# A cautionary note regarding the consequences of balancing for fair comparisons in population ecology

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**NB:** For the convenience of reviewers, we have placed figures and their captions close to where they are first referenced in the text. If accepted, we will re-format the placement of figures according to journal guidelines.

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# Abstract

Population ecology has amassed a significant volume of demographic data across the Tree of Life. Together, these data enable comparative analyses at unprecedented taxonomic and biogeographic scales to examine patterns of demographic performance and their mechanisms. However, macroecological analysis of heterogeneous data and models from diverse study systems comes with risks, and care must be taken to ensure that the patterns from comparative approaches are biologically meaningful, rather than driven by model-specific artifacts. Recently, a balancing approach has been proposed as a solution to 'distorted' population structure, particularly for evaluating transient (short-term) population dynamics. We argue that some distortion is the result of true biological processes, and that balancing over-corrects for distortion due to census timing (pre- vs. post-breeding). We lay out the relationship between demographic census design and the issues purported to be solved by balancing. Using a large dataset of carefully-selected matrix population models from plants and animals, we demonstrate that balancing changes biological interpretation of the relationship between reproductive traits and demographic resilience. We also highlight how application of balancing outside of its narrow original application to transient metrics can be problematic. We argue that meaningful comparisons require tailored approaches that respect the structure and context of demographic data. A more nuanced strategy–based on the biological realities of life cycles, census design, and reproductive strategies–will improve the robustness and interpretation of comparative demographic analyses.

**Keywords** comparative demography, post-breeding census, pre-breeding census, matrix population model (MPM), transient dynamics.

# 1 Introduction

The open-access data revolution has transformed ecological research providing high-resolution data to examine large-scale ecological questions. Notable examples include BIEN for plant occurrence and traits (Maitner et al., 2018), Movebank for animal movement (Kays et al., 2022), and TRY for plant traits (Kattge et al., 2020). These and other resources have enabled macroecological insights into trait evolution (Bruelheide et al., 2018), species distributions (Kissling et al., 2018), and biodiversity responses to global change (Newbold et al., 2016).

Population ecology and demography have also benefited from the open-access revolution. Of relevance in this context are efforts like the Living Planet Index (Collen et al., 2009), the Global Population Dynamics Database (CPB, 1999), Amniote (Myhrvold et al., 2015), DATLife (MPIDR, 2013), MALDABBA (Gaillard et al., 2021; Lemaître et al., 2020; Ronget et al., 2025), SPIBirds (Culina et al., 2021), the COMPADRE Plant Matrix Database (Salguero-Gómez et al., 2015), the Human Mortality (MPIDR, 2025a) and Fertility databases (MPIDR, 2025b), the COMADRE Animal Matrix Database (Salguero-Gómez et al., 2016a), and PADRINO (Levin et al., 2022). The increasing availability of open-access demographic data is fueling comparative research in ecology, evolution, and conservation biology, providing key insights into species' life histories (Healy et al., 2019; Salguero-Gómez et al., 2016b; Van de Walle et al., 2023), invasion biology (Jelbert et al., 2019), and responses to environmental change (Compagnoni et al., 2021).

Population ecologists are now faced with a key challenge: high volumes of heterogeneous demographic data. Specifically, what demographic data do we choose to run our comparative demographic analyses? Demographic database curators have spent a significant amount of their professional lives making sure that the data are as clean, error-checked, and interoperable as possible (Salguero-Gómez et al., 2021). However, the authors of the contributing papers in those databases likely did not have in mind a common protocol to produce data and demographic models that directly allow comparison across populations and species (but see Gascoigne et al. 2023). As such, researchers wanting to capitalize on these open-access resources must set some criteria to make sure that the patterns that may emerge from their analyses are due to biological processes, and not due to artifacts in model choice. In pursuit of fair comparisons, population ecologists have been pointing out key aspects of heterogeneity among structured population models and proposing solutions. Examples include ramet- vs. genet-based demographic models (Salguero-Gómez, 2018), where to determine the beginning of life in populations with a seedbank stage (Franco and Silvertown, 2004; Venable and Brown, 1988), modelling state variables as continuous vs. discrete (Doak et al., 2021; Ellner et al., 2022), and differences or errors arising from the timing of field censuses (Che-Castaldo et al., 2020; Kendall et al., 2019).

Recently, Hinrichsen (2024) introduced another key aspect of heterogeneity, and a mathematical tool that could solve it: "distortion" in indices of transient dynamics, and mathematical balancing as a solution. Specifically, distortion here refers to how far a population's stable distribution is from a uniform or flat distribution. The stable population distribution is defined as the proportion of individuals in each of the examined stages when the population is growing at its asymptotic growth rate. For instance, the stable population distribution of the common carp (*Cyprinus carpio*) in the COMADRE database is right-skewed and therefore more distorted, with the population concentrated in the youngest developmental stage (Figure 1a; Stratford et al. 2016), whereas the stable population distribution of the snow goose (*Anser caerulescens*) is less distorted (more evenly split) across the five stages in its life cycle (Figure 1b; Cooch et al. 2001). Hinrichsen introduces a way to account for the diversity of population structures associated with the matrix population models. Specifically, the author uses a mathematical method called 'balancing', which involves rescaling the projection matrix according to the stable population distribution. This rescaling ensures that indices of transient dynamics become scale-invariant. The author argues that this approach provides a more accurate and meaningful assessment of short-term population changes.

We see the proposal by Hinrichsen as an important addition to the toolbox of comparative demography. However, we are concerned by the ways that balancing causes changes to biological and ecological inference about metrics of transient dynamics (Stott et al., 2011) and the relationship between resilience and life history traits (e.g. Capdevila et al., 2020; Capdevila et al., 2022). It is our opinion that most of the distortion among age/stage/size classes that balancing is designed to solve is not an issue, but a biological feature of the models. The exception, and a major focus of this note, is distortion or unfair comparison that arises due to 'lumping' together models with both pre- and post-breeding census designs. Below, we try to disentangle census design from the general effects of balancing on transient metrics, and discuss the implications for analyses of transient metrics and the accompanying life history traits that macroecologists study. Finally, we offer examples of a couple of alternative approaches that researchers could take to ensure that the scale of their metrics matches the question that they seek to answer.

## 2 The issue of census timing

Because matrix population models operate in discrete time, the structure of the model depends on the order and timing of biological events relative to the model's time step. Because many species reproduce seasonally, annual demographic surveys (*i.e.*, the census) are usually carried out at a day/week/month of the year that is close to the breeding period. This timing can also help researchers to more accurately count individuals, such as for animals that aggregate only during the breeding period, and to more accurately identify the

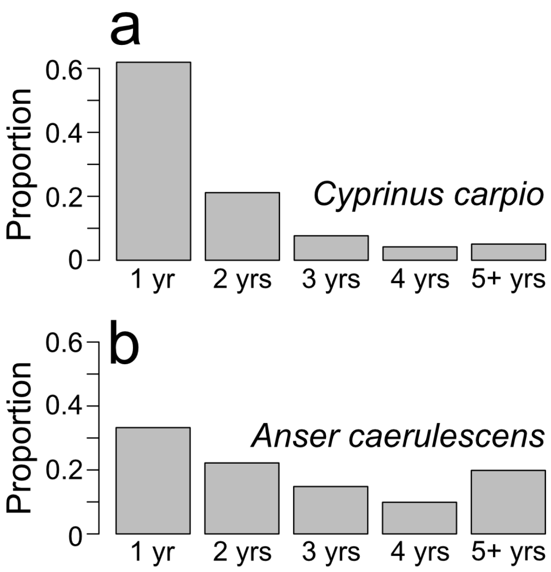

**Figure 1:** The differing stable population distributions among populations and species capture important biological information. Although these two example populations from the COMADRE database are both pre-breeding census designs with five age-structured classes, the stable distribution for (a) common carp (a fish; *Cyprinus carpio*) is more skewed than the stable distribution for (b) snow goose (a bird; *Anser caerulescens*).

reproductive status of individuals, such as in plants with ephemeral reproductive tissues. As a result, demographic censuses and the resultant models can generally be classified as pre- or post-breeding (*sensu* Caswell 2001, Ch. 2)[1].

In a pre-breeding census, individuals are counted immediately before the breeding season, and so new individuals are first counted when their age is approximately one time step (Figure 2a). In contrast, in a post-breeding census, individuals are counted immediately after the breeding season, such that new individuals are first observed at an age of approximately 0 time steps. In a pre-breeding design *model*, reproductive elements (orange arrows in Figure 2a) must account for production of offspring and offspring survival for the first

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[1] There are also birth-pulse models where individuals are assumed to reproduce continuously throughout the time interval. Since these are not as common in the plant and animal literature, we do not dwell on them here.

time step. Conversely, in a post-breeding design model, reproductive rates must account for survival of adults until the next breeding event and production of (age-0) offspring.

Matrix population models (MPMs) based on pre- and post-breeding censuses can yield different estimates of transient dynamics because of these distinctions in the way that vital rates map onto matrix elements (Figure 2a). These differences can lead to different transient behaviors, such as reactivity, amplification, and damping ratio (Figure 2b), even if asymptotic metrics like the population growth rate ($\lambda$) are similar (Figure 2c). For example, in a plant species with seed dormancy, a pre-breeding model would begin with the seedling stage (already accounting for losses due to seed predation, incomplete germination, and seedling competition), while a post-breeding model would begin with the seed stage. By counting each seed as an individual, the post-breeding version of the model would exhibit stronger transient responses. To correct for this, there are methods available to convert models to the same census design, essentially by converting post-breeding models into pre-breeding models before calculating metrics that will be compared across models (see Capdevila et al. 2022 for an application of this approach to macroecological analysis of transient metrics).

The timing of census is key to the patterns reported by Hinrichsen (2024). Indeed, in the examples of species with the highest and lowest distortion in his comparative analysis, the three with highest distortion are all post-breeding models, while the three with lowest distortion are all pre-breeding models. Furthermore, to demonstrate the importance of scale, Hinrichsen uses an illustrative example about a fish biologist who either counts eggs or counts groups of eggs that will survive the first year of life (Hinrichsen, 2024, page 4). When the author points out that the reactivity and Henrici metrics for these two possible models would be drastically different, this is functionally the same as calculating those metrics for a pre-breeding or post-breeding design for the same population.

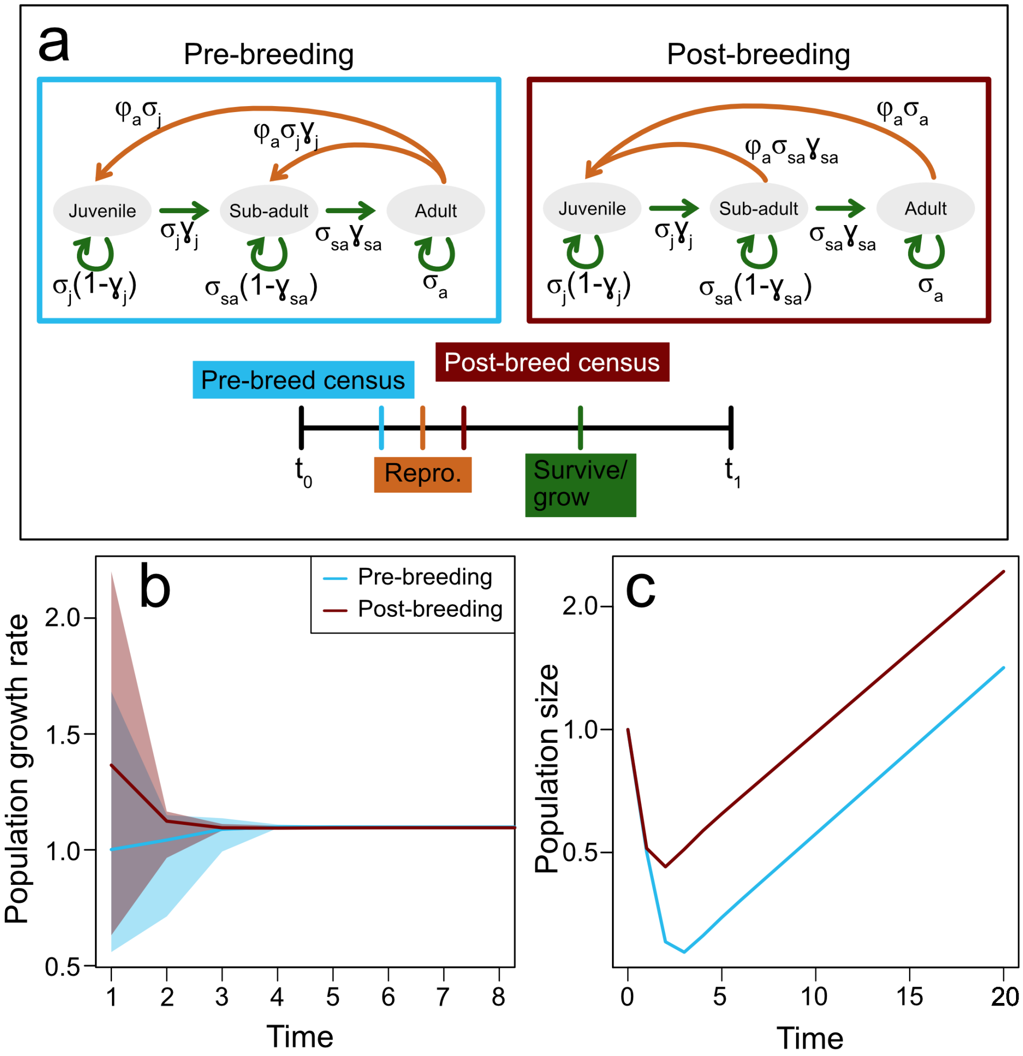

**Figure 2:** The timing of the demographic census impacts the resulting matrix population model's transient dynamics, even though the long-term population growth rate is the same. In (a), we show the life cycle and timing of events across the year, for a species with three stages: juveniles, sub-adults, and adults. This species experiences a single reproductive pulse per time step, followed by a concentrated period of mortality and growth. We simulated this population, collecting two demographic datasets corresponding to pre-breeding vs. post-breeding census. (b) Matrix population models built for the two census designs have different transient dynamics, with the post-breeding model exhibiting a greater propensity to 'boom' after a disturbance. (c) The pre- and post-breeding design models have very similar long-term behavior. Further details of the simulations are available in the Appendix.

Balancing via the stable distribution implicitly assumes that the relative abundance of a given stage class is inversely proportional to its importance or value to the population. The verbal examples used by the author tend to focus on when eggs *vs.* 1-year-olds or eggs *vs.*. adults are counted. However, distortion can arise from a steep survivorship curve, rather than due to differences in how reproduction is counted. We can imagine an example where 1-year-olds and 2-year-olds are counted (*e.g.*, biennial plants), but they are still present in a very distorted distribution. In that case, the distorted distribution is an important and *real* feature of the species' biology, rather than an artifact of counting. As such, the biological implications of balancing may be counter-productive. Furthermore, in cases such as these, balancing could erase variation in the biology that we are primarily interested in understanding. As such, we must ask ourselves: is balancing always re-scaling individuals to their 'adult equivalents' and, if so, is that really desirable?

## 3 How does balancing impact biological interpretation?

Balancing is a valid mathematical approach to produce scale-invariant metrics of transient dynamics (Hinrichsen, 2024) or other population metrics (Hinrichsen, 2025), but biological interpretation of balanced metrics may be more important than mathematical elegance. To examine the potential consequences of balancing on biological interpretation, we analyzed two common measures of transient dynamics: compensation (also called reactivity or first-time-step amplification) and resistance (also called first-time-step attenuation) (Capdevila et al., 2020; Stott et al., 2011; Stott et al., 2012). We calculated these metrics for both the 'raw' (*i.e.*, as produced by the original studies) and balanced version of a subset of models from the COMADRE (v. 4.21.8.0; Salguero-Gómez et al. 2016a) and COMPADRE databases (v. 6.22.5.0; Salguero-Gómez et al. 2015). Here, we used the same set of models that were selected for use in Hernández et al. (2024) - briefly, primitive and irreducible models for full life cycles of populations observed under unmanipulated conditions (*i.e.*, no experimental treatments that could potentially affect the actual biology of the examined species). The data set includes 445 matrix population models for animals, and 1020 for plants.

In general, balancing reduces the range of possible values by several orders of magnitude (Figure 3), as demonstrated by Hinrichsen (2024). Although we expected to see a clear divide in the effect of balancing on the resilience metrics of pre- vs. post-breeding models, the pattern is not as clear-cut as expected. In animals, the most striking effects of balancing on both compensation and resistance are seen in post-breeding models. Before balancing, animal MPMs showed values of compensation ranging as high as 100,000, although the vast majority (93%) have a compensation value of less than 10 (Figure 3a). The models with values greater than 10 before balancing tend to be post-breeding models. After balancing, all values are below 2.5. A similar pattern is observed for the effect of balancing on resistance in MPMs from animals (Figure 3c). In plants, we do not see very much of a pre- vs. post-breeding census divide in the effect of balancing on resilience metrics (Figure 3b,d). It is possible that the distinct effects of balancing on plant vs. animal MPMs could be related to the fact that plant MPMs are more often stage- or size-based, while animal MPMs are more likely to be age-based (Römer et al., 2024; Salguero-Gómez et al., 2015; Salguero-Gómez et al., 2016a).

Balancing showed an expected, but difficult to interpret effect on the relationship between per-capita reproductive output and compensation. Per-capita reproductive output has a natural and interpretable biological relationship with compensation, whose role allows differentiating the transient dynamics of native and invasive species (Jelbert et al., 2019), and whose positive relationship is found in both the full statistical analysis of Capdevila et al. (2022) and the much simpler plots shown in Figure 4a,b. However, balancing removes

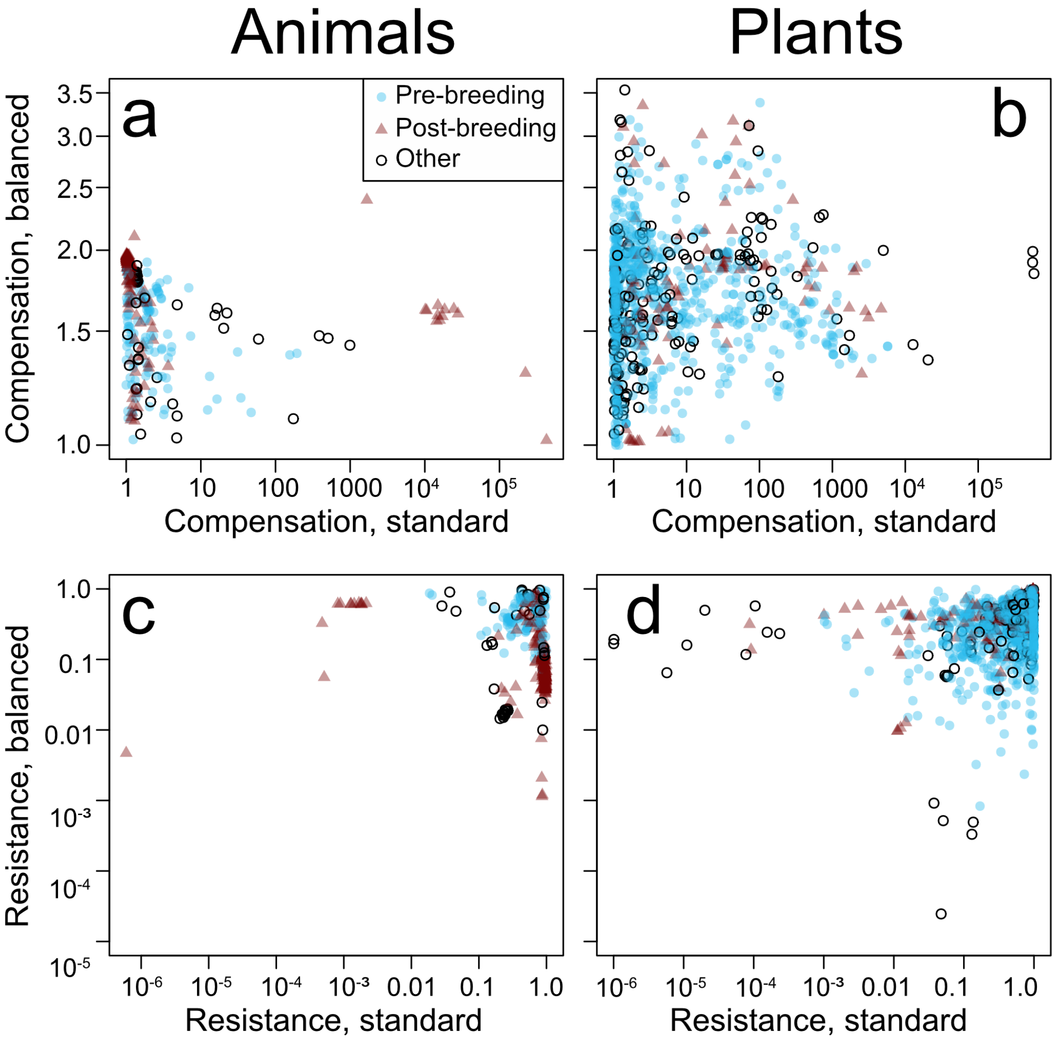

**Figure 3:** The effects of balancing on the resilience metrics of compensation and resistance. Each point is a single matrix population model from the COMADRE or COMPADRE databases, in the subset of models used in Hernández et al. (2024). Pre-breeding and post-breeding census designs are defined as in Figure 2a.

or even reverses this relationship, such that populations with higher per-capita reproductive output have lower compensation after balancing has been applied (Figure 4c,d). In other words, calculating transient metrics in population models after balancing leads to the interpretation that populations with high per-capita reproductive output have a low propensity to ‘boom’ after a demographic disturbance. This, combined with the results of Jelbert et al. (2019), is counter to the ecological pattern that invasive species tend to be those that can thrive in disturbed habitats (Marvier et al., 2004; Meyer et al., 2021). Following the logic above and the finding in Jelbert et al. (2019), if we balance we are likely to lose our ability to predict invasions from transient dynamics, or to even get it backwards.

In light of the recent debate about whether and how to apply balancing in analyses of asymptotic dynamics (interstage flows, Hinrichsen 2025; Yokomizo et al. 2024; Yokomizo et al. 2025), we also caution researchers to think carefully about which metrics should be calculated from a ‘raw’ vs. a balanced matrix population model. As an illustrative example of a gross misapplication of balancing, we calculated generation time (Bienvenu and Legendre, 2015) and expected lifespan (Jones et al., 2022) for both the ‘raw’ and balanced version of the same subset of models discussed above. Our analyses show that balancing has no effect on generation time (Figure 5a,b) but it has profound impacts on the estimation of mean lifespan (Figure 5c,d). For the 70 animal species here examined, balancing tends to decrease lifespans more strongly than it increases them, while the opposite is true in the 151 plant species we balanced.

From the perspective of ecological interpretation, it is worrying that the direction of the impact of balancing on the mean life expectancy depends on life history speed. For fast life histories (those with short expected lifespans, *sensu* Stearns (1998)), balancing increases our perception of life expectancy. Meanwhile, for slow life histories (those with long expected lifespans), balancing decreases our perception of life expectancy. It is also worth noting that the application of balancing causes the projection matrices to be row-stochastic, and therefore under this approach the transition sub-matrix ($\mathbf{U}$) can no longer

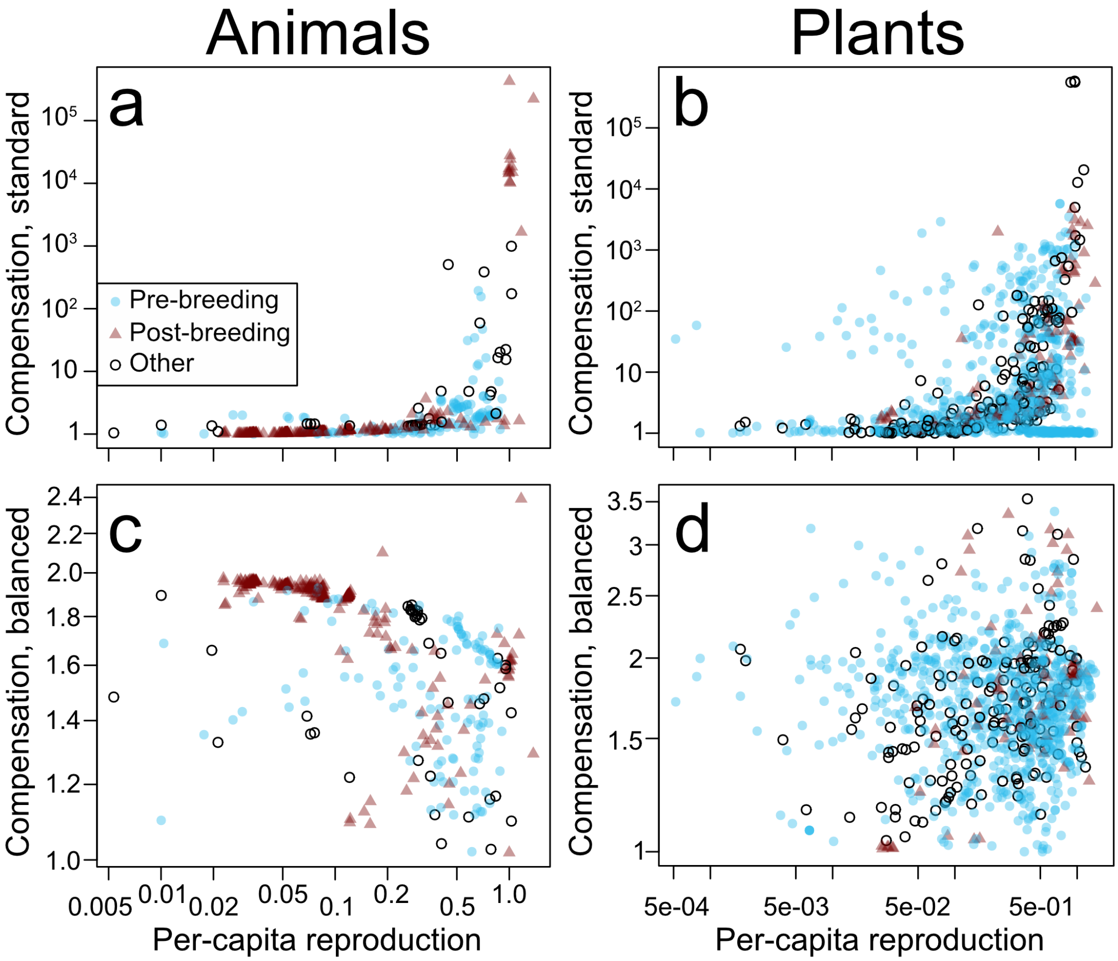

**Figure 4:** The effects of balancing on the relationship between compensation and per-capita reproductive output. Each point is a single matrix population model from the COMADRE or COMPADRE databases, in the subset of models used in Hernández et al. (2024). Pre-breeding and post-breeding census designs are defined as in Figure 2a.

be interpreted as the survival matrix. Very frequently (14%, 76% of the 445, 1020 matrices we examined for animals and plants, respectively), the 'balanced' matrix $\tilde{\mathbf{U}}$ has column sums greater than 1. In a traditional matrix population model, a column sum greater than 1 implies the spontaneous production of individuals in the corresponding age, stage, or size class. While this particular (mis)application of balancing may be unrealistic, it

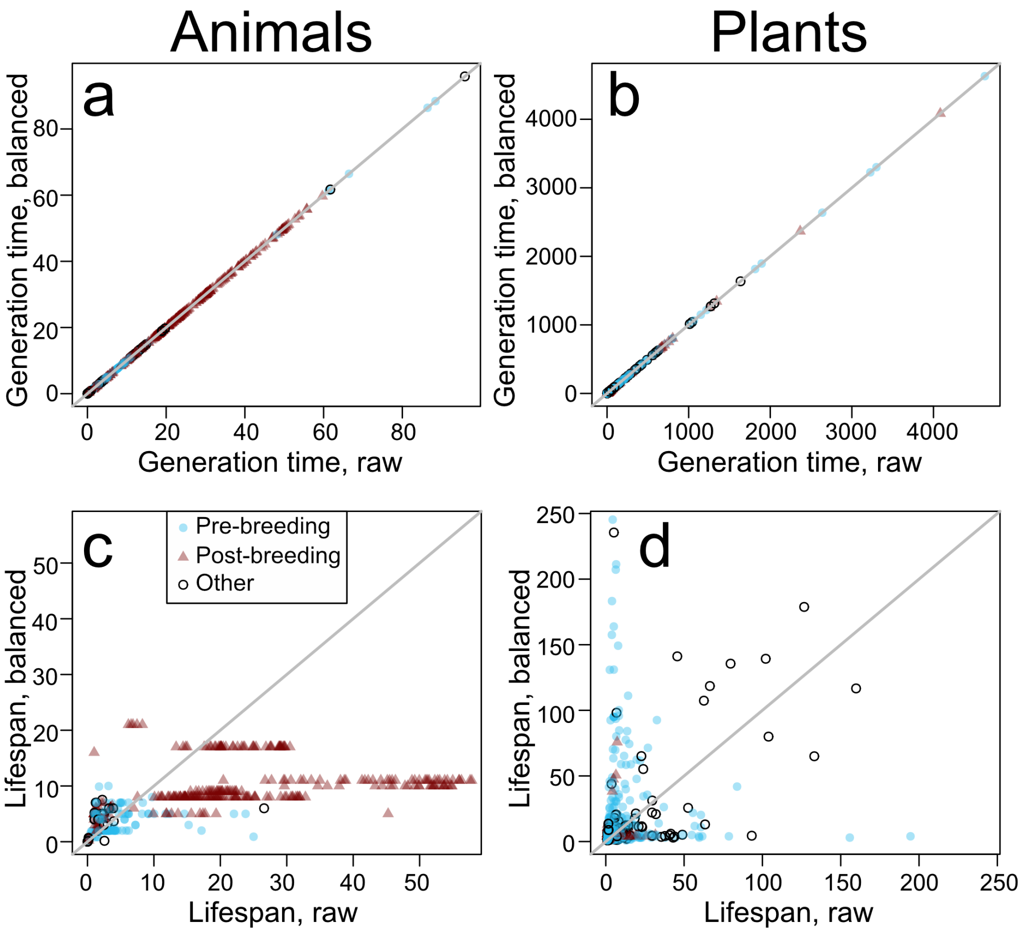

**Figure 5:** Generation time is unchanged by applying balancing, but the expected lifespan is profoundly affected by balancing, with the direction of change influenced by life history speed itself. Each point is a single matrix population model from the COMADRE (animals) or COMPADRE (plants) databases, in the subset of models used in Hernández et al. (2024). Pre-breeding and post-breeding census designs are defined as in Figure 2a. We calculated generation time as the mean age between successive generations in a lineage (Bienvenu and Legendre, 2015). We calculated lifespan as the expected lifespan starting from the first stage or size class using the Rage package (Jones et al., 2022). In all four panels, the grey line is the 1:1 line. For ease of visualization, we have excluded points that fall outside of the 99th percentile of values for each panel (raw and balanced values, combined).

is illustrative of the importance of carefully considering when scale invariance, achieved through balancing, may be helpful and when it may be harmful for answering biological and ecological questions.

At first glance, scaling an MPM by the asymptotic (stable) population vector may seem antithetical to the goal of measuring transient dynamics produced by perturbed (unstable) population vectors. Still, we understand the appeal of this approach by analogy of scaling an MPM by the asymptotic population growth rate, which is standard practice in the analysis of transient dynamics (Stott et al., 2011). However, the asymptotic population vector is not necessarily the 'natural' way to standardize the size of one class relative to others because it may itself contain distortion (skew) among classes (Figure 1), and as we have shown it can distort life history outcomes determined by an MPM (Figure 5). If, for certain objectives, it is unreasonable to compare offspring to adults, or small classes to large classes because of biological distortion, we suggest scaling the state variable vectors (*i.e.*, structured abundance) as the dynamics unfold for both the transient and asymptotic dynamics. A simple way to accomplish this objective is to multiply the state variable vector at each time step by a weighting vector: $\mathbf{c}^\top$. Weighting could be measured in units of mass, size, primary productivity, carbon sequestration or other scales relative to the class of largest unit. If a given class should be discounted entirely, such as fish eggs in the beluga sturgeon example of Hinrichsen (2024), the class could be given a weight of 0. In a comparative analysis, the weighting scheme must be comparable across MPMs.

A concrete example of such a weighting scheme was used in Hernández et al. (2024), which explored patterns of variation in lifespan and lifetime reproductive output across the same subset of plant and animal population models analyzed above. In this study, differences in maternal investment, age of offspring, and gestational periods made it difficult to directly compare lifetime reproductive output calculated from the 'raw' population models. In other words, counting a fish egg and a polar bear cub as the same amount of reproductive output would distort the answer to the research question "What are the patterns of variation in lifespan and lifetime reproductive output across the tree of life?". To address this distortion, the reproductive output was re-scaled by an offspring's probability of reaching maturity, bringing the definition of lifetime reproductive output closer to an evolutionary definition of reproductive success. This re-scaling, which yielded lifetime reproductive output in consistent units of 'offspring which reach sexual maturity' was applied only for the calculation of moments of reproductive output; lifespan, measured in units of years, did not require a similar re-scaling.

## 4 Concluding remarks

It is often necessary to rescale some aspect of the models to compare the life histories and population dynamics of species with extremely different life histories. Without such standardization, demographic metrics like population growth rate ($\lambda$) and life history traits like generation time or reproductive value can be misleading when applied across species that differ drastically in pace of life, such as annual plants *vs.* long-lived vertebrates. For instance, comparing the population growth of *Arabidopsis thaliana*, which completes its life cycle in a few weeks, to that of the African forest elephants (*Loxodonta cyclotis*) or giant sequoias (*Sequoiadendron giganteum*), which reproduce after decades, requires adjusting time scales or normalizing transitions to a per-generation basis (de Vries et al., 2023; Keyfitz, Caswell, et al., 2005). One common approach is to rescale the projection matrix by generation time (Caswell, 2001), allowing demographic metrics to be interpreted in terms of relative timing rather than absolute years. Additionally, standardizing vital rates—such as survival or fecundity—by body size or metabolic rate can help account for life-history variation shaped by allometric constraints (Brown et al., 2004). These rescaling efforts are essential to avoid confounding biological insight with mathematical artifacts, especially when using demographic models in comparative studies or conservation prioritization.

Researchers have developed a number of ways to achieve fair comparisons in demography and adjacent fields. Doing so generally requires a tailored approach for the particular demographic metric and question being addressed. Here, we re-iterate that combining models with pre-breeding and post-breeding designs without any re-scaling would be inappropriate. Balancing, as proposed by Hinrichsen (2024) may be one option for re-scaling. However, we critically demonstrate that balancing does more than account for differences in pre- vs. post-breeding census designs: it changes the relationship between resilience metrics and life history traits, in some cases reversing the biological interpretation. Instead, we invite researchers to re-visit the issues with comparison between pre- and post-breeding models as discussed here and in previous work (Che-Castaldo et al., 2020; Kendall et al., 2019). To facilitate the careful consideration of pre- and post-breeding models, we announce that the census timing information is being added into the COMADRE and COMPADRE databases for all of the models from Hernández et al. (2024), which we use here. This new addition covers 928 and 3975 matrices from 158 and 256 species of animals and plants, respectively. This information (also available in Supplemental Table S1) will be found in the next release of COMADRE (5.0.0.0) and COMPADRE (7.0.0.0) in the metadata field "CensusType". Efforts will continue to further populate this variable across the remaining species in these demographic sources. We hope that this information will serve researchers in their pursuit of careful and fair macroecological comparisons.

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## Figure Legends

**Figure 1.** The differing stable population distributions among populations and species capture important biological information. Although these two example populations from the COMADRE database are both pre-breeding census designs with five age-structured classes, the stable distribution for (a) common carp (a fish; *Cyprinus carpio*) is more skewed than the stable distribution for (b) snow goose (a bird; *Anser caerulescens*).

**Figure 2.** The timing of the demographic census impacts the resulting matrix population model's transient dynamics, even though the long-term population growth rate is the same. In (a), we show the life cycle and timing of events across the year, for a species with three stages: juveniles, sub-adults, and adults. This species experiences a single reproductive pulse per time step, followed by a concentrated period of mortality and growth. We simulated this population, collecting two demographic datasets corresponding to pre-breeding vs. post-breeding census. (b) Matrix population models built for the two census designs have different transient dynamics, with the post-breeding model exhibiting a greater propensity to 'boom' after a disturbance. (c) The pre- and post-breeding design models have very similar long-term behavior. Further details of the simulations are available in the Appendix.

**Figure 3.** The effects of balancing on the resilience metrics of compensation and resistance. Each point is a single matrix population model from the COMADRE or COMPADRE databases, in the subset of models used in Hernández et al. (2024). Pre-breeding and post-breeding census designs are defined as in Figure 2a.

**Figure 4.** The effects of balancing on the relationship between compensation and per-capita reproductive output. Each point is a single matrix population model from the COMADRE or COMPADRE databases, in the subset of models used in Hernández et al. (2024). Pre-breeding and post-breeding census designs are defined as in Figure 2a.

**Figure 5.** Generation time is unchanged by applying balancing, but the expected lifespan is profoundly affected by balancing, with the direction of change influenced by life history

speed itself. Each point is a single matrix population model from the COMADRE (animals) or COMPADRE (plants) databases, in the subset of models used in Hernández et al. (2024). Pre-breeding and post-breeding census designs are defined as in Figure 2a. We calculated generation time as the mean age between successive generations in a lineage (Bienvenu and Legendre, 2015). We calculated lifespan as the expected lifespan starting from the first stage or size class using the Rage package (Jones et al., 2022). In all four panels, the grey line is the 1:1 line. For ease of visualization, we have excluded points that fall outside of the 99th percentile of values for each panel (raw and balanced values, combined).

# Appendix: Demographic simulation and comparison of pre- vs. post-breeding models

To demonstrate the difference in pre- and post-breeding models, we simulated a single population that our 'virtual ecologist' (Zurell et al., 2010) observed via both a pre-breeding and post-breeding census each year (Figure 2). The population experiences a single reproductive pulse per year, followed by a concentrated period of mortality and growth. Probability of survival, probability of growth to the next developmental stage, and reproductive rate are determined by the individuals' classification into developmental stages termed 'juvenile', 'sub-adult', and 'adult.' Individuals are classified as juveniles as soon as they are produced, and they reproduce once they reach the adult stage. This is a simplified model of a population that lives in a strongly seasonal environment.

We initiated the population ($t_0$ in Figure 2) with 1000 individuals sampled from the stages ['juvenile', 'sub-adult', 'adult'] with probabilities [0.4, 0.4, 0.2]. These individuals were then immediately counted during the first pre-breeding census. Next, the adults reproduced according to a Poisson process with mean reproductive output of two. These new individuals were assigned to the juvenile class and counted, along with all existing individuals, in the post-breeding census. All individuals had a unique identification number, such that we assume our virtual ecologist observed all individuals in the population and could recognize individuals on subsequent observations.

After the post-breeding census, we simulated mortality and growth. For each individual, we sampled the binomial distribution with a probability of survival given by their developmental stage ($\sigma_i$; Table S1). Next, surviving individuals were subject to growth. For juveniles and sub-adults, we drew from the binomial distribution with a probability of growth (progressing to the next developmental stage) given by their current developmental stage ($\gamma_i$; Table S1). At this point, the simulated population was at $t_1$, and the number of surviving individuals in each stage could be counted by the virtual ecologist in the pre-breeding census for $t_1$. The steps were repeated until $t_3$ to ensure that both the pre-breeding and post-breeding census information was recorded for two years.

| Stage | Survival probability ($\sigma_i$) | Growth probability ($\gamma_i$) |
|---|---|---|
| Juvenile (j) | 0.5 | 0.6 |
| Sub-adult (sa) | 0.7 | 0.4 |
| Adult (a) | 0.85 | – |

**Table S1:** Annual survival probability and growth probability according to developmental stages. The growth probability represents the probability that a juvenile becomes a sub-adult, or a sub-adult becomes an adult. Surviving juveniles and sub-adults stay in the same state with a probability of $1 - \gamma_i$, and surviving adults stay adults with a probability of 1.

To demonstrate how the population dynamics of the same population would be interpreted differently based on census timing, we next built matrx population models (MPMs) for both the pre-breeding and post-breeding census data. We calculated transition probabilities based on the number of individuals in each developmental class at the first and second census for each census type. Because we assumed perfect detection and identification of individuals, the survival and growth rates (*i.e.*, the **U** matrix) were nearly identical.

Conversely, reproduction was calculated differently for the two census designs. For both census designs, we used 'anonymous reproduction' such that we do not assign offspring to particular parents. For the pre-breeding design, the number of new individuals counted/observed in a focal year ($t_x$) must be assigned as reproductive output to the adults observed the previous year ($t_{x-1}$). Because individuals can progress to the sub-adult stage in the same year that they are 'born' (or hatched, germinated, etc.), adults can produce both juveniles and sub-adults in the pre-breeding census design (Figure 2a). For the post-breeding design, the number of new individuals counted/observed in a focal year ($t_x$) must be assigned as reproductive output to the adults observed in the same year. Because survival and growth happen *before* reproduction in the time-step of the post-breeding census, the fertility matrix (**F**) must incorporate the survival probability of adults, as well as the fact that some of the sub-adults counted at time $t$ will have matured into adults and reproduced by time $t + 1$ (Figure 2a).

Our virtual ecologist would then estimate the following matrix population models:

$$\mathbf{A}_{pre} = \mathbf{U}_{pre} + \mathbf{F}_{pre} = \begin{bmatrix} 0.211 & 0 & 0.423 \\ 0.290 & 0.411 & 0.577 \\ 0 & 0.266 & 0.821 \end{bmatrix}, \tag{S1}$$

and

$$\mathbf{A}_{post} == \mathbf{U}_{post} + \mathbf{F}_{post} = \begin{bmatrix} 0.217 & 0.509 & 1.572 \\ 0.296 & 0.411 & 0 \\ 0 & 0.266 & 0.821 \end{bmatrix}. \tag{S2}$$

These models, built from data on the same population collected using different methods, yield the same predictions about asymptotic population dynamics (Figure 2b). The $\lambda$ values are 1.098 and 1.095 for the pre-breeding and post-breeding models, respectively. However, their transient dynamics differ (Figure 2c), with the post-breeding model exhibiting a transient envelope that is shifted 'up' on the population growth rate axis.

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