

**Title:** Introduction to the Special Issue: The role of seed dispersal in plant populations: perspectives and advances in a changing world

**Authors:** Noelle G. Beckman<sup>1</sup>, Clare E. Aslan<sup>2</sup>, Haldre S. Rogers<sup>3</sup>

**Corresponding author:** noelle.beckman@usu.edu

**Running Title:** The role of seed dispersal in plant populations

**Author affiliations:**

<sup>1</sup> Department of Biology and Ecology Center, Utah State University, Logan, Utah

<sup>2</sup> School of Earth and Sustainability, Northern Arizona University, Flagstaff, AZ

<sup>3</sup> Department of Ecology, Evolution, and Organismal Biology, Iowa State University, Ames, IA

**Abstract**

Despite the importance of seed dispersal as a driving process behind plant community assembly, our understanding of the role of seed dispersal in plant population persistence and spread remains incomplete. As a result, our ability to predict the effects of global change on plant populations is hampered. We need to better understand the fundamental link between seed dispersal and population dynamics in order to make predictive generalizations across species and systems, to better understand plant community structure and function, and to make appropriate conservation and management responses related to seed dispersal. To tackle these important knowledge gaps, we established the CoDisperse Network and convened an interdisciplinary, NSF-sponsored Seed Dispersal Workshop in 2016, during which we explored the role of seed dispersal in plant population dynamics (NSF DEB Award # 1548194). In this Special Issue, we consider the current state of seed dispersal ecology and identify the following collaborative research needs: (1) the development of a mechanistic understanding of the movement process influencing dispersal of seeds; (2) improved quantification of the relative influence of seed dispersal on plant fitness compared to processes occurring at other life history stages; (3) an ability to scale from individual plants to ecosystems to quantify the influence of dispersal on ecosystem function; and (4) the incorporation of seed dispersal ecology into conservation and management strategies.

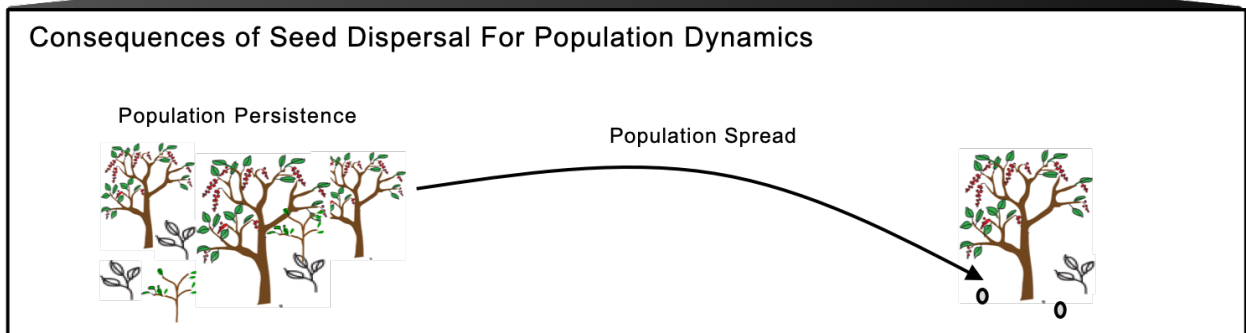
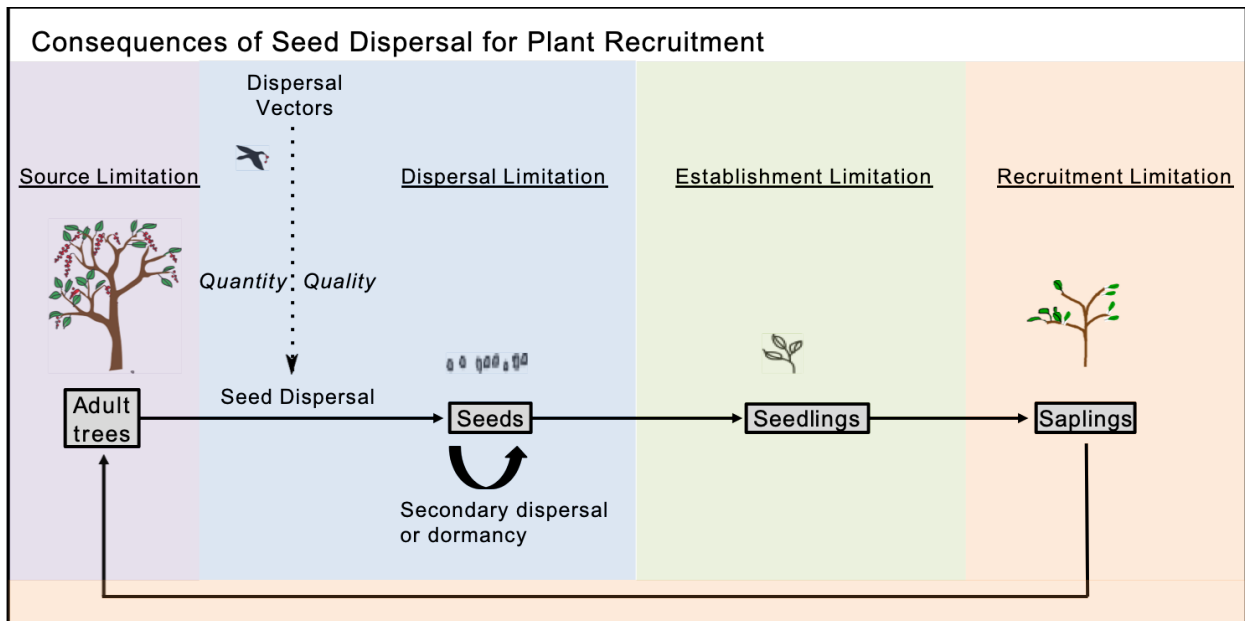
## Keywords

Seed dispersal, plant recruitment, defaunation, population spread, population dynamics, frugivores, CoDisperse

## Introduction

Dispersal is a central component of conceptual frameworks within ecology and evolution (Clobert et al. 2012, Vellend 2016). Movement of individuals affects the spread of populations (Cain et al. 2000), patterns of biodiversity across local, regional, and global scales (Vellend 2010), genetic diversity and adaptive capacity (Kremer et al. 2012), and species' responses to global change (Travis et al. 2013). For a plant, movement of the seed provides the single opportunity in its entire life cycle to change its geographic location. As the seed is deposited within the seedscape (Beckman and Rogers 2013), this life history event sets the template for all future interactions in a plant's life (Fig. 1; Nathan and Muller-Landau 2000). Seed dispersal is of great conservation importance, since it is both affected by global change and affects the ability of plants to move or adapt to global change (McConkey et al. 2012, Travis et al. 2013). As such, seed dispersal holds the potential to affect patterns of biodiversity by mediating population- and community-level dynamics.

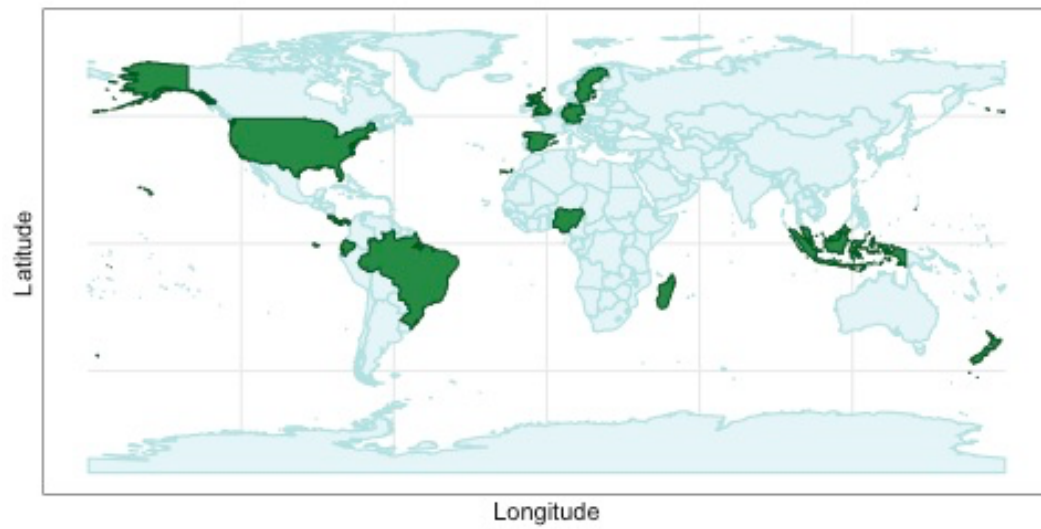
In spite of the importance of seed dispersal as a driving process behind plant community assembly, our understanding of the role of seed dispersal in plant population persistence and spread remains incomplete. As a result, our ability to predict the effects of global change on plant species populations is hampered. This lack of knowledge persists primarily because the processes underlying the dispersal of seeds, as well as their consequences, are complex and context-dependent (Fig. 1; Wang and Smith 2002, Beckman et al. 2019). *In order to make predictive generalizations across species and systems, to better understand plant community structure and function, and to make appropriate conservation and management decisions related to seed dispersal, we need to better understand the fundamental link between seed dispersal and population dynamics.* In this Special Issue, we propose interdisciplinary approaches to advance our understanding of the importance of seed dispersal for plant population dynamics.



**Figure 1. Consequences of Seed Dispersal for Plant Recruitment and Population Dynamics.** Shadings indicate limitation imposed at different stages by the seedscape, the local environment surrounding a seed following seed dispersal that influences later stages of plant recruitment, such as conspecific distance and density, substrate, and light (Beckman and Rogers 2013).

## 1    **Insights from the Special Issue**

2            Progress in basic research into seed dispersal ecology and its application in conservation  
3    and management has been limited by a lack of interactions among disciplines and  
4    biogeographical regions. Often individual researchers attend only disciplinary conferences and  
5    read disciplinary journals; therefore, researchers using mathematical biology approaches to  
6    model the dispersal process may not interact with ecologists empirically studying the dispersal  
7    process, for example. However, seed dispersal links disciplines and subdisciplines from  
8    physiological ecology to community ecology to biogeochemistry to computational and  
9    mathematical modeling. Geographical boundaries are also limiting, often with little interaction  
10   among researchers working in temperate *vs.* tropical systems and Old World *vs.* New World  
11   systems. Even the research focus on a dispersal mode produces boundaries, with little interaction  
12   between groups studying wind dispersal and vertebrate dispersal, for example. To identify and  
13   tackle knowledge gaps on the role of seed dispersal in plant population dynamics, we established  
14   the CoDisperse Network of researchers and convened an interdisciplinary, NSF-sponsored Seed  
15   Dispersal Workshop in 2016 (NSF DEB Award # 1548194). Thirty workshop participants came  
16   from 6 countries (Canada, Germany, Nigeria, Switzerland, United Kingdom, and the United  
17   States) and were actively conducting research in 15 countries across North and South America,  
18   Europe, Africa, Asia, and Oceania (Fig. 2). Participants brought a range of expertise including  
19   ecology, evolution, animal behavior, conservation biology, environmental policy, math, theory,  
20   biogeography, molecular biology, genomics, physics, statistics, and complex systems.



**Figure 2. Map of countries.** Participants were actively conducting research in 15 countries (shown in green).

1           Using small- and large-group guided discussions designed to capture the varied  
2 perspectives of workshop participants, we explored the current state of seed dispersal ecology,  
3 specifically focusing on the consequences of seed dispersal for plant populations. We identified  
4 the following collaborative research needs: (1) the development of a mechanistic understanding  
5 of the movement process influencing dispersal of seeds; (2) improved quantification of the  
6 relative influence of seed dispersal on plant fitness compared to processes occurring at other  
7 plant life history stages; (3) an ability to scale from individual plants to ecosystems to quantify  
8 the influence of dispersal on ecosystem function; and (4) the incorporation of seed dispersal  
9 ecology into conservation and management strategies. The workshop and papers in this Special  
10 Issue focus on strategies to advance the first three research needs, and we urge researchers and  
11 managers to continue discussions to advance the fourth research need.

12           To address these research needs, we argue that multiple epistemologies, or ways of  
13 knowing, are necessary and that discovering generality in patterns and processes requires  
14 comparing knowledge across systems. Overcoming epistemological barriers – disciplinary  
15 differences regarding research goals, theoretical frameworks, assumptions, rigor, and causal  
16 explanation (Brister 2016) – to value multiple ways of knowing can lead to more integrative and  
17 innovative solutions to complex problems (Miller et al. 2008). We propose that seed dispersal is  
18 measurable and more predictable than traditionally assumed, and research advances and  
19 interdisciplinary collaborations are necessary to generalize across species and systems and make  
20 predictions in the context of global change. The reviews and viewpoints in this Special Issue  
21 provide specific recommendations for future research to make seed dispersal ecology  
22 generalizable and predictable utilizing interdisciplinary approaches, while the research papers  
23 give examples of applying novel empirical, mathematical, statistical, and integrated approaches  
24 to address the identified knowledge gaps.

25           Aslan et al. (2019), Beckman et al. (2019), and Rogers et al. (2019) review our current  
26 standing in the field of seed dispersal ecology and propose interdisciplinary advances to  
27 approach the complexity of seed dispersal processes for generalization and prediction. Beckman  
28 et al. (2019) focus on promising interdisciplinary approaches for studying, generalizing, and  
29 predicting seed dispersal and its demographic consequences. They begin with a general approach  
30 for studying the context-dependency of seed dispersal, discuss strategies to reduce and embrace  
31 complexity, and encourage simultaneous and iterative data collection and model development.

1 They consider advances and challenges associated with the first two aforementioned research  
2 needs, specifically 1) the mechanisms underlying the movement and resulting patterns of seeds  
3 and 2) integrating seed dispersal with demography to examine the demographic consequences of  
4 this movement. Aslan et al. (2019) propose a functional approach to reducing the complexity of  
5 studying seed dispersal. They propose categorizing plants based on whether it matters (a) if seeds  
6 are dispersed, (b) into what context they are dispersed, and (c) what vector disperses them. They  
7 explore the use of these functional group categories to achieve generalization across species and  
8 systems in seed dispersal ecology, a key challenge in the field. Rogers et al. (2019) revisit an  
9 existing but under-utilized concept in seed dispersal - the total dispersal kernel. While most  
10 plants have multiple dispersal vectors, few studies incorporate the relative role of each vector on  
11 the overall dispersal kernel. Rogers et al. (2019) review empirical, theoretical, and statistical  
12 challenges associated with studying the total dispersal kernel and suggest promising ways  
13 forward. Understanding the influence of each vector is critical as disperser communities are  
14 altered in today's changing world.

15 Another key theme that emerged from the workshop was the importance of intraspecific  
16 variation in seed dispersal-related traits. Intraspecific variation can have important ecological and  
17 evolutionary consequences; however, most ecological models that investigate these  
18 consequences for population dynamics, species interactions, and global change use mean values  
19 for species (Bolnick et al. 2011, Moran et al. 2016). Schupp et al. (2019) delve into the intrinsic  
20 and extrinsic drivers of intraspecific variation in seed dispersal. They find evidence that, while  
21 drivers of intraspecific variation in seed dispersal are diverse and pervasive, there are large gaps  
22 in our understanding, and they propose research to fill those gaps. Snell et al. (2019) synthesize  
23 research on the consequences of intraspecific variation in dispersal for population, communities,  
24 evolution, and responses to global change. As an example of these consequences, Schreiber and  
25 Beckman (in press) use a mathematical approach to examine how intraspecific variation in  
26 dispersal and fecundity and their covariation influence the spread rates of populations and apply  
27 this approach to a well-studied example, *Acer rubrum*. They find that population spread is  
28 highest when variation in dispersal covaries positively with fecundity. Johnson et al. (2019)  
29 examine evidence for rapid changes in seed dispersal and the potential underlying mechanisms,  
30 including the role of phenotypic plasticity, epigenetics, and rapid evolution. These papers

highlight the importance of estimating intraspecific variation in dispersal and its drivers for predicting the persistence and spread of populations, community dynamics and coexistence.

One of the driving motivations behind the workshop was to understand how dispersal is influenced by global change drivers. Using an accidental experiment of previously logged, hunted and protected forests in the northern Republic of Congo, Nuñez et al. (2018) evaluate the effects of hunting and logging on tree fecundity and seed dispersal in the northern Republic of Congo. They find that low-intensity logging affected seed dispersal distances, though the direction and magnitude varied by species. Olsson et al. (2019) investigate how plant performance is affected by competition and reduced seed dispersal due to hunting and found that dispersal limitation was more important than competition for seedling recruitment in hunted forests. Both studies show that anthropogenic pressures influence seed dispersal. As the Earth continues to warm and overharvesting, logging, and landscape fragmentation escalate, future work should continue to disentangle the effects of interacting pressures on seed dispersal and assess their implications for future plant communities.

#### **Interdisciplinary collaboration to Advance Seed Dispersal Ecology.**

This Special Issue resulted from new collaborations across disciplines forged during the week-long Seed Dispersal Workshop. The workshop facilitated collaboration among empirical ecologists who conduct observational and experimental studies to examine the role of seed dispersal in plant ecosystems around the world; theoretical ecologists applying conceptual, statistical, and mathematical models to generalize the importance of dispersal to plant populations across systems and species; and applied mathematicians, physicists, and systems biologists identifying mathematical challenges and developing novel analytical tools, modeling approaches, and efficient simulation platforms to deal with these multiscale problems.

There are many challenges and opportunities associated with bringing together a diverse group of experts for a short amount of time (Palmer et al. 2016). Having a diverse group of participants draws attention to the differences that exist across disciplines, ways of knowing, and perspectives, including distinct language/jargon and disparate conceptualizations of the problem. We found that successful interdisciplinary interactions required a variety of approaches including defining discipline-specific jargon to provide a common language for researchers from all disciplines and collectively developing a framework for synthesis. Building on practices



developed by the National Socio-Environmental Synthesis Center for interdisciplinary research (Palmer et al. 2016), we provide an overview of the approach we used for organizing and structuring an interdisciplinary workshop (Box 1) and more details in the Supporting Information. Throughout the Special Issue, we provide guidelines for researchers interested in crossing disciplinary boundaries.

### **Box 1. Overview of Organizing an Interdisciplinary Workshop**

- In selecting the group, leaders must balance the breadth of representation of research areas while keeping the overall size to a manageable number for productive collaboration. Carefully select participants who offer diverse perspectives, are committed to achieving a common goal, and will do their part to create an open and welcoming environment.
- Select a location that has one large room and several breakout rooms, all with whiteboards and audio-visual capabilities.
- If IT support is available, virtual participants can be included, but we recommend carefully planning activities with virtual participants in mind in order to ensure seamless participation and positive group dynamics (Fraser et al. 2017).
- Start preparing and engaging participants early to set up an atmosphere of shared responsibility for the workshop's success. Survey participants for advice on topics, strategies for organizing effective workshops, and shared outcomes and common goals.
- In a pre-workshop meeting, summarize results of pre-workshop surveys and provide expectations for workshop goals, objectives, outcomes, communication, and participation before, during, and after the workshop.
- Assign clear and differentiated roles and tasks to participants before, during, and after the workshop.
- Keep focused. Set out a series of tractable questions that can be tackled in the period of time allotted. We suggest 1 overarching question and no more than 2-3 sub-questions for the duration of a one-week workshop. Visibly display these guiding questions in the central gathering place and revisit them often.
- Schedule the week carefully, making sure to allow time for team-building and open discussion, while also steering the group towards the final goals.

- Provide plenty of icebreakers that promote communication and expose differences and similarities in perspectives.
- Get everyone on the same page with regard to the state of the field from various perspectives with short overview presentations and panel discussions.
- Develop a shared vocabulary.
- Use teaching techniques designed to elicit contributions from all participants including small group discussions, think-pair-share, brainstorming and sharing ideas anonymously on post-its, etc. Limit the use of large-group discussions to information sharing, initial brainstorming, and report-backs, to reduce the likelihood of having a few voices dominate.
- Do not let discussions be derailed. Enforce this by requiring frequent report-backs from small groups using structured templates and providing a space for interesting ideas to be recorded and revisited later during the workshop or in future collaborations.
- Ensure interest/buy-in from all disciplines by allowing people to choose working groups of most interest and move to different working groups if they feel so inclined.
- Provide drinks, snacks, and lunches to build group cohesion.
- Demonstrate strong, shared leadership before, during, and after the workshop to create a respectful, open, inclusive, and positive environment and to lead products to completion.
- Have groups identify next steps and select a leader for any projects that emerge from the workshop.
- Check in with project leaders and set deadlines for manuscripts. Conference symposia are useful for consolidating ideas for a review paper, and a Special Issue is a helpful tool for providing a single deadline for multiple papers emerging from a workshop.

## Conclusions

Seed dispersal is fundamental to the structure and function of plant communities, but its complexity and heterogeneity impede mechanistic understanding and quantitative prediction of seed dispersal processes and their disruption. Although it requires careful planning to bridge various vocabularies and epistemologies, assembling interdisciplinary working groups that leverage diverse approaches, tools, and perspectives provides the potential for novel insights to emerge and new tools to bridge knowledge gaps. The diversity of disciplines, geographic regions, and expertise represented in this Special Issue yield a range of perspectives and insights

and, we hope, will stimulate further collaborations to advance seed dispersal ecology and conservation.

#### Sources of Funding

Ideas for this Special Issue initiated during the Seed Dispersal Workshop held in May 2016 at the Socio-Environmental Synthesis Center in Annapolis, MD and supported by the US National Science Foundation Grant DEB-1548194 to NGB and the National Socio-Environmental Synthesis Center under the US National Science Foundation Grant DBI-1052875.

#### Contributions of the Authors

NGB, CEA, and HSR discussed the overall structure of the manuscript. NGB wrote the initial draft with revisions by all authors.

#### Acknowledgements

We thank the past and current Chief Editors of *AoB PLANTS*, Hall Cushman and Tom Buckley, and the Managing Editor Joanne Ferrier for facilitating this Special Issue; all of the participants of the Seed Dispersal Workshop for their collegiality and engendering an overall fun and intellectually inspiring adventure; and the staff of the National Socio-Environmental Synthesis Center (SESYNC) for logistical support during the workshop. We thank Dr. Jonathan G. Kramer, the Director for Interdisciplinary Science at SESYNC, for his feedback and insights on structuring an interdisciplinary workshop.

#### References

- Aslan, C. E., N. G. Beckman, H. S. Rogers, J. L. Bronstein, D. Zurell, F. Hartig, K. Shea, L. Pejchar, M. G. Neubert, J. R. Poulsen, J. HillRisLambers, M. N. Miriti, B. A. Loiselle, E. O. Effiom, J. Zambrano, E. W. Schupp, G. Pufal, J. Johnson, J. M. Bullock, J. F. Brodie, E. M. Bruna, R. S. Cantrell, R. Decker, E. C. Fricke, K. Gurski, A. Hastings, O. Kogan, J. A. Powell, O. H. Razafindratsima, M. Sandor, S. J. Schreiber, R. S. Snell, C. Strickland, and Y. Zhou. 2019. Employing plant functional groups to advance seed dispersal ecology and conservation. *AoB Plants* **11**:plz006.
- Beckman, N. G., C. E. Aslan, H. S. Rogers, O. Kogan, J. L. Bronstein, J. M. Bullock, F. Hartig, J. HilleRisLambers, Y. Zhou, D. Zurell, J. F. Brodie, E. M. Bruna, R. S. Cantrell, R. R. Decker, E. Effiom, E. C. Fricke, K. Gurski, A. Hastings, J. S. Johnson, B. A. Loiselle, M. N. Miriti, M. G. Neubert, L. Pejchar, J. R. Poulsen, G. Pufal, O. H. Razafindratsima, M. E. Sandor, K. Shea, S. Schreiber, E. W. Schupp, R. S. Snell, C. Strickland, and J.

- 1 Zambrano. 2019. Advancing an interdisciplinary framework to study seed dispersal  
2 ecology. *AoB Plants*:plz048.
- 3 Beckman, N. G., and H. S. Rogers. 2013. Consequences of Seed Dispersal for Plant Recruitment  
4 in Tropical Forests: Interactions Within the Seedscape. *Biotropica* **45**:666-681.
- 5 Bolnick, D. I., P. Amarasekare, M. S. Araújo, R. Bürger, J. M. Levine, M. Novak, V. H. W.  
6 Rudolf, S. J. Schreiber, M. C. Urban, and D. A. Vasseur. 2011. Why intraspecific trait  
7 variation matters in community ecology. *Trends in Ecology & Evolution* **26**:183-192.
- 8 Brister, E. 2016. Disciplinary capture and epistemological obstacles to interdisciplinary research:  
9 Lessons from central African conservation disputes. *Studies in History and Philosophy of*  
10 *Science Part C: Studies in History and Philosophy of Biological and Biomedical Sciences*  
11 **56**:82-91.
- 12 Cain, M. L., B. G. Milligan, and A. E. Strand. 2000. Long-distance seed dispersal in plant  
13 populations. *American Journal of Botany* **87**:1217-1227.
- 14 Clobert, J., M. Baguette, T. Benton, and J. Bullock, editors. 2012. *Dispersal Ecology and*  
15 *Evolution*. Oxford University of Press, United Kingdom.
- 16 Fraser, H., K. Soanes, S. A. Jones, C. S. Jones, and M. Malishev. 2017. The value of virtual  
17 conferencing for ecology and conservation. *Conservation Biology* **31**:540-546.
- 18 Johnson, J. S., R. S. Cantrell, C. Cosner, F. Hartig, A. Hastings, H. S. Rogers, E. W. Schupp, K.  
19 Shea, B. J. Teller, X. Yu, D. Zurell, and G. Pufal. 2019. Rapid changes in seed dispersal  
20 traits may modify plant responses to global change. *AoB Plants* **11**:plz020.
- 21 Kremer, A., O. R. J. u. J. Robledo-Arnuncio, F. Guillaume, G. Bohrer, R. Nathan, J. R. Bridle, R.  
22 Gomulkiewicz, E. K. Klein, K. Ritland, A. Kuparinen, S. Gerber, and S. Schueler. 2012.  
23 Long-distance gene flow and adaptation of forest trees to rapid climate change. *Ecology*  
24 *Letters* **15**:378-392.
- 25 McConkey, K. R., S. Prasad, R. T. Corlett, A. Campos-Arceiz, J. F. Brodie, H. S. Rogers, and L.  
26 Santamaria. 2012. Seed dispersal in changing landscapes. *Biological Conservation* **146**:1-  
27 13.
- 28 Miller, T. R., T. D. Baird, C. M. Littlefield, G. Kofinas, F. S. Chapin, and C. L. Redman. 2008.  
29 *Epistemological Pluralism*  
30 *Reorganizing Interdisciplinary Research*. *Ecology and Society* **13**.
- 31 Moran, E. V., F. Hartig, and D. M. Bell. 2016. Intraspecific trait variation across scales:  
32 implications for understanding global change responses. *Global Change Biology* **22**:137-  
33 150.
- 34 Nathan, R., and H. C. Muller-Landau. 2000. Spatial patterns of seed dispersal, their determinants  
35 and consequences for recruitment. *Trends in Ecology & Evolution* **15**:278-285.
- 36 Nuñez, C. L., J. S. Clark, C. J. Clark, and J. R. Poulsen. 2018. Low-intensity logging and hunting  
37 have long-term effects on seed dispersal but not fecundity in Afrotropical forests. *AoB*  
38 *Plants* **11**.
- 39 Olsson, O., G. Nuñez-Iturri, H. G. Smith, U. Ottosson, and E. O. Effiom. 2019. Competition,  
40 seed dispersal and hunting: what drives germination and seedling survival in an  
41 Afrotropical forest? *AoB Plants* **11**.
- 42 Palmer, M. A., J. G. Kramer, J. Boyd, and D. Hawthorne. 2016. Practices for facilitating  
43 interdisciplinary synthetic research: the National Socio-Environmental Synthesis Center  
44 (SESYNC). *Current Opinion in Environmental Sustainability* **19**:111-122.
- 45 Rogers, H. S., N. G. Beckman, F. Hartig, J. S. Johnson, G. Pufal, K. Shea, D. Zurell, J. M.  
46 Bullock, R. S. Cantrell, B. Loiselle, L. Pejchar, O. H. Razafindratsima, M. E. Sandor, E.

- 1 W. Schupp, W. C. Strickland, and J. Zambrano. 2019. The total dispersal kernel: a review  
2 and future directions. *AoB Plants* **11**:plz042.
- 3 Schreiber, S. J., and N. G. Beckman. in press. Individual variation in dispersal and fecundity  
4 increases rates of spatial spread. *AoB Plants*.
- 5 Schupp, E. W., R. Zwolak, L. R. Jones, R. S. Snell, N. G. Beckman, C. Aslan, B. R. Cavazos, E.  
6 Effiom, E. C. Fricke, F. Montaña-Centellas, J. Poulsen, O. H. Razafindratsima, M. E.  
7 Sandor, and K. Shea. 2019. Intrinsic and Extrinsic Drivers of Intraspecific Variation in  
8 Seed Dispersal Are Diverse and Pervasive. *AoB Plants* **11**:plz067.
- 9 Snell, R. S., N. G. Beckman, E. Fricke, B. A. Loiselle, C. S. Carvalho, L. R. Jones, N. I. Lichti,  
10 N. Lustenhouwer, S. J. Schreiber, C. Strickland, L. L. Sullivan, B. R. Cavazos, I. Giladi,  
11 A. Hastings, K. M. Holbrook, E. Jongejans, O. Kogan, F. Montaña-Centellas, J. Rudolph,  
12 H. S. Rogers, R. Zwolak, and E. W. Schupp. 2019. Consequences of intraspecific  
13 variation in seed dispersal for plant demography, communities, evolution, and global  
14 change. *AoB Plants* **11**:plz016.
- 15 Travis, J. M. J., M. Delgado, G. Bocedi, M. Baguette, K. Bartoń, D. Bonte, I. Boulangeat, J. A.  
16 Hodgson, A. Kubisch, V. Penteriani, M. Saastamoinen, V. M. Stevens, and J. M. Bullock.  
17 2013. Dispersal and species' responses to climate change. *Oikos* **122**:1532-1540.
- 18 Vellend, M. 2010. Conceptual synthesis in community ecology. *The Quarterly Review of*  
19 *Biology* **85**:183-206.
- 20 Vellend, M. 2016. *The Theory of Ecological Communities*. Princeton University Press,  
21 Princeton.
- 22 Wang, B. C., and T. Smith. 2002. Closing the seed dispersal loop. *Trends in Ecology &*  
23 *Evolution* **17**:379-385.
- 24