

Predicting and understanding forest dynamics using a simple tractable model

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The perfect-plasticity approximation (PPA) is an analytically tractable model of forest dynamics, defined in terms of parameters for individual trees, including allometry, growth, and mortality. We estimated these parameters for the eight most common species on each of four soil types in the US Lake states (Michigan, Wisconsin, and Minnesota) by using short-term (≤ 15 -year) inventory data from individual trees. We implemented 100-year PPA simulations given these parameters and compared these predictions to chronosequences of stand development. Predictions for the timing and magnitude of basal area dynamics and ecological succession on each soil were accurate, and predictions for the diameter distribution of 100-year-old stands were correct in form and slope. For a given species, the PPA provides analytical metrics for early-successional performance (H_{20} , height of a 20-year-old open-grown tree) and late-successional performance (\hat{Z}^* , equilibrium canopy height in monoculture). These metrics predicted which species were early or late successional on each soil type. Decomposing \hat{Z}^* showed that (i) succession is driven both by superior understory performance and superior canopy performance of late-successional species, and (ii) performance differences primarily reflect differences in mortality rather than growth. The predicted late-successional dominants matched chronosequences on xeromesic (*Quercus rubra*) and mesic (codominance by *Acer rubrum* and *Acer saccharum*) soil. On hydromesic and hydric soils, the literature reports that the current dominant species in old stands (*Thuja occidentalis*) is now failing to regenerate. Consistent with this, the PPA predicted that, on these soils, stands are now succeeding to dominance by other late-successional species (e.g., *Fraxinus nigra*, *A. rubrum*).

climate change | community ecology | SORTIE | TASS | trade-offs

There is an urgent need to develop a predictive understanding of the carbon and ecological dynamics of natural and seminatural forests (1). Forests harbor approximately two thirds of terrestrial biodiversity (2) and half of terrestrial carbon (3), but we currently know little about how the biology and demography of trees lead to regional and global patterns in the biomass, structure, and species composition of forests (4). This problem limits our ability to predict how, and how quickly, forests, and hence the Earth's climate system, might respond to climate change (5). In part, this problem reflects the lack of consensus on a conceptual and modeling framework for forest dynamics (6). At local scales, complex, spatially explicit, individual-based simulation models (hereafter referred to as virtual forest models) have been developed that successfully reproduce observed dynamics. For example, forest gap models [JABOWA-FORET (7, 8) and its derivatives (9, 10)] have reproduced the species composition of old-growth, seminatural forests and are widely used to guide forest management (11–13). Also, the tree and stand simulator (TASS) model and its derivatives (14, 15) can accurately predict the dynamics of size distributions and wood volume and, hence, carbon in even-aged plantation monocultures. However, the complexity of virtual forest models means that they cannot readily be scaled up to address regional and global questions, both because they require detailed data that are rarely available [e.g., light interception, crown transmissivity,

seed-dispersal kernels (9, 16)] and because they are computationally demanding to simulate (6, 17). The complexity of virtual forest models also renders them mathematically intractable, which limits the level of understanding that can be extracted from them.

We recently developed a simple model of the dynamics of a forest stand, the perfect-plasticity approximation (PPA), which simultaneously predicts the dynamics of biomass, stand structure (e.g., tree-size distributions), and ecological succession (e.g., species compositional changes after disturbance). Unlike virtual forest models, the PPA can be parameterized from forest inventory data, is simple enough to simulate at broad geographic scales, and is mathematically tractable (18–20). The purpose of the work presented here was to assess whether the PPA can predict the dynamics of real forest communities.

Fig. 1 shows PPA predictions for the 100-year dynamics of forest stands on four different soil types (in order of increasing soil moisture: xeromesic, mesic, hydromesic, and hydric) in the US Lake states (Michigan, Wisconsin, and Minnesota). For each soil type, we estimated PPA parameters for each of the most common eight species by using forest inventory data. We then initialized the model by using inventory data from young (i.e., recently disturbed) forest stands and ran an ensemble of model simulations to provide predictions for dynamics over 100 years. Finally, we compared these model predictions with observed 100-year chronosequences [supporting information (SI) Appendix, Appendices 1 and 2]. Crucially, the PPA parameters are defined at the level of the individual tree and, thus, were estimated by using only individual-level, short-term data (c. 12-year growth and survival from inventory plots remeasured in the 1990s, and allometry from additional inventories; see Table S1), whereas predictions were evaluated against long-term, stand-level data. The PPA parameters were not adjusted to reproduce the stand-level data (Table S2). Thus, the comparison of predictions vs. observations shown in Fig. 1 is an independent test of the model's ability to predict long-term, community-scale dynamics from short-term, individual-scale observations. However, it is also important to note that chronosequences are generated from a single survey by comparing stands of different ages. Therefore, a match between predictions and observations would be expected only if the processes driving forest dynamics have remained close to constant during the period in which the chronosequences were formed (21).

As Fig. 1 shows, the PPA is able to predict the 100-year dynamics of basal area (an index of carbon storage) recorded in the chronosequences (Fig. 1 Top), predicting the basal area of

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SORTIE is modified to include a realistic level of crown plasticity (19). Second, we found that a perfect-plasticity canopy model accurately reproduced the observed species and size dependencies of crown radius, crown depth, and canopy status (understory vs. canopy) in US forests (18). Together, these results suggest that the deviations from perfect plasticity that occur in reality are, to a first approximation, not critical to either canopy structure or the development of stands. However, it is important to note that the perfect-plasticity assumption is only tenable within a stand, where trees experience a relatively homogeneous physical environment and relatively similar neighborhoods.

To understand the implications of perfect plasticity, consider the case in which the total crown area in a stand is between one and two times the ground area, as is typically the case in mid- to late-successional temperate forests (results not shown). In this case, perfect plasticity implies that all crown area above a critical height Z^* receives full sunlight and that all other crown area is in the understory. The height Z^* needs to satisfy the logical condition that the total sun-exposed crown area is less than or equal to the ground area. Thus, Z^* depends in a simple way on the height and crown geometry of the trees in the stand (18, 19).

Perfect plasticity makes each individual's fate independent of its spatial location and, thus, removes any effects of spatially explicit processes including seed dispersal and understory heterogeneity in light. Thus, individuals of the same species and size have the same expected fate (no trees become "lucky" or "unlucky" as a result of their spatial position), which enables the individual-based model to be recast as a demographic model (19), tracking the fate of cohorts rather than individuals. The definition of a cohort is a group of trees with identical properties (e.g., species, size, demographic rates) and an associated spatial density (number per unit area). The use of demography makes simulations orders of magnitude faster and mathematical analysis possible (19, 20). However, it still allows for a great deal of freedom in the functions controlling the biology of trees (i.e., growth, mortality, fecundity, and allometry and how they depend on tree size, age, and light availability).

The results in this article are from a special case of the PPA that makes very simple assumptions. We make tree crowns flat-topped, with area equal to a circle with radius proportional to an individual's diameter at breast height (dbh); i.e., crown area = $\pi(\phi_j \text{dbh})^2$ for a tree of species j . The flat-top assumption means that an individual's crown is either completely sun-exposed (if the tree is taller than Z^*) or completely shaded (shorter than Z^*). We assume a power law for height allometry (i.e., height = $\alpha_j \text{dbh}^{\beta_j}$). We allow a pair of size- and age-independent dbh-growth rates (cm yr^{-1}) for individuals in the canopy ($G_{L,j}$) and understory ($G_{D,j}$) and an analogous pair of annual mortality rates ($\mu_{L,j}$ and $\mu_{D,j}$), thereby avoiding any explicit consideration of light. We assign a species-independent fecundity parameter F (new recruits per unit sun-exposed crown area per unit time), and within each soil type we disregard random tree-to-tree, plot-to-plot, and/or year-to-year variation in parameters, making growth, mortality, allometry, and fecundity entirely deterministic.

The simplicity of this version of the PPA is illustrated by the following algorithm, which implements its dynamics over 1 year (see *SI Appendix, Appendix 1*, and *Table S3* for details):

1. calculate Z^* ;
2. implement mortality:

$$w(i) \rightarrow (1 - \mu_{L,j})w(i) \quad \text{if height of cohort } i \geq Z^* \quad [1]$$

$$(1 - \mu_{D,j})w(i) \quad \text{if height of cohort } i < Z^* \quad [2]$$

3. implement growth:

$$\text{dbh}_i \rightarrow \text{dbh}_i + G_{L,j} \quad \text{if height of cohort of } i \geq Z^* \quad [3]$$

$$\text{dbh}_i + G_{D,j} \quad \text{if height of cohort of } i < Z^* \quad [4]$$

4. create one new cohort i for each species j in the stand, with $\text{dbh}_i = 0$ and $w(i)$ proportional to the total exposed crown area of species j ,

where $w(i)$ is the spatial density of cohort i (trees ha^{-1}), dbh_i is the diameter at breast height of the trees in cohort i , and the subscripts j refer to the species identity of particular cohorts. Iterating steps 1–4 predicts the dynamics of the stand.

Analytical Predictions for Succession

The special case of the PPA considered here is of special interest, because important features of its dynamics are analytically tractable (19, 20). For example, in the absence of stand-replacing disturbance, the eventual winner in interspecific competition (i.e., the late-successional dominant) is the species j with the greatest value of \hat{Z}_j^* [canopy closure height in an equilibrium monoculture (19, 20)]:

$$\hat{Z}_j^* \approx \alpha_j [G_{D,j} / \mu_{D,j}]^{\beta_j} [\ln(2\pi\phi_j^2 F G_{L,j}^2 \mu_{L,j}^{-3})]^{\beta_j} \quad [5]$$

where \hat{Z}_j^* is in meters. Also, the species with the largest share of the canopy at the time of canopy closure (i.e., the early-successional dominant) is the species with the fastest height growth rate, assuming (i) equal, and realistically high, initial densities of size-zero individuals of all species and (ii) realistically small interspecific differences in μ_L and ϕ . In this region we estimate that canopy closure occurs ≈ 20 years after stand-replacing disturbance on all soil types (results not shown). Thus, as a measure of competitive ability for the early-successional niche, we use the height of a 20-year-old open-grown tree: $H_{20,j} = \alpha_j (20G_{L,j})^{\beta_j}$.

To test the predictive ability of these metrics, we calculated \hat{Z}_j^* and $H_{20,j}$ for each species on each soil type and compared them to the observed successional status (early or late) of each species, calculated from the observed correlation of basal area vs. stand age in the chronosequences (see *SI Appendix, Appendix 1*). Note that \hat{Z}_j^* and $H_{20,j}$ were calculated directly from individual-level parameters without the need for model simulations.

In most cases, these metrics correctly predicted which species were early- or late-successional on each soil type (Fig. 1 *Middle*; Fig. S2). On mesic soil, a group of four species (*Acer rubrum*, *Acer saccharum*, *Quercus rubra*, and *Tilia americana*) had much greater \hat{Z}_j^* values than the others, and these were the four species observed to be significantly late-successional (*SI Appendix, Appendix 1*). Similarly, on xeromesic soils, *A. rubrum* and *Q. rubra* had the greatest \hat{Z}_j^* values, and these were the two species observed to be significantly late-successional. The pattern was less clear on hydromesic and hydric soil, but in both cases the significantly late-successional species were among the species with the greatest \hat{Z}_j^* values. Finally, *Populus tremuloides*, the only significantly early-successional species on all four soil types, had a very low \hat{Z}_j^* but a high H_{20} on all soil types.

Understanding Succession

Secondary succession in forests is often considered to proceed from shade-intolerant to shade-tolerant species (e.g., see refs. 22 and 23). However, there are other, interrelated hypotheses (e.g., see refs. 24–26). For example, according to the differential longevity hypothesis (27), late-successional species dominate old stands because they survive longer. The \hat{Z}_j^* and $H_{20,j}$ metrics allow us to take a formal approach to understanding forest succession in this region. The \hat{Z}_j^* metric (Eq. 1) naturally decomposes into three multiplicative terms separating height allometry (α_j), canopy performance $[\ln(2\pi\phi_j^2 F G_{L,j}^2 \mu_{L,j}^{-3})]$ and understory performance ($G_{D,j} / \mu_{D,j}$), with the latter two terms

being determined, in part, by the height allometry parameter β (Table S4). Only the last term can be said to correspond to shade tolerance, because only understory trees experience shade.

We find that, on each soil, late-successionals tend to have greater understory performance than the early-successional (*Populus tremuloides*) on the same soil (Fig. S2). Examination of parameter estimates (Table S4) shows that the superior understory performance of late successionals is primarily attributable to lower understory mortality ($\mu_{D,j}$) rather than faster understory growth ($G_{D,j}$). Late successionals also tend to have superior canopy performance (Fig. S2), again primarily because of lower canopy mortality ($\mu_{D,j}$) rather than faster canopy growth ($G_{D,j}$) (Table S4). Differences in height allometry (Table S4) are generally not important in determining differences in \hat{Z}^* . The exception is *Thuja occidentalis*, which has a much lower α_j than the other species (Table S4), which is why *T. occidentalis* has an intermediate value of \hat{Z}^* on hydromesic and hydric soils despite good understory and canopy performance (Fig. S2). These results provide support for the differential longevity hypothesis: high \hat{Z}^* of late-successional species is primarily attributable to low mortality rates (understory and canopy). The results are also consistent with the shade-tolerance hypothesis (greater understory performance of late successionals) via understory mortality rather than growth.

We also find that each soil type contains a group of species spread along a successional axis from high $H_{20,j}$, low \hat{Z}^* (early successional) to low $H_{20,j}$, high \hat{Z}^* (late successional). This pattern is clearly seen on the xeromesic and mesic soils (Fig. 1). However, each soil also contains apparently inferior species with relatively low values of both \hat{Z}^* and H_{20} (Fig. 1 Middle, gray symbols), which have, nonetheless, not been lost from these communities. In addition, hydromesic and hydric soils have one species (*A. rubrum*) that seems superior to all others in the sense that it lies substantially above the successional axis defined by the other species (Fig. 1 Middle). Yet, *A. rubrum* does not dominate these communities. Taken together, these observations indicate that the analysis has missed some important processes responsible for the current species composition of old stands in this region (see Discussion).

Predictions for Species Composition

For each soil type the PPA predicted the 100-year dynamics for each species and, hence, the species composition of 100-year-old stands. Again, a match between these predictions and observations would only be expected if the processes controlling the dynamics have remained close to constant during the 100 years up to the 1990s. Therefore, we expected, *a priori*, mismatches between predictions and observations for three species that are considered to have gone through important changes in dynamics over the previous century. *T. occidentalis* is currently thought to be suffering a lack of recruitment, with stands on wet soils in this region no longer succeeding to *T. occidentalis* dominance despite the fact that *T. occidentalis* currently dominates old stands on wet soils, implying that it recruited well in the past (28–31). *A. rubrum* has become increasingly dominant on a variety of soil types in the eastern United States since European settlement [the red maple paradox (32)]. Also, *Abies balsamea* suffers from regular outbreaks of spruce budworm, during which a large percentage of trees are often killed (33, 34). At least one such outbreak occurred between surveys in the inventory data that we used here [Michigan 1985–1988 (35)].

On xeromesic soil, predictions match observations in terms of the species composition of 100-year-old stands and the shift in dominance from *Populus tremuloides* and *Pinus banksiana* to *Q. rubra* and *A. rubrum* (Fig. 1 Bottom). On mesic soil, the match between predictions and observations is close, but the relative positions of *A. rubrum* and *A. saccharum* are reversed (observed,

saccharum > *rubrum*; predicted, *rubrum* > *saccharum*). This mismatch is consistent with the red maple paradox.

On hydromesic and hydric soils, the predictions and chronosequences showed a qualitative mismatch. On both soil types, 100-year-old stands are dominated by *T. occidentalis* (Fig. 1). In contrast, the PPA predicts that 100-year-old stands should not be dominated by *T. occidentalis* (Fig. 1 Bottom) or succeeding to eventual dominance by *T. occidentalis* (Fig. 1 Middle; *T. occidentalis* does not have the greatest \hat{Z}^* on either soil). Instead, the PPA predicts dominance by *Fraxinus nigra* and *A. rubrum* on hydromesic soil, and by *Larix laricina*, *F. nigra*, *T. occidentalis*, *A. rubrum*, and *Picea mariana* on hydric soil. However, on both soils, the predictions for the 100-year change in abundance of *Populus tremuloides* were accurate (Fig. 1).

Discussion

The purpose of this article was to assess whether the PPA might be a useful model for predicting and understanding the dynamics of real forest communities. We found that predictions generally matched observations for the dynamics of basal area, the timing of succession, and size distributions, as did several detailed predictions for the dynamics of particular species, including simple analytical metrics predicting the outcome of interspecific competition (Fig. 1; Figs. S1–S3). Moreover, species-level mismatches between predictions and observations (Fig. 1) correctly identified previously recognized changes in forest dynamics in the region. These mismatches underscore the independence of the tests used here. If the individual and stand-level data had been tautologically related, the model could not have failed to predict the stand-level data. Taken together, our results indicate that the PPA is a potentially useful model for studying forest dynamics.

Theoretical findings from the PPA have been highlighted previously (19, 20). These findings are now bolstered by our demonstration that the PPA model can predict the dynamics of real forest communities. One such finding is a pair of metrics (\hat{Z}^* and H_{20}) that predict competitive ability for the early- and late-successional niche from individual-level species parameters. It is perhaps obvious that these parameters must combine to determine the competitive ability for a given niche (9, 36–38), but exactly how was largely opaque before the development of the PPA. In this case, H_{20} and \hat{Z}^* were relatively successful in predicting the outcome of succession on each soil type. Also, they allowed us to formally test hypotheses about the causes of succession and to formally identify successional trade-offs operating in this region. These results suggest that the PPA might prove useful in interpreting the large body of empirical work on interspecific differences in, and trade-offs among, species traits in forest communities (e.g. see refs. 39–41).

The results also point to the importance of processes not captured by the simple special case of the PPA used here. These and other considerations point to extensions of the model and statistical methods. For example, we found that approximately half of the species studied here deviated from the successional axis (Fig. 1 Middle), and yet these species have not disappeared or outcompeted all other species (as would be expected for inferior or superior species, respectively). Closer examination suggests several explanations including environmental specialization within the soil-type classification used here [e.g., *Betula papyrifera* to cold locations or poor soils (34)], specialization to disturbance by fire [*Pinus banksiana* (34)], and changes in performance either directionally (decreasing for *T. occidentalis*, increasing for *A. rubrum*) or intermittently (e.g., insect outbreaks affecting *Abies balsamea*). Several aspects of the dynamics might be affected by variation in understory light [e.g., as a result of interspecific and ontogenetic variation in canopy transmissivity (39)], which was not included explicitly here. We also assumed a single fecundity value F for all species on each soil type. We

could not estimate F from the inventory data, because it only included trees with a dbh of >2.5 cm (SI Appendix, Appendix 2). A potential problem that could be resolved by including species-specific F is the estimate, for some species on some soils, of negative \hat{Z}^* (plotted as zero in Figs. 1 and Figs. S1–S3), implying that these species cannot persist, even in monoculture, on these soils (19). Although the species in question are likely to have low \hat{Z}^* values, it is likely that the true \hat{Z}^* values are positive, perhaps because, in reality, these species have greater fecundity than the other species.

At a more fundamental level, it is important to note that the PPA, in scaling from trees to stands, occupies the center of a much broader scaling from leaves and roots (or even lower levels of biological organization) to the globe. The other parts of this scaling need to be understood before we can accurately predict the response of global forests to climate change (42). Our current understanding of the response of global forest dynamics to climate change comes from dynamic global vegetation models (DGVMs), the current generation of which scale directly from physiology to ecosystem properties, giving little attention to the individual, population, and community scales in between (5, 6). Because the PPA scales from trees to stands and can be simulated rapidly, it could form the basis of a new generation of

DGVMs. However, it would first be necessary to understand how increased CO_2 and associated changes in climate might affect the growth, mortality, fecundity, and allometry of individual trees. This requirement highlights the need for improved ecophysiological models that scale properly from leaf and root physiology (and their interaction with CO_2 , light, and temperature) to whole-tree growth and mortality (43) and for statistical studies that relate variation in vital rates to chronic differences in climate and soils (e.g., see ref. 44). Also, the PPA applies only to a single forest stand (a region of forest with a relatively homogeneous environment and shared recent history), whereas forested landscapes are composed of tens of thousands of stands, at different stages of disturbance, and subject to varying physical environments. Therefore, to create a tenable model of regional or global forest dynamics on the basis of the PPA, it would be necessary to couple the PPA with models that operate at the landscape scale (45).

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