



Quantifying secondary succession: a method for all sites?

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Abstract: Quantifying and documenting succession has been a challenge to ecologists for many years. A variety of measures have been generated but do not seem to have been widely adopted. We propose the use of an intuitive and quantifiable measure that is amenable to both model building and hypothesis testing, and apply the method to a long-term, ongoing succession project in southeastern Ontario. We compare our measure with turnover rate (Diamond 1969) and lambda (Shugart and Hett 1973). We found that although these measures can determine when change within the community is occurring, the nature of this change and the resultant composition of the community is not readily gleaned from the measure. Our measure, by grouping plants as either 'early' or 'late', allows the relative composition of the community to be understood with a single number. The benefit of using an aggregate measure such as ours, is that a variety of questions can be examined, such as 'when will a community revert to its original composition following fire?' As an example, we utilized our measure on a post-fire succession data set from northern Montana. The results estimate that sites will take anywhere from 3 to 100 years to return to their pre-fire composition, based on current environmental conditions.

Nomenclature: Morton and Venn (1990)

Introduction

The composition of many plant communities changes over time, often following a transition from one form to another, a progression labeled succession. In some cases, this progression proceeds from an initial state to a final state, while in other cases it can be described as cyclical (Grosshans and Kenkel 1997, Armstrong and Bullock 2003), oscillating between 2 states. Regardless if a specific community is typically viewed as linear, moving from initial state to final state, or cyclical, moving from state 1 to state 2, then back to state 1, the process of succession is directional; communities are moving from one set of species to another. Several measures have been proposed to capture the position of the community along this process. A simple, easy to calculate measure can provide a useful summary for comparative purposes. We propose the use of a ratio of the species found in the initial state (early species) to those not found in the initial state (late species). Once the community members have been assigned to the early or late groups, this ratio can be used to compare the rate of succession between different sites, exploring the impact of site specific characteristics or events on this rate. The benefit of such an aggregate measure is that it is simple to calculate, easy to interpret and amena-

ble to correlation between other variables such as herbivore dynamics or soil characteristics.

Plant communities occupy a spatially defined region. For most communities, identifying replicates within the area occupied by the community is difficult due to spatial heterogeneity with respect to soil characteristics, surrounding vegetation, seed bank, and herbivore pressure. When long term community dynamics are studied, appropriate sites may be spatially or temporally isolated, further complicating the potential for replication. To address these issues, studies have sought numerous collections of community data for pattern analysis (Wildi and Schütz 2000). The general result of these studies is that the length of time and specific pathway toward the endpoint community, as defined by Pickett (1989), is difficult to predict. However, it has been shown to depend upon initial community composition and soil characteristics (Pickett 1982, Myster and Pickett 1994). The difficulty in achieving accurate predictions stems largely from the fact that communities tend to be complex, containing a mixture of numerous species (Anand and Orłóci 1997, Anand 2000). Within this community, plant species will exhibit a range of tolerances for drought, sunlight, nutrients, competition and herbivory. However, despite the complexity and irre-

spective of the individual plant species within the community, most plant communities will undergo a process of succession following a disturbance. While a prediction of species abundance and the diversity that will comprise the final community is ideal, at present the ultimately defining mechanism driving this determination is not understood. Until such time as this mechanism can be determined, all long-term community studies continue to add information to this understanding.

Community studies examining the process of succession take one of two basic approaches: 1. allow all species to be included (with the exception of very rare or inconstant species) or 2. to develop groupings, e.g., functional or botanical, to capture the essence of the community. While the first approach is ideally the 'best', often the second approach has to be chosen for clarity or statistical power. Regardless of the approach, the discussion which follows the analysis focuses on the individual species or groups that will be present at some point in the future. We develop an aggregate measure, similar to the second approach, which provides useful information for studying the succession process itself. Aggregate measures of community status enable comparison between sites based on gross characteristics. Such measures permit overall patterns to be detected which are not evident when looking at finer details. Below we describe other measures used to depict succession and discuss their characteristics in relation to the process we are attempting to quantify.

Diamond (1969) published a measure of species turnover rates, first applied to bird species inhabiting islands, and used in other bird studies (Glowacinski and Jarvinen 1975). This measure was modified by Frye (1978) and applied to plant communities. For this measure, the 'rate' of succession was deemed to be increasing as the species turnover rate increased. The equation is as follows:

$$\% \text{ turnover} = 100 \times (E+I)/2 \times (n_1+n_t)$$

where: E is the number of extinctions, I is the number of invasions, n_1 is the total number of species at time 1 and n_t is the total number of species at time t .

This measure relies on species numbers, accounts for extinctions and invasions but does not keep track of the original species or their identity. Without accounting for the species identity, this measure is directionless. Succession may not proceed smoothly, often due to herbivory or other disturbances (McBrien et al. 1983, Brown et al. 1988, Bach 1994). As an example, some herbivores preferentially attack particular species. Such attacks can accelerate or retard succession, an effect that the turnover rate cannot distinguish. Another issue is the sampling ef-

fort required to ensure that each and every species is accounted for within the site being studied. This level of detail renders this measure awkward to use in a practical context and sensitive to sampling effort. Further, it is not clear what increases or decreases in turnover rate signify. For example, a high turnover rate can occur for an abandoned field changing from one set of grass species to another, or when this field shifts from grasses to perennials and woody species. Also, if the field shifts from perennials back to grasses, or from trees back to thorny species, the turnover rate will be high, but the process is no longer moving towards the next sere. Turnover rate can only give an indication that change is occurring in the species composition, it cannot adequately indicate the type or direction of this change.

Shugart and Hett (1973) also developed a measure of species turnover, which quantified the rate of succession occurring over time. Its one unwritten assumption, pointed out by Myster and Pickett (1994), was the nature of the equation itself:

$$\lambda_t = \ln [(n_t - n_t n p_1) / n_1] / t$$

where n_t is the number of species at time t , $n_t n p_1$ is the number of species only at time t and not at time 1, n_1 is the number of species at time 1 and t is the time interval since time 1. If it is assumed that λ_t decays smoothly over time, then its evolution can be expressed as

$$\lambda_t = a t^b$$

where b is assumed to be negative, while a is positive. This structure embodies the assumption that species richness decreases with time. Taking logarithms allows us to perform the regression:

$$\ln \lambda_t = b \ln (t) + \ln (a) + u_t$$

where b is the slope, $\ln (a)$ is the intercept, and u_t is a disturbance term satisfying all the usual assumptions. The regression relationship is strictly for empirical convenience. We were unable to find a generating model for the species numbers n_t and $n_t n p_t$ from which a theoretical specification of the distribution could be derived. Examination of these will indicate the rate of species loss (b) and the initial species loss (a).

If the right conditions are met, then λ can capture the direction of a successional process. These conditions include mostly early species present when n_1 is determined, and these early species go extinct and are replaced by late successional species which are represented in $n_t n p_t$. How-

ever, if most early species are not represented in n_1 , then one cannot use λ to distinguish between two communities, one that changes from one set of early species to another and a second that changes from early to late successional species. Thus, in using λ one assumes that individual species only inhabit, grow, reproduce, senesce and are replaced by new species; suppression and resurgence are presumed to not occur, contrary to findings by Pickett (1982) and our studies (Blatt et al. 2001, in press). Further, the implementation of this measure requires that species numbers fall over time, for if $n_1 - n_t n p_t$ is negative, then λ is undefined. As such, this form cannot capture a community regressing to a prior vegetative composition, such as would occur for cyclical succession (Grosshans and Kenkel 1997, Armstrong and Bullock 2003).

Some of the problems pointed out for the turnover rate which follow from the use of species counts also cause problems for this measure. In particular, since these measures use species numbers and not abundance, they are highly dependent on sampling intensity in both space and time. Increasing the sampling effort will undoubtedly reveal new species that are consistently rare. An alternative to species number is species abundance, which is easier to use in statistical tests and can also capture more complex dynamics related to species' relative dominance. Finally, another problem stems from the concepts of 'rate of species loss' and 'initial species loss'. In both of these instances, these do little to indicate whether the initial species composition was replaced by species associated with the later stages of succession or other species associated with the earlier stages.

The final, and most extensively used, means to describe succession is the Markov chain model (Leps 1987). Although extensively used, a transition probability matrix is neither easy to calculate nor interpret. The Markov chain model determines the probability that community i will become community j , k or l . This is calculated by breaking the plant community down into groups. These have been based on individual species or their dominance (Leps 1987, Scott et al. 1990, Thorhallsdottir 1990, Anand and Heil 2000), floristic composition (Leps 1987, Scott et al. 1990, Thorhallsdottir 1990, Anand and Heil 2000, Wildi and Schütz 2000) or guilds (Wildi and Schütz 2000). The largest number of groups utilized in the Markov chain models presented in these papers is 8, so chosen for reasons of simplicity and ease of calculation. The aggregate measure we propose is, by comparison, more easily calculated and readily interpreted. Our measure also groups the plants, and examines the rate at which community i becomes community j , using 2 categories: early and late. These groupings can be viewed as arbitrary

but are no more so than the groupings used in any other Markov chain model. We use two methods to group the species in the empirical examples that follow. For the abandoned field analysis, we combined published data (Crowder 1986, Geomatics-International 1995) and expert opinion to assign species to the early and late groups. For the recovery after fire, those species present prior to the disturbance were categorized as 'late', i.e., the end-point to which the community 'should' return, and all other species 'early'. These groupings are subject to researcher bias, and we do not suggest that these are the ideal methods. Non-subjective groupings might include clustering based on temporal correlation or some other more objective measure. Explorations of such methods are left for a future paper.

The objective of this work is to compare our succession ratio with turnover rate (Frye 1978) and λ (Shugart and Hett 1973) for an old-field community in southeastern Ontario, then apply the succession ratio to a post-fire succession study in northern Montana.

Methods

Study site

Twenty-seven permanent plots measuring 15 m \times 6.7 m (100 m²) were established in two fields located near the Queen's University Biological Research Station (QUBS), at Lake Opinicon, in South Frontenac Township, Frontenac County (44° 03' N, 76° 09' W), Ontario, in 1975. Both fields were originally mixed deciduous forest (white ash, hickory and white pine) until cleared to become hay fields. They were seeded with *Phleum pratense*, *Trifolium repens*, *Poa pratensis* and *Agropyron repens*, during the early 1930's, annually mown and harvested until 1969 (Field 2) and 1974 (Field 1). Following this final harvest, they were abandoned then purchased by Queen's University in 1975. Within each plot, a 50 cm \times 50 cm quadrat was randomly placed 5 times in June and again in September for 1976-1988, 1995 and 1998. Absolute percent cover for each plant species was determined according to Phillips (1959) with species identified according to Morton and Venn (1990). Absolute percent cover was chosen for a number of reasons: 1. it provides the best proxy for biomass without the time-consuming effort (Smartt et al. 1974), 2. it takes into account the life form of the plants (particularly their ability to shade out other species), and 3. it provides an indication of dominance within the community. Although biomass can be considered the ideal measure to determine which species are most dominant or important within the community (Smartt et al. 1974, Watkins and Wilson 1994), the amount of time required to obtain these measures is often excessive. As we were interested in

how the community changes over time, and the type of change (with respect to the species), percent cover was deemed the most suitable, and practical, measure to use.

Succession ratio

We observed wide variation in the succession process across the 27 plots. We speculate that this heterogeneity is related to factors such as insect outbreaks, soil characteristics and local seed bank content. Since we are interested in how the overall successional process is affected by these factors, and not strictly species counts or the status of some select group or guild, we needed an aggregate measure. To this end, we propose using a 'succession ratio' as a measure. Our succession measure (y_t) can be written as

$$y_t = \frac{\sum e}{\sum l}$$

where e is the total percent cover of early species and l is the total percent cover of late species.

The justification for grouping species is critical and the distinction between species present at t_1 and species 'expected' to be present needs clarification. When an abandoned agricultural field is first observed, it will contain a mixture of species. Some of these will be species that were present at t_1 (usually by intentional seeding) while other species, either arrived or presented themselves (from the seed bank) at a later date. We included in the 'early' category those species that were seeded (t_1 species) and those which are typically found within the first three years of a primary succession sequence ('expected' species). We consulted the single publication describing species for this region (Crowder 1986), local botanists and the Ministry of Natural Resources (Geomatics-International 1995) to obtain a list of species that are typically observed. When a community is observed immediately following a disturbance, any species that appears can easily be considered 'early'. However, in our study, one of the hayfields was abandoned 5 years prior to the start of the research. It already contained a mixture of *Solidago* spp., *Aster* spp., *Taraxacum officinale* and *Asclepias syriaca*, species typically not associated with the first stages of succession after hayfield abandonment in south-eastern Ontario. To use these plant species as representatives of the early stages of succession would be inaccurate. Further, agricultural fields are an artificial setting as species are selected, largely for a particular use, and planted in a specific area. The mixture of plants found within agricultural fields will not generally reflect the composition found in nature. Further, these plants are managed for maximum production, with competition and

herbivory being controlled, commonly using pesticides. Hay fields routinely contain a mixture of grass species that would not typically appear until 5 or 6 years following disturbance in a natural successional sequence. Additionally, some of these species, under natural conditions, may never achieve dominance. Yet in an agricultural environment, these species are dominating the community. The successional sequence in this circumstance will not proceed according to the pathways observed in natural fields because particular species are unnaturally abundant. To account for this situation, we have included the intentionally planted species as part of the 'early' category. As an aide to appreciate the communities found within the plots, plant species dominant (achieving percent cover of >10%) within each plot in 1976 and 1998 are listed (Table 1). We do not suggest that this simple 'Delphi', or consensus finding (Fink et al. 1984) process is the only way or even the best way to categorize the species. In our burned plots from Montana, we used the species present immediately before the disturbance as 'late' and categorized all others as 'early'.

It can be easily shown by the following example that our measure is a simple summary of the Markov chain. Let's say we have a plot, observed for 10 years, that contains 36 plant species. Of these 36 plants, 6 were present in year 1 with all others invading at some point during the successive 9 years. If these original 6 species are grouped as 'early', all subsequent species are grouped as 'late', and then followed over time, the pattern of succession can be observed. Divide the plot into 100 cells which are assumed to each independently follow a Markovian process. Let the Markovian transition matrix be:

$$\mathbf{A} = \begin{bmatrix} 0.8 & 0.0 \\ 0.2 & 1.0 \end{bmatrix}$$

where 0.2 is the probability that a plot will change from early to late, 0.8 is the probability it remains dominated by early species, and 1 is the probability that a plot dominated by late species will remain dominated by late species. If \mathbf{x}_0 is a vector with the number of cells initially dominated by early species and the number initially dominated by late species, then the expected composition of the plot at period t is $\mathbf{x}_t = \mathbf{A}^t \mathbf{x}_0$. For concreteness, suppose that the 100 cells are all initially dominated by 'early' species. After one period, we would expect 80 of those cells to remain dominated by early species, with the remainder becoming dominated by late species. The early to late ratio after one period will be $80/20=4$. After two periods, the number of early species dominated cells is expected to drop to 64, the late species dominated plots increase to 35. The ratio then becomes $64/36=1.78$. Ten iterations yield

$$\mathbf{A}^{10} = \begin{bmatrix} 0.1074 & 0.0 \\ 0.8926 & 1.0 \end{bmatrix}$$

which when applied to the vector \mathbf{x}_0 results in 11 cells remaining dominated by early species and 89 dominated by late species. This results in a ratio of 0.124. By simple analogy, we use percent cover in place of cells, and follow the same logic to arrive at our measure.

Markov models can certainly be more complex, both in terms of dimension and dynamic process. For a case with more dimensions, the succession ratio is calculated by dividing the population composition vector's elements into two groups, early and late, adding their percent cover, and taking their ratio. Clearly, much information is lost in this process. However, if one's primary goal is to make statements about where the community is along the successional process, then our succession ratio will be adequate.

Our measure is effective if one is interested in how the rate of succession is affected by spatially and/or temporally specific events, such as rainfall or soil characteristics (see Blatt et al., in press). If more detailed information regarding the community is wanted, such as the specifics of which species are declining or increasing over time, the succession ratio can serve to identify those sites or time periods where a more detailed inspection is most likely to produce interesting results. If individual species are of interest, it would be quite simple to categorize those as the 'early' or 'late' and examine their relationship over time. With respect to the concept of succession converging to an equilibrium or attractor state, our measure can neither predict specific endpoints nor identify species compositions. Rather, it is intended to examine the aggregate community. If the community were to achieve a stable 'ratio' with little fluctuation over time, it could be said that the community has reached an equilibrium. Our measure is not able to predict what ratio will achieve this equilibrium. As a result of being an aggregate measure, it cannot provide a detailed description of the community, rather, it can determine which group has achieved dominance. Another benefit of our measure is that it is independent of temporal stage. While a plant community can be viewed as 'changing state' with the appearance of specific shrubs or trees, our measure will not distinguish a state change until such time as these species achieve dominance within the community. It has been observed in our plots that tree species not fitting the definition of 'pioneer species', such as apple, were present during the first years of the study (Crowder and Harmsen 1998). Further, more 'orthodox' pioneer species, such as pine and birch, did not colonize the plots as widely as predicted by theory (Geomatrix-International 1995, Crowder and Harmsen 1998). If our measure were able to distinguish these species as part of a temporal stage

then the succession status of our plots would have been determined as being farther along than it actually was. That our measure does not make any species-specific temporal stage distinctions, outside of which general group should appear first and which should appear later, renders it more useful to observing the process of succession itself.

Data analysis

We selected six of the 27 plots to demonstrate our measure: 4 from Field 1 and 2 from Field 2 (see Blatt et al., in press) for further details on field characteristics and plot location). Plots in Field 1 (G1, G7, P4 and P5) were abandoned in 1975 while plots from Field 2 (S1 and S3) were abandoned 5 years earlier in 1970. These plots were selected as 3 represented areas that showed considerable successional change (plots P4, P5 and S1) and 3 represented plots that have shown no significant successional change (plots G1, G7 and S3). The amount of successional change was determined using the succession ratio. When the ratio dropped to <1 , succession was considered to be occurring rapidly; in plots where the ratio was initially <1 (as occurred for Field 2, abandoned in 1970), we considered succession to be occurring rapidly when the ratio dropped to <0.5 . Although it was suggested that we use a similarity index as a means to determine which plots were progressing through succession, we did not. The difficulty in using a similarity index, like the Bray-Curtis, is that these comparisons have to be done across years within-plot. In this case, a change from one set of early species to a second set of early species would generate a low similarity and yet not indicate anything about the status of the succession process. Also, if a plot is farther along in its succession process and contains species more typically associated with later stages of succession, but then reverts to early species as a result of an herbivore outbreak, this change will generate a low similarity suggesting that succession is progressing when in fact it is not (see Blatt et al., in press, for comparisons of our measure against this index).

λ and turnover rate were generated for each plot. Each measure was then compared with our succession ratio for ease in describing and understanding the succession process. With respect to λ , we compared the slopes and intercepts between plots using regression analysis in R (Ihaka and Gentleman 1996). For the purpose of pair-wise comparison, the intercepts and slopes from each equation were compared with all other intercepts and slopes using multiple pair-wise t tests, with P values adjusted using Bonferroni (Zar 1984) as implemented in R. These tests were conducted separately ($H_{0a}: \ln(a_i) = \ln(a_j)$, $H_{0b}: b_i = b_j$,

for all $i \neq j$) and jointly (H_{0ab} : $\ln(a_i) = \ln(a_j)$ and $b_i = b_j$, for all $i \neq j$).

Finally, we conducted regression analysis $\arcsin(y_t) = \beta(1/t) + \alpha + \epsilon_t$ where y_t is the ratio at time t , α is the asymptote the ratio will approach, and β is the slope indicating the rate of convergence. Ratios were transformed using $\arcsin(y_t)$ to ensure normality and adherence to ANOVA assumptions. Equations were generated for 2 groups of plots: those where succession is occurring rapidly and those where succession is occurring slowly, for both fields. All 27 plots from the study were grouped based upon the succession ratio at t_{1998} and comparing it with the ratio at t_{1976} . If $y_{1998} < y_{1976}/2$, then succession was considered to be occurring rapidly. If $y_{1998} \geq y_{1976}/2$, then succession was considered to be occurring slowly. Plots present in the study were categorized as follows: Field 1 (Rapid Succession) - G2, G3, G4, G5, G6, G9, P1, P2, P3, P4, P5, P6 and P9; Field 1 (Slow Succession) - G1, G7, G8, P7, P8; Field 2 (Rapid Succession) - S1, S2, S8 and S9; Field 2 (Slow Succession) - S3, S4, S5, S6 and S7. Examination of these equations for the groups allows for comparison of the likely outcome of the succession process.

Further applications

We also used the succession ratio to examine the succession process in northern Montana Rocky Mountain forests (Stickney and Campbell 2000). In this database, fifty-four sites were surveyed to document the succession process post-fire in either broadcast burn or wildfire scenarios. We chose eighteen of these sites, from the broadcast burn portion of the study, as these were surveyed prior to the burn. The succession process was then documented over the following 25 years. We used the 'pre-burn' survey to determine our 'late' species, generated the succession ratio, and conducted regression analysis to estimate the asymptote. Sites were grouped into 6 regions based on geographical proximity, ecological similarity and exposure. Regions 1 through 4 were located in the Miller Creek Demonstration Forest on the Tally Lake Range District in Flathead National Forest (lat. $48^{\circ}31'N$, long. $114^{\circ}45'W$), and Regions 5 and 6 were located Newman Ridge in the Superior Range District in Lolo National Forest (lat. $47^{\circ}15'N$, long. $115^{\circ}20'W$). Regions 1-4 were all the same habitat type: *Abies lasiocarpa/Clintonia uniflora* but from different elevations and exposures: 1600-1630 m South-West to East (Region 1), 1630-1650 m North to North-West (Region 2), 1530-1560 m West (Region 3) and 1520-1560 m South to West (Region 4). Region 5 was of the *Abies grandis/Clintonia uniflora* to *Pseudotsuga menziesii/Vaccinium globulare* habitat, elevation 1700-1760 m East to South and Region 6 was of

the *Abies grandis/Clintonia uniflora* to *Thuja plicata/Clintonia uniflora* habitat, elevation 1630-1700 m North-East to West.

Results and discussion

General observations

Of the 125 plant species observed in these six plots, only 39 achieved dominance (>10% cover) at some time during the study. Of these 125 species, 16 were classified as 'early', the remaining 109 being classified as 'late'. Table 1 provides a list of these dominant species for 1976 and 1998. For both G1 and G7, slow-succession plots, two of the three dominant plant species remain the same with only one other species being replaced by 1998. For P4 and P5, rapid succession plots, both begin with a high dominance of grass species in 1976, and contain a high percentage of woody species by 1998. Although *Poa pratensis* in P5 is present at high levels (48%) in 1998, it is now present as an understory species. Both S1 and S3 begin with a high percentage of *Aster*, *Solidago* spp. and *Taraxacum officinale* (combined percent cover 41 and 82, S1 and S3, respectively) in 1976, with S1 becoming dominated by woody species in 1998. In S3, the *Aster* and *Solidago* spp. lose their dominance and are replaced by *Poa pratensis* in 1998.

Theoretically, succession should proceed in a monotonic fashion where early species are replaced by later species over time (Clements 1916, Tansley 1935, Margalef 1968, Odum 1969, Connell and Slatyer 1977). Our ratio demonstrates this process empirically (Blatt et al. 2001). Succession ratios for G1 and G7 do not show succession to occur between 1976 and 1998 (Figure 1Ia and 1IIa, G1 and G7, respectively). The patterns observed for these plots, show that the ratio, while approaching 0, remains well above 1. Succession ratios for plots P4 and P5 show gradual decline, consistent with the conclusion that succession is occurring in these plots (Figure 2Ia and 2IIa, P4 and P5, respectively). In P4, there is little variation in the course of succession, with the ratio quickly dropping below 1, by 1977, and remaining low throughout the remainder of the study. In P5, the pattern is more erratic, with the ratio suddenly increasing in years 1981 and 1985. Following the latter surge, the ratio remains high for 3 years before dropping in 1988 and remaining below 1 (Figure 2IIa). In all these cases, from Field 1, the ratio began quite high (ratio range: 2.0 - 46.8), and then dropped to just above 1 (slow-succession plots) or below 1 (rapid-succession plots). The differing plant compositions found within these plots confirm this determination.

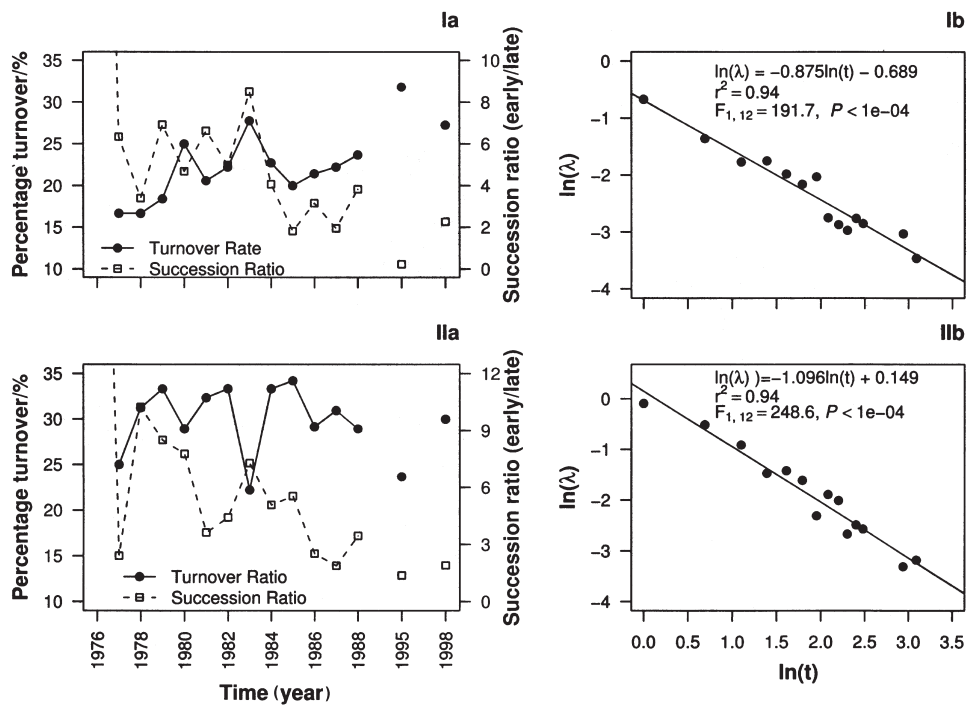


Figure 1. Succession ratio and turnover rates for two plots in Field 1 in an abandoned hayfield in southeastern Ontario. These plots, G1 - Ia and G7 - IIa, were not ploughed prior to abandonment and are not proceeding through succession. Plots were abandoned in 1975 and data collected in 1976. Regressions of $\ln(\lambda_t)$ vs. $\ln(t)$ are also shown for each plot (G1 - Ib, G7 - IIb).

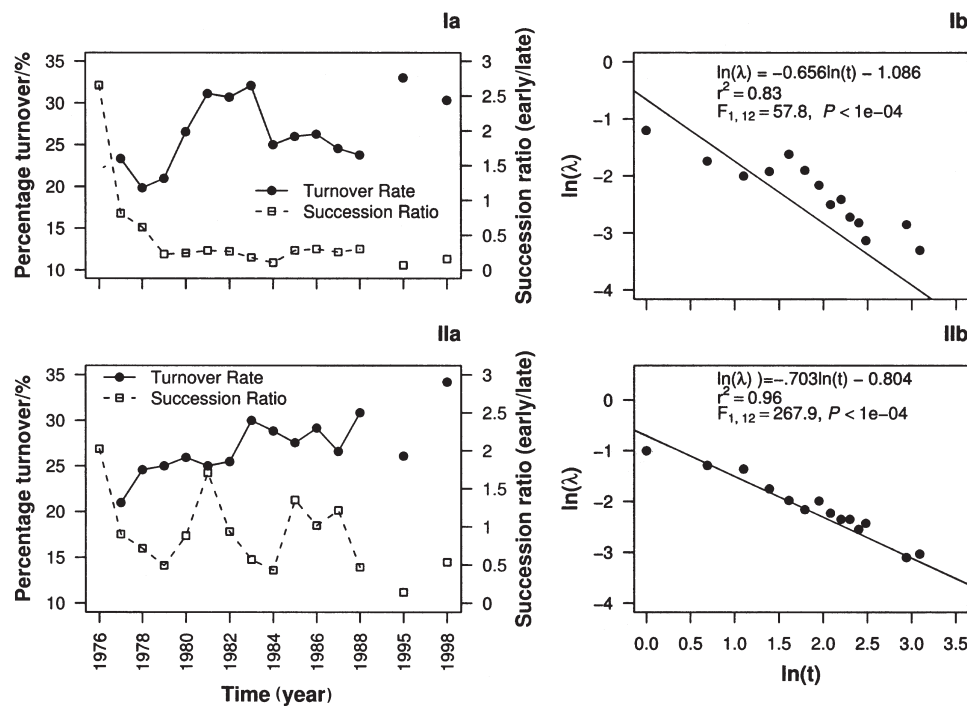


Figure 2. Succession ratio and turnover rates for two plots in Field 1, part of a long-term succession project in an abandoned hayfield in southeastern Ontario. These plots, P4 - Ia and P5 - IIa, were ploughed prior to abandonment and are proceeding through succession. Plots were abandoned in 1975 and data collected in 1976. Regressions of $\ln(\lambda_t)$ vs. $\ln(t)$ are also shown for each plot (P4 - Ib, P5 - IIb).

In Field 2, the ratio begins low for both S1 and S3 (0.4 and 0.2, S1 and S3, respectively, Figure 3Ia and 1IIa), indicating that succession has been occurring and the plots are dominated by later species (see Table 1). Over time, the ratio declines in plot S1, with only two surges, in years 1978 and 1985. During both of these years, the plot had a resurgence of early species with a decline in the later species (predominantly *Solidago* spp.) By 1998, the ratio had continued its decline and was 0.07 - indicating that succession was progressing. Plot S3 gives a different story. Here the ratio begins at 0.2, even lower than the initial ratio in S1, and over time shows a gradual increase. The plant community, by 1998 is dominated by an early species, *Poa pratensis*, with the *Aster* and *Solidago* spp. undergoing significant decline (Figure 3IIa).

Comparison with other measures

Comparing the ratio with turnover rate illustrates that while the pattern of succession may be erratic, the turnover rate does little to describe what is occurring. When the succession ratio is increasing, succession is reversing and the community is becoming dominated by grass or 'early' species. When the succession ratio is decreasing, succession is proceeding and the plant community changing to late species. For all of the plots presented here, the turnover rate showed increases and decreases regardless

if the community was advancing towards late species or regressing towards early species. This can be most clearly observed in plot S1, where the turnover rate is increasing rapidly both when the ratio is declining (Figure 3Ia, years 1980-1983) and increasing (Figure 3Ia, year 1985). Turnover rate has been shown to decrease over time; hence as succession proceeds, the turnover rate declines (Frye 1978). For this study, even in plots where succession was occurring (P4, P5 and S1), this trend did not hold true. Some of the highest turnover rates were achieved during the latter years of succession, well after the ratio had dropped below 1, and the plot was dominated by later species. As the turnover rate relies on an accurate measure of the number of species present, these high turnover rates are probably a result of the rarer species being included in the sampling in some years and overlooked in others. It is for this same reason that the turnover rate can either increase or decrease regardless of which species are acquiring dominance.

Regression analysis of $\ln(\lambda_t)$ vs. $\ln(t)$ disclosed essentially identical patterns for all plots (Figures 1Ib, 1IIb, 2Ib, 2IIb, 3Ib, 3IIb, plots G1, G7, P4, P5, S1 and S3, respectively). The intercepts ranged from -1.086 to 0.149 and the slopes ranged from -0.656 to -1.096. As the slope reflects the rate of change and the intercept the original species loss, it follows that, theoretically, plots rapidly proceeding

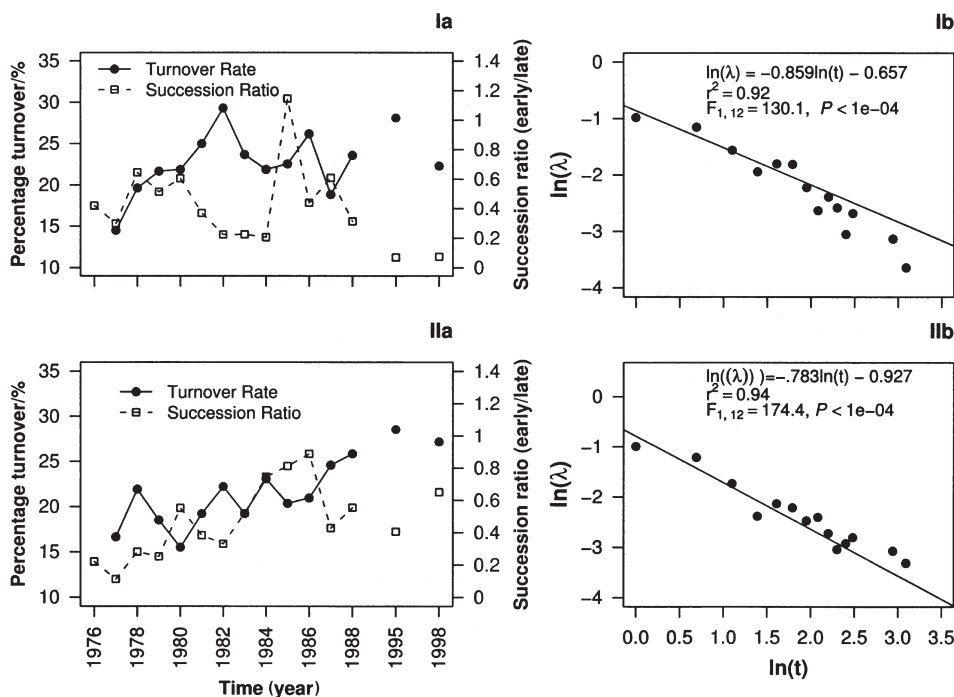


Figure 3. Succession ratio and turnover rates for two plots in Field 2, part of a long-term succession study, in an abandoned hayfield in southeastern Ontario. These plots, S1 - Ia and S3 - IIa, were not ploughed prior to abandonment. This field was abandoned in 1970 but not observed until 1976. Plot S1 is proceeding through succession, plot S3 is not. Regressions of $\ln(\lambda_t)$ vs. $\ln(t)$ are also shown for each plot (S1 - Ib, S3 - IIb).

Table 1. Dominant plant species (>10% cover) within the 6 plots during 1976 and 1998. Differences in community composition can be observed both between plots within years and within plots between years.

Plot	Year	
	1976	1998
G1 ^a	<i>Poa pratensis</i> (53) - G ^b <i>Phleum pratense</i> (48) - G <i>Agropyron repens</i> (19.4) - G	<i>Poa pratensis</i> (25) - G <i>Agropyron repens</i> (22) - G <i>Asclepias syriaca</i> (10) - F
G7 ^a	<i>Poa pratensis</i> (68) - G <i>Phleum pratense</i> (46) - G <i>Agropyron repens</i> (12) - G	<i>Agropyron repens</i> (48) - G <i>Poa pratensis</i> (18) - G <i>Vicia cracca</i> (18) - F
P4	<i>Poa pratensis</i> (25) - G <i>Phleum pratense</i> (20) - G <i>Cerastium vulgatum</i> (10) - F	<i>Pinus strobus</i> (40) - W <i>Poa pratensis</i> (19) - G <i>Carex gracillima</i> (15) - M <i>Alnus rugosa</i> (14) - W <i>Betula papyra</i> (14) - W <i>Carex</i> spp. (11) - M <i>Populus tremuloides</i> (10) - W <i>Solidago canadensis</i> (10) - F
P5	<i>Poa pratensis</i> (65) - G <i>Vicia cracca</i> (10) - F	<i>Poa pratensis</i> (48) - G <i>Aster lateriflorus</i> (12) - C <i>Populus tremuloides</i> (11) - W <i>Asclepias syriaca</i> (10) - F <i>Aster simplex</i> (10) - C <i>Carex</i> spp. (10) - M <i>Salix</i> spp. (10) - W
S1	<i>Fissidens</i> spp. (24) - L <i>Poa pratensis</i> (21) - G <i>Phleum pratense</i> (20) - G <i>Solidago canadensis</i> (16) - F <i>Fragaria virginiana</i> (15) - F <i>Taraxacum officinale</i> (13) - C <i>Aster cordifolia</i> (12) - C	<i>Xanthoxylum americanum</i> (33) - W <i>Rhus radicans</i> (22) - W Creeping mosses (21) - L <i>Solidago canadensis</i> (19) - F <i>Acer saccharum</i> (15) - W <i>Poa pratensis</i> (10) - G
S3	<i>Solidago canadensis</i> (44) - F <i>Phleum pratense</i> (22) - G Creeping mosses (16) - L <i>Aster simplex</i> (14) - C <i>Taraxacum officinale</i> (14) - C <i>Asclepias syriaca</i> (10) - F <i>Aster cordifolia</i> (10) - C <i>Carex laxiflora</i> (10) - M <i>Fissidens</i> spp. (10) - L	<i>Poa pratensis</i> (48) - G <i>Fragaria virginiana</i> (15) - F Creeping mosses (12) - L <i>Solidago canadensis</i> (11) - F <i>Vicia angustifolia</i> (10) - F

^a plots where succession is not occurring.

^b boldface type denotes 'early' species. 'C' denotes Compositae, 'F' - forbs, 'G' - grasses, 'L' - lower plants, 'M' - other monocots, 'W' - woody species (trees and shrubs).

through succession should have different slopes and intercepts when compared with plots that are slowly proceeding through succession. t-test analysis did not yield expected results. Plots G1 and S3 (slow-succession plots) did not have significantly different slopes or intercepts when compared with plots P4, P5 and S1 (rapid-succession plots) (P values ranged from 0.43 - 1.00, slopes; 0.76-1.00, intercepts). Plot G7 was the exception having a significantly different slope when compared with plots P4, P5 and S3 (P = 0.0005, 0.003, 0.046, respectively). Plot G7 also differed significantly from all other plots with respect to intercept (P < 0.0001 for all comparisons). Given that the intercept for G7 was 0.149 when all other plots had a negative intercept, this result is not surprising. Com-

parison of both slopes and intercepts simultaneously disclosed only two significant relationships between plots proceeding rapidly or slowly through succession. Plot S1 (rapid-succession) and S3 (slow-succession) were significantly different (P = 0.03) from each other. This result is most likely anomalous as the only other significant result was for plot G7. G7 was significantly different from all other plots (P < 0.0001, all comparisons), a situation easily explained by the intercept.

The difficulty with using a measure such as λ is that while it may be useful in comparing fields across a broad geographical range and as a means to average the species retention and rate of change (Shugart and Hett 1973), on a smaller scale, when slight differences may be important,

Table 2. Regression equations, based on $\arcsin(y_t \text{ (succession ratio)}) = \beta(1/t) + \alpha + \epsilon_t$, for all 27 plots, in the long-term succession study in southeastern Ontario. Results are grouped by Field and, within Field, according to succession ratio at t_{1998} (see text for details). Time to approach asymptote within $\pm 5\%$ calculated in years.

Field	Succession Progress	Coefficients	Estimate	Standard Error	t-value	P	Time /years
Field 1	Rapid	α (Intercept)	0.007	0.00112	6.75	1×10^{-10}	51
		β (Slope)	0.0179	0.00346	5.18	5.38×10^{-7}	
	Slow	α	0.0139	0.00985	1.42	0.16	240
		β	0.1670	0.03039	5.49	5.42×10^{-7}	
Field 2	Rapid	α	0.00428	0.00058	7.38	6.6×10^{-10}	4
		β	-0.0006	0.00179	-0.34	0.735	
	Slow	α	0.0051	0.00057	9.136	1×10^{-13}	12
		β	-0.0028	0.00175	-1.59	0.115	

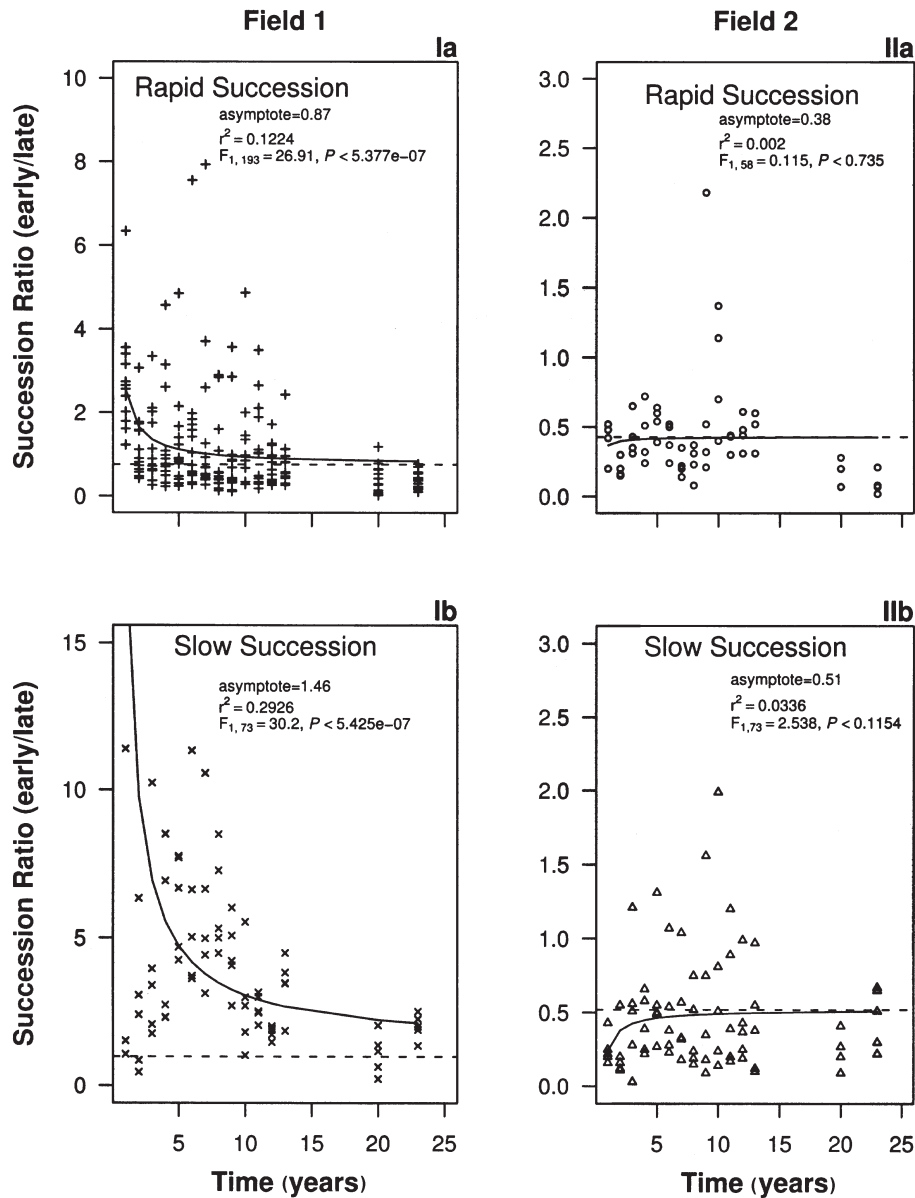


Figure 4. Regression figures showing asymptotic (dotted line) outcome of succession process for all 27 plots from the long-term succession study in southeastern Ontario. Plots were grouped as ‘Slow’ if the succession ratio at t_{1998} was greater to or equal to half the ratio at t_{1976} and ‘Fast’ if the ratio at t_{1998} was less than half the ratio at t_{1976} (see text for further details).

this measure does not appear effective. By definition, the measure cannot determine the direction of succession, and can only measure the rate of change of species, without identifying which ones are part of the change.

Examination of the regression equations for each of the plot groups discloses significant relationships (Table 2 and Fig. 4). In Field 1, for plots where succession is progressing rapidly, the intercept (asymptote) is 0.87 (the inverse of the transformation has been applied to restore original units) and significantly different from 0 ($P = 1 \times 10^{-10}$). The rate of succession is 1.03 or a change in the ratio of 1.03 per year. This rate is faster than that associated with those plots proceeding slowly through succession (rate=16.15). The intercept in this case is 1.45, indicating that the later species do not become dominant for these plots. Solving this equation indicates that the number of years required to reach this asymptote (within 5%) is approximately 240 years. Plots in Field 2 were already partway through the succession process, and consisted of more later species than early species when first observed (Table 1). As such, initial ratios were <1 for the plots. However, even though these plots were ahead of Field 1 with respect to the succession process, they did not proceed uniformly. Plots proceeding quickly through the process (rate = 0.03) approach a lower asymptote than those proceeding slowly (intercepts = 0.38 and 0.511, quickly and slowly, respectively). In the case of the slowly proceeding plots, the rate is 0.33, a 10-fold increase over those plots proceeding rapidly.

The assumption made for both the turnover rate and λ is that those species present initially following field abandonment, are the 'early' species. For fields that have been scraped bare by a glacier or burned such that the bulk of the seed bank is destroyed, this assumption is probably accurate. For most agricultural fields, undergoing secondary succession following abandonment, this is not the case. Further, not all fields are observed immediately following abandonment. Even if the field is plowed, the seed bank can be a large repository of species that are not typically associated with the early stages of succession. To illustrate the difficulty in allowing those species that are initially present to be considered the 'early' species, we have recalculated the succession ratio for the plots (Figure 5). With this figure, it is more difficult to intuitively understand what is occurring, or even what should theoretically occur. Although it is apparent that there are changes occurring, it is not clear whether grass species or woody species are dominating the community. All that can be said is that the community is less like or more like its initial community, which, in abandoned agricultural fields, could easily be a mix of typically early and typically late

species. In a typical 'pure' secondary succession you start with a community in equilibrium and disturb it, e.g., burning, slashing or a hurricane, then leave it alone to repair itself. In an abandoned hayfield, this process is not so simple. Sometime in the 19th century, the land was cleared for agriculture and secondary succession was arrested by annual mowing or plowing with seeding of a grass and legume mixture. At the time of abandonment, we expect to see: a) some remnants of the seeded species persisting well into the experimental (observational) years, and b) a guild of species (some native, some introduced, some seeded, most wild) that have formed and co-existed in an environment that included annual mowing. When the mowing stops and the field is ploughed for the last time, the hayfield community is disturbed, allowing for the introduction of new species, either from the seed bank or avian and wind dispersal. If the mowing ceases with no plowing, the conditions under which the community was able to coexist have changed, enabling new plant-plant competition and plant-insect interactions to be manifest.

The question of concern with succession is whether the plant community is changing, and how fast. Using initial species as the 'early' species will indicate whether the community is changing but it cannot readily indicate what it is changing to. The only reference point is the initial population that can vary quite drastically for each plot (see Table 1). By standardizing the species for an area as being 'early' or 'late' and calculating a ratio, it becomes more obvious that the community is changing from one set to the other, and in which direction this change is occurring. There will no doubt be instances where the initial plant community is comprised of those species typically considered 'early'. However, in abandoned agricultural fields, there is more likely to be a mix, and it becomes more difficult, when using the initial plant community only, to interpret what the community dynamics are in a succession context.

When comparing across geographical ranges, species can vary considerably. Examination of the dominant species given in Frye (1978) shows that of the 42 species listed for the New Jersey piedmont, only 6 of these same species achieve dominance in our succession study. Similarly for Monte (1973), of the 36 dominant species listed, only 3 achieve dominance in our study. Further, of those species achieving dominance in Frye's and Monte's studies, only 26 and 17 species, respectively, are common to our succession study. Both of these studies are on sandy-loam soil types (similar to that in our succession study) and located in New Jersey (40° latitude compared with our 44° latitude). Given these differences, generating a measure that is specific on a small-scale, but standardized on a

large-scale may reveal more useful patterns between sites and across geographic regions. Sub-dividing the plant species into general categories may elucidate some of the elusive unifying patterns.

Application to post-fire succession studies

Post-fire succession plots in the Rocky Mountains generated significant regressions (Table 3 and Figure 6). All intercepts for the Miller Creek and Newman Ridge regions were significantly different from 0 (P ranged from 2×10^{-16} to 0.002, 2×10^{-16} to 5.45×10^{-6} , Miller Creek

and Neman Ridge, respectively). This indicates that none of these plots will revert to the same community that was present pre-fire. For Newman Ridge, the communities, after 25 years, are still dominated by 'early' species (intercepts = 1.4 and 1.6, NR1 and NR2, respectively). This suggests that although the communities that are growing back have constituents similar to those that were present pre-fire, other constituents are now able to gain an advantage and become dominant. The rate of succession, as indicated by the slope, was significantly different from 0 for MC1, MC2 and MC4 (P ranged from 0.0003-0.006). Slopes were not significantly different from 0 for MC3,

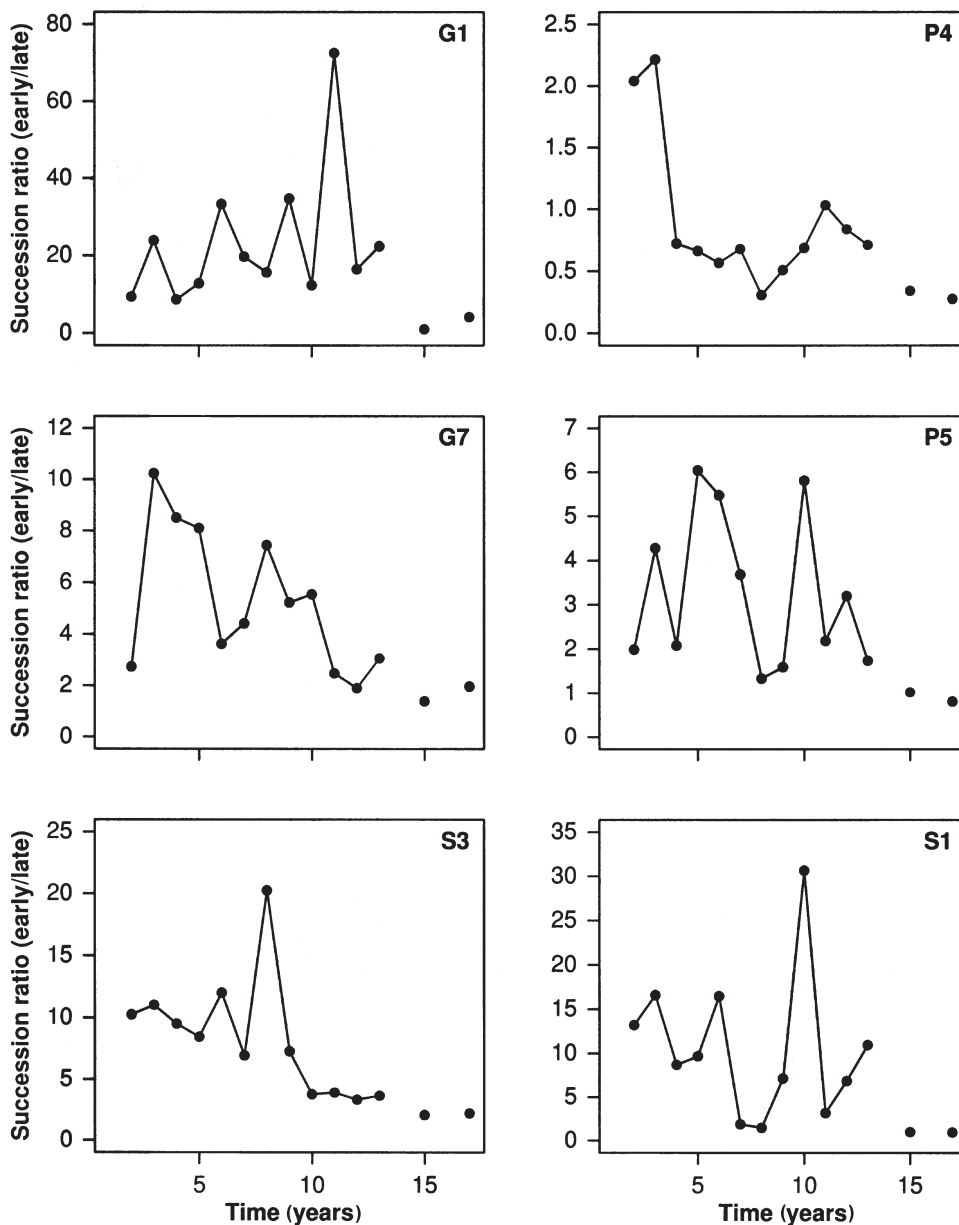


Figure 5. Succession ratio (early/late) over time for 6 plots from a long-term succession study in southeastern Ontario. To generate the ratio, plant species present in year 1 were categorized as the 'early' species, any new species present in subsequent years were categorized as 'late'.

Table 3. Regression equations, based on $\arcsin(y_t)$ (succession ratio) = $\beta(1/t) + \alpha + \varepsilon_t$, for 18 post-fire succession study sites in northern Montana, grouped by geographical proximity and ecological similarity. Four regions are located in Miller Creek (MC), 2 regions are located in Newman Ridge (NR). Each region contains 3 sites. Estimated time required to approach asymptote within $\pm 5\%$ calculated in years.

Region	Coefficients	Estimate	Standard Error	t-value	P	Time /years
MC1	α (Intercept)	0.008	0.0005	16.46	2×10^{-16}	15
	β (Slope)	-0.006	0.002	-3.35	0.002	
MC2	α	0.007	0.002	3.31	0.002	100
	β	0.035	0.009	3.84	0.0003	
MC3	α	0.007	0.0009	8.43	9.9×10^{-11}	3
	β	-0.001	0.003	-0.39	0.696	
MC4	α	0.009	0.001	6.69	7.14×10^{-9}	31
	β	0.014	0.005	2.85	0.006	
NR1	α	0.014	0.003	5.09	5.45×10^{-6}	17
	β	-0.012	0.009	-1.27	0.208	
NR2	α	0.016	0.001	15.05	2.0×10^{-16}	8
	β	-0.006	0.004	-1.58	0.118	

NR1 and NR2. It is also these regions which require the shortest time to reach their asymptote (time = 3, 17 and 8 years, MC3, NR1 and NR2, respectively). Use of the ratio in this context demonstrates both quickly and easily whether regions are reverting to their original composition or not and how quickly this is occurring.

Final remarks

The proposed succession measure captures more information than either Shugart's lambda or turnover rates, particularly by providing a direction that is absent in these other measures. However, this comes at the cost of making a potentially subjective judgment about which species are early and which are late. An alternative to our succession ratio is the use of a Markov model. Markov models have the advantage of allowing more complex processes to be captured. However, they also require potentially subjective groupings to be made, and can be more complicated to estimate and interpret than a ratio.

For the analyses reported here, percent cover by species in each group was used to determine the relative dominance of that group. Both lambda and turnover rate use number of species. We feel that percent cover is superior to species number, as it is not impossible for a large number of species to be present throughout much of the succession process for a given plot, but not achieve abundance levels adequate to influence the community. An alternative may be the number of individuals, but this will not effectively represent life form.

We do not propose the succession ratio as an alternative to Markov models, but rather as a measure that provides an easy summary of the state of a community. In this regard, it is like providing a numerical descriptor of the

seasons. If days without an overnight frost are considered summer days and days with a frost are considered winter days, then a 'seasonality' ratio for a month could be calculated as the ratio of summer days to winter days for that month. A very similar measure that is commonly used in agriculture is growing degree days, which is calculated as the total number of degrees above a specific threshold temperature over a particular period of time. This measure is used as a predictor of insect and fungal populations. We expect that the succession ratio can be used in a similar manner, not as a highly detailed measure of plant community composition, but as a simple measure that can be correlated with other observed characteristics of plant community dynamics.

Conclusion

The succession ratio has been used to develop a model of succession (Blatt et al. 2001) and is amenable to hypothesis testing. Further, the influence of herbivore dynamics, soil characteristics or rainfall patterns over time can easily be compared with our ratio to determine which variations are more or less likely to influence plant community change. Should the field contain a herbivore species with a tendency to achieve outbreak levels that specializes on early species, the plant community should respond with an increase in later species, driving the ratio downward. Conversely, a late species herbivore will reverse the progression (McBrien et al. 1983) causing an increase in the succession ratio. With respect to rainfall or soil characteristics (see Blatt et al., in press), our measure can easily show whether a community will change, how quickly and toward which state.

It can be argued that if the community is farther along in its succession pathway and the 'early' species are fairly

rare, utilizing an early to late ratio will not yield effective results, or disclose useful patterns. If the latter stages of succession are of interest, the ratio can be adjusted to highlight the change from ‘late’ species to ‘woody’ species. Again, if succession is proceeding in a species-replacement linear manner, then the ratio would theoretically decline. It is also useful to utilize the succession ratio

to highlight the progression to the next equilibrium community by listing those species associated with that community (e.g., woody species) as the ‘late’ species and all those present prior to that state as ‘early’. This approach was taken on post-fire succession plots in the Rocky Mountains with favorable results. We showed that plots from the Rocky Mountains, where pre-fire plant species

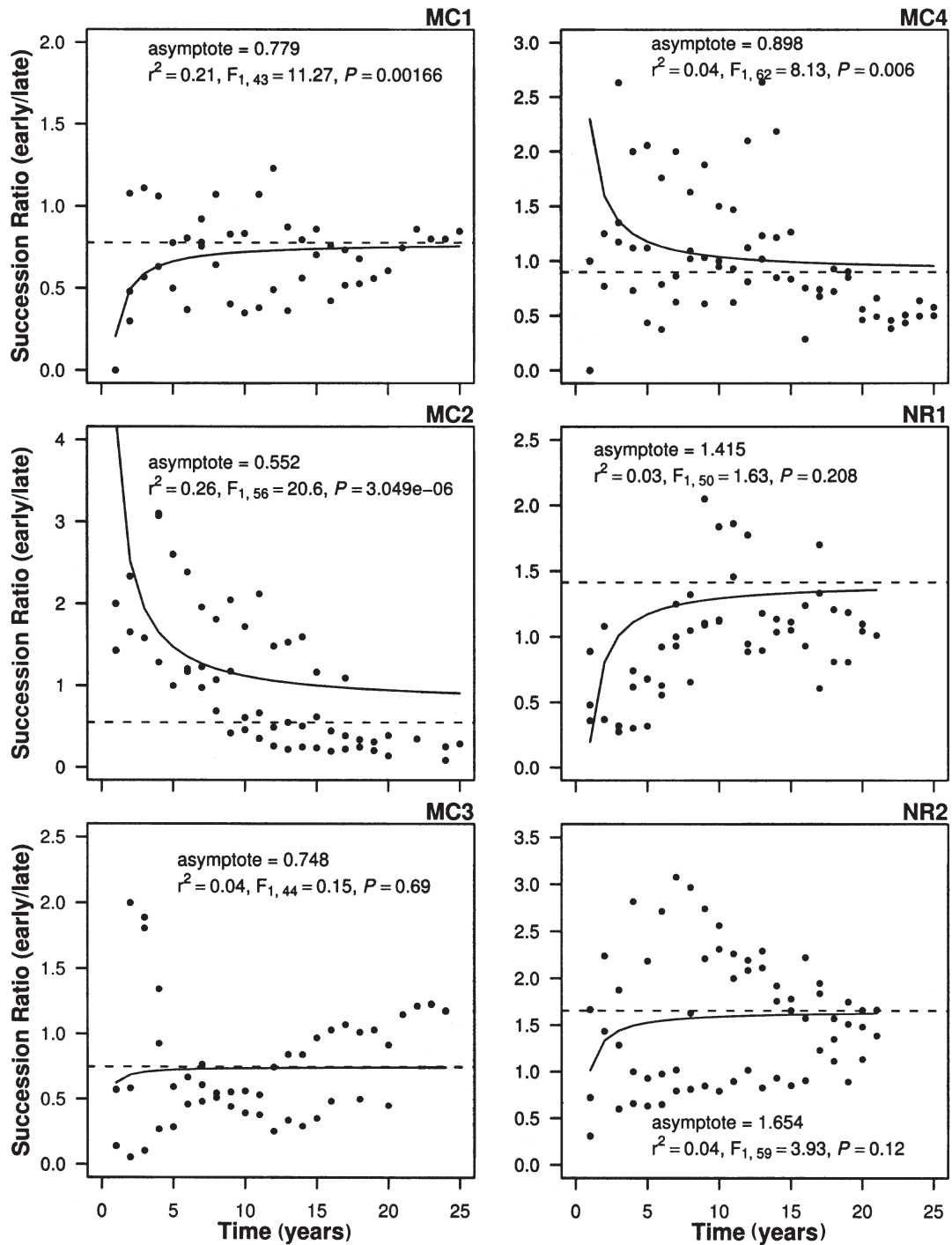


Figure 6. Regression equations for post-fire succession plots located at Miller Creek (MC1-MC4) and Newman Ridge (NR1 and NR2) in Montana showing asymptotes (dotted line) for succession ratio. Pre-fire composition was used for ‘late’.

were categorized as 'late' and all others 'early', will approach their pre-fire composition in 3-100 years (Blatt et al., in press, Anand and Orlóci 1997). In some cases, the plots immediately returned to their pre-fire species mix while others deviated widely from the pre-fire composition. The next step for these data would be to obtain soil, rainfall and seed-bank data in an attempt to determine the underlying mechanism for the observed deviation. Further uses of our measure could apply to comparing N-fixing and non-N-fixing to examine the relationship between these two groups across a range of soil characteristics, particularly those low in N. Regardless of how it is determined, the use of a ratio allows patterns of succession to be more readily observed, while providing a quantifiable measure for the correlation of influencing factors.

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References

- Anand, M. 2000. The fundamentals of vegetation change: complexity rules. *Acta Biotheoretica* 48: 1-14.
- Anand, M. and G.W. Heil. 2000. Analysis of a recovery process: Dwingelose Heide revisited. *Community Ecology* 1: 65-72.
- Anand, M. and L. Orlóci. 1997. Chaotic dynamics in a multispecies community. *Ecological and Environmental Statistics* 4: 337-344.
- Armstrong, H. and D. Bullock. 2003. Stock grazing in woodland - Part 1. *Biotype* 24 (April): 2-5.
- Bach, C.E. 1994. Effects of a specialist herbivore (*Altica subplicata*) on *Salix cordata* and sand dune succession. *Ecological Monographs* 64: 423-445.
- Blatt, S.E., A.A. Crowder and R. Harmsen. (in press) Patterns of secondary succession in old-field communities in southeastern Ontario. *Plant Ecology*.
- Blatt, S.E., J.A. Janmaat and R. Harmsen. 2001. Modelling succession to include an herbivore effect. *Ecological Modelling* 139:123-136.
- Brown, V.K., M. Jepsen, M. and C.W.D. Gibson. 1988. Insect herbivory: effects on early old-field succession demonstrated by chemical exclusion methods. *Oikos* 52:293-302.
- Clements, F. E. 1916. Plant succession: an analysis of the development of vegetation. Technical Report Publication 242, Carnegie Institute of Washington.
- Connell, J. R. and R.O. Slatyer. 1977. Mechanisms of succession in natural communities and their role in community stability and organization. *American Naturalist* 111:1119-1144.
- Crowder, A.A. 1986. The vegetation of the Kingston region. *Bluebill* 33: 37-40, 45.
- Crowder, A. and R. Harmsen. 1998. Notes on forest succession in old fields in Southeastern Ontario: the woody species. *Canadian Field Naturalist* 112: 410-418.
- Diamond, J.M. 1969. Avifaunal equilibria and species turnover rates on the Channel Islands of California. *Proceedings of the National Academy of Science* 64: 57-63.
- Fink, A., J. Kosecoff, M. Chassin and R. H. Brook. 1984. Consensus methods: characteristics and guidelines for use. *Amer. J. Public Health* 74: 979-983.
- Frye, R.J. 1978. Structural dynamics of early old-field succession on the New Jersey Piedmont: a comparative approach. Ph.D. Thesis, Rutgers University.
- Geomatics-International. 1995. Management option for old-field sites in southern Ontario. Guidelines and literature review. Technical Report TR-009, Southern Region Science and Technology Transfer Unit.
- Głowacinski, Z. and O. Järvinen. 1975. Rate of secondary succession in forest bird communities. *Ornis Scandinavica* 6: 33-40.
- Grosshans, R.E. and N.C. Kenkel. 1997. Dynamics of emergent vegetation along natural gradients of water depth and salinity in a prairie marsh: delayed influences of competition. UFS (Delta Marsh) Annual Report 32: 83-93.
- Ihaka, R. and R. Gentleman. 1996. R - A language for data analysis and graphics. *Journal of Computational and Graphical Statistics* 5: 299-314.
- Jassby, A. D. and C. R. Goldman. 1974. A quantitative measure of succession rate and its application to the phytoplankton of lakes. *American Naturalist* 108: 688-693.
- Leps, J. 1987. Vegetation dynamics in early old field succession: a quantitative approach. *Vegetatio* 72:95-102.
- Margalef, R. 1968. *Perspectives in Ecological Theory*. University of Chicago Press, Illinois, USA.
- McBrien, H., R. Harmsen and A. Crowder. 1983. A case of insect grazing affecting plant succession. *Ecology* 65:1035-1039.
- Monte, J.A. 1973. The successional convergence of vegetation from grassland and bare soil on the Piedmont of New Jersey. *William L. Hutcheson Memorial Forest Bulletin* 3: 3-13.
- Morton, J.K. and J. M. Venn. 1990. A checklist of the flora of Ontario: Vascular plants. University of Waterloo, Waterloo, Ontario.
- Myster, R.W. and S. T. A. Pickett. 1994. A comparison of rate of succession over 18 years in 10 contrasting old fields. *Ecology* 75: 387-392.
- Odum, E. 1969. The strategy of ecosystem development. *Science* 164: 262-270.
- Phillips, E.A. 1959. *Methods of Vegetation Study*. Holt, Rinehart and Winston, New York, New York.
- Pickett, S.T.A. 1982. Population patterns through twenty years of old-field succession. *Vegetatio* 49:45-59.
- Pickett, S.T.A. 1989. Space-for-time substitution as an alternative to long-term studies. In: E. Likens (ed.), *Long-term Studies in Ecology: Approaches and Alternatives*. Springer, New York, pp. 110-135.
- Scott, D., J.S. Robertson and W.J. Archie. 1990. Plant dynamics of New Zealand tussock grassland infested with *Hieracium pilosella* II. Transition matrices of vegetation changes. *Journal of Applied Ecology* 27: 235-241.
- Shugart, H.H. and J.M. Hett. 1973. Succession: similarities of species turnover rates. *Science* 180: 1379-1380.
- Smartt, P.F.M., S.E. Meacock and J.M. Lambert. 1974. Investigations into the properties of quantitative vegetational data: I. Pilot study. *Journal of Ecology* 62: 735-759.

- Stickney, P.F. and R.B. Campbell, Jr. 2000. Data Base for Early Post-fire Succession in Northern Rocky Mountain Forests. General Technical Report RMRS-GTR-61-CD. United States Department of Agriculture - Forest Service - Rocky Mountain Research Station.
- Tansley, A.G. 1935. The use and abuse of vegetational concepts and terms. *Ecology* 16: 284-307.
- Thorhallsdottir, T.E. 1990. The dynamics of a grassland community: A simultaneous investigation of spatial and temporal heterogeneity at various scales. *Journal of Ecology* 78: 884-908.
- Watkins, A.J. and J.B. Wilson. 1994. Plant community structure, and its relation to the vertical complexity of communities: dominance/diversity and spatial rank consistency. *Oikos* 70: 91-98.
- Wildi, O. and M. Schütz. 2000. Reconstruction of a long-term recovery process from pasture to forest. *Community Ecology* 1: 25-32.
- Zar, J.H. 1984. *Biostatistical Analysis*. (2nd edition.) Prentice-Hall, Inc., Englewood Cliffs, New Jersey.