Textbook Misconceptions: The Climax Concept of Succession

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SUCCESSION is the process and pattern of changes following a disturbance in communities through time at a site. It is an important concept in an understanding of ecological dynamics; this definition incorporates White & Pickett's (1985) view of disturbance as any relatively discrete event in time that disrupts ecosystem, community or population structure. As a teaching tool, succession allows students to understand the changing nature of communities, as well as conceptualize the result of species' interactions.

Since Clements' seminal paper (1916), the idea of a deterministic end point to the process, called the climax stage, has become entrenched in the literature. This view was challenged in the 1950s and is now regarded as extreme (Simberloff 1982). Despite modern views of the process of succession (McCook 1994), and a rejection of the Clementsian climax thesis, current introductory ecology and environmental science college textbooks retain outdated and simplistic views of succession. In this article I review the development of the climax concept of succession, illustrate the misconceptions in current textbooks, and provide a conceptual model for an updated view of succession useful in teaching at the introductory level.

Development of the Climax Concept of Succession

Cowles (1899) and several Europeans (see review in Whittaker 1953) developed the early ideas on the nature of community change through time. These ideas were codified into a theoretical framework by Clements in 1916. Clements proposed that successional sequences were climatically determined leading to a single self-perpetuating climax community; i.e. the monoclimax. Each climax community was viewed as similar to an organism that grows, matures and dies. Although immediately challenged (Gleason 1917; Tansley 1935), this view became embodied in the literature.

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Gleason (1917, 1926) criticized Clements' monoclimax theory because it lacked accommodation of individual plant population behaviors (see also Peet & Christensen 1980). Tansley (1935) proposed the polyclimax theory, in which a climax community exists but consists of a mosaic controlled by local soil moisture, nutrients, parent material, topography, slope exposure, fire, and animal activity. Despite these concerns, the concept became the central tenet of range condition analysis used by the USDA for range management (Dyksterhuis 1949) and is still used today even though it is recognized as conceptually flawed (Joyce 1993; Tausch et al. 1993).

Whittaker (1953) proposed the climax-pattern hypothesis as a modification of the polyclimax viewpoint. The climax-pattern hypothesis combines community and environmental gradients to yield a variety of climax stands in an area that forms part of a continuous mosaic. Succession proceeds toward one of an infinite number of alternative climax communities, each in equilibrium with its own, unique site as a function of the success of populations of species in relation to local environmental gradients. Nevertheless, even with this pluralistic view of the process, the climax was recognized as a partially stabilized steady-state community that was deterministic within the bounds of local environmental gradients.

Like Harry Houdini's wager of money for scientific evidence of spiritualism, the ecologist Frank Egler offered a $10,000 challenge to the scientific community to present evidence in support of the plant succession-to-climax viewpoint (Egler 1977). Although this challenge was made for several years, the money was never paid out.

More recently, ecologists have sought a mechanistic rather than pathway-oriented understanding of succession (Pickett et al. 1987a). Various models have been proposed such as population-based approaches (Peet & Christensen 1980; Finegan 1984), e.g. the Vital Attributes model (Noble & Slayer 1980); the facilitation, inhibition and tolerance models (Connell & Slayer 1977); Grime's C-S-R hypothesis (1979); and Tilman's (1985) resource-ratio hypothesis. Space precludes a description of each of these here, but a discussion can be found in some science major textbooks (see below) or in the original papers.

Table 1. Textbooks evaluated for their coverage of the climax concept of succession.

Nonscience Major Texts

BSCS. (1992). *Biological science: An ecological approach, 6th ed.* Dubuque, IA: Kendall/Hunt Publishing.
Chiras, D.D. (1993). *Environmental science: Action for a sustainable future, 4th ed.* Redwood City, CA: Benjamin/Cummings Publishing Company.
Cunningham, W.P. & Saigo, B.W. (1995). *Environmental science: A global concern, 3rd ed.* Dubuque, IA: Wm. C. Brown Publishers.
Enger, E.D. & Smith, B.F. (1992). *Environmental science: A study of interrelationships, 5th ed.* Dubuque, IA: Wm. C. Brown Publishers.
Kupchella, C.E. & Hyland, M.C. (1993). *Environmental science: Living within the system of nature, 3rd ed.* Englewood Cliffs, NJ: Prentice Hall.
Miller, G.T. (1996). *Living in the environment: Principles, Connections and Solutions, 9th ed.* Belmont, CA: Wadsworth Publishing Company.
Morgan, M.C., Moran, J.M. & Wiersma, J.H. (1993). *Environmental science: Managing biological & physical resources.* Dubuque, IA: Wm. C. Brown Publishers.
Nebel, B.J. & Wright, R.T. (1993). *Environmental science: The way the world works, 4th ed.* Englewood Cliffs, NJ: Prentice Hall.

Science Major Texts

Begon, M., Harper, J.L. & Townsend, C.R. (1990). *Ecology: Individuals, populations and communities, 2nd ed.* Sunderland, MA: Sinauer Associates.
Brewer, R. (1994). *The science of ecology, 2nd ed.* Philadelphia, PA: Saunders College Publishing.
Colinvaux, P. (1993). *Ecology 2.* New York: Chapman & Hall.
Krebs, C.J. (1994). *Ecology: The experimental analysis of distribution and abundance, 4th ed.* New York, NY: Harper/Collins.
Odum, E.P. (1971). *Fundamentals of ecology.* Philadelphia: W.B. Saunders Company.
Smith, R.L. (1996). *Ecology and field biology, 5th ed.* New York: Harper & Row.
Stiling, P. (1992). *Introductory ecology.* Englewood Cliffs, NJ: Prentice Hall.

Modern perspectives of succession are presented by Pickett and McDonnell (1989), Glenn-Lewin et al. (1992) and McCook (1994). Pickett and McDonnell (1989) contend that the successional climax is an 'ideal' and an abstraction of reality. Reasons for this include:

1. There is never an absence of disturbance.
2. Some communities are not in equilibrium with the present climate.
3. For some vegetation types a recurrent natural disturbance (e.g. fire in tallgrass prairie) maintains the community in what Clements would call a pre-climax condition.
4. The length of time necessary for some species to dominate a site is less than the return time of disturbance.

For example, McCune and Allen (1985) had difficulty applying the climax concept to old-growth forests in Montana and suggested caution in using the concept. Lertzman (1992) described subalpine hemlock forests near Vancouver, Canada, that had not reached equilibrium despite being undisturbed for more than 1500 years. Indeed, Miles (1987) pointed out that the idea of a successional climax is now out of favor. Pickett and McDonnell (1989) go further and suggest that the term climax should be avoided to prevent acceptance of the incorrect assumptions of classical theory.

As pointed out by Allen and Hoekstra (1992), perhaps the main problem in adequately defining ecological concepts is one of scale. At the largest physical scale, say the eastern U.S., it is entirely reasonable to suggest that successional pathways will likely produce the equivalent of a climatically-controlled climax vegetation recognizable as the eastern deciduous forest biome; deserts and grasslands are unlikely to occur there without large-scale climatic shifts. However, as the spatial scale of resolution decreases, the certainty of predicting the eventual outcome of succession decreases as does the self-maintaining nature of these later stages. Thus, the climax concept becomes untenable as site factors and recurrent disturbance become more important at scales below that of the biome. Typically, the teaching of succession operates at the smaller scales, e.g. the oft-cited, but erroneous old-field succession from an annual weedy stage to so-called climax forest.

Misconceptions in Modern Textbooks

Texts used in teaching college environmental science and ecology were examined for their views on the climax theory of succession (Table 1). Texts were separated according to their intended use for nonscience major courses (n = 8), versus science major courses (n = 7).

Nonscience Major Texts

Textbooks intended for nonscience major courses in environmental science or ecology generally oversimplified the current view of succession. Worst of all, they perpetuated the outdated climax viewpoint.

The eventual, and inevitable, state was the climax community:

> *Succession will proceed until a balanced state between all species and their environment is reached. The final state is referred to as a climax ecosystem.* Nebel & Wright (1993).

> *The natural sequence of such changes in community structure is called ecological succession. It occurs in amazingly regular patterns tending toward a climax or steady-state situation.* Kupchella & Hyland (1993).

> *Climax community: A relatively stable, long-lasting community reached in a successional series; usually determined by climate and soil type.* Cunningham & Saigo (1992).

> *A biotic community destroyed by natural or human causes often recovers in a series of changes in which one community is gradually replaced by another until the mature, or climax, community is reached.* Chiras (1993).

> *Ultimately, a relatively stable stage is reached, called the climax community.* Enger & Smith (1992).

> *The climax vegetation that eventually emerges on a site. . . .* Morgan et al. (1993).

The green BSCS high-school-level text written specifically from an ecological perspective presents a similar outdated view:

> *The community that ends a succession, at least for a long period of time, is called the climax community.* BSCS (1987).

In all these texts, the climax community is seen as the usual final stage of succession, and as a long-lasting, self-perpetuating state. Miller (1996) in his analysis does not mention the climax community by name, and the end of succession is called a mature community which has all the same attributes as the traditional climax.

Despite the shortcomings in emphasis mentioned above, several texts did mention that the climax stage is *not always reached in every location* (Kupchella & Hyland 1993). Further, the prevailing doubts that modern ecologists have about the climax theory were occasionally raised: e.g. *Recent studies have thrown a few key tenets of this theory into question.* (Chiras 1993). *Thus, ecologists increasingly believe that climax communities are relatively rare in nature* (Morgan et al. 1993). Despite these disclaimers, comprehensive and alternative viewpoints are rarely offered by these authors [although see the most recent editions of Miller's (1996) and Cunningham & Saigo's texts (1995)], and the emphasis is on presenting successional concepts within the framework of the mono- or polyclimax view of Clements (1916) and Tansley (1935).

Science Major Texts

The seven texts intended for science majors that were reviewed (Table 1) for the most part presented a more balanced and up-to-date view of succession. All seven texts devoted a complete chapter to the topic of succession. All reviewed, in greater or lesser detail, the history of the development of successional theory.

Despite the more current approach of the science major texts, they differed in their treatments of the climax theory of succession. Four of the seven (i.e. Begon et al. 1990; Brewer 1994; Smith 1996; Krebs 1994) compared Clement's monoclimax, Tansley's polyclimax and Whittaker's climax-pattern models. Odum (1971) mentioned only the monoclimax and polyclimax theories, Colinvaux (1993) discussed the monoclimax theory without using the term, and Stiling (1992) makes no mention of either of the three theories. The majority of texts recognized that current theories do not accept the Clementsian view of an inevitable climax community. Nevertheless, opinions ranged from the now outdated:

> *A good compromise between these viewpoints [monoclimax and polyclimax] is to recognize a single theoretical climatic climax and a variable number of edaphic climaxes, depending on the variation in the substrate* (Odum 1971),

to

> *. . . climax vegetation is an abstract concept that is, in fact, seldom realized . . .* (Krebs 1994).

In offering alternatives to the original Clementsian viewpoint, and Tansley's (1935) and Whittaker's (1953) modifications, most authors discussed Connell & Slayer's (1977) tolerance/facilitation/inhibition models (Smith 1996; Stiling 1992; Krebs 1994). Both Smith (1996) and Colinvaux (1993) discuss Gleason's (1917) challenge to Clements' view of succession. Colinvaux even provides a facsimile of Gleason's later (1926) critique of Clements. Other modern mechanistic explanations of succession that are discussed include Egler's (1954) relay floristics and initial floristic composition concept (Smith 1996), Tilman's (1985) resource-ratio hypothesis (Smith 1996), Horn's (1974) Markovian models (Colinvaux 1993, Stiling 1992) and Huston and Smith's (1987) non-equilibrium model (Smith 1996). Colinvaux (1993) also includes discussion of Grime's (1979) C-S-R hypothesis, Lindeman's (1942) energy flow hypothesis, and Odum's (1969) information theory of successional development. It should be noted that the latter two approaches were developed to explain patterns of successional development toward the theoretical climax.

Overall, I found the science major texts to provide a more comprehensive and modern presentation of the concept of ecological succession, and in particular, the climax concept. Nevertheless, the plethora of approaches to the topic reveals a lack of general agreement and calls for the development of a more comprehensive conceptual model, especially for introductory teaching. As noted by Miles (1979), Clements' ideas on succession have an enduring influence—even in modern textbooks.

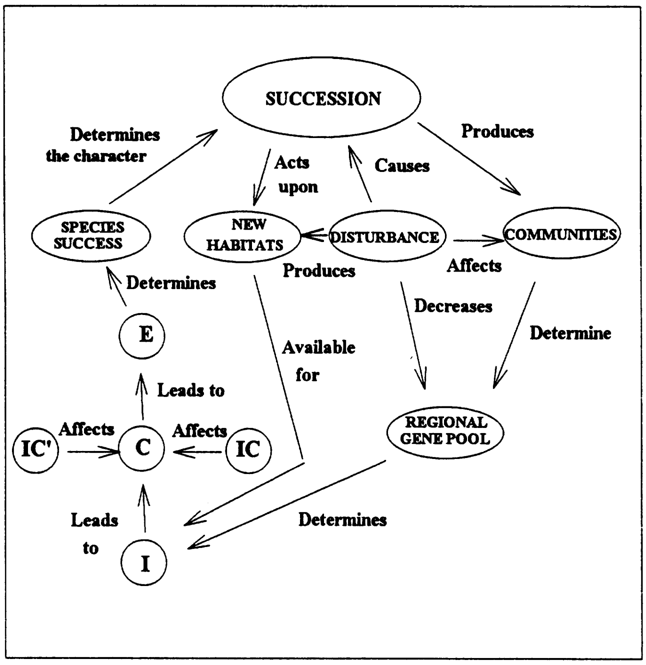

Figure 1. Concept map of succession. I = Immigration, C = Colonization, E = Establishment, IC = Intraspecific Competition, and IC' = Interspecific Competition. In addition to disturbance, other features of the environment not shown here (e.g. soil, climate) also influence all aspects of succession.

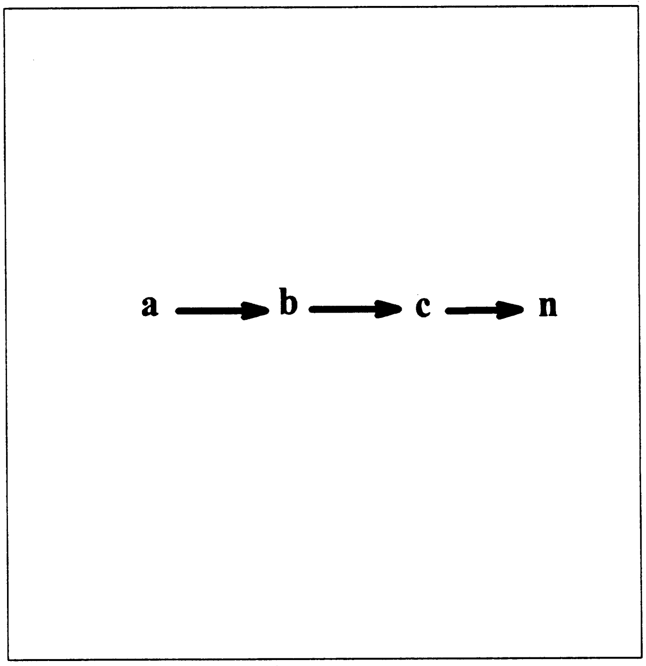

Figure 2. Schematic outline of Clement's monoclimax theory of succession with separate stages (*a, b, c*) leading ultimately to a deterministic climax (*n*).

A Modern Conceptual Model

In the models presented below, I am not attempting to produce a "new synthesis" of successional theory. As noted recently by Morgan et al. (1993), there is no consensus among ecologists as to the best model to explain succession. Rather, I am attempting here to show what is generally accepted and downplay the outdated concepts, namely that of the climax concept. The heavy pedagogical baggage accompanying the term "climax" in successional theory (Scheiner et al. 1993) persuades me, as it has others (Pickett & McDonnell 1989), that we should drop the use of the term altogether. The goal is to produce a model that can be useful in the teaching of succession to students with little ecological background.

Two approaches are proposed. The first is a concept map (Novak 1981) of succession (Figure 1). Briscoe & LaMaster (1991) showed that this approach is useful for the teaching of concepts in college biology. With this approach, key concepts are organized in a hierarchical arrangement with linkages depicting relationships among the concepts. The hope is that this will help teachers and students in understanding the important components of the successional process. An important point to emerge from the concept map is that succession is a process of change in communities caused by disturbance. Directionality toward a theoretical endpoint is de-emphasized. Disturbance affecting new communities and producing new habitats is a central process. Immigration, colonization and establishment are key in affecting succession and hence the path toward new communities. The nature of communities determines, and disturbance can reduce, the regional gene pool that determines immigration (Collins & Glenn 1990).

The second model follows Horn's (1974) probabilistic approach in that we can, and should, recognize for any one successional sequence that there are several likely pathways (Pickett et al. 1987b). I use Miles' (1979) schematic outline of Clements' model of succession as the starting point on the basis that this is the outdated viewpoint that prevails in many textbooks (Figure 2). The problem with this approach is that succession is viewed as a deterministic process with separate stages leading to a single self-maintaining climax. I have enlarged this (Figure 3) to illustrate a theoretical successional sequence in which there are three possible late stages (d_1, d_2, d_3)—each is potentially self-maintaining, but may also develop under certain conditions into something else. The late stages d_1, d_3 have a lower probability of being reached than d_2. In this scheme, there is no end point to succession; rather a succession is seen as a series of changes that communities undergo with the changes from one stage to another taking shorter or longer timeframes, depending upon the particular stage. Again, as with the concept map, this view is intentionally simplistic and intended to de-emphasize the climax concept. Many other alternate stages may be realized in actual successional sequences (e.g. Olson 1958).

Good examples of actual successional sequences that would be useful in teaching a modern view of

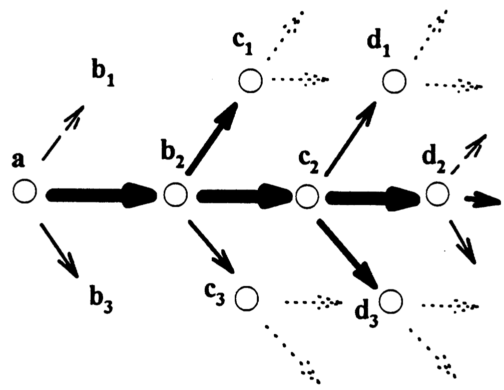

Figure 3. Generalized schematic view of succession. Circles indicate successional stages, labeled *a, b, c, d*. Arrows indicate the direction of successional change from one stage to another with the thickness of the arrow reflecting the probability of that particular change occurring. Note that succession is most likely to follow the sequence *a, b, c, d* but alternate pathways exist at all times; e.g. *b* is most likely to change to c_2 but might also change to either of c_1 or c_3. Three possible alternative pathways are shown for each stage, although in reality there are likely many more.

succession include Olson's (1958) classic representation of alternate dune successions in Lake Michigan sand dunes, although as drawn it too culminates in so-called climax communities. Miles' (1987) representations of multiple successional pathways from dune slacks in The Netherlands and upland grasslands in Britain could also be adapted for teaching since in both a deterministic end-point to succession is not identified.

Conclusions

Nonscience major textbooks are continuing to espouse an incorrect, outdated and misleading view of succession. The reasons are, no doubt, due to the necessarily simplistic approach required for the level of teaching. Nevertheless, there is an inherent danger in oversimplification, especially when a misleading viewpoint is taught (Grubb 1992). Science major textbooks are more up-to-date in their treatment, but many still use Clementsian climax successional concepts as the central organizing theme for their treatment of succession. I propose that the term "climax" be dropped from the ecological teaching lexicon and an emphasis be placed on mechanisms rather than pathways. A concept map and generalized schematic are proposed to help teachers in developing this approach. It is hoped that textbooks will also follow suit.

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