12

Community Dynamics: Succession and Assembly

Concepts

- Communities are dynamic over time; their composition changes over days, years or centuries.
- Primary succession occurs on newly created land, whereas secondary succession occurs after a disturbance removes only part of the plant biomass and substrate.
- Some processes that influence the type and rate of succession are facilitation, tolerance and inhibition. Succession is directed by site availability, species availability and species performance.
- Communities are assembled over time. Membership of a community will be determined by the interaction of species traits and the biotic and abiotic filters of the habitat.
- Species present in a community (actual species pool) must be members of the total, habitat, geographical and ecological species pools.

Introduction

In Chapter 11, we focused on how communities 'look' at one point in time; that is community structure as related mainly to diversity. The composition of any community will fluctuate daily, seasonally, annually, and will change over decades, centuries and millennia (Fig. 12.1). Over a year, communities change visibly as a result of phenology and short-term weather patterns. Even when we try to maintain a stable community, such as in a perennial garden, composition is dynamic. Year-to-year species composition changes in response to environmental factors. A wet year may favour some species, increasing their abundance over another species. Even the most fastidious of gardeners will have different species abundances from year-to-year and some species will be inadvertently lost or introduced over time. Weed communities in agricultural systems will change over time even when the cropping and tillage systems are consistent. Such short-term fluctuations in community composition may or may not result in long-term compositional changes.

Over the long term (centuries to millennia), communities change as a result of selection pressures. Over intermediate time

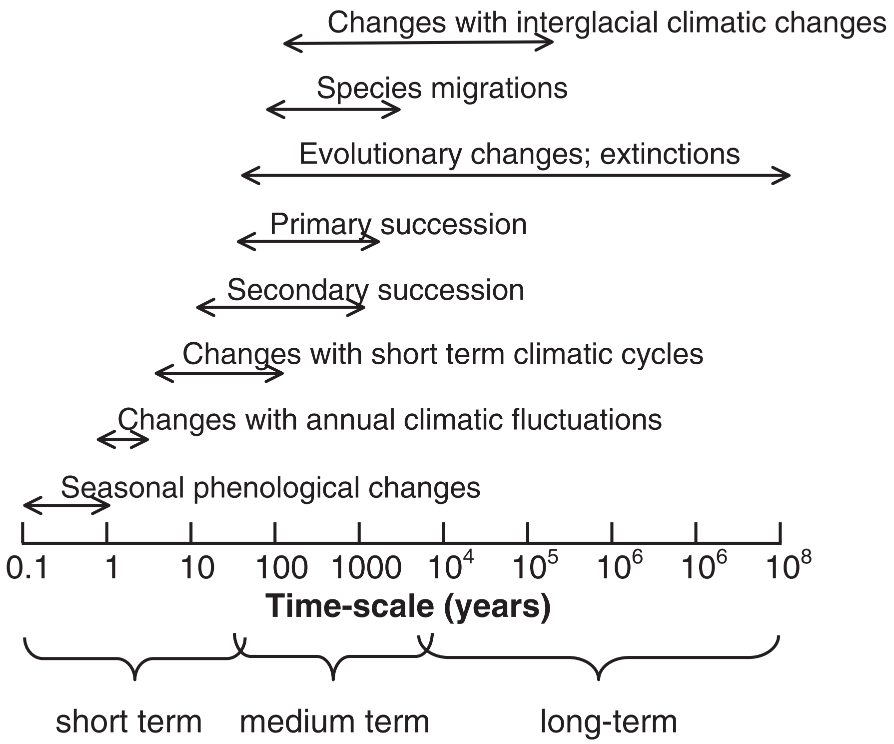

Fig. 12.1. Vegetation change over different time scales (redrawn from Miles, 1987).

scales (decades to centuries), there are changes in vegetation that we call succession. Succession is the directional change in community composition and is different from seasonal or random fluctuations in vegetation. This intermediate scale of vegetational change is the focus of this chapter. In some cases we can observe a community change over our life span. For example, we can watch an abandoned field proceed from a community of annual and perennial weeds during our childhood, to one with scattered shrubs in our adulthood, and possibly to the initial stages of a forest in our old age. In other cases, the development of vegetation and its change over time is almost imperceptible; for example, succession following the retreat of a glacier is very slow (Fastie, 1995).

Community Dynamics

The classical ecological theory assumed that natural communities existed in a state of ‘dynamic equilibrium’. Communities were said to develop over time into a specific stable community type (the climax community). Equilibrium communities were thought to be controlled primarily by competition, and species co-existence was thought to be dependent on niche differentiation and resource partitioning. Implicit in this was the idea that following a disturbance, a community would return to its original state (Perrings and Walker, 1995). These ideas, however, do not fit with current empirical evidence (Pickett *et al.,* 1992; Holling *et al.,* 1995). For example, we now know that following a disturbance, different types of communities can develop and therefore there is no such thing as a single climax community (Walker, 1981; McCune and Allen, 1985; Dublin *et al.,* 1990). Abrams *et al.* (1985), for example, showed that clear-cut jack pine (*Pinus banksiana*) stands can develop into either sedge meadows, hardwood and shrub communities, or return to a jack pine community depending on the season of cutting and whether the site was burned by natural or controlled burns (Fig. 12.2).

The theory of communities reaching equilibrium has now been replaced by the

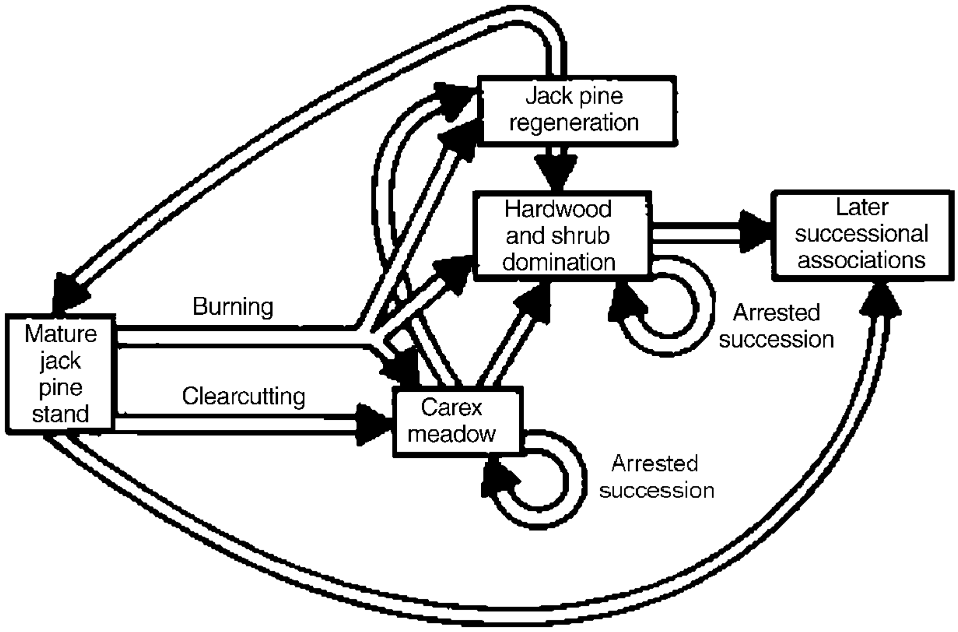

Fig. 12.2. Multiple successional pathways following burning or clearcutting of a mature jack pine forest (Abrams *et al.*, 1985; Copyright 1985, with permission from Elsevier Science).

non-equilibrium concepts that focus on community-level processes and changes over time rather than on any single climax community state (DeAngelis and Waterhouse, 1987). According to Pickett *et al.* (1994), the 'balance [equilibrium] of nature' is a cultural myth or metaphor rather than a scientific concept. Non-equilibrium concepts recognize that while some communities may be at equilibrium at some scales, this is not necessarily the 'normal' situation. Pickett *et al.* (1992) suggested that we use the 'flux of nature' as our metaphor rather than considering nature to be in balance.

Once we accept that communities are not necessarily at equilibrium we can begin to describe how they change over time. The term *stability* is often used to describe how communities resist change in response to disturbance or stress, but it is a vague term and has been defined in many ways (Lĕps *et al.,* 1982; Pimm, 1991). Community stability is broken into three components: persistence, resistance and resilience (Table 12.1). Thus, a community's stability is a function of how long it remains the same (persistence), whether it resists stress or disturbance (resistance), and its ability to return to its original state following a disturbance (resilience). The combination of these three components determines stability; however, a community very strong in one component is not necessarily strong in the others. For

Table 12.1. Terms associated with descriptions of community stability.

Term	Definition	Source
Persistence	'The ability of a community to remain relatively unchanged over time'	Barbour *et al.* (1999)
Resistance	'The ability of a community to remain unchanged during a period of stress'	Barbour *et al.* (1999)
Resilience	'The ability of a community to return to its original state following stress or disturbance'	Barbour *et al.* (1999)
Elasticity	'The speed at which the system returns to its former state following a perturbation'	Putman (1994)

example, a community may be persistent but not resistant or resilient, and therefore will be susceptible to disturbance. A community may be highly resilient under a certain magnitude of disturbance, but once a threshold is passed, a transition will occur and an alternative state will be reached with either the same or new species composition. Such changes in community structure and function can be irreversible and quite abrupt (Perrings and Walker, 1995).

History and Development of Successional Theory

The term succession was originally used by Thoreau in 1860 to describe changes in forest trees (McIntosh, 1999). It remained largely unused until Cowles (1899) studied primary succession on the sand dunes of Lake Michigan near Chicago. He described how they developed through various associations to a forest climax. Cowles (1901) recognized that succession is 'not a straight-line process. Its stages may be slow or rapid, direct or tortuous and often they are retrogressive.'

Clements (1916, 1936), a contemporary of Cowles, was a more forceful individual and therefore his rather dogmatic writing on succession overshadowed those of Cowles (McIntosh, 1999). Clements described in detail what we now think of as the classical succession paradigm. He described it as a directional, progressive, orderly change in vegetation that would ultimately converge to a stable, predictable climax community. Clements believed that the vegetation in each successional pathway altered the environment and ameliorated it for later invading species. Thus, early species facilitated the invasion of later species. From this, Egler (1954) later developed the idea of 'relay floristics' where early species prepared the environment for later ones. Thus, Clements' view of succession proposed that autogenic (internal) processes controlled the development of the community climax. Clements believed that communities were more than the sum of their species and that they had properties of a superorganism (Chapter 11).

Two criticisms arose about Clements' ideas. First, Clements invoked climate as the sole determinant of community composition and neglected other factors. As we have seen in earlier chapters, other biotic and abiotic factors can be important community determinants. Second, Clements did not recognize the possibility of multiple successional pathways, an idea already hinted at by Cowles. Nevertheless, Clements' work is important for his observations of community dynamics and his recognition of the importance of disturbance to the process of succession (Walker, 1999).

In response to Clements' work, Gleason (1917, 1926) noted that successional events were *not* predictable and that succession proceeded *independently* following a disturbance. He believed that communities were simply collections of species with similar environmental tolerances. One criticism of Gleason's work was that he ignored the importance of species interactions in determining community composition, instead focussing almost entirely on abiotic processes (Tansely, 1935).

Gleason's views were greeted sceptically at first, and not taken seriously until decades later in the 1950s. By then ecologists had begun to recognize the work of Watt (1947) and others, who said that communities were a mosaic of patches at different successional stages. While overall community structure might remain constant, individual patches were dynamic. The differences between Clements and Gleason are not as extreme as they first appear. Clements looked at overall change in species composition over a pathway, whereas Gleason looked at smaller-scale changes in individual patches. Therefore, Clements observed temporal changes, and Gleason, spatial patterns.

Patterns of Primary and Secondary Succession

There are two main types of succession: primary and secondary. Primary succession occurs on newly created land (e.g. following a volcanic eruption), whereas secondary

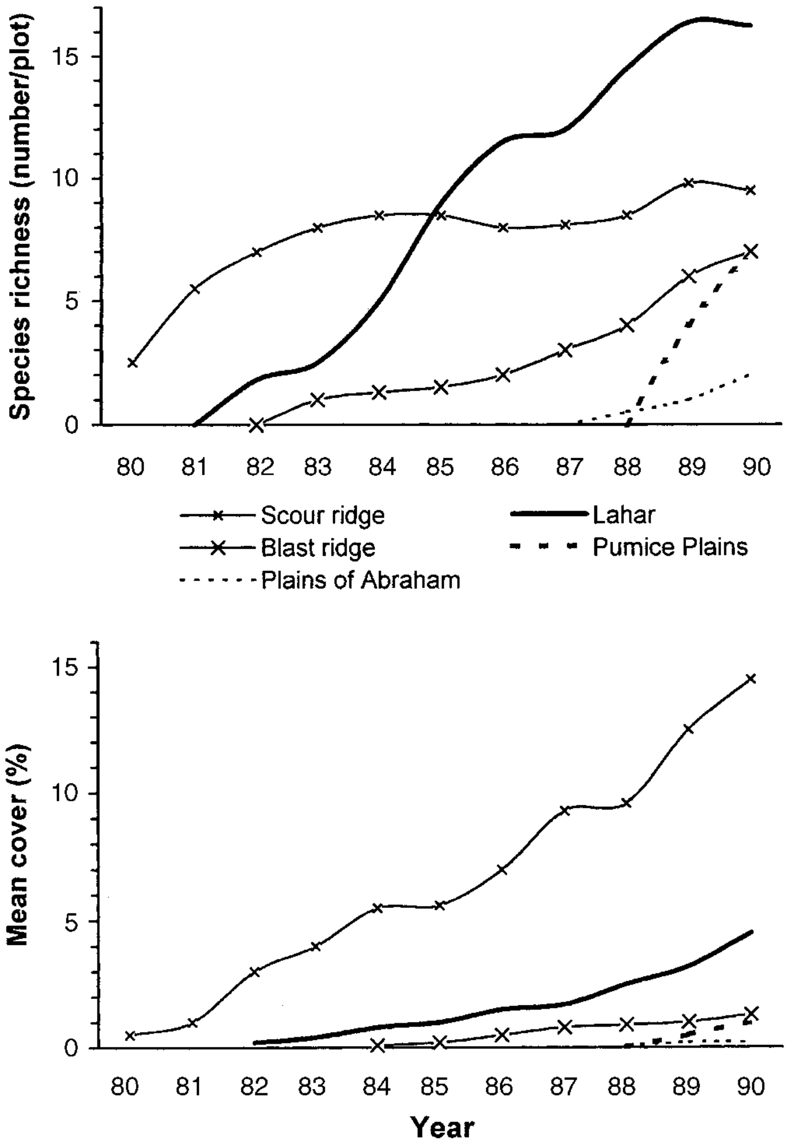

Fig. 12.3. Change in: (a) species richness (number in 250-m^2 plots), and (b) percentage cover during primary succession at five sites on Mount St Helens (redrawn from del Moral and Bliss, 1993).

succession occurs after a disturbance removes only part of the plant biomass and substrate (e.g. following a forest fire).

Primary succession

Primary succession occurs on newly created land where no plants have grown previously or where there is no effective seed bank on site. Habitats undergoing primary succession are usually environmentally harsh because there is no vegetation to ameliorate the abiotic environment and there tends to be few nutrients and little water. Primary succession is a slow process because there is no soil structure or remnants of vegetation to aid regeneration.

del Moral and Bliss (1993) compared the rate of primary succession in five habitat types following the eruption of Mount St Helens in 1980 (Fig. 12.3). They found that the type of soil substrate and vegetation that remained influenced the rate and types of successional pathway. Species richness (α-diversity) increased faster when some vegetation remained or was nearby (on the scour and lahar). After 10 years, the mean percentage cover was low at all sites except on the scour habitat where some original vege-

Table 12.2. Five dominant species in the major study areas of del Moral and Bliss (1993). Species are ranked according to percentage cover. The Scoured Ridge omitted and intact late successional vegetation site added for comparison (from del Moral and Bliss, 1993).

	Sites				
Species	Secondary succession, up to 15 cm of ash (tephra) deposited on vegetation	Lahar, mud flow leaving barren substrate	Blasted ridge, lava, ash and residual soil remaining	Pumice plains, heterogeneous pumice desert	Abraham pumice, pumice of 2–3 cm diameter, desert pavement
Thin bentgrass, *Agrostis diegoensis*	1				5
Dwarf lupin, *Lupinus lepidus*	2	2	1		
Spreading phlox, *Phlox diffusa*	3				
Newberry's fleeceflower, *Polygonum newberryi*	4	1			
Pink mountain-heather, *Phyllodoce empetriformis*	5				
Cardwell's penstemon, *Penstemon cardwellii*		3			
Common catsear, *Hypochaeris radicata*		4	4	4	3
Alpine buckwheat, *Eriogonum pyrolifolium*		5			
Western pearly everlasting, *Anaphalis margaritaceum*			2	1	1
Fireweed, *Epilobium angustifolium*			3	2	2
White hawkweed, *Hieracium albiflorum*			5	3	4
Rusty saxifrage, *Saxifraga ferruginea*				5	

tation and soil remained. Even the lahars, which showed increasing richness over time still had only 5% cover. Species composition also differed among the habitat types (Table 12.2). Species composition in three habitats (ridge, pumice and plains) was similar, but these differed substantially from the relatively unaffected tephra habitat. Communities established on mud flows (lahar) were intermediate in species composition reflecting its proximity to propagules. Even though the lahar and tephra vegetation had similar species composition, their structure varied considerably as the mean percentage cover for these sites in 1990 was 4% and 47%, respectively.

del Moral and Bliss (1993) noted that the characteristics of early invading species may determine how succession proceeds because once a species is established, its own seed production will outnumber propagules of other species that immigrate from other communities. Furthermore, early invaders tended to be located in the more favourable microhabitats, thus improving their own survival. Finally, environmental conditions during the establishment phase may favour some species over others, further directing the successional pathway.

Secondary succession

Secondary succession is the most commonly observed type of succession. It is usually initiated by a natural or human-caused disturbance; for example, fire, hurricanes and flooding initiate secondary succession. Cessation of human activities can also initiate secondary succession, such as when an agricultural field is abandoned. In all cases, there are existing vegetation or seed banks available to aid regeneration.

The rate at which secondary succession proceeds is dependent on the type of soil substrate remaining and on whether established vegetation is nearby and can provide propagules for regeneration. The rate is also dependent on the type of agent initiating succession. For example, a hurricane, clearcut forest or small brush fire can initiate secondary succession, but the vegetation will develop at different rates.

Old field succession is probably the most studied type of secondary succession. It follows the cessation of farming activity such as ploughing and herbicide usage. A classic example of secondary succession is described in Brown and Southwood (1987) who characterized the succession of old fields on sandy soils at Silwood Park in southern Britain. When ploughing stopped, annuals were the first to colonize. Biennials briefly dominated in the second year, followed by an increase in perennials. These changes were reflected in the rapid increase in α-diversity over the first year followed by a gradual decline as perennials and then shrubs and trees dominated (Fig. 12.4).

Patterns and Processes of Succession

Patterns of succession

We have looked at specific examples of primary and secondary succession, but what generalizations can we make about communities undergoing succession, and what ecological processes are important over the course of a successional pathway? As communities develop, the types of plants growing there will change, often in a predictable manner. There are some general patterns as succession proceeds. First, plant cover, biomass and species richness tend to increase over time, at least to a point after which they may level off or decrease. The most obvious

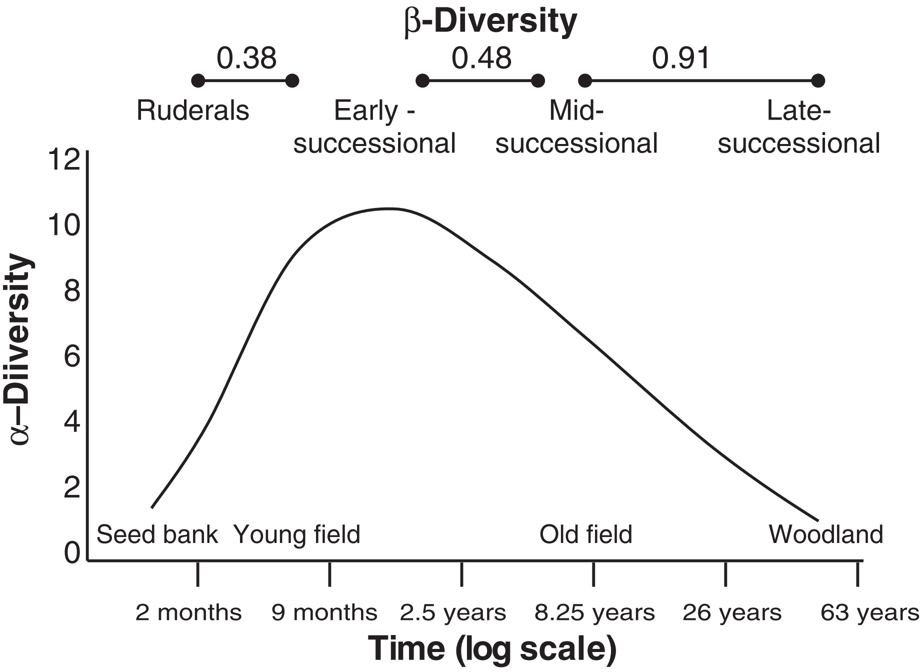

Fig. 12.4. Changes in α-diversity of green plants along a secondary successional pathway. Differences between stages in terms of β-diversity are shown along the top (redrawn from Brown and Southwood, 1987).

Table 12.3. Comparison of physiological and life history traits and population dynamics of plants from early and late stages of successional (from Pianka, 1970; Bazzaz, 1979; Huston and Smith, 1987).

Trait	Early succession	Late succession
Seed and dispersal		
Seed size and number	Many, small seeds	Few, large seeds
Dispersal distance	Long	Short
Dispersal mechanisms	Wind, birds, bats	Gravity, mammals
Seed viability	Long	Short
Size at maturity	Small	Large
Maximum life span	Short (often < 1 year)	Long (usually > 1 year)
Timing and frequency of reproductive events	Early, often monocarpic	Late, usually polycarpic
Growth rate	Fast	Slow
Structural strength	Low	High
Survivorship	Often Deevy Type III	Often Deevy Type I and II
Population size	Often variable over time	Fairly constant over time
Resource acquisition rate	High	Often low
Recovery from nutrient stress	Fast	Slow
Root to shoot ratio	Low	High
Photosynthetic rate	High	Low
Photosynthetic rate at low light	Low	High
Respiration rate	High	Low

change is the increase in canopy height from small annuals and herbaceous perennials to shrubs and trees during many successional pathways in temperate and tropical environments.

Huston and Smith (1987) summarized plant traits associated with early and late successional species (Table 12.3). These traits have been equated with *r*- and K-selected species (see also Chapter 3); however, Grubb (1987) cautioned against this. The high intrinsic rate of population increase (*r*) associated with early successional species can be achieved both by *r*- and K-selected species. A high *r* results from high fecundity in *r*-selected species and from low mortality in K-selected species (Grubb, 1987). During early stages of succession there is a high rate of species change and replacement, but as the community ages, species turnover rate declines. This is due primarily to the rapid growth rate and short life span of early successional species compared to late successional species.

Grime (1977) illustrated patterns of succession on his C-S-R triangle (Fig. 12.5a). In early secondary succession, species are ruderals (R) because there is abundant light and nutrients. The successional pathway favours competitive species (C) and then long-lived stress-tolerators (S) as nutrients and light become limiting. The direction of the pathway will vary with the level and consistency of potential productivity (nutrient status). Higher potential productivity will lead to species that are competitive in the intermediate stages. Potential productivity rarely stays constant throughout a pathway. Nutrients can also be added or removed through human actions. Using this model, successional pathways of specific habitats can also be mapped; for example, in a fertile forest, the pathway favours competitive species for approximately 25 years, and then favours toward stress-tolerators as the biomass continues to accumulate (Fig. 12.5b). Conversely, in an annually harvested meadow, the pathway begins with competitive species and the ruderals as biomass decreases.

This way of illustrating succession is unlikely to fit all situations. Ecke and Rydin (2000) examined the C-S-R model and found that primary succession on uplifted sea coast meadows did not follow the expected trend.

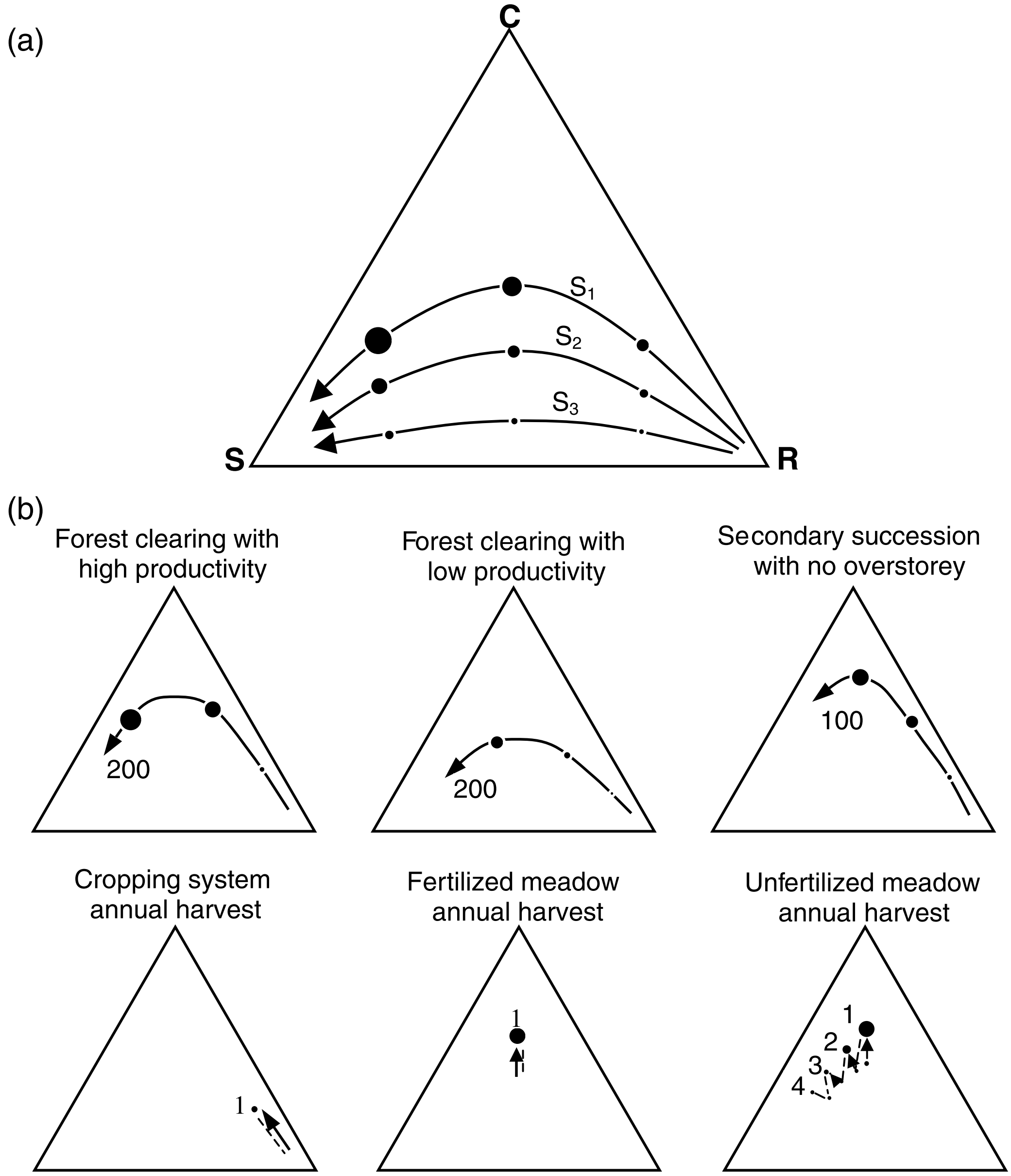

Fig. 12.5. Succession represented on Grime's C-S-R triangle showing: (a) general successional patterns under conditions of high (S_1) medium (S_2) and low (S_3) potential productivity, and (b) successional pathways of specific habitat types. Size of circles indicates the amount of plant biomasss present at that stage of succession. Numbers indicate the approximate time (years) in the successional pathway (redrawn from Grime 1977, 1987).

Here they found that ruderals were not able to colonize the disturbed sites, but that species tolerant of disturbance were dominant in early succession. This is a strategy not considered in the C-S-R model (Steneck and Dethier, 1994; Ecke and Rydin, 2000). Thus we can gain general insight using the C-S-R model but it may not be applicable in all situations.

Processes of succession: facilitation, inhibition and tolerance

In 1954, Egler proposed two models to explain succession. The 'initial floristics model' described how most species were present at the initial stages of succession but that the later successional species became more prominent over time as a result of longer lifespan, slower growth rate and larg-

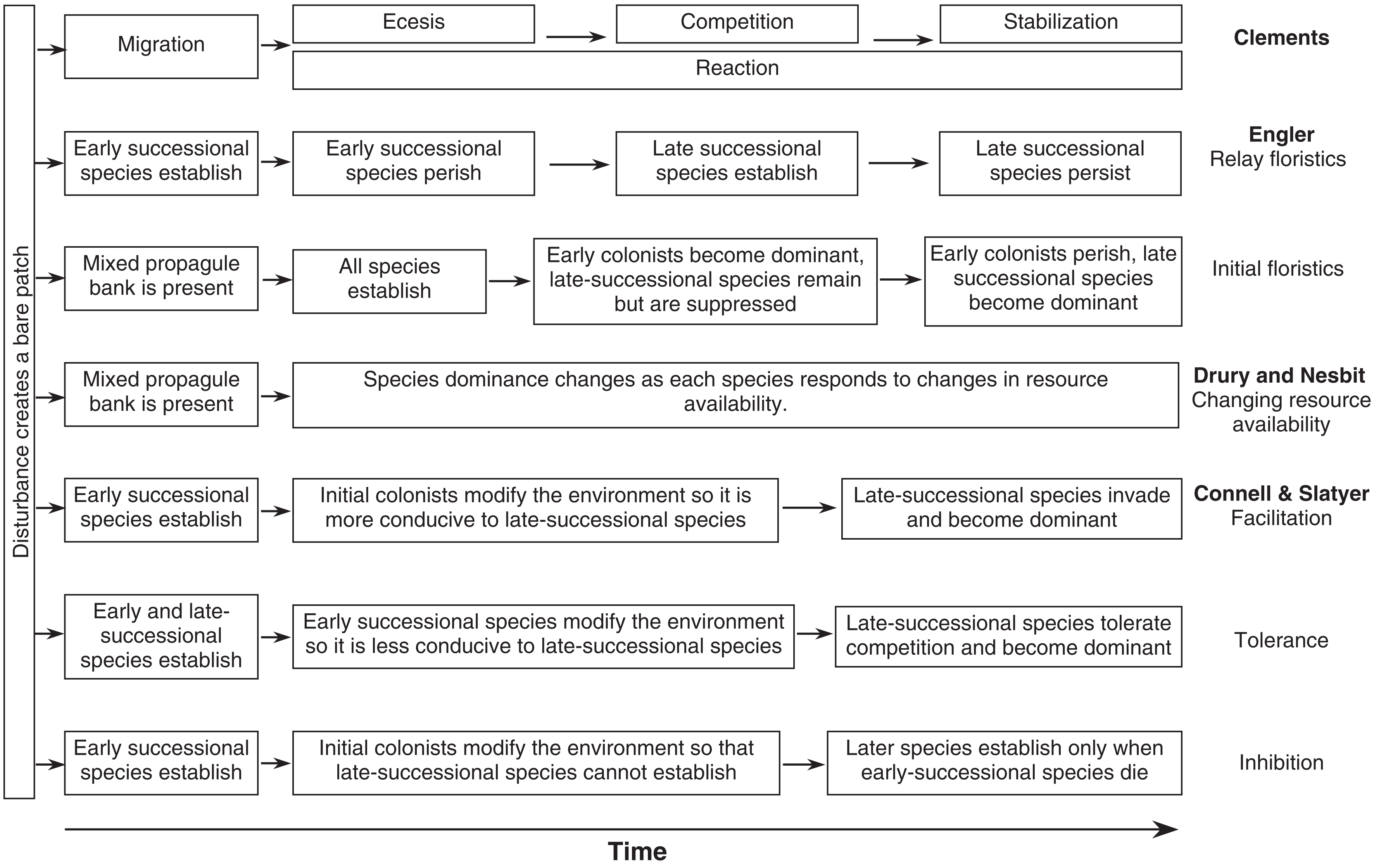

Fig. 12.6. Models of succession (Luken, 1990).

er size at maturity (Fig. 12.6). Drury and Nisbet (1973) expanded on this idea and tested whether physical stress and competition might also be important processes in succession. Second, Egler's 'relay floristics model' proposed that species prepare the environment for later appearing species, making it inhospitable to themselves.

In 1977, Connell and Slatyer further developed some of these ideas and presented three models to explain the mechanisms of succession: facilitation, inhibition and tolerance (Fig. 12.6). These models are still used as a basis to describe the processes underlying succession. These processes interact and the development of most pathways is a combination of all three. Furthermore, the relative importance of the three processes will change over time.

Facilitation

This model develops Clements' original ideas that early species facilitated the invasion of later ones. For example, they may ameliorate temperatures by providing shade, or may increase soil nitrogen by fixing atmospheric nitrogen. In this way, late invading species cannot appear until after the environment is 'improved' by earlier species. There are many examples of facilitation in natural communities; however, these occur mostly in primary succession where early environments are severe (Walker and Chapin, 1987). For example, after Mount St Helens erupted, nitrogen-fixing lupins (*Lupinus lepidus*) were among the first species to colonize. When they died, other species could then take advantage of the released nitrogen (del Moral and Bliss, 1993).

Early accounts of primary succession often reported the importance of lichens, moss and algae in facilitating the establishment of pioneer vascular plants (Griggs, 1933; Booth, 1941) because they were thought to build soil and create microhabitats for vascular plants. In fact, this is not necessarily the case. On Mount St Helens, for example, lichens, moss and algae did not establish in many habitats because of the dry summers and porous rock, and therefore they did not play a role in primary succession (del Moral and Bliss, 1993). In other situations, moss and lichens may actually inhibit the succession of vascular plants on volcanic soils (Frezen *et al.*, 1988).

Inhibition

Inhibition occurs when existing plants prevent or inhibit the establishment of subsequent species. This is caused by a combination of physical, chemical or biotic means. Usually, the early plant becomes established in a site and pre-empts biological space. There are numerous examples of inhibition in succession. In fact the lupins, mentioned in the above section on facilitation, inhibited establishment of other individuals while they were alive. It was only after their death that lupins facilitated the establishment of others.

The inhibitory effect of a species can last long after the individual has died. Litter, for example, can have an inhibitory effect that favours some species over others. In an old field succession, for example, the litter of giant foxtail (*Setaria faberii*) is a physical and chemical deterrent to annual fleabane (*Erigeron annuis*) (Facelli and Facelli, 1993). When the litter is removed, annual fleabane is able to establish and then reduces the growth of giant foxtail. The process of inhibition tends to favour early colonists over late colonists, thus dispersal ability and getting established first are very important.

Tolerance

Connell and Slatyer (1977) viewed facilitation and inhibition as extremes on a continuum, and placed tolerance in the centre. Under this model, early species have no effect on subsequent ones. The timing and success of each species' colonization is determined by its tolerance to environmental conditions; for example, late successional, long-lived species are more likely to tolerate shade than early successional species.

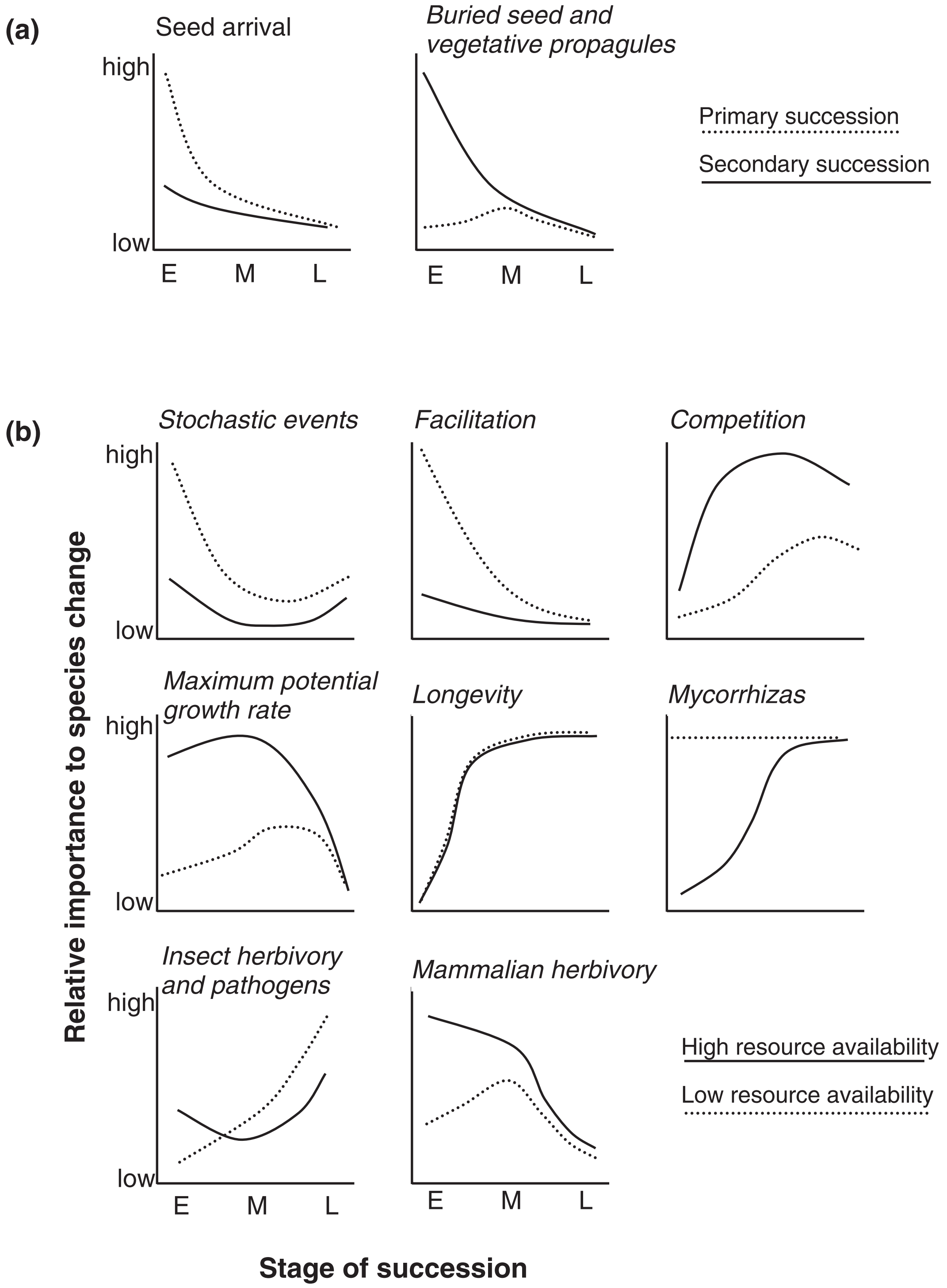

Fig. 12.7. Influence of the: (a) type of succession, and (b) level of resource availability on successional process over the course of early (E), middle (M), and late (L) succession (redrawn from Walker and Chapin, 1987).

Effect of environmental severity on successional processes

The types of processes that are important in determining species change will change with the stage of succession (early, mid- and late), the types of succession (primary vs. secondary) (Fig. 12.7a) and the level of available resources (water and nutrients) (Fig. 12.7b) (Walker and Chapin, 1987). For example, seed arrival is highly important in the early stages of primary succession because

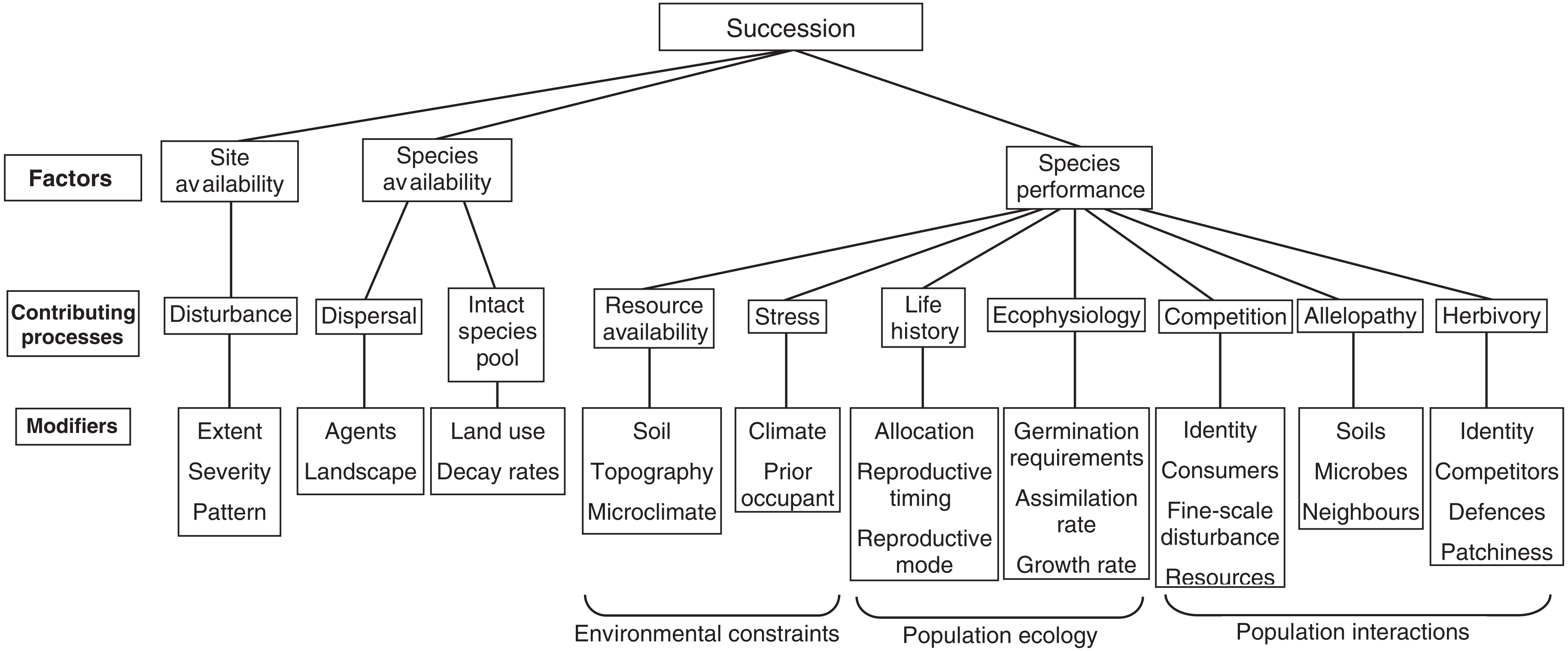

Fig. 12.8. Causes of succession and their contributing processes and modifying factors (redrawn from Pickett *et al.*, 1987a).

seeds will be limiting and the first species establishing at a newly exposed environment can determine what subsequent species will be successful. Conversely, buried seeds and propagules will be more important in secondary succession because these will determine early species composition. Facilitation is more important in nutrient poor environments, but this decreases over the course of succession because vegetation will moderate the environment. Mycorrhizal associations are important throughout succession when nutrients are lacking. When nutrients are available, mycorrhizae will not be important early in succession because there will be little competition, but their importance will increase as the competition for resources increases.

Hierarchy of successional processes

When Connell and Slatyer (1977) developed their three models, they did not look at interactions among processes. Therefore, Pickett *et al.* (1987a,b) proposed a hierarchy of successional processes. This model has also been applied to agricultural weed management (Swanton *et al.*, 1993; Sheley *et al.*, 1996). At the largest scale, Pickett *et al.* said that succession is determined by three factors: site availability, species availability and species performance (Fig. 12.8). These in turn, are influenced by contributing processes and their modifiers.

Site availability

The process of succession is initiated when a disturbance creates or alters a site. Disturbances can be characterized by their extent (area affected), frequency (probability of occurrence over a time period) and magnitude (Walker and Willig, 1999). Magnitude is a combination of intensity (physical force) and severity (impact on vegetation), but the terms are often used interchangeably. The extent of a disturbance determines the environmental conditions and the heterogeneity of the patch, whereas the magnitude will determine its openness and the number and types of propagules available for regeneration (Pickett *et al.*, 1987a,b).

Generally, anthropogenic disturbances are greater in extent and severity than natural disturbances, but they have similar frequencies. Human activities can accentuate or prevent natural disturbances (Luken 1990, p. 12); for example, fire suppression can lead to more extensive and intense fires in the long run (Bond and van Wilgen, 1996). Turner *et al.* (1997) showed that the extent and pattern of fire influenced the successional pathway following the 1988 fires in Yellowstone National Park.

Species availability

The ability of a species to colonize a newly disturbed site will depend on:

- whether it is present in an intact species pool, such as vegetation or in the seed bank;
- its ability to disperse into the site.

Succession following an intense and extensive disturbance will be more dependent on long-distance dispersal, whereas the seed bank and remnant vegetation will be the source of propagules following less intense disturbance (Walker and Chapin, 1987). Del Moral and Bliss (1993) found that proximity to vegetation influenced succession on volcanoes. Lupins and other large-seeded species were early colonists because there were remnant populations serving as seed sources. Sites further from remnant vegetation were composed mostly of small-seeded wind-dispersed species.

Species performance

A species' performance is dependent on its population ecology, how it interacts with other populations, and on environmental factors such as resource level and abiotic stress. A species' performance can be influenced by idiosyncratic events that occur during succession. For example, the timing of the Mount St Helens eruption, in May 1980, may have changed which species were successful (del Moral and Bliss, 1993). When the eruption occurred, much of the ground was still covered in thick snow, and this allowed some plants to persist. Also, ice blocks left crevices when the ice melted and this created moist habitats suitable for

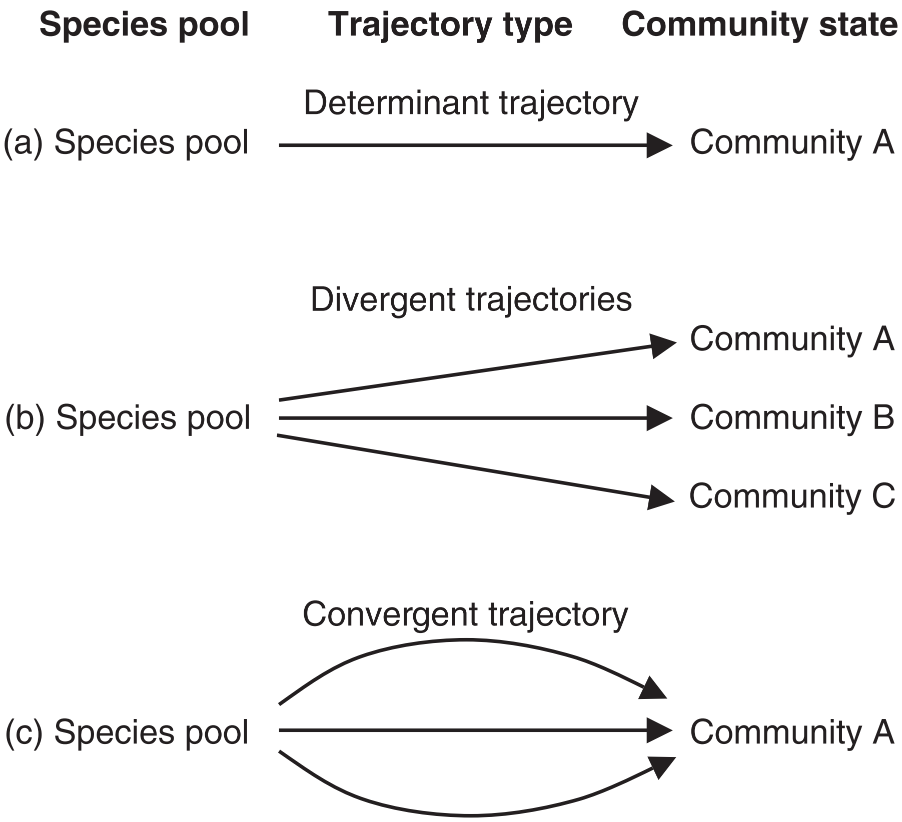

Fig. 12.9. Examples of how different community configurations may be produced from one species pool. (a) Assembly trajectories are deterministic when a species pool consistently produces the same extant community. These deterministic trajectories are relatively immune to historical influences such as invasion sequence. This is the classical view of succession. (b) Different communities may be produced from one species pool when trajectories diverge. These indeterminant trajectories are more sensitive to historical influences such as invasion sequence and changes in the assembly environment. (c) One community type may be produced when assembly trajectories converge (adapted from Drake, 1990).

seedling establishment. Furthermore, the favourable conditions during the three summers following the eruption probably increased seedling establishment allowing new recruits to get a 'foothold'. If conditions had been dry during these first summers, succession might have been delayed or altered. Slight changes in the abiotic environment can alter the competitive balance, or other interactions among colonizing species.

Community Assembly: a Broader Interpretation of Succession

Communities are complex entities and as a result, the thought of looking at 'whole communities' is daunting because there are so many interacting parts. Some scientists deal with complexity by trying to understand all of the community parts individually, and then trying to put the parts together. Another way to deal with complexity is to look at the community as a whole entity and to ignore the details. As the large-scale processes are understood, then more detail can be added. Community assembly theory allows us to do this (Booth and Swanton, 2002).

In recent years the ideas of succession have been reworked and reworded under the theory of community assembly. While there is extensive overlap of these theories, many think of succession as a process of individual replacement whereas community assembly takes a broader approach to community dynamics. Young *et al.* (2001) attempted to summarize the differences between succession and assembly and reconcile the two

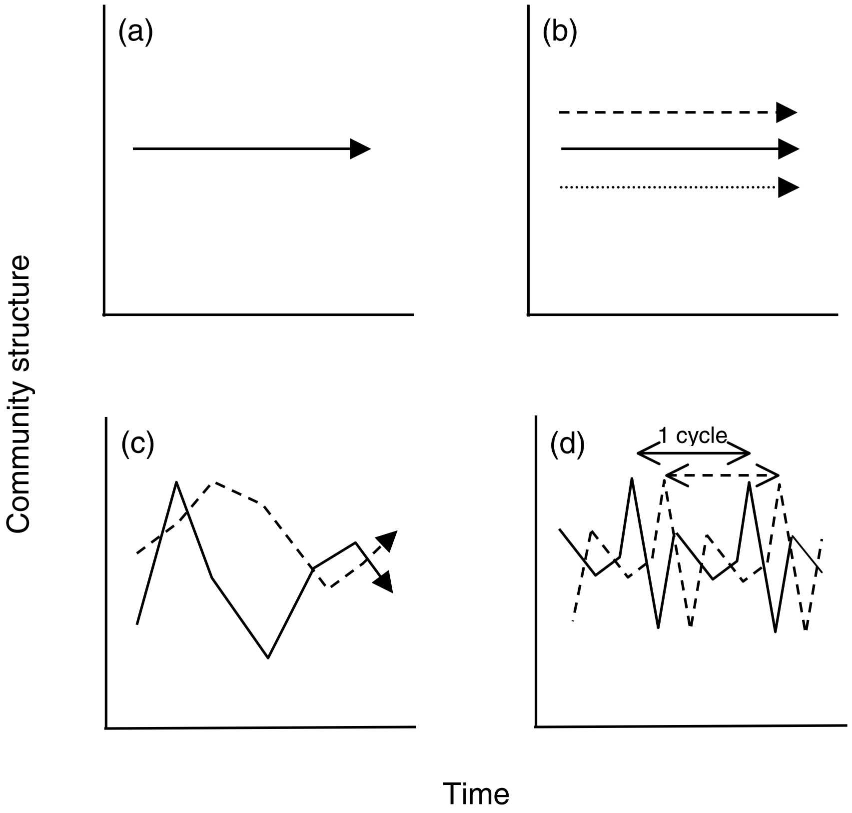

Fig. 12.10. Examples of the divergence and convergence of community trajectories over time. In: (a) communities will converge to a persistent state determined by environmental conditions; in (b) trajectories diverge, and multiple stable states arise out of the same species pool; in (c) communities are random or chaotic and trajectories will continue to converge and diverge, and in (d) one trajectory is reached, but the two communities are cycling out of sync (adapted from Samuels and Drake 1997).

theories. Unfortunately, succession and assembly theories were developed in isolation and only recently have people begun to consider where they overlap and diverge. Really, assembly is the broadening out of the ideas of community dynamics. The basic premise of community assembly is that all biological communities are assembled over time as they follow trajectories and that the membership of a community is limited by filters acting on the species pool. We will first consider how communities follow trajectories through time.

Communities follow trajectories through time

To help us think about communities as dynamic entities we can think of a community as following a trajectory through time (Drake *et al.,* 1999). A trajectory is a path through a series of community states. In a traditional Clementsian view of succession, community development follows a single trajectory: that is, given a species pool, only one community type develops along a deterministic trajectory (Fig. 12.9a). Alternatively, many types of communities can result from a species pool if trajectories are divergent (Fig. 12.9b). Sometimes divergent trajectories may converge producing identical community states (Fig. 12.9c).

It may be difficult to distinguish between a deterministic and an indeterministic trajectory. Over time, trajectories can repeatedly diverge and converge (Fig. 12.10) and this may or may not be predictable (Rodriguez, 1994; Samuels and Drake, 1997). In field experiments, for example, Inouye and Tilman (1988, 1995) found that old-field communities converged after 4 years of nitrogen addition, but after 11 years, these communities had diverged. Sometimes a community reaches a state of predictable cycling (i.e. similar to a population's stable limit cycle) and if viewed over too short a time span, the trajectory will appear indeterministic (Fig. 12.10). Furthermore, two communities following the same trajectory but offset in time will appear different, even though their dynamics are the same. Such communities must be observed over a long enough time scale to distinguish them from random or chaotic trajectories.

Species pools

Only some members of the available species pool will become part of a community. Other species will be removed or filtered out by biotic and abiotic processes at various life stages. Every community is composed of a subset of the total species pool – that is, the group of species available to colonize (Fig. 12.11). Belyea and Lancaster (1999) differentiated among five types of species pools.

- total species pool – large-scale species pool determined by landscape scale ecological and evolutionary processes;
- habitat species pool – the subset of the total species pool that could establish and survive in the habitat;
- geographical species pool – species able to disperse into the habitat;
- ecological species pool – overlap of species present in both the geographical and habitat species pool;
- actual species pool – species present in the above-ground community.

Thus, we have a series of species pools containing subsets of the total species pool. The only time when all types of species pools would be the same is in a closed and stable community where there is no dispersal into the community.

Ecological filters

The processes that remove species from a community are commonly called filters (or constraints). Thus filters limit membership to each species pool, and different types of filters will operate under different conditions. Dispersal constraints determine the geographical species pool, environmental constraints determine the habitat species pool and biotic constraints determine the actual species pool.

Dispersal filters – arriving at the party

Dispersal filters determine what species arrive at a site (see Chapter 6). Communities

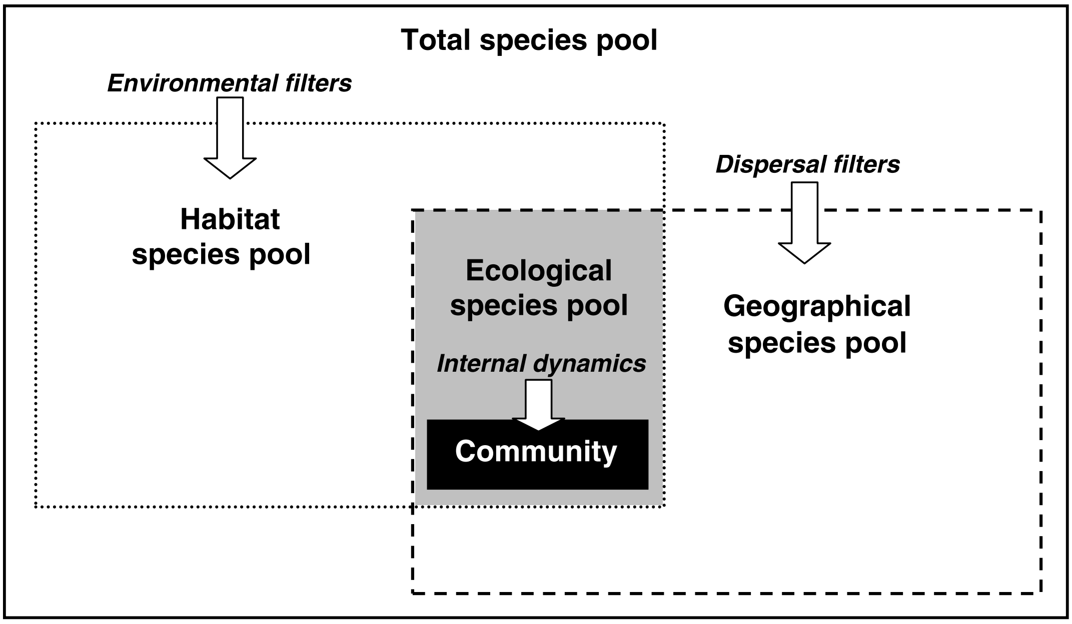

Fig. 12.11. Types of species pools (redrawn from Belyea and Lancaster, 1999).

do not have an unlimited and continuous supply of propagules (Belyea and Lancaster, 1999) because propagules are not produced at a constant rate, nor do they disperse evenly over space. Earlier in this chapter, we discussed the importance of proximity to seed sources (del Moral and Bliss, 1993). As well, seed characteristics, plant phenology and abiotic conditions determine when and whether a propagule can arrive at a site. There has to be the right combination of seed type, dispersal agent and environmental conditions for dispersal to occur.

The timing, sequence, frequency (number of times a species' invasion is repeated) and rate (how quickly invasions are repeated) of species introductions into a community can alter trajectories. The effect of invasion sequence is the most well understood of these. Numerous studies using natural communities (Abrams *et al.*, 1985; McCune and Allen, 1985) and microcosms (Robinson and Dickerson, 1987; Drake, 1991; Drake *et al.*, 1993) have shown that the order in which species are introduced can influence the community trajectory. Early invaders may have the advantage simply because they occupy biological space, inhibiting the invasion of late species, but this is not always the case. Later invaders may drive early ones to extinction by direct or indirect means. They may directly out-compete early invaders, or they may change the abiotic environment, making it inhospitable to the earlier species.

Early species may have a significant role in the assembly process even if the species is not dominant or if its presence is ephemeral. For example, a 'chaperone' species (Kelly, 1994) may facilitate the invasion of another species either by directly assisting it or by inhibiting a third species. Even though the chaperone species is not a dominant species, or is present only temporarily, it could alter significantly the trajectory and have cascading effects on community structure. These 'indirect effects' have also been demonstrated in natural systems (reviewed by Strauss, 1991) and may continue even after a chaperone species has become extinct.

Less studied are the effects of invasion rate and frequency on the trajectory. In experimental studies, species introductions are done singly and at a constant rate, but this is not how invasions occur in natural situations. Generally, increasing the invasion rate and/or frequency increases a community's richness and decreases the likelihood of there being a single stable trajectory because different species will be favoured over time (Hraber and Milne, 1997; Lockwood *et al.*, 1997). A high invasion rate and frequency minimize the influence of historical events (Lockwood *et al.*, 1997). Communities will be more persistent when the invasion rate and frequency are low because the assembly process is not disrupted.

Environmental constraints – crashing the party

After a species is dispersed into a community, it must be able to survive in the physical environment. We can get some indication of a plant's suitability to an environment; for example, by looking at a plant's growth rate versus average temperature and rainfall (Chapter 2). However, the environment can have subtle persistent effects on a community (Chesson, 1986). When we consider only average or typical environmental conditions, we neglect occasional environmental extremes which could have long-term persistent effects on a community. For example, the distribution of the saguaro cactus in Arizona is limited by periodic frosts that kill seedlings, rather than by the cactus's physiological response to average temperature (Hastings and Turner, 1965). Periods of stress, or environmental fluctuation or extremes, may in fact, have a greater impact on the long-term community dynamics than average, relatively predictable environmental conditions. An extreme event may cause some species to go extinct or severely reduce their abundance allowing other species to gain an edge. Environmental variation will alter a community's susceptibility to invasion. Species not usually able to establish may gain an advantage during a period of unusual environmental conditions.

Internal dynamics – being the life of the party

Seeds or propagules can arrive at a site and may be able to survive the abiotic conditions, but not all species will become part of the extant community. Internal dynamics act on the ecological species pool. Population interactions (Chapters 8 and 9) drive internal dynamics. This is possibly the most complicated aspect of community assembly because we cannot possibly understand all interactions. We cannot predict the outcome of all interactions between all species under all dispersal and environmental constraints, nor would this have any predictive value. To make this approach possible and useful, some researchers have used plant characteristic or traits to examine assembly dynamics (Box, 1981; Keddy, 1992a,b; Díaz *et al.*, 1999a,b; McIntyre *et al.*, 1999a,b; Weiher *et al.*, 1999). We will examine this more fully in the next section.

Plant Traits and Functional Groups

We have been taught to classify plants according to their phylogeny – that is, we place them in their family, genus and species. But it might also be useful to classify plants by the traits. Traits are the physical and physiological characteristics that determine a species' ecological function.

Environmental filters remove species from a species pool. In reality, filters act to remove species that lack specific traits (Fig. 12.12) and thus, *traits* rather than species are filtered (Weiher and Keddy, 1999; Booth and Swanton, 2002). Species without the suite of requisite traits will not be able to pass through the series of environmental filters. Plants respond at scales from the climate to disturbance to biotic interactions (Woodward and Diament, 1991). Each type of filter selects against a unique set of traits; therefore, the ability of a species to pass through one filter will not necessarily affect its ability to pass through another because different traits may be required for each. When we work with traits, we first have to decide what traits are important.

Selecting plant traits

How do we determine what traits are biologically relevant? We need to select traits

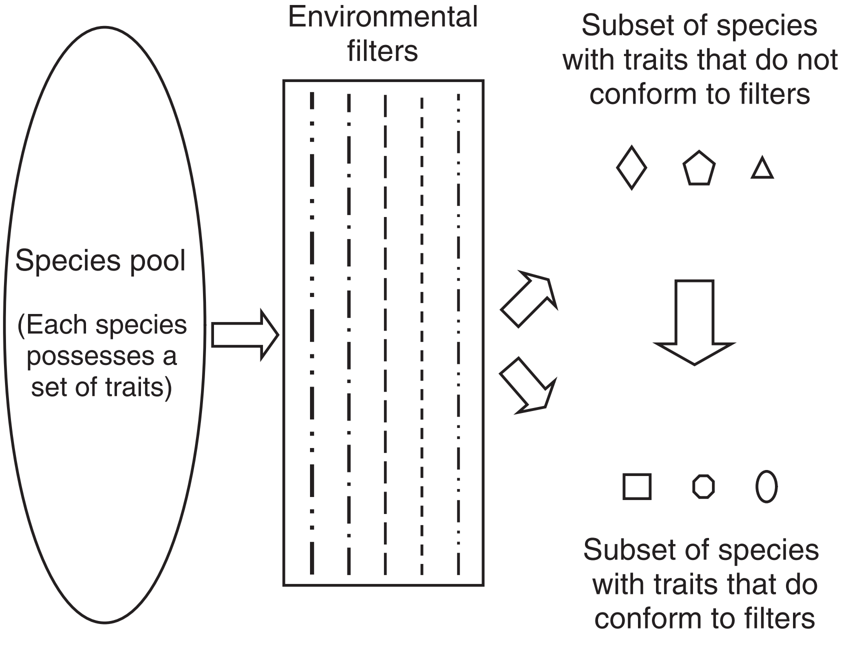

Fig. 12.12. A conceptual model of the trait-based approach to community assembly. A large pool of species is available but they must pass through a series of biotic and abiotic filters that remove species that do not possess specific traits (adapted from Weiher and Keddy, 1999).

Table 12.4. List of traits that could be used as a starting point for a trait-based approach to community assembly and possible ways to quantify them. Some or all of the traits could be selected to record, and of these only some traits would be ecologically important. Based on lists in Díaz *et al*. (1999b), Díaz, Barradas *et al*. (1999), Kleyer (1999) and McIntyre *et al*. (1999b).

Vegetative traits	Classification of trait
Vegetative traits	
Size	<10 cm; 11–20 cm; 21–50 cm; 51–100 cm; >100 cm
Height:width ratio	h:w>1; h:w/1; h:w<1
Specific leaf area	Aphyllous; <1 cm^2; 1.1–2 cm^2; 2.1–3 cm^2; 3.1–5 cm^2; >5 cm^2
Life cycle	Summer annual; winter annual; biennial; perennial monocarpic; perennial polycarpic
Life span	<1 year; 2–5 years; 5–10 years; 11–20 years; >20 years
General form	Prostrate; rosette; erect; tussock; vine; shrub
Leaf form	Aphyllous; evergreen; deciduous
Leaf angle	<90°; >90°
Leaf size	Aphyllous; <1 cm^2; 2–5 cm^2; 6–10 cm^2; 10–25 cm^2; 25–50 cm^2; >50 cm^2
Leaf shape (length:width)	l:w>1; l:w/1; l:w<1
Photosynthetic metabolism	CAM; C_3; C_4
Potential relative growth rate	Low; medium; high
Drought avoidance	None; succulent stem, taproot or other storage organ
Palatability	Unpalatable; low or just at juvenile stage; moderate; high
Leaf texture	Smooth; hairy; spines
Root morphology	Taproot; mostly horizontal; mostly vertical
Maximum rooting depth	<10 cm; 10–25 cm; 25–50 cm; 50–100cm; >100 cm
Extent of clonal expansion	None; some (dm); high degree (m)
Resprouting ability	None; moderate (daughter plants remain attached to parent plant for some period of time); high (daughter plants rapidly become independent)
Mycorrhizal associations	None; ectomycorrhizal; vesicular-arbuscular
Storage organs	None; tubers; bulbs; rhizomes
Reproductive traits	
Seed size (max. length)	<1 mm; 1–2 mm; 3–5 mm; 6–10 mm; >10 mm
Seed shape (variance of seed length, width and depth)	<0.15; 0.15–<1; 1–5; >5
Seed number (per plant)	<100; 100–999; 1000–5000; >5000
Weight of dispersal unit (fruit or seed)	<0.2 mg; 0.3–0.5 mg; 0.6–1 mg; 1–2 mg; >2 mg;
Seed dispersal	No mechanism; wind; by highly mobile animals (birds, bats); by low mobility animals (ants, rodents)
Fruit type	Dry indehiscent; dry dehiscent; fleshy
Season of germination	Plastic; early spring; late spring; summer; autumn
Age of first reproduction	<3 months; 3 months–1 year; 1–3 year; >3 year
Peak period of flower and fruit production	None; autumn to early spring; spring; late spring to late summer; late summer to autumn
Pollination mode	Wind; specialized animals; unspecialized animals
Position of dormant buds (physiognomic types)	thero-; geo-; hemi-; crypto-; chamaephyte
Agricultural specific traits	
Herbicide tolerance	
Weed size relative to crop	Smaller; same; larger

that address the multiple scales of environmental filters. Traits associated with both growth and reproduction should be included (Díaz *et al.*, 1999a). The former influences resource acquisition and storage, and the latter, recolonization and regeneration. Furthermore, both physiological and morphological traits are important. One trait may be important to several processes. For example, seed size affects dispersal, germination, risk of predation and seedling competitive ability. The selection of traits will depend on the habitat type, regional flora and on the goals of the study. Table 12.4 is a list of potential traits to consider.

Forming functional groups

We have reduced the complexity of our community from a list of species to a list of traits. We can simplify it still further by constructing functional groups from the traits. A functional group contains species with a similar set of traits. They serve similar ecological functions in a community and are therefore filtered from species pools in a similar manner, but how do we divide our traits into functional groups? There are a number of ways to do this (Smith *et al.*, 1997); we present two examples.

Nobel and Slatyer (1980) formed functional groups based on their ecological understanding of traits important to the community type. They identified a number of functional groups (Table 12.5) based on three sets of traits:

- arrival and persistence after disturbance;
- their ability to grow following a disturbance;
- the time to reach important life stages.

Using these functional groups they were able to describe vegetation changes of a wet sclerophyll forest in Tasmania following various disturbances (Fig. 12.13). The authors concluded that grouping plants by functional group ‘could be applied to man-modified communities, and to such phenomena as weed invasion or suppression’.

Kleyer (1999) used another approach to

Table 12.5. List of nine functional groups derived by Nobel and Slatyer (1980) based on traits required to arrive or persist following a disturbance, ability to establish following a disturbance, and time to reach important life stages. Species types, their life stage parameters, and a general description of their functional group (modified from the original 15 groups presented in Nobel and Slatyer, 1980). Critical life history events indicated are: m, reproductive maturity, l, longevity of the population, e, longevity of the seed pool.

Type	time since disturbance 0 - - - - - - - - - - - - - - - - - ∞	Characteristics of species
1	- - m - - - - - - - - - - - - - - le	Tolerant of disturbance, and able to establish quickly and continue to establish following disturbance by various means
2	m - - - - - - - - - - - - - - le	Tolerant of disturbance, but propagules only available if vegetation is mature and can release seeds
3	- - m - - - l - - - - - - - - - - e	Pioneer species, with propagules capable of long-distance dispersal into disturbed site
4	- - m - - - l - - - - e	Pioneer species, with propagules always available (usually in seed pool)
5	m - - - l - - - - e	Pioneer species, with propagules available as long as disturbance occurred after the juvenile stage of growth
6	m - - - le	Pioneer species, with short-lived seed pool available
7	- - m - - - le	Pioneer species, able to regrow vegetatively
8	- - m - - - - - - - - - - - - - - le	Require mature vegetation to re-establish, and propagules from dispersal or species pool
9	m - - - - - le	Pioneer species, capable of vegetative reproduction

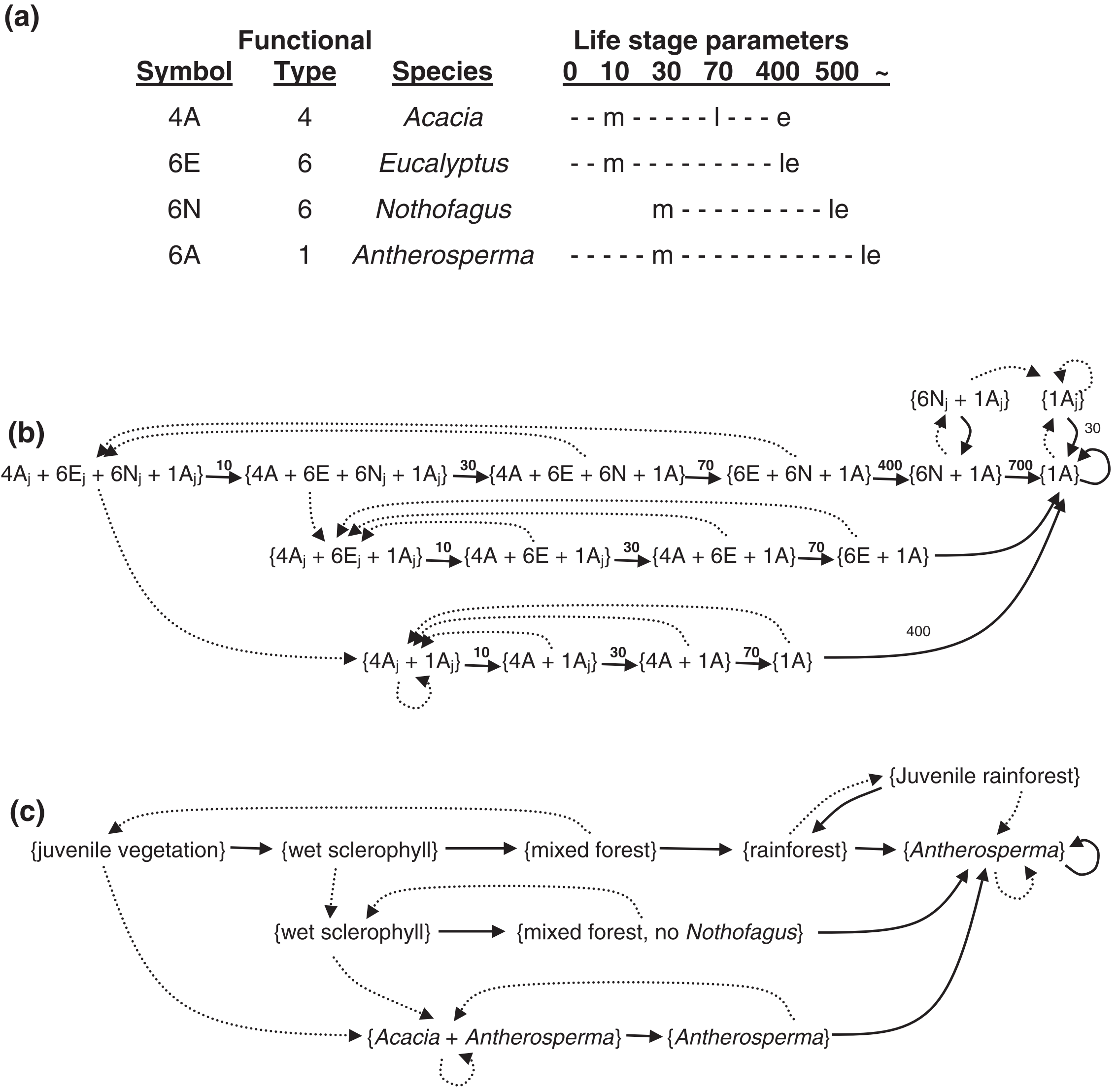

Fig. 12.13. Vegetation replacement series for a wet sclerophyll rainforest in Tasmania (Nobel and Slatyer, 1980). Part (a) describes the four dominant species, their functional types and life history parameters; (b) shows the replacement sequence; (c) summarizes the transition sequences by showing community types. Solid arrows indicate transitions where no disturbance occurs, whereas dotted arrows indicate transitions following disturbance. Numbers are years and subscript j ($_j$) indicates plants in the juvenile stage (redrawn from Nobel and Slatyer, 1980).

delineate functional groups. Kleyer sampled 129 agricultural and disturbed sites in Germany and noted three types of features:

- level of disturbance (from frequently disturbed field to 60-year-old undisturbed field);
- resource supply (level of nitrogen, phosphorus and soil moisture);
- plants species composition.

Species were then characterized using many of the traits listed in Table 12.4. Clustering techniques (see Chapter 15) were used and these identified 30 functional groups containing species with similar traits. Table 12.6 shows six examples, and lists representative species and associated traits. Kleyer was able to predict what functional groups were likely to occur under various combinations of disturbance and resource level (Fig. 12.14). For example, species in type I are more likely to be found in either frequently disturbed sites, or in less disturbed but resource-rich sites.

Table 12.6. Examples of functional groups with similar biology as resulting from the cluster analysis (based on information in Kleyer, 1999).

Functional groups and their representative species	Traits associated with functional group
I. Lambsquarters type *Amaranthus retroflexus, Atriplex patula, Avena fatua, Chenopodium album, Echinochloa crus-galli, Fallopia convolvulus, Polygonum lapathifolium, P. persicaria, Setaria verticillata*	Summer annual. Seed weight > 0.2 mg, seed number 1–10,000. Seed bank long-term persistent, long-range dispersal, plant height mostly 0.3–0.9 m, leaves regularly distributed
II. Chickweed type *Capsella bursa-pastori, Cardamine hirsuta, Matricaria discoidea, Poa annua, Senecio vulgaris, Stellaria media, Veronica persica*	Several generations per vegetation period. Seed weight > 0.2 mg, seed number 1000–10,000. Seed bank short-term to long-term persistent, long-range dispersal, plant height < 0.3 m, leaves regularly distributed. Regeneration from detached shoots reported for *C. hirsuta, S. media, V. persica*
III. Yarrow type *Achillea millefolium, Campanula persicifolia, C. rapunculoides, C. rotundifolia, Cerastium holosteoides, Poa compressa, Sedum acre*	First reproduction at 2–3 years (except *C. holosteoides, P. compressa*). Seed weight mostly < 0.2 mg, seed number 1000–10,000. Seed bank longevity various and dispersal mostly short-range. Plant height 0.3–0.9 m (or < 0.3 m), leaves regularly distributed. Lateral clonal extension some dm or m, vegetative growth mostly slow
IV. Yellow toadflax type *Artemisia vulgaris, Hypericum hirsutum, H. perforatum, Linaria vulgaris, Origanum vulgare, Solidago canadensis, Tanacetum vulgare*	Seed weight mostly < 0.2 mg, seed number mostly > 10,000. Seed bank longevity and dispersal various, plant height 0.3–0.9 m or > 0.9 m, leaves regularly distributed. Lateral clonal extension some m (except *A. vulgaris, H. hirsutum*), vegetative multiplication facultative or slow
V. Creeping buttercup type *Fragaria vesca, Glechoma hederacea, Poa subcoerulea, Potentilla anserina, Ranunculus repens, Rumex acetosella, Trifolium repens*	First reproduction at 1 year for *R. repens*, 2 years for the rest. Seed weight > 0.2 mg, seed number mostly low. Seed bank mostly long-term persistent and long-range dispersal. Plant height low, leaves semirosette or rosette. Lateral clonal extension some dm to m, vegetative multiplication mostly rapid.
VI. Blackthorn type *Corylus avellana, Malus domestica, Prunus spinosa, Salix caprea*	Woody, age at first reproduction 6–15 years. Seed weight > 0.2 mg, seed number 1000–10,000. Seed bank transient and medium- to long-range dispersal. Plant height > 0.9 m, leaves regularly distributed. Lateral clonal extension some m, vegetative multiplication slow

Summary

If we can accurately characterize a community based on its structure, why go the next, more difficult step to describe or predict a community's dynamics? First, we must remember that communities are dynamic, and their present structure may not be representative of their future structure. Second, there are practical applications to be gained from understanding how a community will change in the future, especially for weed ecologists. Thus, we gain predictive knowledge from an understanding of community dynamics.

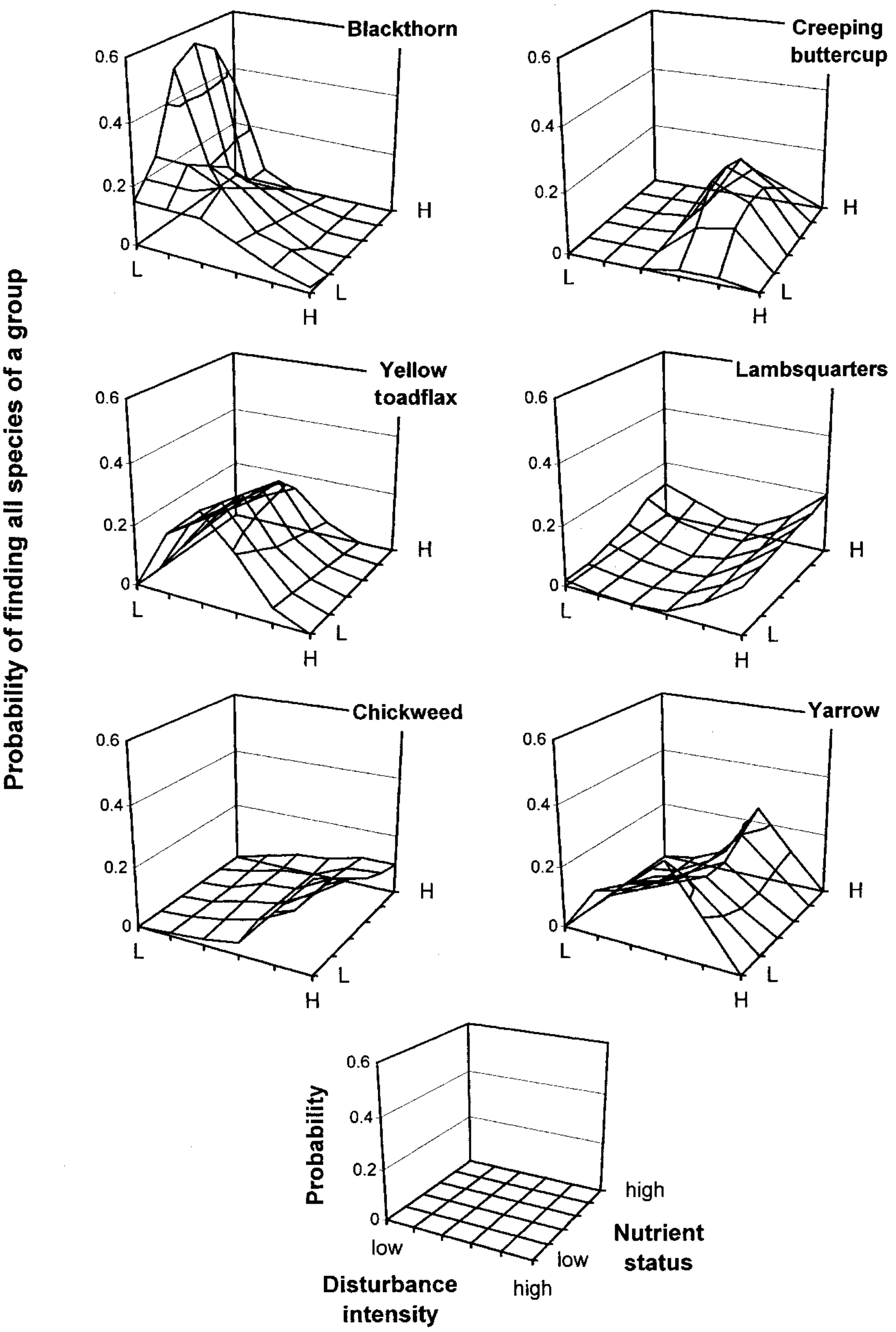

Fig. 12.14. Regression surfaces for six of Kleyer's (1999) functional groups. The probability of finding all of the species in a group is shown in relationship to disturbance intensity and resource supply. Disturbance intensities are (from low to high) 1, old field (disturbed 1×/60 years); 2, field balk (disturbed 1×/20 years); 3, field balk (disturbed 1×/ 10 years); 4, meadow (disturbed 1×/ year); 5, field road (disturbed 30×/year at soil surface); and 6, field (disturbed 6×/ year below soil surface) (redrawn from Kleyer, 1999).

Questions

1. What role does your species play in community dynamics? Is it an early-, mid- or late successional species?
2. Explain why more competitors (C) occur in Grime's model when there are higher levels of potential productivity.
3. Draw a successional trajectory of a no-till annual cropping system under the C-S-R model.
4. Why are the terms 'stability' and 'equilibrium' misleading when describing communities?
5. Refer to Fig. 12.7 (Walker and Chapin, 1987) and explain each of the ten patterns displayed.
6. Refer to Fig. 12.14 (Kleyer, 1999). In what type of community would you expect to find species of each of the six functional groups? Explain your answer.

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