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The use of chronosequences in studies of ecological succession

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and soil development

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Summary

1. Chronosequences and associated space-for-time substitutions are an important and often
32 necessary tool for studying temporal dynamics of plant communities and soil development across
multiple time scales. However, they are often used inappropriately, leading to false conclusions
about ecological patterns and processes, which has prompted recent strong criticism of the
approach. Here, we evaluate when chronosequences may or may not be appropriate for studying
36 community and ecosystem development.

2. Chronosequences are appropriate to study plant succession at decadal to millennial time scales
when there is evidence that sites of different ages are following the same trajectory. They can
also be reliably used to study aspects of soil development that occur between temporally linked
40 sites over timescales of centuries to millennia, sometimes independently of their application to
shorter-term plant and soil biological communities.

3. Some characteristics of changing plant and soil biological communities (e.g. species richness,
plant cover, vegetation structure, soil organic matter accumulation) are more likely to be related
44 in a predictable and temporally linear manner than are other characteristics (e.g. species
composition and abundance) and are therefore more reliably studied using a chronosequence
approach.

4. Chronosequences are most appropriate for studying communities that are following
48 convergent successional trajectories and have low biodiversity, rapid species turnover and low
frequency and severity of disturbance. Chronosequences are least suitable for studying
successional trajectories that are divergent, species-rich, highly disturbed or arrested in time
because then there are often major difficulties in determining temporal linkages between stages.

52 5. *Synthesis*. We conclude that, when successional trajectories exceed the life span of
investigators and the experimental and observational studies that they perform, temporal change
can be successfully explored through the judicious use of chronosequences.

Key-words: chronosequences, disturbance, plant communities, retrogression, soil biological
56 communities, soil development, succession, temporal change

Introduction

Ecologists who study temporal change are challenged by how to study successional and soil
60 developmental processes that span centuries to millennia. Direct, repeated observations (e.g.
through historical photography or long-term plot studies; del Moral 2007) began formally with
studies of dunes in Denmark (Warming 1895) and Michigan (USA; Cowles 1899), and such
observations provide the best source of evidence about temporal changes in plant and soil
64 biological communities over years to decades. However, few studies extend beyond several
decades in duration (but see Chapin *et al.* 1994; Webb 1996; Whittaker *et al.* 1999; Walker *et al.*
2001; Silvertown *et al.* 2002; Meiners *et al.* 2007), so indirect measures are needed to determine
the age successional stages and reconstruct historical vegetation or soil conditions over longer
68 time scales. The most frequently used indirect approach for measuring temporal dynamics
involves the use of chronosequences and associated space-for-time substitution which represents
a type of ‘natural experiment’ (Pickett 1989; Fukami & Wardle 2005). However,
chronosequences may not always be correctly used, and this can lead to misinterpretations about
72 temporal dynamics (Pickett 1989; Fastie 1995; Johnson & Miyanishi 2008), particularly when
mechanisms are inferred from the descriptive patterns that chronosequences supply. In Glacier
Bay, Alaska, USA, for example, erroneous assumptions about temporal linkages between sites

dominated by *Alnus* and *Picea* trees led to incorrect generalizations that *Alnus* facilitated *Picea*
76 growth through fixation of atmospheric nitrogen (Fastie 1995). Extrapolations about the role of
facilitation to other studies were then made without appropriate caveats (Walker 1995; Walker &
del Moral 2003). In this example and others (Johnson & Miyanishi 2008), a chronosequence
approach has led to more confusion than clarity about temporal change.

80 Johnson & Miyanishi (2008) highlighted the misuse of the chronosequence concept for
studying vegetation succession and suggested that the problems they identified also applied to
the use of chronosequences for studying ‘temporal changes in biodiversity, productivity, nutrient
cycling, etc.’. We maintain that there are many instances in which the chronosequence approach
84 may usefully clarify ecological processes in a manner that cannot be achieved in any other way,
and that the wholesale dismissal of the chronosequence approach is likely to impede, rather than
advance, understanding of long-term ecological processes. In this light, we first address the
concept of a chronosequence, how to measure it and its links to succession, soil development and
88 temporal scales. Then, we evaluate under which circumstances chronosequence use is most or
least appropriate. Finally, we discuss how the use of chronosequences can be improved. Our
overarching goal in addressing these issues is to clarify when chronosequences are essential tools
to understanding temporal change and when they should not be used in order to avoid
92 misinterpretations of that change.

Concepts and Approaches

Ambiguity about the meanings of commonly used terms could be contributing to confusion
96 about the applicability of chronosequences. We therefore provide some definitions of relevant
concepts (Table 1) and explore several critical assumptions and concerns involving these

concepts. A fundamental assumption about chronosequences is that the communities and ecosystems of the younger sites are currently developing in a temporal pattern that resembles how the older sites developed (termed a space-for-time substitution). When the date of the initial disturbance and subsequent history of the site are known, chronosequences provide the opportunity to study ecological processes over time periods that are longer than direct observation would permit. Concerns about using chronosequences include whether there is any predictable link between young and old sites, whether the chronology is readily interpretable, whether and at what rate characteristics actually change over time and whether landscape context and chance may confound chronosequence assumptions (del Moral 2007). Various lines of independent evidence are essential to justify the space-for-time assumption before applying the chronosequence approach to studies of temporal dynamics.

Chronosequences imply the presence of ecological succession. Therefore, important concerns about ecological succession impact chronosequence studies. These include the balance of deterministic and stochastic elements, whether a sere (successional sequence) is directional (i.e. encompassing a linear replacement of plant communities to a defined endpoint), whether trajectories converge or diverge and whether many trajectories form a network from a single or several starting points (Lepš & Rejmánek 1991; Samuels & Drake 1997). Trajectories (Fig. 1) can also be parallel, deflected, cyclical, arrested (stalled) or simply involve direct replacement of a former dominant species (Walker & del Moral 2003). As with chronosequences, it is important to discern what characteristics change at what rates over time.

Temporal scales used to study chronosequences depend on the factor or process of interest and on the life span of the dominant organisms or the organisms of interest. For example, microbial succession in soil can be studied over periods of just several days or weeks, whereas

heterotrophic succession (e.g. of decomposers on rotting logs or carcasses) encompasses weeks to years (Bardgett *et al.* 2005). Secondary plant succession (e.g. colonization of abandoned agricultural fields) is normally examined at decadal scales (Meiners *et al.* 2007). Primary plant
124 succession (e.g. on lava or dune surfaces) can involve centuries to thousands of years (Walker *et al.* 1981), while soil development, or pedogenesis, can encompass periods of up to millions of years (Crews *et al.* 1995). Therefore, details about chronosequences that matter at shorter time intervals (e.g. availability of labile nutrients, species interactions) become less relevant as
128 temporal scales expand and the focus shifts to processes such as the formation of humus, accumulation of soil carbon and phosphorus loss or occlusion. Many processes such as primary productivity, decomposition and nutrient immobilization can be addressed at several temporal scales.

132 The presence of a more or less linear relationship between sites can be established in a variety of ways. Techniques include investigating oral and historical records (Engstrom 1995), repeat photography (Webb 1996), tree ring analysis (Fastie 1995), lichenometry (Calkin & Ellis 1980), use of micro- and macro-fossils (Bhiry & Filion 1996; Clarkson *et al.* 2004), palynology
136 (Birks 1980), determining carbon isotope ratios (Kume *et al.* 2003), thermoluminescence dating (Tejan-Kella *et al.* 1990), potassium-argon dating (Funkhouser *et al.* 2007), analysing podzol development (Thompson 1981; Walker *et al.* 1981) or studying soil depth (Poli Marchese & Grillo 2000). Temporal change on inferred chronosequences can be measured with simple, one-
140 time surveys of vegetation and soils that facilitate conclusions about succession or with repeated measurements when these are logistically feasible. Little effort has been made to design the ideal chronosequence study (e.g. number and temporal spacing of sites, number of replicates within each age group) or duration (e.g. temporal duration that a chronosequence can have and still

144 maintain a valid linkage among stages) (Thompson & Moore 1984; Myster & Malahy 2008).
Ultimately, chronosequence measurements should be determined by the parameters of interest,
their rate of change and the degree of spatial heterogeneity within chronosequence stages. In the
following sections, we review the conditions under which the use of chronosequences is most
148 and least appropriate.

Where Chronosequences Are Most Appropriate

Chronosequences are multi-faceted as they can be used to track many ecosystem patterns and
152 processes in developing communities through time, some of which may develop independently
of each other. For example, Myster & Malahy (2008) found a convergence of species richness
and total plant cover on pastures in Puerto Rico over time, but no such directionality for species
composition and abundance. These results reflect a more rapid and deterministic recovery of
156 structural components of vegetation than parameters based on species composition, a result
applicable to both primary (Walker & del Moral 2003) and secondary (Guariguata & Ostertag,
2001; Chazdon *et al.* 2007) succession. We discuss several general situations where
chronosequences are appropriate and provide examples from the ecological literature.

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1. Short-term Seres

When there are demonstrable linkages between stages (i.e. the successional trajectory is
predictable), chronosequences provide a useful approach to studies of short-term temporal
164 change with time frames of c. 1-100 years, unless organisms with very short life spans such as
soil microbes are involved. Such links come from direct observation of relatively short-term
change in permanent vegetation plots or soil microbial and faunal communities, physical remains

of previous stages (e.g. tree stumps) or indirect but robust corresponding observations such as
168 overlapping patterns in tree rings. Many studies use chronosequences of this kind and thereby
extend our knowledge of successional dynamics. For example, short-term chronosequences such
as those on sand dunes have long been used to demonstrate that soil and plant communities
change in tandem during succession (Brown 1958). Inferences from these types of studies have
172 subsequently been made: that the build-up of species-specific pathogens in the root zone can
accelerate species replacement and hence vegetation change (Van der Putten *et al.* 1993). More
recent studies on abandoned fields of known age that differ in time since abandonment have led
to significant insights about how below-ground communities and plant–soil feedbacks serve as
176 drivers of species replacement and vegetation successional development (e.g. De Deyn *et al.*
2003, Kardol *et al.* 2006). Our understanding of the successional development of soil biotic
communities has also advanced through studies of recently exposed glacial substrates. These
substrates are initially composed of simple, heterotrophic, microbial communities (Bardgett &
180 Walker 2004; Bardgett *et al.* 2007) and photosynthetic and nitrogen-fixing bacteria (Schmidt *et al.*
2008) that over time develop more complex, fungal-based food webs (Ohtonen *et al.* 1999;
Bardgett *et al.* 2007). Also, advances have emerged from applying the chronosequence approach
to substrates of differing decay stage and therefore age, such as fungal communities on decaying
184 leaves (Frankland 1998) and microarthropod communities on decaying tree stumps (Setälä &
Marshall 1994).

2. *Convergence of Seres and Vegetative Structure*

188 There are multiple potential trajectories for succession, including single or multiple pathways
that can be parallel, convergent or divergent, but that also can be cyclic or form complex

networks (Fig. 1; Walker & del Moral 2003). Single and cyclic pathways are the most easily adapted to space-for-time inferences because they typically have few dominant species and few stages (Watt 1947). Chronosequences can also be useful for the study of convergent seres, particularly when convergence occurs early in succession. Whenever multiple pathways are present along a chronosequence, sufficient within-stage sampling is required to detect the pathways and avoid erroneous inferences about non-existent pathways (Fig. 1). In the case of an incomplete chronosequence (missing stages) additional historical, retrospective, observational or experimental data is critical before robust inferences can be made about the missing links.

Convergence occurs as a reduction in heterogeneity of species composition among sites over time or as a growing resemblance among different trajectories (Christensen & Peet 1984; del Moral 2007). Convergence is most likely where there is some biological legacy from the initial disturbance, where a deterministic sequence of species or life forms is driven by biological processes or where environmental conditions are predictable (Nilsson & Wilson 1991; Inouye & Tilman 1995; Wilson *et al.* 1995). Decreasing beta-diversity is one way to measure convergence along a sere (del Moral & Jones 2002). Convergence to a dominant growth form such as tussock grasses, dense shrub lands, or trees can potentially reduce the typically stochastic processes of dispersal and establishment, and distinctly alter ecosystem properties and environmental conditions (Walker & del Moral 2003). For example, where succession proceeds from relatively open vegetation to closed forest canopy, one might expect a convergence (reduction of variation) among stands of plant traits such as specific leaf area and root:shoot ratios, soil microbiological traits such as the relative biomass of bacteria and fungi or environmental changes such as amount of understorey light and soil and air temperatures. Despite some evidence of predictable directional shifts in these variables (Tilman 1988; Wood & Morris 1990; Chapin *et al.* 1994;

Llambí *et al.* 2003; Bardgett & Walker 2004), more needs to be done to investigate convergence among stands along the lines of the study by Fukami *et al.* (2005) on the convergence of plant functional traits during secondary succession. Trait convergence is also complicated by spatial
216 heterogeneity in most plant (Armesto *et al.* 1991) and soil (Boerner *et al.* 1996) communities, and a lack of uniformity in the effects of similar structures such as trees on the environment (Binkley & Giardini 1998). Such spatial variability compounds the difficulty of interpreting temporal variability within sites and suggests the need for caution in interpreting
220 chronosequences, even those based on convergence of vegetative structure. Although convergence (especially of life and growth forms) is a common phenomenon in some long-term seres (Poli Marchese & Grillo 2000; Rydin & Borgegård 1991), other seres show increased heterogeneity of life forms as we discuss later.

224 Glacier Bay, Alaska, USA, is a well-studied sere that illustrates many of the points we make about convergence, including the need for multiple sources of information, intense sampling and an understanding of the role of the dominant plant species. The retreating glaciers at Glacier Bay have exposed moraines that have been dated by geological records, direct
228 observation and repeat photography (Vancouver 1798; Field 1947; Goldthwait 1966). A chronosequence of early successional plants has been validated through permanent plots initiated by Cooper (1923) and several additional observational and experimental studies (summarized in Chapin *et al.* 1994). However, links to the next stage are less well established. Detailed
232 sampling determined that the early successional plants (notably the nitrogen-fixing *Alnus*) do not always precede stands of *Picea* (Fastie 1995), the dominant tree species on moraines > 200 years old, as previously assumed. *Picea* forests contribute greatly to soil acidification (Alban 1982) and promote a retrogressive stage (Wardle *et al.* 2004) when *Picea* stands degenerate after about

236 10 000 years (Ugolini & Mann 1979; Noble *et al.* 1984) and understorey diversity increases.
Assuming that early successional stages converge to *Picea* forests (a likely, although not directly
observed linkage), concerns about *Alnus–Picea* sequences during the first 200 years become less
critical when addressing longer time scales where *Picea* and its accompanying ecosystem-level
240 effects predominate. Therefore, for measures of soil biota, soil fertility and plant physiognomy
encompassing several millennia, the exact replacement sequence for plant species at hundred-
year scales is of marginal importance, if the processes of interest have converged. More
important at the longer time scales are the frequency, intensity and spatial distributions of fire,
244 insect outbreaks, logging and other disturbances that destroy forests and initiate secondary
succession, because of the presence of residual forest soil following such disturbances (Walker &
del Moral 2003).

248 3. Long-term and Retrogressive Seres

Over time frames encompassing thousands to millions of years, dramatic shifts can occur in soil
properties and accompanying plant, animal and microbial communities. These changes negate
the previously held assumption that plant communities reach a stable and self-replacing climax
252 (Whittaker 1953). At such temporal scales, chronosequences are usually the only tool available
to interpret changes in ecosystem processes, such as net primary productivity and rates of
decomposition, nutrient mineralization and nutrient immobilization (Vitousek 2004; Wardle *et*
al. 2004, 2008). Long-term chronosequences have also long been recognized as valuable for
256 understanding processes of soil formation and development over time (Walker & Syers 1976),
often independently of their application to plant and soil biological communities. However, the
linkages between long-term soil development, shorter-term changes in microbial and faunal

communities and vegetation development are relatively predictable (Wardle 2002; Bardgett *et al.* 2005), making the chronosequence approach a reasonable template for interpretation of change at many temporal scales.

Predictable shifts during stages of progressive succession include increasing plant and soil microbial biomass, nutrient availability and rates of nutrient cycling (Chapin *et al.* 2003). While such increases can continue for thousands of years (Vitousek 2004; Walker & Reddell 2007), in the absence of catastrophic disturbances that reset the system, ecosystem retrogression can occur, which involves a marked decrease in nutrient availability, often accompanied by reductions in plant biomass (Walker *et al.* 2001, Wardle *et al.* 2004). This pattern has been widely documented in many climates and vegetation types, with the possible exceptions of arid systems (Lajtha & Schlesinger 1988; but see Selmants & Hart 2008) and tropical lowland rainforests (Ashton 1985; Kitayama 2005). Retrogression is typically driven by conversion of soil nutrients and especially phosphorus to less available forms, and in some cases leaching of nutrients below the rooting zone or the development of impermeable soil pans leading to water-logging (Walker & Syers 1976; Vitousek 2004, Coomes *et al.* 2005; Peltzer *et al.* in press). Long-term (millennial scale) changes in soil processes track, and are impacted by, mid-term (100 – 1000 year) to short-term (1 – 100 year) decreases in litter quality, decomposition rates, nutrient use efficiency and nutrient accumulation in plants (Cordell *et al.* 2001; Richardson *et al.* 2005; Wardle *et al.* 2009) and very short-term (days to months) alterations in soil microbial and animal populations (Wardle *et al.* 2004; Bardgett *et al.* 2005; Doblás-Miranda *et al.* 2008). Therefore, retrogression does not simply involve shifts in community- and ecosystem-level properties at longer time scales, but an integration of short- to long-term processes that are distinct from progressive succession. To the extent that plant and soil characteristics of interest are predictable

across stages of retrogression, chronosequences remain a valid tool. We use two examples to illustrate the benefits of applying the chronosequence approach to long-term series that each has a relatively short progressive phase followed by a much longer retrogressive phase.

The current Hawaiian Islands represent an excellent, > 7 million-year chronosequence, because the ecological consequences of their sequential development over an oceanic hotspot are well-documented (Vitousek 2004), making them ideal for between-island comparisons (Mueller-Dombois & Fosberg 1997). Both progressive (Mueller-Dombois 1987) and retrogressive (Wardle *et al.* 2004) succession have been documented in this system, with progressive succession dominant on the younger island of Hawaii (0 – 0.43 M years) and retrogressive succession more widespread on older islands such as Maui (0.8 – 1.3 M years) and Kauai (5.1 M years). Within-island chronosequences have also been characterized on the reliably dated and mapped series of volcanic surfaces on the Island of Hawaii that range from 1 year to > 4000 years old (Drake & Mueller-Dombois 1993; Aplet & Vitousek 1994; Kitayama *et al.* 1995). For example, one can compare succession and soil development on several surfaces (a’*a* lava, pahoehoe lava) across a wide range of elevations (900 - > 3000 m a.s.l.), spatial scales (local to > 500 km²) and climates. Under such conditions, studies of chronosequences can thus be designed to meet various assumptions, variation can be quantified through replication within categories, and multivariate approaches can correct for incomplete designs where chronosequence assumptions are not met. Domination of the Hawaiian forests by a single tree species (*Metrosideros polymorpha*), albeit with several ecotypes, further facilitates comparisons between stages of plant morphology or soil development during both the progressive and retrogressive phases of succession. However, given the numerous climatic changes and variable allochthonous inputs, such as phosphorus inputs from Asian dust, that have occurred during the long history of

the current Hawaiian Islands (Chadwick *et al.* 1999), age-specific processes necessarily become less precise (Vitousek 2004).

The Cooloola Dune sequence in eastern Australia is another example of a long-term sere
308 with a retrogressive phase where a chronosequence approach has been useful. The progressive
phase lasted for c. 250 000 years as soil carbon, nutrients and forest biomass accumulated, and
was followed by c. 350 000 years of retrogression as podzolic soils developed, leaching occurred
to 20-m depth and forest productivity declined (Thompson 1981, Walker *et al.* 1981, Walker *et*
312 *al.* 2000, Wardle *et al.* 2004). The oldest soils support a diverse understorey plant community
(Wardle *et al.* 2008) adapted to extreme infertility. As in Hawaii, other disruptions inevitably
occur over such long time spans (fire is a recurring phenomenon in Australia), but the
chronosequence as a soil age gradient remains robust. In both Hawaii and Australia, research
316 questions that are best answered in studies of the older stages shift to the effects of soil age on
community and ecosystem processes, rather than the generation of hypotheses about mechanisms
of succession and species replacements best addressed in younger seres.

320 4. Chronosequences as Null Models and Predictive Tools

The assumption that a chronosequence exists across various sites with certain patterns of
changing traits provides a useful null model that can be verified or refuted with further
observation and experimentation. With this approach, useful lessons can be learned even when
324 erroneous assumptions about the chronosequence have been made. For example, studies on sand
dunes (Olson 1958; Boerner 1985) that initially assumed a linear successional trajectory have led
to the discovery of non-linear successional networks. Similarly, assumptions about the
progressive nature of successional properties have been modified by the recognition of the

328 retrogressive phase of long-term chronosequences (Walker & Reddell 2007). The development
of predictive models of successional trajectories is difficult because of our poor understanding
about how complex processes such as dispersal, colonization and competition unfold in space
and time (Pickett *et al.* 2009). Lessons learned from chronosequence studies about convergence,
332 deterministic consequences of certain dominant life forms, or patterns of retrogression can
become inputs into a chronosequence function of a general model of succession (Fig. 2; Walker
& del Moral 2003). Clarifying such variables can help interpret successional pathways through
either interpolation between data on stages of known ages or extrapolation beyond known data to
336 future pathways (completing the dotted lines – particularly for the trajectories shown on the left
side of Fig. 1). For example, if short-term chronosequence observations (years to decades) on
landslides suggest initial convergence within a progressive succession caused by biotic
colonization processes (Guariguata 1990; Walker *et al.* 1996) and soil development (Zarin &
340 Johnson 1995), extrapolation to longer time periods will be robust and interpolations can be
made about intermediate stages. If restoration of a landslide is desired, manipulations improve
when trajectories are understood (Walker *et al.* 2009). Chronosequences become essential
predictive tools when considering trajectories of community and ecosystem processes at long-
344 term (millennial) scales (Walker *et al.* 2000). Any such model must account, of course, for the
often nonlinear nature of vegetation change by allowing for both deterministic and stochastic
aspects of temporal dynamics (Cramer 2007).

348 **Where Chronosequences are Least Appropriate**

The assumption of many ecologists in the early 20th century was that the present repeats the past
(McIntosh 1985), so chronosequences were widely used to interpret temporal patterns. The

subsequent shift to a more reductionistic perspective and decades of experimental manipulations
352 indicate that succession is often not deterministic (Glenn-Lewin *et al.* 1992). Therefore, we
assert that chronosequences should not be used to infer short- and mid-term successional
dynamics when the sites are not temporally related in a linear fashion or when they have
different vegetation histories due to climatic, landscape or stochastic factors (Walker & del
356 Moral 2003). One such example involves toposequences, where differences in plant communities
are influenced by their position on the landscape (Matthews & Whittaker 1987; Avis & Lubke
1996) more than by temporal dynamics. Other conditions where chronosequences are least
appropriate include divergent trajectories, highly disturbed seres, or seres with slow rates of
360 turnover, which we now discuss in turn.

1. Divergent and Non-linear Seres

When successional trajectories are divergent or are configured as non-linear networks, the
364 chronosequence approach is less useful and may require more intensive sampling than for
parallel or convergent seres (Fig. 1). Divergence is common due to priority effects (i.e. sequence
of species arrivals), sensitivity to minor differences in initial conditions, stochastic effects and
initial site heterogeneity (Matthews & Whittaker 1987). Early successional communities may
368 more closely resemble each other, particularly in severely disturbed habitats with few successful
colonists, while later successional stages with higher biodiversity diverge. High regional
biodiversity can contribute to high within-stand diversity and therefore also increase the
likelihood of divergence. Local convergence may occur where certain successful species
372 dominate, but divergence may exist at larger spatial scales (Lepš & Rejmanek 1991). Networks
occur when there are multiple stages that arise from a single stage, resulting in alternative

pathways to a convergent endpoint or continued divergence. Causes of networks include different initial site conditions or stochastic dispersal that results in different pioneer communities, leading to independent and sometimes parallel trajectories (Walker & del Moral 2003). Each additional layer of complexity challenges assumptions of connectivity where interpolation is used because of missing data sets and makes the application of the chronosequence approach more difficult.

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2. *Disturbed Seres*

When severe or frequent disturbances reset a sere, succession may be deflected, thus reducing the value of the chronosequence approach. Deflections occur in a variety of ways due to the differential responses of organisms over time and the nature of the repeat disturbances such as moving dunes (Castillo *et al.* 1991) or repeated floods (Baker & Walford 1995). Alternatively, subsequent disturbances may not reset a general successional trend, even if they are relatively severe, as found for early succession on Puerto Rican landslides (Walker & Shiels 2008) or in fire-driven ecosystems in northern Sweden (Wardle *et al.* 1997). Deflected seres are typically caused by allogenic disturbances (e.g. flood, invasive species) but can be reinforced through autogenic processes (e.g. grazing), especially those leading to retrogression (Walker & del Moral 2009). When the timing or severity of the disturbance is unknown (e.g. historic dune migrations) there is no historic baseline and chronosequences are hard to apply. Conversely, with well-documented disturbances (e.g. abandonment of agricultural fields; Cramer & Hobbs 2007) or artificial events (e.g. experimental blow-downs of trees; Cooper-Ellis *et al.* 1999), details about the timing and severity of the disturbance can help to clarify subsequent trajectories and improve the application of the chronosequence approach.

3. *Slow or Arrested Seres*

Rates of plant succession vary from rapid change to almost no change at all. Chronosequences
400 are most applicable to the former; however, changes in ecosystem processes can occur even
when all stages are dominated by the same plant species, such as in monospecific New Zealand
mountain beech (*Nothofagus solandri*) stands (Clinton *et al.* 2002). Succession can be arrested
due to abiotic constraints (e.g. nutrient limitation), limitations in the size of the regional species
404 pool, or resource-use domination by a species leading to competitive inhibition of other species,
at least until the dominant species senesces (Walker & del Moral 2003). Both native and invasive
species can dominate a successional stage, typically by monopolizing light, water and nutrients
through the formation of mats or thickets composed of algae (Benedetti-Cecchi & Cinelli 1996),
408 mosses (Cutler *et al.* 2008), cryptogamic crusts (Kaltenecker *et al.* 1999), grasses (Nakamura *et*
al. 1997), vines (Melick & Ashton 1991), ferns (Russell *et al.* 1998), shrubs (Young *et al.* 1995)
or trees (Dickson & Crocker 1953). Early recognition of arrested states will allow examination of
the cause and potentially lead to the discovery of other controlling variables, but the
412 chronosequence approach is not easily applied to such situations.

How to Improve the Use of Chronosequences

Categorical generalizations about when it is appropriate or inappropriate to use chronosequences
416 to study succession or soil development are not possible, because successional trajectories can be
complex and difficult to predict (Walker & del Moral 2003). However, the relative merits of
applying chronosequences can be compared for different trajectories and community
characteristics (Table 2). We suggest that chronosequences work better with predictable than

420 unpredictable seres, but unpredictable, convergent seres can often be analysed with some
reliability. These relationships apply to either progressive or retrogressive seres. In contrast, we
propose that local community biodiversity and disturbance effects on the usefulness of
chronosequences differ between progressive and retrogressive seres for studies of plant
424 succession under conditions of high disturbance. High plant species diversity in the regional
species pool can make chronosequence approaches difficult because of the greater potential for
colonization of different sites at the same stage by different species leading to alternative
trajectories (Prach 1994; Matthews 1992), especially in highly disturbed habitats (MacDougall *et*
428 *al.* 2003). Soil development is less affected than plant succession by plant species diversity, but it
is still less likely to be amendable to study by chronosequence approaches when diversity is high
and when there is high disturbance. In retrogressive seres, chronosequences can also sometimes
be difficult to apply (especially for plant succession), even at low levels of biodiversity, due to
432 the larger potential for divergence (Table 2). Again, soil development is somewhat buffered from
these problems.

The process of soil development encompasses a time span of centuries to millennia and is
arguably more deterministic than succession once the roles of climate and parent material are
436 clarified (Jenny 1980). Chronosequences are thus interpreted as a series of soils of different ages
that formed on the same parent material, and can be highly appropriate for addressing questions
about soil development and its effects on community and ecosystem properties. Such uses of
chronosequences have significantly advanced our understanding of how soil nutrients change
440 during pedogenesis (Walker & Syers 1976; Vitousek 2004) and the impact of changes in soil
nutrient availability on plants (Wardle *et al.* 2008), decomposers (Williamson *et al.* 2005;
Doblas-Miranda *et al.* 2008), foliar herbivores (Gruner 2007) and above-ground and below-

ground ecosystem processes (Crews *et al.* 1995; Wardle *et al.* 2004; Whitehead *et al.* 2005).

444 Chronosequences can be used in this way to clarify the effects of soil age on current plant
community attributes (Wardle *et al.* 2008), even when they do not generate insights about
patterns of plant succession.

When observations of long-term chronosequences are combined with experiments
448 (Fukami and Wardle 2005), further insights are gained about the mechanistic basis of community
and ecosystem change. For example, controlled fertilizer experiments performed along both the
progressive and retrogressive stages of the Hawaiian chronosequence (Vitousek 2004) have
greatly enhanced our understanding of how the relative importance of nitrogen and phosphorus
452 limitation influences ecosystem development both above and below ground. Similarly, plant
removal experiments along a 6000-year, fire-driven chronosequence in northern Sweden (Wardle
& Zackrisson 2005; Gundale *et al.* **in press**) have clarified the shifting linkages between plant
community composition and soil biogeochemical processes during succession. Although few
456 manipulative experiments have been performed across successional gradients, such studies offer
tremendous potential for better understanding the role of both biotic and abiotic factors in driving
community and ecosystem change during succession.

The appropriate use of chronosequences relies on at least five site-specific issues that
460 serve as limitations, if not addressed (Table 3). First, chronosequences are most useful when
there is a clear pattern of temporal change between multiple stages. Second, there should be
several lines of evidence about the history of the site. For short-term chronosequences, such
evidence might include oral histories, tree rings or historical maps, whereas for long-term
464 chronosequences, these data might include good geographical or stratigraphic dating or
biological indicators such as micro- and macro-fossils. If such independent verification of a time

series is present, the chronosequence approach is more likely to be justified. Third, locating replicate plots randomly within each stage of the chronosequence (not just the progressive phase), when possible, can help address the structure of the (non-age-related) variation among chronosequence stages. Fourth, if there are previously established plots that can be relocated, then earlier measurements can be repeated in order to directly observe any subsequent changes and verify chronosequence assumptions (e.g. Clarkson 1997). Finally, site-specific measurements must be made to record relevant changes, but if these measurements do not employ standardized methodology, extrapolations can be difficult to extend to other studies.

Conclusions

We agree with recent concerns that the misuse of chronosequences can mislead ecologists, particularly in relation to understanding vegetation successional pathways (Johnson & Miyanishi 2008). However, we do not believe that these problems are sufficiently universal or severe to invalidate their use for addressing questions about certain types of ecosystem change. The judicious use of chronosequence studies has greatly advanced our understanding of short-term vegetation change where temporal connections have been confirmed (Foster & Tilman 2000; Meiners *et al.* 2007). Chronosequences have also significantly aided our understanding of long-term landscape processes (Milner *et al.* 2007) and soil development (Walker & Syers 1976) and associated functional changes in above-ground and below-ground processes and organisms (Vitousek 2004; Wardle *et al.* 2004; Bardgett *et al.* 2005), even when the plant successional trajectories do not exactly parallel changes in soil development. Chronosequences are most suited for measuring plant and soil community characteristics that change in a relatively predictive, linear fashion over time, such as plant cover and species richness, pedogenesis, soil

organic matter accumulation and rates of ecosystem processes, and least suited for those traits that are more diffuse and less predictable such as species composition and abundance. Further, chronosequences work better for studying successional trajectories that are convergent, have low
492 diversity and are infrequently disturbed than for trajectories that are divergent, more diverse and frequently disturbed. Finally, chronosequences can often provide information critical to manipulating successional processes for restoration, even where there is an imperfect understanding of the ecosystem (Hobbs *et al.* 2007). We maintain that when appropriately
496 applied, the chronosequence approach offers invaluable insights into temporal dynamics of vegetation change and soil development that cannot be achieved in any other way and that wholesale dismissal of this approach is more likely to impede than to stimulate understanding of these topics.

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Table 1. Definitions of conceptual terms as used throughout this article

Concept	Definition
Chronosequence	A set of sites formed from the same parent material or substrate that differs in the time since they were formed.
Ecological succession	The change in species composition and/or structure over time following either a severe disturbance that removes most organic matter (primary succession) or a less severe disturbance where some biological legacy remains (secondary succession). Biomass, nutrient availability and vegetation stature can either increase (progressive succession) or decrease (retrogressive succession; Walker <i>et al.</i> 2001; Wardle <i>et al.</i> 2004).
Soil development	All temporal change in both the abiotic and biotic aspects of soil, including nutrient and water availability, structure, texture and biota (Bardgett 2005). Often tightly coupled to above-ground changes and subject to the same array of potential trajectories as ecological succession (Wardle 2002).
Disturbance	The relatively abrupt loss of biomass or structure from an ecosystem that creates opportunities for establishment through alteration of resources or the physical environment (Sousa 1984; White & Pickett 1985; Walker 1999). Disturbances both initiate and modify succession and organisms have complex responses to disturbance that impact biodiversity.
Temporal scale	Influences the interpretation of the previous concepts. Succession is typically studied on a temporal scale that represents 1 to 10 times the life span of the dominant species (Walker & del Moral 2003).

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Table 2. Relative appropriateness of the chronosequence approach varies depending on a) predictability and trajectory type (divergent or convergent) and b) plant biodiversity and disturbance impact (frequency plus severity). ++ = very useful, + = useful, - = not useful, -- = potentially misleading

856 a.

	DIVERGENT		CONVERGENT	
	Plant Succession	Soil Development	Plant Succession	Soil Development
PREDICTABLE	+	+	++	++
UNPREDICTABLE	-	-	+	+

b.

	LOW DISTURBANCE		HIGH DISTURBANCE	
	Plant Succession	Soil Development	Plant Succession	Soil Development
HIGH BIODIVERSITY	-	+	--	-
LOW BIODIVERSITY	+	+	+ ¹ or - ²	+

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¹ progressive succession
² retrogressive succession

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Table 3. Guidelines for developing appropriate chronosequence studies in terms of the elements

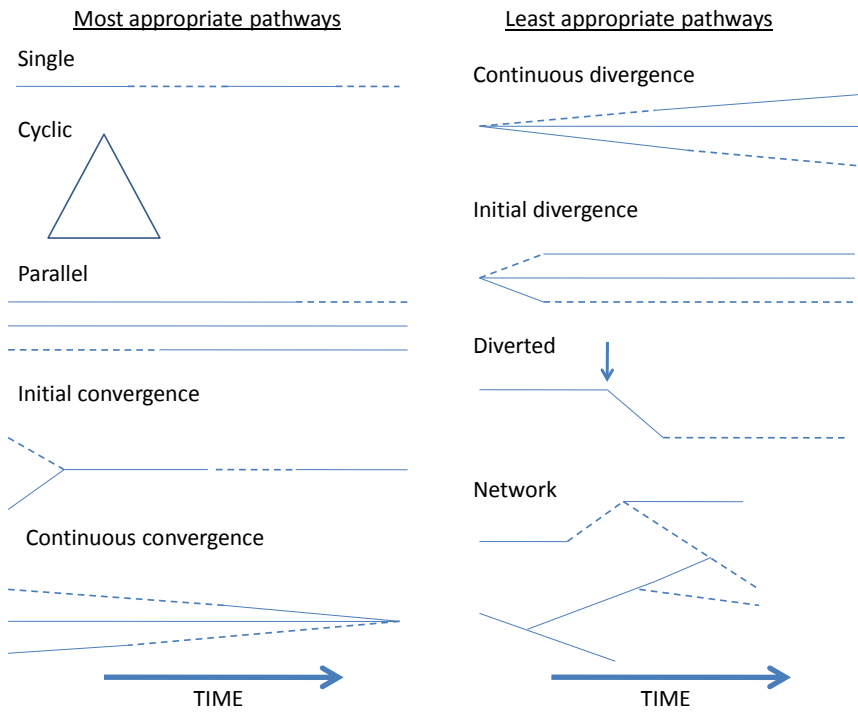
868 needed and potential limitations of studies when these elements are missing

Elements Needed	Potential Limitations if Element is Missing
Two or more stages (duration of time series depends on parameter of interest)	Chronosequence study of ecosystem parameters only
Multiple stand characteristics that vary across stages	Reduced ability to interpret temporal dynamics
At least one independent verification of time series	Faulty assumptions about temporal linkages
Replication within stages (number and spacing depends on spatial heterogeneity)	Misrepresentation of stage characteristics
Sampling intervals within life span of every dominant species of interest or duration of process of interest	Missed stages, inaccurate trajectories
Multiple visits to study plots	Missing verification of short-term dynamics
Sere-appropriate measurements	Failure to record relevant changes
Standardized measurements	Lack of ability to extrapolate to other studies

872 Fig. 1. The most common trajectories of successional development, representing several stages
of development from left to right (modified from Walker & del Moral 2003). The left column
includes those trajectories most appropriate for chronosequence interpretation; the right column
includes those least appropriate for chronosequence interpretation. Within each column,
876 appropriateness decreases from top to bottom, so initial convergence and networks need more
intensive sampling than those at the top of the same column. Dotted lines indicate how
presumed connections between stages can be erroneously assumed when direct evidence is not
available due to incomplete field sampling. For example, the upper line under Continuous
880 Divergence may actually represent a trajectory that had a separate origin. The vertical
downward arrow represents a disturbance that diverts a successional trajectory.

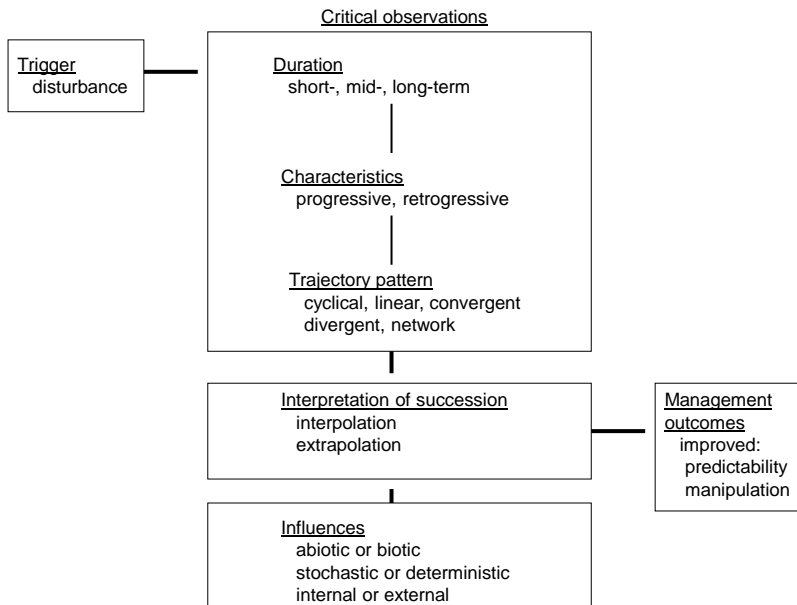
Fig. 2. Elements for a chronosequence function of a general successional model. Following a
884 disturbance, changes in vegetation or soil occur and the chronosequence approach can be used to
determine the duration, characteristics and trajectory patterns. In addition, critical abiotic and
biotic influences can be determined and characterized. The more extensive description and
quantification that can be obtained about an ecosystem, the better the interpretation can be of
888 successional patterns via interpolation within and extrapolation beyond the available data sets.
Ultimately, chronosequence tools can aid management by improving the prediction of
successional change and its manipulation through such efforts as conservation or restoration.

892 Fig. 1.



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Fig. 2.



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