



The twelve theories of co-existence in plant communities: the doubtful, the important and the unexplored

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Keywords

Aggregation; Chance; Circular Interference networks; Co-evolution; Competitive ability; Cyclic succession; Disturbance; Environmental fluctuation; Initial patch composition; Interference/dispersal trade-offs; Niche differentiation; Paradox of the Plankton; Pest pressure; Spatial mass effect

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Abstract

Background: Twelve distinct explanations have been proposed for the co-existence of species in ecological communities.

Types of mechanism: The mechanisms can be divided into those that are stabilizing, i.e. with an increase-when-rare mechanism, and those that are equalizing, the latter on their own only delaying the exclusion of species. However, by evening out fitness, equalizing mechanisms can facilitate the operation of stabilizing mechanisms.

Importance: It is suggested that circular interference networks, co-evolution of similar interference ability, cyclic succession, equal chance (neutrality) and initial patch composition are likely to be unimportant, or perhaps not even occur. Equal chance is an equalizing mechanism. Allogenic disturbance, alpha-niche differentiation, environmental fluctuation (relative non-linearity and/or the storage effect) and pest pressure are probably important. All four are stabilizing. More evidence is needed on aggregation, interference/dispersal trade-offs and the spatial mass effect. Aggregation and the spatial mass effect are equalizing. Suggestions are made of the evidence needed to make informed judgements on which contribute the most to co-existence in plant communities.

Introduction

Ecology has few laws, but the one almost invariable feature of plant communities is that they contain more than one species. Long-term studies such as the Park Grass experiment (Silvertown 1987) show us that much of this is persistence rather than transience. Indefinite co-existence of species contravenes the logic of Gause (1934) that the species with the highest interference ability, i.e. the highest long-term relative population growth rate (PGR) in admixture with other species, should out all others. Hutchinson (1941, 1961) termed this the "Paradox of the Plankton", asking: "How [is it] possible for a number of species to co-exist in a relatively isotrophic or unstructured environment, all competing for the same sorts of materials?" The same question arises for all vegetation. Having combed the literature and sorted synonyms, I find there are 12 distinct mechanisms proposed and possible (Wilson 1990). The 12 are compared with other classifications of co-existence mechanisms in Table 1. Those classifications have been

hierarchical, but the differences are actually multi-faceted (Table 2).

There is a basic distinction between stabilizing mechanisms and equalizing mechanisms (Chesson 2000). For indefinite co-existence, some stabilizing mechanism must operate, i.e. one that includes an increase-when-rare process. Moreover, species abundances always fluctuate and an increase-when-rare mechanism is required to counter this. Equalizing processes, which simply decrease the differences between species in replacement rates (i.e. fitness); do not contain an increase-when-rare mechanism, but by slowing replacement may allow a weak stabilizing mechanism to overcome a fitness difference (Chesson 2000). It is also possible for a stabilizing mechanism to operate as an equalizing one: even if its stabilizing effect is not strong enough alone to permit long-term co-existence, (increase-when-rare), it can reduce the fitness difference between species sufficiently that another weak stabilizing mechanism can effect co-existence.

Table 1. Various classifications of mechanisms of species co-existence. The original mechanism names that can best be recovered from the original paper are given, with *the names used here in italics* for comparability.

Connell (1978)

Non-equilibrium hypotheses
 intermediate disturbance hypothesis: *allogenic disturbance*
Equal chance
 Gradual change: *environmental fluctuation*¹

Equilibrium hypotheses
 Niche diversification: *alpha-niche differentiation*
 Circular networks: *circular interference networks*
 Compensatory mortality
 Herbivores attack and kill seeds or seedlings of common species more frequently: *pest pressure*
Cyclic succession

Apparently not considered
 Co-evolution of similar interference ability
Initial patch composition
Interference/dispersal trade-offs
Spatial mass effect
Aggregation

Wilson (1990)

Density-dependent mechanisms
 Niche diversification: *alpha-niche differentiation*
Pest pressure

Competitive exclusion is a weak force
Equal chance

There is never time for competitive exclusion to operate
 Gradual climate change: *environmental fluctuation*²
 Intermediate-timescale disturbance: *allogenic disturbance*

Colonization mechanisms
 Life-history differences: *interference/dispersal trade-off*
Initial patch composition
Spatial mass effect

Continuous autogenic change
 Circular competitive networks: *circular interference networks*
Cyclic succession

Aggregation (including temporal inertia)

Stabilizing co-evolution: *co-evolution of similar interference ability*

Bengtsson et al. (1994)

Large-scale processes
 Immigration-extinction dynamics (metapopulation dynamics, mass effect)
 Close similarity in competitive ability: *equal chance*
 Trade-off between dispersal and competitive ability: *interference/dispersal trade-offs*
 Mass effect: *spatial mass effect*
 Centrifugal organisation of plant communities: [*beta-niche differentiation*]

Processes within the community
 Based on niche differences
 Niche differentiation: *alpha-niche differentiation*
 Gradual change: *environmental fluctuation*¹
 Regeneration niche: *allogenic disturbance*

Based on similarities in competitive ability
 Environmental filtering: *equal chance*
 Competitive combining ability: *co-evolution of similar interference ability*
 Lottery models: *equal chance / environmental fluctuation*¹
 Species aggregation: *aggregation*

Apparently not considered
Circular interference networks

Cyclic succession
Initial patch composition
Pest pressure

Chesson (2000)

Stable co-existence
 Fluctuation-independent mechanisms
 Resource partitioning: *alpha-niche differentiation*
 Frequency-dependent predation: *pest pressure*
 Fluctuation-dependent mechanisms (*relative non-linearity* and *storage effect*): *environmental fluctuation*

Spatial effects
 Spatial storage effect and spatial relative non-linearity: *spatial mass effect*
 Competition-colonization trade-offs: *allogenic disturbance* and *interference/dispersal trade-offs*

Unstable co-existence: *equal chance*

Not seen as a mechanism of co-existence: *aggregation*

Apparently not considered³
Circular interference networks
Co-evolution of similar interference ability
Cyclic succession
Initial patch composition

Barot & Gignoux (2004)

Stabilizing processes
 Space+time as resources: *cyclic succession*
 Space as a resource
 Exogenous heterogeneity
 Regional co-existence: [*beta-niche differentiation*]
 Disturbance: *allogenic disturbance*

Endogenous heterogeneity
 Deterministic recruitment limitation
 Janzen-Connell: *pest pressure*
 Colonization-competition trade-off: *interference/dispersal trade-offs*
 Heteromyopia: *initial patch composition*⁴
 Limited resource transport: *equal chance + aggregation + spatial mass effect*

Time as a resource
 Exogenous variability
 Disturbance: *allogenic disturbance*
 Each species is the best competitor in given local environmental conditions that are available during given periods: *environmental fluctuation*¹
 Endogenous variability [no mechanism indicated]

Equalizing processes
 Small fitness differences, trade-off: *equal chance*
 Intraspecific aggregation: *aggregation*
 Demographic stochasticity: *equal chance*
 Recruitment limitation as a rule: *equal chance + aggregation (spatial and temporal) + pest pressure + interference/dispersal trade-offs*

Ecological drift: *equal chance*

Apparently not considered
Circular interference networks
Co-evolution of similar interference ability

(1) But without the *storage effect* or *relative non-linearity*, without which it cannot operate. (2) including the *storage effect* but not *relative non-linearity*. (3) But Chesson would see many of these as special cases of fluctuation-independent mechanisms, the *storage effect* or *relative non-linearity* (Chesson 2000, p. 353). (4) However, it is unclear how the patches originate in their interpretation.

Table 2. A classification of mechanisms of species co-existence.

			Patch model	Uniform community model
Stabilizing	Requiring allogenic changes	Requiring only competitive interactions	<i>Allogenic disturbance</i> ³ <i>Interference/dispersal trade-offs</i> ³	<i>Environmental fluctuation</i>
		Requiring non-competitive interactions	<i>Initial patch composition</i>	–
	Not requiring allogenic changes	Requiring only competitive interactions	<i>Cyclic succession</i>	<i>Alpha-niche differentiation</i> <i>Co-evolution of similar interference ability</i>
		Requiring non-competitive interactions	–	<i>Circular interference networks</i> ¹ <i>Pest pressure</i> ²
Equalizing		<i>Aggregation</i>	<i>Equal chance</i> <i>Spatial mass effect</i> ⁴	

(1) This mechanism could possibly operate via competition, but it is difficult to see how. (2) The non-competitive interaction here is via pests. (3) Under *allogenic disturbance* the species can reach all patches equally well, under *interference/dispersal trade-offs* some do not. (4) It is difficult to characterise this as Stabilizing versus Equalizing, and as Patch versus Uniform community. See text.

Terminology notes:

1. "Interference" is used here when "competition" has sometimes been used in the past, in order to include non-competition forms of interference, such as allelopathy and red/far-red effects, especially since we rarely know for sure what type of interference is involved. "Competition" is used *sensu* Clements et al. (1929), Grime (2001) and Begon et al. (2006).
2. "PGR" is used to include the whole of population growth – number of individuals, plant size and vegetative reproduction – thus generalising *r*, which is commonly used with the number of "individuals". RGR could well be generalised in the same way.
3. "Increase-when-rare" is used to mean locally rare, sparse perhaps, with no implication of global rarity.

The problem of spatial scale and the environment

The spatial scale (grain) of the question is impossible to define. Warming (1909) described documenting the fact that different species grow in different places and hence under different environmental conditions (i.e. in different beta niches) as an "easy task". There is considerable current interest in such "environmental filtering", particularly in documenting the extent to which fine-scale vegetation mosaics are caused by environmental heterogeneity. However, I am not concerned with these here, however small the scale. Several of the mechanisms do involve spatial patchiness (*aggregation*, *allogenic disturbance*, *cyclic succession*, *initial patch composition*, *interference/dispersal trade-offs*, *spatial mass effect*), but by definition of the paradox none rely on allogenic environmental heterogeneity within the area where co-existence is being questioned.

The focus is the paradox of how species co-exist locally, in one community, in one small patch of two-dimensional space. But what is "locally"? The appropriate spatial scale (grain) is the one at which we look at the community and ask: "how can the species be co-existing?" but this is impossible to define and it will differ greatly between communities. Shmida & Wilson (1985) regarded 10^2 – 10^4 m² as the upper limit of the scale. A quadrat of 10^2 m² is commonly used for forests, and 0.5^2 – 2^2 m² in grassland, but sometimes habitat heterogeneity and therefore expression of beta-niche differences are clear on a scale smaller than this, e.g. bryophyte species responding to microhabitat differences on logs. The real scale at which we need to ask questions about co-existence is the one at which beta-niche explanations fail and a paradox exists.

Aim

The 12 mechanisms of co-existence have been known for decades, at the latest since the 1920s (*equal chance*), 1940s (*alpha-niche differentiation*, *cyclic succession* and *environmental fluctuation*), 1950s (*interference/dispersal trade-offs*), 1960s (*circular interference networks*, *co-evolution of similar interference ability* and *pest pressure*), 1970s (*allogenic disturbance*, *initial patch composition* and *spatial mass effect*) and 1980s (*aggregation*). By 1990 it was possible to review these 12 mechanisms (Wilson 1990, q.v. for history of the mechanisms) and to my knowledge and careful watching no distinct mechanisms have been described since. In 1990 I exhaustively evaluated the evidence on these mechanisms for one region, and evidence has been gradually accumulating worldwide since then. This paper gives an overview and evaluation of progress so far.

My particular aim is to consider which mechanisms are likely to be important, so they are organised into three sections: doubtful (unimportant or unrealistic), important and unexplored (more investigation is needed). The truth is that all need more evidence and I indicate what evidence we need for each. Estimates of the contribution of the 12 mechanisms to real communities are frankly guesswork/speculation, and are labelled as such.

The doubtful: unimportant or unrealistic mechanisms

Circular interference networks – stabilizing

Interference relations between a set of species are said to be non-transitive if the species cannot be arranged in a pecking order, i.e. an order in which a species higher in the order is always able to displace one lower down. Non-transitivity implies that there is at least one circular interference network (Fig. 1). Laird & Schamp (2006) modelled communities with different networks, and more than one species persisted only in those containing a circular network. A rare species will increase rapidly because the species that it can displace will be abundant.

Circular networks have never been found for plants. For example, Roxburgh & Wilson (2000a) found a perfect pecking order between seven lawn species. Taylor & Aarssen (1990) claimed evidence for circularity, but in fact their three species (and it is circularity between species that concerns us here) show a perfect competitive hierarchy of *Phleum pratense* → *Agropyron repens* → *Poa pratensis*. They claim non-transitivity between genotypes of different species. Out of 435 pair-wise competitive interactions they found 94 significant at $P < 0.05$ without protection for multiple significance tests. There are three genotype-genotype interactions that are at variance with complete transitivity. Since with 435 possible interactions we would expect 21 spurious Type I significances it seems likely that the three are some of these 21.

Lack of evidence for non-transitivity is reasonable, since it is hard to think of a mechanism for it. There cannot be a network of the type shown in Fig. 1 that is based solely on competition for the same limiting factor. It is possible that the species might themselves change the resource that is limiting. For example, species A may be

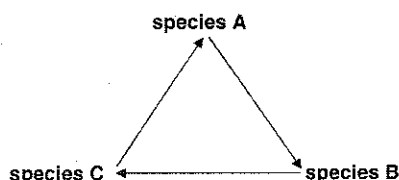


Fig. 1. A circular interference network between three species. An arrow $A \rightarrow B$ indicates that A has superior interference ability to B, and increases at B's expense.

water-spending and cause water stress when it is competing with C or B, yet when C and B are competing without A water may be abundant and competition may be for another factor. The details of the mechanism seem unlikely, and there has been no analysis of whether this would work: by algebra, simulation or experiment. So far as we know, for there to be circular networks, interference of some other type must be involved, such as allelopathy.

Speculation: I suggest that *circular interference networks* are extremely rare, or non-existent.

Evidence required: Clearly, interference abilities of a number of species are needed in a field-realistic situation. In a mixture with no other stabilizing mechanism, the species that will take over is that with the higher population growth rate (PGR, via seeds or vegetative growth) in the mixture (Connolly 1997). Since the relative interference abilities may vary with the proportions of the two species, the relevant PGRs will be those near equilibrium. Practical problems are that: (a) waiting for near-equilibrium and then measuring PGRs will be lengthy; (b) with several species, the experiment becomes large, replication has to be low, and usually most effects are non-significant; and (c) if a third (or more) species can co-exist by some other mechanism, two-species interference abilities may not be relevant.

Co-evolution of similar interference ability – stabilizing

Aarssen (1983) suggested that, in a mixture of two species, stronger selection pressure on the one with lower interference ability would cause it to become the stronger in interference of the two. Superiority in interference would therefore alternate between the two species' populations, an increase-when-rare situation.

Recent work has emphasised that, as agronomists have long known, genotypes of a species can differ widely in their interference ability (Whitlock et al. 2007). We know that a population, put into a different environment, will usually change genetically, and if that change is by selective screening it can occur on a time-scale of a few decades, even months (Walley et al. 1974). Martin & Harding (1981) found evidence of genetic adaptation in interference ability, although circumstantial because the comparison was of field populations. Aarssen (1989) presented evidence that *Senecio vulgaris*, grown with *Phleum pratense* for three generations, increased in its interference with the latter. The *S. vulgaris* study is a rare example of this being shown for a biotic environment. Presumably, the increase in interference ability in this experiment could not continue indefinitely.

Speculation: The mechanism in its "alternating superiority" form would be stabilizing, but this form seems

unrealistic because: (a) even if there is selection in the subordinate species it is hard to see how it could overshoot the other species, and (b) it is hard to see how the two species could increase their interference abilities indefinitely. Without overshoot, this would be a process working towards the equalizing *equal chance* mechanism (see below). It would be operating on an evolutionary time-scale, although recent work is tending to suggest this can sometimes be quite short.

Evidence required: An experiment like that with *Senecio vulgaris*/*Phleum pratense* would be needed, but should be continued for longer and with selection possible in both species. Becks et al. (2010) demonstrated by modelling and by experiments with plankton that co-evolution (here defence against herbivory) can occur surprisingly quickly. Similar work with vascular plant-plant co-evolution would be fascinating.

Cyclic succession – stabilizing

The increase-when-rare mechanism here is similar to that of *circular interference networks*, but the cycle is between vegetation phases, not individual species. Moreover, it can operate with only two phases. Patches are involved, but their environmental differences are autogenic, not allogenic. Watt (1947) excellently reviewed the subject, but unfortunately none of his examples have been supported by subsequent work. The evidence of Yeaton (1978) from a shrub and a cactus in an American desert is interesting, although no actual succession was observed; a hypothesis was made from spatial comparisons with evidence for suggested mechanisms. There seems to be no unequivocal documentation of *cyclic succession*.

Speculation: In the light of inability to document *cyclic succession*, there must be doubt as to whether it exists.

Evidence required: Permanent quadrats could, over a possibly long time, give evidence if one knew in advance where to put them. Long-term records, such as those of Park Grass, Rothamsted, UK, and The Desert Laboratory, Tucson, USA, might just give examples. Ideally, there would be evidence/experiments to indicate the mechanism of species replacement at each stage.

Equal chance (neutrality) – equalizing

It is a long-standing idea that there is an element of chance in which species occurs at a particular spot (Lippmaa 1939; Sale 1977). Chance will make a much larger contribution to species composition when the interference abilities of the species and of individual plants are close to equal (Hubbell 2001; Chesson & Rees 2007).

Speculation: *equal chance* is the equalizing mechanism *par excellence*: Although Connell (1978) emphasised the

chance aspect, the core of this mechanism is the similarity in interference ability, i.e. the neutrality. Practically, all species must be morphologically different and this requires them to be physiologically and functionally different, so the *equal chance* mechanism can never be the sole mechanism of co-existence (Chave 2004). *Equal chance* is simply a statement that whereas between species with different interference ability one will exclude the other, that process will occur more slowly when the difference is less. The equality in interference ability could arise from co-evolution (see above), but will more commonly be caused by ecological sorting, i.e. the screening out of species with low interference ability.

Evidence required: Munday (2004) demonstrated that two fish species seemed to have very similar ecological distributions and equal interference abilities, although with priority effects; Siepielski et al. (2010) found a similar situation with two damselfly species. It would be interesting to find a similar situation with plants. *Equal chance* is a component (but only one) of Hubbell's "Unified Neutral Theory", and almost all tests of the latter have been weak: failure to find departure from null-model predictions (e.g. Lieberman & Lieberman 2007). The same is true for *equal chance* co-existence: proving equality is impossible, but confidence limits around very small differences in interference ability would be compelling.

Initial patch composition – stabilizing

Levin (1974) proposed a model in which two species occupy small, transient patches. Some patches will by chance have more individuals of one species than the other. If between-species interference is greater than within-species interference, the species in the majority will suppress the other in that patch. Although the model involves spatial differences, the patches are identical in environment so this is not beta-niche differentiation.

Speculation: The condition of greater between-species than within-species interference is beloved of ecological modellers, but seems unlikely for plants in the real world. It cannot happen via competition, because resource use will always be at least as similar within-species as between species (I am considering co-existence of species here, not genotypes). Mutual allo-allelopathy might provide a mechanism, but it is very difficult to demonstrate that allelopathy is significant in the field. More likely mechanisms can be envisaged for animals, such as mutual predation and behavioural interference. "Heteromyopia" (Barot & Gignoux 2004) is the same mechanism but without explicit explanation of how the patches arise.

Evidence required: (a) the existence of the small-scale meta-community structure described above; (b) that within-species interference is less than between-species

interference; and (c) that this type of interference is ecologically significant. It seems unlikely all three will occur and can be demonstrated in the same situation.

Important mechanisms

Alpha-niche differentiation – stabilizing

Gause's principle says that no two species can permanently occupy the same niche, but if species differ in their alpha niche (resource niche: Pickett & Bazzaz 1978; Wilson 1999), exclusion by interference could be prevented. The increase-when-rare process is that when a species is rare the resource that it particularly takes up and requires will be present in greater abundance, although luxury uptake of nutrients would complicate this process (cf. Revilla & Weissing 2008). The niche differentiation can include nutrient source (e.g. NO_3 versus NH_4^+), nutrient requirement (Titman 1976; notably Si for diatoms), depth of rooting, phenology of growth, flowering and fruiting (the latter two via reduced competition for pollinators/dispersers), light requirement, etc. Niches can also be constructed by other species, a type of benefaction, notably for epiphytes and parasites, or via heterotrophs, notably N_2 fixation by *Rhizobium* spp. The "Forest architecture" and "Stratification" mechanisms (Kohyama & Takada 2009) are clearly *alpha-niche differentiation*, but personally I would like to see an ecological explanation of the increase-when-rare aspect, and closer matching of the models with observed data.

Speculation: Niche differences are visible in all communities, although sometimes it is difficult to see all the species as having different niches. We rarely know whether the niche differences are sufficient for co-existence. It is not easy to think of a single experiment where niche differentiation has been shown to lead to stability. However, since all species have by definition different niches, as an act of blind faith, I declare that it must often be important.

Evidence required: There have been attempts to conclude, from failure to find niche differences between co-existing species, that co-existence is not due to *alpha-niche differentiation* (e.g. Mahdi et al. 1989). Clark et al. (2007) point out that negative evidence is unreliable because niche differences can be due to an interaction of niche axes. Silvertown (2004) made the point that there is evidence for various types of niche differentiation in plant communities, but full documentation of the alpha niches for all of the species present in a community would be needed in order to determine for which species co-existence might be due to *alpha-niche differentiation* (complete information is sometimes available for the phenology niche of trees).

Experiments on mesocosms with different numbers of species can give evidence that there is over-yielding and greater reliability in mixtures of species, although the

results have been controversial, and rarely is it known that this is due to niche differentiation, nor what the differences might be. For example, Tilman et al. (2006) examined plots at Cedar Creek sown and maintained to a range of species richness. Greater reliability (lower variation in biomass from year to year) was seen in plots with more species. We can suspect that with more species more niches were occupied, and we can see reliability as an informal guide to stability. However, evidence to demonstrate that the mechanism could have been niche differentiation would be very helpful. Often mixtures that include legumes and non-legumes over-yield most, presumably due to niche differentiation. For a full demonstration, a test for true stability sensu May (1973) is needed (cf. Roxburgh & Wilson 2000a, b).

In all the stabilizing mechanisms the question arises of how strong the effect has to be in order to ensure co-existence, given the particular differences in fitness between the species and the operation of any other mechanisms; but the question is asked especially for *alpha-niche differentiation* because of the limiting-similarity concept and calculations of MacArthur & Levins (1967). This remains unanswered for the real world. There are three pieces of information available: (a) a theoretical limiting similarity can be calculated (Szilágyi & Meszéná 2009); (b) the existence of limiting similarity can be seen in the field, but not the exact limiting-similarity value (e.g. Stubbs & Wilson 2004); and (c) the stabilization effect can be measured from the field or experimentally but without our knowing how much of this is due to *alpha-niche differentiation* (Adler et al. 2007). These three need to be brought together, perhaps with experimental removal of the opportunity for niche differentiation or of other mechanisms.

Environmental fluctuation – stabilizing

Environmental fluctuation – seasonal, annual and decadal change – does not necessarily give co-existence. In the absence of any explicitly stabilizing process, one out of co-occurring species must have the greatest long-term PGR over such fluctuations, and will in the absence of other mechanisms of co-existence eliminate its associates.

Chesson (2008) has shown that either of two mechanisms can result in stable co-existence via *environmental fluctuation: relative non-linearity* and the *storage effect*, and only these two can do so. *Relative non-linearity* requires that two species differ in the shape of their response to a resource. All plants affect their environment ("reaction": Clements 1904), and the two species with different response shapes will have different reactions. The effect of environmental fluctuation on the balance between the two species and their different reactions will necessarily give an increase-when-rare mechanism, but

which of the two species has the higher PGR depends on the degree of environmental fluctuation.

The *storage effect* is that a rare species will be able to take advantage of environmental conditions that are favourable for it because there will be little competition. Four conditions are required: (1) the species are competing for a resource; (2) they respond differently to an environmental (i.e. non-resource) factor; (3) competition impacts more on a species in more "favourable" conditions, i.e. when the species is present with higher biomass; and (4) the effect of competition on the population of a species depends on the environment, and this implies some persistence of the population through environmental fluctuations, i.e. buffering. The term "regeneration niche" is difficult to pin down precisely, but seems to be part of item (2) above.

Speculation: The four conditions for the *storage effect* seem almost inevitable, so it must be present often. The conditions for *relative non-linearity* are also obvious, but Chesson's (2008) calculations show it to be a much weaker force. I therefore conclude that *environmental fluctuation* will often cause stabilization, primarily through the *storage effect*.

Evidence required: Chesson's models are very significant for theories of co-existence. Their parameters need to be determined for real-world co-existing organisms, and found to be consistent with the models. The closest approaches so far have been by Adler et al. (2006) in a Kansas prairie, Verhulst et al. (2008) with shrubs in a Mexican desert, Angert et al. (2009) with annuals in an Arizona desert, and Adler et al. (2009) in Idaho sagebrush. These last workers found the processes required for the *storage effect* were very weak, but of course models that are correct and realistic will not operate in all communities.

Pest pressure – stabilizing

All types of pest – herbivores, from insects to large mammals, and also pathogens – have the potential to give an increase-when-rare process. For this, three conditions are required.

1. **Impact**: the pests involved must significantly reduce the fitness of the plant species in terms of survival, growth and/or reproduction.
2. **Abundance-dependence**: the challenge from pests must be less on a species when it is rare than when it is abundant. The requirement is for a lower impact on the fitness of a species when rare, but this will usually be through reduced *grazing/infection*.
3. **Host specificity**: the plant species must differ in the extent to which their fitness is reduced by particular pests.

If these three conditions are all met, then when any one of the plant species in the mixture becomes more abundant, its host-specific pest (Condition 3) will move more

rapidly among its host population and the degree of infestation/infection will increase (Condition 2). This will reduce its fitness (Condition 1), but will not directly impact other species, or will do so only to a lesser extent (Condition 3). Conversely, when a species becomes rare and in danger of being eliminated, infestation by its specific pests will decrease and its fitness increase: increase-when-rare.

Any environmental condition that slows growth will tend to slow species replacement, but also slow stabilizing mechanisms of co-existence. Non-selective shoot herbivory may reduce competition for light. Competition for light is asymmetric because it is based on height difference, and therefore cumulative, with the results of competition changing competitive abilities (Wilson 1988). Non-selective herbivory will reduce this height-based process and thus may reduce species replacement more than it slows stabilizing mechanisms, representing an equalizing mechanism. This is also a reminder that the 12 known mechanisms cannot be seen in isolation.

Speculation: Seeds and seedlings are often heavily predated (Condition 1) and abundance-dependence (2) has often been shown (e.g. Jonzen et al. 2002). Specificity (3) is the problem. There is a huge literature assuming that bird granivores are restricted by beak size to a particular range of fruit/seed sizes, but not to one species. Most mammal and insect granivores are not specific to one species, although species of Bruchid beetle are generally restricted to the seeds of one or a few species of Fabaceae. Seedlings are eaten by invertebrates, but they are likely to be quite generalist in their munching.

Invertebrate and vertebrate herbivores of vegetative parts cause appreciable damage (Condition 1, e.g. Carson & Root 2000), but abundance-dependence (2) is less clear. Again, host specificity (3) is the main issue. With a few notable exceptions, insect vegetative herbivores are not host-specific, even though they have preferences. Vertebrates of vegetative parts have facultative preferences but they are usually polyphagous, some necessarily so since their bite size is larger than individual plants. They often live longer than their herbaceous food plants and are mobile, so in response to reduced plant availability they will switch food or hunt out preferred species rather than decline in population size, having the reverse effect from that required. Pathogens often have a significant impact (Condition 1, e.g. Mihail et al. 1998) and there is evidence for abundance-dependence (2, e.g. Mitchell et al. 2002). The weak link is how often pathogens are species-specific (3), and this seems to vary between ecosystems, from rarely to usually (Gilbert 2002; Mitchell et al. 2002).

In view of the above, I do not believe that herbivory/granivory is generally an effective stabilizing mechanism. Pathogens will often be a major force for co-existence via the *pest pressure* mechanism.

Evidence required: Information on impact, specificity and abundance-dependence are required simultaneously for single systems. Yamazaki et al. (2009) have made a start by recording seedling mortality and its causes (disease or herbivory) in relation to seedling density, distance from conspecific adults and the microenvironment. The evidence could be in the spatial context of the Janzen-Connell model (Yamazaki et al.'s was, but the model can operate in equilibrium without the distance-from-parent element).

The *storage effect* mechanism of *environmental fluctuation* operates via competition. Kuang & Chesson (2010) have shown mathematically that since *pest pressure* tends to reduce competition, it will reduce the effectiveness of the *storage effect* and hinder co-existence. Data to parameterise these models would be very useful, and empirical demonstration of the effect would be fascinating.

Allogenic disturbance – stabilizing

Disturbance is a pulse perturbation that removes biomass from, or kills, plants of most species (Grime 2001). As a mechanism of co-existence, *allogenic disturbance* is a between-patch mechanism (Wilson 1994), that is to say, within a local area there are patches that have very recently been disturbed, others with pioneer species still on them, others in mid succession and yet others in a climax state. However, these patches are not different in the allogenic environment.

The necessary conditions are: (1) there is disturbance of patches at a scale smaller than the one we are considering for the paradox; (2) this disturbance occurs with a frequency such that there will be a mixture of patches of different time since disturbance (this is the "Intermediate Disturbance Hypothesis" of Connell 1978; "successional niche" has been used; this may be another aspect of the rather general term "regeneration niche"); and (3) there are species that occur with differential frequency in patches of different ages since disturbance. The process is stabilizing because when a species inhabiting a particular patch age becomes rare, there is less within-species interference during its phase of patch succession.

Speculation: It seems that there are pioneer species (early successional ruderals) in most communities, but not all. When both pioneer and later successional species are present, the possibility of the mechanism is obvious. This was demonstrated in experimental mesocosms by Questad & Foster (2008). The question is its importance – when we look at a community not disturbed in detail by man how much of the heterogeneity that we see is due to time since disturbance? We do not know, but probably more than we think (Wells et al. 2001). King (1977)

found that only 5% of the plant species in British grasslands were significantly more abundant on recognizable ant hills, but it is possible that other species occurred on old ant-hill sites. Woods (2000) found that in forests of Michigan, USA, some quadrats (0.8 or 0.1 ha) contained more of two species he considered successional, and suggested these were old gaps. Whether these comprise co-existence by *allogenic disturbance* depends on the scale examined. I suspect *allogenic disturbance* is often an important factor.

Evidence required: We now know that disturbance is endemic to communities, and can presume that most communities comprise a mosaic of patches of different times since disturbance, but this is poorly documented. The pattern of spatial vegetation heterogeneity needs to be recorded over time, either by observing changes in permanent quadrats or by tree ageing (since the disturbance cycle will occur over many decades in forests). It then needs to be documented that different species occur in the various post-disturbance successional stages. Most importantly, the latter two pieces of evidence need to be available for a single community.

The unexplored: mechanisms on which more investigation is needed

Interference/dispersal trade-off – stabilizing

This concept originated with Skellam (1951) and Hutchinson (1951). It has been known under a variety of names, including "competition/colonization" and "musical chairs" (Wilson 1990). The concept is of two species in a habitat that contains transient disturbance patches, intrinsically identical. Species *I* is a poor disperser but has strong interference ability, and will take over in all the patches that it reaches. Species *D* is a good disperser so it reaches all patches, but it has low interference ability so it will remain only in the patches that *I* does not reach. Species *I* will eventually reach and dominate the latter patches, but by then disturbance has opened other patches for *D* to colonise. It seems that even the difference in dispersal ability is not required, just that the dispersal patterns are different (Berkley et al. 2010).

Speculation: There have been many mathematical models of the mechanism (e.g. Levins & Culver 1971; Tilman 1994). There is indeed often a negative correlation between interference ability and dispersal ability (Ehrlén & van Groenendael 1998), and Turnbull et al. (1999) gave evidence that large-seeded species, perhaps with lower dispersal ability, were more dominant when more seeds were sown. However, there is very little evidence for this mechanism. The scale and timing of disturbance needs to be right and the trade-off needs to be present, which make it unlikely to operate often.

Evidence required: The negative interference/dispersal needs to be documented for the florule of a community with patchy disturbance, with evidence that the better dispersers reach all (or most) patches, but the species with higher interference ability take over patches that they do reach. Demonstrating this for one community would be an achievement, although it would not indicate how widespread this situation is.

Spatial mass effect – equalizing?

The *spatial mass effect* occurs when the local population of a species has a negative growth rate according to its own survival and reproduction (i.e. $PGR < 0$, $\lambda < 1$), but is maintained by constant immigration from outside the community (Clements 1905). It has also been called the “sink effect”. Snyder & Chesson (2004) applied and extended the temporal *storage effect* and *relative non-linearity* (see “Environmental variation” above) to an environmental mosaic, incorporating the *spatial mass effect* but also considering persistence of species in the whole landscape, source and sink patches. Sears & Chesson (2007) parameterised this model.

The *spatial mass effect* is difficult to categorise. It is equalizing in that there is no increase-when-rare process, yet stabilizing in that there can be indefinite co-existence. It is a patch model in that it requires an external patch with a different environment (beta-niche differentiation on a larger scale) to provide the source of propagules. However, it is a mechanism of co-existence without patches at the scale examined, and can certainly explain why we see species co-existing and the mixture persisting within an intrinsically uniform area (Table 2).

Evidence is sparse. A dramatic example occurs in the Lost World Cavern, northern New Zealand, where 13 species of angiosperm grow without any of them ever setting seed (de Lange & Stockley 1987). In a population of *Cakile edentula* on a sand dune system, Keddy (1982) observed that plants at the seaward edge produced many seeds and had high survival (it is a strand-line species). However, in the rear dunes, the few plants surviving to maturity did not produce enough seeds to balance mortality, and the population was maintained by seeds blown inland from the strand.

Speculation: Wherever there is vegetational heterogeneity, seeds will surely germinate in foreign territory and ramets invade, so the *spatial mass effect* will be present almost always.

Evidence required: The population growth rate within the community must be shown to be $PGR < 0$, and the propagule influx must be quantified. Both of these are very difficult to do, and they need to be done for the same community.

Aggregation (Spatial Inertia) – equalizing

Spatial aggregation of the plants of a species gives inertia, delaying exclusion by interference since replacement occurs only at patch boundaries if dispersal is limiting. We assume the patches are intrinsically identical, in environment but perhaps different in species for historical reasons. The process was described analytically by Clifford & Sudbury (1973) and modelled by Silvertown et al. (1992). It has been demonstrated with real plants in an artificial community (Stoll & Prati 2001). However, theory shows that aggregation does not necessarily slow down exclusion by interference (Chesson & Neuhauser 2002) and Chesson (2008) argues that the effect of aggregation is an artefact caused by not considering the right time-scale.

Temporal Inertia (Cowles 1901) refers to the ability of plants to persist for some time when conditions are unsuitable for them, as adult plants or as a reproducing but gradually declining population. It is really not a mechanism of co-existence, simply an artefact of using a time-scale inappropriate for the life history of the plants.

Speculation: Species are aggregated almost everywhere, so this seems likely to have very wide importance as an equalizing mechanism.

Evidence required: Experiments like that of Stoll and Prati (2001) are needed, but under realistic field conditions.

Conclusion

Since we see multi-species communities all around us, in apparent breach of the law of Gause, it is not surprising that 12 explanations have been proposed. Some are related (Table 2). For example, three depend on disturbance. One of these and a fourth include autogenic succession. The mathematics of the storage effect can be used to describe the *spatial mass effect*, storage in space rather than time. Five explanations require patches within the area we are considering, although not in the intrinsic environment, as I have eschewed such beta-niche effects. However, I believe all 12 mechanisms are distinct. The need is now for hard evidence from nature on these mechanisms. Too often, in vegetation science, observation and theory proceed happily without either bothering the other. That has largely been the case here.

Stable co-existence raises the concept of “stability”. Early workers had taken low variability, now more precisely called “reliability”, as equivalent to stability. This fails because low variability can also be due to low perturbation, and anyway how low does the variability have to be in order for us to call it stability? An “equilibrium” can be stable, or unstable. The concepts of “resistance” and “resilience”, applied to a stable community, describe features of the stabilizing process, not the existence of it, and resistance can be asked also of an unstable

community. Stability *sensu stricto* (Lyapunov stability, local stability) is defined as the ability of a community to return eventually to its former state after an extremely small pulse perturbation (May 1973). Taken from mathematics, it is clear and consistent, and the only one we can use. Objections are raised that: (a) we cannot observe extremely small perturbations, (b) we cannot wait for "eventually", and (c) before we could wait, another disturbance would happen and the environment would change, as it is always doing. But we must remember that although determining stability *sensu stricto* is beyond the ability of mortals, observing stabilizing processes is not. The study of Harpole & Suding (2007) is an example. It is therefore preferable, and practical, to think of stabilizing processes, especially the ability to increase when rare.

The opposite question is why monospecific stands are occasionally seen, in obedience to Gause's law but as a surprise because of their rarity. They usually occur in aquatic or intermittently wet habitats such as lakes and the lower zones of salt marshes, but occasionally in stress habitats such as saline deserts. I do not know of any theory directed at this. P.W. Richards suggested that in tropical rain forests, normally diverse, mono-dominance was to be found in unfavourable habitats (Salisbury 1931), but Connell (1979) suggested that mono-dominance is the climax situation, and the iconic species-rich tropical rain forest communities are recovering from disturbance.

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