endemism relative to their percentage New Zealand endemism). The psilopsids, lycopods, and quillworts are the least regionally endemic plant group in New Zealand (28%). Remaining plant groups have intermediate to low and highly predictable scores for both measures of endemism. The relationship between average aggregate regional endemism of species and the species richness of plant groups is positive and significant ($R^2 = 0.31$, $P = 0.04$), indicating a tendency for species in the larger plant groups to have more restricted distributions. However, this trend is strongly influenced by the four largest, most regionally restricted plant groups (non-composite and composite dicot herbs, dicot trees and shrubs, and grasses), and is not seen across the smaller plant groups. Thus, the correlation of endemism and richness rank is not quite significant ($R^2 = 0.24$, $P = 0.07$). Percentage New Zealand endemism and species richness of plant groups are not significantly related ($R^2 = 0.06$, $P = 0.39$ by rank correlation). This is because some highly New Zealand endemic plant groups (e.g., gymnosperm and monocot trees and shrubs) are widespread, while others have more restricted distributions (e.g., grasses, dicot trees and shrubs, composite dicot herbs).

Nine of the 14 plant groups show significant relationships between average aggregate regional endemism of species and latitude across botanical provinces (Table 5). The two speciose herbaceous dicot groups, along with monocot herbs and rushes, share positive relationships with latitude (i.e., their more regionally restricted species tend to occur in southern botanical provinces), whereas ferns, gymnosperms, and monocot herbs and lianes have negative relationships (their more widespread species occur in southern northern provinces).

Taxonomic richness (radiation) and endemism

The relationship between residual species-per-genus ratios (after correcting for species richness) as an expression of radiation (phylogenetic diversity) and the average aggregate regional endemism of species for the 171 list-regions (regional endemism) has highlighted five groups of outliers in relation to the mean values for both indices (Fig. 7):

1 A combination of exceptionally high values for radiation and high values of regional endemism of species is shown by Campbell and the Auckland islands only.

2 High values of regional endemism of species and average values for radiation are shown by the Kermadec and Stewart islands.

3 The Chatham, Antipodes, and Three Kings islands and the North Cape and Surville Cliffs mainland regions show high regional endemism of species, combined with low radiation.

4 Mainly average values for regional endemism of species but exceptionally high values for radiation (Table 3) are seen in many list-regions, predominantly east of the main divide in the South Island (west and Central Otago, Mt Cook National Park, throughout Marlborough), in two geological substrates of west Nelson, and also in the Rangitoto Range, Maungataniwha Forest, and Mt Tunurangi (Ahimanawa Range) list-regions of central North Island.

5 More or less mean values for regional endemism of species and low values for radiation apply to many North Island list-regions (Table 3). The syndrome is best expressed in mainland Hicks Bay (East Cape), Ahipara Gumfields (Tauroa Peninsula), Pukeamaru Scenic Reserve (Raukumara Range), and White Cliffs (Taranaki) list-regions. Rangitoto Island in the Hauraki Gulf is represented, along with several Northland list-regions. d'Urville Island, and the hills south-west of Cape Campbell are the only South Island representatives of this syndrome.

DISCUSSION

Species richness

Corrected for area, there is broad consistency at all three taxonomic ranks in the geographic pattern of list-regions that show exceptionally high or low

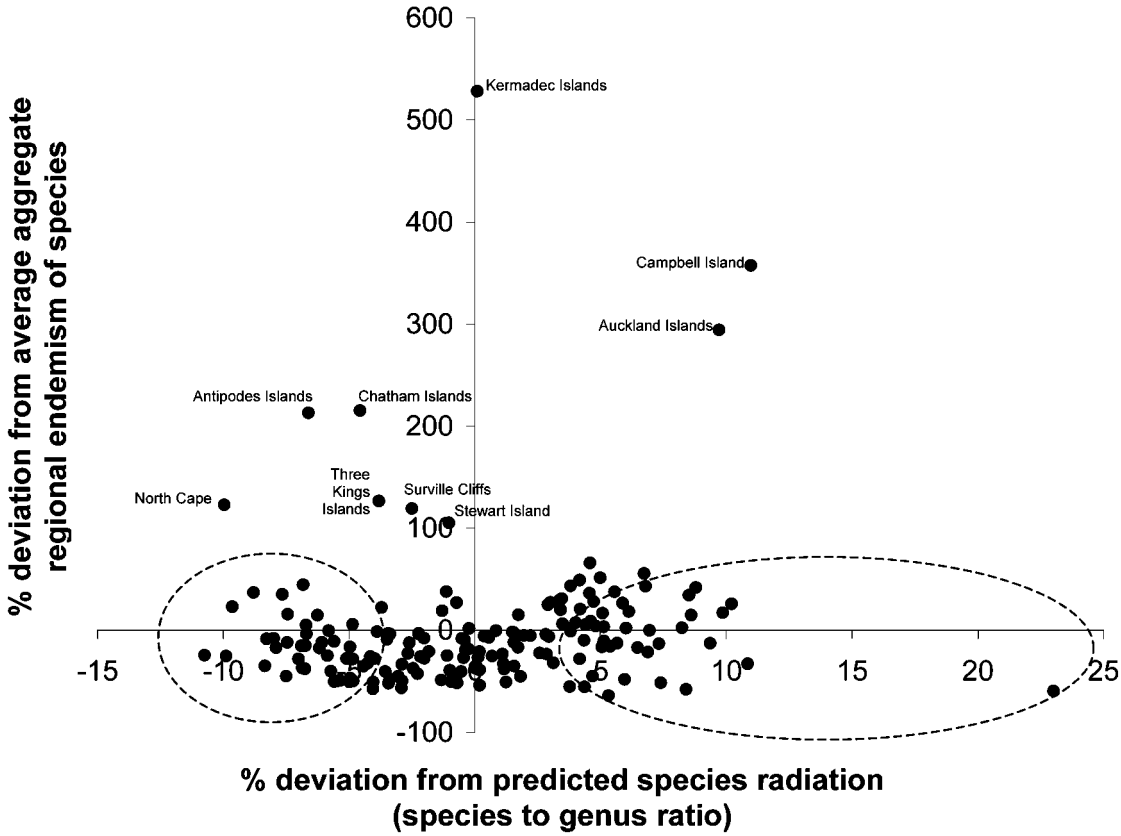

Fig. 7 Relationship between endemism and radiation: showing percent deviation (% dev.) from mean values for average aggregate regional endemism of species, and percent deviation (% dev.) from the expected species-per-genus ratios (calculated using rarefaction) from the regression on species richness, for the 171 list-regions. The dashed circles show arbitrary aggregations of list-regions ("syndromes") discussed in the text.

richness. Most of the species-rich regions are in central New Zealand from west Nelson and Marlborough to central North Island, with three southern mainland additions (Table 2). Richness in the higher taxonomic ranks is concentrated around Auckland and Cook Strait. This northern concentration, in combination with the significant negative trend in family and genus richness with latitude, supports the notion of greater survival of families and genera in the warmer north with the onset of late Cenozoic climate deterioration. Only the south Wellington coast deviates from the consistent latitudinal decline in family and genus richness by being unusually genus-rich. Two influences may be at work there: first, south Wellington-Wairarapa is the southern margin of the lower North Island floristic gap, harbouring a strong representation of disjunct species from both central and northern North Island and an extension across Cook Strait of a predominantly South Island flora (Rogers 1989); second, the region is likely to be landfall for propagules of south and east Australian origin carried by trans-Tasman sea currents (de Lange et al. 1998).

List-regions that are exceptionally family-, genus-, and species-poor relative to land area are somewhat more geographically dispersed. Species-depauperate regions often have no alpine zones or low environmental heterogeneity (Rogers & Overton 2000).

Whereas we suggest that the majority of the unexplained variance in the species-area relationship is due to differences in environmental heterogeneity or earth history, we acknowledge that an unquantifiable portion will be due to database issues such as differential sampling effort, variable taxonomic rigour in inventory, and regional extinction of species in the last 800 years of human occupation.

New Zealand is popularly depicted as predominantly a forest environment, comprising a highly mobile contingent flora of trees, shrubs, ferns, lianes, and orchids. However, 64% of species in the present dataset are from non-forest specialist plant groups (i.e., composite and non-composite herbs, grasses, sedges, rushes, psilopsids, lycopods, and quillworts; Table 5). Average aggregate regional endemism is particularly high in the first three of these non-forest plant groups; this conforms with earlier observations that, outside Northland, endemism is concentrated in the non-forest flora (Druce 1984; Williams & Courtney 1998). Accordingly, much richness and endemism are products of adaptation to non-forest ecosystems characterised by extremes of rock chemistry, soil moisture, topography, disturbance, and productivity-constraining climates. In southern New Zealand, richness-promoting environments were found to be centred just east of the main divide where indices of environmental heterogeneity are greatest (Rogers & Overton 2000).

Many empirical examples show that after controlling for area, certain biota show increasing richness toward the equator (e.g., bat and marsupial richness increase throughout the North and South American continents; Lyons & Willig 2002). However, we show no significant relationship between species richness and latitude in the New Zealand flora. Strong floristic regionalism, as reflected in variations in richness, endemism, and radiation, combined with a comparatively narrow latitudinal span, may have confounded such a relationship.

Taxonomic richness (radiation)

Although species-per-genus and species-per-family ratios are likely to be only rudimentary measures of phylogenetic diversity (Rodrigues & Gaston 2002), they remain the best surrogate in the absence of comprehensive molecular-based measures for the New Zealand vascular flora.

Floras that have the least radiated genera and families in New Zealand are invariably those of coastal, lowland, and island list-regions, predominantly in the North Island, although the list includes the more southern Chatham Islands and Otago Peninsula floras. These environments may not be novel in terms of evolutionary processes; or may have much genetic interchange with surrounding floras; or may be of recent geological origin.

Exceptionally highly radiated floras are predominantly South Island list-regions that lie near to and usually east of the main divide, in Otago, mid Canterbury, and Nelson-Marlborough. Just five North Island list-regions have highly radiated floras (Mt Tunurangi, the Maungataniwha, Rangitoto, and Black Birch Ranges, and the Upper Kaingaroa Plains; Table 3). Auckland and Campbell Islands are family-, genus-, and species-poor in relation to area, but comprise a small number of disproportionately highly radiated families and genera. Wardle (1978) suggested that the subantarctic islands' flora was mainly derived from or via Antarctica and that this flora, in common with the Chatham Islands (Godley 1975), probably experienced less profound Quaternary disturbances than the mainland. Our results simply point to colonisation by and/or survival of just a few source lineages, and a high level of subsequent speciation, despite these islands' low topographic profiles and ostensibly low environmental heterogeneity as a constraint.

Using rarefaction, we show that the amount of radiation within a list-region is negatively correlated with its species richness. In other words, smaller floras have an increasing presence of highly radiated genera, and, conversely, larger floras have an increasing presence of conservatively radiated genera. No correlation is evident between list-regions with highly radiated floras and those with exceptionally high species richness relative to their land area. In fact, the most radiated floras are the most family- and genus-poor relative to their land area. With family and genus richness increasing northward, and species-per-family and species-per-genus ratios increasing southward, again there is evidence that a few cosmopolitan families and genera compensated for a late Cenozoic loss of lineages with species-radiation in the novel habitats of the more mountainous south.

Endemism

The species richness of list-regions and botanical provinces within New Zealand is strongly correlated with their land area, yet extrapolation of these relationships to the total New Zealand land area predicts just one-third and two-thirds of the total flora, respectively. This is strong evidence for insularity in the evolution of the flora, leading to a high degree of regional endemism.

Our measure of aggregate regional endemism measuring the sum of the inverse range sizes of all species in an area overcomes the confounding influences of area and size of the flora on orthodox measures of endemism (Kier & Barthlott 2001; see also Williams et al. 1996). The positive but somewhat dispersed relationship between the number of particularly range-restricted species and the aggregate

measure of endemism shows that the two indices are complementary but not interchangeable. They have different applications in assessing biogeographic distinctiveness: the former highlights the few most restricted taxa while disregarding the more widely dispersed remainder of the flora, whereas the latter indicates the relative dispersibility and ecological specialisation of the entire flora.

Corrected for floristic richness, most of the major offshore islands (and North Cape) show much greater endemism at genus and species ranks than mainland regions (and at the rank of family for the Three Kings Islands). The mainland has quite predictable levels. Clearly, insularity as an evolutionary driver has its most extreme expression on isolated islands within the New Zealand botanical region, but taxonomic rank provides different flavours across the subtropical to subantarctic latitudinal gradient. The northern islands probably retain a greater number of Cenozoic families and genera, whereas the source pool for high species endemism on southern offshore islands is just a few, more widespread families.

Within the alpine vascular flora, McGlone et al. (2001) found a negative relationship across plant groups between the degree of New Zealand endemism and their internal range within New Zealand. They suggested that species selection in the Pleistocene was, for most species, to follow the movement of suitable environments across the landscape, or to retreat to small, often atypical refugia in response to interglacial-glacial cycles. In using almost the entire flora, the present study reinforces that finding and explains the pattern in terms of plant group dispersibility and adaptation to narrow-range or widespread ecosystems in the following terms.

1 Ferns, orchids, sedges, rushes, and psilopsids, lycopods, and quillworts have relatively low New Zealand endemism and low aggregate (i.e., regional) endemism within New Zealand.

2 The composite and non-composite dicot herbs along with dicot trees and shrubs and grasses have high degrees of both New Zealand endemism and aggregate regional endemism within New Zealand.

3 Gymnosperms deviate from both these patterns by having high New Zealand endemism and low regional endemism.

There are also contrasting latitudinal patterns in radiation and aggregate regional endemism by plant group:

1 The highly speciose composite and non-composite dicot herbs and grasses and the less speciose monocot herbs and rushes increase southward.

2 Conversely, endemism decreases southward for monocot and gymnosperm trees and shrubs, ferns, orchids, and dicot and monocot lianes.

3 Sedges, psilopsids, lycopods, and quillworts show no latitudinal trends.

High regional endemism of the speciose plant groups that increases southward implies ecological specialisation to narrow-range, often non-tall forest ecosystems that would confer little opportunity to migrate in response to shifting patterns of resource availability as a response to Pleistocene climate change. These ecosystems include turfs of coastal headlands, ephemeral wetlands, the inland saline ecosystem, dune slacks, wet/dry frosty hollows and margins of floodplain forest, cliffs (often limestone), and dryland pavements on outwash fans, terraces, and braided riverbeds, all characterised by extremes of rock chemistry, soil moisture, and topography (Rogers & Walker 2002). Alternatively, ferns, orchids, sedges, rushes, and psilopsids, lycopods, and quillworts are highly dispersible and adapted to either extensive or non-specialised narrow-range ecosystems, such as forest, scrub, seral tussockland, and wetlands. Monocot and gymnosperm trees and shrubs and dicot and monocot lianes may be derivatives of relictual elements of the subtropical and warm temperate biota of mid-Cenozoic forests.

Implications for conservation policy

A comprehensive biodiversity strategy for New Zealand should incorporate the evolutionary or phylogenetic complexion of the flora as reflected in patterns of species richness, radiation, and endemism. We highlight striking contrasts in taxonomic structure within the offshore islands, and between offshore island and mainland floras. Nature conservation reserves created from tenure review of the pastoral leasehold land of the South Island high-country will capture 1) radiated floras, with many closely related species of low lineage diversity and rapid evolutionary processes and 2) endemism at low taxonomic rank.

Alternatively, perhaps the most phylogenetically important regions are in northern coastal and lowland environments, with their high phylogenetic diversity and likely older lineages. Either way, evolutionary processes can only be accommodated in generous reserves, with particular emphasis on altitudinal sequences for global climate change.

Finally, better understanding of the environmental drivers of these divergent geographic patterns of richness, radiation, and endemism may come from their correlation with environmental parameters,

such as Leathwick et al.'s (2003) classification of New Zealand's physiographic environments.

CONCLUSIONS

Our investigations of New Zealand plant biodiversity at regional and provincial scales first addressed the question of whether the Late Cenozoic radiation of the New Zealand flora produced divergent patterns of richness, radiation, and endemism. To answer this, we examined the relationship between richness at different taxonomic levels and land area, latitude, radiation, and endemism.

List-regions with exceptionally high species richness in relation to area are concentrated in central New Zealand. Family-, genus-, and species-poor areas are mostly uplands of the North Island without alpine zones, ranges in Otago and Southland, and the subantarctic islands. Our results suggest that exceptionally species-rich floras do not tend to be highly endemic-rich or radiated. Overall, there were significant decreases in area-corrected family and genus richness southward, coinciding with increasing species radiation. Consequently, area-corrected species richness shows no latitudinal trend.

The species richness to area relationship reveals a wide disparity between the predicted size of the whole New Zealand flora and the actual, much greater total number of species. This result provides strong evidence for insularity-driven endemism within the New Zealand botanical region.

Small floras tend to be sourced from fewer, highly radiated families or genera, while larger floras have a greater presence of conservatively radiated lineages when a random selection of species is drawn from them. Corrected for the size of the flora, degree of radiation increases southward. A large group of mainly South Island regions has above-average radiation (i.e., low phylogenetic diversity), while a large group of mainly North Island regions (but also a number of lowland South Island regions) shows below-average radiation (i.e., high phylogenetic diversity). No mainland list-regions or botanical provinces show exceptionally high degrees of endemism relative to the size of their floras. However, the offshore islands show extreme degrees of radiation and endemism that can be categorised into three evolutionary syndromes:

1 High radiation from a small source pool of antecedents and high endemism is evident in the southern subantarctic islands (Campbell and Auckland islands).

2 Stewart, Three Kings, and Kermadec islands, the Surville Cliffs (a geological island in Northland), and North Cape are also distinctive for comparatively highly endemic floras showing predictable or intermediate degrees of endemism.

3 The Chathams and Antipodes islands have comparatively poorly radiated but highly endemic floras.

Our second question asked whether the least New Zealand endemic plant groups show the most widespread distributions (i.e., less regional endemism) within New Zealand, reflecting less environmental specialisation or occupation of widespread habitats. Our work confirms that the more New Zealand endemic plant groups also have the more restricted internal ranges as noted by McGlone et al. (2001) for the alpine flora. Gymnosperms are a notable exception; they are 100% New Zealand endemic but widespread within New Zealand. In addition, we show that species from the larger plant groups tend to be more regionally restricted within New Zealand and to have a higher percentage of New Zealand endemics, although the latter relationship is less strong. Contrasting latitudinal trends in endemism within New Zealand are evident for the 14 different plant groups that reflect their dispersibility and evolutionary adaptation to habitat dispersion. Two adaptive strategies are evident: a smaller pool of species that can tolerate cyclical appearance and disappearance of environments by regional mobility (McGlone et al. 2001), and a much larger pool of more sedentary, stress-tolerant specialists confined to narrow-range, non-tall forest ecosystems during cyclical environmental change.

In seeking to extend the debate on regional endemism by correcting for area and floristic richness, we show that the offshore islands have the most endemic floras at all taxonomic ranks, and that southern mainland regions and offshore islands show the most radiation from a limited pool of progenitors.

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Appendix 1 Published and unpublished vascular plant species lists used to compile a database of species by list-region.

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Druce AP 1992as. Indigenous higher plants (lycopods, ferns, gymnosperms, flowering plants) of upper Saxton River catchment, Marlborough, 4000–6650 ft (1225–2025 m). Unpublished checklist held at Landcare Research, Lincoln, New Zealand.

Druce AP 1992at. Higher plants (lycopods, ferns, gymnosperms, flowering plants) of mountains west of upper Glenroy River and west of Alpine Fault, southern Nelson, 1700–5500 ft (500–1675 m). Unpublished checklist held at Landcare Research, Lincoln, New Zealand.

Druce AP 1992au. Indigenous higher plants (lycopods, ferns, gymnosperms, flowering plants) in area of Tertiary calcareous rocks between "Aniseed Valley" and Puhipuhi Valley, southern Marlborough, including Blue Duck Scientific Reserve and Puhipuhi Scenic Reserve, 150–1200 m (500–3932 ft). Unpublished checklist held at Landcare Research, Lincoln, New Zealand.

Druce AP 1992av. Indigenous vascular plants (psilopsids, lycopods, ferns, gymnosperms, flowering plants) in vicinity of Charming Creek walkway and Ngakawau Gorge, northwest Nelson, sea-level to 150 m. Unpublished checklist held at Landcare Research, Lincoln, New Zealand.

Druce AP 1992aw. Indigenous vascular plants (ferns, flowering plants) of coastal cliffs, beaches, dunes, and wetlands, Cape Foulwind, sea-level to 65 m. Unpublished checklist held at Landcare Research, Lincoln, New Zealand.

Druce AP 1992ax. Higher plants (lycopods, ferns, gymnosperms, flowering plants) of upper Hope Valley (including Little Hope Valley, Lamb Valley, Teal Valley, and Cow Valley) at foot of south Hope Range, northwest Nelson, 400–600 m. Unpublished checklist held at Landcare Research, Lincoln, New Zealand.

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