Community Dynamics

Caveats

Caveat 1: While most of the examples are of terrestrial plant communities, the same concepts can be applied to wetland, fresh-water, and marine communities.

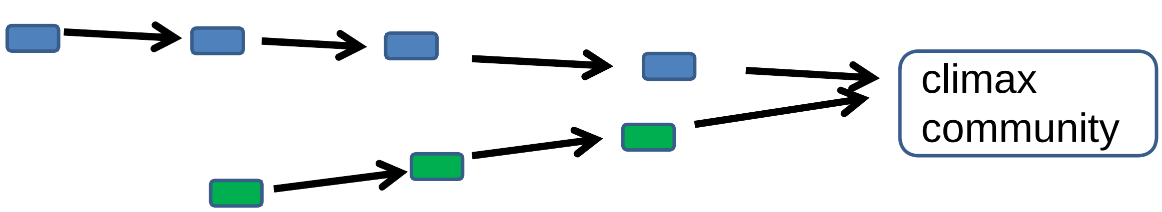
Caveat 2: The emphasis is mostly on the dominant plant species, following the scientific literature. However the changes in the dominant plants affect subdominant plant species, animals, microorganisms, and ecosystem-level processes such as nitrogen fixation, carbon sequestration, and soil erosion.

Caveat 3: In this scheme, community dynamics are categorized as one of five alternatives (A-E). As we consider actual examples, the category that best describes the particular scenario will depend upon our choice of temporal and spatial scales.

Types of community dynamics

A. Communities in a successional sequence

Succession is classically defined as a linear temporal sequence of communities, each replacing the one before it, without direct human intervention. In classical succession theory, this sequence ends with a persistent community called the *climax community*. Also in classical succession theory, prior land use may determine the starting point and therefore some or all of the intermediate stages, but a site has a single climax community that is determined only by its physical environment (climate, geology, topography) and the available species pool. Because soils develop over time as succession proceeds, soil is usually not considered part of the physical environment that determines the climax community.



Since soil-building is so slow, it often determines the rate of succession. *Primary succession* begins in the absence of soil. *Secondary succession* begins with soil present. If a soil-like material is present, such as fine-grained alluvial deposits, it is considered secondary succession. Both primary and secondary succession can be initiated by natural events or by anthropogenic (human-made) disturbances. Note that the initiating disturbance is NOT part of the succession.

Table 1. Examples of disturbances that can initiate primary and secondary succession.

	type of succession initiated	
initiating disturbance is	primary	secondary
non-anthropogenic	lava flow deep pumice field glacier retreat leaving behind gravel or bedrock sand dune deposition alluvial deposit (gravel)	hurricane damage to forest salt water overwash that kills plants flood (soil not removed) loess deposition after glacier retreat alluvial deposit (fine-grained)
anthropogenic	mine or quarry (soil not saved and replaced) road cut soil erosion due to human activities, down to parent material	mine or quarry (soil saved and replaced abandonment of a field abandonment of a pasture clearcut soil erosion due to human activities, not down to parent material

The goals of some land management activities such as tree-planting after a fire or clearcut are essentially attempts to duplicate succession, but at an accelerated rate.

Many, though certainly not all, endangered species are species whose habitat is restricted to the later stages of succession. Leaving large logs and snags after logging are examples of interventions to increase the rate at which a forest develops old-growth characteristics and thereby becomes habitat for old-growth species such as the northern spotted owl.

B. Community maintained by frequent disturbance

A good example of this type of community, familiar to everyone restoring or managing "prairies" in the US, is tall-grass grasslands, which require frequent (every 1-5 years, depending on the site) fires to persist. In the central US, tall-grass grasslands occur in regions where there is enough rainfall for forests to grow. Yet the early European explores and later the American settlers reported finding grasslands or oak savannas there. The soils of this region indicate that grasslands or savannas have been the dominant type of community for millennia. Some combination of Native American-set fires and lighting-set fires maintained these grasslands and savannas.

Another example is the longleaf pine (*Pinus palustris*) savannas of the southeastern US coastal plain. Surface fires in this community does not kill the adult longleaf pine trees, but does prevent the savanna from becoming a forest.

The ponderosa pine savannas of the southern Rocky Mountains have a similar relationship with fire. Years of fire suppression have allowed young pine trees and hardwoods to form an understory layer in these former savannas, so that now fires 'crown' and kill the pines.

It is likely that most of the rest of the world's grasslands and savannas are, or were, fire-maintained. Fires are known to have maintained for example.

Management of these communities requires re-instating the necessary disturbance regime. This may require considerable study and experimentation to determine. To use fire effectively, we must know the frequency, season, intensity, and spatial scale required to produce the desired community. Likewise river, stream, and wetland communities are often dependent upon a hydrologic regime in which water levels fluctuate at the right season, in the right amount, with the right year-to-year variation, with water of the right quality.

The hallmark of a community maintained by frequent disturbance is that the above-ground species composition is minimally changed by the disturbance.

C. **After a disturbance, two or more sequential communities occupy a site, but before a stable community is achieved, disturbance restarts succession.**

In many parts of the world, succession rarely or never reached a climax community. Instead a disturbance such as fire or flooding intervened.

Examples of this type of community dynamics include many montane forests in the western US dominated by species such as Douglas fir and lodgepole pine that require high-light conditions to establish. If crown fires could be prevented for a long enough period, they would presumably become dominated by one or more species of fir or spruce whose seedlings and saplings are shade-tolerant. Because Douglas fir and lodgepole pine can live for centuries, a crown fire almost always occurs before the hypothetical climax is reached. Note that the old-growth Douglas fir forests occupied by the northern spotted owl, although they may be 400 years old and have the structure and species of an old-growth forest, are not technically climax forests due to the light requirements of Douglas fir seedlings.

When managing such communities, it is important not only to impose the correct disturbance regime, as discussed above, but also to have sufficient land to allow some of it to be temporarily unsuitable for the target species at any given time.

This type of community dynamics and the previous one (B. disturbance maintains the community) are not always distinct. For example, consider some Mediterranean-climate shrublands in which fires do not kill the dominant shrub species but do burn off their above-ground stems so that they must re-sprout after a fire. Immediately after a fire, herbaceous species that have been present in the seed bank have the opportunity to grow. If we focus on the herbaceous community, we would identify at least two sequential communities; if we focus on the shrubs and include burned-back stumps in our census, we would say that this is a disturbance-maintained community.

The distinction between B and C comes down to one of our focus and of our temporal scale. We say the disturbance maintains a community when the community or ecosystem characteristics on which we are focusing are unchanged by the disturbance, or when changes in them are slight from our perspective, and/or when recovery to a pre-disturbance state is very rapid from our perspective. Thus when an Illinois grassland is burned, very few individuals of the dominant grasses are killed (unchanged characteristic), there is little post-fire erosion (change is slight), cover returns to its pre-fire level within a year (very rapid recovery); all of these properties put it into category B. In comparison, it may take 200 or more years for an Oregon Douglas fir forest to development the old-growth characteristics that make it suitable for the northern spotted owl (large change, slow recovery), putting this example into category C.

D. alternate stable communities

Examples of alternate stable states come from systems where, after a prolonged period without fire, the system will no longer carry a fire.

One example is the <u>oak-hickory forests of the northeastern US versus the maple-dominated forests</u> that are replacing them. It is now thought (Abrams 1992 and many subsequent papers by him and others) that the oak-hickory forests of the northeastern US were maintained by frequent surface fires, that is, were an example of B, above. This state is stable, given an appropriate climate and fire regime and climate. Without fire, the oaks and hickories are replaced by maples and other fire-intolerant hardwoods. These latter species have leaf litter that does not burn, so once the replacement has occurred the system has entered a second stable state.

Another example is some of the <u>forests in the states around the Great Lakes</u>. These were white pine forest when the area was settled and presumably had dynamics that resembled those of the conifer forests of the northern Rocky Mountains and the Pacific northwest, so they would have fit into category C. Intense logging of these pine forests in the late 1800's (origin of the folk tales of Paul Bunyan), followed by post-logging burning of the slash, and then years of fire suppression, have converted the area into beech-maple forests. These winter-deciduous forests do not burn, due to their high tissue water content during the growing season and their damp, packed-down leaf litter. Beech-maple forest appears to be an alternate stable state.

Sometimes the alternate stable state is in part the result of the introduction of a non-native species. In the Great Basin and parts of Wyoming, the pre-settlement vegetation was a <u>shrub savanna dominated by sagebrush and perennial grasses</u>, a stable state. Cheatgrass, an annual Eurasian grass, invaded, in part because of over-grazing. Cheatgrass burns readily. The pre-cheatgrass fire frquency was probably every 50-100 years; cheatgrass stands can burn every year to two. Frequent fires prevent sagebrush from recolonizing a site, making the <u>cheatgrass-dominated community</u> an alternate stable state.

Alternate stable states where one state is desirable and the other is not present enormous management challenges. It is often extremely difficult, and perhaps impossible, to move the system from the undesired to the desired state.

E. multiple alternate states, without clear stable points

In many systems, the composition of the vegetation (and associated animals, microorganisms, carbon cycle, etc.) depends strongly upon the disturbance regime, and relatively small differences in disturbance regime will alter the community substantially. For example, the composition of the community may depend upon the precise frequency, intensity, and season of fire or the precise season, duration, depth, and water quality of flooding.

In this situation, there may be particular combinations of, for example, fire frequency, intensity, and season that reliably produce a particular community (as in case B above; community maintained by disturbance) or reliably produce a particular sequence of communities (as in case C above). However a slightly different fire frequency or intensity or season may send the community off on a different trajectory. This situation is therefore probably best conceptualized as something more akin to a 'lumpy blanket' on which the system wanders than an attracting well into which it tends to roll.

Systems that vary between woodland, savanna, and grassland seem particularly likely to have dynamics of this sort. Woody plant encroachment, fire suppression, and grazing push these systems towards woodland; fire, mechanical clearing, and elephant browsing push them towards grassland. The result is a density of woody plants that depends upon site history, with no clear stable state unless fire, clearing, and elephants are all excluded.

On the Edwards Plateau of central Texas, surface fires apparently maintained savannas before settlement c. 1850 in some sites. Decades of fire suppression have lead to an increase in woody cover, especially juniper (*Juniperus ashei*, 'cedar'), in central Texas savannas, converting them to juniper-dominated woodlands. With lower deer densities, it is possible that juniper would not dominate wood plant encroachment. Mechanical clearing followed by surface fires has been successfully used by the City of Austin to restore savannas; the degree of woody cover depends upon, among other factors, time elapsed since burning or clearing. Season of fire is known to affect the composition of the herbaceous community . However, once juniper has reached a sufficiently high density and cover, surface fires are not longer possible; if a site burns at all, the fire will crown. Crown fires occurred in juniper woodlands in the drought year 2011; it is not yet clear what will follow crown fires in these woodlands.

Oak savannas in the upper Midwest of the United States provide another example. A site can support a variety of communities, depending on its fire history (Tester 1989; Peterson and Reich 2001). Good examples also come from east Africa, where poaching levels determine elephant densities which in turn determine woody cover (Leuthold 1996; Mapaure and Campbell 2002).

Literature cited

Leuthold, W. 1996. Recovery of woody vegetation in Tsavo National Park, Kenya, 1970-94. African Journal of Ecology 34:101-112.

Mapaure, I. N. and B. M. Campbell. 2002. Changes in miombo woodland cover in and around Sengwa Wildlife Research Area, Zimbabwe, in relation to elephants and fire. African Journal of Ecology 40:212-219

Peterson, D. W., and P. B Reich. 2001. Prescribed fire in oak savanna: fire frequency effects on stand structure and dynamics. Ecological Applications, 11(3):914-927.

Tester, J. R. 1989. Effects of fire frequency on oak savanna in east-central Minnesota. Bulletin of the Torrey Botanical Club 116:134-144.

TERRESTRIAL AND WETLAND COMMUNITIES

A classification of major terrestrial plant communities

(*: fire may be important; ** fire likely is very important)

A. Forests

	angiosperm (‘hardwood’)	coniferous (needle-leaved)
evergreen	**tropical lowland wet forests** (‘rainforests’)	**boreal forests**** (taiga)
	tropical montane forests	**montane coniferous forests****
		lowland pine forests**
deciduous	**winter-deciduous temperate forests***	
	dry-season-deciduous tropical forests	

B. Other communities in which woody plants are dominant or at least common

1. **woodlands** - lower, more open canopy than true forests
examples: pinyon/juniper woodlands of lower elevations in the southern Rocky Mountains; the cerrado of Brazil

2. **thorn scrub** - tropical and subtropical vegetation dominated by woody plants, often without thorns
example: acacia woodlands of southern and eastern Africa; caatinga of Brazil

3. **shrublands**** - vegetation dominated a more-or-less continuous cover of short-stature woody vegetation
example: shrublands of regions of Mediterranean climate (called chaparral) in southern California, matorral in central Chile, fynbos in the Cape of Good Hope, garigue in southern France, batha in Israel, etc.)

4. **shrub-steppe, shrub savanna*** - scattered shrubs in a grassland matrix
example: sagebrush steppe of northern Great Basin, US

5. **savanna**** - scattered trees in a grassland or low shrub matrix
examples: tropical savannas of east Africa; many of the eucalyptus-dominated plant communities of Australia; pine savannas of parts of the southeastern US

6. **shrub-dominated desert vegetation** - primarily scattered shrubs

examples: Karroo desert of souther Africa; sonoran Desert of Arizona, northern Mexico, creosote bush desert of western Argentina

C. Plant communities in which shrubs and trees are uncommon or absent

1. **tallgrass grasslands**** - treeless vegetation, primarily found in temperate regions, in regions with sufficient precipitation to support trees
example: prairie of Illinois, Iowa, etc.

2. **shortgrass grasslands*** - treeless vegetation, primarily found in temperate regions, in regions too dry to support trees but with more precipitation (or better distributed precipitation) than deserts
example: grasslands of eastern Colorado

3. **desert grassland**
example: southwestern US, at higher elevations than shrub-dominated desert vegetation but below the pinyon-juniper woodlands

4. **tundra, paramo** - found in regions too cold for shrubs and trees, both in temperate and tropical alpine areas <u>and</u> in the arctic and antarctic

The role of fire

I. North American terrestrial communities greatly affected by fire

[...] indicates some uncertainty about pre-settlement role of fire

1. boreal forests (Canada, Maine, lowland Alaska)

2. almost all western montane coniferous forests (Rocky Mts, Cascades, Sierras, coast ranges]

[3. pre-settlement pine forests of New England, Great Lakes States]

4. jack pine forests of Great Lakes States (habitat of endangered Kirtland's warbler)

5. long-leaf pine savannas of southeast US, including southeast TX

[6. oak savannas of Edwards Plateau (central TX)]

7. shrublands of southern California (chaparral)

[8. shrublands of lower montane sites in southwest US]

9. tallgrass grasslands, between the 100th meridian, the eastern forests of the US and Canada, and the boreal forest of Canada, including the prairies of east TX and of coastal TX

II. North American terrestrial communities probably not affected by fire

1. deciduous forests of north-eastern US, south-eastern Canada, including those of the Appalachian mountains; they extend into northeast TX

2. bottomland hardwood forests of southeast US, including southeast TX

3. pinyon/juniper woodlands of lower Rocky Mountain elevations (but these may have spread following fire suppression)

4. thorn scrub of south TX (but this has probably replaced grassland and savanna due to fire suppression)

5. sagebrush-dominated shrub steppe of Utah, southeastern Washington, etc. = the Great Basin desert (but fires now are causing this to be replaced by a cheatgrass-dominated desert grassland)

continued on the next page ....

6. shrub-dominated desert communities of the Sonoran, Mojave, and Chihuahuan deserts of

southwestern US, including west TX

7. alpine and arctic tundra communities

8. shortgrass grasslands, found between the 100th meridian and the Rocky Mountains, including Texas panhandle

9. desert grasslands, historically found just above the shrub-dominated desert lowlands in the southwest, but often now replaced by shrub-dominated communities due to overgrazing

A classification of wetlands, with examples

wetlands = ecosystems that have soil saturated for some period of time each year (or most years), but do not always have standing water.

	fresh water	**salt water**
forests	bald cypress swamps white cedar swamps black gum swamps palm swamps	mangrove forests
shrublands	pocosins sphagnum bogs	shrubby mangrove stands
herbaceous vegetation	cattail marshes *(Typha spp.)* sawgrass marshes	salt marshes *(Spartina spp.)* black rush marshes *(Juncus spp.)*