4

8

The use of chronosequences in studies of ecological succession

12 and soil development

Lawrence R. Walker[1*], David A. Wardle[2], Richard D. Bardgett[3] and Bruce D. Clarkson[4]

16

[1]School of Life Sciences, University of Nevada Las Vegas, 4505 Maryland Parkway,
20 Las Vegas, NV 89154-4004, USA, [2]Department of Forest Ecology and Management,
Swedish University of Agricultural Sciences, SE-901 83 Umeå, Sweden, [3]Soil and Ecosystem
Ecology Laboratory, Lancaster Environment Centre, Lancaster University, Lancaster LA1 4YQ,
UK, and [4]Department of Biological Sciences, Private Bag 3105, University of Waikato,
24 Hamilton 3240, New Zealand.

28 *Correspondence author. E-mail: walker@unlv.nevada.edu

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

3

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.

160

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

192   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

196   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;

200   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

204   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

208   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

212   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*.

260   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).

264   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

268   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

272   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

276   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; Doblas-Miranda *et al*. 2008). Therefore,

retrogression does not simply involve shifts in community- and ecosystem-level properties at

280   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

12

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 seres that each has a

284   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-

288   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

292   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,

296   pahoehoe lava) across a wide range of elevations (900 - > 3000 m a.s.l.), spatial scales (local to >

500 km^2) 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

300   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

304   inputs, such as phosphorus inputs from Asian dust, that have occurred during the long history of

13

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 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 occured 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 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.

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 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

376   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.

380

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

384   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

388   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)

392   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

396   the application of the chronosequence approach.

17

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

468   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

472   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

476   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

480   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

484   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

488   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.

500

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.

516   Kolasa & S.T.A. Pickett), pp. 256-269. Springer, New York.

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

520   Eastern Cape, South Africa. *Landscape and Urban Planning*, **34**, 237-253.

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 3rd 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*

Deglaciated 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.

Kitayama, K. (2005) Comment on: Ecosystem properties and forest decline in contrasting long-

664   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 oppostifolia* 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.,

Condron, 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

752   North Stradbroke Island, Australia. *Australian Journal of Soil Research*, **28**, 465-481.

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

756   River area, Queensland. 1. Introduction, general description and research approaches.

      CSIRO Australian Division of Soils Report 73, Canberra, Australia.

Tilman, D. (1988) *Plant Strategies and the Dynamics and Structure of Plant Communities.*

      Princeton University Press, Princeton.

760 Ugolini, F.C. & Mann, D.H. (1979) Biopedological origin of peatlands in southeast Alaska.

      Nature, **281**, 366-368.

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

768   University Press, Princeton, New Jersey, USA.

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 41st 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) *Plantesamfund: Grunträk 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.

Zarin, D.J. & Johnson, A.H. (1995) Nutrient accumulation during primary succession in a

840   montane tropical forest, Puerto Rico. *Soil Science Society of America Journal*, **59**, 1444-

1452.

844

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 *et al.* 2001; Wardle *et al.* 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).

848

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]	+

860

[1] progressive succession
[2] retrogressive succession

864

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

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.

Most appropriate pathways

Single

Cyclic

Parallel

Initial convergence

Continuous convergence

TIME

Least appropriate pathways

Continuous divergence

Initial divergence

Diverted

Network

TIME

896

Fig. 2.

```
                              Critical observations
                    ┌──────────────────────────────────────────┐
  ┌─────────────┐   │         Duration                         │
  │ Trigger     │───│           short-, mid-, long-term        │
  │  disturbance│   │                                          │
  └─────────────┘   │                  │                       │
                    │                                          │
                    │         Characteristics                  │
                    │           progressive, retrogressive     │
                    │                                          │
                    │                  │                       │
                    │         Trajectory pattern               │
                    │           cyclical, linear, convergent   │
                    │           divergent, network             │
                    └──────────────────────────────────────────┘
                    ┌──────────────────────────────┐   ┌──────────────────┐
                    │ Interpretation of succession  │   │ Management       │
                    │   interpolation               │───│ outcomes         │
                    │   extrapolation               │   │   improved:      │
                    └──────────────────────────────┘   │     predictability│
                    ┌──────────────────────────────┐   │     manipulation  │
                    │ Influences                    │   └──────────────────┘
                    │   abiotic or biotic           │
                    │   stochastic or deterministic │
                    │   internal or external        │
                    └──────────────────────────────┘
```

900

904