Understanding the drivers of intraspecific demographic variation: needs and opportunities

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Background:

Plant ecologists have long sought to quantify the drivers of variation in growth, survival, and reproductive output (Harper and White 1974). Global studies have had some success in explaining variation in these demographic metrics among species by including functional traits in analyses (Adler et al. 2014). Shifting focus from among to within species studies of intraspecific demographic variation and functional traits is needed, since climate change impacts on demography may vary among populations of the same species. Some fields of study already focus on intraspecific, population-level variation, such as population biology, invasion ecology, and restoration and conservation biology. Typically, though, studies focus on single species, limiting application of findings to other species or higher scales (i.e., community-level). In contrast, other fields of study include many species and make inferences at larger spatial and biological scales but ignore population-level variation that can lead to contrasting responses to climate among populations of species in a community. By combining perspectives and methods across fields, we can fully leverage the promise of traits to transcend species or system-specific patterns to better understand the drivers of demographic variation, quantify the individual and collective importance of demographic rates to fitness, and predict complex ecological patterns from individual to landscape scales.

Current State of Thought:

High levels of trait variation within and among populations may contribute to variation in demographic rates, including growth, survival, and reproduction, driven by interactions between individuals' traits and the environment (Figure 1). However, species-level trait values are often applied to all individuals, regardless of their population or its abiotic and biotic environments, thus ignoring the range of trait variation within and among populations (Figure 1A). Beyond traits, Buckley and Puy (2022) note that ecologists often use data and models from a few populations to explain dynamics in other populations or for entire species. These methods are used despite research showing correlation among traits, demography, and the environment (Oldfather and Ackerly 2019). This is particularly an issue for wide-ranging species and those that span extensive environmental gradients.

Indeed, there have been several calls for population-level focus and sampling of intraspecific traits and demographic variation with recent studies tackling these challenges. Oldfather and Ackerly (2019) demonstrated population-level variation in multiple demographic rates across microclimatic gradients, finding that demographic rates were influenced by interactions between individual size and microclimate, and size-demographic rate relationships varied in direction and magnitude across a microclimatic gradient (Figure 1B). Further application of this research across macro-environmental gradients is needed to better understand population dynamics and range dynamics now and in future climates. Beyond empirical work, reviews have highlighted the importance of population-level variation when linking functional traits to demographic rates (Laughlin et al. 2020; Buckley and Puy 2021). Laughlin et al. (2020) suggest estimating population fitness (λ), in place of individual fitness, and determining the effects of interactions between functional traits and the environment on population fitness with explicit inclusion of trade-offs among demographic rates. Lasky et al. (2020) highlight the complexity involved in understanding current and predicting future regional-scale population dynamics. They provide a novel framework that incorporates genetic and phenotypic variation, abiotic and biotic factors, and demographic components. Together, this recent work builds on previous work to reinforce the context-dependency of demographic relationships within and among populations, but also provides frameworks for incorporating this complexity into predicting emergent patterns in ecology.

Looking Forward:

Integrating these perspectives and approaches is critical in the face of anthropogenic change, but does increase the complexity of experiments, observations, and data analyses needed to do so. It will also require incorporation of biotic and abiotic conditions (Swenson et al. 2020; Lasky et al. 2020). For example, Yang et al. (2020) showed that models of individual tree growth rate including climate data, biotic neighborhood, and multiple trait variables outperformed those lacking these contexts. They also showed that individual-level trait measurements explained more variation than species-level measurements assigned to all individuals of a species. Beyond the inclusion of environmental contexts, we need to recognize that different demographic metrics may respond in different ways across the same environmental gradient and vary in their influence on population growth rates (Figure 1C). For example, DeMarche et al. (2018) showed that temperature can have opposing effects on different demographic rates where mean individual growth rates increased, but survival rates decreased, with increasing temperature in an alpine plant species, contributing to its ability to persist across a broad climatic range through demographic compensation (i.e., opposing demographic rate trends across populations (Villellas et al. 2015). Further, both life-history plasticity and local adaptation shaped range-wide responses to climate suggesting population specific responses to climate change, which has implications for distribution across the landscape.

Better integration of feedbacks between ecology and evolution will also lend insight into how traits, environment, and demography interact to drive population dynamics. We can think of traits as reflecting past contexts with implications for future responses. For instance, intraspecific trait variation can reflect historical patterns of selection across a species range, including local adaptation to spatial and temporal environmental variation, which provides insight into trait variation and its influence on past and future performance (Oldfather et al. 2021). Further, trait values may not be static. As an example, Nguyen et al. (2016) demonstrated that two invasive species responded to selection on traits characteristic of drought escape following a reduced precipitation experiment simulating future climate change. Studies like these will improve understanding of how changes in climate may alter selection patterns and shift species' ranges. Here, we can incorporate perspectives from additional fields, since restoration and invasion ecology have a history of investigating how traits vary among populations and bridging research with practice (Funk 2021).

The largest factor limiting progress in explaining intraspecific variation in demographic metrics is missing data at the population level. Ideally, we would measure multiple demographic rates, traits, local biotic factors, along with local and regional abiotic factors across multiple populations across the species' range. While access to environmental variables has increased through climate databases, availability of biotic contexts, demographic data, and population specific trait measurements are less common. Fortunately, for trait data, biodiversity databases may already have many of the resources needed to overcome these challenges. TRY (Kattage et al. 2011) and Global Inventory of Floras and Traits (GIFT; Weigelt et al. 2020) are two plant trait databases that include geographic information on where traits were measured. The structure of many trait databases reflects the history of the field (community ecology) and type of analyses (global) they were established to benefit and are thus often at coarse scales that are inadequate for the integration we propose. Fortunately, a simple way to increase the value of the data would be adding information on the biological scale and locality of measurements to databases. The newly released AusTraits database is making raw, individual-level measurements a priority, while also having explicit labels for when measurements are from an individual, species-means within one site, or species-means across sites (Falster et al. 2021).

Demographic data are not only less available than trait data, but also slower to become available due to the difficult nature of its collection. COMPADRE (Salguero-Gómez et al. 2015) and PADRINO (Levin et al. 2022) databases, however, are lowering barriers to population-level demographic data. Compagnoni et al. (2021) used population models from these databases to show that precipitation has a stronger effect than temperature on population growth rates and that species with shorter generation times respond more strongly to climate. However, these databases currently include mainly species from cold, dry areas that are represented by few populations and do not span the climate and geographic ranges of the species. Beyond demographic data, modeling approaches that capitalize on more readily available abundance data, such as that found in LOTVS (Sperandii et al. 2022), may facilitate analyses of trait-demographic relationships across species ranges (Laughlin et al. 2020). Chalmandrier et al.

(2021) calibrated trait-demographic relationships using abundance data to address patterns of plant community structure across a temperature gradient. These works showcase how updated methodology and context inclusion can allow for improved understanding at larger biological and spatial scales.

Conclusion:

Species distributions and community composition are intricately tied to variation in population dynamics across space and time, which are directly related to the successes and failures of individual plants. This has led to calls for studies to investigate intraspecific demographic variation and integrate intraspecific trait variation and environmental contexts (Laughlin et al. 2020; Swenson et al. 2020). While these studies remain rare, recent work shows progress in pushing our understanding of the drivers of intraspecific demographic variation forward. Research that investigates axes of co-variation among traits, demography, and the environment within and among populations will allow a better understanding of how dynamic functional responses to environmental variation drive population dynamics and species persistence. Knowledge gained from this research will also allow improved parameterization of models to predict future community dynamics and species ranges along with broad applications to management, restoration, and conservation practices all while advancing basic science of societal importance (Funk 2021).

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Author Contributions

S.J.W. led conceptual development and drafted the manuscript with input and assistance from J.R.G. Both authors contributed equally to manuscript edits and revisions.

Literature Cited

Adler, P. B., R. Salguero-Gómez, A. Compagnoni, J. S. Hsu, J. Ray-Mukherjee, C. Mbeau-Ache, and M. Franco. 2014. Functional traits explain variation in plant life history strategies. *Proceedings of the National Academy of Sciences USA* 111: 740-745.

Buckley, Y. M., and J. Puy. 2022. The macroecology of plant populations from local to global scales. *New Phytologist* 233: 1038-1050.

Chalmandrier, L., F. Hartig, D. C. Laughlin, H. Lischke, M. Pichler, D. B. Stouffer, and L. Pellissier. 2021. Linking functional traits and demography to model species-rich communities. *Nature Communications* 12:2724.

Compagnoni, A., S. Levin, D. Z. Childs, S. Harpole, M. Paniq, G. Römer, J. H. Burns, J. Che-Castaldo, N. Rüger, G. Kunstler, J. M. Bennett, C. R. Archer, O. R. Jones, R. Salguero-Gómez, and T. M. Knight. 2021. Herbaceous perennial plants with short germination time have stronger responses to climate anomalies than those with longer generation time. *Nature Communications* 12: 1824.

DeMarche, M. L., D. F. Doak, and W. F. Morris. 2018. Both life-history plasticity and local adaptation will shape range-wide responses to climate warming in the tundra plant *Silene acaulis*. *Global Change Biology* 24: 1614-1625.

Falster, D., R. Gallagher, E. H. Wenk, I. J. Wright, D. Indiarto, S. C. Andrew, C. Baxter, J. Lawson, et al., 2021. AusTraits, a curated plant trait database for the Australian flora. *Scientific Data* 8: 254.

Funk, J. L. 2021. Revising the trait-based filtering framework to include interacting filters: Lessons from grassland restoration. *Journal of Ecology* 109: 3466-3472.

Harper, J. L., and J. White. 1974. The demography of plants. *Annual Review of Ecology and Systematics* 5: 419-463.

Kattage, J., S. Díaz, S. Lavorel, I. C. Prentice, P. Leadley, G. Bönisch, E. Garnier, M. Westoby, et al. 2011. TRY - a global database of plant traits. *Global Change Biology* 17: 2905-2935.

Lasky, J. R., M. V. Hooten, and P. B. Adler. 2020. What processes must we understand to forecast regional-scale population dynamics? *Proceedings of the Royal Society B* 287: 20202219.

Laughlin, D. C., J. R. Gremer, P. B. Adler, R. M. Mitchell, and M. M. Moore. 2020. The net effect of functional traits on fitness. *Trends in Ecology & Evolution* 35: 1037-1047.

Levin, S. C., S. Evers, T. Potter, M. P. Guerrero, D. Z. Childs, A. Compagnoni, T. M. Knight, and R. Salguero-Gómez. 2022. Rpadrino: An R package to access and use PADRINO, an open access database of integral projection models. *Methods in Ecology and Evolution* 13: 1923-1929.

Nguyen, M. A., A. E. Ortega, K. Q. Nguyen, S. Kimball, M. L. Goulden, and J. L. Funk. 2016. Evolutionary responses of invasive grass species to variation in precipitation and soil nitrogen. *Journal of Ecology* 104: 979-986.

Oldfather, M. F., and D. D. Ackerly. 2019. Microclimate and demography interact to shape stable population dynamics across the range of an alpine plant.

Oldfather, M. F., C. L. Van Den Elzen, P. M. Heffernan, and N. C. Emery. 2021. Dispersal evolution in temporally variable environments: implications for plant range dynamics. *American Journal of Botany* 108: 1584-1594.

Salguero-Gómez, R., O. R. Jones, C. R. Archer, Y. M. Buckley, J. Che-Castaldo, H. Caswell, D. Hodgson, A. Scheuerlein, et al. 2015. The COMPARDE plant matrix database: an open online repository for plant demography. *Journal of Ecology* 103: 202-218.

Sperandii, M. G., F. de Bello, E. Valencia, L. Götzenberger, M. Bazzichetto, T. Galland, A. E-Vojtkó, L. Conti, et al. 2022. LOTVS: a global collection of permanent vegetation plots. *Journal of Vegetation Science* 33: e13115.

Swenson, N. G., S. J. Worthy, D. Eubanks, Y. Iida, L. Monks, K. Petprakob, V. E. Rubio, K. Staiger, and J. Zambrano. 2020. A reframing of trait-demographic rate analyses for ecology and evolutionary biology. *International Journal of Plant Sciences* 181: 33-43.

Villellas, J., D. F. Doak, M. B. García, and W. F. Morris. 2015. Demographic compensation among populations: what is it, how does it arise and what are its implications? *Ecology Letters* 18: 1139-1152.

Weigelt, P., C. König, and H. Kreft. 2020. GIFT - A global inventory of floras and traits for macroecology and biogeography. *Journal of Biogeography* 47: 16-43.

Yang, J., X. Song, J. Zambrano, Y. Chen, M. Cao, X. Deng, W. Zhang, X. Yang, G. Zhang, Y. Tang, and N. G. Swenson. 2020. Intraspecific variation in tree growth responses to neighbourhood composition and seasonal drought in a tropical forest. *Journal of Ecology* 109: 26-37.

Figure 1. Conceptual figure showing how intraspecific trait variation contributes to complex relationships between traits and the environment, leading to variation in demographic rates. We expect these relationships will be trait and/or environmentally dependent with the expectation that different demographic metrics may be driven by different variables. **(A)** Sampling a functional trait from one or a few populations (red and blue curve) may not capture the full range (bold curve) of intraspecific trait variation of a species. This trait variation may be driven by differences in genetic variation among populations, which is known to interact with the environment to influence trait expression. **(B)** Trait-demographic rate relationships are sensitive to micro- and macro-environmental gradients (trait x environment interactions) such as across elevation as highlighted here where there is a negative relationship between the trait and a demographic rate within a high elevation population (red line), but a positive relationship within a low elevation population (blue line). Different demographic rates may respond in different ways across the same environmental gradient leading to compensatory relationships. **(C)** These relationships may be evident by differences in relationships among demographic rates across an environmental gradient. As an example, fecundity is higher at lower elevations and decreases as elevation increases (solid line), whereas survival rate shows the opposite pattern, higher at higher elevations and decreasing as elevation decreases (dashed line). Compensation between fecundity and survival along this elevation gradient may contribute to population stability.