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RESEARCH ARTICLE

Several candidate size metrics explain vital rates across multiple populations throughout a widespread species' range

Maude E. A. Baudraz[1] | Dylan Z. Childs[2] | Ruth Kelly[1,3] | Annabel L. Smith[1,4] | Jesus Villellas[5] | Martin Andrzejak[6,7] | Benedicte Bachelot[8] | Lajos K. Benedek[9] | Simone P. Blomberg[10] | Judit Bodis[11] | Francis Q. Brearley[12] | Anna Bucharova[13,14] | Christina M. Caruso[15] | Jane A. Catford[16,17] | Matthew Coghill[18] | Aldo Compagnoni[19] | Anna Mária P. Csergő[9] | Richard P. Duncan[20] | John Dwyer[21] | Johan Ehrlén[22] | Bret D. Elderd[23] | Alain Finn[1] | Lauchlan Fraser[18] | Maria B. García[24] | Jennifer R. Gremer[25] | Ronny Groenteman[26] | Liv Norunn Hamre[27] | Aveliina Helm[28] | Maria Höhn[29] | Lotte Korell[6,7] | Lauri Laanisto[30] | Anna-Liisa Laine[31] | Michele Lonati[32] | Caroline M. McKeon[1] | Aoife Molloy[1] | Joslin L. Moore[33,34] | Melanie Morales[35,36] | Sergi Munne-Bosch[35] | Zuzana Münzbergová[37] | Siri L. Olsen[38,39] | Adrian Oprea[40] | Meelis Pärtel[28] | Rachel M. Penczykowski[41] | William K. Petry[42] | Satu Ramula[43] | Pil U. Rasmussen[44] | Simone Ravetto Enri[32] | Deborah A. Roach[45] | Anna Roeder[7,46] | Christiane Roscher[7,46] | Marjo Saastamoinen[47] | Cheryl Schultz[48] | R. Drew Sieg[49] | Olav Skarpaas[50] | Ayco J. M. Tack[22] | Joachim Töpper[51] | Peter A. Vesk[52] | Gregory Vose[53] | Elizabeth M. Wandrag[54,55] | Glenda M. Wardle[56] | Astrid Wingler[57] | Yvonne M. Buckley[1]

Correspondence
Yvonne M. Buckley
Email: buckleyy@tcd.ie

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Abstract

1. Individual plant size often determines the vital rates of growth, survival and reproduction. However, size can be measured in several ways (e.g. height, biomass, leaf length). There is no consensus on the best size metric for modelling vital rates in plants.
2. Demographic datasets are expanding in geographic extent, leading to choices about how to represent size for the same species in multiple ecological contexts. If the choice of size variable varies among locations, inter-population comparative demography increases in complexity.

For affiliations refer to page 14.

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3. Here, we present a framework to perform size metric selection in large-scale demographic studies. We highlight potential pitfalls and suggest methods applicable to diverse study organisms.
4. We assessed the performance of five different size metrics for the perennial herb *Plantago lanceolata*, across 55 populations on three continents within its native and non-native ranges, using the spatially replicated demographic dataset PlantPopNet. We compared the performance of each candidate size metric for four vital rates (growth, survival, flowering probability and reproductive output) using generalized linear mixed models. We ranked the candidate size metrics based on their overall performance (highest generalized R^2) and homogeneity of performance across populations (lowest total magnitude of, and variance in, population-level error).
5. While all size variables performed well for modelling vital rates, the number of leaves (modelled as a discrete variable, without transformation) was selected as the best size metric, followed by leaf length. We show how to interrogate potential trade-offs between overall explanatory power and homogeneity of predictions across populations in any organism.
6. *Synthesis*. Size is an important determinant of vital rates. Using a dataset of unprecedented spatial extent, we find (a) consistent size-based models of growth, survival and reproduction across native and non-native populations of this cosmopolitan plant species and (b) that several tested size metrics perform similarly well. This is encouraging for large-scale demographic studies and for comparative projects using different size metrics, as they may be robust to this methodological difference.

KEYWORDS
demography, landscape demography, large scale spatial demography, plant population ecology and macroecology, population models, size variable selection, state variable selection

1 | INTRODUCTION

The size of individuals is critical for modelling individual vital rates, such as fecundity, growth and survival, particularly in plants (Caswell, 2001; Easterling et al., 2000; Morris & Doak, 2002; Roff, 1986; Stearns, 1992). Larger, same-age individuals are often interpreted as having a higher performance (Stearns, 1992). Nonetheless, larger is not necessarily better, as size can also increase visibility to herbivores, susceptibility to disturbances and lead to architectural instability (Díaz et al., 2007).

'Size' is not simple to measure, particularly in perennial plants that display considerable structural variation. Therefore, many size metrics are used for plant population modelling, such as stem diameter in trees (Ellner & Rees, 2006; Meunier et al., 2007), number of leaves (Oldfather, 2018a, 2018b), as well as combinations of different variables (e.g. length of the longest leaf times the number of leaves in a rosette in Van Groenendael (1986) and Van Groenendael and Slim (1988)). The appropriate size metric may vary depending on the focal study organism, which makes it difficult to determine the 'optimal' metric for capturing size as a determinant of individuals demographic fate.

The selection of an appropriate size variable is typically only briefly mentioned in publications (Ellner et al., 2016; Oldfather, 2018b). There is some advice about how to select the best state variable for demographic studies, which mostly focuses on comparing different candidate variables using the Akaike information criterion (AIC; Akaike, 1974; Caswell, 2001; Morris & Doak, 2002; but see also Younginger et al., 2017). AIC, however, is used to compare models using the same response variable. To compare the performance of multiple size metrics as explanatory variables for explaining variance in multiple vital rates as response variables (e.g. size at the next time point (continuous response), probability of flowering (binary response), probability of survival (binary response)), AIC is not appropriate and other approaches are needed (Akaike, 1974). Other metrics of goodness of fit should be implemented, such as the root mean square error or mean absolute error (Willmott & Matsuura, 2005), but guidance is lacking. Furthermore, advice is mostly aimed at demographic studies including one or a few populations, generally spatially close and in similar environments (Coutts et al., 2016; Pironon et al., 2017; Salguero-Gómez et al., 2015).

There have been efforts in recent years to increase the geographical extent of demographic datasets. Demographic data are collected at larger spatial and environmental scales through harmonized protocols, such as PlantPopNet (gathering information about *Plantago lanceolata* on three continents; Buckley et al., 2019; Smith et al., 2020; Villellas et al., 2021) and other spatially distributed demographic studies (such as Colautti et al., 2014 on *Alliaria petiolata*; Doak & Morris, 2010 on *Polygonum viviparum* and *Silene acaulis*; Jongejans et al., 2011 on *Carduus nutans*; Merow et al., 2017 on *Berberis thunbergia* and *Alliaria petiolata* and Sheth & Angert, 2018 on *Erythranthe cardinalis*). New challenges in analysing such data will undoubtedly emerge. In particular, different size variables might be good predictors of vital rates in different populations, as individuals in those populations may need to invest in different 'aspects' of size to face different biotic and abiotic conditions. For instance, the number of leaves per rosette in a rosette-forming plant might be more important in an alpine location to avoid damage by winter frost, while plant height may be of more importance in a mesic temperate meadow with strong competition for light (Falster & Westoby, 2003; Givnish, 1982; Halbritter et al., 2018). Size and its implications might also differ between the non-native and native range of a species due to different selective pressures (Paynter et al., 2016).

The existing size variable selection approaches do not, to our knowledge, account for between-population variation in the performance of size metrics. The overall performance of a model could be high, yet some vital rates may be much better explained in some populations than others. A lack of homogeneity in explaining demographic processes across multiple populations may affect the accuracy of predictions of the demography of populations occurring in new locations or under new climatic, land use or biotic contexts.

The homogeneity of performance of size metrics is of pressing importance as datasets grow in extent, to overcome the most commonly cited limitations in demographic studies, which are the limited geographical range of available data to answer questions (Coutts et al., 2016; Salguero-Gómez et al., 2012; Tredennick et al., 2018) and the lack of spatial replication (Csergő et al., 2017; Salguero-Gómez et al., 2012, 2015). One example of a project aiming to fill these gaps in data availability is PlantPopNet, a spatially distributed model system for population ecology (www.plantpopnet.com) monitoring multiple populations of the perennial plant *Plantago lanceolata* across three continents, including both native and introduced ranges (Buckley et al., 2019; Smith et al., 2020; Villellas et al., 2021). Populations are censused annually for growth, survival and fecundity of all individuals by a network of local collaborators using a standardized protocol (Buckley et al., 2019). *Plantago lanceolata* is a cosmopolitan perennial plant (Sagar & Harper, 1964; Smith et al., 2020) and PlantPopNet includes populations across a wide range of environmental conditions, from six different biomes (Figure 1). Given the broad range of climates faced by the studied populations, the PlantPopNet data are a good example of the need for a state variable that performs consistently across geographic and climatic space, populations and vital rates.

Using the PlantPopNet data, we developed a framework to select the best state variable (from candidate variables using different above-ground size metrics) across populations and vital rates as a critical first step in developing a spatially distributed population model. Our objective was to test whether different size metrics varied in explanatory power and performance across vital rates and across populations. While we use a case study of *Plantago lanceolata*, the core questions we raise and methods we suggest could be applied to other organisms. We discuss the application of these methods to other study organisms and systems.

2 | MATERIALS AND METHODS

2.1 | Overview

We used the internationally distributed demographic dataset from PlantPopNet to compare the performance of different size metrics as predictors in demographic models of growth, survival and reproduction across 55 populations of *Plantago lanceolata* from the sub-Arctic to the sub-Tropics (Figure 1). Using generalized linear mixed-effects models of growth, survival, probability of flowering and reproductive output, we compared six candidate size metrics to explain these vital rates. We assessed the size variables by comparing the explanatory performance of the different size metric models across vital rates, populations and native versus non-native ranges. Models were compared using R^2 and mean absolute error (MAE) per population.

2.2 | The species

Plantago lanceolata L. is a short-lived, perennial, rosette-forming herb (Kuiper & Bos, 1992; Sagar & Harper, 1964). Each individual (genet) is composed of one to several rosettes (ramets), which are generally connected and in close proximity. Small flowers (4 mm diameter) are arranged in spikes which vary in length and are organized on a variable number of flowering stems per rosette and per individual plant (Sagar & Harper, 1964). Each flower produces up to two seeds in a circumcissile capsule (Lauber et al., 2018). The plant is variable in size and shape, with leaves ranging from 2 to 45 cm in length (Sagar & Harper, 1964). Native to Eurasia, *P. lanceolata* is now present on all continents except for mainland Antarctica (CABI, 2019). As this species is widespread, of relatively low impact as a non-native species, not intensively managed as a weed, perennial, easy to recognize in the field, and was already being studied in multiple fields of biology and ecology (Kuiper & Bos, 1992), it was selected as a study organism for PlantPopNet.

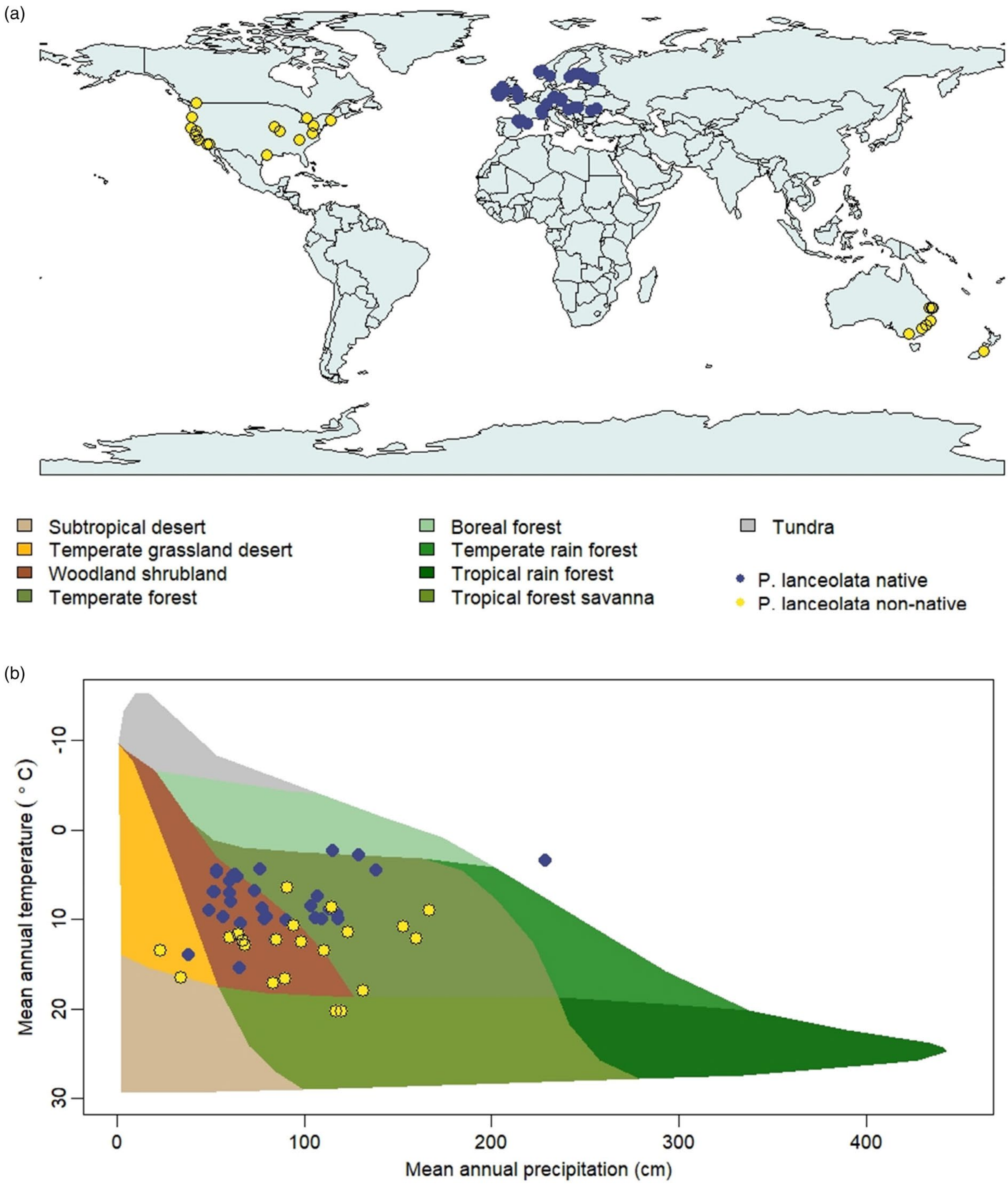

FIGURE 1 The distribution of the 55 populations of *Plantago lanceolata* included in this study in geographical (a) and environmental (b) space. Panel (b) shows the biomes of the world where *P. lanceolata* occurs. The biomes are classified by their mean annual precipitation values and mean annual temperature (Whittaker, 1970). Due to high local precipitation, one population in Norway lies outside the definition of Whittaker's biomes. Plots were developed with the BiomePlot (Kunstler, 2014) and rworldmap packages (South, 2011).

2.3 | Dataset

PlantPopNet (www.plantpopnet.com; Figure 1) collaborators collect demographic information on 65 naturally occurring populations of *P. lanceolata* across three continents. The present study included 55 populations that had at least two consecutive yearly censuses (Supporting Informations S1 and S2). Each population consists of an initial 100 individuals marked in naturally occurring populations and re-visited yearly at the peak of the flowering season.

We considered one genet to be one individual. Rosettes (ramets) linked by the same rooting system were added to the size of the overall genet. New recruits within the original plots were recorded and followed in subsequent years. The number of rosettes, number of leaves per rosette, length of the longest leaf and width of the longest leaf for each rosette, flowering status (flowered, not flowered), reproductive output and survival or death of each individual were recorded at each annual census. We used the first transition (from start of the study at that site to 1 year after, that is, the first 2 years of census data) for each population. For further information on the PlantPopNet protocol, see Buckley et al. (2019).

Permits to perform fieldwork were required where necessary. Data were collected from site SC with authorization from the National Parks and Wildlife Service for work in the Burren National Park (no permit number), from sites SW729 and SW242 with authorization from the Direction générale de l'environnement du Canton de Vaud (DGE) Section Biodiversité et Paysage in Switzerland (no permit number), from sites ACR, HAS, NRM and JSJ with authorization from the University of California Natural Reserve System (no permit number), from site HU with authorization from the Hungarian University of Agriculture and Life Sciences, Georgikon Campus (no permit number), from site TY with authorization from Tyson Research Center, Washington University in St. Louis (no permit number), from site CDF with authorization from University College Cork (no permit number), from site PC with authorization from the University of California, Davis Putah Creek Riparian Reserve (no permit number), from site BG with authorization from the Luster municipality (no permit number), from site IT with authorization from the University of Torino, Department of Agricultural, Forest, and Food Sciences (no permit number) and from site WIN with authorization from the Hampshire and Isle of Wight Wildlife Trust (no permit number).

2.4 | Choice of candidate size metrics

Several size metrics have been used to characterize growth, survival and reproduction for *P. lanceolata* using a variety of different approaches (Antonovics & Primack, 1982; Hamre et al., 2010; Van Groenendael, 1986; Van Groenendael & Slim, 1988), including on populations monitored by PlantPopNet (Villellas et al., 2021). Based on these sources and the availability of measurements via PlantPopNet, we estimated size using five candidate size metrics: number of leaves, estimated biomass, total leaf area, total leaf length and length of the longest leaf (Table 1). These five size metrics use the three basic measurements of number of leaves, length of longest leaf and width of longest leaf as individual measurements or in arithmetic combinations. The computation of the metrics is detailed in Table 1 and in Supporting Information S1. The use of the length of the longest leaf was dictated by the sampling

TABLE 1 Candidate size metrics considered in this study.

Metric	Calculated as	Transformation	Rationale
Number of leaves	No. of leaves	No transformation	Intuitive measure, easy to compute and measure in the field. Treating number of leaves as a discrete count variable enables appropriate error distribution and link function to be used. Bounding at zero is retained
Number of leaves	No. of leaves	Log_e transformation	Intuitive measure, easy to compute and measure in the field. Treating number of leaves as a continuous variable through a log transformation enables the use of normal errors and a continuous scale
Total leaf area	Length of longest leaf × width of longest leaf × no. of leaves	Log_e transformation	Strong link to light capture
Total leaf length	Length of longest leaf × no. of leaves	Log_e transformation	Commonly used in literature, strong link to light capture and ease of measurement in the field
Leaf length	Length of the longest leaf	Log_e transformation	Quickest to measure in the field, low level of expected causal links to light capture
Regressed biomass	$\exp(0.556$ $+1.924\times\log(\text{no. leaves})$ $-0.213\times\log(\text{no. leaves})^2$ $+0.003\times\text{leaf length}$ $+0.833\times\log(\text{leaf width}))$	Log_e transformation	Integrated measure that estimates biomass using several non-destructive size measures. Requires destructive measurement to develop the parameterization which is time consuming

Note: The variables were selected based on their occurrence in the literature (Antonovics & Primack, 1982; Hamre et al., 2010; Van Groenendael, 1986; Van Groenendael & Slim, 1988; Villellas et al., 2021) and the availability of measurements via PlantPopNet. Number of leaves was modelled as a count variable and as a continuous variable in the growth model where size is both a response and explanatory variable. The transformed and untransformed number of leaves are treated as different size metrics in the rest of the analysis. The use of other untransformed size variables did not have a strong justification due to low conceptual impact (e.g. continuous versus discrete growth model), and some convergence issues for untransformed variables. The biomass equation was calibrated using an approach similar to Villellas et al. (2021; see Supporting Information S1).

protocol, which may bias upwards some of these size metrics. The number of leaves was the only non-continuous candidate size variable in our study. We used the untransformed number of leaves as a discrete measure of plant size. We also used a log transformation of the number of leaves to enable use of a continuous scale. This facilitated comparisons with other size metric models using continuous response variables and normal errors.

All other variables were also log transformed as it normalized the residuals of the models and reduced the skewness where applicable. All model diagnostic plots without log transformation are available in Supporting Informations S3 and S4.

2.5 | Development of the vital rate models

We modelled the following vital rates: survival probability, individual growth (modelled as $\text{size}_{t+1} = f(\text{size}_t)$), flowering probability and reproductive output. We built a series of generalized linear mixed models to explain the variation in each of these vital rates. Six models were built for each vital rate, each testing one size variable as a candidate fixed effect, for a total of 24 models. The models included random slopes and random intercepts at the population level, and a random intercept at the plot level, matching the study design (following the PlantPopNet protocol, all populations are monitored in plots with marked individuals (Buckley et al., 2019)). To ensure comparability between the model outputs, we used the same dataset for each model, that is, no missing values for any size metric.

The reproductive output was captured as the product of the length of the longest inflorescence and the number of flowering stems, as a proxy for the number of seeds produced (Villellas et al., 2021). It was modelled as a function of size, using a Gaussian distribution with an identity link. Survival and flowering probability were both modelled as a function of size, using a binomial distribution with a logit link. Growth was modelled as $\text{size}_{t+1} = f(\text{size}_t)$, and the same size metric variable was used as the response and explanatory variables for each growth model. For the continuous response variables, Gaussian errors were used. The number of leaves, used as a response count variable, was modelled using negative binomial errors, with a square root link function in the package GLMMTMB (Brooks et al., 2017). The use of the negative binomial family and square root link was data driven, as a Poisson model showed signs of overdispersion. All other models were fitted using the lme4 package (Bates et al., 2015). The *viridis* colour-blind friendly palette was used to produce all figures, using the Turbo option (Garnier et al., 2021). All analyses were performed in R version 4.4.1 (R Core Team, 2024) and the code used is provided in Supporting Information S5.

2.6 | Best size variable selection

Our objective was to compare size metrics in their ability to produce models that (a) met all applicable statistical assumptions, (b) had consistent performance across vital rates and had both (c) high explanatory power across populations and (d) homogeneous performance across populations. Each point (b–d) was assessed as a separate criterion (see text hereafter). The candidate size metrics were ranked for each criterion. Metrics that did not meet the model assumptions (criterion a) were removed from the model ranking process. We applied equal weighting of the criteria, but note that weighting could easily be changed if justified by the objective of the study.

2.7 | Evaluation metrics

We used two different model performance metrics to assess each criterion: Nakagawa's R^2 adapted to generalized linear mixed models (Johnson, 2014; Nakagawa et al., 2017; Nakagawa & Schielzeth, 2013), and the mean absolute error (MAE) (Chai & Draxler, 2014; Willmott & Matsuura, 2005). We used R^2 as an overall metric of model performance, and MAE to quantify the error of the model within each population. Nakagawa's R^2 includes conditional and marginal R^2. Marginal R^2 (R^2_{m}) can be understood as related to the variance explained by the fixed effects in the model, while the conditional R^2 (R^2_{c}) is related to the variance explained by the entire model including the random structure. The equations to derive R^2 for generalized linear mixed models differ depending on the error distribution and the link of the model (Nakagawa & Schielzeth, 2013). Therefore, we use R^2_{c} to compare metrics in their ability to explain each vital rate, but normalize the R^2_{c} values prior to averaging them across the different vital rates:

$$\text{Normalized } R^2_{c\,r,u} = \frac{R^2_{c\,r,u} - \min\left(R^2_{c\,r}\right)}{\max\left(R^2_{c\,r}\right) - \min\left(R^2_{c\,r}\right)}, \tag{1}$$

where r is the vital rate and u is the size metric.

MAE is the sum of the absolute values of the (standardized) residuals from each population (a measure of the ‘total error’ of the model in this population) divided by the number of individuals in the population. We preferred MAE to the *root mean square error* (RMSE), another well-used metric of goodness of fit, as the RMSE is sensitive to the effect of outliers. Using the square of the error works well for normally distributed processes but would penalize any response variable with a distribution skewed to the right (Willmott & Matsuura, 2005). Finally, the division by the number of individuals will render MAE more robust to varying population size than other metrics such as the variance within the population, which will increase with population size.

The mean absolute error is computed as follows:

$$\text{MAE}_{r,u,p} = \frac{\sum_1^n \left|e_{r,u,p,i}\right|}{n}, \tag{2}$$

where $e_{r,u,p,i}$ is the standardized residual of plant i from the model for vital rate r with the size variable u, with n observations within population p. The raw residuals of the model were computed as the difference between the observed and predicted values for each individual i. As the response variables of the models for each vital rate r, as well as the growth models using each size variable u, are in different units, we standardized the raw residuals by subtracting the mean ($\mu_{r,u}$) and dividing by the standard deviation ($\sigma_{r,u}$) of each model to compute the standardized residuals $e_{r,u,p,i}$.

2.8 | Selection process

2.8.1 | Criterion (a) Assumptions check

We verified that assumptions were met for each model. As generalized linear mixed models with non-Gaussian errors are hard to diagnose, we used the DHARMa package (Hartig, 2020; see Supporting Information S3). The DHARMa package helps with the diagnosis of overdispersion, zero inflation (or depletion) and model misspecification in the case of non-Gaussian response metrics and can also be applied to Gaussian response metrics. We used DHARMa to assess the uniformity of DHARMa residuals (homoscedasticity and homogeneity), the normality of random intercepts and slopes and the occurrence of zero inflation or depletion. We also used the sjPlot package to display random effect normality (Lüdecke, 2020). We display examples of the results of the DHARMa model diagnostic procedure in Supporting Information S3 and the code in Supporting Information S5.

2.8.2 | Criterion (b) Performance across vital rates

We used R^2 (Nakagawa & Schielzeth, 2013) to assess the goodness of fit for each vital rate model (see Section 2.7 for more details). A model with greater R^2 was ranked higher. We investigated both the R^2_c and R^2_m for our models but used only the R^2_c for the final variable selection step, as it includes the role of random effects in capturing the variance in vital rates. Nakagawa's R^2 was computed using the 'performance' R package for each model (Lüdecke, 2020). The equations used to derive the R^2_c differ based on the family and link function of each model (Nakagawa & Schielzeth, 2013). The R^2_c values were therefore normalized across each vital rate as detailed in Equation (1) prior to computation of the final score. For each size variable u, the final score on criterion b was the average of the *normalized* $R^2_{c\,r,u}$ over all four rates r. We have three types of models involved in this study; binomial models with logit link (survival, flowering probability), negative binomial models with square root link (growth modelled as number of leaves) and Gaussian models with log transformed variables and identity link (reproductive effort, continuous growth models). For one of the growth models the number of leaves, untransformed, is modelled using a negative binomial error distribution, with a log link. As it is the only model with this error distribution and link, we excluded it from the comparison of R^2 values and obtained the *normalized* $R^2_{c\,u=\text{number of leaves}}$ as the average over three rates (survival, fecundity and reproductive output).

2.8.3 | Criterion (c) High explanatory power across populations

We determined how well the model performed within each population by computing the mean absolute error for each population $\mathrm{MAE}_{r,u,p}$ (Willmott & Matsuura, 2005, see above). A low $MAE_{r,u,p}$ means that the model for vital rate r using the size variable u performs well for population p. We then summed MAE across all populations to reach the value for criterion (c) for metric u and vital rate r (see Supporting Information S1.1.4).

2.8.4 | Criterion (d) Homogeneity of the within population performances

We compared candidate size variables for homogeneous model performance across populations by calculating criterion d *as* the variance in $\mathrm{MAE}_{r,u,p}$ across all populations; $d_{r,u} = \sigma^2\left(\mathrm{MAE}_{r,u,p}\right)$. The rationale is that even if a metric has a low summed $\mathrm{MAE}_{r,u,p}$ value, it does not mean the spread of performance between populations will be narrow.

2.9 | Application of the criteria

The performance of each size metric against each criterion was measured in units of standardized R^2_c, MAE or variance in MAE as applicable (criterion b—highest R^2_c, criterion c—lowest population MAE, d—lowest variance in population MAE). As the various criteria were measured in different units, we normalized the scores for each criterion to a 0 to 1 scale. We then used (1 − c) and (1 − d) to ensure common directionality from 0 (worst performing) to 1 (best performing) for each criterion. The normalized scores for each criterion were averaged over all criteria to obtain the overall scores. The overall score therefore ranges from 0 (worst performing metric) to 1 (best performing metric).

2.10 | Further explorations

In addition, we assessed whether the relationship between size and vital rates was constant across populations by plotting the random slopes and intercepts for all populations. To do so, we extracted the conditional modes from each model. Very distinct, or even opposite slopes, would indicate either an ecologically different relationship between size and any vital rate in different populations (or regions of the world).

Finally, we explored if environmental gradients could explain the observed changes in size to vital rates relationship. The environmental gradients used were mean temperature and mean annual precipitation, sourced as bioclim layers at a 10-min resolution (Fick & Hijmans, 2017). To test for the effects of the environmental gradients, or interaction between size metrics and environmental gradients, we built a linear mixed effects model for population MAE as a function of the temperature and precipitation values, together with the range (native, non-native), the size metric (categorical) and the interaction between the size metrics and the two environmental gradients. The random structure allowed the intercept to vary for each vital rate and population of origin, and the slope of the relationship between MAE and temperature or precipitation was allowed to vary between vital rates. More complex random structures, including the size variables as a random intercept, produced convergence warnings or did not converge. Both temperature and precipitation were normalized and scaled to avoid convergence issues. This model was built using the lme4 R package (Bates et al., 2015).

3 | RESULTS

3.1 | (a) Model diagnostics

The assessment of all 24 models against their respective assumptions can be seen in Supporting Informations S3 and S5. All models were deemed to adequately conform to their respective assumptions and were used for further analysis.

3.2 | (b) Performance across vital rates

All size metrics performed well across vital rates. For the binomial models, the conditional R^2_c ranged from 0.55 to 0.7 for survival and 0.6 to 0.73 for flowering probabilities (Figure 2). For the Gaussian models, the conditional R^2_c ranged from 0.55 to 0.73 for reproductive output and 0.54 to 0.68 for growth models. The negative binomial growth model had a conditional R^2_c of 0.8. The number of leaves (untransformed) consistently emerged as the top ranked variable where it could be compared to the other size metrics (Figure 2; Table 2). The ranks of the other size metrics differed between rates; for example, total leaf area was ranked second for probability of flowering in terms of R^2_c, but ranked last for reproductive output. The size metrics, being the only fixed effect in our model, were responsible for the following R^2_m portions of explained variance: $R^2_m = 0.21$ to 0.35 for the Gaussian growth models (0.53 for the negative binomial model), $R^2_m = 0.06$ to 0.21 for the Gaussian reproductive output model, $R^2_m = 0.10$ to 0.22 for survival and $R^2_m = 0.18$ to 0.30 for the flowering binomial models (Figure 2).

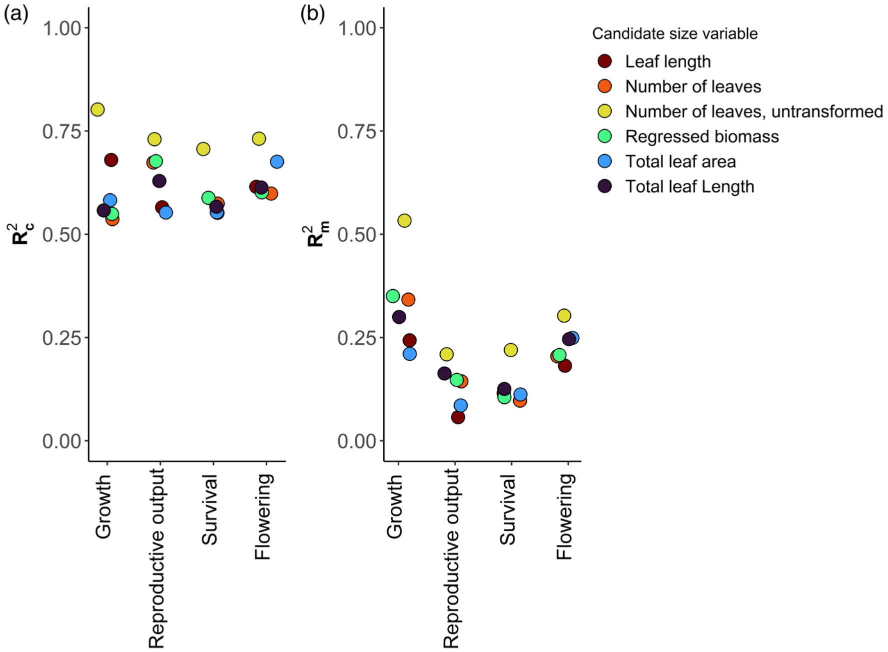

FIGURE 2 Performance of the candidate size metrics across vital rates (growth, reproductive output, survival and flowering probability on the *x*-axes), expressed in terms of (a) conditional and (b) marginal R^2 (R^2_c and R^2_m respectively, on the *y*-axes). R^2_m is a measure of the variance explained by the fixed effects in the model, R^2_c of the variance explained by the fixed effect and the random effects taken together. The equations to compute R^2_c differ slightly between Gaussian (growth, reproductive output) and binomial (survival, flowering probabilities) models. Absolute values are only comparable within these model types; yet the relative performance of each size variable remains comparable. Colours represent different size metrics. Overlapping points appear through the use of jitter on the *x*-axis. All size variables are log-transformed ($\log_e$), except for the number of leaves which is a count and therefore is used both as a discrete variable and as a continuous, log-transformed ($\log_e$) variable. The R^2_c for the growth model using the discrete, untransformed number of leaves as a response variable (0.8) is not exactly comparable with the values of the other size metrics for the same vital rates, as the model uses a different error distribution.

TABLE 2 Comparison and ranking of size metric candidate variables.

Variable	Criterion (b) performance across rates		Criterion (c) performance across populations		Criterion (d) homogeneity across populations		Overall standardized score	Overall rank
	Standardized score	Score in original metric^1	Standardized score	Score in original metric^2	Standardized score	Score in original metric^3		
Number of leaves, untransformed	1	1	1	151.58	0	0.361	0.66	1
Leaf length	0.13	0.30	0.81	152.9	0.8	0.288	0.58	2
Total leaf area	0.04	0.23	0.61	154.21	1	0.27	0.55	3
Total leaf length	0	0.20	0.28	156.48	0.83	0.285	0.37	4
Number of leaves	0.01	0.21	0.03	158.22	0.61	0.306	0.22	5
Regressed biomass	0.08	0.26	0	158.42	0.56	0.31	0.22	6

Note: No candidate metric was excluded based on unmet model assumptions (criterion a). The performance of candidate metrics was then assessed over criteria b–d: Performance across rates (criterion b), performance across populations (criterion c) and least variable performance across populations (criterion d). The superscripts correspond to the units of the criteria: ^{1}mean normalized R^2_c across vital rate models, ^{2}summed mean absolute error (MAE) across all populations, ^{3}variance in MAE across populations (see Section 2). The original scores were standardized (value − minimum, divided by the range) to obtain comparable scores between response metrics. We used (1 − c) and (1 − d) as standardized scores to maintain the directionality between 0 (worst performance) and 1 (best performance). The scores were averaged across criteria to obtain the final score. Values presented here are rounded to the last meaningful decimal.

3.3 | (c) Performance across populations

The performance of the size metrics across populations is illustrated in Figure 3. In general, size metrics performed similarly across populations for the same vital rate (Figure 3, mode of the distributions, Table 2), with the exception of the growth model (Figure 4a) where the mode of the MAE values using untransformed number of leaves was lower than other size metrics.

3.4 | (d) Homogeneity of the within population performances

The variance in population error is displayed in Figure 3 (spread of the values). The growth model using the number of leaves (untransformed) had a longer tail towards high MAE values than other size metrics (Figure 3a), implying some populations were poorly explained.

Number of leaves (untransformed) also yielded the highest variance among populations for the growth model (0.12, against a mean value of 0.06 for all size variables; Table 2).

3.5 | Performance along climatic gradients

The analysis of performance along environmental gradients showed little difference between candidate metrics and vital rates (Figure 4). However, there was a general and consistent positive effect of temperature on population MAE. Vital rates models were therefore consistently poorer at capturing demography as temperature increased. There was no effect of the precipitation gradient (Figure S1.2.1), nor of the native versus non-native ranges (Figure 4; Figure S1.2.1) on population MAE.

3.6 | Homogeneity of predictions across populations

The relationships between size and vital rates were mostly homogeneous over all populations (Figure 5); larger plants tended to be larger at the time of the next census, and to be more likely to flower and more likely to survive, although the magnitude of the relationship differed between populations. For survival, flowering probability and reproductive output, the relationship with size was inverted in a few populations, with larger plants being more likely to die, less likely to flower and producing fewer seeds per flowering event.

3.7 | Size variable selection

Ranking size metrics using our variable selection framework yielded different results for each criterion (Table 2). Overall, the number of leaves as a discrete variable was the best performing metric,

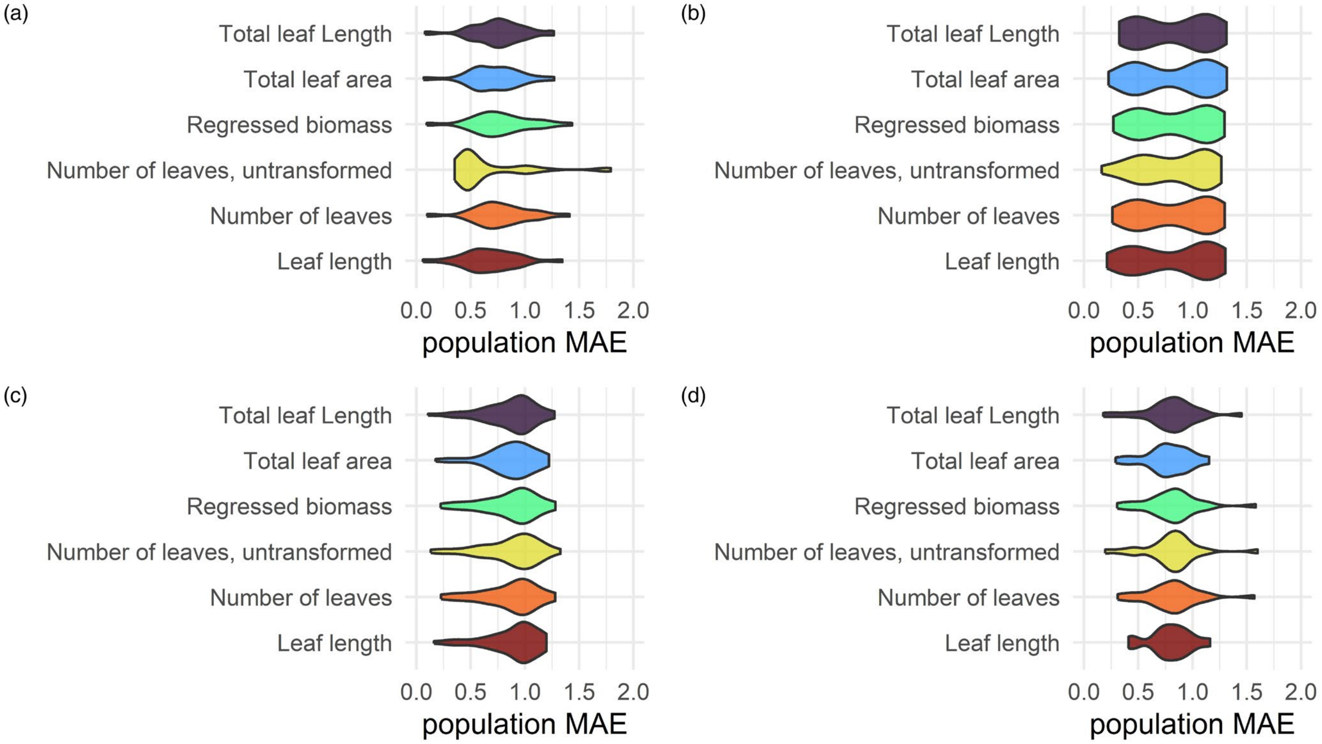

FIGURE 3 Performance of the different size metrics (*y* axis), illustrated by the density plot of the populations' mean absolute errors (MAE, *x* axis) from the models for (a) growth, (b) survival, (c) flowering probability and (d) reproductive output. Residuals were standardized for all models. Wider density plots imply a broader spread of performance across populations; a tail to the right means that a few populations are poorly explained using the corresponding size variable. Conversely, a tail to the left implies a few populations are very well explained.

followed by leaf length (Table 2). The number of leaves was the best metric for two of our three criteria; however, it performed poorly at criterion d, the between-population variance in MAE. That is probably driven by the right skew of the MAE distribution for the number of leaves (Figure 3a, fourth row). The metric that was most homogeneous between populations (high values for criterion d) was the Total Leaf Area, which performed worse than all other methods at explaining the vital rates (Figure 2).

4 | DISCUSSION

We found that we can build informative vital rates models for multiple populations across the native and non-native ranges for the common herbaceous perennial *Plantago lanceolata* using simple size variables, derived from straightforward field measurements. In our final ranking, the number of leaves was the best performing metric across all criteria, when used as a discrete variable and not log transformed to force a count variable into a Gaussian distribution (Table 2). The percentage of explained variance in vital rates was high for all vital rates (R^2_c; Nakagawa & Schielzeth, 2013). The relationships (slopes) between size and vital rates were consistent between size metrics (Figure 5), although a few populations had contrasting behaviour; in most cases, larger plants are more likely to both survive and flower, whereas in a few populations, smaller plants had a higher probability to survive, as well as to flower. The two best performing metrics (number of leaves and leaf length) are straightforward to measure in the field and do not require proxies or estimation (which is the case for biomass (Villellas et al., 2021)). These size metrics are non-destructive, which is a distinct advantage over the destructive collection of whole specimens for the estimation of parameters for the biomass equation, which ranked fifth. Interestingly, they are also direct field measurements rather than combinations of multiple measurements. Our identification of a simple size metric that can be used with confidence across many different populations is of significance for collaborative projects such as PlantPopNet. Simplified protocols have the greatest practical longevity (Pocock et al., 2014) which is important for the collection of long time series data, as is done in the PlantPopNet, but also on an increasing number of other species (DeMarch et al., 2017; Sheth & Angert, 2018).

Ultimately, the choice of a size metric may vary depending on the focal research question and organism. In the case of *P. lanceolata*, our suggested best size metric (untransformed number of leaves as a discrete variable) was the best against two of our suggested criteria, but the worst against the third criterion. We advise other authors to address such patterns and their consequences in their own data, species and research questions. In the present case, while the number of leaves explains all vital rates well, and across all populations, some populations are explained much better than others (low homogeneity of the within population performances, criterion d). Figure 3 shows that, in our case, this is mostly due to two aspects: a tail of high MAEs for the growth model, and a distribution of population

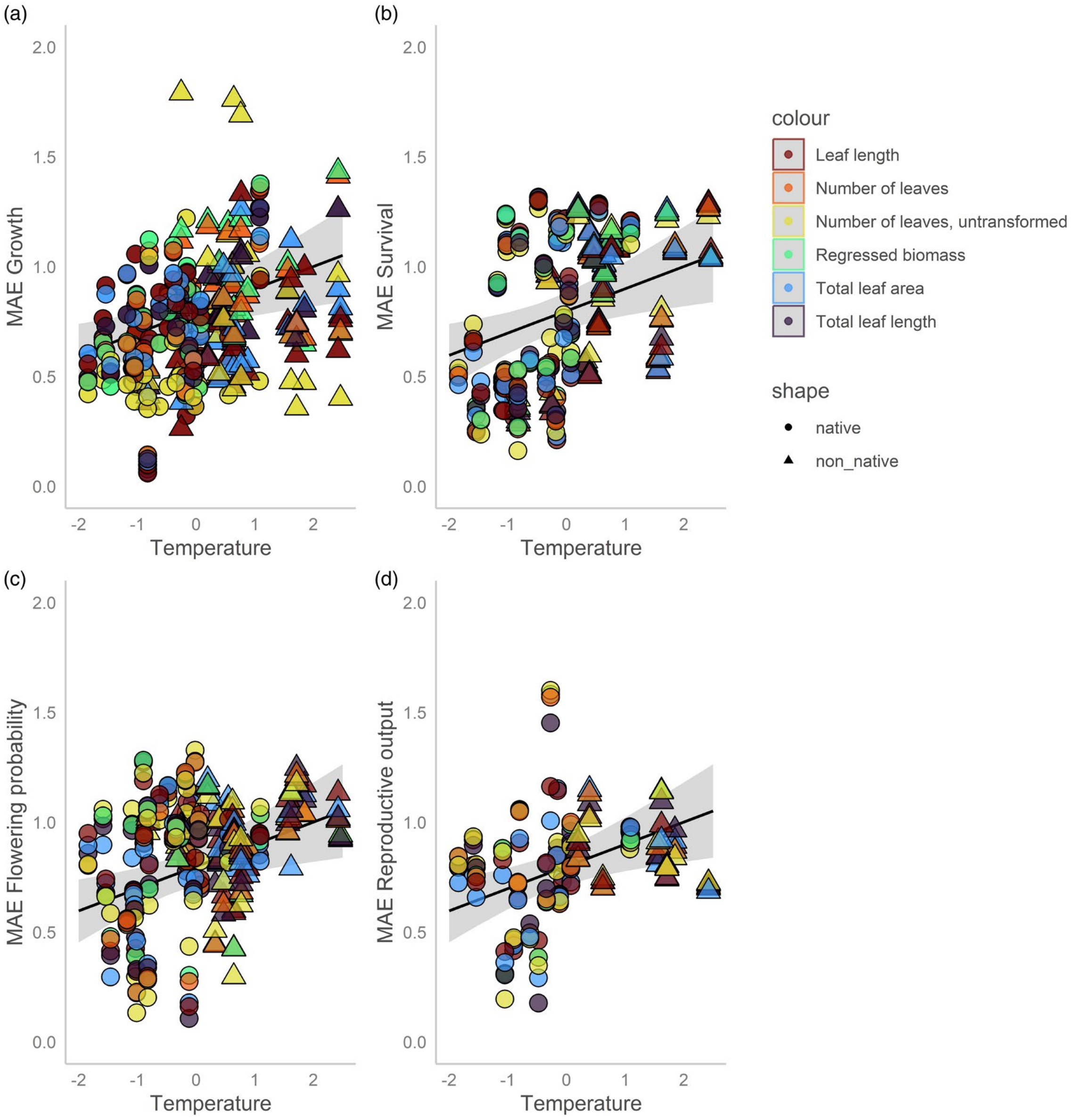

FIGURE 4 Homogeneity of the performance of the vital rates models along climatic gradients. In panels (a)–(d), each point is the mean absolute error remaining in the residuals of one population once the growth (a), survival (b), probability of flowering (c) and reproductive output (d) have been modelled as a function of size. The populations are presented in order of increasing temperature (*x*-axis), where temperature values were scaled (mean centred and divided by the standard deviation). The black line and greyed areas show the prediction and confidence interval of a mixed effect model where MAE is predicted as a function of temperature, precipitation, the part of the range (native, non-native) and the size metric as fixed effects and the vital rate and population of origin as random effects (see methods). The trends over the temperature gradients are displayed with all other variables set to their average. The same figure over the global precipitation gradient can be seen in Supporting Information S1.2.

MAEs for flowering and survival probabilities starting at lower values than other size metrics. We are therefore confident in our choice of size metric for our study organism, as it will capture those last two rates better than any other size candidate. Nonetheless, in our case, caution is needed in interpreting the results of future studies, as, although the growth in most populations will be well explained (the mode of the MAE distribution is lower than for other candidate size metrics, Figure 3), the growth of a few populations might be poorly explained. One can also see in Figure 5 that our fixed effect models had very different slopes for the relationship between size and vital rates in certain populations. Therefore, while the explanatory power of our models is very good, the predictive ability of our model in new populations may be biased. For studies focusing on invasive species and how to manage them upon entering a new study or area (Jongejans et al., 2011; Merow et al., 2017), this may be of major importance.

Interestingly, all candidate size metrics capture a bimodality in explaining survival (Figure 3b). This was due to the observed survival rates being very high in some populations. Models therefore had no difficulty capturing the patterns as they just predicted

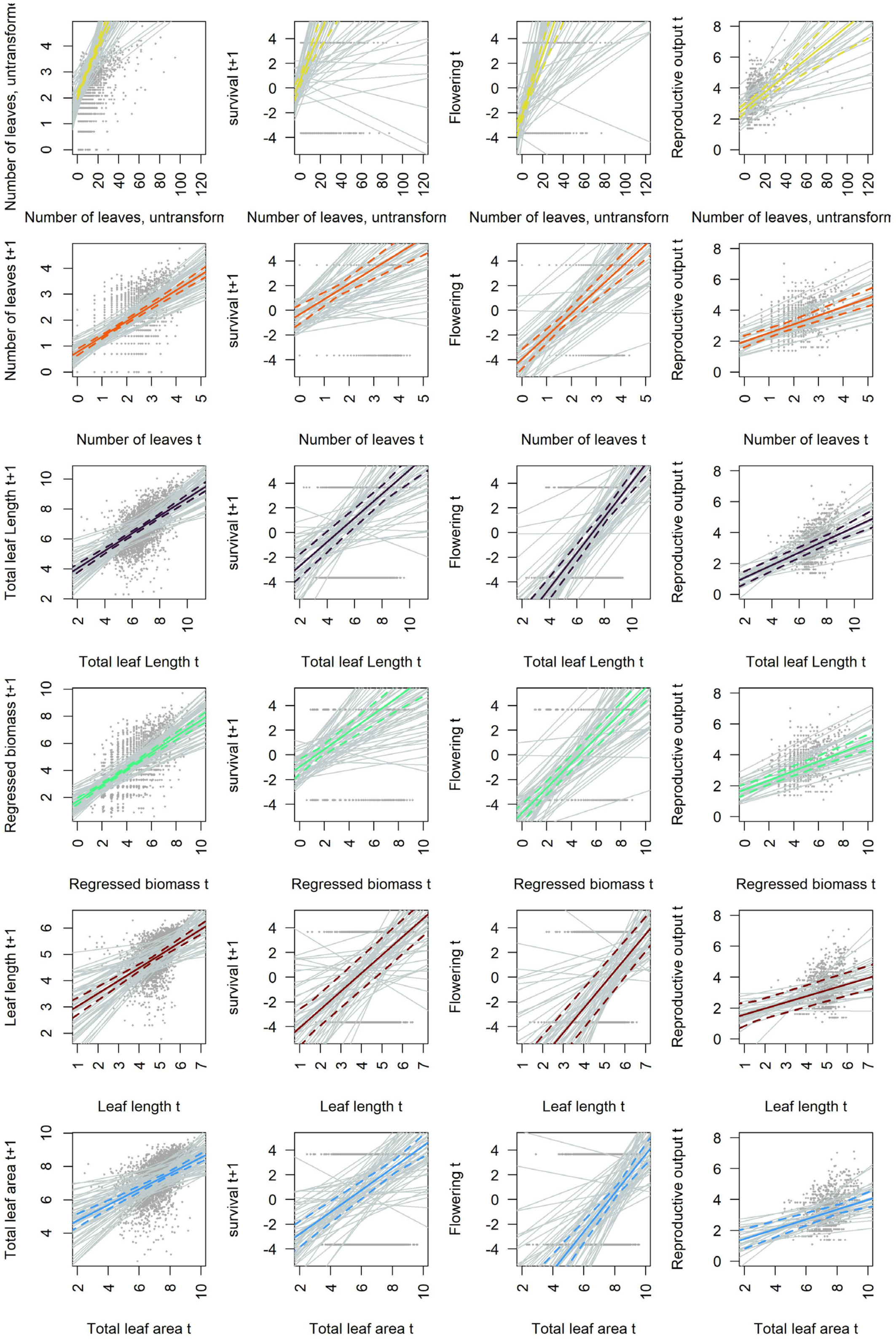

FIGURE 5 Homogeneity of the relationship between the vital rates and different candidate size metrics in 55 populations of the perennial herb *Plantago lanceolata* monitored by PlantPopNet. Each grey line represents the relationship between the size metric and vital rate in a single population, where each row is a different size metric and each column is a different vital rate. This relationship is the best linear unbiased predictor (BLUP) from a mixed effects model of the vital rate as a function of size with a random slope and intercept for population. The panels are therefore in different units and can only be compared qualitatively. Solid colour-coded bold lines show the fixed effect of the model, with dotted lines for the 95% CIs. Grey dots in the background show original observations, on the link scale if applicable (logit scale for survival and flowering probability). Binary observations are plotted as their logit values, 3.66 and −3.66, respectively.

survival for all plants, producing the low mode. However, there is greater difficulty explaining survival in populations where it is not extremely high, as variance is highest for probabilities around 0.5. This produced the high mode. As the pattern was similar using all candidate size metrics, it does not affect the results of the current study. This showcases how our multi-dimensional assessment of differences between size metrics enables nuanced evaluation of size variables for their research question (much more so than a simple use of AIC values) and across different types of organisms. Depending on the research question, we suggest considering weighting the selection criteria differently to emphasize certain properties expected from the size metric. For example, phenotypic or genetic differences between populations may be indicative of important ecological or evolutionary processes (Paynter et al., 2016). In such cases, a lack of homogeneity in predictions between populations as evidenced through criterion d may be upweighted.

The number of leaves was not the best predictor in our study when modelled using a Gaussian distribution through a log transformation (O'Hara & Kotze, 2010). This shows that the careful consideration of the nature of a demographic variable or parameter (is it a count variable? Is it continuous? What distribution does it follow?) remains extremely important (Bolker, 2019; Zuur et al., 2010, 2013). The decision to use a discrete or continuous size variable as a state variable has important consequences for further demographic analyses. On the one hand, count variables will be addressed via statistical distributions truncated at 0. This will avoid the prediction of individuals of negative sizes. In addition, when building size-structured population models, the choice of a continuous size variable lends itself to an integral projection model, whereas if a discrete variable is used, a matrix projection model is the appropriate choice (Caswell, 2001; Easterling et al., 2000; Ellner et al., 2016). In this specific case and with our data, we would build a matrix model that uses the number of leaves as a size metric, where the size of adult individuals is modelled through a negative binomial distribution. The use of a count variable has a drawback, though: in our dataset with only one transition and the possibility of dormancy of plants, zero leaf-sized adult individuals are confounded with dead individuals, which leaves our negative binomial zero depleted (Supporting Informations S3 and S5). This will strongly affect a negative binomial model (Bolker, 2019; Bolker et al., 2009). With more years of data added to the analysis, the dead individuals can be recognized from dormant individuals, which will diminish the impact of that issue. Another alternative would be to build an IPM with the leaf length as a size metric, which is our second-best candidate in the selection process (Table 2). Again, the importance of doing or not doing this might depend on the research question or the morphology of the focal species.

Although the purpose of this study was to select an appropriate size metric prior to studying the effects of potential environmental drivers of demographic processes (see for instance Römer et al., 2021), our results give some insights on the importance of environmental predictors to be added in future demographic models. There was little overall trend in MAE along precipitation gradients, but an increase in MAE with temperature (Figure 4). Temperature seems an important candidate in the investigation of large scale drivers of demographic patterns (Kelly et al., 2021; Römer et al., 2021; Shea et al., 2005). We therefore advise the inclusion of relevant climatic variables within large scale demographic models. This will shed light on the causes of large scale demographic variation (Buckley & Puy, 2022; Greiser et al., 2020), and probably increase model quality. The explanatory power of population of origin varies depending on the vital rate (R^2_c vs. R^2_m comparison, Figure 2). This probably indicates differences in the strengths of the mechanisms influencing vital rates and highlights the need for further exploration of drivers of demographic processes at large scales (Ehrlén et al., 2016; Merow, Dahlgren, et al., 2014; Merow, Latimer, et al., 2014; Römer et al., 2021).

Much current comparative demographic work uses collated demographic models across multiple species (Kelly et al., 2021; Salguero-Gómez et al., 2015; Silvertown et al., 1993). If the choice of size variable were to be mainly locally influenced, differences between model outputs at the species level, developed on one or few local populations in different places, may require complex interpretation as species-level and local differences are confounded. On the contrary, our results provide support for studies of collated works, as the comparison of populations modelled using different size metrics may be robust to this methodological difference, at least at the intraspecific level. This support for collated works, as well as our framework to select simple, non-destructive, homogeneously performing size metrics, helps to address the biggest limitations in existing demographic datasets, namely the small geographical range of datasets (Coutts et al., 2016; Salguero-Gómez et al., 2012; Tredennick et al., 2018) and their lack of spatial and temporal replication (Csergő et al., 2017; Salguero-Gómez et al., 2012, 2015).

5 | CONCLUSIONS

Using a unique spatially extensive replicated dataset, we shed light on size-structured changes in demography across the range of a cosmopolitan plant species. We found that simple size metrics can perform very well in size-structured demographic studies, despite the wide geographic and climatic range included. We provided a method for, and a case study of, the implications of size variable selection in demographic studies including numerous populations. Careful consideration ought to be taken to the statistical properties of candidate variables. Our study offers support for works in the field of demography seeking generalization through compilation of models from different studies or populations.

AUTHOR CONTRIBUTIONS

Yvonne M. Buckley, Anna-Liisa Laine, Anna Mária P. Csergő, Bret Elderd, Deborah A. Roach, Dylan Z. Childs, Glenda M. Wardle, Johan Ehrlén, Jesus Villellas, Maria B. García, Maude E. A. Baudraz, Rachel M. Penczykowski, Simone P. Blomberg and

Sergi Munne-Bosch designed the concept and methods behind the plantpopnet. Maude E. A. Baudraz conceived the research idea for the current paper with Yvonne M. Buckley. Maude E. A. Baudraz performed the analysis with contributions from Yvonne M. Buckley and Dylan Z. Childs. Ruth Kelly and Christina M. Caruso provided intellectual input on the analysis. Maude E. A. Baudraz wrote the first draft with contributions from Yvonne M. Buckley. Anna Bucharova, Aldo Compagnoni, Alain Finn, Aveliina Helm, Ayco J. M. Tack, Anna-Liisa Laine, Annabel L. Smith, Anna Mária P. Csergő, Adrian Oprea, Anna Roeder, Astrid Wingler, Benedicte Bachelot, Bret Elderd, Christina M. Caruso, Caroline M. McKeon, Christiane Roscher, Cheryl Schultz, Deborah A. Roach, Dylan Z. Childs, Elizabeth M. Wandrag, Francis Q. Brearley, Glenda M. Wardle, Gregory Vose, Jane A. Catford, John Dwyer, Joslin L. Moore, Jennifer R. Gremer, Joachim Töpper, Jesus Villellas, Judit Bodis, Lajos Benedek, Lauchlan Fraser, Lotte Korell, Lauri Laanisto, Liv Norunn Hamre, Martin Andrzejak, Maria B. García, Matthew Coghill, Maude E. A. Baudraz, Mária Höhn, Michele Lonati, Melanie Morales, Meelis Pärtel, Marjo Saastamoinen, Olav Skarpaas, Peter A. Vesk, Pil U. Rasmussen, R. Drew Sieg, Richard Duncan, Ronny Groenteman, Ruth Kelly, Rachel M. Penczykowski, Siri L. Olsen, Sergi Munne Bosch, Satu Ramula, Simone Ravetto Enri, William K. Petry, Yvonne M. Buckley and Zuzana Münzbergová gathered the data and made it available for this research. Alain Finn and Yvonne M. Buckley curated the data with contributions from Maude E. A. Baudraz, Ruth Kelly, Caroline M. McKeon and Aoife Molloy. Annabel L. Smith provided a first cleaned version of the plantpopnet data used at the start of the study. Jesus Villellas provided the regression biomass equations. Aoife Molloy helped format the code into Supporting Information. All co-authors edited the manuscript. Simone P. Blomberg, Aldo Compagnoni and Joachim Töpper provided useful additional comments on analyses. Maude E. A. Baudraz monitored and incorporated all co-authors comments.

AFFILIATIONS

[1]Co-Centre for Climate + Biodiversity + Water, School of Natural Sciences, Trinity College Dublin, Dublin 2, Ireland; [2]Ecology and Evolutionary Biology, School of Biosciences, University of Sheffield, Sheffield, UK; [3]Environment and Marine Sciences Division, Agri-Food and Biosciences Institute, Belfast, UK; [4]School of Environment, University of Queensland, St Lucia, Queensland, Australia; [5]Departamento de Ciencias de la Vida, Universidad de Alcalá, Alcalá de Henares, Spain; [6]Department of Community Ecology, Helmholtz Centre for Environmental Research—UFZ, Halle (Saale), Germany; [7]German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Leipzig, Germany; [8]Department of Plant Biology, Ecology, and Evolution, Oklahoma State University, Stillwater, Oklahoma, USA; [9]Department of Botany, Hungarian University of Agriculture and Life Sciences, Budapest, Hungary; [10]School of the Environment, University of Queensland, St. Lucia, Australia; [11]Hungarian University of Agriculture and Life Sciences, Institute for Wildlife Management and Nature Conservation, Keszthely, Hungary; [12]Department of Natural Sciences, Manchester Metropolitan University, Manchester, UK; [13]Department of Biology, University of Tübingen, Tübingen, Germany; [14]Department of Biology, Philipps University Marburg, Marburg, Germany; [15]Department of Integrative Biology, University of Guelph, Guelph, Ontario, Canada; [16]Department of Geography, King's College London, London, UK; [17]Fenner School of Environment & Society, The Australian National University, Canberra, Australian Capital Territory, Australia; [18]Department of Natural Resource Science, Thompson Rivers University, Kamloops, British Columbia, Canada; [19]German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Martin Luther University Halle-Wittenberg, Halle, Germany; [20]Centre for Conservation Ecology and Genomics, University of Canberra, Canberra, Australian Capital Territory, Australia; [21]School of the Environment, The University of Queensland, St Lucia, Queensland, Australia; [22]Department of Ecology, Environment and Plant Sciences, Stockholm University, Stockholm, Sweden; [23]Department of Biological Sciences, Louisiana State University, Baton Rouge, Louisiana, USA; [24]Pyrenean Institute of Ecology (CSIC), Zaragoza, Spain; [25]Department of Evolution and Ecology, University of California, Davis, California, USA; [26]Manaaki Whenua—Landcare Research, Lincoln, Canterbury, New Zealand; [27]Faculty of Technology, Environmental and Social Sciences, Western Norway University of Applied Sciences, Sogndal, Norway; [28]Institute of Ecology and Earth Sciences, University of Tartu, Tartu, Estonia; [29]Department of Botany, Institute for Agronomy, MATE, Hungarian University of Agriculture and Life Sciences, Budapest, Hungary; [30]Chair of Biodiversity and Nature Tourism, Estonian University of Life Sciences, Tartu, Estonia; [31]Organismal and Evolutionary Biology Research Program, Faculty of Biological and Environmental Sciences, University of Helsinki, Helsinki, Finland; [32]Department of Agricultural, Forest and Food Sciences, University of Torino, Grugliasco (TO), Italy; [33]Department of Energy, Environment and Climate Action, Arthur Rylah Institute for Environmental Research, Heidelberg, Victoria, Australia; [34]School of Biological Sciences, Monash University, Clayton, Victoria, Australia; [35]Department of Evolutionary Biology, Ecology and Environmental Sciences, Faculty of Biology, University of Barcelona, Barcelona, Spain; [36]Institut de Recerca de la Biodiversitat, University of Barcelona, Barcelona, Spain; [37]Department of Botany, Faculty of Science, Institute of Botany, Czech Academy of Science, Charles University, Prague, Czech Republic; [38]Faculty of Environmental Sciences and Natural Resource Management, Norwegian University of Life Sciences, Ås, Norway; [39]Norwegian Institute for Nature Research, Oslo, Norway; [40]Botanic Garden 'Anastasie Fatu' of University 'Alexandru Ioan Cuza', Iasi, Romania; [41]Department of Biology, Washington University in St. Louis, St. Louis, Missouri, USA; [42]Department of Plant and Microbial Biology, North Carolina State University, Raleigh, North Carolina, USA; [43]Department of Biology, University of Turku, Turku, Finland; [44]The National Research Centre for the Working Environment, Copenhagen, Denmark; [45]Department of Biology, University of Virginia, Charlottesville, Virginia, USA; [46]UFZ, Helmholtz Centre for Environmental Research, Department Physiological Diversity, Leipzig, Germany; [47]Faculty of Biological and Environmental Sciences, University of Helsinki, Helsinki, Finland; [48]School of Biological Sciences, Washington State University, Vancouver, Washington, USA; [49]Department of Agricultural and Biological Sciences, Truman State University, Kirksville, Missouri, USA; [50]Natural History Museum, University of Oslo, Oslo, Norway; [51]Norwegian Institute for Nature Research, NINA Bergen, Bergen, Norway; [52]School of Ecosystem and Forest Sciences, The University of Melbourne, Parkville, Victoria, Australia; [53]Department of Biology, Merritt College, Oakland, California, USA; [54]Institute for Applied Ecology, University of Canberra, Canberra, Australian Capital Territory, Australia; [55]Department of Biology, University of York, York, UK; [56]School of Life and Environmental Sciences, The University of Sydney, Sydney, New South Wales, Australia and [57]School of Biological, Earth & Environmental Sciences and Environmental Research Institute, University College Cork, Cork, Ireland

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CONFLICT OF INTEREST STATEMENT

Yvonne M. Buckley, Jane A. Catford and Peter A. Vesk are editors of *Journal of Ecology*, but took no part in the peer review and decision-making processes for this paper.

PEER REVIEW

The peer review history for this article is available at https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/1365-2745.70148.

DATA AVAILABILITY STATEMENT

The data for this study can be found here: https://datadryad.org/dataset/doi:10.5061/dryad.mw6m9067c (Baudraz et al., 2025). This dataset is based on a subset of the Standard Data Products (PLANTPOPNET_Y0_V1.02_2020-11-18 and PLANTPOPNET_Y1_V1.1_2021-03-31, see Supporting Information S1) for the first 2 years of demographic data in the PlantPopNet.

ORCID

Maude E. A. Baudraz https://orcid.org/0000-0001-7252-8419
Dylan Z. Childs https://orcid.org/0000-0002-0675-4933
Ruth Kelly https://orcid.org/0000-0001-7982-5993
Annabel L. Smith https://orcid.org/0000-0002-1201-8713
Jesus Villellas https://orcid.org/0000-0001-7805-5683
Martin Andrzejak https://orcid.org/0000-0002-5847-5098
Benedicte Bachelot https://orcid.org/0000-0003-3348-9757
Lajos K. Benedek https://orcid.org/0009-0002-3218-7749
Simone P. Blomberg https://orcid.org/0000-0003-1062-0839
Judit Bodis https://orcid.org/0000-0002-3707-1684
Francis Q. Brearley https://orcid.org/0000-0001-5053-5693
Anna Bucharova https://orcid.org/0000-0002-5468-5426
Christina M. Caruso https://orcid.org/0000-0001-7069-9572
Jane A. Catford https://orcid.org/0000-0003-0582-5960
Matthew Coghill https://orcid.org/0000-0003-1476-1567
Aldo Compagnoni https://orcid.org/0000-0001-8302-7492
Anna Mária P. Csergő https://orcid.org/0000-0003-3325-2995
Richard P. Duncan https://orcid.org/0000-0003-2295-449X
John Dwyer https://orcid.org/0000-0001-7389-5528
Johan Ehrlén https://orcid.org/0000-0001-8539-8967
Bret D. Elderd https://orcid.org/0000-0001-5853-1136
Alain Finn https://orcid.org/0000-0002-2209-9553
Lauchlan Fraser https://orcid.org/0000-0003-3998-5540
Maria B. García https://orcid.org/0000-0003-4231-6006
Jennifer R. Gremer https://orcid.org/0000-0001-8983-5482
Ronny Groenteman https://orcid.org/0000-0003-3444-5262
Liv Norunn Hamre https://orcid.org/0000-0002-9033-4260
Aveliina Helm https://orcid.org/0000-0003-2338-4564
Maria Höhn https://orcid.org/0000-0002-8587-8271
Lotte Korell https://orcid.org/0000-0001-7051-8903
Lauri Laanisto https://orcid.org/0000-0003-2215-7298
Anna-Liisa Laine https://orcid.org/0000-0002-0703-5850
Michele Lonati https://orcid.org/0000-0001-8886-0328
Caroline M. McKeon https://orcid.org/0000-0002-6864-6380
Aoife Molloy https://orcid.org/0000-0002-1540-8768
Joslin L. Moore https://orcid.org/0000-0001-9809-5092
Melanie Morales https://orcid.org/0000-0002-2931-4543
Sergi Munne-Bosch https://orcid.org/0000-0001-6523-6848
Zuzana Münzbergová https://orcid.org/0000-0002-4026-6220
Siri L. Olsen https://orcid.org/0000-0002-4443-8261
Adrian Oprea https://orcid.org/0000-0003-4875-877X
Meelis Pärtel https://orcid.org/0000-0002-5874-0138
Rachel M. Penczykowski https://orcid.org/0000-0003-4559-0609
William K. Petry https://orcid.org/0000-0002-5230-5987
Satu Ramula https://orcid.org/0000-0001-7795-0352
Pil U. Rasmussen https://orcid.org/0000-0003-0607-4230
Simone Ravetto Enri https://orcid.org/0000-0002-3584-8031
Deborah A. Roach https://orcid.org/0000-0002-5273-5370
Anna Roeder https://orcid.org/0000-0001-7101-5726
Christiane Roscher https://orcid.org/0000-0001-9301-7909
Marjo Saastamoinen https://orcid.org/0000-0001-7009-2527
Cheryl Schultz https://orcid.org/0000-0003-3388-8950
R. Drew Sieg https://orcid.org/0000-0002-1322-1393
Olav Skarpaas https://orcid.org/0000-0001-9727-1672
Ayco J. M. Tack https://orcid.org/0000-0002-3550-1070
Joachim Töpper https://orcid.org/0000-0002-6996-7223
Peter A. Vesk https://orcid.org/0000-0003-2008-7062
Gregory Vose https://orcid.org/0000-0002-4170-2143
Elizabeth M. Wandrag https://orcid.org/0000-0001-8140-539X
Glenda M. Wardle https://orcid.org/0000-0003-0189-1899
Astrid Wingler https://orcid.org/0000-0003-4229-2497
Yvonne M. Buckley https://orcid.org/0000-0001-7599-3201

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Data S1. Supplement to methods and results.

Data S2. Input data.

Data S3. Illustration of the approach used to explore the model diagnostics of the vital rate models under criterion (a).

Data S4. Diagnostic plots of models where all size metrics are log transformed.

Data S5. Code.

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