

A critique on overstory/understory comparisons based on transition probability analysis of an old growth spruce-fir stand in the Appalachians

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Abstract

Compositional stability in forests has traditionally been evaluated by comparing understory with overstory composition. Such comparisons have generally been qualitative. Transition probability analysis has recently allowed quantitative prediction of future community states. We used transition probability analysis of an undisturbed spruce-fir forest to evaluate the sensitivity of the overstory/understory comparison to underlying assumptions. The predictions of future composition differed widely depending on understory size class used, ecological situation (gap versus forest plots), and stand descriptor (density versus frequency). Species longevities and interactions between understory and overstory species also affected the predictions. Understory data generally led to a predicted increase in importance for the most tolerant species (*Abies fraseri*) and the conclusion that a previous disturbance allowed the least tolerant species (*Betula lutea*) to become established. Inventory of stems in gaps led to a predicted increase in importance for the least tolerant species (*Betula*) and the conclusion that disturbance frequency was increasing in the stand. Data incorporating more detailed observations of the gap capture process led to the inference that this old growth stand was in compositional equilibrium. In this community, the species that was densest in the understory species (*Abies*) had the shortest lifespan and thus, the fastest canopy turnover rate. This led to counter-intuitive behavior in the models; in some cases *Abies* had a 40% higher relative density in the understory than in the overstory at equilibrium.

Introduction

A common technique in the evaluation of forest stability is the comparison of overstory with understory composition (see, for example, Langford & Buell's (1969) development of the climax concept). The frequent use of the overstory/understory comparison in forest vegetation (it has less frequently been used in analyses of grasslands, shrublands, and other vegetation) is due to several spatial and temporal attributes of forests: dominant individuals are long-lived, forests have a layered structure, and understory individuals (comprising the 'advanced regeneration' of American forestry literature and including the 'seedling bank' of Grime (1979)) are usually younger than overstory in-

dividuals. Historically most projections based on overstory/understory differences have been qualitative (e.g. Daubenmire, 1936; Dix, 1957; Buell *et al.*, 1966); more recently, transition probability analysis (Horn, 1975; Usher, 1979a, 1979b, van Hulst, 1980) has provided a means of quantitative prediction.

Transition probability analysis is the philosophical descendant of the overstory/understory comparison, but is more powerful because predictions are explicit and precise (their accuracy is, of course, a separate question – Usher 1979b, van Hulst 1980). Transition probability analyses are mixed-aged, mixed-species, non-spatial models as defined by Shugart (1984). In this paper we used both tree-based (i.e., using data collected beneath canopy individuals; cf. Horn, 1975) and gap-based formula-

tions (i.e., using data collected in forest gaps; cf. Barden, 1981). In these models, a population parameter (most often fractional relative density) is used as the probability that a given understory species will replace a given overstory species (Horn, 1975).

We collected traditional size class data in an old growth, undisturbed forest and predicted equilibrium composition based on various permutations in the data set. These predictions were compared to each other and to present stand composition to address the following questions:

- 1) How do predictions based on different size classes of reproduction differ from one another?
- 2) How do predictions based on forest shade plots differ from those based on gap plots?
- 3) How do predictions based on knowledge of the identity of canopy species differ from those based on average, stand-wide, composition?
- 4) How do predictions based on realistic lifespans differ from those based on equal lifespans?
- 5) How do predictions based on density and frequency differ?
- 6) How do predictions based on observed gap captures differ from those based on understory composition and from those based on inventory of gap stems?
- 7) Do the different predictions lead to different interpretations of stand history or stability?

In the strictest sense, the overstory/understory comparison assumes a narrow set of conditions with regard to these questions. It assumes that relative understory density is sufficient to predict future canopy composition, that positive or negative canopy/understory interactions are absent, and that differences in longevity among species are not important to prediction. We discussed the general validity of the overstory/understory comparison by examining these assumptions in the context of 14 predictions of compositional equilibrium based on various kinds of data collected from a single stand. Our null hypothesis was that the predictions would lead to similar conclusions concerning the stability and past history of the stand; our alternative hypothesis was that predictions would lead to different interpretations of stand stability and past history.

Our purpose was thus to contrast various predictions of stand composition as a way of examining the assumptions of the overstory/understory com-

parison. This comparative use of transition probability analysis is similar to that recently used in analyses of successional mechanisms in heathland (Hobbs, 1983; Hobbs & Legg, 1983) and grassland (Usher 1979b). Although we will make inferences about realism, our primary purpose was not to prove which of the predictions was most realistic for the vegetation we studied (in any case, the question of realism in our predictions has become a moot point because of a recent invasion by an exotic insect pest see below). It is difficult to establish the realism of stand predictions in forest communities because generation times are long and are similar in temporal scale to environmental change. Even if we could observe multiple generations of trees on one site, natural disturbances and climatic change can potentially deflect stand trajectories from those predicted (White, 1979; Pickett, 1980). Objections to the use of the overstory/understory comparisons that are based on environmental instability are valid, but less critical than the one we examined here. The overstory/understory comparison has always been based (implicitly or explicitly) on the assumption of an invariant environmental context, i.e., that outside factors would not deflect the stand from some otherwise inevitable path. Therefore, we chose to examine the overstory/understory comparison with the assumption (however, unrealistic) of an invariant environmental context. We carried out this analysis in an old growth, low diversity forest lacking spatially large natural disturbances.

Methods

The study site was a 7 ha old growth spruce-fir stand at 1800 m on the north slope of Mt. Collins, Great Smoky Mountains National Park, Tennessee, USA (35°36'N). We studied a gentle (0-10°) upper slope dominated by *Picea rubens* Sarg., *Abies fraseri* (Pursh) Poir, and *Betula lutea* Michaux f. (Oosting & Billings, 1951). The stand had no history of logging, fire, or other human disturbance; however, an exotic insect, *Adelges piceae*, invaded several years before our analysis was carried out. We distinguished and avoided the standing dead *Abies* canopy trees killed by this pest in our sample because the invasion of this insect represents a shift to larger scale disturbance and we sought to examine the overstory/understory comparison in the

context of spatially small processes. Since *Adelges* did not infest the younger stems on which this analysis was based, and because increased mortality of mature *Abies* began only the year before sampling, this insect outbreak had minimal influence on the data we collected.

The field sampling had three objectives: 1) to characterize the overstory composition; 2) to characterize the distribution of tree regeneration; and 3) to characterize gap capture events using the methods of Barden (1981). Canopy composition was sampled with ten random Bitterlich prism tallies using a 5-factor metric prism. Diameter of tallied trees was recorded and used to derive overstory density. In the regeneration plots, individuals were sampled in four height classes, using a nested series of quadrats: 1) less than 25 cm tall (using a 1 by 1 m quadrat), 2) 26 cm to 1 m tall (using a 2 by 2 m quadrat), 3) 1-2 m tall (using a 4 by 4 m quadrat), and 4) 2-4 m tall (using a 4 by 4 m quadrat). Sampling for regeneration density was carried out in five ecological situations: 1) 5-10 yr gaps ($n=25$), 2) random forest shade plots ($n=100$), and plots positioned under individual trees of the three canopy dominants, 3) *Abies fraseri* ($n=25$), 4) *Picea rubens* ($n=25$), and 5) *Betula lutea* ($n=25$). The 4 by 4 m quadrats were randomly positioned, with the smaller quadrats nested within. Absolute and relative frequency and density were computed from these data.

The third part of the study consisted of an analysis of 60 forest gaps created by the death of 1 to 3 canopy trees (gapmakers) (Barden, 1981). The species, size, and age of the gapmaker trees was recorded. Mean lifespan was computed as the average age at death. The dominant subcanopy individuals in the gaps were designated as successor trees. If no single tree in the understory had achieved gap dominance then codominant trees were designated.

Transition probability tables were constructed from the field data. These tables consisted of the probabilities that a given understory species would replace a given overstory species. The tables thus consisted of nine elements in our three species system (3 overstory species \times 3 possible successor trees). We constructed probability tables for each of the four size classes of regeneration, using relative density (four probability tables) and relative frequency (four probability tables). Probability tables based on relative density and frequency in the 2-4 m height class were also constructed from the

random understory plots (two probability tables) and from the gap plots (two probability tables). In these tables, identity of the overstory or gapmaker species was ignored (i.e., the traditional approach in overstory/understory comparisons) and each understory species thus had a constant probability of replacing each canopy species. By contrast, the identity of the overstory species was explicitly used in the tables based on the plots positioned below individual overstory trees.

The observed gap capture rates were also used to construct a probability table. Because the identity of the gapmaker was known, these tables included nine unique probabilities. In order to test the sensitivity of these predictions to differences in species longevity, the models were run twice, once for the observed mean lifespans, and once assuming all species had the same lifespan.

We contrasted relative density and relative frequency in these predictions because of the following argument. Below any canopy tree in our stand, there were about 65 understory stems <4 m tall (see Results). On average, only one of these understory stems will survive to replace an overstory tree. Hence, if survivorship is high, presence of a single individual in the quadrats is potentially as important as total density. Survivorship may also differ among species such that total understory density at a single point in time is not a reliable index of potential survivorship.

Relative frequency was derived in the following manner. The absolute frequency of each species in each quadrat was 0 (absent) or 1 (present); this number was divided by the sum of the absolute frequencies for the quadrat to produce relative frequency (for example, if all three species were present, irrespective of their relative density, each species had an equal probability of succeeding to the canopy - 0.33 in this case). The underlying assumption of this method is that only one understory stem will replace a given canopy individual; a frequency tally (0 or 1) was thus used as an index of potential canopy density in the place of absolute density (which can vary from 0 to about 50 in canopy quadrats).

We then solved each of the 14 probability tables for equilibrium stand composition, using differential equations (Appendix I). This method meets the same set of ecological assumptions and produces similar results to Markov chains used by Horn (1975).

Results

Field data

The canopy was dominated by *Abies fraseri* (320 stems/ha, 55.9% of total canopy density), *Picea rubens* (170 stems/ha, 30.1%), and *Betula lutea* (80 stems/ha, 14.0%). Absolute density of understory stems in random forest shade plots was 32000 stems/ha in size class 1 (stems less than 25 cm tall), 3 000 stems/ha in size class 2 (26 cm to 1 m tall), 840 stems in size class 3 (1 to 2 m tall), and 1 180 stems/ha in size class 4 (2 to 4 m tall). The total for all understory stems, 37020 stems/ha, was 65 times total overstory density.

Abies fraseri dominated the reproduction in the shade, with 72% of all understory stems (Table 1). *Betula lutea* was relatively scarce in the understory (2% of all stems), but even this species had higher absolute understory density (740 stems/ha) than total overstory density for all species (570 stems/ha). First year *Betula* seedlings (sampled in size class 1) were especially dense under *Betula* trees (Table 1, column 9). The understory density of *Picea* was intermediate to that of *Abies* and *Betula* (Table 1).

Distribution of understory stems varied with identity of the canopy species (Table 1). *Abies* reached its highest values below *Picea* (80 to 90% of all understory stems in the three largest size

classes). Except for size class 1, *Picea* reached its highest relative density below *Abies* (23–40% of all understory stems). *Betula* was unimportant under any of the three canopy species, except for size class 1 under *Betula* trees.

Density of understory stems was higher in the 5–10 yr gaps than in the shade. The ratios of gap to shade densities increased from smaller to larger size classes. This ratio was 1.1 in size class 1, 1.4 in size class 2, 1.5 in size class 3, and 2.3 in size class 4. Much of this difference was due to the higher density of *Betula* in gaps compared to shade plots: in the 2–4 m height class, this species was 10 times denser in gaps than in shade. The relative density of *Betula* was 20 times higher in gaps, compared to forest plots (Table 1, last two columns). *Abies* and *Picea* also were denser in gaps than in shade, but the difference was less marked than for *Betula*. In the 2–4 m height class *Abies* was 1.7 times denser and *Picea* was 2.5 times denser in gap compared with shade quadrats. Thus, the absolute density of the two conifers was higher in gaps than in shade plots, but their relative density was lower.

Abies also possessed higher relative frequencies than the other two species, but the relative strength of this dominance was generally lower than for relative density (Table 1). Hence, the difference between *Abies* and *Picea* was less extreme for frequency than for density. Relative frequency of *Betula* was 4 times higher in gaps compared to forest

Table 1. Relative density and frequency of the three dominants in four understory size classes and in shade and gap plots.

Canopy tree:	Relative density and frequency by size class below three dominants												Relative density and frequency in size class 4	
	<i>Abies fraseri</i>				<i>Picea rubens</i>				<i>Betula lutea</i>				Shade	Gaps
Size class: n =	1 25	2 25	3 25	4 25	1 25	2 25	3 25	4 25	1 25	2 25	3 25	4 25	100	25
<i>Abies fraseri</i>														
Relative density	0.58	0.60	0.68	0.77	0.46	0.84	0.80	0.90	0.50	1.0	0.87	0.86	0.72	0.44
Relative frequency	0.61	0.56	0.63	0.70	0.52	0.57	0.68	0.63	0.57	1.0	0.63	0.62	0.54	0.37
<i>Picea rubens</i>														
Relative density	0.38	0.40	0.28	0.23	0.46	0.16	0.18	0.08	0.25	0	0.07	0.11	0.26	0.17
Relative frequency	0.35	0.44	0.32	0.30	0.35	0.43	0.23	0.30	0.29	0	0.31	0.36	0.39	0.33
<i>Betula lutea</i>														
Relative density	0.04	0	0.04	0	0.08	0	0.02	0.02	0.25	0	0.06	0.03	0.02	0.39
Relative frequency	0.04	0	0.05	0	0.13	0	0.09	0.07	0.14	0	0.06	0.02	0.07	0.30
Total absolute density (stems/0.01 ha)	250	25	60	8	500	38	8	14	100	11	6	10	12	27

quadrats and relative frequency of *Abies* and *Picea* was lower.

Abies had the highest gap capture values under all three species of canopy trees. *Abies* captured 80% of all *Picea* gaps, 62% of all *Betula* gaps, and 56% of all *Abies* gaps (Table 2). The peak importance of *Picea* was in *Betula* gaps (38%, but the sample size is low for these gaps - Table 2). *Betula* had its peak importance in *Picea* gaps (25% of gap captures).

Picea reached larger sizes and ages than *Abies*. Of the two, only *Picea* exceeded 50 cm d.b.h. (diameter breast height), at which size it had a density of 90 stems/ha. Mean age at death for the three species was *Abies*, 137 yr (SD=24.1); *Picea*, 225 yr (SD=69.8); and *Betula*, 154 yr (SD=21.1). Maximum ages in the study area are 160 yr for *Abies* and 350 yr for *Picea* (Oosting & Billings, 1951).

Transition probability analysis

For illustration, only the transition probability table for the gap capture observations is shown (Table 2). The data used in the other twelve probability ta-

Table 2. The transition probability table based on observed gap captures in gaps created by the fall of 1 to 3 trees.

Gap successor	Gap maker		
	<i>Ab fr</i> <i>n</i> = 28	<i>Pi ru</i> 28	<i>Be lu</i> 4
<i>Abies fraseri</i>	0.56	0.80	0.62*
<i>Picea rubens</i>	0.18	0.07	0.38*
<i>Betula lutea</i>	0.25	0.13	0

* These figures are not multiples of 0.25 because codominant trees were recognized.

bles are contained in Table 1. The 14 predictions of equilibrium composition (recall that the probabilities of Table 2 were used in two tests) are presented in Tables 3 to 5.

When relative density below the three dominants was used in the analysis, predictions varied with size class of reproduction. The prediction based on the smallest size class was that *Picea* would dominate the stand (52% of canopy stems versus 42% for *Abies*), despite the fact that *Abies* had a higher relative density in this size class than *Picea*. This surprising result derived from the differences in lifespans between the two species. Because it lived only about half as long as *Picea* (Table 4), *Abies* created a greater number of gaps, than would be expected from its canopy density at any one point in time.

Using data from the three largest size classes, *Abies* dominance was predicted, with the concentration of dominance in *Abies* increasing from size class 2 (51% of canopy density) to size class 4 (70%). This corresponded to an increasing concentration of understory dominance in *Abies* from size class 2 to size class 4 (Table 1). When the random understory data were used (constant probabilities that a given understory species would replace the three canopy species), *Abies* dominance was also predicted (Table 3).

Data from gap plots predicted shared dominance by *Abies* and *Betula* (both with 38%), with *Picea* third in importance (26%). Data from the gap capture data, however, predicted a composition very close to that of the present stand: *Abies*, 54%; *Picea*, 28%; and *Betula*, 18%. This result was counter-intuitive in that *Abies* captured 56-80% of gaps (depending on the identity of the gapmaker species). Again, the effect of *Abies*'s relatively

Table 3. The effect of reproductive size class and situation (gap vs. shade) on transition analysis predictions using relative density.

Species	Equilibrium composition based on:							
	Rel. density in four classes below canopy trees				Rel. density in random plots		Obs. Gap Capture	Obs. Canopy Density
	<25 cm	26 cm - 1 m	1 - 2 m	2 - 4 m	Shade 2 - 4 m	Gap 2 - 4 m		
<i>Abies fraseri</i>	42	51	62	70	61	38	54	56
<i>Picea rubens</i>	52	49	35	29	37	24	28	30
<i>Betula lutea</i>	6	0	3	1	2	38	18	14

Table 4. The effect of lifespan on transition analysis predictions of equilibrium, using the data for observed gap captures.

Species	Constant lifespan	Obs. mean lifespan	Obs. mean lifespan (yr)
<i>Abies fraseri</i>	62	54	137
<i>Picea rubens</i>	20	28	225
<i>Betula lutea</i>	18	18	155

short lifespan was seen: *Abies* captured a majority of gaps but it also created the largest share of gaps.

The differences between the predictions based on gap inventories and gap capture observations suggested that the dynamics of the stand are not a direct function of gap stem densities. Predictions based on advanced regeneration, as described above, also differed from the gap capture observation predictions, suggesting that capture of gaps is not a simple function of advanced regeneration density or frequency.

The gap capture probability table was used to test the effect of lifespans on the predictions (Table 4). Using constant lifespans resulted in higher *Abies* importance and lower *Picea* importance, but *Betula* importance was not greatly affected.

Predictions based on relative frequency gave lower values for *Abies* than did the other predictions, but the predictions based on the two largest size classes still showed *Abies* dominating the stand (Table 5). *Picea* was predicted to dominate using data from the two smallest size classes, and for both shade and gap plot data. Predictions of *Picea* and *Betula* were always higher when frequency was used than when density was used (Table 5 compared with Table 3).

In summary, predictions of future *Abies* canopy density ranged from 29–70% (compared to a cur-

rent relative canopy density of 56%), predictions of *Picea* canopy density ranged from 24–56% (compared to a current relative density of 30%), and predictions of *Betula* canopy density ranged from 0–38% (compared to a current relative density of 14%). Only the predictions based on the observed gap captures (which incorporated knowledge of the overstory or gapmaker species) and realistic lifespans were similar to current stand composition (Table 3). When data on species lifespans were ignored, the predicted importance of the longest-lived species (*Picea*) declined compared to predictions based on realistic lifespan data. When data from gaps were ignored, the predicted importance of the least shade tolerant species (*Betula*) declined compared to predictions based on gap data. Frequency data resulted in higher predictions for *Picea* since that species occurs at lower relative densities, but has similar relative frequencies, when compared to *Abies*.

From these predictions we derived the following insights into species behavior. *Picea*'s low gap capture rate was compensated by a long canopy residence time. *Abies* had high relative understory density but had the shortest lifespan, thereby creating a disproportionate share of the gaps as a function of its canopy density. Because of this, some predictions showed that *Abies* maintained higher relative densities in the understory than in the overstory at equilibrium. *Betula* was predicted to be persisting in the stand only when gap information was used and was the best of the three species in exploiting the gap event (i.e., it had a higher ratio of gap to shade density than the other two species and was a codominant of gap density). Performance of *Abies* and *Picea* in the models was a reflection, to one degree or another, of advanced regeneration – and

Table 5. The effect of reproductive size class and situation (gap vs. shade) on transition analysis predictions based on relative frequency.

Species	Equilibrium composition based on:					
	Rel. frequency in four size classes below canopy trees				Rel. frequency in random plots	
	<25 cm	26 cm – 1 m	1 – 2 m	2 – 4 m	Shade 2 – 4 m	Gap 2 – 4 m
<i>Abies fraseri</i>	46	44	54	56	42	29
<i>Picea rubens</i>	47	56	41	42	52	44
<i>Betula lutea</i>	7	0	5	2	6	27

hence of the period of 10s to 100s of years between gap events. For *Betula* this long period between gaps was not necessarily a good index of its future stand importance and one must turn to an analysis of the gap process to understand its role.

Discussion

In the introduction we posed seven questions concerning the overstory/understory comparison. The first six of these dealt with the effect of various permutations in the data set on prediction. We have shown above that the six kinds of permutations in the data set resulted in quantitatively different predictions. We turn now to the seventh question: how do these different predictions effect interpretations of vegetation stability and stand history?

If traditional ideas had been applied to these data, the following conclusions would have been reached. *Abies* accounted for 72% of all understory stems, while *Betula* accounted for only 2%. Since *Abies* accounted for 55% of overstory density and *Betula* 14%, we would have concluded that *Abies* was increasing and *Betula* decreasing in stand importance. *Picea* was also overrepresented in the canopy and would have been predicted to be declining in importance. One might even have conjectured that a previously undetected natural disturbance, such as a large windthrow, allowed *Betula* to become established. However, no such disturbance need be postulated to explain current composition. Current composition can be accounted for by observations of gap capture in relatively small gaps. The more detailed the information on the gap capture process (e.g., when probabilities were based on identity of the overstory species, realistic longevities, and sampling of gap events), the more congruent the predictions were with current stand composition. However, predictions based on gap densities (versus those based on gap captures) were equally divergent from current stand composition – they suggested that *Betula* would increase in the stand (from 14–38%) and that *Abies* would decrease (from 55–38%). Based on gap density, one would have concluded that there was an increasing disturbance frequency in the stand – the opposite conclusion from that based on understory relative densities. Thus, an uncritical analysis of sapling density in gaps would also lead to potential erroneous interpretations.

Although current canopy composition was virtually identical to that published thirty years earlier by Oosting & Billings (1951) for the same stand and the stand has no history of human disturbance, we do not contend that our stand is necessarily in compositional equilibrium. Indeed, such an equilibrium would be difficult to establish, and has become a historical question in any case due to the recent invasion by the exotic insect *Adelges picea*. However, the results we obtained are important in a critique of the overstory/understory comparison, whether or not one of our 14 predictions is more accurate than the others, because these predictions diverged in ways that showed the sensitivity of the approach to differences in the kinds of assumptions and data that are used.

The basic assumption of the overstory/understory comparison is that the understory of a forest stand is alone sufficient for prediction of future overstory composition. This assumption is equivalent to the assumption that species survivorship is reflected in understory density. This assumption implies further that: 1) density measured at one time reflects survivorship (however, note that no one size class has been universally used for the density measurement), 2) species do not differ in the characteristic shape of their survivorship curves, and 3) understory processes that take place between gap events can be extrapolated to predict overstory composition (i.e., that shade processes integrate all relevant interactions needed for prediction). Since the overstory/understory comparison usually does not include information on either species longevity or overstory/understory interactions, there are two further assumptions to add to the list above: 4) longevity (or canopy residence time) is unimportant and 5) there are no significant pairwise interactions (positive or negative) between the overstory and understory stems related to the specific identity of the stems in question.

There is a growing literature that supports the importance of gap events in the composition of old growth forests (Runkle, 1985). This literature has shown that gap size influences subsequent composition: shade tolerant species are dependent for release on small gaps, while shade intolerant species are dependent on larger gaps (Runkle, 1984). Barden (1981) showed that mature intolerant trees tended to have larger crown sizes, thus promoting larger gaps after treefall. Runkle (1984)

showed changes with time since gap creation: as gaps became older, the importance of shade tolerant (slow growing) saplings increased. However, gaps also tended to enlarge as additional treefall occurred on gap edges, thus promoting shade intolerant species. Both Runkle (1981, 1984) and Barden (1980, 1981) supported the interpretation reached here, that canopy composition is a probabilistic outcome of competition between advanced regeneration and gap exploiting species. Accurate prediction of future composition depends on analysis of the canopy turnover process. Such process oriented research has also shown that there is some tendency for negative and positive associations between species in the canopy and understory (Fox, 1977; Runkle, 1981; Woods, 1984; Woods & Whittaker, 1981). Our analysis thus supports the view that an understanding of succession must emerge from research on population processes (Peet & Christensen, 1980).

In short, the overstory/understory comparison has usually lacked detail on the processes of canopy turnover. Since the gap event occurs in a single year and gap closure occurs within several decades, it may seem at first reasonable to extrapolate from the phase of understory establishment. Temperate trees may live 100-250 years or more, and the period of shade establishment thus lasts an order of magnitude longer than the gap opening phase.

Predictions based on the overstory/understory comparison were sensitive to the validity of the inherent assumptions. We did not measure actual survivorship, but we can state that the gap event had a large effect on stand composition (out of proportion to its brief occurrence in stand history). Further, species longevity played a critical role and interaction between species was important. Beyond these direct observations, we also suspect that species do differ in the shape of their survivorship curves in our stand and that static density profiles do not reflect actual survivorship (survivorship varies between gap and shade situations). Since there was an exponential increase in stem density from larger to smaller size classes, and since even the most intolerant species in our data set was present in greater density in the understory than total overstory density, relative density itself is not directly coupled to long term survivorship. The data on sapling density in gaps also supported the general conclusion that probability of survivorship

cannot be directly deduced from relative density. Given these observations, it is understandable that transition probability analysis led to the following counter-intuitive prediction for *Abies*: that species was predicted to be declining in importance in some models in which it dominated the understory size classes at equilibrium.

Conclusions

Traditional methods relying solely on relative understory density for prediction of future forest composition result in divergent predictions depending on the kind of data and assumptions that are used. Predictions vary with size class and stand descriptors (density, frequency) used. The traditional methods do not account for canopy/understory interactions, differential survivorship among species, longevity of canopy species, and the influence of the gap event. Predictions based on understory density are substantially different from those based on information about the process of gap capture. However, predictions based on relative density in gaps are not necessarily more realistic than predictions based on forest shade density. In our case, only when predictions were based on observation of the identities of gapmakers and successor trees did they resemble current composition of an old growth spruce-fir. Canopy residence time played a critical role: the shorter-lived species in our data set had higher understory density than the other two species, but created a disproportionate share of the gaps. For species such as this, relative understory density may exceed relative canopy density at equilibrium and may not lead to increased canopy importance. In our data set, this was the case even when relative understory density exceeded relative overstory density by 40% or more. The failure of understory density to adequately predict the importance of species which exploit gaps is a less surprising, but an equally important problem when applying the overstory/understory comparison. Forest dynamics can only be understood with a finer scale analysis of the process of tree replacement.

Appendix I.

Differential equations used in transition probability analysis. Three simultaneous equations were solved for the condition that $dy/dt=0$ (equilibrium composition):

$$\frac{dY_f}{dt} = \frac{(P_{ff}-1)Y_f}{L_f} + \frac{P_{fs}Y_s}{L_s} + \frac{P_{fb}Y_b}{L_b} \quad (1)$$

$$\frac{dY_s}{dt} = \frac{(P_{ss}-1)Y_s}{L_s} + \frac{P_{sf}Y_f}{L_f} + \frac{P_{sb}Y_b}{L_b} \quad (2)$$

$$\frac{dY_b}{dt} = \frac{(P_{bb}-1)Y_b}{L_b} + \frac{P_{bf}Y_f}{L_f} + \frac{P_{bs}Y_s}{L_s} \quad (3)$$

where Y_f is the fraction of canopy trees of *Abies*; Y_s is the fraction of canopy trees of *Picea*; Y_b is the fraction of canopy trees of *Betula*; L_f is the lifespan of *Abies*; L_s is the lifespan of *Picea*; L_b is the lifespan of *Betula*; P_{ff} is the probability that *Abies* replaces *Abies*; P_{fs} is the probability that *Abies* replaces *Picea*; P_{fb} is the probability that *Abies* replaces *Betula*; P_{ss} is the probability that *Picea* replaces *Picea*; P_{sf} is the probability that *Picea* replaces *Abies*; P_{sb} is the probability that *Picea* replaces *Betula*; P_{bb} is the probability that *Betula* replaces *Betula*; P_{bf} is the probability that *Betula* replaces *Abies*; P_{bs} is the probability that *Betula* replaces *Picea*.

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