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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 km<sup>2</sup>) 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).

308 The Cooloola Dune sequence in eastern Australia is another example of a long-term sere 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 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 20<sup>th</sup> 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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508

### **References**

Alban, D.H. (1982) Nutrient accumulation by aspen, spruce, and pine on soil properties. *Soil Science Society of America Journal*, **46**: 853-861.

- 512 Aplet, G.H. & Vitousek, P.M. (1994) An age-altitude matrix analysis of Hawaiian rain-forest succession. *Journal of Ecology*, **82**, 137-147.
- Armesto, J.J., Pickett, S.T.A., & McDonnell, M.J. (1991) Spatial heterogeneity during succession: A cyclic model of invasion and exclusion. *Ecological Heterogeneity* (eds J. Kolasa & S.T.A. Pickett), pp. 256-269. Springer, New York.
- 516 Ashton, P.S. (1985) Species richness in tropical forests. *Tropical Forests* (eds L.B. Holm-Hielsen, I.C. Nielsen & H. Balslev), pp. 239-251. Academic Press, London.
- Avis, A.M. & Lubke, R.A. (1996) Dynamics and succession of coastal dune vegetation in the Eastern Cape, South Africa. *Landscape and Urban Planning*, **34**, 237-253.
- 520 Baker, W.L. & Walford, G.M. (1995) Multiple stable states and models of riparian vegetation succession on the Animas River, Colorado. *Annals of the Association of American Geographers*, **85**, 320-338.
- 524 Bardgett, R.D. (2005) *The Biology of Soil: A Community and Ecosystem Approach*, Oxford University Press, Oxford.
- Bardgett, R.D., Bowman, W.D., Kaufmann, R. & Schmidt, S.K. (2005) A temporal approach to linking aboveground and belowground ecology. *Trends in Ecology and Evolution*, **20**, 528 634-641.
- Bardgett, R.D., Richter, A., Bol, R., Garnett, M.H., Baumler, R., Xu, X.L., Lopez-Capel, E., Manning, D.A.C., Hobbs, R.J., Hartley, I.R. & Wanek, W. (2007) Heterotrophic microbial communities use ancient carbon following glacial retreat. *Biology Letters* **3**, 532 487-490.

- Bardgett, R.D. & Walker, L.R. (2004) Impact of coloniser plant species on the development of decomposer microbial communities following deglaciation. *Soil Biology and Biochemistry*, **36**, 555-559.
- 536 Benedetti-Cecchi, L. & Cinelli, F. (1996) Patterns of disturbance and recovery in littoral rock pools: Nonhierarchical competition and spatial variability in secondary succession. *Marine Ecology Progress Series*, **135**, 145-161.
- Bhiry, N. & Filion, L. (1996) Holocene plant succession in a dune-swale environment of  
540 southern Quebec: A macrofossil analysis. *Ecoscience*, **3**, 330-342.
- Binkley, D. & Giardini, C. (1998) Why do tree species affect soils? The warp and woof of tree-soil interactions. *Biogeochemistry*, **42**, 89-106.
- Birks, H.J.B. (1980). Modern pollen assemblages and vegetational history of the moraines of the  
544 Klutlan Glacier and its surroundings, Yukon Territory, Canada. *Quaternary Research*,  
**14**, 101-129.
- Boerner, R.E.J. (1985) Alternate pathways of succession on the Lake Erie Islands. *Vegetatio*, **63**,  
35-44.
- 548 Boerner, R.E.J., DeMars, B.G. & Leicht, P.N. (1996) Spatial patterns of mycorrhizal  
infectiveness of soils along a successional chronosequence. *Mycorrhiza*, **6**, 79-90.
- Brown, J.C. (1958) Soil fungi of some British sand dunes in relation to soil type and succession.  
*Journal of Ecology*, **46**, 641-664.
- 552 Calkin, P.E. & J.M. Ellis. 1980. A lichenometric dating curve and its application to Holocene  
glacier studies in the central Brooks Range, Alaska. *Arctic & Alpine Research*, **12**, 245-  
264.



- Castillo, S., Popma, J. & Moreno-Casasola, P. (1991) Coastal sand dune vegetation of Tabasco  
556 and Campeche, Mexico. *Journal of Vegetation Science*, **2**, 73-88.
- Chadwick, O.A., Derry, L.A., Vitousek, P.M., Huebert, B.J. & Hedin, L.O. (1999) Changing  
sources of nutrients during four million years of ecosystem development. *Nature*, **397**,  
491-497.
- 560 Chapin, F.S., III, Matson, P.A. & Mooney, H.A. (2003) *Principles of Terrestrial Ecosystem  
Ecology*. Springer, New York.
- Chapin, F.S., III, Walker, L.R., Fastie, C.L. & Sharman, L.C. (1994) Mechanisms of primary  
succession following deglaciation at Glacier Bay, Alaska. *Ecological Monographs*, **64**,  
564 149-175.
- Chazdon, R.L., Letcher, S.G., van Breugel, M., Martinez-Ramos, M., Bongers, F. & Finegan, B.  
(2007). Rates of change in tree communities of secondary neotropical forests following  
major disturbances. *Philosophical Transactions of the Royal Society of London, Series B  
568 - Biological Sciences*, **362**, 27-289.
- Christensen, N.L. & Peet, R.K. (1984) Convergence during secondary forest succession. *Journal  
of Ecology*, **72**, 25-36.
- Clarkson, B.D. (1997) Vegetation succession (1967-1989) on five recent montane lava flows,  
572 Mauna Loa, Hawaii. *New Zealand Journal of Ecology*, **22**, 1-9.
- Clarkson, B.R., Schipper, L.A. & Lehmann, A. (2004) Vegetation and peat characteristics in the  
development of lowland restiad peat bogs, North Island, New Zealand. *Wetlands*, **24**,  
133-151.

- 576 Clinton, P.W., Allen, R.B. & Davis, M.R. (2002) Nitrogen storage and availability during stand  
development in a New Zealand *Nothofagus* forest. *Canadian Journal of Forest  
Research*, **32**, 344-352.
- Cooper, W.S. (1923) The recent ecological history of Glacier Bay, Alaska. II. The present  
580 vegetation cycle. *Ecology*, **4**, 223-246.
- Cooper-Ellis, S., Foster, D.R., Carlton, G. & Lezberg, A. (1999) Forest response to catastrophic  
wind: result from an experimental hurricane. *Ecology*, **80**, 2683-2696.
- Coomes, D. A., Allen, R.B. Bently, W.A., Burrows, L.E., Canham, C.D., Fagan, L., Forsyth,  
584 D.M., Gaxiola-Alcantar, A. Parfitt, R.L., Ruscoe, W.A., Wardle, D.A., Wilson, D.J. &  
Wright, E.F. (2005) The hare, the tortoise, and the crocodile: the ecology of angiosperm  
dominance, conifer persistence and fern filtering. *Journal of Ecology* **93**, 918-935.
- Cordell, S., Goldstein, G., Meinzer, F.C. & Vitousek, P.M. (2001) Regulation of leaf life-span  
588 and nutrient-use efficiency of *Metrosideros polymorpha* in N and P limited Hawaiian  
forests. *Oecologia*, **127**, 198-206.
- Cowles, H.C. (1899) The ecological relations of the vegetation on the sand dunes of Lake  
Michigan. *Botanical Gazette*, **27**, 95-117, 167-202, 281-308, 361-391.
- 592 Cramer, V.A. (2007) Old fields as complex systems: New concepts for describing the dynamics  
of abandoned farmland. *Old Fields: Dynamics and Restoration of Abandoned Farmland*  
(eds V.A. Cramer & R.J. Hobbs), pp. 31-46. Island Press, Washington, D.C.
- Cramer, V.A. & Hobbs, R.J. (eds) (2007) *Old Fields: Dynamics and Restoration of Abandoned*  
596 *Farmland*. Island Press, Washington, D.C.

- Crews, T.E., Kitayama, K., Fownes, D., Herbert, D., Mueller-Dombois, D., Riley, R.H. & Vitousek, P.M. (1995) Changes in soil phosphorus and ecosystem dynamics along a long term chronosequence in Hawaii. *Ecology*, **76**, 1407-1424.
- 600 Cutler, N.A., Belyea, L.R. & Dugmore, A.J. (2008) Spatial patterns of microsite colonization on two young lava flows on Mt. Hekla, Iceland. *Journal of Vegetation Science*, **19**, 277-286.
- De Deyn, G.B., Raaijmakers, C.E., Zoomer, H.R., Berg, M.P., de Ruiter, P.C., Verhoef, H.A., Bezemer, T.M. & van der Putten, W.H. (2003) Soil invertebrate fauna enhances grassland  
604 succession and diversity. *Nature*, **422**, 711-713.
- del Moral, R. (2007) Limits to convergence of vegetation during early primary succession. *Journal of Vegetation Science*, **18**, 479-488.
- del Moral, R. & Jones, C.C. (2002) Early spatial development of vegetation on pumice at Mount  
608 St. Helens. *Plant Ecology*, **161**, 9-22.
- Dickson, B.A. & Crocker, R. L. (1953) A chronosequence of soils and vegetation near Mt. Shasta, California. I. Definition of the ecosystem investigated and features of the plant succession. *Journal of Soil Science*, **4**, 123-141.
- 612 Doblas-Miranda, E., Wardle, D.A., Peltzer, D.A. & Yeates, G.W. (2008) Changes in the community structure and diversity of soil invertebrates across the Franz Josef Glacier chronosequence. *Soil Biology & Biochemistry*, **40**, 1069-1081.
- Drake, D.R. & Mueller-Dombois, D. (1993) Population development of rain forest trees on a  
616 chronosequence of Hawaiian lava flows. *Ecology*, **74**, 1012-1019.
- Engstrom, D.R. (ed) (1995) Proceedings of the 3<sup>rd</sup> Glacier Bay Science Symposium, 1993. National Park Service, Anchorage, Alaska.

- Fastie, C.L. (1995) Causes and ecosystem consequences of multiple pathways on primary  
620 succession at Glacier Bay, Alaska. *Ecology*, **76**, 1899-1916.
- Field, W.O. (1947) Glacier recession in Muir Inlet, Glacier Bay, Alaska. *Geographical Review*,  
**37**, 369-399.
- Foster, B.L. & Tilman, D. (2000) Dynamic and static views of succession: Testing the  
624 descriptive power of the chronosequence approach. *Plant Ecology*, **146**, 1-10.
- Frankland, J.C. (1998). Fungal succession – unraveling the unpredictable. *Mycological Research*,  
**102**, 1-15.
- Fukami, T. & Wardle, D.A. (2005) Long-term ecological dynamics: reciprocal insights from  
628 natural and anthropogenic gradients. *Proceedings of the Royal Society of London, Series  
B - 272*, 2105.
- Fukami, T., Bezemer, T.M., Mortimer, S.R. & van der Putten, W.H. (2005) Species divergence  
and trait convergence in experimental plant community assembly. *Ecology Letters*, **8**,  
632 1283-1290.
- Funkhouser, J.G., Barnes, I.L. & Naughton, J.J. (2007) Problems in the dating of volcanic rocks  
by the potassium-argon method. *Bulletin of Volcanology*, **29**, 709-717.
- Glenn-Lewin, D.C., Peet, R.K. & Veblen, T.T. (eds) (1992) *Plant Succession: Theory and  
636 Prediction*. Chapman & Hall, London.
- Goldthwait, R.P. (1966) Glacial history. *Soil Development and Ecological Succession in a  
Deglaciaded Area of Muir Inlet, Southeast Alaska* (ed A. Mirsky), pp 1-18. Institute of  
Polar Studies Report Number 20, Ohio State University, Columbus, Ohio, USA.

- 640 Gruner, D.S. (2007) Geological age, ecosystem development, and local resource constraints on  
arthropod community structure in the Hawaiian Islands. *Biological Journal of the  
Linnean Society*, **90**, 551-570.
- Guariguata, M. (1990) Landslide disturbance and forest regeneration in the upper Luquillo  
644 Mountains of Puerto Rico. *Journal of Ecology*, **78**, 814-832.
- Guariguata, M. & Ostertag, R. (2001) Neotropical secondary forest succession: changes in  
structural and functional characteristics. *Forest Ecology and Management*, **148**, 185-206.
- Gundale, M.J., Wardle, D.A. & Nilsson, M.-C. (**In press**) Vascular plant removal effects on  
648 biological N-fixation vary across a boreal forest island gradient. *Ecology*.
- Hobbs, R.J., Walker, L.R. & Walker, J. (2007) Integrating restoration and succession. *Linking  
Restoration and Ecological Succession* (eds L.R. Walker, J. Walker & R.J. Hobbs), pp.  
168-180. Springer, New York.
- 652 Inouye, R.S. & Tilman, D. (1995) Convergence and divergence of old-field vegetation after 11  
yr of nitrogen addition. *Ecology*, **76**, 1872-1887.
- Jenny, H. (1980) *The Soil Resource: Origin and Behavior*. Springer, New York.
- Johnson, E.A. & Miyanishi, K. (2008) Testing the assumptions of chronosequences in  
656 succession. *Ecology Letters*, **11**, 419-431
- Kaltenecker, J.H., Wicklow-Howard, M. & Pellant, M. (1999) Biological soil crusts: natural  
barriers to *Bromus tectorum* L. establishment in the northern Great Basin, USA.  
*Proceedings of the VI International Rangeland Congress* (eds D. Eldridge & D.  
660 Freudenberger), pp. 109-111. Bureau of Land Management, Boise, Idaho, USA.
- Kardol, P., Bezemer, T.M. & van der Putten, W.H. (2006) Temporal variation in plant-soil  
feedback controls succession. *Ecology Letters*, **9**, 1080-1088.

- 664 Kitayama, K. (2005) Comment on: Ecosystem properties and forest decline in contrasting long-term chronosequences. *Science*, **308**, 633a.
- Kitayama, K. Mueller-Dombois, D. & Vitousek, P.M. (1995) Primary succession of Hawaiian montane rain forest on a chronosequence of eight lava flows. *Journal of Vegetation Science*, **6**, 211-222.
- 668 Kume, A., Bekku, Y.S., Hanba, Y.T. & Kanda, H. (2003) Carbon isotope discrimination in diverging growth forms of *Saxifraga oppositifolia* in different successional stages in a High Arctic glacier foreland. *Arctic, Antarctic, and Alpine Research*, **35**, 377-383.
- Lajtha, K. & Schlesinger, W.H. (1988) The biogeochemistry of phosphorus cycling and  
672 phosphorus availability along a desert soil chronosequence. *Ecology*, **69**, 24-39.
- Lepš, J. & Rejmánek, M. (1991) Convergence or divergence: What should we expect from vegetation succession? *Oikos*, **62**, 261-264.
- Llambí, L.D., Fontaine, M., Rada, F., Saugier, B. & Sarmiento, L. (2003) Ecophysiology of  
676 dominant plant species during old-field succession in a high tropical Andean ecosystem. *Arctic, Antarctic, and Alpine Research*, **35**, 447-453.
- MacDougall, A.S., Wilson, S.D. & Bakker, J.D. (2008) Climatic variability alters the outcome of long-term community assembly. *Journal of Ecology*, **96**, 346-354.
- 680 Matthews, J.A. (1992) *The Ecology of Recently-deglaciated Terrain: A Geoecological Approach to Glacier Forelands and Primary Succession*. Cambridge University Press, Cambridge.
- Matthews, J.A. & Whittaker, R.J. (1987) Vegetation succession on the Storbreen glacier foreland, Jotunheimen, Norway: A review. *Arctic and Alpine Research*, **19**, 385-395.
- 684 McIntosh, R.P. (1985) *The Background of Ecology*. Cambridge University Press, Cambridge.

- Meiners, S.J., Cadenasso, M.L. & Pickett, S.T.A. (2007) Succession on the Piedmont of New Jersey and its implications for ecological restoration. *Old Fields: Dynamics and Restoration of Abandoned Farmland* (eds V.A. Cramer & R.J. Hobbs), pp. 145-161. 688  
Island Press, Washington, D.C.
- Melick, D.R. & Ashton, D.H. (1991) The effects of natural disturbances on warm temperate rainforests in South-eastern Australia. *Australian Journal of Botany*, **39**, 1-30.
- Milner, A.M., Fastie, C.L., Chapin, F.S., III, Engstrom, D.R. & Sharman, L.C. (2007) 692  
Interactions and linkages among ecosystems during landscape evolution. *BioScience*, **57**, 237-247.
- Mueller-Dombois, D. (1987) Forest dynamics in Hawaii. *Trends in Ecology and Evolution*, **2**, 216-219.
- 696 Mueller-Dombois, D. & Fosberg, F.R. (1997) *Vegetation of the Tropical Pacific Islands*. Springer, New York.
- Myster, R.W. & Malahy, M.P. (2008) Is there a middle way between permanent plots and chronosequences? *Canadian Journal of Forest Research*, **38**, 3133-3138.
- 700 Nakamura, F., Yajima, T. & Kikuchi, S. (1997) Structure and composition of riparian forests with special reference to geomorphic site conditions along the Tokachi River, northern Japan. *Plant Ecology*, **133**, 209-219.
- Nilsson, C. & Wilson, S.D. (1991) Convergence in plant community structure along a disparate 704  
gradient: are lakeshores inverted mountainsides? *The American Naturalist*, **137**, 774-790.
- Noble, M.G., Lawrence, D.B. & Streveler, G.P. (1984) Sphagnum invasion beneath an evergreen forest canopy in southeastern Alaska. *Bryologist*, **87**, 119-127.

- Ohtonen, R., Fritze, H., Pennanen, T., Jumpponen, A., & Trappe, J.M. (1999). Ecosystem  
708 properties and microbial community changes in primary succession on a glacier forefront.  
*Oecologia*, **119**, 239-246.
- Olson, J.S. (1958) Rates of succession and soil changes on southern Lake Michigan sand dunes.  
*Botanical Gazette*, **119**, 125-170.
- 712 Peltzer, D.A., Wardle, D.A., Allison, V.J., Baisden, W.T., Bardegett, R.D., Chadwick, O.A.,  
Condrón, L.M., Parfitt, R.L., Porder, S., Richardson, S.J., Turner, B.L., Vitousek, P.M.,  
Walker, J., & Walker, L.R. In press. Understanding ecosystem retrogression. *Ecological  
Monographs*.
- 716 Pickett, S.T.A. (1989) Space-for-time substitutions as an alternative to long-term studies. *Long-  
term Studies in Ecology* (ed G.E. Likens), pp. 110-135. Springer, New York.
- Pickett, S.T.A., Cadenasso, M.L. & Meiners, S.J. (2009) Ever since Clements: From succession  
to vegetation dynamics and understanding to intervention. *Applied Vegetation Science*,  
720 **12**, 9-21.
- Poli Marchese, E. & Grillo, M. (2000) Primary succession on lava flows on Mt. Etna. *Acta  
Phytogeographica Suecica*, **85**, 61-70.
- Prach, K. (1994) Vegetation succession on river gravel bars across the northwestern Himalayas.  
724 *Arctic and Alpine Research*, **26**, 349-353.
- Richardson, S.J., Peltzer, D.A., Allen, R.B. & McGlone, M.S. (2005) Resorption proficiency  
along a chronosequence: Responses among communities and within species. *Ecology*, **86**,  
20-25.



- 728 Russell, A.E., Raich, J.W. & Vitousek, P.M. (1998) The ecology of the climbing fern  
*Dicranopteris linearis* on windward Mauna Loa, Hawaii. *Journal of Ecology*, **86**, 765-  
779.
- Rydin, H. & Borgegård, S.- O. (1991) Plant characteristics over a century of primary succession  
732 on islands, Lake Hjälmaren. *Ecology*, **72**, 1089-1101.
- Samuels, C.L. & Drake, J.A. (1997) Divergent perspectives on community convergence. *Trends  
in Ecology and Evolution*, **12**, 427-432.
- Schmidt, S.K., Reed, S.C., Nemergut, D.R., Grandy, A.S., Cleveland, C.C., Weintraub, M.N.,  
736 Hill, A.W., Costello, E.K., Meyer, A.F., Neff, J.C. & Martin, A.M. (2008) The earliest  
stages of ecosystem succession in high-elevation (5000 metres above sea level), recently  
deglaciated soils. *Proceedings of the Royal Society, Series B - Biological Sciences* **275**,  
2793-2802.
- 740 Selmants,. P.C. & Hart, S.C. (2008) Substrate age and tree islands influence carbon and nitrogen  
dynamics across a semiarid retrogressive chronosequence. *Global Biogeochemical  
Cycles*, **22**, GB1021.
- Setälä, H., & Marshall, V. (1994) Stumps as a habitat for Collembola during succession from  
744 clear-cuts to old-growth Douglas-fir forests. *Pedobiologia*, **38**, 307-326.
- Silvertown, J., McConway, K.J., Hughes, Z., Biss, P., Macnair, M. & Lutman, P. (2002)  
Ecological and genetic correlates of long-term population trends in the park grass  
experiment. *American Naturalist*, **160**, 409-420.
- 748 Sousa, W.P. (1984) The role of disturbance in natural communities. *Annual Review of Ecology  
and Systematics*, **15**, 353-391.

- Tejan-Kella, M.S., Chittleborough, D.J., Fitzpatrick, R.W., Thompson, C.H., Prescott, J.R. & Hutton, J.T. (1990) Thermoluminescence dating of coastal sand dunes at Cooloola and North Stradbroke Island, Australia. *Australian Journal of Soil Research*, **28**, 465-481.
- 752
- Thompson, C.H. (1981) Podzol chronosequence on coastal dunes in eastern Australia. *Nature*, **91**, 59-61.
- Thompson, C.H. & Moore, A.W. (1984) Studies in landscape dynamics in the Cooloola – Noosa River area, Queensland. 1. Introduction, general description and research approaches. CSIRO Australian Division of Soils Report 73, Canberra, Australia.
- 756
- Tilman, D. (1988) *Plant Strategies and the Dynamics and Structure of Plant Communities*. Princeton University Press, Princeton.
- Ugolini, F.C. & Mann, D.H. (1979) Biopedological origin of peatlands in southeast Alaska. *Nature*, **281**, 366-368.
- 760
- Van der Putten, W.H., Van Dijk, C. & Peters, B.A.M. (1993) Plant-specific soil-borne diseases contribute to succession in foredune vegetation. *Nature*, **362**, 53-56.
- 764
- Vancouver, G. (1798) *A voyage of discovery to the North Pacific Ocean, and round the world; in which the coast of North-west America has been carefully examined and accurately surveyed*. **3**, 244-245. Robinson, London.
- Vitousek, P.M. (2004) *Nutrient Cycling and Limitation: Hawaii as a Model System*. Princeton University Press, Princeton, New Jersey, USA.
- 768
- Walker, J. & Reddell, P. (2007) Retrogressive succession and restoration on old landscapes. *Linking Restoration and Ecological Succession* (eds L.R. Walker, J. Walker & R.J. Hobbs), pp. 69-89. Springer, New York.

- 772 Walker, J., Thompson, C.H., Fergus, I.F. & Tunstall, B.R. (1981) Plant succession and soil development in coastal sand dunes of subtropical eastern Australia. *Forest Succession. Concepts and Application* (eds D.C. West, H.H. Shugart & D.B. Botkin), pp. 107-131. Springer, New York.
- 776 Walker, J., Thompson, C.H., Reddell, P. & Olley, J. (2000) Retrogressive succession on an old landscape. *Proceedings of the 41<sup>st</sup> Symposium of the IAVS* (ed P. White), pp. 21-23. Opulus, Press, Uppsala.
- Walker, J., Thompson, C.H., Reddell, P. & Rapport, D.J. (2001) The importance of landscape  
780 age in influencing landscape health. *Ecosystem Health*, **7**, 7-14.
- Walker, L.R. (1995) How unique is primary plant succession at Glacier Bay? *Proceedings of the Third Glacier Bay Science Symposium, 1993* (ed D.R. Engstrom), pp. 137-146. National Park Service, Anchorage, Alaska.
- 784 Walker, L.R. (ed) (1999) *Ecosystems of Disturbed Ground*, Elsevier, Amsterdam.
- Walker, L.R. & del Moral, R. (2003) *Primary Succession and Ecosystem Rehabilitation*. Cambridge University Press, Cambridge.
- Walker, L.R. & del Moral, R. (2009) Lessons from primary succession for restoration of severely  
788 damaged habitats. *Applied Vegetation Science*, **12**, 55-67.
- Walker, L.R. & Shiels, A.B. (2008) Post-disturbance erosion impacts carbon fluxes and plant succession on recent tropical landslides. *Plant and Soil*, **313**: 205-216.
- Walker, L.R., Velázquez, E. & Shiels, A.B. (2009) Applying lessons from ecological succession  
792 to the restoration of landslides. *Plant and Soil*, **324**, 157-168.

- Walker, L.R., Zarin, D.J., Fetcher, N., Myster, R.W. & Johnson, A.H. (1996) Ecosystem development and plant succession on landslides in the Caribbean. *Biotropica*, **28**, 566-576.
- 796 Walker, T.W. & Syers, J.K. (1976) The fate of phosphorus during pedogenesis. *Geoderma*, **15**, 1-19.
- Wardle, D.A. (2002) *Communities and Ecosystems: Linking the Aboveground and Belowground Components*. Princeton University Press, Princeton, New Jersey, USA.
- 800 Wardle, D.A. & Zackrisson, O. (2005) Effects of species and functional group loss on island ecosystem properties. *Nature*, **435**, 806-810.
- Wardle, D.A., Bardgett, R.D., Walker, L.R. & Bonner, K.I. (2009) Among- and within-species variation in plant litter decomposition in contrasting long-term chronosequences.
- 804 *Functional Ecology*, **23**, 442-453.
- Wardle, D.A., Bardgett, R.D., Walker, L.R., Peltzer, D.A. & Lagerström, A. (2008) The response of plant diversity to ecosystem retrogression: evidence from contrasting long-term chronosequences. *Oikos*, **117**, 93-103.
- 808 Wardle, D.A., Walker, L.R. & Bardgett, R.D. (2004) Ecosystem properties and forest decline in contrasting long-term chronosequences. *Science*, **305**, 509-513.
- Wardle, D.A., Zackrisson, O., Hörnberg, G., & Gallet, C. (1997) Influence of island area on ecosystem properties. *Science*, **277**, 1296-1299.
- 812 Warming, E. (1895) *Plantefund: Gruntræk af den Ökologiska Plantegeografi*. Philipsen, Copenhagen.
- Watt, A. S. (1947) Pattern and process in the plant community. *Journal of Ecology*, **35**, 1-23.

- Webb, R.H. (1996) *Grand Canyon, a Century of Change*. University of Arizona Press, Tucson,  
816 Arizona, USA.
- White, P.S. & Pickett, S.T.A. (1985) Natural disturbance and patch dynamics: an introduction.  
*The Ecology of Natural Disturbance and Patch Dynamics* (eds S.T.A. Pickett & P. S.  
White), pp. 3-13. Academic Press, Orlando.
- 820 Whitehead, D., Boelman, N.T., Turnbull, M.H., Griffin, K.L., Tissue, D.T., Barbour, M.M.,  
Hunt, J.E., Richardson, S.J. & Peltzer, D.A. (2005) Photosynthesis and reflectance  
indices for rainforest species in ecosystems undergoing progression and retrogression  
along a soil fertility chronosequence in New Zealand. *Oecologia*, **144**, 233-244.
- 824 Whittaker, R.H. (1953) A consideration of climax theory: The climax as a population and  
pattern. *Ecological Monographs*, **23**, 41-78.
- Whittaker, R.J., Partomihardjo, T. & Jones, S.H. (1999) Interesting times on Krakatau: Stand  
dynamics in the 1990s. *Philosophical Transactions of the Royal Society of London, Series*  
828 *B – Biological Sciences*, **354**, 1857-1867.
- Williamson, W.M., Wardle, D.A. & Yeates, G.W. (2005) Changes in soil microbial and  
nematode communities during ecosystem retrogression across a long term  
chronosequence. *Soil Biology and Biochemistry*, **37**, 1289-1301.
- 832 Wilson, J.B., Allen, R.B. & Lee, W.G. (1995) An assembly rule in the ground and herbaceous  
strata of a New Zealand rain forest. *Functional Ecology*, **9**, 61-64.
- Wood, D.M. & Morris, W.F. (1990) Ecological constraints to seedling establishment on the  
Pumic Plains, Mount St. Helens, Washington. *American Journal of Botany*, **77**, 1411-  
836 1418.

Young, D.R., Shao, G. & Porter, J.H. (1995) Spatial and temporal growth dynamics of barrier island shrub thickets. *American Journal of Botany*, **82**, 638-645.

840 Zarin, D.J. & Johnson, A.H. (1995) Nutrient accumulation during primary succession in a montane tropical forest, Puerto Rico. *Soil Science Society of America Journal*, **59**, 1444-1452.

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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	+	+	+ <sup>1</sup> or - <sup>2</sup>	+

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<sup>1</sup> progressive succession  
<sup>2</sup> retrogressive succession

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

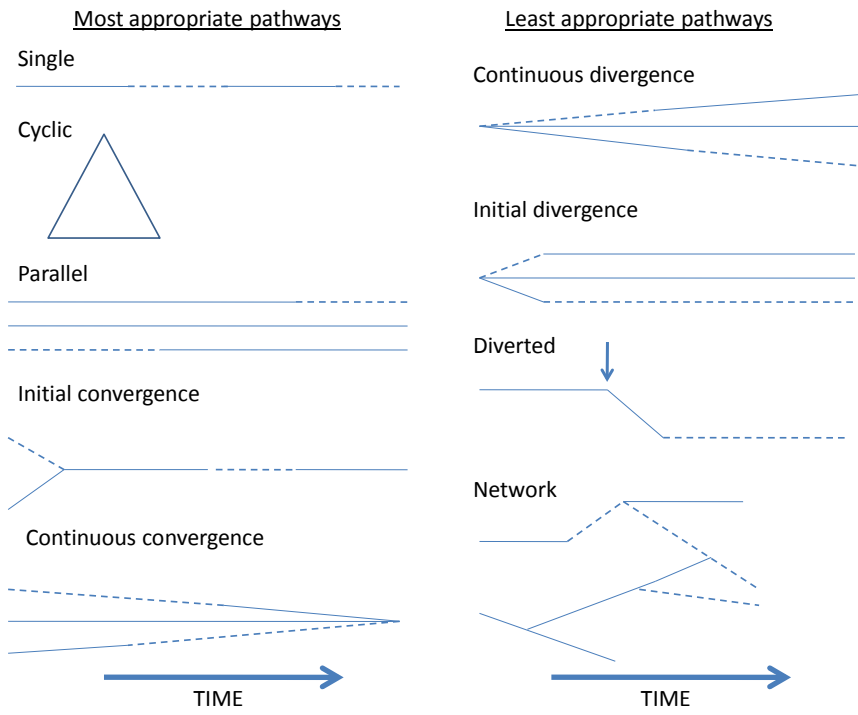
868 needed and potential limitations of studies when these elements are missing

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.

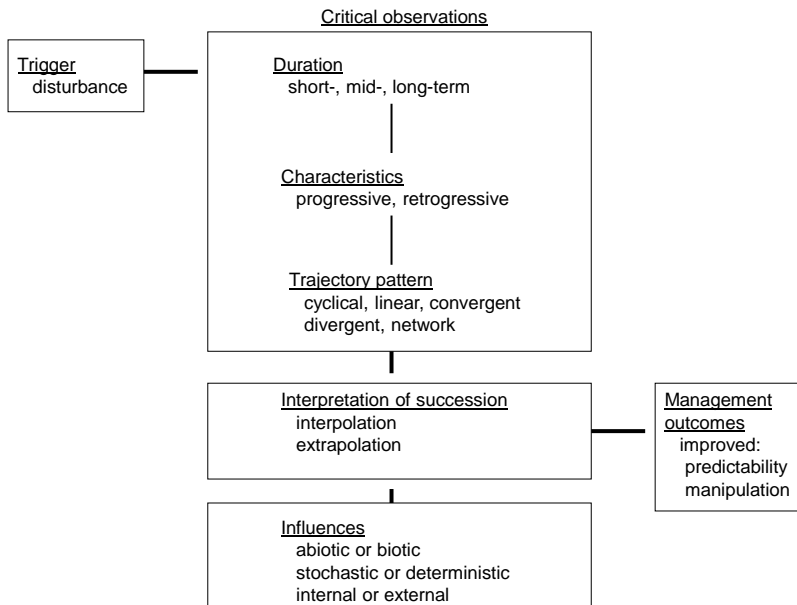
Fig. 2. Elements for a chronosequence function of a general successional model. Following a  
884 disturbance, changes in vegetation or soil occur and the chronosequence approach can be used to  
determine the duration, characteristics and trajectory patterns. In addition, critical abiotic and  
biotic 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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