Botany Department, University of Otago, P.O. Box 56, Dunedin, New Zealand.

MECHANISMS OF SPECIES COEXISTENCE: TWELVE EXPLANATIONS FOR HUTCHINSON'S 'PARADOX OF THE PLANKTON': EVIDENCE FROM NEW ZEALAND PLANT COMMUNITIES

Summary: A problem perplexing many ecologists studying natural communities has been how the species of a community coexist without competitive exclusion occurring. Hutchinson named this the 'Paradox of the Plankton', though the question has been asked especially for tropical rain forest and coral reef communities. Twelve mechanisms have been proposed to explain the paradox:

1. Niche Diversification,
2. Pest Pressure,
3. Equal Chance,
4. Gradual Climate Change,
5. Intermediate-timescale Disturbance,
6. Life History Differences,
7. Initial Patch Composition
8. Spatial Mass Effect
9. Circular Competitive Networks,
10. Cyclic Succession,
11. Aggregation,
12. Stabilising Coevolution.

Evidence is reviewed for the relative importance of these twelve mechanisms in New Zealand indigenous vegetation.

From the available evidence, it is suggested that (4) Gradual Climate Change is probably a major explanation of the Paradox of the Plankton in New Zealand. (10) Cyclic Successional processes are probably involved in this change, though there is so far only speculation for N.Z. (8) Spatial Mass Effect and (1) Niche Diversification are probably also important, though poorly documented. Aggregation (11) may facilitate these processes.

(5) Intermediate-timescale Disturbance is probably unimportant for within-community coexistence, with the notable exception of small forest gaps. Elements of (3) Equal Chance and (6) Life History Differences are probably involved in this, though there is no evidence available for N.Z.

Some of the elements necessary for Pest Pressure (2) appear to occur.

(7) Initial Patch Composition, (9) Circular Competitive Networks, and (12) Stabilising Coevolution are probably unimportant, or even non-existent.

Keywords: Coexistence; diversity; New Zealand; Paradox of the Plankton; vegetation.

Introduction

The paradox

In 1961, Hutchinson posed his classic question: "How [is it] possible for a number of species to coexist in a relatively isotrophic or unstructured environment, all competing for the same sorts of materials?". Indeed, the almost ubiquitous existence of multi-species communities is one of the few firm facts in ecology. How can alpha species diversity be as high as it is within most actual communities, in the face of the Principle of Gause that no two species can permanently occupy the same niche? Why does competitive exclusion not occur, leaving only one species - the one with the highest competitive ability? The paradox has still not been solved (Ghilarov, 1984). Hutchinson gave the particular example of the phytoplankton, from which the paradox is named. Most species of phytoplankton are autotrophic, requiring light, CO_2 and about 17 mineral elements, not all of which will be limiting in any particular waters. Yet considerably more species than implied by this can coexist. A similar problem exists for almost all plant communities. For example, Connell (1978) asked the same question - "How is high diversity maintained near equilibrium?" - taking as his particular examples tropical rain forest and coral reef.

Explanations

Some possible answers to the paradox have been discussed by Connell (1978), Shmida and Ellner (1984) and others. The mechanisms are:

1. Niche Diversification,
2. Pest Pressure,
3. Equal Chance,
4. Gradual Climate Change,
5. Intermediate-timescale Disturbance,
6. Life History Differences,
7. Initial Patch Composition

  8. Spatial Mass Effect
  9. Circular Competitive Networks,
10. Cyclic Succession,
11. Aggregation,
12. Stabilising Coevolution.

(Alternative terms to those above are given in the heading to each section.) (1) Niche Diversification and (2) Pest Pressure are both equilibrium explanations based on density-dependent mechanisms, giving an advantage in growth or survivorship to the minority component, thus preventing competitive exclusion. The density-dependence is caused by either (in mechanism 1) less severe depletion of the minority species' resources or (in mechanism 2) fewer pests on it. The (3) Equal Chance hypothesis suggests that competitive exclusion does not eliminate species because it is a weak force, and the success of one species or another at a particular point is partly due to chance.

   Another possibility is that there is never time for competitive exclusion to operate. The (4) Gradual Climate Change and (5) Intermediate-timescale Disturbance explanations are non-equilibrium ones, suggesting that equilibrium is never reached in real communities because of changes in the external environment. In the case of Gradual Climate Change this is because there are slow environmental changes, and the community always includes relict species from vegetation that developed under the previous climate. In the case of Intermediate-timescale Disturbance the lack of equilibrium is because of repeated sudden disturbances, creating 'gaps'. In either case, the changes are suggested to occur frequently enough for equilibrium never to be achieved.

   The (6) Life History Differences mechanism also depends on the presence of gaps, but they are caused by natural plant death, not by external factors. Some of these gaps are colonised by a highly-competitive but poorly dispersed species, the remainder by a more ruderal species. Thus, there is a random element, as in mechanism 3. Initial Patch Composition (7) also depends on colonisation in transient opportunities. Once a species has established a patch, it holds the space. In this model the species need not differ in life history, but must inhibit their own growth less than that of the other ,species.

   The (8) Spatial Mass Effect suggests that competitive exclusion is prevented by repeated invasion from nearby habitats. The two explanations (9) Circular Competitive Networks and (10) Cyclic Succession also imply continuous change, but the change is autogenic. In the case of Circular

Competitive Networks, individuals of different species replace each other by interference; in Cyclic Succession communities replace each other because of their effects on the environment.

   Aggregation of plants of a species (11), and the length of life of woody plants, are processes which will at least slow competitive exclusion.

   In Stabilising Coevolution (12) the change is genetic, not ecological. Natural selection is suggested to improve the competitive ability of a minority species, either in general or against the majority species.

Evidence

There have been a number of reviews of the theory of various of these mechanisms (e.g. Connell, 1978; Aaarssen, 1983; Shmida and Ellner, 1984; Shmida and Wilson; 1985; Grubb, 1986; Chesson, 1986), but no review has been made of evidence on which of the proposed mechanisms operate, or on their relative importance. This paper examines evidence for the various mechanisms in the case of New Zealand indigenous terrestrial vascular plant communities. There are two reasons for choosing N.Z.:

(a)   A world-wide review would be impracticable. N.Z. offers a discrete area for examination.
(b)   New Zealand vegetation developed completely free of human influence until 1000 years B.P. Until the advent of Europeans about 150 years B.P., human impact was much lower than in most areas of the world. Even 1000 years is within a generation or two for some species. Therefore, the original vegetation can be reasonably reconstructed.

The problem of spatial scale

Solutions to Hutchinson's paradox are scale-dependent (Grubb, 1987). The Paradox of the Plankton is how so many species coexist *within* a community (high alpha diversity). Ecologists are generally less worried how there can be different species in different communities, since this can be explained by environmental differences, though other factors such as disturbance or chance are sometimes invoked.

   Since discrete communities usually cannot be distinguished, the appropriate scale is difficult to determine and essentially arbitrary, but we can set some limits. In most terrestial communities, sites 10 m apart would be seen as being in the same community (though with obvious exceptions); a site 1000 m away would be seen as potentially in a different community, even in tropical rain forest (Williams *et al.,* 1969).

Whittaker used 10^3 m^2 (0.1 ha) for his within-community (alpha diversity) studies (e.g. Naveh and Whittaker, 1979). Shmida & Wilson (1985) regarded the area 10^2 - 10^4 m^2 as the upper limit of within-community scale. Here the value of 10^3 m^2 is used when a definite scale is required.

1. Niche diversification
(Connell, 1978; 'Gaussian coexistence' and 'Selection leading to niche differentiation' - Aarssen, 1983; 'Niche relations' and 'Habitat diversity' - Shmida and Wilson, 1985)
Concept
The oldest explanation for coexistence is that co-occurring species differ in niche (Connell 1978). The difference in niche will often be intrinsic to the species, though it could arise from co-evolutionary character displacement (Connell, 1980). For stability to result, there must be density-dependent performance (growth or survivorship), such that when a species is rare relative to its equilibrium frequency, the particular resource it uses is depleted proportionately more, and the species performs better.

Only alpha niche (= resources niche) differences can explain within-community coexistence; Beta niche (= geographical niche = conditions niche) differences are irrelevant to within-community richness (Pickett, 1980) unless they are on a fine spatial scale.

Niche differentiation can occur in time, but it is not sufficient for there to be a simple oscillation in advantage as some have suggested ("first one species, then another, then the first again (etc.) has the competitive advantage" - Aarssen 1983), because one of the two species will have the lesser long-term population growth rate, and competitive exclusion will occur. As in non-temporal niche differentiation, a density-dependent mechanism is required, so that a species gains more in its favoured phase when it is rare than when it is common.

(Differences between *r* and *K* species are the Intermediate-timescale Disturbance (5) mechanism. 1 do not believe Grubb's (1977) term the 'Regeneration Niche' to be a useful one.)
Evidence
The synusial niche
Differences in stratum/synusia are very obvious. Stratification is particularly well developed in N.Z.'s forests (Dawson and Sneddon, 1969; Bee *et al.,* 1989), with several strata and with many climbers and epiphytes (Oliver, 1930), but even grasslands in N.Z.

show considerable stratification (Scott, 1965). However, Wilson (1989) could find little evidence that stratification was important in community structure.
The phenological niche
Elsewhere, staggering of species' flowering times within a community has been observed, sometimes with indication of statistical significance (e.g. Ranta *et al.,* 1981, in Scandinavia), and interpreted as pollination niche differentiation. This is of relevance for coexistence only if there is competition for pollinators or dispersers.

Bliss and Mark (1974) observed a range of species' flowering times in Rock and Pillar Range alpine vegetation. However, in alpine vegetation in Nelson, Clarke (1968) found that 25-28 of the 31 species were in flower together in January. It might be expected that phenology would be less varied with the shorter season of alpine environments.

Scott (1977) gave evidence for differences in timing of shoot extension growth in Mt Ruapehu subalpine communities, for example maximum extension in *Schoenus pauciflorus* was in December, but maximum dry-weight growth in *Dracophyllum recurvum* was in January-February. It is not easy to see this as a mechanism for coexistence in evergreen species, unless nutrient uptake patterns are correlated with morphological growth (Rogers and Westman, 1979; Veresoglou and Fitter, 1984).

Leathwick (1984) found that vegetative phenology of shrubs and small trees in North Island forests was similar between species, though several canopy trees showed a different pattern. Flowering and fruiting phenology was more varied, which could show evolutionary divergence. He made no analysis of whether phenology tended to be more different between species that often co-occurred. Bussell (1968) found differences in vegetative phenology between native tree species; for example maximum rate of leaf appearance for *Nothofagus solandri* was in October, that of *N. fusca* in January.
The rooting-depth niche
Cameron (1963) showed that, at least in pumice soil, the root distribution of *Dacrydium cupressinum* was deeper than that of *Beilschmiedia tawa* - potentially niche differentiation.
The beta niche
Beta niche differentiation smaller than the spatial scale considered can explain the Paradox of the Plankton. Little is known of small-scale environmental/vegetation variation in N.Z., though it

has been found in alpine herb fields (Weir and Wilson, 1987), alpine fellfields (Mark and Bliss, 1970), ephemeral stream channels in forest (Stewart, 1986) and forest pit and mound topography (Adams and Norton, in prep.).

Conclusion

It seems likely that there is considerable niche differentiation within N.Z. communities, but little attempt at documentation has been made.

Another approach is that if the number of niches is the main determinant of species richness, variance in species richness within a community should be lower than in a null model (Wilson *et al.,* 1987). Wilson and Sykes (1988) examined a number of communities around Dunedin by this method, and found no evidence for niche limitation.

2. Pest pressure

(Gillett, 1962; 'Compensatory mortality' - Connell, 1978; 'Escape hypothesis' - Howe and Smallwood, 1982; 'Predator pressure' - Shmida and Ellner, 1984).

The concept

When pests ('pest' here includes diseases) reduce growth or survivorship, and such reduction is greater in the currently more common species, mixtures can be stable (Gillett, 1962; Connell, 1970; Janzen, 1970). Janzen *(op. cit.)* suggested that the spatial result would be maximum regeneration at some distance from the parent (Fig. la). Armstrong (1989) produced a formal model of the process.

Three conditions are needed for this mechanism to operate:
i.   Impact: the pest has to significantly reduce the growth or survivorship, and eventually the reproduction, of the host.
ii. Specificity: the pest has to be more or less species-specific.
iii. Density-dependence: spread of the pest must be slower in mixtures of the host with plants of non susceptible species than in monoculture.

Selective vertebrate herbivory can operate in the same manner (Fowler, 1988a). In indigenous N.Z. this would be mainly by flightless birds.

Evidence

Insects: impact

In N.Z. grassland, scarabaeid beetle larvae are important pests, especially *Costelytra zealandica* in lowland and montane tussock grassland, *Odontria* spp. in subalpine and alpine grassland and *Pyronota*
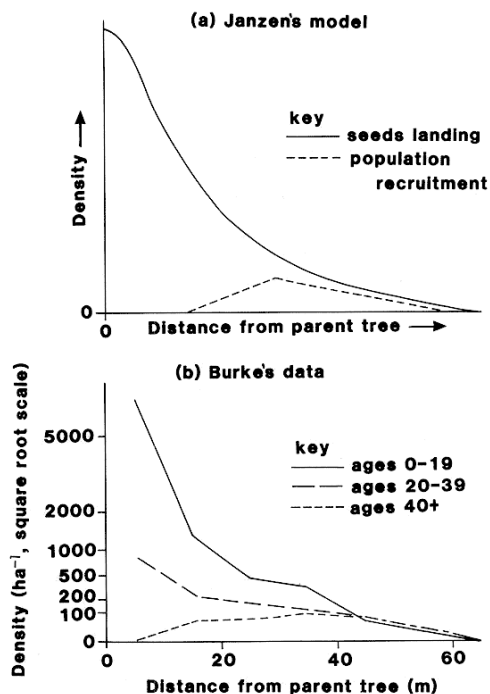

Figure 1: *Density of tree seedlings of different ages at various distances from a parent tree. (a) Janzen's model, based on his Pest Pressure theory, (b) Data for Podocarpus hallii on Mt Tarawera N.Z. (equal area basis: Burke, 1974).*

spp. in scrub (Scott, 1984).

Dawson and Ie Comte (1978) report mealy bugs that kill *Aciphylla* spp.

Insects are also important pests of all *Nothofagus* forests (Milligan, 1974). The greatest literature on pests of N.Z. plants is of *Nothofagus* pests; indeed the total of 22 monophagous insects is the second highest in the flora (Dugdale, 1975). Epidemics of *Nascioides enysi* larvae occur on *Nothofagus* spp., perhaps causing significant mortality (Morgan, 1966), at least predisposing it to *Platypus* beetle attack (Milligan, 1974); however, *N. enysi* normally attacks after other damage (Conway, 1949; Morgan, 1966), and may not be a cause of *Nothofagus* mortality at all (Wardle, 1984). Epidemics of *Proteodes carnifex* larvae can occur on *Nothofagus solandri* over wide areas and last 2-3 years (Dugdale, 1965); infestation can completely defoliate a tree, remove the lower

buds, and kill the tree (Wardle, 1984). *Epichorista emphanes* larvae epidemics (Milligan, 1974) can defoliate over extensive areas (Wardle, 1984). The armoured scale *Inglisia fagi* can be epidemic on *Nothofagus fusca,* especially after ecological stress (Hosking and Kershaw, 1985), defoliating the upper crowns over wide areas, with associated and perhaps resulting mortality (Milligan, 1974; Wardle, 1984).

Insects: specificity

Pest host-specificity, the second condition above, is high in N.Z.; 27% of N.Z. tracheophyte genera have monophages, including many gymnosperms (Dugdale, 1975).

All of the *Nothofagus* pests mentioned above have narrow specificities. *Nascioides enysi, Proteodes carnifex* and *Epichorista emphanes* larvae are found only on *Nothofagus* (Milligan, 1974; Rawlings, 1953). *Inglisia fagi* is almost specific to *N. fusca* (Spiller and Wise, 1982).

Insects: density-dependence

The only N.Z. study of the effect of host density on insect populations seems to be that of Frazer (1984), who examined the distribution of the scale insect *Anoplaspis metrosideri* on its host *Metrosideros umbellata*. There was no evidence for greater infestation when the host plants were denser.

Burke (1974) found young seedlings of *Podocarpus hallii* clustered close to the parent, but older offspring were at maximum density further away (Fig. 1b). This exactly matches the pattern Janzen (1970) predicted due to pest dispersal and density-dependent survival (Fig. 1a), though Burke interpreted it by allelopathy.

There has certainly been no direct experiment in N.Z. on the effect of insects on diversity, comparable to that of Henderson and Clements (1980).

Diseases: impact and specificity

There are many native disease organisms of N .Z. higher plants (Dingley, 1969). Whilst some, mainly wood rots (e.g. the fungus *Phellinus scruposus),* have been found on many unrelated hosts, most have been recorded on only one (e.g. the rust *Puccinia aucta* on *Lobelia anceps),* or on several related species (e.g. *Mycosphaerella coacervata* on *Coprosma* species). In contrast to insect pests, few parasitic fungi attack *Nothofagus* species (Gilmour, 1965). *Cyttaria* species attack only *N. menziesii* (Dingley, 1969), and weaken the tree appreciably (Gilmour, 1965). Very few bacterial diseases of native plants are recorded, though *Xanthomonas laureliae* infects (only) *Laurelia novae*

zelandiae, and can cause severe defoliation (Dingley, 1969). No significant nematode pest is known of native plants, and only Phormium yellow leaf virus amongst viruses.

Diseases: density-dependence

I know of no quantitative estimate of the effect of taxon-specific diseases on N.Z. native plants, comparable to the survey by Burdon and Chilvers (1974) for Australia. *Cyttaria* is said to spread more *slowly* in dense stands (Gilmour, 1965).

Birds: impact, specificity and density-dependence

Before extinction, about 1400 AD, grazing moas (large flightless rattites) probably had a large impact on N.Z. vegetation (Batcheler, 1989). Caughley (1989) estimates a moa biomass in southern N.Z. of 2000 kg km^{-2}. They could have promoted Pest Pressure coexistence if moa species, to some degree specific in diet, coexisted at any site. There is evidence that often many moa species did coexist (Caughley, 1989; Atkinson and Greenwood, 1989). Atkinson and Greenwood *(op. cit.)* suggested that because of differences in body weight, height, bill and gizzard characters, species of moas would have fed on different plant species. However, the diet of moas in general is controversial (Burrows, 1989; Batcheler, 1989), let alone the diet of particular species. There is little possibility of testing density dependence. The possibility of moa-mediated Pest Pressure remains untestable.

Conclusion

Pest Pressure may foster diversity, but evidence is sparse. The weakest link in the evidence for N.Z. Pest Pressure is that for density-dependence, as elsewhere (Augspurger, 1988).

Nothofagus species, to a far greater extent than other native woody plants, frequently form almost arboreally-monospecific communities. By the Pest Pressure theory, pests of *Nothofagus* should be particularly abundant in such communities, and although no direct comparison has been made this is indeed the impression one gets from the literature. This can be taken as support for the Pest Pressure theory, which predicts that pests should more more prevalent in monocultures. Yet the continued existence of these monocultures is also evidence that Pest Pressure has not been effective in causing arboreal diversity.

3. Equal chance

(Connell, 1978; 'Lottery' - Sale, 1977; 'Equal-chance lottery competition' - Shmida and Ellner, 1984; 'Ecological equivalency' - Shmida and Wilson, 1985).

The concept

Chance explanations have been advanced for vegetation patterns in a wide range of communities (e.g. Palmgren, 1929; Martin, 1959; Schafale and Christensen, 1986). Several workers have suggested that within an area of tropical rain forest there exists a pool of species that are ecologically very similar, and that chance of dispersal determines which will occupy a particular site (e.g. Schulz, 1960; Hubbell and Foster, 1986). In New Zealand, Veblen and Stewart (1980) advanced a similar explanation for the colonisation of canopy gaps by *Dacrydium cupressinum, Weinmannia racemosa* or *Metrosideros umbellata*. The latter workers emphasised seed/seedling availability, no doubt bearing in mind the prevalence of mast seeding, and the ability to remain as suppressed seedlings, of many New Zealand tree species.

Equal chance implies equal competitive ability. Recently, some ecologists have come to believe that whilst competition in many plant communities is intense, many species can be similar in their competitive ability (Goldberg and Werner, 1983). The crucial moment may be at the seedling stage; it is possible that once a plant occupies a site others are excluded, though only when competition is for light (Wilson, 1988a). Differences in establishment success might be due to year-to-year environmental fluctuation (Fowler, 1988b), which is temporal Niche Diversification (Mechanism 1). It might be due to variation in seed rain (Agren and Fagerstrom, 1984; Roberts & Christensen, 1988; Sharik *et al.,* 1989), though the seed rain is likely to be environmentally-controlled. However, where establishment is purely by chance, and site pre-emption occurs, the Equal Chance mechanism will operate.

Evidence

Smida and Wilson (1985) considered that when a species-area curve for an apparently uniform habitat showed a steady upward trend, this was evidence for the operation of Equal Chance, especially when curves from other habitats in the area showed saturation. At best this is very indirect evidence. The only species-area curve that I know has been published for N.Z. is that of Beever *et al.* (1968).

Sykes and Wilson (1987) eschewed chance as an explanation in a vegetation type (slack) where several ecologists have invoked it.

On islands, a direct test of determinacy versus chance (assuming that incidence functions are not important) is available in a test for nesting. Wilson (1988b) found plant species nesting among islands of Lake Manapouri to be significant, but far from complete. His analyses pointed to habitat control rather than chance, at least for native species.

The most well-known invocation of chance is the Island Biogeography model of MacArthur and Wilson (1963), based on probabilistic immigration and extinction. However, Quinn *et al.* (1987) and Kelly *et al.* (1989) could find little evidence for its operation in Lake Manapouri islands.

Conclusions

Few have suggested a role for chance in determining the composition of N.Z. vegetation. Chance is very difficult to prove or disprove; it is usually invoked when other explanations are not apparent.

4. Gradual climate change

('Gradual change' - Connell, 1978; 'Competitive equilibrium is prevented by fluctuating conditions' - Huston, 1979; 'Temporal mass effect' - Shmida and Ellner, 1984; 'Storage effect' - Warner and Chesson, 1985).

The concept

Hutchinson's original (1941) explanation for the Paradox of the Plankton was that if there is environmental change, some species will be favoured in some conditions, other species in others. This is a non-equilibrium explanation - that the community is constantly changing in response to climate change. Thus, the community will comprise a mixture of species favoured by the current environment, with remnants of species favoured by the previous environment. The latter species may fail to regenerate completely under the current environment, and so be represented only by old individuals. The alternative name 'Storage effect' emphasises that it is based on carryover from the previous environment, either because of the length of life of individuals/clones, or because of storage in the seed pool (Grubb, 1988). Alternatively, remnant species may regenerate, but at an insufficient rate to maintain the species long-term (i.e. a negative population growth rate), so that the species will be eliminated only after several generations. Either way, there is a lag in the

vegetational response to climate change. Levins (1979), Warner and Chesson (1985), Comins and Noble (1985) and others demonstrated the effect was mathematically possible.

Connell (1978) suggested the process would operate only for environmental change on an intermediate timescale. Rapid environmental change will not allow coexistence by this mechanism because there will not be time for the vegetation to change, so all species must be able to tolerate the range of conditions (though opportunity for temporal niche differentiation would exist). For example, a ubiquitous rapid environmental change is the day:night cycle. All species must be able to tolerate this daily environmental change, and over many such cycles one of two competitors occupying the same niche will tend to be eliminated (Hutchinson, 1953). Therefore, diversity is not promoted. Very slow environmental change will not promote coexistence, because the community composition will have time to change, and competitive exclusion will occur (Hutchinson, 1953).

Even if the mechanism does not lead to permanent coexistence, the storage effect may slow competitive exclusion enough for other mechanisms to operate (Fowler, 1988a).

The Gradual Climate Change mechanism differs narrowly from temporal Niche Differentiation (mechanism 1) in that some of the species involved are on their way to local extinction, and thus there is a turnover of species.

Evidence

Holloway Climate Change hypothesis

Speight (1911) and later workers (notably Holloway, 1948, 1954) proposed that there had been significant climate change in N.Z. within the recent past (Holloway suggested within the last millennium, probably 1200-1300 AD), viz. increasing aridity and decreasing temperature (Holloway, 1948). Later workers have estimated a later time for the climatic deterioration: 1600-1800 AD (Wardle, 1963), 1500-1900 AD (June, 1982). Holloway's evidence and that of later workers (especially Wardle, 1963; June 1982) was largely from the population size structure of existing forests, especially lack of regeneration in such species as *Dacrydium cupressinum, Prumnopitys taxifolia* and *Libocedrus bidwillii*. Some of this evidence has also been explained in other ways (Foweraker, 1923; Poole, 1953; Veblen and Stewart, 1982; and see Wardle, 1985). For example, Beveridge (1983) and Norton *et al*. (1988) suggested regeneration would not be expected beneath a dense canopy;

regeneration would occur when the canopy broke. Molloy (1969) reviewed the literature, and concluded that all the forest structure evidence could be explained in alternative ways.

Independent evidence has been claimed for climate change: subfossil logs above the current treeline (Raeside, 1948), lack of *Chionochloa* spp regeneration (Raeside, 1953), invasion of *Chionochloa* spp grasslands by *Festuca novae-zelandiae* (Tussock Grassland Research Committee, 1954), changes in *Nothofagus* establishment (Haase, 1989b), soil/climate relations in Otago and Canterbury (Raeside, 1948), pollen analysis (Harris, 1955; Moar, 1966; McGlone and Bathgate, 1983; Lees, 1986), glacial advance/retreat (Gellatly and Norton, 1984; Gellatly, 1985), sediment patterns on the Canterbury plains (Raeside, 1948), speleothems (Burrows and Greenland, 1979) and direct temperature records (Salinger *et al.,* 1983). Burrows and Greenland (1979) concluded there was evidence for climate change, but conflict on the details. Norton *et al*. (1988) saw more basic difficulties, for example of how a small temperature drop could affect regeneration of *Dacrydium cupressinum* throughout New Zealand. Any climate change is likely to affect severely only those populations at one end of the ecological/geographic range, and cause only local extinction. McGlone (1988) suggested a change in the wind pattern, especially incursion of cold polar air, could have effects on climate over much of N.Z. He cites effects of polar air as increased evapotranspiration, stunting of tree growth and felling of trees.

Bathgate (1981) carefully re-evaluated Holloway's evidence at one of the latter's principal sites, the Longwood Range. The population structure suggested there had been little regeneration of *Dacrydium cupressinum* from about 1600 to 1850 AD. Ring widths showed diameter growth had been lower in this period. Bathgate took this as evidence that there had indeed been a cooler and perhaps damper period, at least in Southland, though at a later period than Holloway suggested.

Some such vegetation change might be only in relative species abundances, and thus not affect richness, but in several situations Holloway envisaged species becoming locally extinct (e.g. podocarps in some Southland forests and Westland hill forests - Holloway, 1954). ('Podocarp' is used to indicate members of Podocarpaceae, in the papers referred to here predominantly *Dacrydium cupressinum*.)

Under the Holloway hypothesis, trees in many forests would be remnants from vegetation in

equilibrium with the previous climate, especially since podocarps can live for a millenium. Thus, Holloway (1947) saw occasional trees of *Nothofagus menziesii* near Dunedin as chance remnants from past *Nothofagus* cover, though Wardle's (1967) interpretation was quite the opposite. Poole (1950) saw a pocket of *N. menziesii* on the Hauhungaroa Range as a remnant. Holloway (1954) saw *Lepidothamnus intermedius* and *Lagarostrobos colensoi* plants in pole *Dacrydium cupressinum* stands as remnants from bog forest under wetter conditions; though succession would be an alternative explanation. He saw pockets of *Nothofagus fusca* in *N. menziesii* / *N. solandri* forest in Southland and south Westland as remnants from a more favourable climate. Franklin (1967) saw *Halocarpus biformis* as a relict species in the Tararua and Ruahine Ranges. This was generalised in Robbins' (1962) interpretation of N.Z. 's lowland forests as a fusion of older podocarp forest and invading angiospermous forest.

A single climate change would not allow long-term coexistence since species composition would re-equilibrate (Connell, 1978), but at least Holloway (1954) envisaged further climate change before adjustment to the previous one was complete.
Successional relics
Relict species in a succession represent a similar process, on a smaller spatial scale and with soil factors sometimes predominant. For example, Smale (1984) found *Dacrycarpus dacrydioides* failing to regenerate in White Pine Bush; he suggested that *D. dacrydioides* became established after a volcanic eruption nearby, and was now failing to regenerate because of shade-intolerance of its seedlings. Sykes *et al*. (1991) found dying plants of *Phormium tenax* and *Carex secta* in the Taieri carr, where taller vegetation had overtopped them. Lough *et al*. (1987) considered that *Chionochloa rigida* was declining in a local 'retrograde succession'; however, their Markovian model did not predict it would be eliminated from the community.
Conclusion
Almost all the suggestions under the Holloway hypothesis are for canopy dominants, perhaps partly because they are conspicuous and also because many of the workers were: foresters. I know of no suggestions on whether understorey species are also remnants. Will understorey species lag for a shorter time, because of their shorter life cycles, or will they lag for longer because they are buffered from the physical environment? Holloway (1954) seems to assume, especially in the case of *Prumnopitys taxifolia*

forests, that the small-tree and herb strata persist after the canopy has gone. Similarly, the Tussock Grassland Research Committee (1954) suggested five lower stratum herbs as indicators of former *Chionochloa* sp. grassland. I know of no suggestions whether subordinate species from the previous climate have disappeared from particular communities, or whether species have immigrated as a result of the climate change. In no case is speculation on vegetation response to climate change supported by experimental evidence on temperature or moisture tolerance of the species.

The Holloway Climate Change theory in N.Z., once widely accepted, has recently been doubted. It is true that some papers advocating it contained little data to directly support their theories. However, Holloway's 1954 paper is obviously based on much careful field observation. Wardle's (1963), Bathgate's (1981) and June's (1982) data for a widespread regeneration gap cannot be easily dismissed, though the removal of moas and other browsers, and the introduction of rats, by Maori, are alternative explanations (Wardle, 1979; June, 1982). Pollen analysis shows considerable vegetation change throughout the past 15,000 years (Burrows, 1979; McGlone *et al.,* 1984; Newnham *et al.,* 1989), and there is no reason to suppose this is not continuing. There is direct and indirect evidence for climate fluctuation on all time scales. This must affect plant establishment and growth, as has occasionally been documented (e.g. Haase, 1989a). The few long-term studies of plant communities have shown continual change in species dominance (Watt, 1981; Grubb, 1986), apparently caused by subtle climate change (Watt, 1981; van der Meijden *et al.,* 1985). Haase (1986a) showed year-to-year variation in the growth of *Brachyglottis buchananii,* that could be related to temperature, but there seems to be no record in N .Z. of variation in species composition. However, it would be surprising if Gradual Climate Change were not a factor currently enabling coexistence in N.Z. plant communities.

5. Intermediate-timescale disturbance
('Intermediate disturbance' - Connell, 1978; 'Colonization hypothesis' - Howe and Smallwood, 1982; 'Patch dynamics and regional coexistence' - Shmida and Ellner, 1984; 'Regeneration niche' - Grubb, 1977).

Concept

Connell (1978) suggested that very frequent disturbances will exclude all species except those maturing quickly. Very infrequent disturbance will also result in low diversity, because competitive exclusion will occur (Huston, 1979; Pickett, 1980). At intermediate frequencies of disturbance, there will be patches of different disturbance ages, newly-disturbed patches bearing *r* species and old patches bearing *K* species (Pickett, 1980), resulting in among-patch coexistence. The *r* species must be able to disperse to the disturbance patches (Pickett, 1980; Armstrong, 1988).

This mechanism helps to explain the Paradox of the Plankton only if the patches are within-community in spatial scale (Pickett, 1980), defined here as less than 10^3 m^2.

Intermediate-timescale Disturbance differs from (4) Gradual Climate Change in that (a) there is premature death of plants (not just failure to regenerate), (b) typically all species are killed, (c) the disturbance is sudden, and (d) the effect is a temporary one, with eventual restoration of the original species composition of a patch. The two mechanisms might also be connected, in that an environmental change might alter the disturbance regime.

Evidence

Types of Disturbance

Many types of disturbance have been suggested for the N.Z. environment (Table 1).

The first five types listed, wind, floods, natural fires, volcanic eruptions and earthquake-induced slips, will typically occur on too large a spatial scale to explain alpha richness. Glaciation, even local glaciation, would occur on too great a spatial scale, and too long a timescale. The next four types, soil erosion/deposition, landslides, snow avalanches and riverbank erosion, probably occur on too large a spatial scale for there to be mosaics within 10^3 m^2. Drought, frost and hail will generally occur on too large a spatial scale, and not all species will be affected (Atkinson and Greenwood, 1972; Allan, 1944). Bird trampling could increase alpha diversity; characteristic species are indeed found in burrow areas (Gillham, 1960; Burrows, 1972), but the semi-permanence of these areas makes this more of an environmental factor.

The last three factors, individual tree death and/or windthrow, snow break and freeze-thaw soil heave in the alpine zone, seem likely to occur on the required spatial scales in space and time. Stewart (1986) found tree-fall gaps 100-500 m^2 in size. Veblen

Table 1: *Types of disturbance suggested for New Zealand terrestrial plant communities.*

	Type	Reference
1	Wind (gales, cyclones)	Hutchinson (1932), Thomson (1936), Greenwood (1949), Grant (1963), Shaw (1983), Jane (1986)
2	Floods	Scott (1963), Cox and Mead (1963)
3	Natural fires	Molley *et al.* (1963), Wraight (1963), Fleming (1963), Dodson *et al.* (1988)
4	Volcanic eruptions, with ash showers, wind blast, avalanches and ash-flow.	Nicholls (1959), Vucetich and Pullar (1963), Taylor (1953), Sykes, (1965), Druce (1966b), Timmins (1982).
5	Earthquake-induced slips	Robbins (1958)
6	Glaciation	Moar and Suggate (1979)
7	Soil erosion and deposition	Archer (1979), McGlone and Topping (1983)
8	Landslides	Dils (1965)
9	Snow avalanches	Conway (1977, in Wardle 1984)
10	Riverbank erosion	Wilson (1985)
11	Drought	Jane and Green (1983, 1986), Grant (1963, 1984)
12	Frost	Baylis (1958)
13	Hail	Shaw (1987)
14	Bird trampling	Fineran (1966, 1973)
15	Individual tree death and/or windthrow	Hutchinson (1932), Thomson (1936), Six Dijkstra *et al.* (1985), Stewart (1986).
16	Snow break	Elder (1959), Druce (1966a), Wardle and Allen (1983)
17	Freeze-thaw soil heave	Bliss and Mark (1974)

and Stewart (1980) interpreted even-aged or bimodally-aged clumps 450 m2 to about 1000 m^2 in areas as erstwhile canopy gaps. However, Six Dijkstra *et al*. (1985) found that once the canopy was opened quite large patches could be affected. Windthrow of individual trees blurs any distinction between climax conditions and disturbance.

Thus, although disturbance patches have been considered the norm in podocarp forests (Hutchinson, 1928; Six Dijkstra *et al.,* 1985), *Nothofagus* forests (Thomson, 1936) and *Agathis australis* forests (Latter, 1932; Ogden, 1985), only individual tree death and/or windthrow, and snow break, could be effective in promoting forest alpha diversity.

Disturbance-requiring species

Is has been suggested that N.Z. has a deficit of early-successional species, with few annuals (Allan, 1937), and few woody mid-successional species (Dansereau, 1964). Indeed, Roxburgh *et al*. (1988) found it hard to identify a single colonist species in the Old Man Range high-alpine. Stewart (1986) analysed the specific composition of forest gaps, and there is no clear evidence in his data that there are species occurring only in gaps, and thus no clear evidence that the gaps increase diversity.

However, some forest species once seen as climax species have been reassessed as incapable of regenerating in climax conditions, (e.g. under their own canopy) and therefore as requiring disturbed patches for their presence in an area (Table 2). Hutchinson (1928) and Six Dijkstra *et al*. (1985) suggested *Dacrydium cupressinum* regenerated mainly after disturbance. However, the more direct evidence

of Baxter and Norton (1989) indicates that after logging disturbance *D*. *cupressinum* regenerated, within the first few decades after disturbance, only from already-established seedlings and saplings and therefore only when the disturbance was mild enough for them to have remained. Other species have been considered to occur only in canopy gaps: *Litsea calicaris* and *Knightia excelsa* (Smale and Kimberley 1983), *Metrosideros excelsa* and *Vitex lucens* (Percy 1955-6).

There is very little autecological evidence for most the species in Table 2. In fact Warrington *et al*. (1989) found *Dacrydium cupressinum* to be rather shade-tolerant.

In stratified communities, disturbance can occur separately in each stratum. For example, Stewart (1986) showed that *Grammitis billardieri* and *Nertera dichondraefolia* occurred predominantly on fallen logs, a disturbance of the lower strata.

Multi-generation effects

Both theoretical models and interpretation of real data have generally assumed that the *r* species are unable regenerate once the *K* species arrive. Ogden *et al*. (1987) suggested an interesting variant for *Agathis australis,* that it was able to produce some regeneration under the succeeding canopy, but not enough to give a positive population growth rate, and therefore not enough to reproduce the population size of the previous cohort. They therefore envisaged a series of *A*. *australis* cohorts of decreasing size. The concept is similar to one mentioned under Gradual Climate Change, except that is it initiated by disturbance, not by climate change.

Table 2: *Suggestions in the literature that species, previously regarded as 'climax' species, require disturbance.*

Species	References
Agathis australis	Latter (1932), Mirams (1957), Pook (1979)[1]
Dacrydium cupressinum	Foweraker (1924), Veblen and Stewart (1980)
Libocedrus bidwillii	Poole (1953), Clayton-Greene (1977), Veblen and Stewart (1982), Norton (1983), Haase (1986b)
Loxoma cunninghammii	Bergquist (1957-60)
Metrosideros robusta	Grant (1963)
Metrosideros umbellata	Veblen and Stewart (1980), Allen and Rose (1983), Stewart and Rose (1989)
Podocarpus totara	Foweraker (1922)
"totara"	Nicholls (1963)
Nothofagus fusca	Grant (1963), Ogden (1988)
Nothofagus solandri var. *cliffortioides*	Ogden (1988)
Phyllocladus trichomanoides	Pook (1979)
Weinmannia racemosa	Veblen and Stewart (1980)

[1]Ogden *et al*. (1987) have a different emphasis

 Direct regeneration

The Intermediate-timescale Disturbance mechanism works by disturbance allowing *r* species to invade before the *K* species can reoccupy the site. This does not necessarily happen. In podocarp-dominated forests, a sere can occur with *r* species later giving way to *K* species (Hutchinson, 1932), but in some *Nothofagus* forests disturbance produces a crop of young *Nothofagus,* not other tree species (Wardle and Allen, 1983), "no species foreign to the association ever gaining a place" (Cockayne, 1926). Thus, *Nothofagus* spp are 'climax' species that readily act as pioneers (Holloway, 1948), especially *N. menziesii* (Holloway, 1946), and even (or especially) when the mineral soil is revealed (Reid, 1948; Thomson, 1936). Similarly, Roxburgh *et al*. (1988) found that in an alpine succession in Central Otago there were no species restricted to the pioneer stages.

Conclusion

Disturbance is now considered an important determinant of the vegetation cover of landscapes, and source of large- and medium-scale community differences (White, 1979; Pickett *et al.,* 1989; Whitmore, 1989). However, it does not necessarily explain coexistence at the spatial scale we are considering. There is a need for documentation on the spatial scale of disturbances in N.Z. communities, and of the vegetational response to disturbance. Different types of disturbance may have different effects (Collins and Glenn, 1988), but there is insufficient documentation to know to what extent this is true for New Zealand.

6. Life history differences

('Alternate [sic] life-history strategies' - Shmida and Ellner, 1984; 'Species differing in regeneration properties' - Fagerstrom and Agren, 1979; 'Musical chairs' - Crawley, 1986).

The concept

Skellam (1951) considered a model in which two (annual) species occupy single-plant safe sites. Species S, is the better competitor, and eliminates species S, if it reaches a site, but it has less efficient reproduction/dispersal, and therefore leaves some sites available for S, to occupy. Hutchinson (1951), Levins and Culver (1971), Geritz *et al*. (1988) and Britton (1989) discussed similar models.

This can be distinguished from (1) Niche Differentiation in that no environmental heterogeneity. nor differences between species in

resources used, are required. It can be distinguished from (5) Intermediate-timescale Distarbance in that (a) the gaps are caused by monocarpic or seasonal death, not by external disturbance, and (b) species S I is limited only by dispersal, not by its ability to tolerate the environment of the gap. It can be distinguished from (3) Equal Chance in that, though there is a random element, it acts via dispersal; the competitive abilities of the two species are very different.

Evidence and Conclusion

Grubb *et al*. (1982) found some evidence for coexistence by this mechanism on an English sand dune, but there is no evidence from N.Z. Although this mechanism is formally distinct from others, nature is rarely that simple, and I doubt whether it could be found in its pure form.

7. Initial patch composition

Levin (1974) suggested that if two species occupy small, transient patches, and each species inhibits its own growth less than that of the other species, coexistence is possible. Some patches will by chance have more individuals of one species than the other, and that species will suppress the other in that patch. I know of no attempt to apply the model to plants, nor do I know how it could apply.

8. Spatial mass effect

(Shmida and Ellner, 1984; 'Mass effect' - Shmida and Wilson, 1985; 'Refuges' - Crawley, 1986).

The concept

Shmida and Ellner (1984) suggested that the species richness of a patch could be increased by the immigration of seeds from nearby habitats, of species that can survive but would not have a positive population growth rate in the patch itself. The population of such a species is maintained in marginal habitats only because seed immigration supplements local seed production in balancing mortality (van Steenis. 1972). Pulliam (1988) referred to these as 'sink habitats'.

Evidence

Edge effects

Shmida and Wilson (1985) showed high richness in some 'floristic transition areas' in Israel near to species-rich and environmentally diverse areas, and took this as evidence for the Spatial Mass Effect. Webb and Hopkins (1984) gave evidence for such an effect with invertebrates in small patches of heathland

in England. Hatton and Carpenter (1986) attempted to test the theory by comparing diversity round the edge of an environmental patch in pasture with that in the middle. However, a higher diversity at the edge could also be because more species were able to tolerate the ecotone conditions, or because the boundary fluctuated, or because the environment was patchy on a small spatial scale there.

Non-selfsustaining populations

The Spatial Mass Effect could be demonstrated by finding a species present in a community in which it could not reproduce. For example, Sykes and Wilson (in press) found *Dacrydium cupressinum* and *Dacrycarpus dacrydioides* in scrub immediately adjacent to the Cole Creek dunes. Not only were there no mature trees (the maximum height was 1.5 m), but because of the exposure to salt-laden winds it was inconceivable that a mature tree of either of those two species could establish there.

Grant (1963) referred to seed of 'foreign' species being distributed beyond the bounds of its mother forest type, but believed such species established only when there was open ground. Holloway (1947) saw the few podocarp trees amongst *Nothofagus* forest in the Waikaia Valley as chance establishments by bird-carried seed.

A dramatic case of the Spatial Mass Effect occurs in the Lost World Cavern, where de Lange and Stockley (1987) described a flora of 13 species of angiosperms; because of the low light few reach reproductive state, and the population is maintained by immigrant seed.

To demonstrate the Spatial Mass Effect it is not necessary that the immigrating species fails to reproduce, only that without immigration the population is not self-perpetuating, i.e. it has a negative population growth rate. The only examples I know of population growth rates calculated for N.Z. native species are one (but with estimated fecundities) for *Nothofagus fusca* (June and Ogden, 1978) and one for *Avicennia marina* (Burns and Ogden, 1985).

Conclusion

It must be common for seeds to be carried into an area in which the species cannot sustain itself otherwise. Few observations of this kind have been made in N.Z. The Lost World Cavern example is a clearcut case. For other cases, population growth rates would need to be calculated. Nevertheless, the paucity of suggestions in the literature of the presence of species that 'do not belong' to a community is surprising.

9. Circular competitive networks

('Circular networks' - Connell, 1978).

The concept

Harper (1964) suggested that competitive ability is not necessarily an absolute character, forming a 'pecking order' (Harper, 1977). It may be relative, i.e. dependent on the species competed against - the 'non-transitive competitive relationship' of Buss and Jackson (1979). This raises the possibility of Circular Competitive Networks, where species A beats B, B beats C, but C beats A. Connell (1978) suggested Circular Competitive Networks as a mechanism for coexistence.

Evidence and Conclusion

I know of no example of circular competitive ability in plants. Keddy and Shipley's (1989) analysis also suggests that competitive ability is normally absolute. Haizel and Harper (1973) claimed to find deviation from a pecking order, but there is no evidence of a circular network in their data. I know of no studies of competitive ability between native N.Z. plants.

10. Cyclic succession

('Cyclic regeneration' and 'Turnover in species composition between different habitat patches' - Shmida and Ellner, 1984).

The concept

Watt's (1947) concept of Cyclic Succession is similar to that of (9) Circular Competitive Networks, except that; (a) whole communities are involved, not individuals of particular species, (b) the cycle between species is caused by their effects on the environment, and (c) as few as two phases may be involved. Armstrong and McGehee (1980) produced competition models in which non-linear response to resource gradients could lead to cyclic coexistence. Cyclic Succession is not fully separable from (5) Intermediate-timescale Disturbance, since many disturbances are initiated partly because of the external environment and partly because of processes endogenous to the plant community (White, 1979).

Autoallelopathy could operate in a similar way (Aarssen, 1983; *contra* Fowler, 1988a); the autotoxins from a plant would reduce the survivorship of an individual, reduce the probability of regeneration on that site, and reduce the chance of individuals of the same species establishing nearby. For example, Newman and Rovira (1975) observed that the two most auto-inhibited species in their experiment
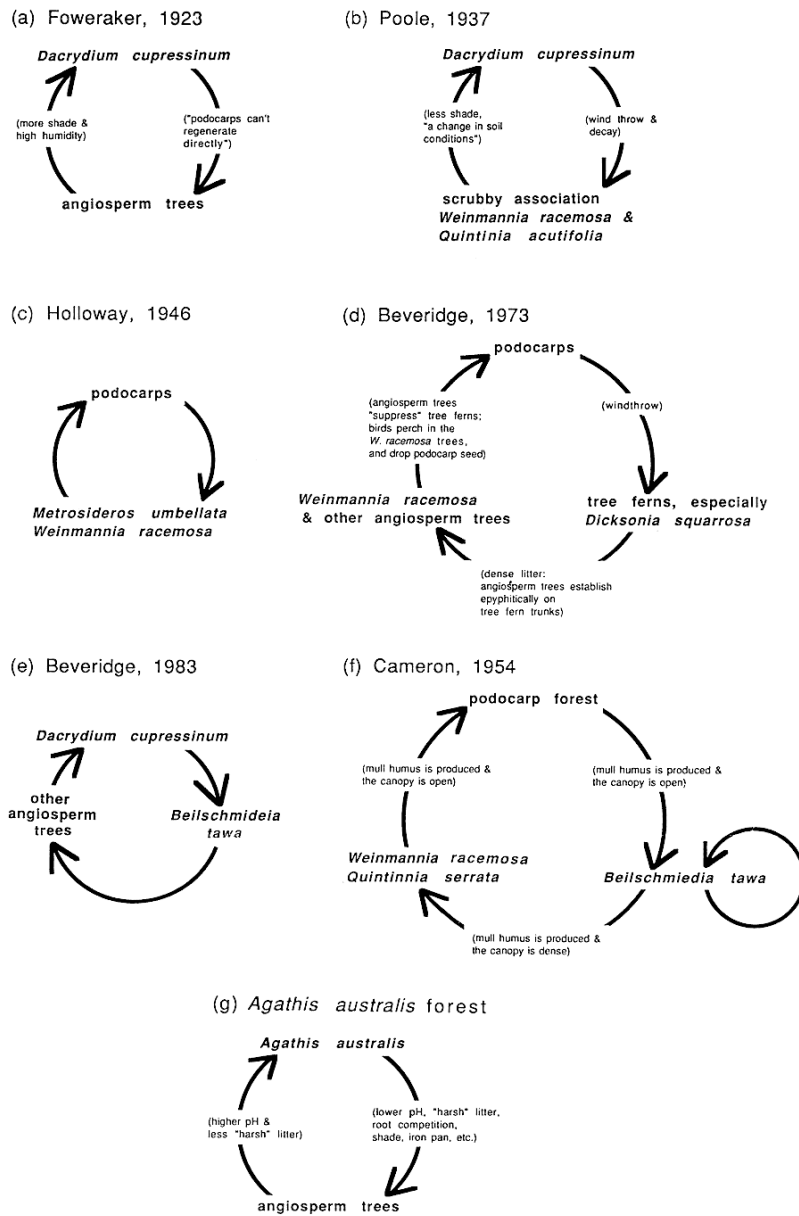
Figure 2: *Published hypothesis of Cyclic Succession for New Zealand forests.*

normally grew, in the wild in permanent grassland, as isolated individuals.

Evidence
Podocarp-angiosperm forest
Foweraker (1923) suggested that in West Coast forests, *Dacrydium cupressinum* cannot regenerate directly, but does under a nurse association of angiosperm trees (Fig. 2a). Poole (1937) made a similar suggestion for the West Coast (Fig. 2b), Holloway (1946) for Southland (Fig. 2c), and Beveridge (1973) for central North Island (Fig. 2d). (Herbert, 1986, gives evidence that birds do indeed drop podocarp seeds.) Beveridge did not explain why podocarps could not regenerate directly. In 1983 he proposed a similar cycle (Fig. 2e), again offering no mechanism. The suggestion remains an idea with no documentation.

Cameron (1954) put forward a similar concept (Fig. 2f). Explanation of the mechanism seems unresolved in parts. Cameron had little evidence, beyond a mosaic of communities in apparently uniform conditions, which Grant (1963) explained by disaster and climate change. Nicholls (1956) could find no evidence for such a cycle in Taranaki forests. Again, Cameron's suggestion remains but an idea.
Agathis australis forest
Mirams (1957) and others have suggested that *Agathis australis* stands are one phase of a cycle (Fig. 2g), that *A. australis* is unable to regenerate under its own canopy for a variety of reasons (Table 3). The authors making the suggestions have rarely provided evidence (Table 3), though *A. australis* litter is indeed slow to decay (Enright and Ogden, 1987). It is suggested (e.g.

Table 3: *Reasons given for the suggested inability of Agathis australis to regenerate under its own canopy, with indication whether the author gave any evidence for his assertion.*

Reason	Author	Evidence given?
amount of litter	Sando (1936)	-
	McKinnon (1945)	-
type of litter	Bieleski (1975b)	-
pH of litter	Blakemore and	-
	Miller (1968)	yes
root competition with	McKinnon (1945)	-
angiosperms	Mirams (1957)	yes
	Bieleski (1959)	-
shade of angiosperms	Sando (1936)	-
	Mirams (1957)	-
	Bieleski (1959)	yes
	Bieleski (1975a)	-
formation of iron pan	Sando (1936)	-

Bieleski, 1975a) that under the succeeding angiosperm trees the supposed soil changes are reversed. *A. australis* can then reinvade, extending above the canopy of angiosperm trees, suppressing their growth. Again no evidence is offered.

Ogden (1985) has questioned the basic assumption of these suggestions - a lack of direct regeneration of *A. australis* - reporting that many *A. australis* stands contain abundant seedlings of different sizes.
Other ecological situations
Weir and Wilson (1987) considered the possibility of cyclic succession between alpine cushion and herb field on the Rock and Pillar range, but rejected it.

There have been only preliminary reports of allelopathy for N.Z. native plants (Scott, 1975; Molloy *et al.*, 1978).

Conclusion
None of the suggestions can be regarded as supported by evidence. For the mechanism to increase alpha diversity, the patches of different phases must be on within-community spatial scale. Those ecologists in N.Z. suggesting cycles have generally envisaged a larger scale, individual patches of the mosaic being a few hectares (Bieleski, 1975b), or tens or even hundreds of acres (Cameron, 1954), though Beveridge (1973) envisaged a single-tree gap process.

11. Aggregation

The concept
Almost all plant species are aggregated in almost all communities (Kershaw and Looney, 1985). Silvertown (1987) and Czm-an and Bartha (1989) pointed out that this within-species aggregation will slow down species replacement, and hence slow competitive exclusion.

When aggregation is due to environmental heterogeneity, it represents beta niche differentiation. However, when aggregation is due to morphology or to limited dispersal, it becomes a mechanism in its own right. The mechanism is comparable to the storage effect aspect of (4) Gradual Climate Change.

Ives (1988) suggested specifically that aggregation would enhance Initial Patch Composition (mechanism 7), and Britton (1989) that aggregation could be the cause of the patches required for operation of Life History Differences (7).

Evidence
There have been few investigations of the pattern of species in New Zealand plant communities. Iball (1989), from surveys of some North Island forests,

concluded that, as in plant communities elsewhere, most species showed aggregation.

Conclusion

This is a mechanism for slowing competitive exclusion, not preventing it.

12. Stabilising coevolution

('Genetic feedback' - Pimentel, 1968; 'Selection leading to balance competitive abilities' - Aarssen, 1983; 'Selection for competitive combining ability' - Aarssen, 1985).

The concept

Aarssen (1983) proposed that, in a mixture of two species, there would be selection for increased competitive ability in the minority species. He suggested this would lead to stable coexistence. The main difficulties with this theory are: (a) species cannot increase their competitive ability indefinitely, especially since there will already have been such selection for many generations; and (b) even allowing for some ecotypic differentiation it is difficult to envisage a species adapting differently to each species it grows with (Goodall, 1966). Aarssen and Turkington (1985) gave some evidence for the process, though Evans and Turkington (1988) cast doubt on the work.

Pimentel *et al*. (1965) and Pimentel (1968) produced a very similar model, but one which overcomes the first objection above by assuming that different species exert different types of competitive pressure.

The mechanism contrasts with another postulated type of coevolution, that of Character Displacement leading to niche diversification (Connell, 1980), in that selection is for increased competitive ability, not separation of resource use.

Evidence

There is some evidence on within-species genetic differentiation in native N.Z. plants (Mark, 1965; Ogden, 1974; Greer, 1979, 1984; Wilcox and Ledgard, 1983; Ronghua *et al.,* 1984), little on within-population variation (Forde, 1964), and certainly no evidence with the detail required to test Aarssen's hypothesis.

Conclusion

The realism of Pimentel's and Aarssen's models depends on the strength of coevolution as a force. Davis (1981) assumed that periods in the order of 10,000 years were insufficient for coevolution; Aarssen and Turkington (1985) considered they had evidence

for its occurring in 40 years. This difference is partly because of different life spans, but I believe it also represents different views on the strength of coevolution as a force.

Rigorous evidence for any type of coevolution is very hard to obtain (Connell, 1980).

General conclusions

A major conclusion must be the lack of relevant information for many of the 12 mechanisms described. Whilst this may partly reflect paucity of study of N.Z. vegetation, and sometimes uncertainty as to what ecological hypotheses it is intended to test when data are collected, information would not be more available for many parts of the world. In spite of the lack of information, I shall attempt an evaluation the importance of the suggested mechanisms.

Some mechanisms I would dispatch. I do not believe that Initial Patch Composition (7) is an ecologically sensible theory. Circular Competitive Networks (9) have never been demonstrated between plants. Stabilising Coevolution (12) is an attractive theory, and potentially very powerful. I do not believe Aarssen's variant, because I cannot conceive of ever-increasing competitive ability. Pimentel's variant is more realistic. However, current ecological evidence is tending to support Gleason's (1917) model of plant community structure, a very loose one. If the controls on species composition are so loose, I find it hard to believe that the controls on genotypes within species are much tighter. Turkington and Harper (1979) claimed to have evidence for tight controls on interspecific genotypic adaptation, but Snaydon (1985) interpreted their results quite differently. Therefore, I do not believe the Stabilising Coevolution mechanism is an important force in plant communities.

Equal Chance (3) is impossible to prove, but many now consider that, although competition is important in structuring plant communities, the difference in competitive effect between different species may sometimes be small (Goldberg and Werner, 1983; Lieberman *et al.,* 1985; Bazzaz, 1987). Such similarity could come about through convergent evolution (Tilman, 1981), converging on optimum utilization of resources (Ghilarov, 1984), though Roughgarden's (1983) model suggests competition will prevent such a process. Equal chance does not itself allow coexistence unless the equality is exact, but it may slow competitive exclusion enough for other mechanisms to operate. Aggregation (11) will also slow competitive exclusion, and thus facilitate other mechanisms of coexistence.

Some of the elements necessary for Pest Pressure (2) appear to occur, but there is no evidence that it is the major explanation for the Paradox as Gillett (1962) suggested.

Intermediate-timescale Disturbance (5) is a currently much-discussed mechanism (White, 1979; Pickett *et al.,* 1989; Whitmore, 1989). It probably accounts for some coexistence, especially with the declining cohort concept of Ogden *et al*. (1987). The importance of disturbance would be less in N.Z. than elsewhere if there really is a paucity of pioneers and an ability of some climax species to act also as pioneers. But although disturbance is important in determining diversity over the landscape, I do not believe it is important in allowing within-community diversity. The problem of spatial scale is greatest with Intermediate-timescale Disturbance, but when ecologists look at vegetation, and wonder how all the species present can coexist, I do not believe the evidence supports the answer of disturbance. The exception to this is tree-gaps, surely an important feature of forest dynamics (Denslow, 1987; Stewart, 1986; Schaetzl *et al.,* 1989). At high altitudes snow break and freeze-thaw are important. Snow break affects mainly adult trees, perhaps with short life expectancy anyway, and this may reduce its impact.

I doubt whether the Life History Differences (6) model is directly applicable to any real situation (cf Pianka, 1976), but the processes may well be involved in more complex time/space patch situations.

I would, on the evidence currently available, list Niche Diversification (1), Spatial Mass Effect (8) and Gradual Climate Change (4), perhaps associated with Cyclic Succession (10), as probably the most important explanations for the Paradox.

Niche Diversification (1) takes several forms. Membership of different synusiae is obvious to the eye, though it has rarely been formally documented in N.Z. Other types of niche differentiation, such as rooting-depth and phenological differences, are not immediately visible, but are probably as important. Again documentation is needed.

Populations with negative population growth rates may be maintained by the Spatial Mass Effect (8) from adjacent habitat patches. Small-scale environmental and hence vegetational patchiness seems common (Williams *et al*. 1969; Weir and Wilson, 1987), so the Spatial Mass Effect is probably very common, though hard to demonstrate.

Watt (1947) suggested Cyclic Succession (10) as an important process in plant communities. Others have been unable to find similarly neat examples, and further investigation has shown some of Watt's own examples to be more complex than he suggests (Svensson, 1988; de Hullu and Gimingham, 1984; Marrs and Hicks, 1986). Evidence for specific cycles in N.Z. vegetation is very weak. However, it seems likely that processes of the type Watt highlighted are a component of vegetational change.

I suggest that Gradual Climate Change (4) is probably the major explanation of the Paradox of the Plankton in N.Z. terrestial plant communities. Although earlier suggestions of a sharp climate change 600-800 years ago now appear simplistic, it seems that all plant communities are always in a state of change in response to climate (Davis, 1981; Fowler and Antonovics, 1981; van der Meijden *et al.,* 1985; Collins *et al.,* 1987), even if that change is sometimes slower than at other times (Gleason, 1927). Although a complete failure of some podocarps to regenerate has been suggested for parts of N.Z., and may occur, changes that cause the population of a species to decline over several generations (a negative population growth rate) must be more common. I could agree with Fowler (1988a) that: "In view of . . . climatic variability. . . few plant populations or communities spend much time near an equilibrium condition". This must apply at least as much in N.Z. as elsewhere.

Acknowledgements

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