Demographic synthesis for global tree species conservation

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Abstract

Conserving the world's tree species requires syntheses on which tree species are most vulnerable to pressing threats, such as climate change, invasive pests and pathogens, or selective logging. We review the population and forest dynamics models that, parameterized with data from population studies, forest inventories, or tree rings, have been used for identifying species' life history strategies and threat-related changes in population demography and dynamics. The available evidence suggests that slow-growing and long-lived species are the most vulnerable. However, a lack of comparative, multi-species studies still challenges more precise predictions of tree species' vulnerability to threats. Improving data coverage for mortality and recruitment, and accounting for interactions among threats would greatly advance vulnerability assessments for conservation prioritizations of trees worldwide.

Demography as a tool for tree species conservation assessments

Trees provide vital ecosystem services, including carbon sequestration, habitat provision, element cycling, timber, and cultural values [1,2]. However, 30% of the 73,000 known tree species on Earth are currently threatened with extinction [3], and more than 100 tree species have been lost in the last 500 years [4,5]. Deforestation is currently the greatest threat to trees, while climate change, the infestation with alien and invasive pests and pathogens, and selective logging for timber threaten specific tree species in the remaining forest ecosystems [5].

Conserving the world's tree species requires information on the occurrence and prevalence of threats as well as on the effects of threats on species demography [6] as **life history strategies** (see **Glossary**) can strongly shape population **resilience** to threats [7]. Plant species' life history strategies are generally structured along two independent axes: the fast-slow continuum, *i.e.*, from fast-growing, short-lived species to slow-growing, long-lived species, and a reproductive strategy axis, ranging from species that reproduce much and often, but only for a short period of time, to those that reproduce at a lower rate for a long period of time [8–10]. Trees occupy a considerable proportion of the life history strategy space of plants [11], but are unique in that they are potentially very long-lived [12]. In the case of long-lived trees, following single individuals over the course of their lives (**Box 1**) to monitor variation in growth or death is challenging, if not impossible, complicating a precise quantification of **vital rates** [13].

Demographic approaches can quantify the **vulnerability** of a tree species to a threat by quantifying vital rates across the species' life cycle (*e.g.*, juvenile, adult), and by using linear operators, such as structured population models [14,15], to estimate the potential effects of a threat on population size and structure. The results of these assessments readily lend themselves to conservation prioritizations [16]. For example, the IUCN red list considers threats that cause declines in population size by more than 30% over three generations to be severe [17].

To help prioritise conservation efforts, we review the effects of important threats on tree species in naturally regenerating forests, and the modelling approaches and data used for assessing which vital rates at which life cycle stages are the most critical to population response to threats. Furthermore, we highlight paths forward to a comparative understanding of the vulnerability of tree species based on their life history strategies, which is essential for improved identification of conservation priorities and potential actions [18].

Demographic modelling approaches and data used for assessing vulnerability

Several types of population and forest dynamics models are applied to assess the consequences of threats on the viability of tree populations (**Box 2**). Structured population models, such as matrix population models (MPMs) and integral projection models (IPMs) [19], are analytically tractable [20] and oftentimes used for **sensitivity analyses** [21] and **population viability analyses** [22]. Their standardised output and widespread application have fuelled comparative analyses across hundreds of species [9]. However, MPMs and IPMs have to date not frequently accounted for competitive interactions and hence community dynamics (but see *e.g.*, [23]). The perfect-plasticity approximation (PPA) is an analytically tractable model of forest dynamics that simulates height-structured light competition based on vital rates in discrete dynamic canopy layers [24,25]. Individual based models (IBMs) can also simulate light competition and community dynamics, but are typically not analytically tractable [26]. Forest landscape models (FLMs) are the most common tool to project how entire forest communities change over time by considering simplified representations of light competition [27]. However, PPA models, IBMs, and FLMs have so far rarely been applied to the analysis of the vulnerability of single tree species to threats (but see [28]).

A variety of data sources can be used for demographic model parameterization (**Table 1**). Single-species population studies provide detailed information on vital rates across the entire life cycle [29]. However, such data are often collected on small plots and within a few years ([29,30]; but see [31]), challenging a robust assessment of long-term tree population dynamics. In contrast, forest inventory data capture the demography of all species in a community and can be used to quantify neighbourhood interactions [32,33]. However, forest inventory data yield little information on the demography of rare species and poorly capture the demography of early life stages as only trees above a relatively large size threshold (*e.g.*, 5 or 10 cm diameter at breast height, dbh) are followed. Another key source for demographic information is tree-ring data, which allows correlations between tree growth, tree age, and past environmental conditions [34]. Tree-ring data are potentially available for all species with seasonal growth, forming clear rings, from boreal to even tropical species [35]. However, tree-ring data are often biased towards successful individuals that have lived long lives, obscuring the dynamics of the whole forest.

The varied role of threats in tree demography - current knowledge and gaps

Species-specific threats act differently on vital rates [36]. For example, high temperature can increase **reproduction** [37], selective logging can favour the growth of juveniles [38], while drought and insects can reduce the survival of the largest trees [39,40]. Here, we review the state of our demographic knowledge on three important species-specific threats to trees: climate change, pests and pathogens, and selective logging. For each, we discuss the challenges and limitations of the demographic data and approaches used to assess species vulnerability and synthesise the available evidence on which tree life history strategies will be most vulnerable to the threat.

Climate change

Climate change will exacerbate the frequency and intensity of heat waves and the magnitude of negative and positive precipitation anomalies. These changes will increase the number and length of droughts and the area and frequency of wildfires [41].

Data, approaches, and challenges

Most demographic models to date have assessed tree species' vulnerability to climate change by estimating the link between climate and vital rates using observations of demography across space [42] or via physiological models [43]. For instance, an IPM based on observational data has shown that drying and warming conditions lead to declines in recruitment and survival, though the strength of responses varied between species [44]. Low recruitment might occur if seedlings tolerate a smaller range of moisture conditions than adults [45]. On the other hand, physiological models predict, and evidence suggests, that tall trees are the most likely to die from drought stress [40]. While these approaches can clearly advance our understanding of population responses to climate change, spatial observations of vital rates must be interpreted cautiously [46] because their variation across sites can be confounded by range position, local adaptation, land use and disturbance history, or plant community composition. Furthermore, physiological models that focus on simulating photosynthesis can miss important processes, such as carbon allocation for modelling growth, hydraulic failure for modelling mortality, and mechanisms underlying seedling establishment and survival [47–49]. Finally, decades of classical plant demography using elasticity analyses may have oversimplified how threats affect the viability of tree populations [50], which could give the incomplete impression that long-lived plants can persist without investing in successful recruitment. Prolonged recruitment failure, however, may drive long-lived species into "**extinction debt**" [51]. Forest models in use today for climate impact assessment do not represent establishment and mortality with the same complexity as growth, highlighting opportunities for incisive future model developments [52].

Synthetic knowledge

There is general consensus across studies that an increase in temperature, drought, and/or fire frequency will lead to a decline of species with slow life history strategies (which are usually called in this literature “late successional species” [53,54]). Because slow species tend to have a long **lifespan** [9], they often have delayed maturity and achieve larger sizes at maturity [55,56]. These traits could make slow species particularly vulnerable to increased mortality of large individuals triggered by climatic extremes. Adult trees are essential to maintain populations in the face of fluctuating climatic conditions [57]. Moreover, slow tree species in temperate and subtropical mountains could also face recruitment failure [54,58]. At the rear range edge, *i.e.*, the low-latitude or low-altitude limit of a species’ distribution, seedling establishment and survival might fail [59]. At the leading range edge, insufficient dispersal ability [58,60,61] might hamper migration. The disadvantages of slow life history strategies seem particularly strong in boreal forests, where fast deciduous species are projected to replace slow conifers [53,60]. Sprouting ability can help populations persist through disturbances such as fire, potentially making them less vulnerable to this threat than seed-obligate species [62].

Pests and pathogens

Invasive alien insect pests and pathogens threaten tree populations worldwide, an effect that is exacerbated by climate change and global trade [63]. Pest or pathogen infestations can increase mortality [39,64] and reduce growth and reproduction of surviving trees [63]. These changes in vital rates ultimately cause population declines and increased extinction risk even of common tree species, such as green ash (*Fraxinus pennsylvanica*) [65].

Data, approaches, and challenges

MPMs and analyses of **life table response experiments** show that the effect of pests and pathogens on tree populations is often determined by increased mortality of large individuals [39,65]. Due to their typically high **longevity**, many tree populations are especially sensitive to changes in adult mortality [66]. These demographic effects can be extreme, for example chestnut blight can kill all of the largest stems of American chestnut (*Castanea dentata*), leaving only small clones to resprout post-infestation [29]. IBMs that assess tree population and forest community dynamics after infestation estimated, for instance, that it will take 300 years before the density of large American beech trees (*Fagus grandifolia*) recovers after beech bark disease [67], or that eastern hemlock (*Tsuga canadensis*) might lose its relative dominance over other tree species in some areas unless it develops at least some resistance to its pest, the adelgid [68].

However, vital rates of infested *versus* non-infested trees before or during outbreaks are often unknown. Hence, model parameters are taken from different populations [64,65,68] that might experience confounding environmental conditions. Moreover, many population models do not include processes that are likely relevant for species' vulnerability, such as (1) positive or negative density-dependence of infestation-related mortality [54,65] (but see [69]); (2) the spatial aggregation of host populations, currently only considered in FLMs (*e.g.*, [70]); (3) resistance traits of individual trees of a population (but see [64]), and (4) a trade-off between reproduction and chemical defence [71] that could influence infestation-related changes in **population growth rates**.

Synthetic knowledge

While comparative studies on how the vulnerability of trees to pests and pathogens is related to tree life histories have not yet been conducted, this is a promising future direction. First, if pests and pathogens primarily cause mortality of large tree individuals [39] (but see [64]), we expect tree species with slow life history strategies to be more vulnerable. Second, we expect that the species' mortality rate during the reproductive stage in conjunction with allocation trade-offs between reproduction and defence [71] might affect the species' overall reproductive output. And third, tree species with longer **generation times** may have a higher potential to show plasticity [72]. Yet, they may also have a lower potential to evolve resistance due to slower responses to selection, especially if there are no resistant genotypes present at the time of infestation [73]. Whether rare or common species are more vulnerable to pest and pathogen infections will depend on the interplay between spatial aggregation, vital rates, and resistancegene diversity of the host-tree (cf. [74]). In addition, our current knowledge on tree vulnerability comes mostly from temperate host-pest systems, and studies in the tropics are needed to achieve a global understanding.

Selective logging

Demographic studies that consider the effects of selective logging on the full life-cycle of trees primarily come from the Neotropics and Africa. In these regions, selective logging is more common and important than in Southeast Asia [75,76], where the tree community is primarily composed of high value timber species. The goal of these studies is to assess the effects of repeated removal of large/reproductive individuals on population size or 'harvestable timber volume', and to identify species-specific requirements for minimum cutting diameters, rotation lengths, and/or the number of retained seed trees that enable sustained timber yields [77].

Data, approaches, and challenges

Although the design of species-specific harvesting regimes is recommended for all high-value timber species [78], detailed demographic studies have only been carried out for a few species, mostly in Brazil (*e.g.*, [79,80]). MPMs, IPMs, and hybrid models are often parameterized using vital rates from intact (*i.e.*, unlogged) forests. Thus, most of these models do not consider that the removal of large trees creates canopy gaps that temporarily increase light availability, potentially benefiting recruitment and growth of remaining individuals [38].

In population models, performance differences between individual trees can be incorporated through growth autocorrelation of individuals [81], *e.g.*, estimated from tree-rings [82]. Spatiallyexplicit IBMs by definition account for spatial and temporal heterogeneity in light. However, only the IBM ‘SELVA’ has been applied so far in the context of selective logging [86]. Incorporating gap-dependent recruitment in this model significantly improved post-logging recovery of *Dicorynia guianensis*, a major timber species in French Guiana [83], but not in other species [81,84].

Many valuable light-demanding timber species require larger canopy openings for successful recruitment than the openings typically created by low-intensity logging [76,85]. However, even for premium timber species, such as mahogany, specific light requirements for successful regeneration are uncertain. This shortcoming hampers reliable assessments of species vulnerability to selective logging and the design of sustainable management strategies [81].

Synthetic knowledge

Many of the highest value timber species in the Neotropics and Africa (*e.g.*, big-leaf mahogany *Swietenia macrophylla*, cedro *Cedrela odorata*, *Tabebuia* spp, and courbaril *Hymenaea courbaril*) are relatively fast-growing and light-demanding as juveniles, and reach relatively large adult sizes [79]. In intact forests, they often show ‘flat’ diameter distributions with few small trees and can be classified as long-lived pioneers [86]. Demographic studies including multiple species show that these fast-growing but poorly-recruiting species as well as species with small size at maturity (*e.g.*, *Jacaranda copaia*, *Simarouba amara*, *Symphonia globulifera*) are less vulnerable to logging than slow-growing species and/or species with large reproductive size [79,80,84,87,88], because they reach their reproductive size/age before the next rotation, ensuring continued recruitment.

This coincides with the recommendation that the logging rotation length should be determined by the ‘age at minimum commercial size’ [89], which is likely correlated with reproductive age.

The proportion of individuals in small size classes is another important indicator for the population recovery of trees after selective logging [35,79,84]. For tree species with a high proportion of small stems, populations recover quickly after logging, and reducing logging intensity by increasing minimum cutting diameters or seed tree retention can improve recovery even more [79]. For species with a low proportion of small individuals, increasing minimum cutting diameters improves recovery for some species [79–81,90], but not for others [79].

Synthesising which demographic knowledge is needed across threats

Our review shows that, to date, we have an often incomplete understanding of how threats affect vital rates of trees, and how trees’ life history strategies, including their reproductive strategy, influence their vulnerability to different threats. Yet, such information is key to improving quantitative vulnerability assessments. To close this gap, we identified three research areas: (1) improving data coverage for mortality and recruitment, (2) performing sensitivity analyses and systematic modelling exercises, and (3) accounting for interactions among threats across different scales.

Improving data coverage for mortality and recruitment

To assess which tree life stages are most critical for species vulnerability to threats, full life-cycle models need to be parameterized, requiring detailed data on mortality and pre-recruitment life-stages. Estimating threat effects on mortality is difficult for most tree species, because overall mortality is low, especially in large old trees, and large sample sizes are necessary to detect change (*e.g.*, a change from 1% to 3% mortality can dramatically decrease tree longevity, but is difficult to detect) [13,57]. However, tree densities in large size classes are low, and in some biomes, *e.g.* temperate forests, old-growth forests are rare, precluding precise mortality estimation for old and senescent trees. Several recent research avenues are already improving tree mortality estimates, such as remote sensing technology to monitor mortality of large trees [91], Bayesian modelling to account for data sparseness [38,92], changepoint detection statistics in mortality analyses [13], and dendrochronological dating of tree deaths to distinguish between continuous and episodic patterns of tree mortality (*e.g.*, related to infestations, or drought) [93].

Data on reproduction, dispersal and seedling vital rates are often lacking [94,95]. Most forest inventories cover only data of individuals that have reached recruitment status (Table 1). To improve our understanding on which of the vital rates in the early life stages are crucial for population viability, extensive data collection efforts are needed, such as forest inventories with nested design covering seeds and seedlings (see *e.g.*, [96], https://www.forestgeo.si.edu/research-programs/flowers-seeds-and-seedlings-initiative). Moreover, seed production and seedling establishment and their responses to climate are highly variable spatio-temporally [97]. The appropriate examination of this pattern calls for distributed observation networks to collect demographic data across the range of a species (*cf*. PlantPopNet, or MASTIF network). Reproductive success likely depends on resource availability, which changes over the course of forest succession. Thus, to better assess the vulnerability of species to threats, data on species' resource requirements are urgently needed, *e.g.*, on light requirements for successful regeneration in selectively logged species [81].

So far, viability analyses have been biased towards temperate tree species as well as high-value timber species of the (sub-)tropics. Comparative studies based on standardised demographic data across many tree species differing in phylogeny, life history and biome (*cf.* ForestGEO network, [98]) are necessary for cross-species vulnerability assessments.

Incorporating sensitivity analyses and performing systematic modelling exercises

As the demographic modelling approaches outlined in our review suffer from different limitations (see Box 2), we suggest combined approaches and systematic modelling exercises. One such combined approach is a sensitivity analysis performed with PPA models based on estimates of vital rates [25,99] to assess the relative importance of different vital rates for population growth rates in variable environments [24,100]. For instance, increased mortality of large individuals due to drought might be more relevant for slow-growing species than for fast-growing species. Such sensitivity analyses may allow conservation management to better target the most sensitive life stages of species with certain demographic strategies.

Much of the demographic data required to parameterize full life-cycle models of trees are difficult to obtain. Even using functional traits to predict demographic rates is still challenging [101]. Thus, in cases where data are scarce, we suggest performing systematic modelling of vital rates with IBMs, which explicitly account for changes in light availability as is caused by threat-related mortality. IBMs could simulate variation in vital rates due to different climatic range positions of a population (cf. [102]) or contingent upon different conservation measures, they could mimic the interplay among the spatial aggregation of host tree species, disease-related density-dependent mortality, and pest dispersal (cf. [103]), or combine parameterisations for single species (harvested species) and those for plant functional types (remaining species) (cf. [25]).

Integrating interactions among threats across different scales

Ideally, the systematic modelling exercises would also incorporate interaction effects between threats, such as between drought-stress, insect attacks, and/or fires [104]. Such an implementation is even more challenging, since the scales at which these threats affect tree populations can vary in space and time [105]. Moreover, as environmental site conditions can alter demographic responses of tree populations to biotic and abiotic threats [102], models would need to incorporate threat interactions while considering the location of a tree population within the distributional range of the species. Though previous FLMs have incorporated threat-interactions across scales (*e.g.*, iLand, [105]), these models are usually not mathematically tractable. This circumstance hampers sensitivity analyses similar to the ones proposed above for stand-scale IBM and PPA models. To understand how life history strategies translate to species vulnerability at the landscape scale, such sensitivity analyses would be urgently needed.

Concluding Remarks

Our review shows that, due to their typically high longevities, trees pose a severe data challenge that so far has hindered a synthetic understanding of the role of tree species' life history strategies for their vulnerability to different threats across space and time. These data gaps can be filled in the future with distributed observation networks (including standardised assessment of early life stages) and through links to other research fields (*e.g.,* remote sensing to improve mortality data). Where threats interact, systematic modelling exercises are a promising option.

Sensitivity analyses with PPA models or FLMs could help test which vital rates are the most critical for vulnerability to a given threat and how this vulnerability changes across a species range (see **Outstanding Questions**). Cross-species analyses are needed to assess which species, based on their demographic strategies, are most vulnerable to each threat. We argue that such a demographic framework will leverage a general understanding of tree species vulnerability to global change drivers, and will help develop targeted conservation measures focusing on the most sensitive life stages of threatened tree species.

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Boxes & Figures

Box 1 Life cycle of a tree

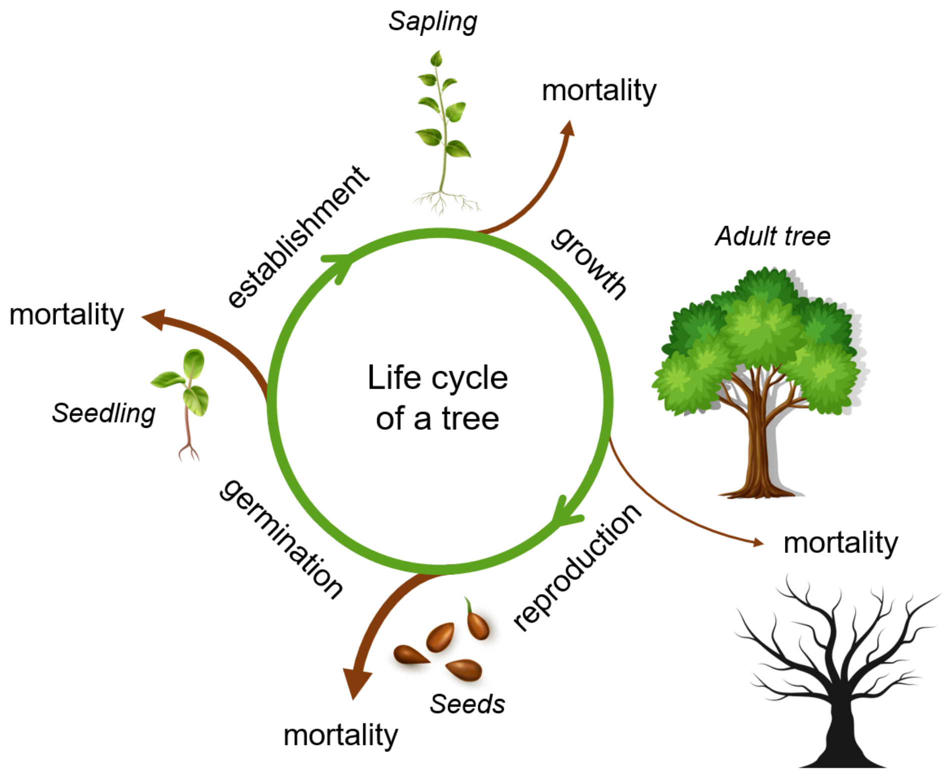


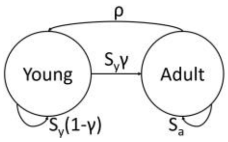
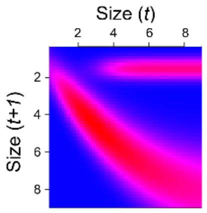
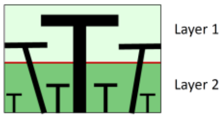
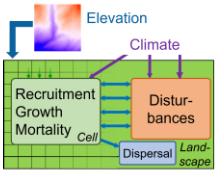
Figure I. Life cycle of a tree with vital rates. *It can take centuries for a tree to fulfil its life cycle, growing from seed to seedling to sapling to a mature tree. How reproduction is quantified varies largely among data sources and demographic modelling approaches (see Box 2 and Table 1), and how strongly reproduction varies e.g., due to climate change or pest/pathogen infestation is rarely assessed. Data on growth rates are abundant, while data availability is sparse at the beginning and end of a tree's life (germination and seedling establishment, and mortality rates of the largest adult trees, respectively), though small changes in large-tree mortality (e.g., through logging) can have large effects on a population's growth rate. Mortality rates may differ by several orders of magnitude, often being highest for seedlings and saplings, and very low for mature trees (indicated here by line thickness), though* *mortality rates may increase for very old trees, resulting in either monotonically decreasing or U-shaped curves of size-dependent mortality, respectively.*

Box 2

Demographic modelling approaches

In Table I we present a comparison of population and forest demographic models and their suitability to derive metrics identified as crucial for conservation.

Table I. Comparison of demographic modelling approaches, their representation of demographic processes, spatial and temporal scales covered, ***life history traits*** *that can be derived, other factors that can be included, and typical questions addressed by the different approaches. (Graphics: MPM – A. Compagnoni; IPM – C. Merow; PPA – N. Rüger; IBM – SpeedTree; FLM – Forest Ecology, ETH Zürich)*

	Population projection models (MPM, IPM)	**Perfect plasticity approximation (PPA) models**	**Individual based models / forest gap models (IBM)**	**Forest landscape models (FLM)**
	 			

Description	represent populations based on the demography of size, and sometimes age classes	sub-divide forest stands into dynamic canopy layers to approximate competitive interactions	simulate the dynamics of individuals or **tree cohorts**; represent demographic processes and their responses to intra- and inter-specific competition and site conditions	represent the cohort dynamics of single species based on their demography and physiology (local scale dynamics typically based on IBMs, landscape scale dynamics incorporate interactions of dispersal and disturbances
Level of representation of vital rates	MPM: discrete classes (*e.g.*, size or age) IPM: discrete (*e.g.*, age) and continuous (*e.g.*, size) classes	dynamics of tree cohorts in discrete canopy layers	dynamics of individual trees or tree cohorts	cohort dynamics of single species

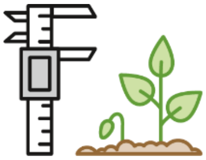
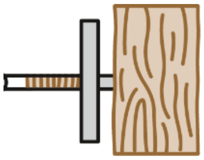
Spatial scale	non-spatial (but see [106])	tree gap to stand scale	tree gap to stand scale	landscape (100k ha or more)
Temporal scale	most studies examine asymptotic population growth rate	up to centuries of forest dynamics	up to centuries of forest dynamics	long-term (>100yrs)
Mathematically tractable	yes	yes	no	no
Sensitivity analyses	common	uncommon, but computationally feasible	uncommon (computationally expensive)	uncommon (computationally expensive)
Life history traits that can be derived (examples)	net reproductive rate (R_0), asymptotic population growth rate (λ), generation time, degree of iteroparity	population growth rate (potentially, more life history traits could be derived)	population growth rate (potentially, more life history traits could be derived)	population growth rate (potentially, more life history traits could be derived)

Including competition for light	no (but see [107])	yes	yes	no (but see exceptions in [27])
Incorporating effects of site conditions and climate	yes	yes	possible (but only a small proportion of the models do this)	yes
Accounting for disturbances	yes	possible	yes	yes
Typical questions addressed	population responses to management, disturbance, climate, pathogens, herbivory. Biological conservation (*e.g.*, Population viability analyses)	forest succession; Embed demography into Earth System Models	forest succession in response to disturbance, climate, and management	effects of disturbances, landscape composition, and dispersal on long-term forest dynamics; effects of forest management

Strengths and limitations of four main demographic modelling approaches and their suitability for conservation assessments: Population projection models are the standard tool for comparative demographic analyses, sensitivity analyses, and population viability analyses [14,22]. On the other hand, MPMs are problematic in trees, because by subdividing the population in a few discrete classes, their estimates can be imprecise in the long term [19]. Moreover, these tools cannot satisfactorily describe light competition among trees [107]. Light competition is modelled successfully by IBMs, which can therefore produce accurate forecasts of population dynamics [42]. However, both population models and IBMs most often refer to single sites because of data (population projection models) and computational (IBMs) limitations. These limitations are addressed by FLMs, which use forest inventory data and employ simplified representations of light competition to project how entire forest landscapes change over time, though assessments of prediction accuracy are generally missing in FLMs [27]. PPA models could in theory address the limitation of FLMs, because they are a tractable model of light competition, they are parameterized with forest inventory data, and they produce accurate predictions at the plot scale [24]. PPA models, like IBMs and FLMs, have occasionally been employed for comparative demographic analyses (see *e.g.*, [108]) but have not incorporated sensitivity analyses. However, this limitation could be in principle overcome in PPA models by exploiting their mathematical tractability. A promising approach are hybrid models that extend IBMs to include growth autocorrelation [81] or size-dependent survival functions (*e.g.* ‘individual-based forward simulation’ in [107], or 'demographic process model' in [96]). These are ways to quantify vital rates over size, or individual heterogeneity, which can improve performance and inference of the original models.

Table 1 Sources of tree demographic data.

Comparison of sources of tree demographic data that can be used as input to the models in Box 2 and beyond.

	Population studies 	**Forest inventory data** 	**Tree-ring data** 
Description	detailed demographic measurements covering all life cycle components of a single species to assess population dynamics and its drivers; data often collected to parameterize population models (MPMs, IPMs)	repeated census of individual size and status (alive, dead) of all trees in a plot above a minimum size threshold: a) large plots b) spatially distributed small plots c) (sub)national forest inventories	tree age and annual growth (ring width) can be derived from tree cores; can be used to assess sensitivity of growth rates of different life stages to environmental variation, incl. climate change or pest and pathogen infection

Measurement interval	most often annually, but up to 10 years	often 5-10 years	annual growth rings
Study duration	most often <5 years	often long-term (>20 years)	lifespan of tree individuals
Spatial scale	often restricted to few populations (locations)	a) single location b) several/many locations across an environmental gradient c) regular grid	often restricted to few individuals at one location or several locations across an environmental gradient
Coverage of life cycle	often extensive, *i.e.*, including reproduction, germination, seedling dynamics	size threshold a) often 1 cm dbh b) often 5 cm dbh c) often 7 or 10 cm dbh	>1.3 m (cores usually taken at breast height), usually no information on smaller life stages and population-level rates (recruitment, mortality)

Miscellaneous	difficult to parameterize for long-lived organisms such as trees	- capture entire community, but little information on rare species - if spatial coordinates are recorded, neighborhood interactions can be quantified - when using national forest inventories, plots without silviculture might need to be selected	- mostly in biomes with seasonal climate, few species with tree rings in the tropics - biases need to be accounted for (*e.g.,* sampling bias towards old trees at marginal sites) - allow inferring climate-sensitivity of growth
Example databases/ networks	COMPADRE, PADRINO	a) ForestGEO b) Afritron, Global Ecosystem Monitoring network (GEM) c) Global Forest Biodiversity Initiative (GFBI), FunDivEurope (including several national forest	International Tree-Ring Data Bank (ITRDB)

		inventories), US Forest Inventory and Analysis	

Glossary

Extinction debt: time for declining populations to disappear following environmental perturbations.

Generation time: the average age of reproductive individuals in a population. In the case of trees, the average age of 'parents' of new germinants.

Life history strategy (also 'Demographic strategy'): a species' tactic with respect to patterns of resource allocation to and timing of survival, growth, and reproduction; the range of strategies is constrained by trade-offs between vital rates.

Life history trait (also 'Demographic metric'): traits derived from vital rates (below) via demographic models, *e.g.*, age at maturity, size at maturity, reproductive value, generation time, lifespan/longevity.

Lifespan/longevity: the expected age at death of individuals in a population. In trees, average lifespan can vary substantially, depending on which individuals are counted as part of the population (*e.g.*, all trees starting from seedlings or only canopy trees). Hence, there can be a large difference between average lifespan and maximum longevity of a species.

Life table response experiment (LTRE): uses the vital rates of an organism as the response variable in studies of the population-level response to different environmental or biological factors (*e.g.*, different drought severity levels; infested *vs.* non-infested).

Population growth rate (λ): the expected, long-term rate of change in population size per unit time, *e.g*., the average annual population growth rate.

Population viability analyses (PVA): evaluate the threats faced by populations of species, their risks of extinction or decline, and their chances for recovery under a variety of conditions, often based on species-specific demographic data and models.

Recruitment: the rate of individuals of a species crossing a specified size threshold (*e.g.*, > 2m height, or >10 cm diameter at breast height), typically expressed as number of individuals per ha per year, or per adult basal area per year.

Reproduction: the reproductive output of an individual; for trees often estimated as seed mass produced by a tree of a given species and size, or approximated based on the recruitment of new trees (see also 'Recruitment' above). This can be done via seed traps, or by assuming the ratio of seedlings in time *t+1* is proportional to the reproductive effort (*e.g.*, number of flowers/cones) in time *t*.

Resilience: the ability of a system to res a disturbance**.**

Sensitivity analysis: quantification of changes in a system's property (*e.g.*, the growth rate of a population) in response to an infinitesimally small change in one of its components (*e.g.*, a vital rate in the population).

Tree cohort: a collection of individual trees of the same species expected to have the same vital rates (in a given microhabitat), often characterized by being the same age and/or size.

Vital rate (also 'Demographic rate'): any of the demographic processes that aid in the completion of the life cycle of a species. *E.g.*, survival, growth, reproduction.

Vulnerability: the sensitivity of a population to a threat, depending on how strongly the threat affects one or several vital rates and how sensitive the population growth rate is to changes in the vital rate(s).

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