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WORKSHOP ON PLANT DISPERSAL AND MIGRATION MODELING

Final Report

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Abstract

Global environmental change is causing shifts in the geographical locations of habitats suitable for particular plant species. While it is established that the future distributions of plant species will be strongly influenced by the ability of plants to migrate to sites of suitable habitat, our ability to predict potential and actual migration rates is rudimentary. This workshop organized by the Global Change and Terrestrial Ecosystems (GCTE) core project of the International Geosphere-Biosphere Program provided scientists with interests and expertise in global change and plant migration with a forum for developing a new collaborative synthesis of understanding on long distance dispersal and migration modeling. This grant from the U.S. Department of Energy, Office of Biological and Environmental Research, provided partial support for the workshop by supporting the participation of U.S. scientists.

Rationale

Global environmental change is causing shifts in the geographical locations of habitats suitable for particular plant species (Davis and Zabinkski 1992). While it is established that the future distributions of plant species will be strongly influenced by the ability of plants to migrate to sites of suitable habitat (Pitelka et al. 1997), our ability to predict potential and realized (as influenced by habitat fragmentation and habitat loss) migration rates is rudimentary. A work group organized by the Global Change and Terrestrial Ecosystems (GCTE) core project of the International Geosphere-Biosphere Program has been tasked with developing capacity to predict plant migration rates in the context of global change. The group aims to (1) improve our empirical knowledge of long distance dispersal, (2) use empirically based dispersal functions to predict plant migration rates as influenced by landscape heterogeneity and (3) develop techniques for scaling up dispersal algorithms. It is the group's premise that these goals can be achieved by developing an intimate relationship between natural history knowledge, data, parameter estimation and modeling.

Capacity to predict potential migration rates has improved markedly recently (Clark et al. 1988, 1999). Although we now understand the processes that determine potential migration rates it should be noted that our empirical knowledge of these processes remains poor. This is because the great majority of quantitative dispersal studies have concentrated on local dispersal and have explicitly ignored the rare (< 5%) long distance (an order of magnitude greater than the modal dispersal distance) dispersal events that determine potential migration rates (Cain et al. in press). Most reports of rare long distance dispersal have been anecdotal. An immediate task is therefore to improve and synthesize our quantitative knowledge of long distance dispersal.

While progress has been made in developing techniques for predicting potential migration rates our ability to predict how habitat loss, fragmentation and other forms of environmental heterogeneity determine realized migration rates is poor. Most studies of migration in heterogeneous landscapes have been theoretical (e.g. Gardner et al. 1987), while empirical work has used microcosm systems (e.g. With et al. 1999). Both the theoretical and microcosm work have identified thresholds of landscape connectivity but more recent work has shown that these thresholds may not exist when rare long distance dispersal is considered (Higgins and Richardson 1999). It is clear that predicting the outcome of the often complex interactions between landscape heterogeneity and dispersal requires more work. Linking theoretical, microcosm and landscape perspectives into an operational framework for predicting migration rates will require creative and innovative work.

The workshop offered an opportunity for interaction between people with empirical and statistical perspectives on dispersal, as well as with modelers working at scales from the patch, to the landscape and to large regions or continents (see list of participants, Appendix 2). The workshop was held in Montpellier, France, on June 19-21, 2001. The workshop was sponsored by the U.S. Department of Energy, the U.S. Forest Service, the Electric Power Research Institute, and the Centre National de la Recherche Scientifique.

Specific questions
Six broad classes of issues appear of interest with respect to long distance dispersal and migration.

1. Methods to sample, analyze and model dispersal kernels
   - Necessity to edit a compilation ('recipe book') to advise new users
   - Comparison of estimates from different methods, e.g. different kernel estimation functions; genetic, paleo-ecological
   - Comparison of modeling approaches, e.g. mechanistic vs. phenomenological
2. Presently available long distance dispersal data:
   - How are they distributed? Geographically (e.g. temperate vs. tropics), across life forms (e.g. herbaceous vs. trees), across methodologies of estimation
   - What are the actual results, e.g. in terms of frequencies for given distances (conditional e.g. on location, plant type, method, etc.)?
   - What are the uncertainties?
   - What are the areas where progress in filling knowledge gaps or improving uncertainties is feasible in the short to medium term?
3. Is LDD related to species adult and/or seed traits? This encompasses a number of sub-questions:
   - Are there relationships between LDD and traits involved in the primary dispersal syndrome?
   - What are the evolutionary constraints on these traits and trade-offs among them?
   - What is the level of genetic variability in these traits, and its effect on LDD?
   - What are the links between LDD and species distribution range size (restricted vs. widely distributed)?
   - Do relationships depend on scale? (stop to apply at larger scale?)
   - If relationships between LDD and plant traits exist, how do these traits relate or not with those involved in response to environmental factors, or effects on ecosystem functioning?

4. Estimation of migration rates from dispersal kernels
   - Effects of fecundity and other life history traits on realized migration rates
   - Effects of habitat fragmentation or landscape heterogeneity: how much does it slow migration rates? Identify non-linearities if they exist.
   - Effects of the recruitment stage: competition from established vegetation
   - What is the best use for paleo rates, what are their limitations, how do they compare with present measured rates (e.g. invasions, range expansions), etc.?

5. Long distance dispersal
   - Will migration rates result in response lags and subsequent effects on ecosystem functioning (and services)?
   - Where will migration rates result in increased extinction risk?
   - Does migration matter when considering the life form level (e.g., plant functional types used in Dynamic Global Vegetation Models)? (i.e. it may be enough if one or a few species of the life form manage to migrate)
   - Need to break up life forms according to migration abilities?
   - Is long-tailed (phenomenological) dispersal across grid cell sufficient?
   - How important is within grid heterogeneity?

6. Communicating policy relevant results: results that convey and simplify what we know / don't know
   - What are the estimated risks posed by migration limitation, and what are the uncertainties about this message?
   - What aspects are more vulnerable? ecosystem function (e.g. carbon cycle) vs. biodiversity may not yield the same answer

Workshop Activities
The workshop focused on two activities, (1) synthesizing of quantitative data on long distance dispersal and (2) developing a conceptual and methodological framework for predicting migration rates at regional and continental scales.

Using life history and seed attributes to predict shapes of dispersal kernels

This working group compiled a database of published studies with the following objectives:

1. An evaluation of the depth and breadth of the existing data assessing where the data gaps are and where studies tend to fall short of presenting data that allow cross-comparison of dispersal kernels.
2. An analysis of how our various categorizing attributes of plants and studies relate to dispersal kernel parameters.
3. An analysis of the form of the dispersal kernel that best fits plants of varying attributes.

There is a growing literature on seed dispersal that may allow an assessment of patterns in the shapes of dispersal kernels. We are attempting to assemble a database of published studies to analyze patterns in seed dispersal kernels across a) methods of study, b) life history attributes, c) seed dispersal characteristics. Over 50 data sets were entered in the base at the workshop, and more are being sought by participants. Data were categorized according to whether a study recorded seeds versus seedlings; whether the data were frequency or abundance, the maximum distance sampled, the sample design (trap, or release,) the biome in which the plant grows and the dispersal vector (e.g., wind, animal, water). Attributes of species included propagule size, mass and morphology; plant growth form, height, longevity and fecundity; whether plants were able to resprout or maintain a seed bank; and the timing of seed release.

Initial analysis of the database will begin by fitting all data to 2Dt and generalized Weibull (exponential family) distributions in order to compare the parameters. Both dispersal kernels are two parameter models. We will use maximum likelihood models to obtain the best fit model for each species. Further analysis will utilize maximum likelihood to assess whether plants with varying attributes are fit more or less well by different types of curves.

We will attempt to reject the null hypothesis of no difference in dispersal kernels across plant and seed traits. We expect that propagule attributes should be strong predictors of seed dispersal. Surprisingly, there is relatively little evidence of these differences that are described through empirical data. We assess the literature in order to characterize the state of seed dispersal studies in order to better understand the breadth of data that has been collected and identify weaknesses in the current suite of ecological data (e.g., discover gaps in life histories of species).

Incorporating Dispersal in Forecasts of Global Vegetation Change

Future human-induced climate change may occur at a rate greater than any experienced in the past 10,000 years. The more rapid the climate change, the greater the potential for temporary disequilibria or permanent changes in ecosystem structure and functioning. The United Nations Framework Convention on Climate Change requires signatories to prevent "dangerous interference" with the climate system (defined broadly as that rate of change which will allow ecosystems to adapt naturally to climate change). Thus, it is critical to resolve not only how the terrestrial biosphere might be altered, but also how rapidly this could happen. Climate-induced changes in the biosphere could occur through potentially very rapid changes in the amount and function of vegetation and animal 'stocks', as well as through slower changes in species composition. Changes in species composition will proceed along two main paths, *in situ* conversion, that is, subdominant species replacing dominant ones, or via migration of species from distant locales. It is likely that *in situ* conversion will proceed more rapidly than off-site migration, but both will be important and must be understood at the planetary scale.

Ecosystem simulations under future climate scenarios suggest that the preferred ranges of many species could shift 10s to 100s of kilometers over only 50-100 years, nearly an order of magnitude faster than observed since the last glaciation. Differences in the capacities of species to migrate such distances could have large effects on the distribution, structure, and functioning of future ecosystems, and thus on the properties humans value. The most rapidly moving species could 'overtake' existing ecosystems; while, the least mobile species could be susceptible to being 'overtaken' and possibly out-competed into local or regional extinction.

Simulation-based forecasts of possible future conditions will help inform policy makers on the vulnerability of ecosystems and on how society should address climate change. However, globally applied models recognize only about 6 to 30 plant functional types (PFT), such as temperate deciduous broadleaf or tropical evergreen trees, to represent the more than 250,000 species of vascular plants already catalogued (and the additional 500,000 estimated to be undiscovered). These PFTs typically are combined to distinguish about 6 to 50 vegetation types for the entire Earth (e.g., Temperate Deciduous Forest or Tropical Savanna). Because of the extent to which such models must aggregate species into PFTs, only general implications for biodiversity can be inferred.

Among the newest large-scale ecosystem models are Dynamic Global (or General) Vegetation Models. They simulate ecosystem change over long time periods, on spatial grids of varying scales. Among the issues they include are: 1) changes in regional to global carbon cycling and sequestration; 2) ecosystem biophysical feedbacks to the climate system; and 3) changes in resources, such as timber and water and other features or services of natural ecosystems valued by society.

Since DGVMs are relatively new and not fully developed, we will examine the processes of plant migration and the challenges in their simulation. Perhaps the two most significant challenges in modeling long-distance migration are: 1) accurately estimating the frequency and distance of long-distance dispersal events and their success in establishing new vegetation communities; and 2) the conceptual problem of aggregating information from individual species into the 'metaphor' of plant functional types as simulated in DGVMs. Also, migration modeling must incorporate *in situ* vegetation change via complex successional shifts in dominance of local PFTs accompanied by rare long-distance, migratory PFTs.

Summary of Workshop Products

A brief summary of the workshop has been published in Trends in Ecology and Evolution as a Meeting Report: Ronce, O. 2001. Understanding plant dispersal and migration. Trends in Ecology and Evolution 16: 663-4.

The workshop activities will improve our ability to make statements about the proportion of floras that will not be able to migrate to sites of suitable environmental quality. A fast track paper is being prepared, comparing required and predicted migration rates in different floras dominated by different life forms

A joint publication using the LH-dispersal kernel meta-analysis will address will address the following questions:

- Does knowledge of seed morphology and local dispersal syndrome define the occurrence of rare long distance dispersal?
- Is the presence of long distance correlated with particular environment, life history combinations?
- What proportion of dispersal data sets examined exhibit evidence of rare-long distance dispersal?

- What distribution of migration rates is generated by migration models parameterized with the dispersal data sets examined?

The tools and protocols we use for the data analyses and guidelines for collecting appropriate data will also be summarized on a website to encourage and empower more work on rare long distance dispersal.

A synthetic paper is being prepared for Bioscience. The objectives of this paper are to outline:

- The challenges that have to be addressed in order to appropriately model species migration over large scales
- How present generic vegetation models could benefit from the growing knowledge about long distance dispersal, both through the accumulation of data sets and the insights into modeling methods.

Literature Cited

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Gardner, R.H., B.T. Milne, M.G. Turner, R.V. O'Neill. 1987. Neutral models for the analysis of broad scale landscape pattern. Landscape Ecology 1: 19-28.

Higgins, S.I. and Richardson, D.M. 1999. Predicting plant migration rates in a changing world: the role of long-distance dispersal. American Naturalist. 153: 464-475.

Pitelka, L.F. and the Plant Migration Workshop Group. 1997. Plant migration and climate change. American Scientist. 85: 464-473.

With, K.A. Cadaret, S.J. and Davis, C. 1999. Movement responses to path structure in experimental fractal landscapes. Ecology. 1340-1353.

Appendix 1 - Workshop Program

19 June		
Time	Author	Title
8h45-09h15	Lavorel	Welcome and introductions
09h15-09h45	Lavorel and Pitelka	Dispersal and migration in the GCTE context
09h45-10h30	Ron Neilson	The challenges of dispersal modeling in DGVMs
10h30-11h00	Tea Break	
11h00-11h45	Jason McLachlan	A paleo-ecological perspective of plant migration
11h45-12h30	Richard Dean, Sue Milton	Long distance dispersal tails from the Karoo, South Africa
12h30-13h15	Ophélie Ronce	Evolution of short and long distance dispersal: what do we know?
13h15-14h15	Lunch Break	
14h15-17h00	Pitelka, Lavorel and Higgins to facilitate	Group discussion, select working groups
17h00-17h30	Higgins and Clark	Software installation and data exchange
20 June		
Time	Author	Title
08h30-09h30	Martin Aguiar Mark Schwartz	Primary and secondary dispersal of grass seeds in the Patagonian steppe Predicting future tree migration under global change scenarios
09h30-10h30	James Clark	Tutorial: Inverse methods for dispersal parameter estimation
10h30-11h00	Tea	
11h00-12h00	James Clark	Tutorial continued
12h00-13h00	Working group activity	
13h00-14h00	Lunch	
14h00-15h30	Working group activity	
15h30-16h00	Tea Break	
16h00-17h30	Working group activity	
21 June		
Time	Author	Title
08h30-09h30	Heike Lischke Niklaus Zimmerman	Linking population dynamics, physiology and dispersal in regional migration models Multi-scale analysis of seed dispersal: calibrating a kernel from life history data of animals
09h30-10h30	James Clark	*Tutorial: From dispersal kernels to migration rates*
10h30-11h00	Tea	
11h00-12h00	James Clark	Tutorial continued
12h00-13h00	Working group activity	
13h00-14h00	Lunch	
15h00		CITY TOUR
22 June		
Time	Author	Title
08h30-09h30	Ken Thompson Jerome Chave	Catching dispersing seeds in the act Long-distance dispersal and the species composition of ecological communities: lessons from a neutral model
09h30-10h30	Eric Imbert	Tutorial: MIGRATE, a program for calculating dispersal distances from molecular data
10h30-11h00	Tea	
11h00-12h00	François Rousset	Tutorial: Limitations of estimation methods of dispersal parameters from Genetic data
12h00-13h00	Working group activity	
13h00-14h00	Lunch	
14h00-15h30	Working group activity	
15h30-16h00	Tea Break	
16h00-17h30	Working group activity	

23 June		
Time	Author	Title
08h30-09h30	Guy Midgley Steve Higgins	Dispersal syndromes, bioclimatic ranges and the moderating role of persistence traits - early indications from the western Cape, South Africa How plants might migrate in heterogenous landscapes
09h30-10h30	Ran Nathan	Tutorial: Aerodynamic models of seed dispersal
10h30-11h00	Tea	
11h00-13h00	Working group activity	Working group reports and wrap up
13h00-	Lunch	

Appendix 2 - Participant list

Name	*Institution*	*Country*	*email*
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