

How temporal and spatial mosaics of reproduction determine forest communities

Temperate forests are a critical global resource and one especially important to Canada—supporting the forestry, maple syrup, and related industries while providing numerous additional services to people. Their persistence and regeneration shapes the global carbon cycle of today and our future. Yet how forest tree communities assemble and are maintained is still a major question in ecology—and one that is more pressing to answer given human-caused climate change. Addressing this question requires understanding how tree seeds and seedlings successfully navigate a world of seed predators (including small mammal and birds) and soil pathogens to become adult trees. This project examines how pulsed tree seed production (called ‘masting’) and spatial mosaics of seed and seedling death may promote forest regeneration. Through a collaborative Canadian-Swiss alliance of two major forest ecology labs this project will gather data across a range of forest sites—across two countries and three years—to test the relative roles of seed predators and pathogens in determining seed and seedling survival over both space and time. Complementary skills from each team will allow the project to build population models of forests that can test competing hypotheses for what drives assembly and provide future predictions. By working across a climatic gradient just south of BC and incorporating tree growth, this project will help improve predictions of the assembly and resilience of Canadian forests as the climate warms, with implications for the global carbon cycle.

RELEVANCE AND EXPECTED OUTCOMES

- Outline the objectives of the proposed international collaboration and explain the potential outcomes and impacts. Explain how the international collaboration will address important research challenges in the natural sciences and engineering (NSE) disciplines and further develop areas of Canadian strength and leadership.
- Describe the global importance of the topic and how the expected outcomes could benefit Canada.

Understanding the major factors that shape forest communities is a fundamental question across ecology and forest science, with decades of research yielding competing hypotheses. Most hypotheses focus on the challenge of understanding how seeds and seedlings survive a world of predators and pathogens to become saplings.¹⁻⁴ This project unites and tests the two major models for forest regeneration from seed in temperate forests: (1) pulsed seed production in only certain years—called ‘masting’ or ‘mast seeding’—as a way to temporally structure seed predators such that they are at low abundance in high seed years;^{5,6} and (2) spatial negative density-dependent survival of seeds and seedlings.^{2,3} This latter mechanism, often called ‘Janzen-Connell,’ is caused by hypothesized high predator or pathogen density near a parent tree that declines with distance from the parent tree, creating spatial mosaics in survival for seeds.^{2,7} While both hypotheses focus on the challenge of seed and seedling survival as the major mystery of forest regeneration, they operate on contrasting axes—with masting focused on temporal patterns of recruitment,⁸ and Janzen-Connell focused on spatial patterns. Importantly, they also make contrasting predictions. Masting uses an economy of scale—high seed production can swamp predator populations assuming most seed sources for the predators mast (produce an abundant seed crop) at the same time—to predict positive density dependence (more seeds lead to more survival), while Janzen-Connell predicts negative density dependence. They also make varying predictions for how environmental factors affect seed production and in turn adult tree growth. Masting suggests plants use environmental cues to time high-reproduction years and experience associated growth declines due to high investment in reproduction.^{6,9-11} In contrast, Janzen-Connell requires no environmental cues and predicts more regular reproduction with less noticeable effects on growth.

We argue that both mechanisms for forest recruitment—masting and Janzen-Connell—may explain recruitment in temperate forests, but have rarely been tested together.¹² Our project leverages collaboration between two forest ecology labs to build on existing data and collect the additional data critical to test these models together. Globally the need for a robust mechanistic model of forest tree dynamics is critical to the global carbon cycle, with Canada’s forests playing a major role.^{13,14} In Canada, this is also an especially pressing challenge as industries related to forests (e.g., tourism, wood products, maple syrup) are critical to the economy and at risk of major shifts with increased warming from human-caused climate change. With improved models of forest dynamics and how they respond to environmental cues, including regeneration from seed—a major focus of this work—Canada will be better poised to mitigate major forest change when possible (for example, through targeted seed or planting programs in actively managed forests), and mitigate impacts.

COLLABORATION:

- List and describe your international collaborator(s).
- Explain the rationale for your selected international collaborator(s) and the added value of the collaboration.
- Describe the role of your team in the collaboration.

The international collaborator, Janneke Hille Ris Lambers, is a world expert in forest ecology,¹⁵⁻²¹ with special expertise in global change ecology of temperate forests—including Mount Rainier (called

Tahoma by local indigenous groups)—where she has worked for over 15 years.^{19,21–23} Her research focus on forest assembly, including the role of Janzen-Connell dynamics,²⁴ makes her uniquely skilled to co-lead this research.

This proposed work is large in scope—designed to potentially reshape how we understand forest dynamics in temperate forests—and is only possible through close collaboration of the Plant Ecology Group (Hille Ris Lambers, ETH) and the Temporal Ecology Lab (Wolkovich, UBC). Each of the proposal's three work packages (WP) require integrated collaboration between the two labs. The Plant Ecology Group provides rare spatially and temporally rich data on seed production and seedling recruitment, while the Wolkovich lab will collect tree growth data through tree cores in the same locations to round out the data required to test the costs and benefits of each hypothesis (outlined in WP1). New studies to assess the role of mammalian seed predators and soil pathogens in structuring seed and seedling dynamics will be carried out by each lab in WP2, with the Temporal Ecology lab leading the soil microbial sequencing aspect of WP2 for US sites.

Both PIs are skilled in modeling complex ecological dynamics, which will be critical for all WPs. Wolkovich is especially adept at Bayesian approaches that can be used for predictions,^{25–28} while Hille Ris Lambers brings expertise in demographic models,^{21,24,29} two skillsets that come together in WP3 where predictive models will estimate demographic costs and benefits of masting. These models can help uncover gaps in each hypothesis—for example by showing cases where model predictions do not match existing patterns in the data—and can be adapted to make useful forecasts of how forests may change with continued climate change.³⁰

This collaboration will strengthen an international scientific network critical for adapting to continued global change. In addition to the exchange for trainees directly involved in the research (outlined in the Training plan below), this project will bring important skills in how to measure and model forest demography for forecasting to UBC and Canada. The proposed US sites are located just south of BC (Mount Rainier), and thus may serve as a sentinel of what warming will bring to BC forests. Further, the Temporal Ecology Lab will learn first-hand the forest-demography methods used by the Plant Ecology Group, and will then have the skills to gather similar data for BC.

TRAINING PLAN:

- Describe how the project and the international collaboration offer opportunities for enriched training experiences that will allow research trainees (undergraduates, graduates and postdoctoral fellows) to develop relevant technical skills as well as professional skills, such as leadership, communication, collaboration and entrepreneurship. Include the nature of the planned interactions with the international collaborators(s) and other relevant activities.

This collaboration will build an international network of trainees skilled in field and lab forest demography and ecology methods alongside robust computational and analytical approaches. As outlined in the SNSF grant, Canadian HQP are integral to the proposed research. A current UBC PhD student (Xiaomao Wang) will play a critical role in collecting and analyzing tree growth data. This student will be joined by a MSc student who will focus on seed predator trials and help with soil pathogen assays (WP2) with support from the proposed Swiss postdoc and additional support through the Temporal Ecology Lab. All students will be supported by and help mentor 8–22 undergraduate students on the project, who will assist in field and lab work while taking on specific components of a task to gain experience in project design. This team will work alongside a Swiss team spanning similar career stages with a project designed around team collaboration and training.

Both PIs (Wolkovich and Hille Ris Lambers) have track records of high quality training and are com-

mitted to trainees on this project becoming well-rounded professionals through an enriched international program of meetings and skill building. The labs plan in-person meetings each year alongside bi-monthly videocalls to maintain momentum, troubleshoot issues and provide additional support as needed. In-person meetings will have focused training components, including forest ecology and demography field methods and data science skills for reproducible research in the first year. Meetings in following years will focus on analytical methods and will provide opportunities for trainees to learn Bayesian methods and the language Stan from Wolkovich, and demographic modeling from Hille Ris Lambers. All meetings will include structured and unstructured opportunities to build collaboration, leadership and communication skills as different trainees will lead different aspects of the project and present their progress regularly. In the last year of the project, these meetings will include time to practice presentations for scientific meetings, alongside career discussions of next steps and opportunities.

EQUITY, DIVERSITY, AND INCLUSION (EDI):

- Describe how EDI will be fostered within the research environment, including 1) how EDI will be considered in the training plan and 2) how EDI has been considered in the academic team composition.

Both the Temporal Ecology Lab and Plant Ecology Group recognize how much academia's failure to attract, retain and promote the full diversity of people in our broader communities limits our research, outreach and makes our related work less useful. Both labs are thus committed to actionable steps to change this current reality, and have a history of efforts to broaden participation and lower barriers to entry and success, which they will build upon in this project. To increase the diversity of HQP, all positions will be open with clear job descriptions that encourage candidates with diverse backgrounds to apply and are reviewed by colleagues specializing in this before being shared widely on job boards and listservs. The PI and at least two lab members will review all candidates with a rubric designed to minimize implicit bias. The Temporal Ecology maintains a suite of additional guidelines and protocols for equitable hiring and science as discussed in the Personal data form.

Work in the field, lab and computationally will also be designed to foster a welcoming and inclusive environment. At the field and lab work stages, the PIs will carefully design tasks so they are approachable for trainees. This includes, for example, using drills or starters for coring trees (WP1) to reduce the physical force needed. Wolkovich will work together with all trainees on an Individual Safety Plan (ISP) so they are aware and prepared for any hazards at Mount Rainier. Computational work and training will be carefully shared and managed in the Temporal Ecology Lab, with trainees from undergraduate to PhD levels given similar structured training in data management, reproducible science and—for Masters, PhD and undergraduates who request it—training in Bayesian modeling. This will include short trainings as part of international team meetings, as well as more frequent one-on-one meetings with individuals working on specific computational or analytical tasks, and additional potential trainings through visitors and collaborators to the lab.

Team meetings will be carefully designed to make sure all lab members can attend and feel fully welcome. Both labs have a proven track record of designing meeting times, locations and structures to support lab members' family, religious, health-related and other life commitments and challenges while also giving them a robust opportunity for collaboration, team science and training. This means the PIs will work out meeting schedules well in advance, carefully choose locations and activities that are inclusive for all and make sure trainees feel they can share concerns. Discussing how to make team meetings equitable and inclusive will be part of the early video-call meetings, including structured readings and discussions as needed.

References:

- [1] Janzen, D. H. (1971). Seed predation by animals. *Annual review of ecology and systematics* pp. 465–492.
- [2] Connell, J. H. (1983). On the prevalence and relative importance of interspecific competition: evidence from field experiments. *The American Naturalist* 122, 661–696.
- [3] Comita, L. S., Queenborough, S. A., Murphy, S. J., Eck, J. L., Xu, K., Krishnadas, M., Beckman, N., and Zhu, Y. (2014). Testing predictions of the Janzen–Connell hypothesis: a meta-analysis of experimental evidence for distance- and density-dependent seed and seedling survival. *Journal of Ecology* 102, 845–856.
- [4] Davies, T. J. and MacPherson, A. (2024). Seed masting as a mechanism for escape from pathogens. *Current Biology* 34, R120–R125.
- [5] Koenig, W. D. (2021). A brief history of masting research. *Philosophical Transactions of the Royal Society B* 376, 20200423.
- [6] Pearse, I. S., Koenig, W. D., and Kelly, D. (2016). Mechanisms of mast seeding: resources, weather, cues, and selection. *New Phytologist* 212, 546–562.
- [7] Janzen, D. H. (1970). Herbivores and the number of tree species in tropical forests. *The American Naturalist* 104, 501–528.
- [8] Pearse, I. S., LaMontagne, J. M., and Koenig, W. D. (2017). Inter-annual variation in seed production has increased over time (1900–2014). *Proceedings of the Royal Society B: Biological Sciences* 284, 20171666.
- [9] Koenig, W. D. and Knops, J. M. (1998). Scale of mast-seeding and tree-ring growth. *Nature* 396, 225–226.
- [10] Hacket-Pain, A., Friend, A., Lageard, J., and Thomas, P. (2016). Tree rings and masting: considering reproductive phenomena when interpreting tree rings? *Tree Rings in Archaeology, Climatology and Ecology* 14, 78–85.
- [11] Bogdziewicz, M., Hacket-Pain, A., Kelly, D., Thomas, P. A., Lageard, J., and Tanentzap, A. J. (2021). Climate warming causes mast seeding to break down by reducing sensitivity to weather cues. *Global Change Biology* 27, 1952–1961.
- [12] Bogdziewicz, M., Kelly, D., Ascoli, D., Caignard, T., Chianucci, F., Crone, E. E., Fleurot, E., Foest, J. J., Gratzer, G., Hagiwara, T., et al. (2024). Evolutionary ecology of masting: mechanisms, models, and climate change. *Trends in Ecology & Evolution*.
- [13] Canadell, J., Monteiro, P., Costa, M., Cotrim da Cunha, L., Cox, P., Eliseev, A., Henson, S., Ishii, M., Jaccard, S., Koven, C., et al. (2021). *Climate Change 2021: The Physical Science Basis. Contribution of Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change*. (New York, NY: Cambridge University Press).
- [14] Friedlingstein, P., O’sullivan, M., Jones, M. W., Andrew, R. M., Gregor, L., Hauck, J., Le Quéré, C., Luijkx, I. T., Olsen, A., Peters, G. P., et al. (2022). Global carbon budget 2022. *Earth System Science Data Discussions* 2022, 1–159.

- [15] Clark, J. S., Silman, M., Kern, R., Macklin, E., and HilleRisLambers, J. (1999). Seed dispersal near and far: patterns across temperate and tropical forests. *Ecology* 80, 1475–1494.
- [16] Hille Ris Lambers, J., Clark, J. S., and Lavine, M. (2005). Implications of seed banking for recruitment of southern appalachian woody species. *Ecology* 86, 85–95.
- [17] Ettinger, A. K. and HilleRisLambers, J. (2013). Climate isn't everything: competitive interactions and variation by life stage will also affect range shifts in a warming world. *American Journal of Botany* 100, 1344–1355.
- [18] HilleRisLambers, J., Harsch, M. A., Ettinger, A. K., Ford, K. R., and Theobald, E. J. (2013). How will biotic interactions influence climate change–induced range shifts? *Annals of the new York Academy of Sciences* 1297, 112–125.
- [19] Ford, K. R., Breckheimer, I. K., Franklin, J. F., Freund, J. A., Kroiss, S. J., Larson, A. J., Theobald, E. J., and HilleRisLambers, J. (2017). Competition alters tree growth responses to climate at individual and stand scales. *Canadian Journal of Forest Research* 47, 53–62.
- [20] Buckley, L. B. and Hille Ris Lambers, J. (2019). Temperate and boreal responses to climate change. *Biodiversity and Climate Change: Transforming the Biosphere*. Yale University Press, New Haven, USA pp. 221–230.
- [21] Ford, K. R. and HilleRisLambers, J. (2020). Soil alters seedling establishment responses to climate. *Ecology Letters* 23, 140–148.
- [22] Ettinger, A. K., Ford, K. R., and HilleRisLambers, J. (2011). Climate determines upper, but not lower, altitudinal range limits of pacific northwest conifers. *Ecology* 92, 1323–1331.
- [23] Anderegg, L. D. and HilleRisLambers, J. (2016). Drought stress limits the geographic ranges of two tree species via different physiological mechanisms. *Global Change Biology* 22, 1029–1045.
- [24] Hille Ris Lambers, J., Clark, J. S., and Beckage, B. (2002). Density-dependent mortality and the latitudinal gradient in species diversity. *Nature* 417, 732–735.
- [25] Ettinger, A. K., Chamberlain, C. J., Morales-Castilla, I., Buonaiuto, D. M., Flynn, D. F. B., Savas, T., Samaha, J. A., and Wolkovich, E. M. (2020). Winter temperatures predominate in spring phenological responses to warming. *Nature Climate Change* 10, 1137–U119.
- [26] Buonaiuto, D. M. and Wolkovich, E. M. (2021). Differences between flower and leaf phenological responses to environmental variation drive shifts in spring phenological sequences of temperate woody plants. *Journal of Ecology* 109, 2922–2933.
- [27] Wolkovich, E. M., Auerbach, J., Chamberlain, C. J., Buonaiuto, D. M., Ettinger, A. K., Morales-Castilla, I., and Gelman, A. (2021). A simple explanation for declining temperature sensitivity with warming. *Global Change Biology* 27, 4947–4949.
- [28] Morales-Castilla, I., Davies, T., Legault, G., Buonaiuto, D., Chamberlain, C. J., Ettinger, A. K., Garner, M., Jones, F. A., Loughnan, D., Pearse, W. D., et al. (2024). Phylogenetic estimates of species-level phenology improve ecological forecasting. *Nature Climate Change* pp. 1–7.
- [29] Clark, J. S., Lewis, M., McLachlan, J. S., and HilleRisLambers, J. (2003). Estimating population spread: what can we forecast and how well? *Ecology* 84, 1979–1988.

- [30] IPCC. (2014). *Climate Change 2014: Impacts, Adaptation, and Vulnerability*. (Cambridge, United Kingdom and New York, NY, USA: Cambridge University Press).