

FORUM

The COMPADRE Plant Matrix Database: an open online repository for plant demography

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Summary

1. Schedules of survival, growth and reproduction are key life-history traits. Data on how these traits vary among species and populations are fundamental to our understanding of the ecological conditions that have shaped plant evolution. Because these demographic schedules determine population

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growth or decline, such data help us understand how different biomes shape plant ecology, how plant populations and communities respond to global change and how to develop successful management tools for endangered or invasive species.

2. Matrix population models summarize the life cycle components of survival, growth and reproduction, while explicitly acknowledging heterogeneity among classes of individuals in the population. Matrix models have comparable structures, and their emergent measures of population dynamics, such as population growth rate or mean life expectancy, have direct biological interpretations, facilitating comparisons among populations and species.

3. Thousands of plant matrix population models have been parameterized from empirical data, but they are largely dispersed through peer-reviewed and grey literature, and thus remain inaccessible for synthetic analysis. Here, we introduce the COMPADRE Plant Matrix Database version 3.0, an open-source online repository containing 468 studies from 598 species world-wide (672 species hits, when accounting for species studied in more than one source), with a total of 5621 matrices. COMPADRE also contains relevant ancillary information (e.g. ecoregion, growth form, taxonomy, phylogeny) that facilitates interpretation of the numerous demographic metrics that can be derived from the matrices.

4. *Synthesis.* Large collections of data allow broad questions to be addressed at the global scale, for example, in genetics (GENBANK), functional plant ecology (TRY, BIEN, D3) and grassland community ecology (NUTNET). Here, we present COMPADRE, a similarly data-rich and ecologically relevant resource for plant demography. Open access to this information, its frequent updates and its integration with other online resources will allow researchers to address timely and important ecological and evolutionary questions.

Key-words: big data, comparative approach, elasticity, matrix population model, open access, plant population and community dynamics, population growth rate, sensitivity, transient dynamics

Introduction

Demography is central to the understanding of ecology and evolution (Metcalf & Pavard 2007). The environment affects populations through its impacts on the vital rates of individuals (e.g. survival, growth, development, reproduction, dispersal), and those effects commonly differ among life cycle stages. Indeed, genetic variance in vital rates represents the foundation of fitness differences and thus the building blocks on which natural selection operates (Lande 1982). Thus, projections of demographic performance such as population growth rate and structure, equilibrium density, viability, and risk of local extinction are appropriately calculated using stage-structured models. Structured population models (Tuljapurkar & Caswell 1996) provide a convenient mathematical framework to connect variation in vital rates throughout an organism's life cycle to its population dynamics. These models have been formulated as partial differential equations (McKendrick 1926; Kermack & McKendrick 1939), matrix population models (Leslie 1945; Lefkovich 1965; Caswell 2001), delay differential equations (Nisbet 1997; Gurney, Blythe & Stokes 1999), integro-difference equations [the most relevant of which are, in the context of this manuscript, integral projection models (IPMs); Easterling, Ellner & Dixon 2000; Ellner & Rees 2006] and other mathematical frameworks, as reviewed elsewhere (Keyfitz 1967; Metz & Diekmann 1986; Nisbet, Gurney & Metz 1989; Tuljapurkar & Caswell 1996; Caswell 2001).

Matrix population models (MPMs hereafter) are the most widely used structured population models among plant population ecologists (Salguero-Gómez & de Kroon 2010;

Crone *et al.* 2011). The popularity of MPMs arose from their (i) straightforward formulation, (ii) value at assembling complex data in an analytically tractable framework, (iii) solid mathematical foundations and (iv) clear biological interpretation of their outputs (e.g. the dominant eigenvalue corresponds to the population growth rate λ). MPMs are constructed by identifying multiple stages into which a species' life cycle can be classified, either based on biological knowledge or various optimization algorithms (Vandermeer 1978; Moloney 1988; Salguero-Gómez & Plotkin 2010). Individuals within each stage are then characterized by their likelihood of surviving and either remaining in that stage or transitioning to another, and their contributions to sexual or clonal recruitment stages (for a detailed treatment, see Caswell 2001). This division of the life cycle into stages allows for the explicit incorporation of one of the most fundamental aspects of the study of demography: not all individuals in a population contribute equally to its dynamics; for example, seedlings have low survival and no reproductive output, whereas large plants typically have high survival and a large reproductive output.

Matrix population models describe the dynamics of populations over a discrete projection interval:

$$\mathbf{n}(t+1) = \mathbf{A} \mathbf{n}(t) \quad (1)$$

where $\mathbf{n}(t)$ and $\mathbf{n}(t+1)$ are population vectors containing the number of individuals in each life cycle stage at times t and $t+1$, respectively, and \mathbf{A} is the population projection matrix. The projection interval can vary from days (Hamda, Jevtic & Laskowski 2012) to weeks (J. Metcalf, pers. comm.), months

(Griffith 2010), a single year (Quintana-Ascencio, Menges & Weekley 2003; Lucas, Forseth & Casper 2008), a quinquennial or more (Shimatani *et al.* 2007; Yamada *et al.* 2007).

The nature of the matrix A determines the type of MPM. If the entries of A are fixed, the model is time invariant and provides all the classical demographic results of linear models. Time-varying models include periodic, density-dependent and stochastic models, depending on the nature of the variation in $A(t)$. In nonlinear models, $A(n)$ depends on the population vector n . The projection matrix may also depend on the state of the environment. All these types of models are reviewed in Caswell (2001). New analytical techniques for MPMs are being developed rapidly, and many of these have already led to applications for plants. Some of these applications include the study of stochastic population dynamics under the impact of fires, floods or hurricanes (Caswell & Kaye 2001; Horvitz, Tuljapourkar & Pascarella 2005; Smith, Caswell & Mettler-Cherry 2005); extraction of age-specific information from stage-specific models (Cochran & Ellner 1992; Lebreton 2005; Caswell 2006, 2009; Tuljapourkar & Horvitz 2006; Horvitz & Tuljapourkar 2008) to explore the evolution of senescence in plants (Baudisch *et al.* 2013; Caswell & Salguero-Gómez 2013); spatial models for stage-structured invasions (Neubert & Caswell 2000; Buckley *et al.* 2005; Caplat, Nathan & Buckley 2012); density-dependent models in plants (Ramula & Buckley 2009), as well as bifurcation and sensitivity analyses in plants (Shyu *et al.* 2013); periodic models for seasonal population dynamics (Caswell & Trevisan 1994; Pico, de Kroon & Retana 2002; Bacaer 2009) (Caswell 2001); and short-term population dynamics (Verdy & Caswell 2008; Stott *et al.* 2010; Stott, Townley & Hodgson 2011) applied to a variety of species, including threatened and invasive species (Le Corff & Horvitz 2005; Hahn, Buckley & Muller-Scharer 2012).

Hundreds of studies in plant population biology have been published using MPMs. This rapid accumulation of demographic data, together with a commitment to open-access information by funding agencies, journals and researchers (Van Noorden 2012), now allows us to (i) address questions not yet answered due to the lack of global demographic data and (ii) revisit conclusions drawn on the basis of smaller data sets. To facilitate these new endeavours, we introduce the COMPADRE Plant Matrix Database (COMPADRE, for short), an open-access online repository of plant (MPM-based) population dynamics. COMPADRE (version 3.0) contains MPMs from 468 studies with 598 plant species, as well as ancillary information that allows for in-depth interpretation of the species' demography, such as geographic location of the study populations, ecoregion, study periods, treatments and plant growth form descriptors (see 'What is in the COMPADRE portal?' below).

COMPADRE is the result of efforts initiated over 25 years ago (Franco & Silvertown 1990) and later continued in parallel by several research groups, before being recently integrated into a single repository. The information in the database has been standardized and error-checked to facilitate user analyses and made publicly available at www.compadre-db.org. The goal of this publication is to introduce and describe this resource.

We first offer a historical description of its origins and development; next, we explain how the database is managed and organized, and detail its current content. Finally, we briefly highlight its research potential and suggest future directions towards improving our understanding of plant population dynamics world-wide.

A historical perspective: from Leslie to COMPADRE 3.0

Introduced by Bernardelli (1941) and Leslie (1945, 1948), MPMs were largely neglected by ecologists, evolutionary biologists and demographers for two decades. The pioneering work of Lefkovich (1965) and Keyfitz (1964) (Fig. 1) indicated the potential of MPMs to examine how individuals contribute to a population's dynamics as a function of attributes such as age, ontogeny, size, spatial location and causes of death. Plant ecologists, who by the 1960s had realized that plant demography often depends more on size or ontogeny than age (Harper 1967; Harper & White 1974; Werner 1975), started adopting stage-structured MPMs in their research (Usher 1966; Sarukhan & Gadgil 1974; Hartshorn 1975; Werner & Caswell 1977).

COMPADRE 1.0, which previously stood for comparative plant demographic research, was founded in 1989 (J. Silvertown & M. Franco). A decade after its creation, it archived 105 plant species with their corresponding MPMs averaged across periods and populations. This number contrasted sharply with the handful of publications with MPMs available by 1986 (Table 8 in Caswell 1986). COMPADRE 1.0 resulted in several seminal publications on comparative demography including the exploration of the fast-slow continuum in the plant kingdom (Franco & Silvertown 1997), the evolution of senescence in plants (Silvertown, Franco & Perez-Ishiwara 2001) and the broad state of the art of plant population ecology (Franco & Silvertown 1990). Silvertown and Franco's approach of partitioning the elasticity of population growth rate into three main components – stasis, growth and reproduction – enabled interspecific comparison of basic demographic properties across the plant kingdom (Silvertown, Franco & McConway 1992; Silvertown *et al.* 1993). Briefly, the authors calculated the relative contribution of the stasis, growth and reproduction matrix elements to the population growth rate (λ) (elasticities *sensu* de Kroon *et al.* 1986) and used them to locate species onto a ternary plot space. Refinement of this method to estimate the elasticity of the basic vital rates survival, growth and fecundity, rather than that of matrix elements that only approximate them (Franco & Silvertown 2004) triggered interest in the comparative use of MPMs for hundreds of plant species (Crone *et al.* 2011). This approach also helped to establish links between demography and conservation biology (Silvertown, Franco & Menges 1996; Crone *et al.* 2013).

Following COMPADRE 1.0, various research teams continued MPM digitization, either building upon COMPADRE 1.0 (COMPADRE 2.0; R. Salguero-Gómez, D. Hodgson), or starting anew (e.g. Iriando *et al.* 2009; Ellis *et al.* 2012). The development of various MPM repositories resulted in publications examining a wide range of topics. These include comparative

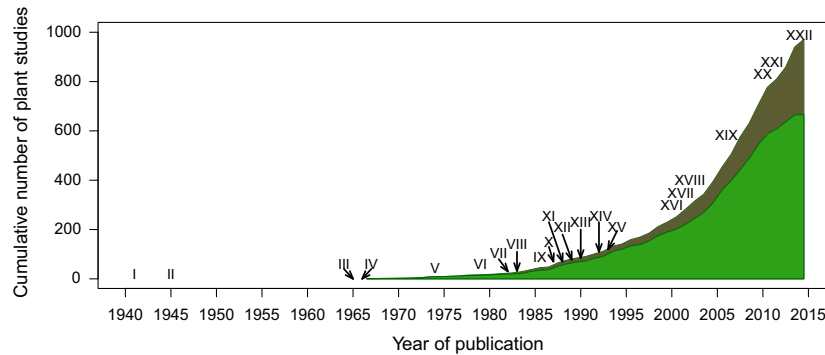


Fig. 1. Timeline of the cumulative number of studies published up until 20 July 2014 containing matrix population models (MPMs) in peer-reviewed journals, books, reports and theses. Light green background corresponds to studies released in COMPADRE 3.0; dark green corresponds to studies under inspection, to be released in future versions of COMPADRE. Pivotal events in the development of the COMPADRE Plant Matrix Database: (I and II) first applications of MPMs to demography (Bernardelli 1941; Leslie 1945), (III) introduction of theory for stage-classified MPMs (Lefkovich 1965), (IV) first application of MPMs to plants (Usher 1966), (V) first plant comparative demographic manuscript using MPMs (Sarukhan & Gadgil 1974), (VI) introduction of life cycle graph methods, with application to plants (Hubbell & Werner 1979), (VII) first stochastic MPM for plants (Bierzychudek 1982), (VIII) the first MPM using age and size in plants (Law 1983), (IX) introduction of elasticity analyses to MPMs illustrated with an example from plant demography (de Kroon *et al.* 1986), (X) first density-dependent MPM for plants (de Kroon, Plaisier & van Groenendaal 1987), (XI) first formalized quantitative approach to distinguish age- and size-dependent demography (Caswell 1988), (XII) birth of COMPADRE and first edition of the *Matrix Population Models: Construction, Analysis, and Interpretation* (Caswell 1989), (XIII) publication of *Population Dynamics in Variable Environments* (Tuljapourkar 1990), (XIV) first plant Life Table Response Experiment analysis (Silva *et al.* 1991), (XV) first comparative plant demography publication (Silvertown *et al.* 1993), (XVI) first special feature on MPMs (Heppell, Pfister & de Kroon 2000) and first analysis of invasion speed for plant populations (Neubert & Caswell 2000), (XVII) second edition of *Matrix Population Models* (Caswell 2001), (XVIII) publication of *Quantitative Conservation Biology: Theory and Practice of Population Viability Analysis* (Morris & Doak 2002) summarizing and stimulating applications of MPMs to conservation, (XIX) development of COMPADRE 2.0, (XX) second special feature on MPMs (Salguero-Gómez & de Kroon 2010), (XXI) development of the COMPADRE Plant Population Database 3.0 and (XXII) its online open access release in www.compadre-db.org.

demography of native and invasive populations (Ramula *et al.* 2008), effects of environmental stochasticity on plant population dynamics (Buckley *et al.* 2010), plant life-history evolution (Burns *et al.* 2010), the importance of plant shrinkage for population dynamics (Salguero-Gómez & Casper 2007), the first comparative exploration of short-term dynamics (Stott *et al.* 2010) and an assessment of utility for recovery of endangered species (Zeigler, Che-Castaldo & Neel 2013).

The current database, COMPADRE 3.0, has been hosted by the Max Planck Institute for Demographic Research since 2011. There, the priorities have been to (i) minimize redundant efforts in data digitization by integrating independent research groups around the world, (ii) continue archiving plant demographic data, adding important ancillary information, and (iii) build an online portal to share the information on an open-access basis. The efforts have entailed incorporating parallel MPM databases into a single repository and significantly scaling up the digitization (See *Internal Organization* below) of both published MPMs and MPMs obtained directly from the authors or calculated by us (Table 1). The third priority, building an online portal, is described in more detail in the section *What is in the COMPADRE portal?* (below).

The COMPADRE Plant Matrix Database

INTERNAL ORGANIZATION

The continuous increase in published MPMs in the recent decades (Fig. 1) requires a coordinated effort to search,

digitize, error-check and release the information (Fig. 2). To facilitate this, COMPADRE is supported by two committees and a digitization team. The core committee (Appendix S1 in Supporting Information) is responsible for creating and updating protocols for data search, digitization, error-check and release, and for the overall infrastructure of the database and the internal organization of COMPADRE. The science committee, composed of a group of expert demographers located world-wide, provides external advice to the core committee on future directions, helps expand the geographic reach of COMPADRE and supplies the COMPADRE digitization team with grey literature. Both committees work together to secure funding for COMPADRE in the long term.

The COMPADRE digitization team primarily digitizes published information containing plant MPMs and ancillary information. The team is composed of students and postdoctoral fellows primarily based at the MPIDR (but see Appendix S1). The team has been trained in population ecology, MPMs and database archiving by the project leaders. In addition to entering information in a standardized format (Table 1; Fig. 3; Appendix S2), they contact authors to request information that is not included in the publication, or for help interpreting demographic information and carrying out error-checks.

FROM THE FIELD TO THE SCIENTIFIC COMMUNITY

Our work in COMPADRE starts when the work of the authors ends. After authors have collected plant demographic data, parameterized MPMs and – for the most part – published

Table 1. Variable names and meaning contain in the COMPADRE Plant Matrix Database, organized by seven general aspects: taxonomy, plant architecture, source, details of study, geolocation and matrix population model. A more detailed description can be found in the user protocol of COMPADRE in www.compadre-db.org

Aspect	Variable	Description
Taxonomy*	<i>SpeciesAuthor</i>	Taxonomic species name as used by the author(s) in the publication. When more than one study exists for the same species, these are given sequential numeric suffixes (e.g. <i>Cirsum_pitcheri</i> , <i>Cirsum_pitcheri_2</i> , <i>Cirsum_pitcheri_3</i>)
	<i>SpeciesAccepted</i>	Currently accepted taxonomic name as used by The Plant List (www.theplantlist.org). See the Appendix S3 for an R script to check accepted and synonym names from <i>SpeciesAuthor</i> above
	<i>Authority</i>	Taxonomic authority of <i>SpeciesAccepted</i>
	<i>TaxonomicStatus</i>	Whether <i>SpeciesAuthor</i> is currently accepted or synonym of <i>SpeciesAccepted</i> , as per The Plant List
	<i>TPLVersion</i>	Version of The Plant List used for taxonomic validation
	<i>InfraspecificAccepted</i>	Taxonomic intraspecific name of study species, as per The Plant List
	<i>SpeciesEpithetAccepted</i>	Taxonomic species epithet of study species, as per The Plant List
	<i>GenusAccepted</i>	Taxonomic genus of study species, as per The Plant List
	<i>Genus</i>	Taxonomic genus of study species, as in <i>SpeciesAuthor</i>
	<i>Family</i>	Taxonomic family of study species
	<i>Order</i>	Taxonomic order of study species
	<i>Class</i>	Taxonomic class of study species
	<i>DicotMonocot</i>	Whether study species is a dicot, a monocot or neither
	<i>AngioGymno</i>	Whether study species is an angiosperm, a gymnosperm or neither
	<i>Phylum</i>	Taxonomic phylum of study species
	<i>Kingdom</i>	Taxonomic kingdom of species. Note that while COMPADRE's main focus is in the Plantae Kingdom, it also contains a few MPMs from species that do not belong to this kingdom. Nonetheless, these are included in COMPADRE due to taxonomic inertia and their demographic similarity with true plants (e.g. 68 MPMs from red algae, kingdom Chromalveolata)
Architecture* Source of information*	<i>AngioGymno</i>	Whether species is an angiosperm, gymnosperm or neither
	<i>GrowthType</i>	General functional type of the species (e.g. annual, fern, liana, herbaceous perennial; Table 2)
	<i>Authors</i>	Last names of full authorship in study
	<i>Journal</i>	Abbreviated journal of publication (www.abbreviations.com/jas.php), otherwise stated as 'PhD thesis' ($n = 44$), 'MSc thesis' (2), 'BSc thesis' (2), 'Book' (53), 'Report' (3) or 'Internet' (1)
	<i>YearPublication</i>	Year of publication of study
	<i>DOI/ISBN</i>	Digital object identifier (for manuscripts) or international standard book number (for books), when available; old publications do not have an assigned DOI. An R script is also provided to obtain full citation from manuscripts based on DOI (Appendix S3)
Details of the study*	<i>AdditionalSource</i>	If additional information was obtained from a secondary source, the abbreviated citation is included here (first author's first last name, abbreviated journal name and publication year; e.g. Godinez-Alvarez <i>Bot Rev</i> 2003 for <i>Escontria chiotilla</i>)
	<i>StudyDuration</i>	Years of observation of the population dynamics of the species, calculated as $StudyEnd - StudyStart + 1$ (e.g. 2005–2000 + 1 = 6)
	<i>StudyStart</i>	Year the study started
	<i>StudyEnd</i>	Year the study ended
	<i>AnnualPeriodicity</i>	Frequency with which seasonal or annual MPMs were constructed (e.g. 1: once per year; 2: twice per year; 0.2: once every five years)
	<i>NumberPopulations</i>	Number of populations examined in the study – These may not match the number of populations with MPMs in COMPADRE 3.0 if the author has not made available all of the MPMs
Location†	<i>MatrixCriteriaSize</i>	Whether and on which biometric aspects of the species was the MPM constructed
	<i>MatrixCriteriaOntogeny</i>	Whether some aspect of the developmental stage of the species was used to construct the MPM
	<i>MatrixCriteriaAge</i>	Whether some aspect of the age of the species was used to construct the MPM
	<i>MatrixPopulation</i>	Name(s) of populations from which the MPM was constructed. When no population name is provided in the source, the name of closest geographic landmark or letters in alphabetical (e.g. 'A', 'B', 'C'...) or numerical order (e.g. '1', '2', '3'...) are used
	GPS location	
	<i>LatDeg</i>	Latitudinal degrees of study population
	<i>LatMin</i>	Latitudinal minutes of study population
	<i>LatSec</i>	Latitudinal seconds of study population
	<i>LatNS</i>	Latitudinal cardinal direction: North or South
	<i>LonDeg</i>	Longitudinal degrees of study population
	<i>LonMin</i>	Longitudinal minutes of study population

(continued)

Table 1. (continued)

Aspect	Variable	Description
Details of matrix population model†	<i>LonSec</i>	Longitudinal seconds of study population
	<i>LonWE</i>	Longitudinal cardinal direction: West or East
	<i>Altitude</i>	Altitude of study population (in metres) obtained from Google Earth
	<i>Country</i>	Country or countries where the study population was studied. Here, only countries currently accepted by the United Nations according to the ISO 3 list were employed (http://unstats.un.org/unsd/tradekb/Knowledgebase/Country-Code)
	<i>Continent</i>	Continent of the study population
	<i>Ecoregion</i>	Description of the terrestrial or aquatic ecoregion, corresponding to Olson <i>et al.</i> 's classification (2001), where the study took place. When the study is undertaken in its majority under controlled, indoor conditions (e.g. laboratory, glasshouse), this is noted as 'LAB'
	<i>StudiedSex</i>	Sex(es) considered to construct the MPM
	<i>MatrixComposite</i>	MPMs were differentiated among matrices that correspond to a given single population, single treatment and single annual period ('individual'; Fig. 4), to a single population, treatment and intra-annual period ('seasonal'), to a MPM that is the result of element-by-element arithmetic mean ('mean'), or where the individual-level data were pooled to construct a MPM over various periods, populations and/or treatments ('pooled'). We must note that by default we calculated the mean MPM when all individual MPMs in the study were made available. The pooled and mean matrices for all the individual, unmanipulated (see <i>MatrixTreatment</i>) MPMs coincide when the sample sizes and stage distributions at time <i>t</i> are the same across all the individual MPMs. Mean MPMs were only calculated by us for unmanipulated individual matrices (see below)
	<i>MatrixTreatment</i>	Treatment to which the demographic data used to parameterize the specific MPM was subjected. We specified 'unmanipulated' as those matrices where no human-led experimentation was carried out. Users are encouraged to carefully examine variable <i>MatrixObservation</i> (below) for additional pertinent information
	<i>Captivity</i>	Whether the study species was in its wild setting, or under controlled conditions (e.g. greenhouse, botanical garden) for most of the demographic data that were collected
	Start and end of study period	
	<i>MatrixStartYear</i>	Beginning year <i>t</i> for MPM <i>A</i> describing the population dynamics between time <i>t</i> and year <i>t</i> +1
	<i>MatrixStartSeason</i>	Beginning season <i>s</i> for seasonal MPM <i>B</i> describing the population dynamics between season <i>s</i> and season <i>s</i> +1
	<i>MatrixStartMonth</i>	Beginning month <i>m</i> for seasonal MPM <i>B</i> describing the population dynamics between month <i>m</i> and month <i>m</i> +1
	<i>MatrixEndYear</i>	End year <i>t</i> +1 for MPM <i>A</i> describing the population dynamics between time <i>t</i> and time <i>t</i> +1
	<i>MatrixEndSeason</i>	End season <i>s</i> +1 for seasonal MPM <i>B</i> describing the population dynamics between seasons <i>s</i> and season <i>s</i> +1
	<i>MatrixEndMonth</i>	End month <i>m</i> +1 for seasonal MPM <i>B</i> describing the population dynamics between month <i>m</i> and month <i>m</i> +1
	<i>MatrixSplit</i>	To facilitate the calculation of various demographic properties (e.g. life expectancy η_e , mean age at first reproduction L_x , vital rate sensitivities), the MPM <i>A</i> (<i>matA</i> , below) has been split into survival (<i>matU</i>), sexual (<i>matF</i>) and clonal reproduction (<i>matC</i>) submatrices (Fig. 3) when sufficient information was provided in the source. In 4% of cases, insufficient information led to us not been able to split <i>A</i> into <i>U</i> , <i>F</i> and <i>C</i> . This matrix is referred to as <i>Indivisible</i>
	<i>Observation</i>	Relevant observation that the user should bear in mind when analysing and interpreting the MPMs. In the present version, 43% of the matrices have observations. Observations include, for instance, warnings about the description by the author of an 'unmanipulated' population that some researchers may wish to treat as a treatment (e.g. natural fires), among others
	<i>MatrixClassAuthor</i>	Classification of the stages in the life cycle of the study species as described by the author
	<i>MatrixClassOrganized</i>	Standardization of <i>MatrixClassAuthor</i> into three stages: <i>prop</i> for seed banks, <i>dorm</i> for vegetatively dormant individuals and <i>active</i> for individuals photosynthetically active. We standardized <i>MatrixClassAuthor</i> in this way to facilitate cross-comparisons of various general life cycle stages. Note that other general classifications are possible, for instance, distinguishing reproductive individuals from non-reproductive individuals by evaluating the <i>F</i> and <i>C</i> submatrices
	<i>MatrixClassNumber</i>	Sequence of numbered classes from 1 to <i>MatrixDimension</i>
	<i>MatrixDimension</i>	Dimension of the MPM
	<i>SurvivalIssue</i>	Reports maximum stage-specific survival in the submatrix <i>U</i> (below). If this value > 1, users are encouraged to carefully evaluate the matrix

(continued)

Table 1. (continued)

Aspect	Variable	Description
Population matrix model [†]	<i>matA</i>	MPM including demographic processes that depend on survival (<i>SubMatrixU</i> below), sexual reproduction (if pertinent and available; <i>SubMatrixF</i> below), and clonal reproduction (if pertinent and available; <i>SubMatrixC</i> below; Fig. 3)
	<i>matU</i>	Submatrix population model describing only survival-dependent demographic processes (e.g. seed bank, stasis, progression, retrogression, vegetative dormancy). Matrix elements corresponding to sexual and clonal reproduction are filled with zeros (Fig. 3)
	<i>matF</i>	Submatrix population model describing only sexual reproduction. All other matrix elements are filled with zeros (Fig. 3)
	<i>matC</i>	Submatrix population model describing only clonal reproduction. All other matrix elements are filled with zeros (Fig. 3)

*Information that is study specific.

†Information that is matrix population model specific.

their study (Fig. 2), the first step in database digitization is for COMPADRE project leaders and the digitization team to find published MPMs. Information reaches us through two main channels: (i) personal communications (currently < 2%) and (ii) periodic searches implemented by the project leaders in the core committee. Every week (*ISI Web of Knowledge* and *Scopus*) and every day (*Google Scholar*) automated literature searches are conducted with a combination of keywords ('demography', 'elasticity', 'life cycle', 'matrix model', 'plant', 'population' and/or 'population growth rate') that target manuscripts potentially containing MPMs. These searches are complemented with automatic alerts for publications that cite important MPM methodological advancements (e.g. de Kroon *et al.* 1986; de Kroon, van Groenendael & Ehrlén 2000; Caswell 2001; Morris & Doak 2002). Finally, the project leaders and digitization team carry out searches with lower frequency (approx. 2 months) on *ProQuest* for PhD, MSc and BSc theses.

Once the publications containing MPMs have been acquired, the matrices and metadata are digitized into COMPADRE under a strict data entry protocol (Appendix S2) before being published online via the COMPADRE portal. Data provided via personal communications may alternatively be placed under an embargo period. The embargo date is chosen by the contributing author(s), and the data are released in the online portal only after the date has passed, and the authors have given explicit written permission.

WHAT IS IN THE COMPADRE PORTAL?

The fundamental piece of information in COMPADRE is the MPM. Each MPM describes the population dynamics of a given study × species × population × period × treatment combination. However, MPMs alone are of limited value. COMPADRE contains ancillary information that is study- or matrix-specific (Table 1) that allows users to interpret the MPM. A description of each variable can be found in Table 1 and in the user's guide. The information can be broadly categorized into taxonomy of the species (and its phylogenetic position in the tree of life; see Appendices S2 and S5), spe-

cies traits such as growth form or architectural organization, primary data source, study details and geographic location of the study populations. Further ancillary information specific to each MPM is also given (Table 1).

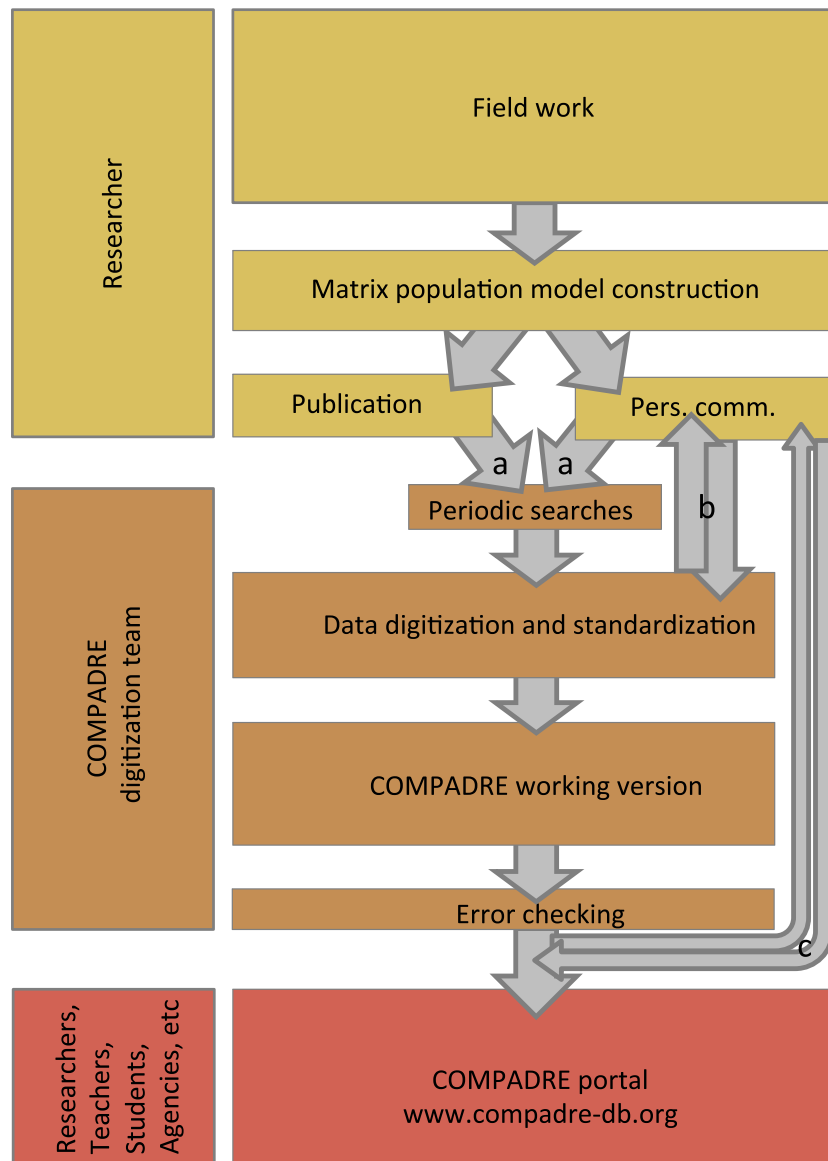
As described in the introduction, MPMs can be parameterized in various ways. The MPMs in COMPADRE contain only the matrix elements, and no underlying relationships that would describe, when available, the relationship between the vital rates and, for instance, density dependence, or environmental impacts. When possible, MPMs measured over a series of years are included, but COMPADRE does not include the stochastic models that might have been developed from that series of matrices (See *The vision: beyond COMPADRE* below).

The information available via the COMPADRE portal is completely open access after registration, and users are encouraged to employ it at their own discretion for research or teaching, but not for commercial uses. Registration and login required to access and download the data provide us with basic information (e.g. status, country, institution, email address) regarding users. This information allows the COMPADRE team to notify users if/when necessary (e.g. new data release, correcting errors, new/updated *R* scripts for matrix manipulations and analyses), as well as to obtain user statistics that will help justify grant support for the database in the long term. For these reasons, users should not share the downloaded data, but rather encourage other potential users to register and obtain the latest data set directly from COMPADRE portal.

Upon login, users are able to download four files: an *R* data object file (COMPADRE_Data-Nov_10_2014.RData) that contains the study-specific and matrix-specific information described in Table 1; the user's guide, which details how the previous file is organized (Appendix S2); a zip file containing *R* scripts for data subsetting and manipulation (Appendix S3); and a nexus file containing the phylogeny of the species included in the first file (Appendix S3).

Once a significant volume of studies has been digitized, standardized and error-checked (see *Data quality* below), that section of the COMPADRE working version is pushed to the COMPADRE portal. Following the initial release of data from 468 studies, at the time of publication of this manuscript,

Fig. 2. Workflow of search for matrix population models (MPMs) and ancillary information, digitization, standardization, error-checking and release of information in the COMPADRE Plant Matrix Database. After plant demographic data are collected, used to parameterize MPMs and published by the researchers, (a) publications containing MPMs for plants are found by the COMPADRE digitization team through frequent searches, or personally communicated by researchers, and incorporated in the COMPADRE Plant Matrix Database initial records. There, the digitization team extracts all pertinent information (Table 1). Missing information is requested directly from the authors (b) or found in alternative sources. MPMs and their metadata also undergo standardization to facilitate their automatic manipulation (Appendix S3). Each MPM is then carefully checked for quality requirements and to fix potential errors (see *Data quality* above); when necessary, (c) the COMPADRE digitization team contacts the author(s) to clarify potential incongruities. Following the first release of COMPADRE v. 3.0 online, and approximately every ~6 months, new digitized, standardized, error-checked sections of the COMPADRE working version will be pushed to the online version. Unpublished information provided to the digitization team by the author(s) under an embargo agreement (< 0.1% currently) is only released once the embargo period has expired and we have received consent from the author(s).



updates of the database will be made publicly available every 6 months – we currently have a total of 992 species in the process of being digitized and error-checked. For every new release, any errors found in previous releases will be corrected and accompanied by a note in the variable *Observation* (see *COMPADRE User's Guide* and Table 1). In order to allow scientific reproducibility, outdated versions will be archived and accessible via the COMPADRE portal.

Future versions of the COMPADRE portal will allow users to upload information. New data uploaded by users will be incorporated into COMPADRE once they have been processed and passed our quality standards. The embargo policy option described above for COMPADRE will also apply to unpublished data provided by users.

DATA QUALITY

Various aspects of the information are checked for quality assurance before the information is released in the COMPADRE

portal. Below, we outline the most important error-checks and standardization procedures conducted on the content of COMPADRE (more details are provided in Appendix S2):

- **Taxonomic names:** For each study species, we report two values: the name used in the original source by the author (s) (*SpeciesAuthor* in Table 1) and the name currently accepted by The Plant List (www.theplantlist.org). In 15% of the species in COMPADRE 3.0, names provided by the authors are not the currently accepted names (i.e. no match, synonym or unresolved as per The Plant List). Citing the correct taxonomic name is vital to cross-database research (see *The vision: beyond COMPADRE*, below). Because taxonomic names may be updated frequently, we provide an R script to check on name spelling, synonyms and accepted taxonomic names based on the R package *Taxonstand* (Appendix S3).
- **Phylogenetic tree:** A phylogenetic tree for species in COMPADRE has been constructed to allow users to account for

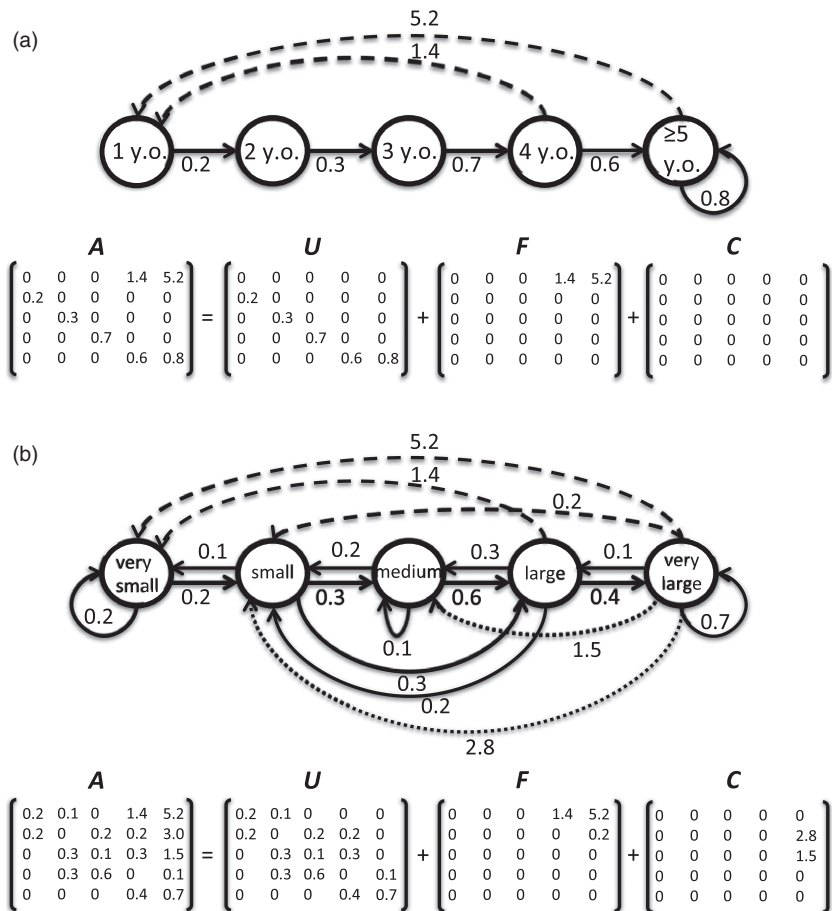


Fig. 3. Life cycle of two idealized plant populations based on age (a) and size (b), with their corresponding matrix population models \mathbf{A} , and underlying basic demographic processes of survival (\mathbf{U} submatrix; solid arrows), sexual reproduction (\mathbf{F} submatrix; dashed arrows) and clonal reproduction (\mathbf{C} submatrix; dotted arrows). In the Leslie matrix model example (a), the division of submatrices is relatively more straightforward than in the Lefkovich matrix model example (b). In the latter imaginary example, individuals can transition into the same stage as they can contribute with sexual and/or clonal offspring (e.g. small stage). In these cases, splitting \mathbf{A} into submatrices \mathbf{U} , \mathbf{F} and \mathbf{C} is only feasible when sufficient information is provided by the authors (see variable *MatrixSplit* in Table 1).

phylogenetic ancestry if they wish to conduct comparative analyses (Appendixes S3 and S5).

- **Geolocation:** The location where the demographic information was collected is important to the interpretation of MPMs. When GPS coordinates were made available, these were checked for consistency with the region and countries where the research took place (e.g. terrestrial plants cannot exist in the middle of an ocean). Information about the location of each population was then used to establish the ecoregion of the study as per the classification by Olson *et al.* (2001; Fig. 1 within).
- **Architectural organization:** The anatomic and physiological organization of plants can constrain their demography (Silvertown *et al.* 1993; Franco & Silvertown 1997; Silvertown, Franco & Harper 1997; Stott *et al.* 2010; Baudisch *et al.* 2013; Adler *et al.* 2014). In COMPADRE, plant habit is characterized according to the classification *GrowthType* (Table 1).
- **Division of demographic processes:** Whenever possible, each projection matrix \mathbf{A} in COMPADRE has been partitioned into a submatrix \mathbf{U} that contains only transitions and survival of existing individuals, a submatrix \mathbf{F} that contains sexual reproduction and a submatrix \mathbf{C} that contains clonal reproduction, as described in Fig. 3. This often requires communication with the authors to clarify what proportion of each element of \mathbf{A} corresponds to each process. In the current version of COMPADRE, 3% of the MPMs \mathbf{A} have not yet been

divided into these components due to lack of information (see variable *MatrixSplit* in Table 1).

- **Stage-specific survival:** Stage-specific survival is given by the column sums of the submatrix \mathbf{U} ; it is constrained to lie between 0 and 1. Values greater than 1 render most analyses of survival and longevity impossible. While rounding errors may result in stage-specific survival probabilities slightly greater than 1, when any probabilities were much greater than 1, authors were contacted for clarification. In some cases, this resulted in a correction in the assignment of proportions of each matrix element in \mathbf{A} to the submatrices \mathbf{U} , \mathbf{F} and \mathbf{C} described in Fig. 3, which was then noted in *Observations* (Table 1). MPMs pending of this correction have a value > 1 in variable *SurvivalIssue* (Table 1).
- **Classification of stages:** To help automate comparative analyses, the life cycle stages in each MPM in COMPADRE have been classified into a standardized set of categories. Although we make available the exact description of the stages as described by the authors (see variable *Matrix-ClassAuthor* in Table 1), we have, based on this information, classified stages into 'prop' (propagules/seed bank stage), 'dorm' (vegetatively dormant individuals) and 'active' (individuals photosynthetically active, neither prop nor dorm). This allows the user to, for instance, derive life expectancy considering the beginning of life to be the point where seeds germinate (Caswell & Salguero-Gómez 2013;

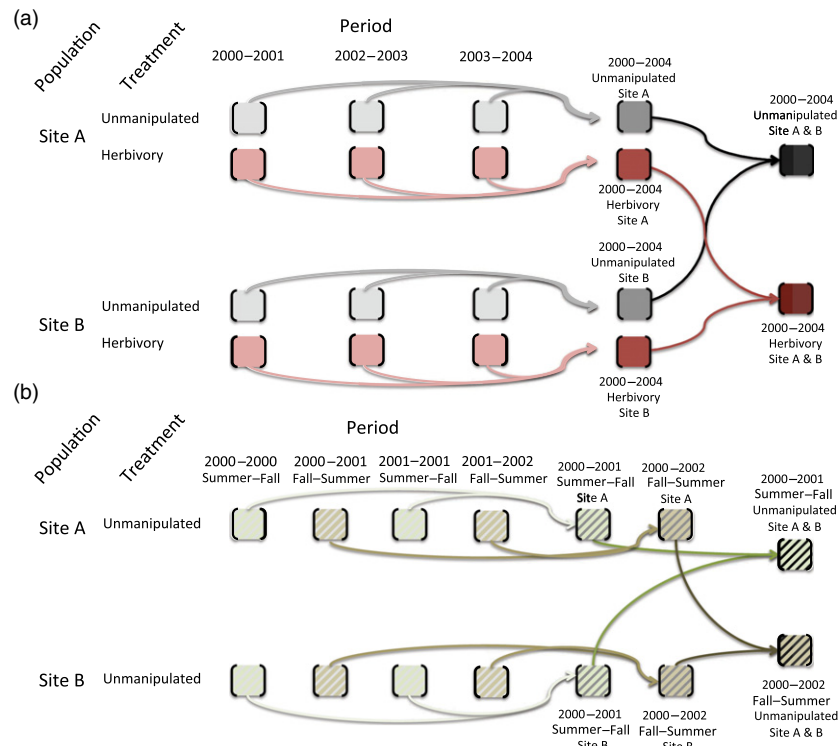


Fig. 4. COMPADRE contains the matrix population models per study corresponding to as many populations, study periods and treatments as the authors have made available, as well as those matrices that we have been able to derive from underlying demographic information. We refer to each matrix under a given study \times species \times population \times period \times treatment combination as the ‘individual’ matrix when the species’ population dynamics have been examined between years (a) or ‘seasonal’ matrix when the study explored intra-annual dynamics (b). Here, we showcase two examples of how matrices are classified in COMPADRE and, when necessary, calculated as summary matrices of individual or seasonal matrices. (a) An imaginary study species where the population dynamics were followed annually between 2000 and 2004, resulting in three annual periods for two populations, each with a baseline (‘unmanipulated’; light grey matrix) control for a treatment, in this case, herbivory (pink matrix). Each set of individual matrices within a given population and under a specific treatment level was used to calculate the mean MPM for that site and treatment across all periods (unmanipulated: grey; herbivory: red); each of the population \times treatment mean matrices was then averaged to produce a grand mean matrix of all periods and populations for a given treatment level (dark grey for unmanipulated; dark red for treatment). Different treatment levels are not averaged due to the lack of foreseeable utility. (b) An imaginary study species where the population dynamics were followed every summer and fall of 2000–2002, resulting in four seasonal matrices (summer–fall: light green hatched pattern; fall–summer: light brown hatched pattern). When not reported by the authors, we calculated the season-specific mean MPM per population (summer–fall: green hatched pattern; fall–summer: brown hatched pattern) and the season-specific mean matrix across all populations (summer–fall: dark green; fall–summer: dark brown). An annual MPM for an annual period of interest, population(s) and treatment(s) (not shown here) can be calculated by back-multiplying seasonal matrices as described by Caswell (2001, p. 349).

Jones *et al.* 2014) (we provide some *R* scripts as basic examples in Appendix S3).

- **Types of MPMs:** When available, we have digitized the MPMs for each study \times species \times population \times period \times treatment combination. We refer to this unique combination of an MPM as an ‘individual’ matrix (variable *MatrixComposite* in Table 1), if they are based on an annual or lower frequency (e.g. every 5 years as in Shimatani *et al.* 2007; see *AnnualPeriodicity* in Table 1), and ‘seasonal’, if they explore the intra-annual population dynamics of a species. The seasons/months corresponding to intra-annual matrix models (Table 1) are identified to permit multiplying the seasonal matrices in the correct order to calculate statistics of interannual survival and population growth. Additionally, to facilitate comparative studies, we have also calculated, when not already available, element-by-element arithmetic ‘mean’ matrices across each of the aforementioned categories (Fig. 4). In addition to ‘individual’, ‘sea-

sonal’ and ‘mean’ MPMs, COMPADRE also includes ‘pooled’ MPMs. The latter is only made available through the author, as they require individual-level data of the study, which COMPADRE does not have (see ‘What COMPADRE is not about’ below). A pooled MPM results from parameterizing the matrix directly from individual-level data, pooling a set of periods and populations, and thus by-passing the aforementioned element-by-element arithmetic mean approach. Depending on the estimation procedures used, the pooled and mean matrices may be identical if each matrix is based on the same number of individuals; they will, however, tend to differ when the sample sizes are different.

The COMPADRE team makes every effort to ensure data accuracy. However, we take no responsibility for consequences of improper use of the database by the user, nor for the possibility of potential typographical errors and omissions. Users who may detect incongruencies are encouraged to contact us at compadre-contact@demogr.mpg.de.

GLOBAL REPRESENTATION IN COMPADRE

The current version in the COMPADRE portal contains an unprecedented sample size for information on plant population dynamics: 468 studies with 598 plant (and algae) species, resulting in 5621 MPMs. This represents a substantial improvement in sample sizes available from previous publications (17 in Jones *et al.* 2014; 290 in Baudisch *et al.* 2013; 207 in Mbeau-Ache & Franco 2013; 36 in Caswell & Salguero-Gómez 2013; 222 Adler *et al.* 2014; 417 in R. Salguero-Gómez, O.R. Jones, E. Jongejans, S.P. Blomberg, D. Hodgson, C. Mbeau-Ache, P.A. Zuidema, H. de Kroon & Y.M. Buckley, in review). The individual MPMs and seasonal MPMs together total 3614 matrices, representing unique com-

binations of studies \times species \times populations \times treatments \times periods (Fig. 5a). The remaining 1997 MPMs are the product of element-by-element arithmetic means of other individuals or seasonal matrices. Given the temporal and population replication in each study (Fig. 5f and g), the relatively high ratio of individual and seasonal MPMs to mean and pooled MPMs (approx. 3:2; Fig. 5a) highlights that not all authors release all the individual/seasonal MPMs they have produced; there seems to be a greater tendency towards making only summary matrices available.

The information in COMPADRE 3.0 is well represented across the phylogenetic tree of plants. The current version contains 5597 (99.5%) MPMs for plants and green and red algae (Kingdom Plantae), as well as 24 (0.4%) MPMs for brown

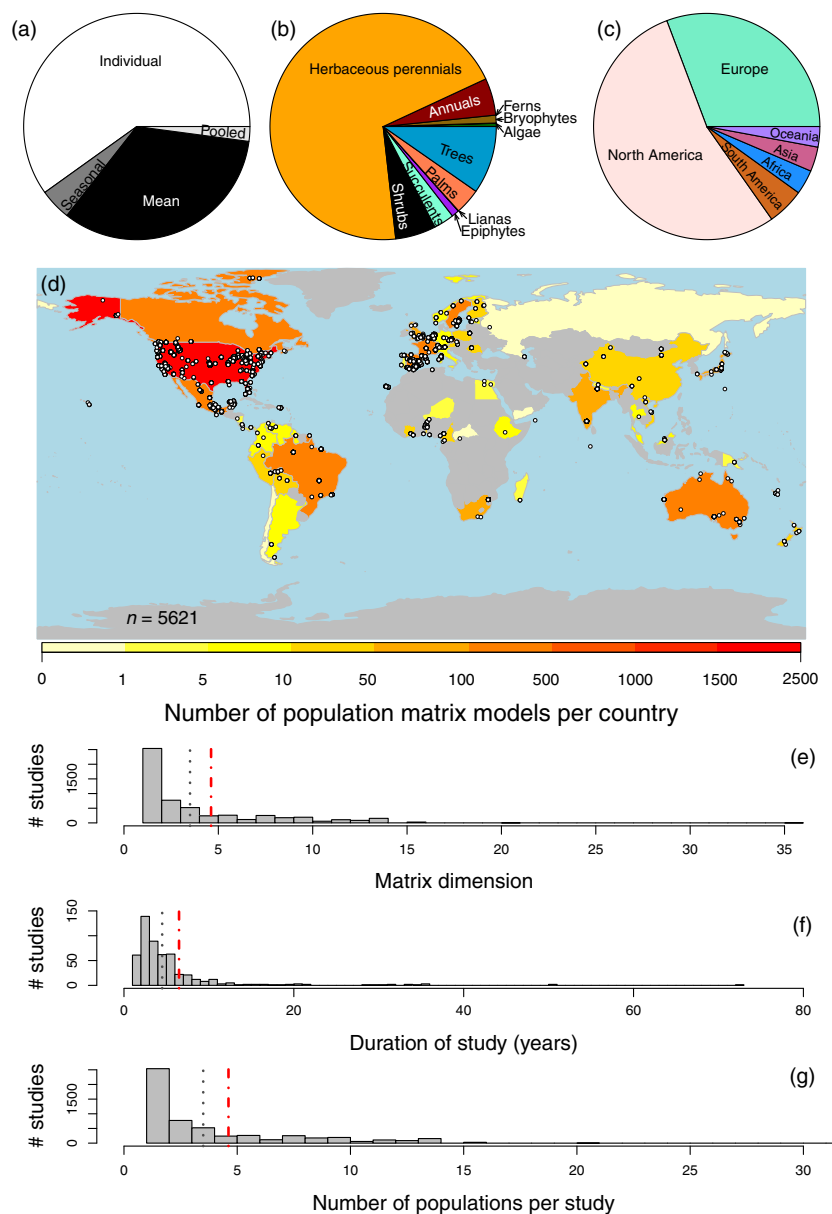


Fig. 5. The current online version of the COMPADRE Plant Matrix Database (3.0) contains 5621 matrix population models. Breakdown of number of MPMs by (a) type of MPM (see Fig. 4), (b) plant growth form, (c) continent, (d) geographic location, where dots represent the approximate locations of each study population (when available), (e) matrix dimension, (f) duration of study and (g) number of populations per study. In (e), (f) and (g), the grey and red vertical lines represent the median and mean values, respectively.

algae (Kingdom Chromalveolata). Within vascular plants, there are 5323 (96.3%) MPMs for angiosperms, and 206 (3.7%) MPMs for gymnosperms; this representation approximates the extant angiosperms/gymnosperms ratio in the world (www.theplantlist.org). Furthermore, the most abundant taxonomic divisions of the Plantae Kingdom are represented in COMPADRE 3.0: mosses (Bryophyta: 2 MPMs, 0.0004%), ferns (Pteridophyta: 65, 0.75%), cycads (Cycadophyta: 43, 0.8%), conifers (Coniferophyta: 163, 2.9%) and flowering plants (Anthophyta: Liliopsida 1163, 20.7%, and Magnoliopsida 4150, 73.8%). Yet, no demographic information exists for liverworts (Hepatophyta), hornworts (Anthocerotophyta), club mosses (Lycophyta), horsetails (Sphenophyta), whisk ferns (Psilotopsida), the charismatic *Ginkgo biloba*, the only representative of the Ginkgoopsida, nor gnetae (Gnetophyta). In total, 117 taxonomic families are represented. The number of MPMs within taxonomic families varies up to three orders of magnitude, with Adoxaceae, Moraceae or Vochysiaceae containing a single MPM each, but other groups such as the Poaceae (286 MPMs), Primulaceae (297), Leguminosae (465) or Compositae (720) contain many more.

COMPADRE also includes information on general plant growth forms (Table 2; Fig. 5b). The number of MPMs in vascular, non-woody species (herbaceous perennials, annuals, algae, lianas, epiphytes and succulents) sums to 4478 (80.6%), whereas the number of woody species (trees, palms and shrubs) results in 1078 (19.4%). These values reflect the relative diversity as indicated by a recent estimate of woody species world-wide (FitJohn *et al.* 2014).

Overall, COMPADRE 3.0 offers a robust geographic coverage of plant population dynamics. The MPMs in COMPADRE are well spread geographically, although countries with a higher gross domestic product clearly appear to have had more opportunities to implement plant demographic studies using MPMs (Salguero-Gómez, unpublished data). Information in COMPADRE 3.0 includes plant and algae population dynamics on all continents except Antarctica (Fig. 5d). Yet, clear gaps exist in our knowledge of plant demography in certain regions, including Africa and Asia. North America (Canada, the USA and Mexico), Europe, Australia and Brazil together provide 89.3% of the MPMs in COMPADRE 3.0 (Fig. 5c). Unfortunately, remarkably few studies report information from countries with high biodiversity such as Honduras, the Democratic Republic of Congo, Paraguay or Indonesia. Furthermore, even some developed countries, such as Saudi Arabia, Turkey, Greece or Ireland, are under-represented.

Replication of studies through time and space is highly variable, but overall is poor. The mode of duration of studies in COMPADRE 3.0 is 4 years (Fig. 5c), corresponding to the length of an average PhD project, as well as that of most funding agencies. Only a handful of studies have followed plant population dynamics for ≥ 10 years for the online portal. This short duration is particularly limiting for our knowledge of plant demography, as many plants rank among the longest-lived organisms (Peñuelas & Munné-Bosch 2010), with many achieving life expectancies much longer than a decade (Brunstein & Yamaguchi 1992; Bowers, Webb & Rondeau 1995). The mode of number of populations studied per publication

Table 2. Breakdown of number of population matrix models in COMPADRE 3.0 by plant *GrowthType* (Table 1) and *Ecoregion* (Olson *et al.* 2001)

	Alga	Bryophyte	Fern	Annual	Herb	Shrub	Succulent	Epiphyte	Liana	Palm	Tree	Sum
BOR	0	2	0	0	176	0	0	0	0	0	0	178
DES	0	0	0	42	277	112	74	4	0	4	7	520
FGS	0	0	0	0	42	0	0	0	0	0	0	42
LAB	0	0	0	4	28	0	0	0	0	0	0	32
MED	0	0	0	1	425	93	6	0	0	33	18	576
MON	0	0	0	0	30	0	0	0	0	0	1	31
POE	10	0	0	0	0	0	0	0	0	0	0	10
TBM	1	0	63	197	1351	70	0	0	0	3	107	1792
TCF	19	0	0	2	595	2	0	1	0	0	95	714
TDB	0	0	0	0	9	0	7	0	0	10	85	111
TEU	2	0	0	0	0	0	0	0	0	0	0	2
TGS	1	0	0	6	700	7	0	0	0	0	11	725
TGV	0	0	0	2	98	16	56	0	0	13	17	202
TMB	0	0	0	2	228	45	0	42	3	91	152	563
TSC	0	0	0	0	3	0	14	13	0	25	5	60
TSS	3	0	0	0	0	0	0	0	0	0	0	3
TUN	0	0	0	0	10	5	0	0	0	0	0	15
Sum	36	2	63	256	3972	350	157	60	3	179	498	5576

Represented ecoregion abbreviations: BOR, boreal forests/Taiga; DES, deserts and xeric shrublands; FGS, flooded grasslands and savannas; LAB, laboratory/glasshouse controlled conditions; MED, Mediterranean forests, woodlands and scrubs; MON, montane grasslands and shrublands; POE, polar ecoregions; TBM, temperate broadleaf and mixed forests; TCF, temperate coniferous forests; TDB, tropical and subtropical dry broadleaf forests; TEU, temperate upwellings; TGS, temperate grasslands, savannas and shrublands; TGV, tropical and subtropical grasslands, savannas and shrublands; TMB, tropical and subtropical moist broadleaf forests; TSC, tropical and subtropical coniferous forests; TSS, temperate shelf and seas ecoregions; TUN, tundra.

For other ecoregions not represented in this version of COMPADRE, see the User's guidelines (Appendix S2).

in COMPADRE is one. This is also a particular concern if we are to gain a basic understanding of the intraspecific demographic variability and to implement optimal conservation management measurements. Indeed, some species can exhibit a great deal of demographic variability, which in some cases can be even greater than among non-closely related species (Oostermeijer *et al.* 1996; Silvertown, Franco & Menges 2000; Menges *et al.* 1996; Jongejans *et al.* 2010).

INFORMATION NOT CONTAINED IN COMPADRE 3.0

The niche of COMPADRE is matrix-based plant (and algae) demography. COMPADRE does not contain the individual-level records of survival, changes in stage, reproduction and death from which MPMs are often parameterized. Likewise, COMPADRE does not contain integral projection models (Easterling, Ellner & Dixon 2000), as another IPM database is currently under construction (63 plant species, PADRINO; R. Salguero-Gómez, unpubl. data). In addition to the MPMs, COMPADRE mostly contains supporting demographic data. Regarding questions for which other information not contained in COMPADRE (e.g. reproductive system, microhabitat conditions, seed mass) would be critical, users are encouraged to explore existing databases [e.g. TRY (Kattge *et al.* 2011), BIEN (<http://bien.nceas.ucsb.edu/bien>), D3 (Hintze *et al.* 2013), BioFlor (<http://www2.ufz.de/biolflor/overview/merkmale.jsp>)].

The potential of COMPADRE is not in the MPMs *per se*, but in the outputs that can be derived from them. We have made a number of simple R scripts available to manipulate and interact with matrices, derive demographic outputs and correct for phylogenetic relationships (Appendix S3). Users are welcome to explore these or other more developed open-source libraries (Stubben & Milligan 2007; Stott, Hodgson & Townley 2012; Metcalf *et al.* 2013) and to carry out their own calculations based on compendia of methods for analysis of MPMs (e.g., Caswell 2001, 2009; Morris & Doak 2002). Users are also encouraged to avail themselves of other existing tools for teaching and mentoring such as the matrix workflows of BioVel (<https://portal.biovel.eu>). Lastly, users must note that the COMPADRE team provides the information and some basic tools, but no technical support.

USES AND MISUSES

Users of COMPADRE, in accordance of scientific ethical standards, are encouraged to acknowledge those who collected the field data, parameterized the MPMs, and made them public. To facilitate study citation, in addition to the variables described in Table 1 under the aspect 'Source', we have also made available an R script that produces a citation list of the studies based on their DOI or ISBN (Appendix S3). Users are also encouraged to visit the Supporting Information Appendix S4 for a comprehensive list of studies made public in the present release. Significant efforts have been made to digitize, standardize, error-check and supplement demographic information with relevant ancillary information such as ecoregion, growth form, taxonomy and phylogeny. Consequently, the information

available in the COMPADRE online portal (www.compadre-db.org) is released under the Creative Commons Attribution-NonCommercial-ShareAlike CC BY-NC-SA license (<http://creativecommons.org/licenses/by-nc-sa/4.0/>). This requires users to cite the present manuscript and the version of the online portal in their works.

To help in the interpretation of the MPM, users are also encouraged to consult the notes provided under the variable *Observation* associated with each MPM. Here, we provide three examples to illustrate the importance of understanding the context and construction of each MPM. First, although we use the term '*unmanipulated*' for those MPMs used as baseline for treatments (note the intentional avoidance of the term 'control' here), the environment under which field data used to build these matrices were collected may not be representative of typical conditions for that population (e.g. fires, herbivory, droughts). These events may or may not be representative of long-term *normal* conditions for that population. Secondly, plant demographers are now aware of accidental addition of a year delay in the population dynamics of plants by specifying an unnecessary seed stage where no permanent seed bank exists (Caswell 2001; p. 60). This artefact has been corrected in most – but perhaps not all – MPMs in COMPADRE. A third aspect to consider here is that some submatrices *F* and/or *C* may have all zero values in their matrix elements; in some cases, quantifying sexual and/or clonal reproduction may not have been the goal of the authors or it may have been logistically impossible. Submatrices *F* or *C* containing only zeros (Fig. 3) may not necessarily represent a failure of reproduction in the population, but rather that reproduction might not have been measured (Kubota 1997). In such cases, calculations involving reproduction (e.g. calculation of population growth rates from $A = U + F + C$) are of questionable relevance. Finally, the information contained in the variables *NumberPopulations* and *Population* (Table 1) assumes that each studied site is a separate population. The term 'population' here is used loosely, following the authors' need to differentiate between sites where the same species was studied, regardless of whether or not those sites constitute biologically the same population or not. Users may want to carefully inspect the published source of each MPM for that purpose. Alternatively, it is possible to derive geographic distances among populations based on GPS coordinates provided here and integrate that information with dispersal kernels (Bullock *et al.* 2012; Hintze *et al.* 2013) for a better understanding of population or meta-population dynamics.

THE VISION: BEYOND COMPADRE

COMPADRE contributes to an ambitious programme envisioned decades ago. Much of that vision has been realized, and here, we detail various expansions that we envisage for the future. Some arise from new technologies or analytical methodologies, while others from the increased interest in gathering natural history records of species and the expansion of biological data repositories.

Several projects have recently enabled users to obtain the real-time biological information of species observed in natural settings, such as iSpot (<http://www.ispotnature.org>). Phenological events such as first flowering are recorded by members of the general public and students via online Websites and apps and verified by experts before ingesting into public databases; NaturesCalendar in the UK (<http://www.naturescalendar.org.uk>) and ClimateWatch in Australia (<http://www.climatewatch.org.au>) are two rather successful examples. We believe that COMPADRE has potential for research, teaching and outreach in a similar way as the aforementioned projects. Our vision is that, after some initial training, *any* user will be able to obtain information on important demographic attributes of a species/population such as life expectancy, the abiotic and biotic agents that most affect its population dynamics, time to quasi-extinction and potential to invade all within the reach of a smartphone with GPS to determine locality and a built-in camera to determine the species of interest and microhabitat conditions. To that end, we are currently developing an R library, COMPADRE-DB (Salguero-Gómez & Jones, unpublished data), that interacts with the online portal to manipulate MPMs, derive demographic output, and interact with other databases.

Naturally, this potential requires integration of COMPADRE with other existing data repositories and their interconnectivity through a central, interconnected platform. Central repositories are already available for most of the relevant disciplines: genetics (GenBank), taxonomy (Catalogue of Life; The Plant List), plant anatomic and physiological traits (TRY, BIEN, D3), occurrence data (GBIF), conservation status (IUCN) and climate information (Fetch). What is missing currently is the central platform and the user interface protocols to allow for real-time interactivity. New online repositories such as the Australian Ecological Knowledge and Observation System (<http://www.ecoinformatics.org.au>) have made progress at integrating rich ecological data at a national level via online tools for data description and publication and serve as a model for future efforts.

The potential of COMPADRE also resides in cross-taxonomic, comprehensive demographic studies. Other databases are available or under development that will help us progress towards this goal: birds [BIDDABA, $n = 857$ species (Lebreton *et al.* 2012)], mammals {Pantheria [life-history traits of all extinct and recently extinct mammals, (Jones *et al.* 2009)]}, or all animals: DATLIFE (life tables for 293, age-specific fertility for 61, maximum life span for 2659, adult/juvenile mortality for 532 animal species; A. Scheuerlein & Vaupel, unpubl. data), COMADRE (MPMs for over 1300 animal species; R. Salguero-Gómez and COMADRE core committee unpubl. data), PADRINO [Integral Projection Models (IPMs) for approx. 100 plant species; R. Salguero-Gómez, unpubl. data] and the Global Population Dynamics Database (NERC Centre for Population Biology 2010).

To date, COMPADRE 3.0 and its predecessors have led to over 30 publications. These have addressed key ecological (Buckley *et al.* 2010; Salguero-Gómez *et al.* 2012; Adler *et al.* 2014), evolutionary (Pfister 1998; Baudisch *et al.* 2013; Jones

et al. 2014), methodological (Salguero-Gómez & Plotkin 2010; Caswell & Salguero-Gómez 2013) and conservation biology questions (Ramula *et al.* 2008). However, these studies have realized only a small proportion of the full potential of COMPADRE. Many pressing questions remain for which COMPADRE will be a useful tool. For example, the coupling of climatic models with MPMs can better inform species distribution models to gain insights into the demographic mechanisms behind range boundaries (Guisan & Zimmermann 2000; Huntley *et al.* 2010). The power of COMPADRE's extensive, comprehensive information will also improve the estimation of extinction risk based on non-demographic characteristics, which can be used to inform the management of threatened and endangered species (Traill, Bradshaw & Brook 2007; Sodhi *et al.* 2008).

Analyses based on the COMPADRE database will also help to identify lacunae in our current understanding of plant demography. For example, comparative analyses would benefit from greater spatial and temporal replication in demographic studies. Variation in demographic parameters within species across years or sites representing its distribution across gradients (Buckley *et al.* 2010; Zeigler, Che-Castaldo & Neel 2013) may be as large as variation among species (Jongejans & de Kroon 2005), limiting ability to draw conclusions or to identify patterns across taxa. In the working version of COMPADRE (Fig. 2), 37% of studies (365/992) contain data on the same species at two or more sites, and only 23% of studies (229/992) contain data for more than 5 years. Yet, such data are critical for improving inferences and incorporating spatial and temporal stochasticity in analyses of MPMs.

As cross-disciplinary and cross-taxonomic research develops with the contributions of COMPADRE, our team will do all within our reach to remain updated on information and user needs. Scientific methods come and go, and we cannot predict how MPMs will be used in the coming decades, or what new ways of parameterizing or formulating MPMs will become common practice (e.g. vital rates are starting to be parameterized as density-dependent, climate-dependent variables). This uncertainty may pose some challenges but may also create opportunities for COMPADRE and for the users. The database and its associated protocol for digitizing, standardizing and error-checking information will likely change to respond to user needs; researchers are encouraged to provide us with feedback. At the same time, we hope that users will be inspired to maximize the usefulness and impact of their own data by collecting the ancillary information that is standardized in COMPADRE; for instance, we found that most studies do not report GPS coordinates of the study populations (Johnson & Barton 2004). To facilitate integration into future versions of COMPADRE, all MPMs and associated metadata should be made available in the publication's supplementary information, or as separate data papers (Ellis *et al.* 2012).

The ultimate goal of COMPADRE is to encourage plant population ecologists to share information and think not only about their specific questions, but also about how addressing a given question with their specific study species fits into the complex collage of what we know and do not know about

plant demography. The 932 species currently in the working version of COMPADRE (Fig. 1) represent 0.374% of the ~250 000 extant species of plants (Govaerts 2001). Given how costly these data are to obtain, this is a fairly impressive representation, particularly when considering the substantial phylogenetic coverage in the data set (Appendix S5), and the youth of plant population ecology as a discipline (Harper 1977). The exponential increase in the number of these types of studies provides further cause for optimism (Fig. 1). Nonetheless, COMPADRE shows gaps and opportunities for the development of research in geographic regions where no plant studies are yet included, for example, in most African countries and the Middle East (Fig. 5d).

One of the great strengths of comparative studies is their use as a tool for identifying generalities that can be extrapolated to poorly known species (Shea *et al.* 1998; Ramula *et al.* 2008). With many plant species threatened with extinction both locally and globally, COMPADRE provides an easily accessible tool for obtaining data for these species, or for identifying useful generalizations for particular taxonomic groups, life-history strategies and regions which should help guide the management and forecasting of threatened populations. The COMPADRE Plant Matrix Database represents a step closer to achieving a global repository of biological information for the management of the planet's biodiversity.

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Data accessibility

The data associated with this manuscript can be accessed at www.compadre-db.org.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Constituency of COMPADRE.

Appendix S2. COMPADRE user's guide.

Appendix S3. COMPADRE R scripts.

Appendix S4. Extended literature used in COMPADRE 3.0.

Appendix S5. COMPADRE phylogeny.

Appendix S6. COMPADRE funding support and extended acknowledgements.

Appendix S7. Author contributions.

Appendix S8. Supplementary information references.