

# Why Pollen-Atmosphere Interplay Matters to Forest Gene Conservation<sup>1</sup>

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Forests are thought to adapt too slowly to anthropogenic climate change, making them highly vulnerable to large-scale loss. Losses can accrue swiftly because generations are lengthy, particularly at higher latitudes (>23° to 73°) where wind-pollinated forest species are commonly found to mature slowly. Losses incurred during adaptation to climate change translates into less allelic richness, or genetic diversity, and one can expect some resilience on this point because forests have more genetic diversity than other seed plants and this feature has shaped the forest fragmentation paradox debate (Bacles and Jump 2011, Kramer et al. 2008, Lowe et al. 2015). These great reservoirs of genetic diversity in forest trees have an overlooked dimension: temporal layering.

To explain temporal layering of genetic variation, consider that a given pollen pool is available to any year's cohort of ovules is shaped by weather conditions during pollen release, transport and deposition (Box 1). Seed and pollen dispersal occurs on far greater distances than once thought (e.g., Ehrlich and Raven 1969, Williams 2017). Seed from that one ovular cohort will thus have an allelic composition distinct from other cohorts. Shaped by weather conditions occurring pollen release, transport and deposition, the pollen pool is a function of certain atmospheric events<sup>3</sup> (Lanner 1966).

Atmospheric turbulence is the prevalent delivery system for wind-delivered forest tree pollen. Turbulence refers to a continuous succession of gusts, swirling eddies and lulls accompanied by swift changes in wind direction or advection. Turbulence is a product of atmospheric motion systems which wax and wane with the seasons. Examples of these systems include low- and high-pressure weather systems, turbulent large-scale eddies and land-sea circulations (Liu 2007 pages 3 to 5). Together these converge into unique atmospheric events during a given year's pollen season which in turn disperse

## Box 1. The pollen-atmosphere model proposed by Lanner (1966)

The pollen-atmosphere interplay model proposed by Lanner (1966) considers the pollen pool for each annual seed cohort, not adult populations. For example, one year's pollen pool might be composed of many long-distance pollen parents. The next year's pollen pool might be composed of a few local pollen parents. The third year's cohort might have a large yet equal composition of local and long-distance pollen parents. This year-to-year variation corresponds to specific set of atmospheric events. One year had dry gusting winds which favored long-distance pollen transport. The next year had steady winds punctuated by afternoon rain showers which scoured pollen out of the atmosphere. The third year had gusting winds with a rare rainstorm. This is part of the reason that the magnitude of gene flow between any two populations is poorly correlated with distance.

pollen grains vertically and horizontally through the atmosphere. This is simply described by Lanner (1966) who wrote: "...forest trees and other perennial seed plants have genetic diversity patterns shaped by annual meteorological events."

Together with pollen phenology, atmospheric events specific to the interval of pollen release shape genetic diversity from one year to the next for a given year's seed cohorts (Box 1). These temporally-layered seed

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<sup>3</sup> A forest tree population's entire life cycle, not only standing forest, is the unit of *interactive* response to rapid climate change. Considering the diplohaplontic life cycle of these long-lived perennial seed plants shapes how general circulation models (GCM) can be linked to forest ecosystems for climate change forecasting.

cohorts contribute to the next sporophyte generation. Any one seed cohort is shaped by that year's pollen pool, not spatial distances between standing adult populations (Box 1). Taking this further, we can hypothesize that a paternity analysis of one single year's seed cohort will reflect more closely the true genetic structure than measuring the horizontal distance between two adult populations.

Next, let us consider how this cohort-level concept behind the pollen-atmosphere interplay model fits with traditional population genetics models. Traditionally, genetic properties of a population are assigned to a group of reproducing adults, i.e. a population or a collection of populations. In our new model (Box 1), genetic properties are ascribed instead to each annual seed cohort.

First, each year's seed cohort from a forest population is assigns its own level of genetic variation. Second, effective population number is now indeterminate, changing from one year to the next (Lanner 1966). Third, dispersal and potential gene flow could be correlated with regional atmospheric events occurring during pollination. Might this explain the structure of genetic variation more than geographical separation between two adult populations? Testing this hypothesis for gene conservation programs of higher-latitude wind-pollinated forest species is the next step for testing the pollen-atmosphere interplay model.

In closing, temperate forest species are long-lived, perennial and wind-pollinated, all of which are life history features distinct from the short-lived animal and plant model species used to develop Sewall Wright's isolation-by-distance theory (Wright 1943). This dimension can be envisioned as a temporal layering of genetic diversity into temperate forest species. Could genetic variation within a forest population have an overlooked temporal dimension which is shaped by year-to-year atmospheric events during pollination? Implicit to the pollen-atmosphere interplay model is how much depends on how much effective gene flow actually takes place. To this end, one must test patterns of genetic variation and gene flow among annual seed cohorts for a given set of populations.

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