Title: How pulsed reproduction shapes temperate forest communities

Relevance and expected outcomes

Understanding the major factors that shape forest communities is a fundamental question across ecology and forest science, with decades of research producing competing hypotheses that have yet to produce one robust mechanistic model. Most hypotheses focus on the challenge of understanding how seeds and seedlings survive a world of pests, predators and pathogens to become saplings, at which point light gaps and other more stochastic processes seem to determine which individuals become canopy trees.

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' usually—as a way to temporally structure seed predators such that they are at low abundance in high seed years; and (2) spatial negative density-dependent survival of seeds and seedlings. This later mechanism, often called 'Janzen-Connell' effects, is caused by hypothesized high predator or pathogen presence near a parent tree that declines with distance from the parent tree, creating spatial mosaics in survival for seeds. While both hypotheses focus on the challenge of seed survival as the major mystery of forest regeneration, they operate on contrasting axes—with masting focused on temporal patterns of recruitment, while Janzen-Connell focuses on spatial patterns—and make somewhat 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. In Janzen-Connell, seed production is highest near the parent tree where survival is also lowest and maximum recruitment is predicted where seed production is lower. They also make varying predictions for how environmental factors effect seed production and in turn adult tree growth; masting suggests plants use cues to time high-production years and would experience associated growth declines due to high investment in reproduction, while Janzen-Connell predicts more regular reproduction with less noticeable effects on growth and due to the environment.

We argue both mechanisms for forest recruitment—masting and spatial negative density-dependent survival—may explain recruitment in temperate forests, but has rarely been tested. Our project leverages collaboration between two forest ecology labs to build on existing data and collect the additional data critical to testing these models together. The international collaborator will importantly provide long-term data temporally and spatially explicit data on seed production and seedling survival that is rare and required to address these questions, while the Canadian collaborator will bring expertise in Bayesian modeling to address these two hypotheses together, and collect the tree growth data that is necessary to predict long-term forest dynamics.

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. 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 which is 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 forest), and mitigate impacts of forest change (for example, through understanding impacts on small mammal and bird communities from this work).

Collaboration: The international collaborator, Janneke Hille Ris Lambers, is a world expert in forest ecology, 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. She is currently Professor and Group Leader at ETH-Zurich, where she runs the Plant Ecology Group of roughly 8-12 trainees (master and doctoral students and postdocs) and 10 research staff, and has now studied Swiss temperate forests for over four years. As detailed further in the accompanying biographical sketch, Hille Ris Lambers is one of the most respected researchers in both forest ecology and global change, and has reshaped how ecologists think about temperate forest assembly. Her research focus on forest assembly, including the role of Janzen-Connell dynamics, makes her uniquely skilled to co-lead this research and the Temporal Ecology lab, run by Wolkovich, will gain from her knowledge, methods, skills and data.

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 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 to test the two major hypotheses for forest regeneration, 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.

Both PIs are skilled in modeling complex ecological dynamics, which will be critical for all WP. Wolkovich is especially adept at building Bayesian models that can be used for predictions, while Hille Ris Lambers brings expertise in demographic models, two skillsets that come together in WP3 where modeling will estimate demographic costs and benefits of masting, with Wolkovich developing predictive models. These predictions can help uncover gaps in each hypothesis—for example by showing cases where model predictions do not match existing pattens in the data—and can be adapted to make useful forecasts of how forest may change with continued climate change. This could be especially beneficial in Canada where climate change is expected to accelerate in the coming decades and forecasts of forest change could help managers mitigate and adapt to climate change.

This collaboration will strengthen an international scientific network critical for advancing fundamental ecology and also for adapting to continued global change. In addition to the exchange for students and postdocs 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. 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 would have the skills to gather similar data for BC. Already, the Temporal Ecology Lab has leveraged some of the

Plant Ecology Group's methods to collect one aspect of long-term forest demography data (seedling counts) in forests along an elevational gradient Smithers, BC, and this collaboration would build the network, that could lead eventually to research across US and Canadian sites.

Training plan:

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 with a current UBC PhD student playing a critical role in collecting tree growth data in WP1. This PhD student will be joined by two proposed MSc students (or one PhD student, depending on candidates who apply to open calls for this position, see also EDI section below) and 3-6 undergraduate students as junior researchers on the project. 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 committed to trainees on this project becoming well-rounded professionals through an enriched international program of meetings and skill building. The labs plan two in-person meetings each year alongside monthly video-calls to maintain momentum, trouble-shoot issues and provide other support as needed. In-person meetings will each have focused training components in the first year, including forest ecology and demography field methods and data science skills for reproducible research, including an introduction to git and GitHub as well as data management skills. Meetings in following years will focus on analytical components of WP and will provide major opportunities for trainees to learn the quantitative approaches of both PIs, including 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 projects, we expect these meetings to include practices talks and other presentations for scientific meetings, as well as career discussions of next steps and opportunities. The Wolkovich lab holds career-focused lab meetings at least once each year and the opportunity to expand these meetings to include a more international perspective will benefit the entire Temporal Ecology Lab.

Equity, diversity, and inclusion (EDI):

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 make our related work narrower and less useful. Both labs are also 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, that 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 work stage, PIs carefully design tasks so they are approachable for many trainees (for example, using drills or starters for coring trees to reduce the physical force needed) and Wolkovich works together with all trainees on an Individual Safety Plan (ISP) so they are aware, trained and prepared for any hazards. The Temporal Ecology Lab makes sure all take Wilderness First Aid and any other field courses for safety that trainees need. These general rules and the use of ISPs continue for lab work. Computational work and training is carefully shared and managed in the Temporal Ecology Lab, with trainees from undergraduate to PhD levels given training in data management, reproducible science and—for Masters, PhD and undergraduates who request it—training in Bayesian modeling. Wolkovich works hard to make sure computational approaches are available to all in the lab, not just the trainees who *think* they can learn such approaches (which is often a biased group) through courses she offers, regular lab meetings focused on a shared computational tasks and inviting visitors who specialize in leveling the playing field for computational ecology.

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, and other life commitments while also giving them a robust opportunity for collaboration, team science and training. Depending on the exact members of the lab, this often means working out meeting schedules well in advance, carefully choosing locations and activities that are inclusive for all. 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. While both labs are an active work-in-progress towards a more inclusive and equitable system in academia, both PIs efforts towards this are clearly recognized: Wolkovich currently serves on the Steering Committee for Harnessing Diversity in Data Science and Hille Ris Lambers ... XX

References • Use this section to provide a list of the most relevant literature references. Do not refer readers to websites for additional information on your proposal. Do not introduce hyperlinks in your list of references. • These pages are not included in the page count.