

Research article

Plant demographic knowledge is biased towards short-term studies of temperate-region herbaceous perennials

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Plant demography has a long history resulting in a large knowledge base. Comparative analysis of this information allows exploration of the drivers of demographic patterns globally and the study of life-history evolution. Studies aiming to generalise demographic patterns rely on data being derived from a representative sample. However, the data are likely to be taxonomically, geographically and methodologically biased. Matrix population models (MPMs) are widely-used in plant demography, so an assessment of publications using MPMs is a convenient way to assess the distribution of plant demographic knowledge using this modelling approach. We assessed bias in this knowledge using data from the COMPADRE Plant Matrix Database, containing MPMs for > 700 species. We show that tree species and tropical areas are under-represented, while herbaceous perennials and temperate areas are over-represented. There is a positive association between the number of studies per country and per capita GDP. Most studies have low spatiotemporal replication with 43% of studies conducted over < four years, and only 17% replicated across > three sites. This limited spatiotemporal coverage means existing data may not represent the environmental conditions the species experience. These biases and knowledge gaps inhibit theory development and limit current utility for identifying useful generalities for management decisions, such as typical responses to climate change. It is likely that similar biases extend to other demographic modelling tools such as integral projection models. We urge researchers to address these biases and close these knowledge gaps.

Keywords: bias, biogeography, comparative biology, population growth rate, population projection matrix

Introduction

Population ecologists aim to understand and predict population dynamics using demographic data including vital rates of survival, reproduction, and development. Their efforts include examining population responses to changes in climate, land use, and

management (Morris and Doak 2002, Crone et al. 2011). Demographic data are also crucial for robust population viability analyses of threatened or invasive species (Morris and Doak 2002, Crone et al. 2011). Besides single-species studies, researchers have conducted comparative analyses investigating broad demographic and life history patterns among species. These comparative analyses have aided the development of general theories of life history variation, including r–K selection theory (MacArthur and Wilson 1967), Grime's C–S–R triangle (Grime 1974, Silvertown et al. 1992), Stearns' fast–slow continuum (Stearns 1992, Franco and Silvertown 1996, Salguero-Gómez et al. 2016) and reproductive strategies continuum (Salguero-Gómez 2017). The empirical exploration of these themes requires large quantities of data from diverse species experiencing a wide range of environmental conditions.

Comparative analyses often rely on the collation of published data to obtain sufficient sample sizes. There are numerous recent examples of this (Dalglish et al. 2010, Bullock et al. 2012, Burns et al. 2013), and large-scale collaborative efforts to collate global demographic and life history and related data are increasingly common (Wright et al. 2004, Loh et al. 2005, Kattge et al. 2011, Salguero-Gómez et al. 2015, Capdevila et al. 2022, Hernández-Yáñez et al. 2022, Cant et al. 2023). Such databases provide a rich resource for workers focussing on life-history strategies and demographic performance.

Matrix population models (MPMs), which describe life cycles in terms of survival, reproduction, and transitions among discrete life stages are frequently-used in plant demography (Caswell 2001, Crone et al. 2011). MPMs are useful because they have well-understood mathematical properties and derived measures that are comparable across diverse species (Caswell 2001). With its extensive collection of plant studies utilizing MPMs, the COMPADRE Plant Matrix Database (Salguero-Gómez et al. 2015) stands as a comprehensive and invaluable resource for understanding plant demography. While other analytical tools, such as integral projection models (IPMs, Easterling et al. 2000) and individual-based models (DeAngelis and Mooij 2005), have also been employed in this field, their use is not yet as prevalent as MPMs. This is changing fast, with IPMs rapidly becoming the tool of choice among plant demographers: since 2000 there have been 211 papers published using IPMs for plant demography (PADRINO database, Salguero-Gomez pers. comm.). It is worth considering that the biases existing in MPM-based work likely extend to other modeling approaches, though they are beyond the scope of the present study. The contents of such databases were not explicitly collected for inclusion in large databases but rather for the disparate purposes of the original studies. Although these databases may contain unbiased samples of the literature, researchers likely focus on species or geographical areas of particular interest, leading to similar taxonomic, life history, or geographic bias. Franco and Silvertown's (1990) assessment of plant demographic knowledge highlighted the existence of such bias. They found that, although the

most speciose families were the best-studied, some groups were poorly represented (e.g. Orchidaceae, vines). They also highlighted a bias towards short-lived species. More recent assessments of similar data (Salguero-Gómez et al. 2015) also highlight obvious taxonomic and geographic knowledge gaps that are broadly similar to those presented by Franco and Silvertown (1990).

Bias of this nature has far-reaching consequences for our understanding of plant demography and could limit the usefulness of databases like COMPADRE for comparative analyses. For example, extrapolating generalities based mainly on analyses of short-lived organisms in temperate regions to long-lived tropical tree species is questionable at best. After evaluating temporal trends in the use of MPMs in the plant demographic literature, we identify and quantify potential biases in plant demographic knowledge and discuss their implications. To do this, we used COMPADRE to address the following questions: 1) where is the research performed? 2) For which species do we have demographic data? 3) How are the studies and MPMs designed? More precisely, we tested the following seven hypotheses (H1–H7):

Where is the research performed?

To assess potential geographic bias in plant demographic studies, we focussed on continental, ecoregion, and country-level biases. We also examined the relationship between the number of studies and the wealth of the country where the study was conducted (as indicated by per capita gross domestic product, GDP). Due to the association between scientific output and GDP (King 2004, van Noorden and Butler 2019), we expected (H1) the relatively wealthy continents of Europe and North America to be over-represented and that studies from temperate ecoregions (which characterise these continents) would dominate. Further, we expected (H2) that wealthier countries would be over-represented compared to their poorer counterparts since they have more funds for research (King 2004, van Noorden and Butler 2019).

For which species and populations do we have demographic data?

We expected (H3) that the representation of growth forms would not be proportional to their natural abundance, with herbaceous perennials being over-represented and some growth forms almost absent due to the challenges of data collection. For example, although vascular epiphytes are a diverse group, many are hard to study due to their location high up in the tree canopy. This potential bias is important because, if true, it would limit opportunities to make general inferences on the demography of poorly-represented growth forms. Furthermore, we expected to find (H4) a tendency to preferentially study threatened species because they are of particular interest in population ecology (Morris and Doak 2002). We also expected (H5) a trend towards choosing flourishing populations (i.e. with $\lambda > 1$) for data collection, reflecting the researchers' desire to ensure the long-term viability of their project.

How are the studies and MPMs designed?

The usefulness of individual demographic studies for comparative analyses can be limited by study design and MPM construction methods. We explored this by examining within-study spatio-temporal replication and MPM dimension. We expected (H6) low rates of temporal and spatial replication reflecting the tenure of research grants (2–5-years), meaning that the data may not adequately represent the environmental conditions experienced by the population/species. This is important because spatiotemporal replication for species is necessary to estimate relationships between demographic traits like population growth and drivers such as weather/climate (Compagnoni et al. 2021). We expected (H7) that matrix dimension would vary widely, with a tendency for the MPMs of long-lived species such as trees to have a greater dimension simply because there is more opportunity to divide a long-lived life course than a short-lived one. This is important, especially for comparative work, because matrix dimension is associated with both derived measures such as population growth rate or generation time and elasticities (Enright et al. 1995, Salguero-Gómez and Plotkin 2010, Takada et al. 2018). Therefore, a bias in matrix dimension with respect to important variables such as growth form, taxonomy, or geography could lead to spurious inferences.

Our results highlight plant demographic knowledge gaps in the MPM literature for assessing general patterns, and we encourage researchers to evaluate the significance of these gaps for their research and to close the gaps with novel research.

Material and methods

To quantify potential biases in our knowledge of plant demography, we used the COMPADRE Plant Matrix Database ver. 6.23.5.0 (release date 5 May 2023) (Salguero-Gómez et al. 2015). Although COMPADRE also contains data on red and brown algae and lichens, we restrict our analysis to plants (i.e. land plants and green algae) (Cavalier-Smith 1981). We analysed our data using R ver. 4.3.0 (www.r-project.org).

Data in COMPADRE are organised by research publication such that particular species can appear multiple times in different articles, and a single publication can include several species. We derived our sample from 641 articles on 759 species. Most articles (541) focussed on single species while 100 focussed on multiple species (2–33 species). In some cases, archived MPMs represent the element-by-element average across several transitions (e.g. the average of five years of data). However, COMPADRE also often includes data for individual transitions (e.g. transitions from year 1 to 2, year 2 to 3 etc.). Similarly, articles often include several MPMs representing different geographic areas or experimental treatments. Our data set included 884 species-by-article combinations and a total of 8845 MPMs. In addition to the MPMs, we use metadata on geolocation, ecoregion, growth form, taxonomy, and study timeframe, as well as the MPM

projection interval, to quantify temporal, biogeographic and taxonomic biases.

Where is the research performed?

Biogeography

We characterised biases in the distribution of studies among continents and ecoregions (H1). We first quantified the density of studied species (i.e. studied species per km² of each country). We then compared the species distribution among ecoregions in COMPADRE with the estimated species distribution in nature using Pearson's chi-squared tests (hereafter, χ^2 -tests) and post hoc proportion z-tests (using 'prop.test' in R, www.r-project.org). We could do this because COMPADRE assigns each studied population to Olson's 14 ecoregions (Olson et al. 2001). In some cases, populations are assigned to multiple closely-related ecoregions (e.g. different types of temperate forests). To simplify analysis, we collapsed Olson's ecoregions into five broader categories: tropical (TMB, TDB, TSC and TGV, see the Supporting information for explanation), temperate (TBM, TCF, TGS), Mediterranean/desert (MED, DES), tundra/boreal (BOR, TUN, MON), and wetland (MAN, FGS). We extracted the estimated number of species naturally occurring in each ecoregion from Kier et al. (2005). Kier et al. (2005) did not include bryophytes or algae, so we excluded them from this comparison.

Country-specific wealth (GDP)

We used country-level mean per capita GDP for 1990–2021 (World Bank 2022) to examine whether wealthy countries are overrepresented in COMPADRE (H2). To do this, we used a Poisson generalised linear model (GLM) (log-link) with log-transformed GDP as the explanatory variable and the number of demographic studies as the response variable. Log-transformation of GDP was necessary to improve the fit of the model.

For which species and populations do we have demographic data?

Taxonomy

To characterise potential biases in taxonomy and growth form (H3), we first analysed the distribution of taxa in COMPADRE among the taxonomic categories of angiosperm versus gymnosperm, monocot versus eudicot (for the angiosperms only), and Family. We then used the COMPADRE database meta-data variable *OrganismType* (hereafter, growth form), which includes a range of paraphyletic growth form categories such as 'tree', 'herbaceous perennial' and 'shrub' (the full list is Herbaceous perennial, Tree, Shrub, Annual, Succulent, Epiphyte, Palm, Algae, Fern, Bryophyte, Liana and Lichen). We compared the distribution of angiosperms versus gymnosperms in COMPADRE with estimates of their diversity across all plant species (Campbell et al. 2018) and the numbers of eudicots and monocots using Evert et al. (2013). We linked numbers of species within families extracted from

COMPADRE with the number of species per Family listed in [The Plant List \(2010\)](#) for the same families. [FitzJohn et al. \(2014\)](#) estimate the proportion of woody species, which we compared with the proportion of trees and shrubs in COMPADRE. We compared the proportion of epiphytes with estimates from ([Zotz 2013](#)). As above, we used χ^2 -tests and post hoc proportion tests for these comparisons.

Conservation status

To characterise potential bias in the conservation statuses of species studied (H4), we obtained the IUCN Red List categories (IUCN 2021) for species using the R package 'rredlist' ver. 0.7.1 ([Chamberlain 2020](#)). We use a χ^2 -test to compare the distribution of COMPADRE species among Red List categories with that of species in [The Plant List \(2010\)](#).

Population growth rates

To assess whether researchers tend to collect demographic data on growing or declining populations and whether researchers tend to start monitoring studies in a boom phase of the population (H5), we examined the asymptotic population growth rates (λ) calculated from each MPM. We first analysed this data using a t-test to check for an overall trend in λ . We then used linear models to check for variation in average λ values across ecoregion and growth form. Subsequently, to check whether there was a tendency for λ to decline during the study, we filtered the data to include only studies spanning at least five years, were experimentally unmanipulated, and for which λ could be calculated (i.e. the MPMs contained no missing values and did not violate ergodicity or irreducibility assumptions, [Stott et al. 2010](#)). We then fitted an ordinary least squares (OLS) regression with λ as the response variable and year as the explanatory variable. The slope of this model indicates the temporal trend in λ : a negative trend supports our hypothesis that researchers preferentially work on initially flourishing sites where population growth rates decline over time. We repeated this with studies spanning at least ten years to ensure our results were robust to the length of the time series.

How are the studies and MPMs designed?

Temporal and spatial replication, matrix model dimension

To explore potential biases in temporal and spatial replication (H6) and matrix dimension, we examined frequency distributions of study duration (years), spatial replication (number of populations, as defined by the original article authors) and matrix dimension for all species-by-article combinations in COMPADRE. We also examined variation in these quantities among ecoregion and growth form (H7) using ANOVA on log transformed counts, followed with Tukey tests.

Results

Where is the research performed?

Biogeography

As expected (H1), geographical bias was obvious, with study density being greatest in Europe (23.6 studies per million

km²) and North America (17.3 studies per million km²), while South American, Oceania, Asian and African countries were relatively poorly-represented, with 7.11, 6.92, 1.64, 1.12 studies per million km², respectively (Supporting information). A post hoc analysis showed that the dominance of Europe and North America in the COMPADRE database has increased slightly since the year 2000: 71.0% of articles post-2000 focussed on these regions compared to 63.9% pre-2000 (Supporting information), though this change in distribution is not statistically significant (Kolmogorov-Smirnov test: D = 0.333, p-value = 0.931).

As hypothesised (H1), there was a significant difference between the species distribution in COMPADRE compared to in nature (χ^2 -test: $\chi^2 = 297.34$, df = 4, $p < 0.001$). Species from temperate ecoregions are over-represented in COMPADRE (46% compared to an estimated 24% of species inhabiting these regions in nature; proportion test: $\chi^2 = 236.77$, df = 1, $p < 0.001$, [Fig. 1B](#)). In contrast, tropical ecoregions are under-represented (29 versus 42%; proportion test: $\chi^2 = 55.864$, df = 1, $p < 0.001$). Similar results were apparent for wetlands (1 versus 5%; proportion test: $\chi^2 = 26.109$, df = 1, $p < 0.001$) and tundra and boreal ecoregions (5 versus 13%; proportion test: $\chi^2 = 45.973$, df = 1, $p < 0.001$). Species from Mediterranean and desert ecoregions are represented in approximately the same proportion as in nature (18% in COMPADRE versus an estimated 17%; proportion test: $\chi^2 = 1.081$, df = 1, $p = 0.299$).

Country-specific wealth (GDP)

As expected (H2), the numbers of articles per country and per capita GDP are positively correlated (Poisson GLM: null deviance = 1523.7, residual deviance = 1189.3, df = 1, 59, $p < 0.001$, [Fig. 1C](#)). Here, 77% of countries (206 of 267) are not represented in COMPADRE. The USA, with 199 research articles, dominates COMPADRE, followed by Mexico with 89 articles, Sweden (32), Australia (28), Canada (26), Spain (23), Japan (20), Brazil and Great Britain (both 19) and France (18). Interestingly, several of the wealthiest countries are not represented (e.g. Iceland, Ireland). The positive correlation between the number of studies in COMPADRE and country GDP ([Fig. 1C](#)) remains statistically significant even when we remove the two outliers with most studies (USA and Mexico).

For which species and populations do we have demographic data?

Taxonomy

As expected (H3), species representation in COMPADRE does not well-reflect natural diversity. COMPADRE categorises species as angiosperm (91.7%), gymnosperm (5.5%), or 'non-seed plants' (2.8%) which includes ferns, mosses etc. ([Fig. 1D](#)). The corresponding figures in nature are 88.5% (angiosperm), 0.2% (gymnosperm) and 11.3% (non-seed plants) ([Campbell et al. 2018](#)). Thus, COMPADRE's taxonomic distribution is different from nature (χ^2 test: $\chi^2 = 1156.6$, df = 2, $p < 0.001$). In fact, COMPADRE

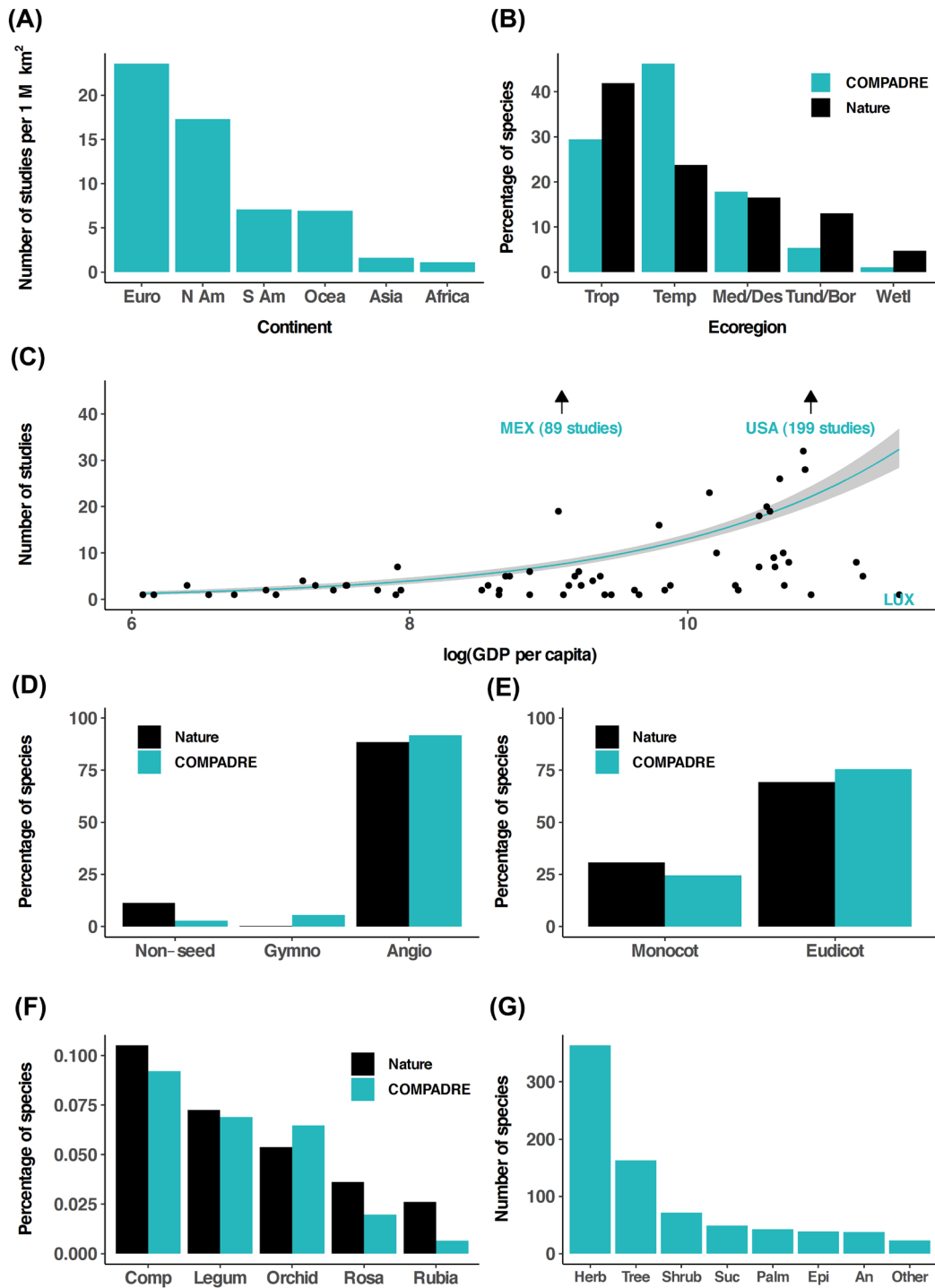


Figure 1. Geographic and taxonomic biases in COMPADRE. (A) The distribution of study density across continents. (B) The species distribution among ecoregions in COMPADRE compared to the natural distribution (Trop=tropical; temp=temperate; Med/Des=Mediterranean and deserts; Tund/Bor=tundra and boreal regions; Wetl=Wetlands). (C) The relationship between country per capita GDP and the number of plant demography studies using MPMs. The regression line represents a gamma-error GLM, conditioned on countries having at least one plant demography study. (D) Comparison of the species distribution among broad categories of angiosperms, gymnosperms and non-seed plants, in COMPADRE and in nature. (E) Comparison of the distribution of angiosperm species among monocot and eudicot categories, in COMPADRE and in nature. (F) Comparison of the distribution of species among the five largest dicot families in COMPADRE and in nature (Comp=Compositae; Legum=Leguminosae; Orchid=Orchidaceae; Rosa=Rosaceae; Rubia=Rubiaceae). (G) The distribution of species among growth form categories (Herb=herbaceous perennials; Tree=trees; Shrub=shrubs; Suc=succulents; Palm=palms; An=annuals; Epi=epiphytes; Other=includes mosses and ferns).

over-represents gymnosperms (proportion test: $\chi^2=1009.3$, $df=1$, $p < 0.001$) and under-represents non-seed plants (proportion test: $\chi^2=67.941$, $df=1$, $p < 0.001$).

Of COMPADRE's angiosperms, 75.5% are eudicots and 24.5% monocots (Fig. 1E), which approximately reflects their natural distribution (69.3% eudicot, 30.7% monocot, Evert et al. 2013). Our χ^2 test nevertheless indicated a significant difference ($\chi^2=16.07$, $df=1$, $p < 0.001$).

To understand the distribution of COMPADRE species across plant families, we examined the five largest eudicot families (according to The Plant List 2010): Compositae (Asteraceae), Leguminosae (Fabaceae), Orchidaceae, Rosaceae, and Rubiaceae (Fig. 1F). The χ^2 test showed that the distributions differed between COMPADRE and nature (χ^2 test: $\chi^2=21.523$, $df=4$, $p < 0.001$). This difference is driven by the Rubiaceae and Orchidaceae, which are under-represented (Rubiaceae: proportion test: $\chi^2=10.496$, $df=1$, $p < 0.001$; Orchidaceae: proportion test: $\chi^2=7.799$, $df=1$, $p=0.007$). The other families are fairly proportionately represented (all $p > 0.05$).

Half of COMPADRE's species are herbaceous perennials (364 of 791 species, 46%), and only 26% are woody plants (trees or palms) (Fig. 1G). This contrasts with estimates that 45–48% of vascular plant species are woody (FitzJohn et al. 2014).

Conservation status

The IUCN has assessed only 30% ($n=239$) of the species in COMPADRE. Of these, contrary to our expectations (H4),

COMPADRE's content with respect to the Red List status well-reflects Red List assessments (χ^2 test: $\chi^2=4.799$, $df=4$, $p=0.309$). Most of COMPADRE's species are assessed as Least Concern (61%), with the rest falling into one of the threatened categories (Vulnerable, Endangered or Critically Endangered) (Fig. 2A).

Population growth rates

As predicted (H5), there is an overall slight but statistically significant tendency to study growing populations (two-sided t -test on $\log \lambda = 0$: $t=7.610$, $df=1565$, $p < 0.001$). However, the effect size is small (mean $\log \lambda = 0.069$, 95% CI = 0.051–0.087, SD = 0.360) (Fig. 2B). Inclusion of growth form as a covariate reveals that this tendency varies among growth form, with trees, shrubs, herbaceous perennials and annual plants all having $\log \lambda$ values greater than 0, while other included growth forms (succulent, palm, epiphyte, algae) show no significant difference (Supporting information). There were no significant differences in $\log \lambda$ between growth forms, except for annual plants, which tended to have a larger population growth rate than the other types (Tukey HSD: $p < 0.05$). Our analysis of OLS regression slopes for populations with at least a five-year time-series shows no tendency for researchers to select populations where λ is initially high but then decreases, leading to negative slope values (Fig. 2C; t -test: $t=0.518$, $df=200$, $p=0.605$). To ensure that this result was robust to the length of the time-series used, we repeated this with time-series of at least ten-years with qualitatively identical results. The non-significant result

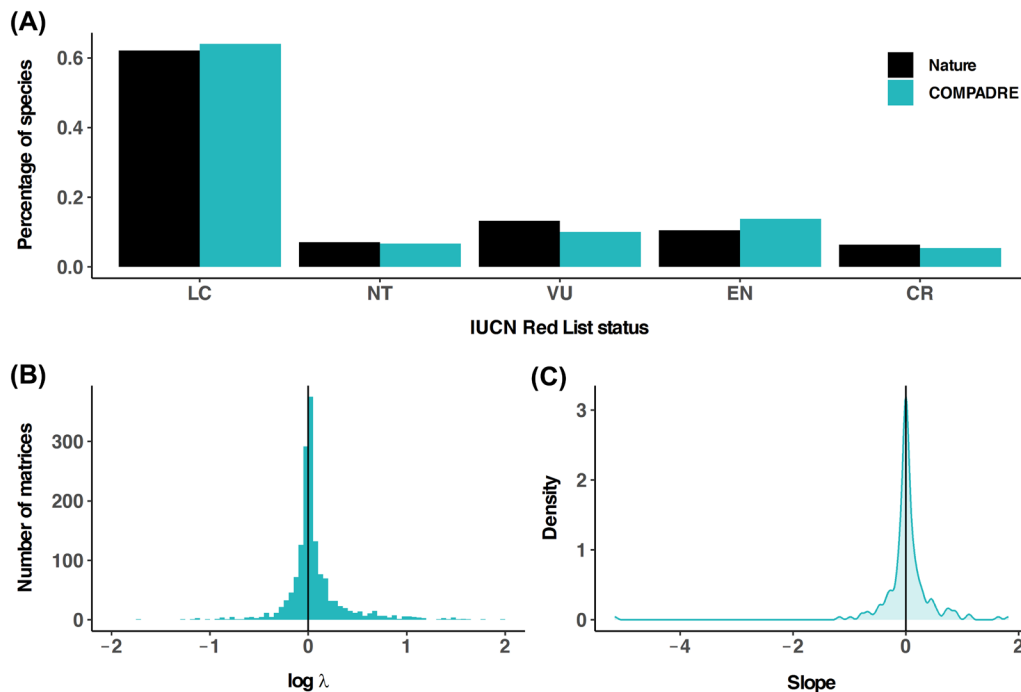


Figure 2. Conservation status and population trend biases in COMPADRE. (A) Comparison of the distribution of species among IUCN Red List conservation status in COMPADRE (blue) and in nature (black) (LC=least concern, NT=near threatened, VU=vulnerable, EN=endangered, CR=critically endangered). (B) The distribution of population growth rates ($\log \lambda$) for MPMs in COMPADRE. (C) The density distribution of the slope of the linear $\lambda \sim \text{year}$ relationship for studies with > five years of data.

is also consistent across growth forms ($F=1.018$, $df=8$, 192 , $p=0.424$) and ecoregions ($F=0.1638$, $df=4$, 196 , $p=0.957$). There were no significant differences between groups in either case (Tukey HSD: all p -values > 0.05).

How are the studies and MPMs designed?

Temporal and spatial replication

As expected (H6), most COMPADRE studies are short-term (Fig. 3A), with 43% running for between one and three years, which is slightly shorter than expected. The median study duration is four years, while the mean is longer (6.466 years), reflecting the skewed distribution. Long-term exceptions include studies of the shrub *Cassia nemophila* (Silander 1983) and the tree *Acer saccharum* (Lin and Augspurger 2008), which both span 51-years. Study duration did not vary much among ecoregions (Supporting information). There was some variation in study duration among growth forms: the study duration for annual plants tended to be shorter than those for other herbaceous perennials, shrubs, and epiphytes (Supporting information). Contrary to expectation, trees (a typically long-lived

growth form) are not studied for longer periods than typically shorter-lived growth forms (Supporting information).

As expected, most studies have a low degree of spatial replication (Fig. 4B), with only 17% of studies replicated across more than three sites. Most studies are carried out at a single site, though the distribution is skewed (mean = 3.126, median = 1, range = 1–96). Interestingly, species studied at four or more sites are mainly herbaceous perennials (57%). The number of MPMs per study does not vary much among ecoregions (Supporting information) or growth form (Supporting information).

Matrix model dimension

We expected (H7) that MPM dimension would vary widely and be greater for long-lived groups like trees. The distribution of matrix sizes is left-skewed (mean = 6.609, median = 5; Fig. 3C), with the largest matrix having a dimension of 60 (for *Rhododendron ponticum* (Travis et al. 2011)). There are four 'matrices' for three species with a dimension of one (*Perilla frutescens*, Levin et al. 2019; *Narcissus poeticus* and *Rosa canina*, Burns et al. 2013). Although unusual, these are

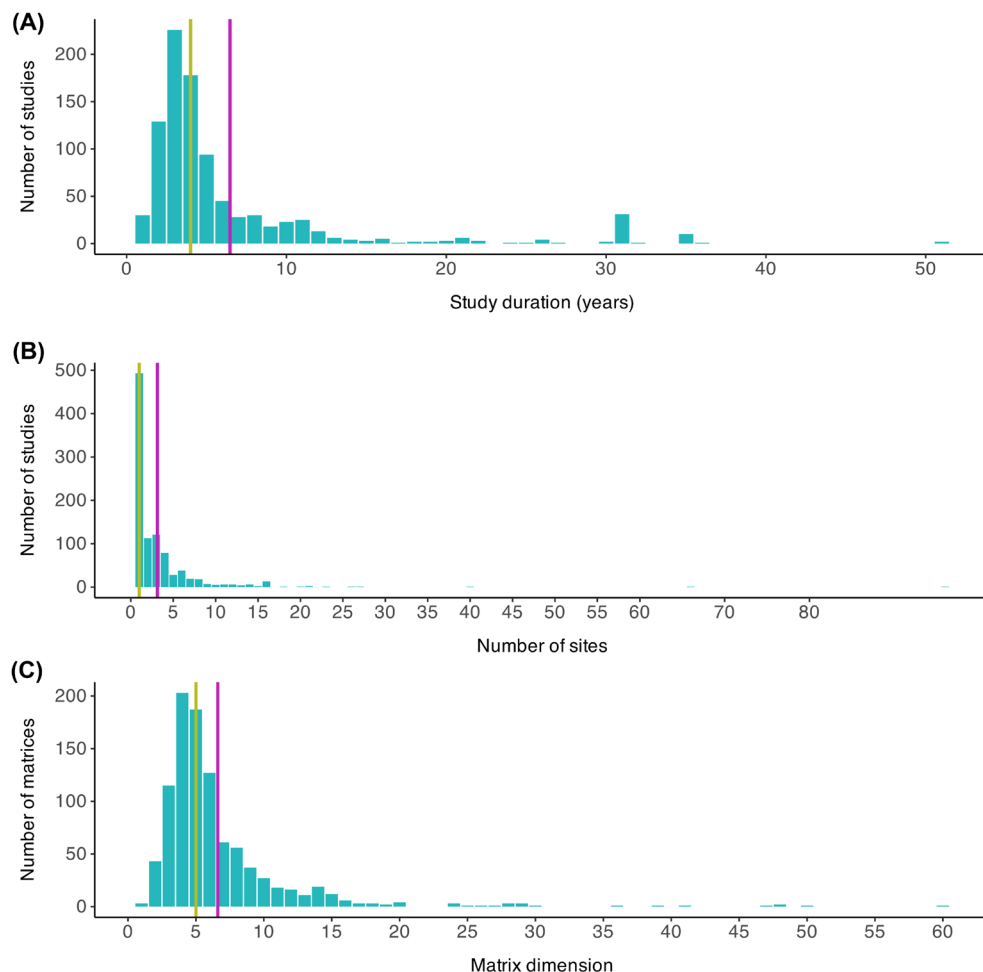


Figure 3. Spatiotemporal replication and MPM construction in COMPADRE. (A) The distribution of study duration. (B) The distribution of the number of study sites (spatial replication). (C) The distribution of matrix dimension across MPMs. The magenta and yellow lines show the mean and median, respectively.

indeed presented and analysed as matrices in studies using matrix methods.

Although the ANOVA indicated that typical matrix dimension varied significantly among ecoregions (ANOVA on log matrix dimension: $F=16.95$, $df=5$ and 948 , $p < 0.001$) (Supporting information), the post hoc Tukey tests indicated no significant pairwise differences (Supporting information). This discrepancy is likely due to the conservative nature of Tukey tests. In contrast, the variation in dimension across growth forms is clearer (ANOVA on log matrix dimension: $F=10.470$, $df=6$ and 894 , $p < 0.001$), and the Tukey tests indicate that tree and palm matrices are significantly larger than annual plants and herbaceous perennials (mean dimension, backtransformed from the log-scale outputs of the Tukey test: Trees=7.494; Palms=7.480; Herb=4.682; Annual=3.140; Supporting information). This supports our initial hypothesis (H7).

Discussion

Plant demographic knowledge has improved in the three decades since Franco and Silvertown (1990), but gaps and biases remain. Understanding such biases is important when using large-scale data to make broad generalisations. For example, under-representation of particular ecoregions, growth forms, or taxonomic groups may lead to incorrect generalisations if species in those under-represented regions or groups have distinct demographic behaviour. Improved knowledge of biases in databases like COMPADRE, and a recognition of their impact on inferences, will enhance our understanding of the natural world. Researchers should carefully consider potential biases in these large-scale datasets, especially when conducting comparative studies seeking to generalise across disparate taxa and geographic regions.

COMPADRE (ver. 6.23.5.0) contains data for 760 species, representing 0.21% of the ~ 370 000 extant plant species (not including green algae) (The Plant List 2010). Although COMPADRE covers only a fraction of plant diversity, it contains most English-language published MPM-based plant demographic work (Salguero-Gómez et al. 2015). It is, therefore, a reasonable indicator for MPM-based plant demographic knowledge. We emphasise, however, that most COMPADRE studies are English language. This is notable because Amano et al. (2016) found that a third of biodiversity conservation literature was non-English and about 16% is unsearchable using English keywords, thus remaining hidden. If similar patterns hold in plant demography, knowledge gaps in the English-speaking research community could be closed by engaging with researchers familiar with non-English language literature.

Where is the research performed?

Biogeography

Plant biodiversity is unevenly distributed. Equatorial regions are usually relatively species-rich, while biodiversity declines

polewards for most groups (Gaston 2000). Biodiversity hotspots are concentrated in the tropics, on equatorial islands, and in the Southern Hemisphere (Kier et al. 2005, 2009). Our finding that approximately three-quarters of demographic studies take place in the largely temperate regions of the western, Northern Hemisphere (Fig. 1A–B, Supporting information) contrasts with those areas, supporting H1. This result is not surprising given similar findings for population dynamics (McRae et al. 2017), biodiversity time-series (Dornelas et al. 2018), and the distribution of ecological studies (Martin et al. 2012). These patterns highlight knowledge gaps for the planet's most threatened ecosystems. For example, sub-Saharan Africa and Southeast Asia have among the least ecological data yet show the most rapid terrestrial ecosystem declines (MEA 2005). Given the importance of demographic data for assessing extinction risk demographic data gaps are a concerning impediment to species-level conservation. Beyond conservation, this biogeographic bias limits our understanding of global ecological trends and drivers of population dynamics and life-history evolution.

Country-specific wealth (GDP)

As anticipated (H2), plant demographic research output was positively associated with the per capita GDP of the country where the work was carried out (Fig. 1C). We expected this because high-GDP countries invest more in research (King 2004, van Noorden and Butler 2019) and researchers tend to conduct research near their home institutions for logistical reasons (Courtts et al. 2016). The high variation around the trendline may reflect the international networks and mobility of researchers carrying out research away from their home institutions. Many high diversity regions tend to have lower GDP and strategies should be explored to encourage plant demographic research in these regions.

For which species and populations do we have demographic data?

Taxonomy

As expected (H3), most of COMPADRE's species are angiosperms, reflecting this group's high diversity. However, COMPADRE over-represents gymnosperms and under-represents the non-seed plants. Within angiosperms, most of COMPADRE's species are eudicots. Although this approximates the natural distribution of eudicot versus monocot species, we nevertheless detect a small statistically significant bias towards the study of eudicots. COMPADRE's species distribution among the major eudicot plant families approximated the natural distribution, except for Rubiaceae and Orchidaceae, which were under-represented. The paucity of Rubiaceae may relate to geographical bias since this group is mainly (sub)tropical, which is not well-represented in COMPADRE. As expected (H3), herbaceous perennials are better-represented than any other growth form. Trees, which are economically and ecologically and ecologically important (Chambers et al. 2001), are under-represented, probably due

to logistic difficulties in studying large, long-lived organisms, but perhaps also due to the relatively low temperate-region tree diversity.

Although some biases may be overcome statistically (e.g. by resampling or rarefaction), the scarcity of demographic data on several growth forms, including ferns, lianas, and bryophytes, reduces our ability to draw inferences for these growth forms to set them in context with more commonly-studied forms. This issue is particularly troublesome for comparative studies of plant life history evolution.

Conservation status

Demographic models are useful to guide management decisions for threatened species (Morris and Doak 2002). Contrary to expectation (H4) that researchers collectively focus on threatened species, the distribution of demographic studies in COMPADRE well-approximates the actual distribution of plant Red List statuses. There is no tendency to favour studies of threatened species. However, we should regard this result with caution because it is based on the small fraction of COMPADRE species that have been Red List-assessed. The true distribution of species among Red List categories may be quite different, especially since species endemic to biodiversity hotspots are less likely to have been assessed.

Population growth rates

There was a overall slight tendency for the preferential study of growing populations and a stronger statistically significant tendency for several growth forms (supporting H5). Still, there was no evidence for a 'regression to the mean' effect where growth rates decline along the time series (contrary to Buckley et al. 2010, who found a consistent decline in growth rates through the course of studies, across all growth forms and species rarity). We initially anticipated this tendency because we expected researchers to select obviously flourishing populations to avoid the risk and logistical cost of local extinction. The difference between our results and those of Buckley et al. (2010) could be due to differences in data or methods. Buckley et al. used a smaller dataset (50 species) but a potentially more statistically powerful phylogenetic Bayesian multi-level regression model. This effect warrants further investigation because biased sampling (e.g. towards growing populations) could lead to incorrect conclusions about population dynamics in comparative research.

How are the studies and MPMs designed?

Temporal and spatial replication

The fact that demographic studies tend to have low spatial and temporal replication supports our hypothesis (H6) and confirms previous findings (Crone et al. 2011, Ehrlén et al. 2016). Limited spatial replication may affect confidence in model inferences. The geographic distribution of plants varies widely, with some occurring in specific small areas (e.g. *Iliamna remota* is endemic to the ~ 8 ha Langham Island, IL, USA; Swinehart and Jacobs 1998) while others span

continents (e.g. *Plantago major*, Sagar and Harper 1964). Widely-distributed species are likely to experience a greater range of environmental conditions than those with small ranges, and demographic data should ideally be collected in representative parts of this range to understand the species' demography more fully. Work by Doak and Morris (2010), Wardle et al. (2014) and Römer et al. (2021) are good examples of such efforts.

The limited temporal extent in most studies is also a concern because accurate forecasting of population dynamics is expected to require a time-series extending well beyond three years, primarily because of the impacts of rare extreme weather events (Ehrlén et al. 2016, Teller et al. 2016). Given the cost and effort required for long-term research, the limited temporal extent of plant demography studies is not surprising. Space-for-time substitution, which enables rapid data accumulation across an extensive range of environmental conditions, can allow modelling of responses to future climate scenarios without the need for long time-series (Blois et al. 2013, Damgaard 2019). However, the approach assumes drivers of spatial demographic variation are equivalent to those that drive temporal variation, which may not be the case (Pickett 1989, Damgaard 2019). In any case, the low spatial replication in COMPADRE limits broad utilisation of this approach.

Matrix model dimension

Researchers constructing MPMs usually select an appropriate model dimension based on species life-history (including longevity or life cycle complexity), the study's purpose, and quantity of data available to parameterise each transition. Modelling the demography of species with more complex life cycles often requires larger matrices. Nevertheless, especially for age or size-based matrices, there is a large degree of flexibility in the choice of matrix dimension. Consequently, species with similar life histories may often be modelled with matrices of different dimensions. While we would hope that inferences from these MPMs are robust to difference in dimension, it is important to realise that matrix dimension can indeed affect the outcomes (Enright et al. 1995, Salguero-Gómez and Plotkin 2010, Takada et al. 2018). Therefore, when systematic variation in matrix dimension occurs across different forms or ecoregions, beyond what is necessary to capture life cycle complexity, it has the potential to introduce unintended biases in the analysis. As expected (H7), matrix dimension varies hugely, with a substantial proportion (~ 20%) having a dimension of three or less. This low dimension could limit utility. For example, this dimension is probably too low for the derivation of measurements relying on calculating age trajectories from stage-based MPMs (Cochran and Ellner 1992, Caswell 2001) such as Keyfitz's entropy (Keyfitz 1977). Furthermore, as mentioned above, derived metrics including elasticities (Enright et al. 1995, Salguero-Gómez and Plotkin 2010, Takada et al. 2018) and transient measures (Stott et al. 2010), are sensitive to MPM dimension. Besides influencing individual metrics, systematic bias in model dimension among growth forms and ecoregion

could produce spurious inferences in comparative studies if not accounted for.

Dealing with bias

Our assessment of the available data in COMPADRE has revealed systematic bias in the availability of demographic data across various factors, including geography, taxonomy, and growth form. Such biases are not surprising, given the well-known biases in biodiversity data (Titley et al. 2017, Conde et al. 2019, dos Santos et al. 2020). The bias in COMPADRE is a form of non-random sampling error, where sample statistics do not reflect the population-level parameters under investigation. In addition to this bias, it is likely that random sampling error, whereby the sample statistics from the available data do not represent the true statistic, is an issue for groups with small sample sizes. Unlike bias, the problem of random sampling error can be alleviated by increasing the sample size for the group in question.

Over the longer term, such sampling error and bias could be reduced by targeting under-represented areas or taxa for research (Fazey et al. 2005, dos Santos et al. 2020). This strategy is expensive and would require community support and/or incentives from funding bodies. An alternative approach that does not rely on collecting additional data, is to acknowledge the existence of such bias and account for it statistically. The appropriate approach is highly dependent on the specifics of the data and hypotheses used, and are beyond the scope of this paper. We recommend that researchers consider carefully some of the numerous ways to do this, including weighting (McRae et al. 2017) and subsampling (e.g. rarefaction) (Gotelli and Colwell 2001). In addition, researchers could use careful hierarchical regression modelling (Harrison et al. 2018) where potential bias-causing terms are explicitly included in the model.

Conclusions

Although knowledge of global plant demography has undoubtedly improved with the extensive use of MPMs in the three decades since Franco and Silvertown (1990), it is still biased. It is founded on geographically biased data heavily focused on herbaceous perennials, leaving important knowledge gaps. Demographic research is constrained by funding, with the temporal length echoing typical grant and PhD tenure, with work concentrated in wealthy countries. We found no significant bias in conservation status or population growth rate, indicating that researchers focus neither on threatened species nor strongly trending populations.

It is worth considering that other demographic methods, including IPMs (Easterling et al. 2000) and individual-based models (DeAngelis and Mooij 2005), have greatly contributed to plant demographic knowledge and may reduce or close some of the knowledge gaps and biases we discuss. Further investigation is required to test this. We expect, however, that the biases will be similar no matter which tool

is considered because the factors that generate these biases remain similar across methods.

To close knowledge gaps and better understand generalities in life-history strategy and population dynamics, research targeting neglected growth forms and ecoregions is desirable, as is increased spatial and temporal replication within species. Furthermore, an improved understanding of the impact of these biases on model predictions and methodological developments to account for known biases would be helpful.

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Gesa Römer: Conceptualization (supporting); Formal analysis (lead); Investigation (equal); Methodology (equal); Visualization (lead); Writing – original draft (lead); Writing – review and editing (equal). **Johan P. Dahlgren:** Conceptualization (equal); Methodology (equal); Project administration (equal); Supervision (supporting); Writing – review and editing (supporting). **Roberto Salguero-Gómez:** Data curation (equal); Writing – review and editing (supporting). **Iain M. Stott:** Formal analysis (supporting); Investigation (supporting); Methodology (supporting); Writing – review and editing (supporting). **Owen R. Jones:** Conceptualization (lead); Data curation (equal); Formal analysis (equal); Funding acquisition (equal); Investigation, Methodology (lead); Project administration (lead); Supervision (lead); Visualization (supporting); Writing – original draft (supporting); Writing – review and editing (equal).

Data availability statement

Most data used here is open access and can be obtained from the following web pages: COMPADRE Plant Matrix Database: <http://www.compadre-db.org> (Salguero-Gómez et al. 2015); IUCN Red List data: <http://www.iucnredlist.org> (IUCN 2019); The Plant List: <http://www.theplantlist.org> (The Plant List 2010); World Bank: <https://data.worldbank.org/indicator/NY.GDP.PCAP.CD> (World Bank 2022). Analysis code is included in the Supporting Information.

Data are also available from the Open Science Framework repository: <https://doi.org/10.17605/OSF.IO/PBZJ7> (Römer et al. 2023).

Supporting information

The Supporting information associated with this article is available with the online version.

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