

SPECIAL FEATURE

ADVANCES IN PLANT DEMOGRAPHY USING MATRIX MODELS

Integral Projection Models for trees: a new parameterization method and a validation of model output

Pieter A. Zuidema^{1,4,*}, Eelke Jongejans², Pham D. Chien^{1,3,4}, Heinjo J. During¹ and Feike Schieving¹

¹Ecology and Biodiversity Group, Institute of Environmental Biology, Utrecht University, Padualaan 8, 3584 CH Utrecht, The Netherlands; ²Experimental Plant Ecology, Radboud University Nijmegen, Heyendaalseweg 135, 6525 AJ, Nijmegen, The Netherlands; ³Forest Science Institute of Vietnam, Dong Ngac, Tu Liem, Hanoi, Vietnam; and ⁴Tropenbos Vietnam Programme, 6/1 Doan Huu Trung Street, Hue, Vietnam

Summary

1. Matrix models are popular tools for plant demographic studies, but their application to long-lived, slow-growing species is hampered by the fact that (i) model output is highly sensitive to category width and (ii) growth variation between individuals can only be partially accounted for. Integral Projection Models (IPMs) – an extension of matrix models – offer a solution to these problems.

2. Here, we introduce a new method to parameterize IPMs for trees – the ‘integration method’ – which allows constructing IPMs for long-lived, slow-growing species. This approach is more suitable than the ‘midpoint rule’, which is customarily used.

3. We built IPMs for six tree species from Vietnamese (sub)tropical forests. For four of these species, population growth rate (λ) was highly sensitive to the number of categories in the transition matrix. Population growth stabilized for IPMs with 100–1000 categories, corresponding to categories of 0.1–1 cm in trunk diameter. This preferred width is much narrower than the 10-cm-wide categories customarily used in tree models.

4. The distribution of elasticity values over transition types (stasis, progression to next and further categories) is also highly sensitive to matrix dimension in IPMs. In addition, elasticity distribution is influenced by including or excluding growth variation.

5. Age estimates obtained from IPMs were also highly sensitive to matrix dimension: an IPM with 1000 size categories yielded 2–4 times higher age estimates for large trees than one with 10 size categories. Observed ages obtained from tree ring analyses for four of the study species allowed validating these estimates. IPMs with 10 categories strongly underestimated age, while those with 1000 categories yielded slight age overestimates. Underestimating age in small matrices is caused by the occurrence of unrealistically fast pathways through the life cycle and is probably widespread among tree models with broad categories. Overestimating ages in IPMs with narrow categories may be due to temporally autocorrelated growth or errors in fitting growth curves.

6. *Synthesis.* IPMs are highly suitable tools to analyse tree demography. We recommend that tree IPMs (and classical matrix models) apply narrow diameter categories (0.1–1 cm width) to obtain reliable model output.

Key-words: age estimates, elasticity, Integral Projection Models, matrix dimension, population growth, population matrix model, tree demography, tree ring analysis, tropical trees

Introduction

Matrix models are a popular tool for demographic analysis of long-lived plant species. So far, these models have been

*Correspondence author. E-mail: p.a.zuidema@uu.nl

constructed for > 100 tree and shrub species (reviews Franco & Silvertown 2004; R. Salguero-Gómez, unpublished data). The parameterization and construction of these models for long-lived species is very different from that for short-lived species. Transition values in matrices of short-lived species are typically based on observed transitions among categories. But for long-lived and slow-growing species – most trees, large palms and large shrubs – the annual change in size is (very) small relative to the maximum size and observing transitions among matrix categories is impossible. Thus, transitions in matrix models for trees and shrubs are typically calculated from growth rates of individuals or passage time through categories (e.g. Bernal 1998; Zuidema & Boot 2002; Chien, Zuidema & Nghia 2008).

There are two limitations of classical matrix models that have important implications for the output of models constructed for long-lived species. First, in their standard form matrix models offer limited possibilities to incorporate variation among individuals within a size category. Growth variation can be incorporated to distinguish between groups of individuals with fast growth, slow growth and those that shrink in size (e.g. Horvitz & Schemske 1995; Salguero-Gómez & Casper 2010), but this does not include variation between *all* individuals. Growth variation among individuals may strongly influence the dynamics and growth rate of populations (Pfister & Stevens 2003), especially for long-lived species (Wisdom, Mills & Doak 2000; Zuidema & Franco 2001; Zuidema *et al.* 2009). Second, the output (population growth rate λ , elasticities) of matrix models is highly sensitive to variation in the number of categories (Enright, Franco & Silvertown 1995; Ramula & Lehtilä 2005). In models for trees, it is customary to define rather wide categories, e.g. of 10 cm diameter from which typically 1–5% of the individuals progress to the next size category every year (e.g. Bernal 1998; Zuidema & Boot 2002; Chien, Zuidema & Nghia 2008). As the transition probabilities in a matrix model depend only on the current situation, there is no obstruction for unrealistically fast pathways through the life cycle. For instance, in matrix models with 10-cm-wide diameter categories and small progression probabilities, a small fraction may reach 50 cm diameter in five time steps, something that is clearly impossible biologically (and physically). This fraction contributes strongly to population growth and probably causes the high estimates of λ for small matrix models (Zuidema 2000; Ramula & Lehtilä 2005). In a model with narrow categories such ‘leaps’ through the life cycle are impossible and such models produce lower values of λ , different elasticity patterns and higher age estimates (Zuidema 2000).

Integral Projection Models (IPMs) provide solutions for both above-mentioned problems. IPMs are extensions of matrix models that yield similar output (population growth, sensitivity, elasticity, age estimates), but use continuous relations of vital rates (growth, survival, reproduction) versus size (or age) as input, instead of category-specific values (Easterling, Ellner & Dixon 2000; Ellner & Rees 2006). The above-mentioned limitations do not apply to IPMs, as these models explicitly incorporate variation among individuals in growth

rates (and any other vital rate), typically use large numbers of categories (or *mesh points*) and allow for transitions of individuals to any other size (be it larger or smaller). So far, IPMs have hardly been used for long-lived, slow-growing species (Metcalfe *et al.* 2009), in spite of their potential to be used for these species groups.

Here, we propose and apply a new method to parameterize IPMs for trees. Specifically, we evaluated the sensitivity of λ , elasticity and ages to changes in matrix dimension (number of categories) of IPMs and validated the age estimates obtained from the models with tree ring data. In the following, we first briefly review approaches to parameterization of matrix models for trees and introduce a new way to parameterize IPMs for long-lived, slow-growing species. Next, we construct and analyse IPMs for six tree species from Vietnam, for which demographic analyses and matrix models have been published (Chien 2006; Chien, Zuidema & Nghia 2008). Finally, we discuss the suitability of IPMs for modelling tree population dynamics.

Constructing matrix models for trees and shrubs

Matrix models use the equation $\mathbf{n}(t+1) = \mathbf{A}\mathbf{n}(t)$, where \mathbf{n} is a vector of size m that contains the number of individuals in each of the categories $i = 1$ to m , and \mathbf{A} is a square matrix of dimension m that contains the transitions from category j to i in one time step (Caswell 2001). So far, two main methods have been applied to parameterize transition matrices in stage-based models for plants (Fig. 1).

In matrix models, the probability of an individual to move from one to another category is the basis for describing population dynamics. The classical and most straightforward approach to constructing matrix models is therefore to use the observed frequencies of transitions among categories as elements in transition matrices (Caswell 2001). Individuals are assigned to size categories at first and subsequent censuses, and the proportions of individuals moving to other categories or staying in the same category are recorded and used as transition values. This approach has the advantage that no assumptions are made about the distribution of sizes or growth rates within a size category. Using observed transitions is especially suitable for species with considerable annual changes in size, as in this case sufficient transitions are observed to larger or smaller size categories. This is a suitable approach for short-lived herbs, or long-lived herbs and shrubs showing large annual changes in size relative to their maximum size, but it may fall short for slow-growing life-forms such as shrubs and trees.

For long-lived and slow-growing species, the frequency of transitions among categories is usually too low to apply observed transitions. Therefore, this approach has hardly been applied to trees and shrubs. Theoretically, there are two solutions to this problem – using very narrow categories or (very) long census intervals – but these are often impractical (requiring very large populations or long study periods). Therefore, for trees and shrubs, it is common to calculate transition probabilities from information on vital rates (growth, survival, reproduction; e.g. Zuidema & Boot 2002; Shimatani *et al.*

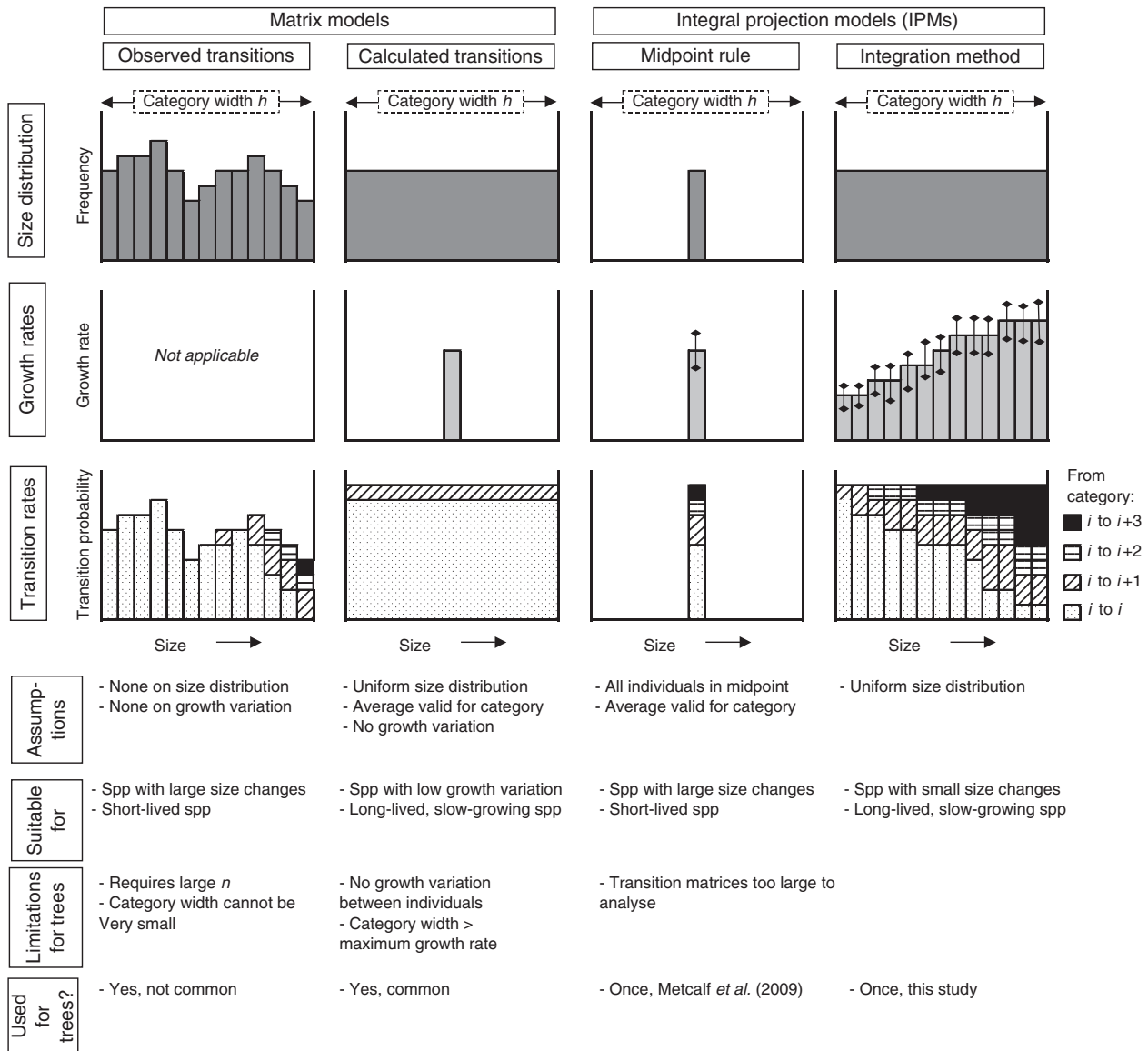


Fig. 1. Parameterization methods of matrix models and Integral Projection Models: calculations, assumptions on distributions, suitability and limitations for tree demography. Note that categories in matrix models are typically much wider than those in IPMs and that the number of sub-categories used in the integration method is much larger than shown here.

2007). The average growth rate or average passage time is used to calculate the transition probability to move to the next category for an average (surviving) individual. This can be done in two ways: using growth data from the category of interest only or using regressions that relate growth and size over the entire size range (Morris & Doak 2002). The latter, in fact, very much resembles the approach of IPMs, in which such overall performance–size relations (kernel) are at the core of the model (see below). Over two-third of matrix models for trees and shrubs have applied the method of calculated transitions (Zuidema 2000).

The method of calculated transitions makes a number of important assumptions (Fig. 1). First, it assumes that the average vital rate or average transition probability reasonably describes the performance of individuals in that category. In other words, variation in vital rates among individuals in a cat-

egory does not have a major role in determining population dynamics, as this method does not allow specifying the proportion of individuals that shrink and move to smaller size categories, or the proportion that leaps one or more categories because of fast growth. Second, it assumes that all individuals in a category have the same (i.e. average) vital rates, in spite of the fact that individuals vary in size within categories. Third, it is assumed that individuals are uniformly distributed in the category. In the case that vital rates are not strongly size-dependent (within a category) and variation in vital rates among individuals is relatively small, these assumptions are reasonable. But in the case that individuals are unevenly distributed over the size range within a category and performance (growth, survival) changes strongly (or nonlinearly) over the size range within the category, erroneous transition values may be obtained. These problems particularly occur if size categories

are rather wide, containing individuals of very different sizes which strongly vary in vital rates. Interestingly, for practical reasons transition matrices for trees and shrubs have a rather low dimension (average \pm SE = 8.7 ± 0.5 categories, $n = 46$; Zuidema 2000). The annual probability of moving to the next category in these models is typically 1–5% (Zuidema 2000). An obvious solution to this problem is to split categories, to reduce size variation within a category (Enright, Franco & Silvertown 1995). There is, however, a lower limit to the category width when applying the ‘calculated transitions’ approach: if category width drops below the average growth rate, transitions to the next larger size category cannot be calculated, as all individuals skip that category and move directly to $i + 2$. IPMs provide a solution to these problems, as they apply a probability distribution of growth rates to calculate transitions to various larger and smaller size categories.

Constructing IPMs for trees and shrubs

Integral Projection Models describe the dynamics of a continuous population distribution vector n as:

$$n(y, t + 1) = \int_L^U K(y, x)n(x, t)dx \quad \text{eqn 1}$$

where $[L, U]$ gives the range of possible states or sizes x at time t , y is the state at $t + 1$, and K is the projection kernel that yields probabilities of individuals of state x at time t to ‘grow’ to state y , or the number of new individuals of state y at $t + 1$ produced by an individual of ‘state’ x at time t . The ‘state’ of an individual can be age, size, some other attribute, or their combination (Easterling, Ellner & Dixon 2000; Ellner & Rees 2006). We will refer to ‘size’ here, as this is commonly used to classify trees and shrubs (diameter, height, crown size). The projection kernel K is built from a function P that relates growth and survival from x to y during one time step, and a function F that gives the production of recruits of size y by adults of size x (Easterling, Ellner & Dixon 2000; Ellner & Rees 2006). P and F are based on continuous functions (mostly regressions) that relate growth, survival and reproduction to size. Growth variation between individuals is explicitly taken into consideration, as the transition probability for individuals of size x to move to size y is based on the statistical relation between size y and size x and the residual variation around that fit.

Although IPMs define size-related vital rates in a continuous fashion and do not bother with size classes and class borders, the implementation of these models requires calculating the integrals in eqn 1, which is most practically conducted by applying fine categorization. For the numerical integration of the integrals, the ‘midpoint rule’ is commonly used (Ellner & Rees 2006). This implies that the entire size range (from L to U) is split into m categories (the number of *mesh points* or *bins*, or the matrix dimension), of width h . Thus, eqn 1 then results in:

$$n(x_i, t + 1) = h \sum_{j=1}^m k(x_i, x_j)n(x_j, t). \quad \text{eqn 2}$$

where x_j is the status at time t and x_i that at time $t + 1$ (Ellner & Rees 2006). This corresponds to the equation for matrix models: $\mathbf{n}(t + 1) = \mathbf{K} \mathbf{n}(t)$, in which \mathbf{K} is a square transition matrix with m categories of width h (Ellner & Rees 2006). Using this matrix equation, the population development can be projected and mathematical properties of transition matrix \mathbf{K} (eigenvalues, eigenvectors) can be obtained to calculate relevant demographic measures (population growth rate, stable size distributions, sensitivity, elasticity; Easterling, Ellner & Dixon 2000).

Thus, using the midpoint rule, the probability of moving from the midpoint of a category to the midpoint of another category is calculated from the projection kernel, and then multiplied by the category width h (Fig. 1). The selection of h is crucial in determining the accuracy with which the growth probabilities are obtained, and narrow categories are recommended (Ellner & Rees 2006). Figure 2 illustrates this using a hypothetical, but realistic, distribution of diameter growth rates, with an average of $0.18 \text{ cm year}^{-1}$ and a 95% confidence interval of $0.08\text{--}0.28$. For a category width of 0.5 cm (Fig. 2a), the probability of moving to the next category (growth = 0.5 cm year^{-1}) is close to zero. For a category width of 0.1 cm (Fig. 2b), progression to category $i + 1$, $i + 2$ and $i + 3$ can be estimated, but not very accurately. Using a category width of 0.01 cm , the frequency distribution is accurately ‘sampled’, yielding reliable transition probabilities (Fig. 2c). It is obvious that model output changes when h is varied from 0.5 to 0.01 , but probably would remain stable when h would be further reduced. The midpoint rule has been successfully applied in IPMs for herbs (e.g. Easterling, Ellner & Dixon 2000; Ellner &

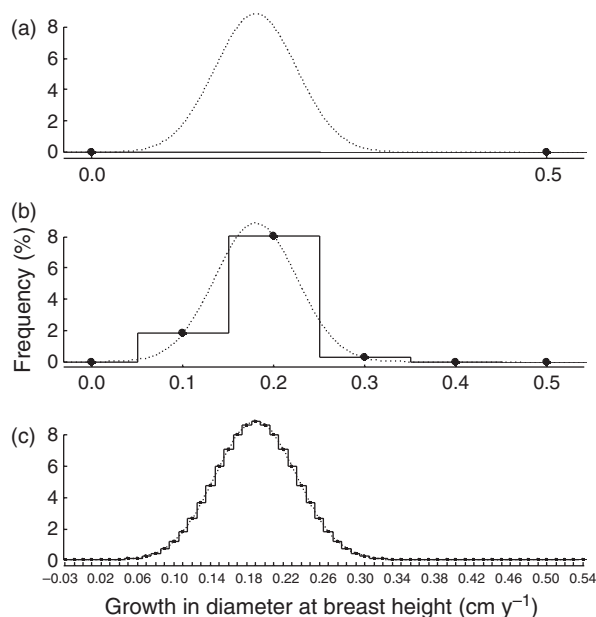


Fig. 2. Consequences of category width for calculation of transition probabilities in Integral Projection Models. Shown is a realistic frequency distribution of diameter growth rates for an imaginary tree species, with probabilities of moving to the next category (dots) for category widths h of 0.5 , 0.1 and 0.01 cm d.b.h. (a, b, c, respectively). Step functions illustrate how accurately the frequency distribution is ‘sampled’ in the three cases.

Rees 2006). The typical matrix dimension (or number of mesh points or bins, m) used in these cases is 10–100.

For slow-growing and long-lived trees and shrubs, in which the annual change in size is very small relative to the maximum size, the midpoint rule would require extremely large transition matrices (Fig. 1). For example, taking the recommended category width from the example in Fig. 2 ($h = 0.01$ cm) and a typical maximum size of 100 cm diameter, this would require 10 000 diameter categories. In theory, such very large matrices can be constructed, but computing power quickly becomes limiting when calculating λ , elasticity values and age estimates. A solution to these calculation problems may be the use of 'sparse matrix' tools, but at this moment it is not possible to obtain eigenvalues and eigenvectors using these tools within R (R Development Core Team 2009).

Therefore, we propose an extension of the midpoint rule that overcomes this problem and yields realistic transition probabilities without requiring very narrow categories. This 'integration method' (Fig. 1) calculates the transition probabilities for many (here we used 200) equal-distance points within each category of width h . For example, let us take the growth frequency distribution from Fig. 2 and a category width of 0.1 cm with 200 subdivisions to calculate the transition probabilities for trees of 7.0–7.1 cm diameter. In the integration method, transition probabilities to the next category (that of 7.1–7.2 cm) and further categories are calculated first for trees of exactly 7.0 cm diameter. In analogy to the midpoint rule, these probabilities are then multiplied by the category width h and divided by 200 to obtain transition probabilities from that subcategory to the equivalent subcategory in the next and further categories. Then, the same is performed for trees of 7.0005 cm ($= 7.0 + 1/200 \times 0.1$), which probably uses a slightly different frequency distribution, as average and SD of diameter growth vary with size. This is repeated for each of the 200 subcategories and transition probabilities to each of the other categories are summed (integrated) to obtain one value per type of transition (i to $i + 1$, to $i + 2$, etc.). The advantage of this approach is that transition probabilities can be accurately calculated also for categories that are relatively wide compared with the variation in growth rates (Fig. 1). Our approach bears resemblance to the calculation of passage distributions in tree populations (Kohyama, Kubo & Macklin 2005), which estimates transitions among size categories based on those individuals that actually pass the category boundary rather than on average growth rate.

IPMs for six tree species

SPECIES, SITES, DATA COLLECTION AND ANALYSES

We constructed IPMs for six Vietnamese tree species which vary in maximum size and diameter growth rate and occur in different forest types (Table 1). All study species are threatened tree species, with small remaining populations. Demographic field studies of these species were performed from 2003 to 2005 in natural populations within national parks in North and Central Vietnam. A detailed report on field sites, data collection and data analysis is provided by Chien, Zuidema & Nghia (2008). Below, we include the information necessary to understand the construction and output of IPMs.

Per study species, 2–3 permanent plots of 2.5–3 ha each were established in 2003. Subplots of 20×20 m were randomly established within plots to study dynamics of seedlings and saplings (< 5 cm d.b.h.). The number of subplots was chosen such that at least 100 seedlings were included for each species. Total number of individuals (seedlings, saplings and trees) ranged from 208 for *Annamocarya sinensis* to 432 for *Dacrydium elatum*. At first census, all trees > 5 cm d.b.h. and all seedlings and saplings in the subplots were located, tagged and measured. Re-censuses were carried out in 2004 and 2005. At each census, d.b.h. was measured and reproductive status assessed for trees > 1 cm d.b.h. Total height was measured for smaller individuals. Survival was recorded for all individuals. Newly recruited seedlings were searched and measured at re-censuses.

For individuals > 1 cm d.b.h., we established relations between vital rates (growth, survival and reproduction) and d.b.h., using nonlinear and logistic regressions. Further information on these analyses is provided in Appendix S1 in Supporting Information.

TREE RING MEASUREMENTS

We performed tree ring analysis to obtain true ages of trees, which could be compared with estimated ages from IPMs as a means of model validation. For four of our study species, increment cores were obtained from 30 to 34 individuals of > 30 cm d.b.h. per species (*A. sinensis*, *Calocedrus macrolepis*, *D. elatum* and *Pinus kwangtungensis*). From each tree, we extracted 1–2 wood cores at c. 1.3 m height. All cores were sanded and ring widths were measured to the nearest 0.1 mm. When the cores did not include the tree pith, we estimated the

Table 1. Characteristics of six Vietnamese tree species used in this study. d.b.h., diameter at breast height; Δ d.b.h., average d.b.h. growth for a tree of 10 cm d.b.h. Data from Chien, Zuidema & Nghia (2008)

Species	Family	Forest type	Max d.b.h. (cm)	Δ d.b.h. (cm year ⁻¹)
<i>Annamocarya sinensis</i> (Dode) Leroy	Juglandaceae	Lowland, closed canopy	150	0.27
<i>Calocedrus macrolepis</i> Kurz	Cupressaceae	Mountain, open canopy	> 100	0.18
<i>Dacrydium elatum</i> (Roxb) Wall ex Hook	Podocarpaceae	Montane, open canopy	50–70	0.26
<i>Manglietia fordiana</i> (Hemsl.) Oliv.	Magnoliaceae	Montane, open canopy	50–60	0.27
<i>Parashorea chinensis</i> Wang Hsie	Dipterocarpaceae	Lowland, closed canopy	> 100	0.27
<i>Pinus kwangtungensis</i> Chun ex Tsiang	Pinaceae	Montane, open canopy	50–70	0.18

distance to the pith and used the average number of rings of the other samples of the same species to obtain an estimate of the number of missing rings. Cores from hollow trees and those which lacked > 5 cm from the pith were excluded. The annual nature of ring formation was checked by correlation with rainfall data from nearby stations (1970–2004) and was proven by significant correlations between standardized ring width and rainfall (Chien 2006). Thus, ring counts are good estimates of tree age.

IPM CONSTRUCTION AND ANALYSES

For individuals > 1 cm d.b.h., we used the regression functions to establish the P (survival and growth) and F (fecundity) functions of the projection kernel. Although it would have been possible to establish such functions also for smaller individuals and combine these into one IPM (Ellner & Rees 2006), we decided not to do so. Trees spend a relative short portion of their life in these small size categories, and including those categories would result in a more complex model. Therefore, for individuals < 1 cm d.b.h., we used the transitions probabilities from the published transition matrices (categories 1–4; Chien, Zuidema & Nghia 2008).

We used nonlinear regressions and step functions to build the projection kernel (see Appendix S1). Note that we established nonlinear relations between tree diameter growth and initial diameter as this better captured size-dependent variation in growth compared with the 'standard' approach in IPMs, in which size at $t + 1$ is related to that at t using linear regressions (Easterling, Ellner & Dixon 2000; Metcalf *et al.* 2009). Next, we applied the integration method to calculate transition probabilities (Fig. 1). We varied the number of d.b.h. categories from 3 to a maximum of 1000, which resulted in category widths of roughly 20–0.1 cm diameter. Diameter categories of 20 cm are sometimes used in tree matrix models (Zuidema & Boot 2002; Chien, Zuidema & Nghia 2008).

We constructed the projection kernel and calculated transition probabilities for various matrix dimensions in R (R Development Core Team 2009). We calculated asymptotic population growth rate λ , the dominant eigenvalue of the matrix, for each of the matrix dimensions applied (Ellner & Rees 2006), using the popbio package in R (R Development Core Team 2009).

We calculated elasticity values (de Kroon, van Groenendael & Ehrlén 2000) for models of 10, 100 and 1000 d.b.h. categories. For each of the matrix sizes, we calculated elasticities for a situation with and without variation in diameter growth among individuals. We did so because we were interested in the impact of including variation on the distribution of elasticity values over transition types. IPMs, in which variation between individuals is not taken into account, are analogous to classical matrix models of the same dimension. In these cases, the average growth rate of a category determines to which category individuals can progress. In implementing the large IPMs (1000 d.b.h. categories), we detected that such large matrix calculations yield erroneous elasticity values in R (R Development Core Team 2009): elasticity values sum to > 1

in many cases. This error is caused by rounding of the very low transition values that occur in such large matrices. The problem has not been solved yet and we therefore used poptools to calculate elasticities (<http://www.poptools.org>), which yielded elasticity sums of exactly 1. There were no problems in calculating λ values and elasticities in poptools.

Finally, we calculated age estimates for each of the d.b.h. categories to compare these values to observed ages from tree ring counts. We used the approach presented by Cochran & Ellner (1992) to calculate age estimates from matrix models to obtain the conditional ages at entering a size category, τ . So far, these age estimates have not been obtained for IPMs, but they can be readily applied to such models.

SENSITIVITY OF POPULATION GROWTH RATE (λ) TO CATEGORY WIDTH

For four of six species, category width had a large impact on population growth rate λ (Fig. 3): population growth rate was considerably higher when using wide categories. For instance, applying 12-cm-wide diameter categories in *Parashorea chinensis* yielded $\lambda = 1.03$, while this was 0.99 for 0.12-cm categories. The largest changes in λ were observed when varying category width from 1 to 10 cm, which is in the range of category widths applied in matrix models for trees (Enright, Franco & Silvertown 1995; Zuidema 2000; Ramula & Lehtilä 2005). Recently, Metcalf *et al.* (2009) applied diameter categories of c. 0.65 cm width in IPMs of Costa Rican tree species, but as their IPMs did not include recruitment, the impact of category width on λ could not be evaluated. It should be noted that the observed change in λ in this study is not caused by errors in estimating transition probabilities from applying the midpoint rule to wide categories (e.g. Fig. 2a). In all calculations, we applied the integration method, with a sufficient number of subcategories to accurately calculate transitions.

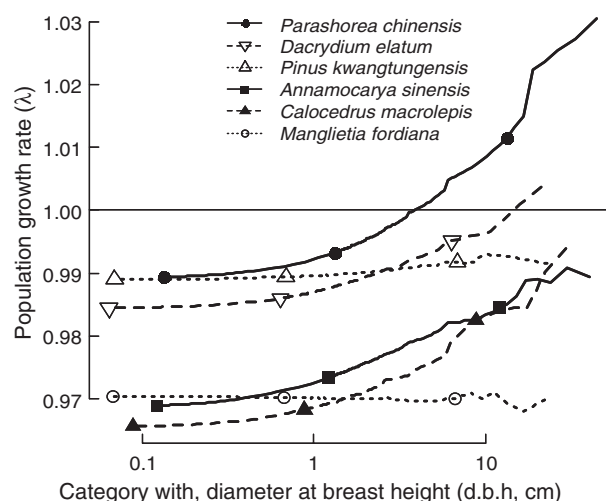


Fig. 3. Effect of category width on population growth rate λ in Integral Projection Models for six Vietnamese tree species. Symbols indicate models with 1000, 100 and 10 d.b.h. categories, from left to right.

High λ values for small matrices are caused by the boosting effect of a small proportion of individuals that pass rapidly through the life cycle and reach reproductive size at very young age (Zuidema *et al.* 2009). The magnitude of this boosting effect of fast growth probably depends on the amount of recruits produced, their initial survival and the increase in reproductive output with size. The two species for which λ is insensitive to category size, *P. kwangtungensis* and *Manglietia fordiana*, produced relatively low amounts of seedlings per adult tree ($< 1 \text{ year}^{-1}$; see Appendix S1). *Annamocarya sinensis* also has a low reproduction rate, but its seedlings have a considerably higher survival ($85\% \text{ year}^{-1}$) compared with the others ($65\text{--}74\% \text{ year}^{-1}$), thus leading to a stronger stimulation of λ when category width is increased. In all, our results show that wide categories may cause higher λ values under certain conditions. Similar increases in λ were also obtained after reducing the dimension of matrix models (Zuidema 2000; Ramula & Lehtilä 2005; Chien 2006), although in other cases λ appeared to be insensitive to category width (Enright, Franco & Silvertown 1995; Ramula & Lehtilä 2005).

ELASTICITY ANALYSES

In our large matrices (1000 d.b.h. categories), transition values are concentrated close to the main diagonal, as average diameter growth is typically 0.2–0.6% of the maximum size and growth standard deviations are 0.1–0.2% of that maximum size. As a result, the elasticity contour plot for this study species shows a thin line of non-zero elasticities close to the main diagonal (Fig. 4a). When zooming in, some variation in elasticity values can be observed (Fig. 4b). This picture is completely different from the elasticity contour plots published for IPMs of herbs so far (Easterling, Ellner & Dixon 2000; Ellner & Rees 2006; Kuss *et al.* 2008). In these cases, non-zero elasticity values were much more spread out over the contour plots, as such species exhibit large annual changes (both negative and positive) in size relative to their maximum size.

As expected, the distribution of elasticity values over categories changed drastically when varying the dimension of transi-

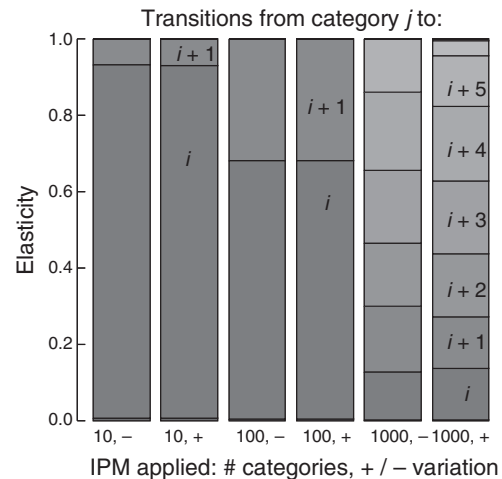


Fig. 5. Elasticity distribution over transition types for Integral Projection Models of *Annamocarya sinensis* with varying number of d.b.h. categories (10, 100, 1000) and including (+) or excluding (–) growth variation between individuals. The results for the other five study species are similar, see Appendix S2.

tion matrices. Figure 5 shows the elasticity distribution for one of the study species and similar results were obtained for the five other species (Appendix S2). With increasing matrix dimension, stasis elasticity is reduced while progression elasticity is increased. In models with 10 and 100 d.b.h. categories, there are (virtually) no individuals that progress from category i to $i+2$ or further. In the model with 1000 categories (category width c : 0.1 cm d.b.h.), individuals do move to categories $i+2$ and further, even beyond $i+10$ in some cases (Appendix S2). Similar shifts in elasticity distribution have been found in studies that varied category width for matrix models (Enright, Franco & Silvertown 1995; Zuidema 2000; Ramula & Lehtilä 2005; Chien 2006). Finally, elasticity of fecundity was inversely proportional to matrix dimension, which is probably a reflection of the generally larger contribution of fecundity for matrix models that yield higher λ (de Kroon, van Groenendaal & Ehrlén 2000).

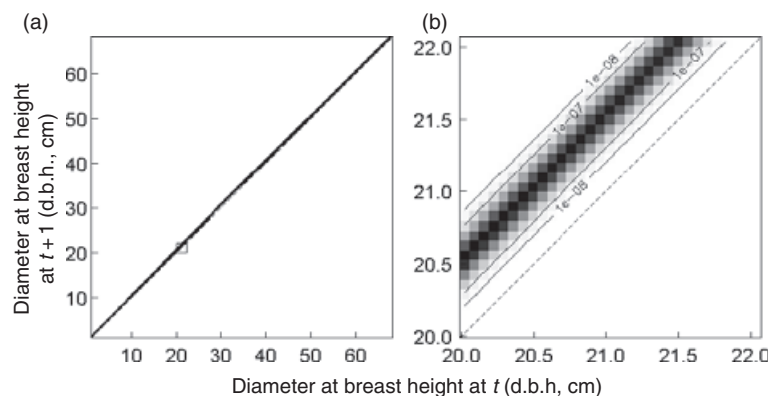


Fig. 4. Example contour plot of elasticity values from an Integral Projection Models with 1000 categories for *Manglietia fordiana* (a) and a detail from this plot for trees of 20–22 cm d.b.h. (b). The interrupted lines indicate stasis. (a) All cells with elasticity $> 1 \times 10^{-8}$ are black. (b) Darker grey indicates higher elasticity. Summed elasticities for growth and stasis transitions are 0.92; elasticities for fecundity (0.0062) and seedling categories (0.076) are not shown. Please note that the orientation of these figures differs from that usually applied for transition matrices (with $t+1$ in columns and t in rows).

Excluding variation among individuals also changed elasticity distributions, particularly for matrices with 1000 d.b.h. categories (Fig. 5 and Appendix S2). IPMs without variation had higher elasticities for progression to the next category and lower or zero values for transitions to further categories. Interestingly, these changes in elasticities were small, probably because of the rather low degree of variation in diameter growth. Thus, the high number of categories to which individuals can progress in a large IPM is mainly the result of the large size-dependent variation in growth (see Appendix S1) and much less so that of growth variation among individuals. For slow growing tree species ($0.1\text{--}1\text{ cm year}^{-1}$) that reach large size ($> 50\text{ cm d.b.h.}$), this may generally be the case.

AGE ESTIMATES AND THEIR VALIDATION

Age estimates were highly sensitive to the dimension of the transition matrix (Fig. 6). The estimated age at reaching 60 cm d.b.h. was 2–4 times higher when applying a model with 1000 d.b.h. categories compared with one with 10 categories. Age estimates increased particularly strongly when matrix dimension was increased from 10 to 100 d.b.h. categories. When comparing age estimates to observed ages from ring counts, it becomes clear that IPMs with just 10 d.b.h. categories strongly underestimated the observed ages for three of the four species. Models with 100 d.b.h. categories yielded age estimates that matched more closely to observed ages, except for *P. kwangtungensis*.

Surprisingly, age estimates obtained from very large matrix models may be considerably higher than the observed ages from ring counts (Fig. 6). There are several possible causes of

this discrepancy. First, temporal growth autocorrelation may cause persistent differences in growth rates among trees. If such persistent growth differences are not included in growth models, ages may be overestimated (Brienen & Zuidema 2006; Brienen, Zuidema & During 2006). Second, the Hossfeld equation that was used to relate d.b.h. growth with d.b.h. passes through the origin (see Appendix S1), which may ‘push’ the curve downwards in its initial part, below the data points for d.b.h. growth. This was indeed the case for *C. macrolepis*, *D. elatum* and *P. kwangtungensis* (Appendix S3). An underestimation of juvenile growth rates resulting from the curve fitting may lead to considerable age increase for juvenile trees. Third, the growth rates of juvenile trees measured in plots may be lower than those obtained from juvenile tree rings in extant large trees (Landis & Peart 2005). This ‘juvenile selection effect’ is probably caused by a preferential survival of fast-growing individuals, which implies that the extant adult trees have had above-average growth rates in the past (Rozendaal *et al.* 2010). Juvenile growth rates from ring data were indeed higher than plot data for *A. sinensis* and *P. kwangtungensis* (Appendix S3).

We performed extra simulations to eliminate the consequences of the last two effects. To this end, we calculated average growth rates for trees of 1–5 and 5–10 cm d.b.h. from ring data. We then built the projection kernel using these values if they were higher than those from the Hossfeld equation, for a given tree diameter. The resulting age estimates for a model with 1000 d.b.h. categories are shown as interrupted lines in Fig. 6. Age estimates are considerably lower compared with the standard model with 1000 categories. For three of four species (*A. sinensis*, *C. macrolepis* and *D. elatum*), these adapted

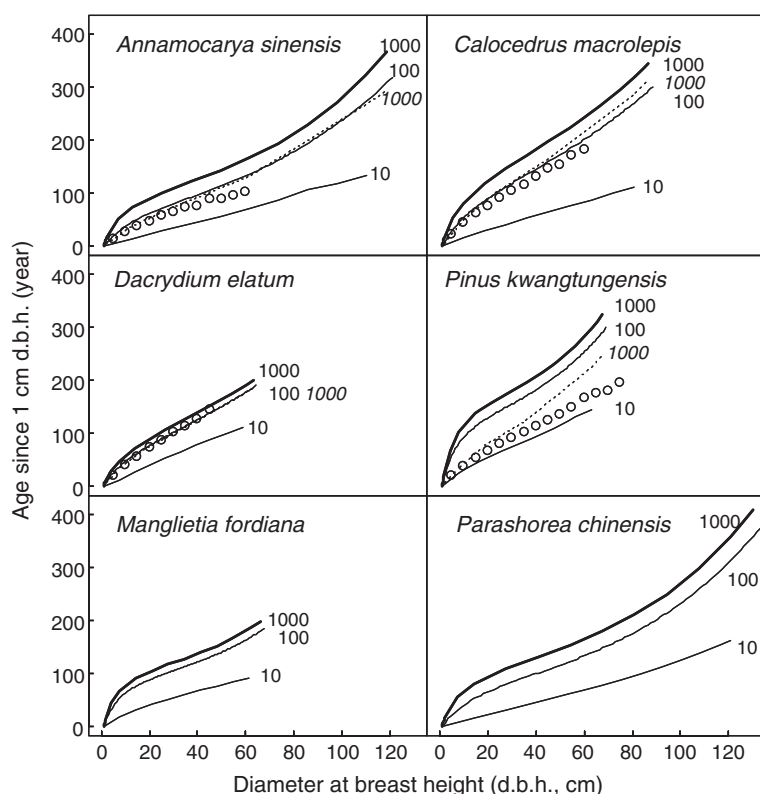


Fig. 6. Estimated (lines) and observed (dots) ages for d.b.h. categories of six Vietnamese tree species, based on Integral Projection Models with varying number of d.b.h. categories (10, 100, 1000). Estimated age is the conditional age upon reaching the category (τ , Cochran & Ellner 1992). Open dots indicate average observed age at reaching a d.b.h. category based on tree ring counts, for four ring-forming species. The interrupted line is conditional age for a modified model in which higher juvenile growth rates were applied.

models yield age estimates that are very close to the observed ages, over the entire d.b.h. range. For *P. kwangtungensis*, estimated and observed ages also match closely up to 20 cm d.b.h. These results suggest that the low growth rates of small trees used to establish the projection kernel for the standard models may be responsible for overestimating tree ages in IPMs with 1000 categories. To what extent this is caused by a poor fit of the Hossfeld curve or a juvenile selection effect is unclear. Probably, in IPMs with low matrix dimension age overestimation is more than compensated for by unrealistically fast growth through the juvenile categories.

Discussion

MATRIX MODELS OR IPMS FOR TREES?

There are clear advantages of using IPMs instead of classical matrix models to analyse tree demography. First, as IPMs are based on overall relations between vital rates and trees size (and/or age), they circumvent problems which arise when calculating transition probabilities separately for every category based on the individuals included in that category. In such cases, an uneven distribution of individuals over size categories and low sample sizes per category may cause random fluctuations in transition probabilities across categories that are unrelated to the biology of the study species. Using IPMs, this does not happen, as these models use all data for one or a few overall analyses (Ellner & Rees 2006). Using scarce data on vital rates to perform a few overall analyses is preferred over the calculation of category-by-category transition values, as in the latter case many more parameters need to be estimated to fill the transition matrix (Ellner & Rees 2006; Ramula, Rees & Buckley 2009). Various matrix model studies have dealt with this problem by establishing overall size-dependent patterns of vital rates (Batista, Platt & Macchiavelli 1998; Bernal 1998; Morris & Doak 2002; Zuidema & Boot 2002; Chien, Zuidema & Nghia 2008). This way of matrix parameterization is in fact very close to the establishment of a projection kernel for IPMs (Ellner & Rees 2006). Whatever the method for calculating transitions, we stress that the quality of model output depends on the quality and quantity of the data input.

The second advantage of using IPMs over matrix models is that variation between individuals is taken into account. Various studies have shown that variation in vital rates among individuals may cause large fluctuations in population growth obtained from matrix models (e.g. Wisdom, Mills & Doak 2000; Zuidema & Franco 2001). Differences in the magnitude of variation across categories or vital rates may cause shifts in the distribution of elasticity values (Zuidema & Franco 2001). In our results, the inclusion of growth variation did not have a large impact on model output, probably because growth variation was relatively small compared with class width even in our IPMs with 1000 d.b.h. categories. However, it is probably that strong growth variation and size dependency in this variation plays an important role in governing population dynamics.

It should be noted that there are some limitations to the inclusion of variation between individuals in deterministic

IPMs. Although these models include variation among individuals in growth rates and in size at recruitment, they are not able to cope with uncertainty in survival rates or variation in reproductive output among individuals. Stochastic IPMs may need to be applied in those cases (Ellner & Rees 2007; Metcalf *et al.* 2009).

Integral Projection Models can yield practically all output that can be obtained from classical matrix models (sensitivities, elasticities, life table response experiments, age estimates; Ellner & Rees 2006; Williams & Crone 2006), but loop analysis in IPMs with large matrix dimension is probably problematic. Loop analysis allows quantifying the contribution of pathways through the life cycle to population growth (van Groenendael *et al.* 1994). In IPMs, the large amount of categories and the possibility to move from one category to various others creates a large amount of possible pathways through the life cycle. In that case, the classical way of loop analysis, in which unique transitions identify a life cycle pathway (van Groenendael *et al.* 1994), cannot be applied and loops need to be identified and selected in a different and automated way. Loop-identifying algorithms based on graph theory are now available (e.g. Güneralp 2007), but the selection of loops and the biological interpretation of results is not straightforward (Adams 2008). Nevertheless, it is certainly of interest for (tree) demographers to be able to analyse the relative contribution of different life cycle pathways to λ in models that use continuous growth–size relations and include growth variation (Zuidema *et al.* 2009). Methodological advances are required in this field.

The question remains what to use in tree demography studies: IPMs or classical matrix models? Overall, we recommend the use of IPMs for the reasons outlined above. Nevertheless, there may be specific reasons to choose classical matrix models. If demographic models are constructed with the specific goal to apply loop analysis, classical matrix models are more appropriate (e.g. Zuidema *et al.* 2009; Salguero-Gómez & Casper 2010). Matrix models are more convenient for species that exhibit strict developmental stages, although in practice we do not expect finding tree species with such type of life history. Finally, multi-state models with subpopulations in different (discrete) habitats or ramets within genets are probably more conveniently constructed using matrix models, although multi-state IPMs can also be constructed (Ellner & Rees 2006; Metcalf *et al.* 2009).

CATEGORY WIDTH AND MODEL OUTPUT

Several studies have shown that category width in matrix models affects model output (population growth, elasticities, ages; Enright, Franco & Silvertown 1995; Zuidema 2000; Ramula & Lehtilä 2005; Chien 2006). Our analyses here illustrate this once again (Figs 3–6). Based on such results, some researchers have suggested to construct matrix models with a low number of categories as this would reduce the amount of data required (Ramula & Lehtilä 2005), while others have made a plea for using narrow categories as this diminishes the possibility for unrealistic fast growth through the life cycle (Zuidema 2000; Chien 2006). These advices are contradictory as they depart

from different ways of model parameterization. If matrix models are based on observed transitions, transition matrices with more categories require a larger sample size to realistically quantify transitions (Fig. 1, Ramula & Lehtilä 2005). On the other hand, if matrix models are parameterized using calculated transitions based on regression models, splitting categories does not require a larger sample size as all available data are used to establish these statistical models (Zuidema 2000; Chien 2006). The results presented here show that small matrix models may greatly overestimate population growth and greatly underestimate ages because of the fast and unrealistic pathways through the life cycle that are possible in small matrices.

On the other hand, our results also show that ages may be slightly overestimated when large transition matrices are used (Fig. 6). As such, these transition matrices are not 'too large', as they yield stable population growth. Rather, they show the issue of temporally autocorrelated growth, which was masked in smaller matrices. As shown by our additional simulations (interrupted lines in Fig. 6), these age overestimations can be partially overcome by adjusting the juvenile growth rates used. Temporal growth autocorrelation can have major impacts on transition rates (Kohyama, Kubo & Macklin 2005), age estimates (Martinez-Ramos & Alvarez-Buylla 1998) and elasticity patterns (Zuidema *et al.* 2009). Standard matrix models and IPMs cannot cope with autocorrelated growth (Pfister & Stevens 2003), but extensions of these models and IPMs do allow including temporal autocorrelation (Ellner & Rees 2006; Zuidema *et al.* 2009). Such models have hardly been applied so far.

In this study, we were fortunate to possess age estimates that we used to validate model output. However, having such data at hand is not a requirement to implement IPMs for long-lived, slow-growing species. In fact, in most cases such additional information is not available to plant demographers. Validation of model output is therefore only sporadically done (e.g. Bierzychudek 1999) but is certainly of great value to understand model behaviour and improve model construction.

Based on our results, we recommend that IPMs for trees are constructed using a sufficiently large number of categories so that population growth stabilizes. The optimal matrix dimension can be evaluated using the stepwise methods included in Appendix S1. In the case that researchers prefer matrix models over IPMs or are unable to construct the latter, we recommend that (i) transitions are calculated from overall relations between vital rates (survival, growth, reproduction) and size (and/or age), and (ii) that narrow categories (0.1–1 cm diameter) are used.

TOWARDS A WIDER APPLICATION OF IPMS

Why have IPMs not been used for long-lived trees and shrubs so far? And why not in general? The adoption of IPMs in plant demographic studies in general has been slow since their introduction 10 years ago (Easterling, Ellner & Dixon 2000). This is not specific for IPMs, as many innovations in population modelling took more than a decade to become incorporated in the

toolbox (matrix models, elasticity, LTRE). In the case of IPMs, the requirements of statistical analyses, complexity of building the projection kernel, unfamiliarity with R language and absence from general text books may have contributed to this slow adoption. For a wider application of IPMs to both long- and short-lived species, clear guidelines are required. Handbooks by Caswell (1989, 2001), Akcakaya, Burgman & Ginzburg (1999) and Morris & Doak (2002) have greatly popularized matrix models and stimulated their application. Accessible and easy-to-use software is also required for a wider application. For matrix modelling, software such as RAMAS and POPTOOLS, or scripts for MATLAB have assisted and stimulated plant demographers to use matrix models. Similar tools should become available for IPMs. To facilitate the uptake, we have included a detailed stepwise description of the construction of tree IPMs, including the R code for our integration method (Appendix S1).

In the case of tree demography, the need for at least two size parameters to describe ontogenetic development (height for seedlings, diameter for trees) may have prevented uptake initially, as the early publications did not treat such complex life cycles (Easterling, Ellner & Dixon 2000; but see Ellner & Rees 2006). Another problem may have been that application of the midpoint rule requires a large number of categories for long-lived tree species. This has now been solved by the introduction of the integration method here. We hope that this method and the example models introduced here will stimulate the application of IPMs for trees, shrubs and other long-lived, slow-growing organisms.

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Supporting Information

Additional supporting information may be found in the online version of this article:

Appendix S1. Model construction: functions and parameters.

Appendix S2. Elasticity distributions of five species.

Appendix S3. Diameter growth rates obtained from plot and ring data.

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