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Ecological scaling of aerobiological dispersal processes

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Abstract

A variety of organisms change their geographic locations during their life history, and many use the atmosphere to accomplish this shift. Biota that flow in the atmosphere range from very small (viruses, bacteria, pollen, and spores) to quite large (weed seeds, aphids, butterflies and moths, songbirds, and waterfowl). As these organisms move, they experience meteorological and ecological conditions that occur at a wide range of spatial and temporal scales. We present an ecological scaling approach that integrates concepts and elements of spatial and temporal scaling to understanding aerobiology and provide examples of the ecological scales important to the long-distance aerial movement of organisms and associated biological events and processes.

An operational framework for ecological scaling of long distance biota movement is achieved by linking spatially-static ecoregion classification systems with temporally-dynamic measures of vegetation phenology. The ecoregions provide ecological boundaries for the phenological dynamics of plants. Operationally, this approach integrates the bi-weekly vegetation greening indices (NDVI) derived from AVHRR or TM satellite data (representing temporal scaling) with the less dynamic land cover–land use classification (IGBP) and the relatively static ecoregion boundaries (representing the spatial scaling). We argue that the correlation of the life histories of species, especially the timing of take-off, to ecosystem phenology through meteorological-based variables and indices (e.g., degree days and moisture indices), allows for dynamic characterization of source ecosystems and can be used to parameterize atmospheric models to forecast the flow of biota in the air.

The scale of these processes, the diversity of the types of biota involved in long-distance movement, and the complexity of the processes require systems thinking. We anticipate that this paper will stimulate studies to enhance our understanding of the flow of organisms in the biosphere.

Keywords: Aerobiology; Long-distance aerial movement; Migration; Dispersal; Scale

1. Introduction

Almost all organisms move from one place to another place at some time during their life. For some organisms, movement occurs within a habitat, while for others, long-range movement is an essential element in their life history. The majority of terrestrial organisms that move long distances use the atmosphere as their transport medium (Dingle, 1996). It is important to monitor aerial flows of biota and the important consequences of these movements as we develop new strategies to understand and manage the diverse natural and human-modified environments. A sound understanding of the biological and meteorological interactions that govern the movement of organisms in the atmosphere is a prerequisite to developing innovative and successful strategies for protecting human health and for sustaining a large number of

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terrestrial ecosystems. This is because many biota, some indigenous to receptor ecosystems and others exotic, that are known to afflict human health and production systems move long distances through the atmosphere. In addition, the inflows and outflows of organisms to and from ecosystems can be as important as their birth and death rates in regulating the dynamics of populations within both natural and human-built environments. Recent improvements in entomological radars (Drake, 1993; Riley, 1993) and remote sensing of the Earth's surface (Field et al., 1995; Robinson, 1995) have improved our capability to identify many of these aerobiota (e.g., large insects and birds) and make long-term quantitative monitoring of the atmospheric flow of some organisms practicable and cost-effective (Reynolds and Riley, 1997; Drake et al., 1998).

The typical components of long distance aerial movement include taking off and ascent, horizontal transport along an atmospheric pathway, and descent and landing (Drake et al., 1995). The primary external controls that influence the movement process are organism population, weather systems that trigger and facilitate the dispersal of the organism population, and the ecosystems involved in the process. Different organism population traits, including morphological, biochemical, physiological, and behavioral, influence long-range dispersal phenomena (Johnson, 1969; Dingle, 1972; Drake et al., 1995). Manifestations of these traits depend on environmental cues that provide information about changes in their current habitats, thus fostering organism movement to other places (Wilson, 1995). In most cases, changes in the habitat are due to the effect of weather. Seasonal changes in temperature, precipitation, and day-length are the main factors which cause organisms to migrate in an attempt to populate suitable habitats or escape from habitats before unfavorable conditions appear (Johnson, 1995; Pedgley et al., 1995). Among the weather factors, wind and convection favor dispersal by providing transportation for large numbers of aerobiota (Drake and Farrow, 1988; Johnson, 1995; Pedgley et al., 1995). A key component in the migration process is the ecosystem (or ecosystems) involved before, during, and after dispersal occurs. The take-off and a successful landing will likely occur in ecosystems to which the organisms are functionally adapted. Unless the movement of organisms is local, the condition of the ecosystem where take-off occurs and the condition of the ecosystem where landing takes place may be different. Many organisms that move long distances in the atmosphere also move locally within source and destination habitats. A spatial and temporal framework is necessary to understand the dynamics of organisms that move long distances and especially those that shift the scale of their movement during their life cycles. This poses an important challenge for researchers in the field of aerobiology. It requires a truly multidisciplinary approach including the participation of scientists with biological, meteorological, and geographical expertise. Because aerobiology encompasses a broad range of organisms (birds, insects, viruses, bacteria, pollen, and seeds), practitioners need to be able to recognize the range of scales at which processes and events impact these organisms. In addition, an understanding of the ecological and meteorological processes that operate at the different scales and impact the population dynamics of aerobiota is required. Current technology enables researchers to increase the scope of aerobiological studies to cover the entire population dynamics of organisms that engage in long-distance movement and presents researchers with the challenge of adopting an ecological hierarchical framework.

In this paper, we provide a perspective on ecological scaling that allows an enhanced comprehension of the long-distance movement process. Furthermore, we discuss how to integrate remote sensing technology with ecological region classification to achieve ecological scaling for the study of aerobiology.

2. The concept of scale for the study of long-distance dispersal of biota

Scale refers to the size of a phenomenon both in time and space (Allen and Hoekstra, 1992). An object or event is large-scale if perceiving it requires observations across large areas or over long time periods. Generally, the more heterogeneous a phenomenon, the larger its scale (Allen and Hoekstra, 1992; Wiens, 1989). The determination of the appropriate scale for studying a phenomenon is highly influenced by the perspective of the observer. Often the human perception of time and space is different from that of the organisms under study (Allen and Hoekstra, 1992; Wiens, 1989; Wiens and Milne, 1989), particularly when such studies involve highly mobile organisms (Isard et al., 1991; Taylor, 1989). An important consideration in aerobiological studies is the correspondence between temporal and spatial scales (Levin, 1992; Wiens, 1989). A mismatch between the temporal and spatial dimensions can lead to misinterpretation of the movement phenomenon. Long-term observations in a small area may exhibit high variability resulting in an inability to distinguish between system patterns and system noise. On the other hand, short-term observations over a large area often result in imperceptible changes (Wiens, 1989).

2.1. Temporal (phenological) scale

Phenology is a state within a sequence of growth stages of the development of an organism. These stages are recurring biological events whose timing is regulated by biotic and abiotic forces (Lieth, 1974). However, phenology of poikilothermic organisms is largely regulated by temperature and thus is predictable. The movement of organisms over long distances is influenced by their own growth as well as changes in the development of their hosts at their geographic source and destination. Therefore, phenology becomes a valuable indicator of organism characteristics (both aerobiota and their hosts) and can aid in the examination of the response of migrant populations to changes in ecosystems at different temporal and spatial scales.

Communities of organisms within a spatial unit at any moment in time are at different stages in their life histories. However, the stages of development or phenological state of many species may be intimately related. For example, the general phenological stages that most plants transition through include emergence, early vegetation, late vegetation, flowering, fructification, and senescence (Fig. 1). Animals that depend on vegetation during their lifetime have evolved such that their phenological stages are synchronized with those of the plants they exploit. Moreover, the rates at which plants and animals in an ecosystem progress through their phenological sequences are linked because variations in phenology are governed largely by weather conditions. For example, a warm spring will hasten the development of many plants and animals within an area while an early frost may result in widespread senescence. From the perspective of a scientist studying the long-distance movement of organisms, two temporal scales at which the seasonal progression of temperature and moisture conditions can impact the phenology of vegetation within a geographic area are of primary importance: intra- and inter-annual. Intra-annual changes in ecosystems, generally observed at weekly or monthly intervals, are influenced by latitude, position on the continent, and elevation. At this scale, the most evident phenological changes on midlatitude landmasses are due to changes in leaf biomass (Plate 1A). Since the seasonal progression of temperature and moisture varies with latitude, the quantity of leaf biomass at different latitudes also varies. In spring and fall, we observe a gradient of greening from the southern to northern United States (Plate 1A). Because the movement of organisms from one geographical area to another can occur within intervals of one week or less, it is imperative that take-off is 'ecologically timed' so there is a high probability of a successful landing in a geographic area with vegetation at the appropriate phenological stage.

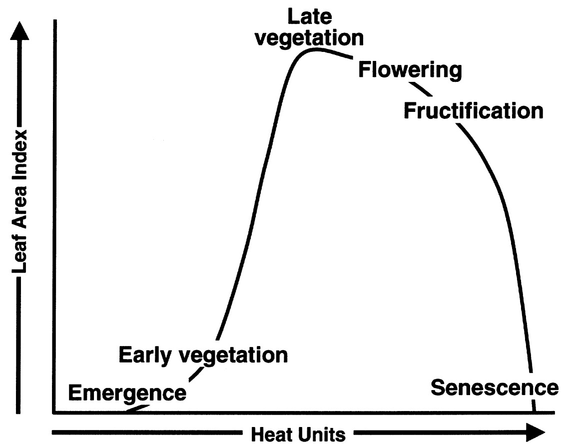
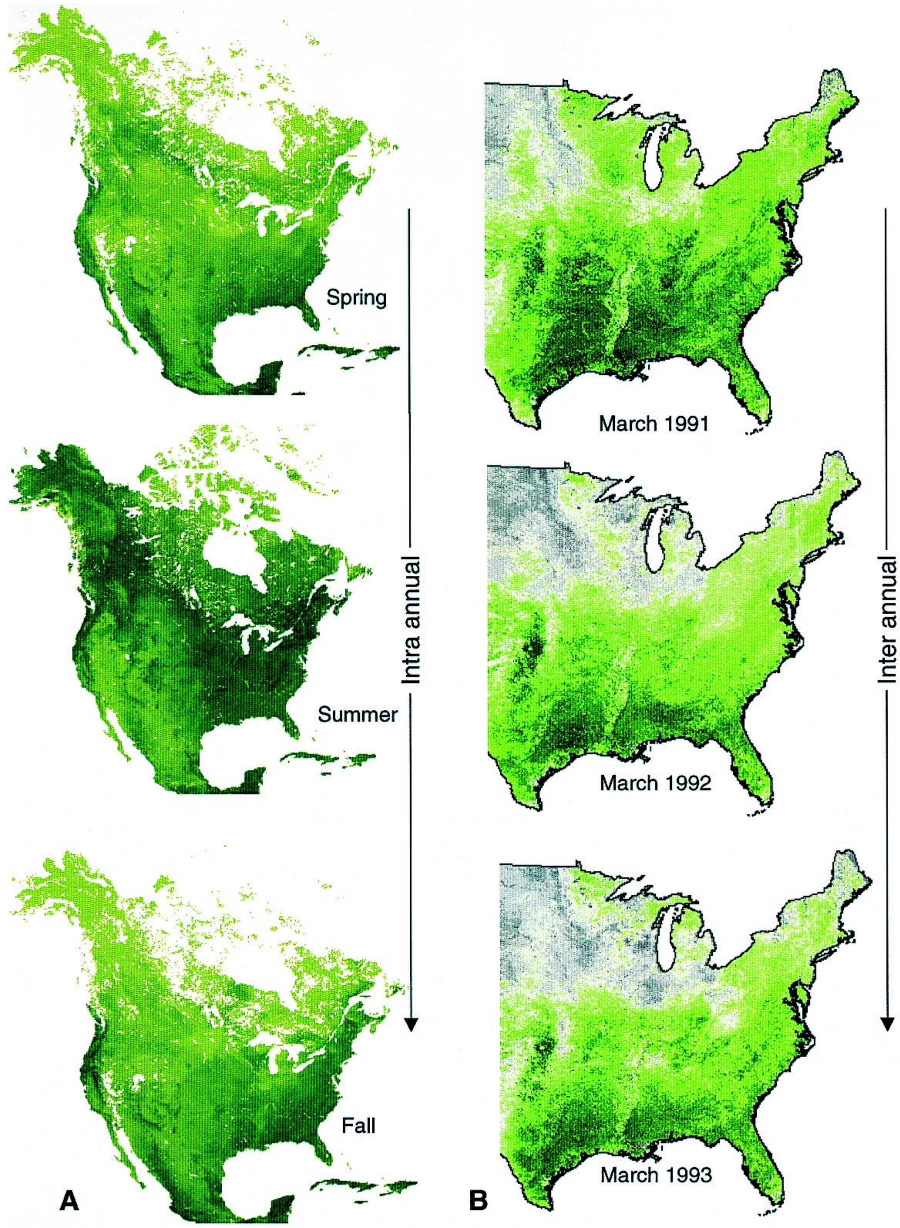


Fig. 1. Representation of the phenological stages in foliage growth of higher plants as measured by the leaf area index shown as function of accumulated heat units.

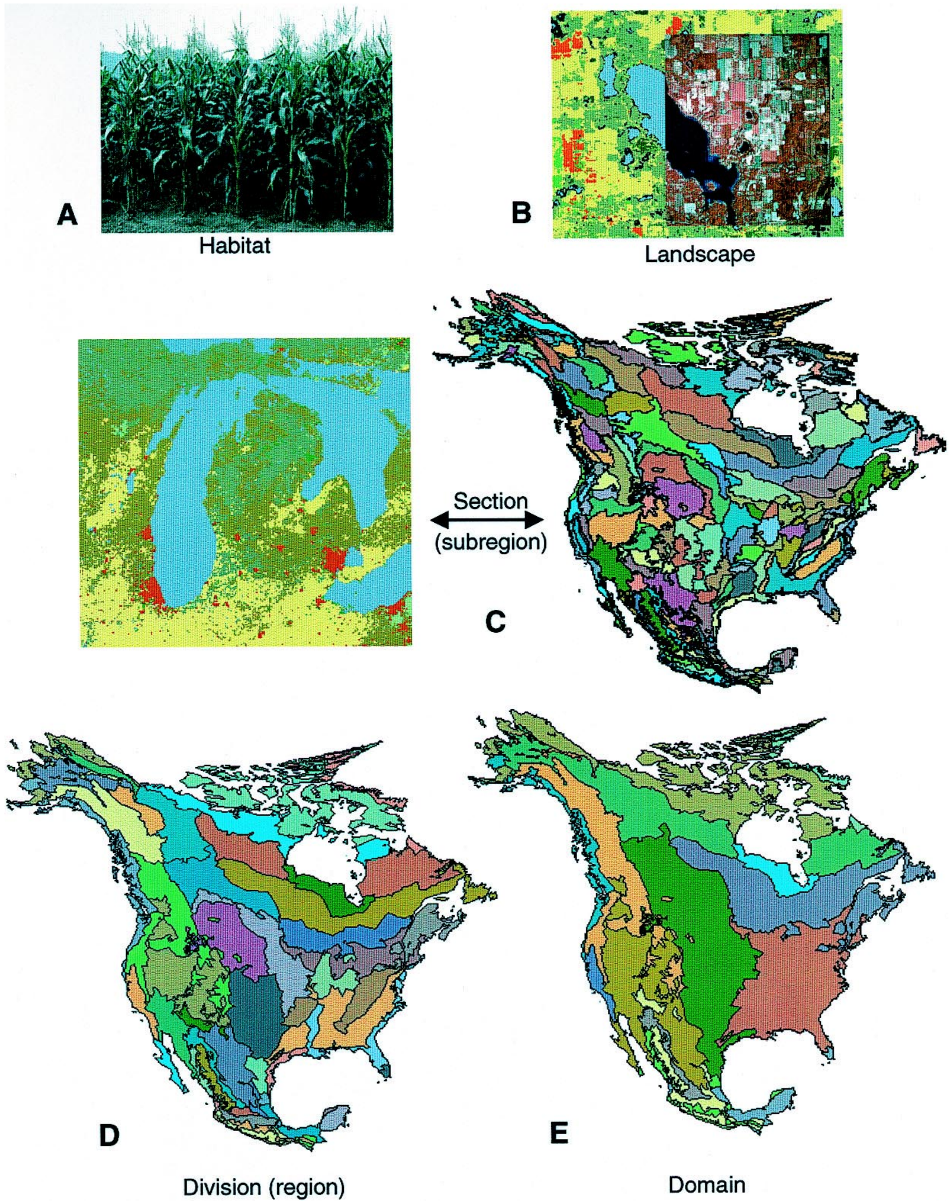
Large-scale human modification of vegetation at landscape scales has increased the synchrony of phenological development in a wide range of organisms. For example, the simultaneous planting of crops in monocultures throughout large portions of the North American continental interior (Corn Belt) has synchronized the life stages of most agricultural pests and their



A, Maps of greening index representing phenological states of vegetation communities within North America for Spring, Summer, and Fall (i.e., depicting intra-annual variations in ecosystem dynamics). B, Maps of greening index representing phenological states of vegetation communities within North America for March 1991, 1992, and 1993 (i.e., depicting inter-annual variations in ecosystem dynamics).

predators. Many organisms move long distances in the atmosphere to exploit these abundant but ephemeral resources, and to survive, some must move again at the end of the growing season to overwintering habitats (Southwood, 1962).

While the intra-annual changes in phenology follow seasonal changes in weather, inter-annual changes are due to the year-to-year variability in climate when the seasonal transitions in large-scale circulation patterns occur earlier or later than normal and as a result of



Hierarchical geographic scaling system useful for studying the flow of organisms in the atmosphere. A, Habitat – animals move from plant to plant (digital photograph). B, Landscape – organisms move from habitat to habitat (aerial photography (red image) at $1\,m^2$ resolution or Thematic Mapper satellite imagery (background) at $30\,m^2$ resolution). C, Section (or subregion) – organisms move longer distances (habitats are indistinguishable and only general patterns of land cover can be determined using AVHRR satellite imagery at $1\,km^2$ resolution and the highest resolution level in the Omernik (1987) ecoregion classification system). D, Division (or region) – organisms move long distances (intermediate resolution level in the Omernik (1987) ecoregion classification system), and E, Domain – continental migrations of organisms (course resolution level in Omernik (1987) ecoregion classification system).

extreme weather conditions. Warm temperatures in spring in high latitudes, for example, may cause early greening of the vegetation, whereas cold temperatures may delay it. For instance, the Great Lakes states exhibited different degrees of greening during early spring in 1991, 1992, and 1993 (Plate 1B). However, the degree of greening of the vegetation in states bordering the Gulf of Mexico remained relatively constant during this period. Organisms that initiated long-distance aerial movement from the Gulf Coast states and landed in the Great Lakes region during March 1993 arrived in habitats with vegetation that was less advanced than those that made the same trip in March 1991.

Long-term monitoring of landscape greening as an indicator of vegetation phenology can be a valuable resource for tracking changes that occur at intra- and inter-annual time scales. It provides a means for better understanding of the seasonal dynamics of migratory populations in relation to ecological conditions in their habitats. Moreover, long-term monitoring allows the detection of extreme events that occur at large temporal scales and that can induce unusual and unexpected mass movement of organisms in the atmosphere. Many populations of animals do not move from their habitats until the ecosystem is under severe stress (Unganai and Kogan, 1998). For example, the migratory grasshoppers in the grasslands of North America have not entered a migratory phase since the 1930s. This is because conditions within the grasslands have not allowed populations to reach high enough levels to cause ecological stress that is sufficiently severe to induce long-distance movement of grasshoppers in search of ecosystems more appropriate for their survival.

2.2. Spatial (geographic) scale

Population stress due to environmental exigencies can increase the readiness of organisms to move (Southwood, 1962; Tauber et al., 1984). Habitat diversity, variations in soils, surface water abundance and quality, and the quantity and distribution of nutrients can modify an organism's responses to population stress as well as to adverse weather conditions. Stress affects an organism's phenology and the likelihood of initiation of dispersal and a successful outcome. The presence of adjacent habitats within a geographic area that can supply organisms with abundant resources for development during the growing season and habitats suitable for overwintering may make long-distance movement for a species unnecessary. At higher latitudes, however, extensive regions become inhospitable for many organisms with the onset of the cold season, making migration to more suitable regions imperative.

Geographic units form a hierarchy of interacting elements that range from habitats, landscapes, sections (subregions), divisions (regions) to domains on continents (Plate 2A–E). Ecosystems are considered functioning units in nature consisting of biological communities and their associated abiotic environments, and hence they are not fixed geographic units (i.e., they could involve many habitats and landscapes). The habitat is generally considered the smallest unit in hierarchical geographic scaling schemes. The meaning and size of habitat when applied to plants as opposed to animals, and among different species of animals, varies because of their respective relative scaling in time and space (Allen and Hoekstra, 1992). For organisms that move long distances in the atmosphere, it is appropriate to designate an area the size of the animal's range or the size of a plant community prior to movement as the source habitat and the area the size of its range or community after movement as the receptor habitat. Because it is more practical to map vegetation patterns than animal ranges, plant communities are generally used to delineate habitats, although many animals cross plant community boundaries in their daily activities (Allen and Hoekstra, 1992). Natural landscapes, commonly delineated by landforms (e.g., river basins and mountains) and soils, are composed of ecosystems interconnected by corridors through which biota freely move. Generally, the topography and the types and arrangement of surface cover units within a landscape exert considerable influence over how the seasonal variation in temperature, precipitation, and wind impacts local ecosystems and populations (Drake and Farrow, 1988). In most cases, however, long-distance movement of organisms encompasses a geographical area that extends beyond the landscape. Ecological regions, or 'ecoregions,' are relatively large geographical areas of 'relative homogeneity with respect to ecological systems involving interrelationships among organisms and the environment' (Omernik, 1995). There are two common hierarchical classifications of ecoregions (Omernik, 1987; Bailey, 1996) that can provide a scalable spatial framework for studying long-range transport of organisms. Here we use the terminology, section, division, and domain, popularized by Bailey (1976, 1996, 1998), for the higher levels in the hierarchical geographic classification system. The ecoregion schemes are especially useful because they provide the potential to link the biology of migratory organisms to ecological factors that influence movement at different spatial scales. For instance, coarser ecoregion units in Bailey's classification (domains) were identified primarily based on climatic conditions and natural vegetation. Delimitation of sections, the smallest ecoregion unit in Bailey's classification, is based on vegetation and geomorphology. In the Omernik's classification, the three levels of ecoregions were derived from climate, geomorphology, soil, vegetation, wildlife, and water. Scaling up and down using ecoregions can be a useful framework to characterize and delimit ecological conditions of the smaller landscapes and habitats of importance during the long-range movement process (see Plate 2). For instance, using the finer resolution of ecoregion levels can provide the ecological boundaries for the take-off and landing sites of migratory organisms. On the other hand, the use of the ecoregion level at coarser resolution can allow the characterization of the ecosystems beneath atmospheric pathways. These classification schemes are readily available in digital format, and efforts are underway to further subdivide them and provide a finer scale of resolution (Omernik, 1995).

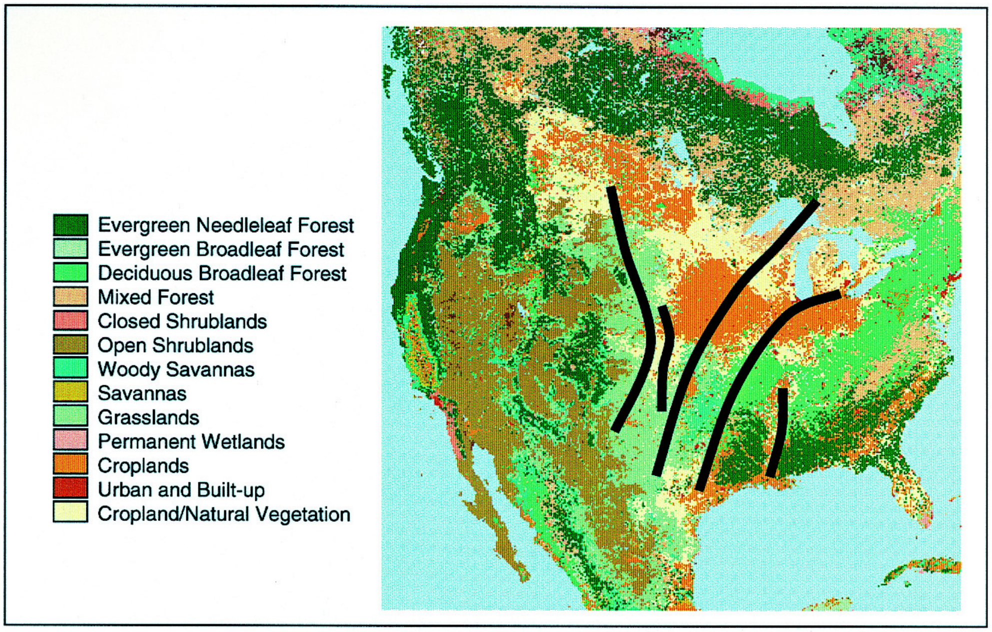
3. Remote sensing measurement of temporal and spatial changes in ecological characteristics of geographic units

Remote sensing can assist in the measurement of ecological information (based on electromagnetic radiation) from large areas of the Earth. (Field et al., 1995; Robinson, 1995). The satellite-mounted Advanced Very High Radiation Radiometer (AVHRR) provides digital images of the Earth that extend 2399 km and have a resolution of 1 km^2 (Eidenshink and Faundeen, 1994). An index of phenology can be computed using a combination of visible and infrared channels on the sensor to produce a plant greening index called the Normalized Difference Vegetation Index (NDVI) (Goward et al., 1991). Due to the large geographic scale and the high frequency of the observations, these data provide a useful phenology index to characterize the vegetative greening of geographic units ranging in area from landscapes to domains at time intervals from days to months (see Plate 1A and B; Johnson and Gage, 1997). This includes the change in phenology that occurs in the geographic areas of take-off, the state of phenology beneath the region of atmospheric transport, and the geographic areas of deposition at scales appropriate for each. The use of indices such as the NDVI can facilitate the study of the interactions between vegetation changes and animal populations (Robinson, 1995).

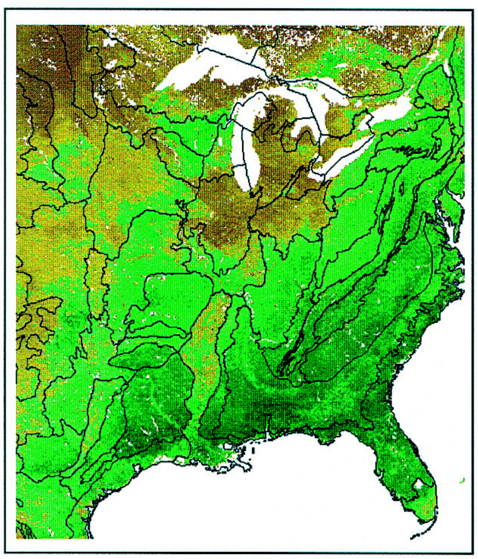
Another advantage of remote sensing in ecological assessments is the identification of major land cover-land use types (Nemani and Running, 1997). Land cover classification with high-resolution imagery (TM) also can be used for studies of long-distance movement of biota. TM images have an extent of 185 km and a resolution of 30 m. However, when studying the ecosystems throughout an atmospheric corridor used by organisms during long-distance movement, it is usually more appropriate to use land use classifications determined from satellite imagery with less resolution (e.g., AVHRR) but with a larger extent. For example, the study of a species that moves from a southern overwintering habitat to an agricultural area in the northern latitudes of North America would require an order of magnitude more TM than AVHRR images. A very useful example of a land cover-land use classification is the IGBP Classification with 1 km resolution (Plate 3A, Belward, 1996). Global and regional information related to different land cover-land use classification schemes are in the public domain at the Earth Resources Observation Systems (EROS) Data Center Distributed Active Archive Center (EDCDAAC).

4. Integration of space and time scales.

There is an array of organisms that use the atmosphere to traverse from source to receptor geographic units. The Canada goose, potato leafhopper,



A



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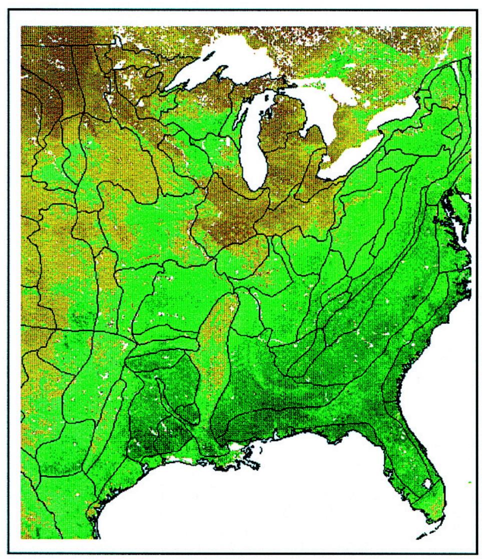

C

A, Land cover-land use patterns in North America based on the IGBP classification. Black lines show the pathways used by aerobiota to move between the Gulf Coast states/Texas and the continental interior of the continent. B and C, Spatial distribution of vegetation greening in the eastern portion of the US in relation to ecoregion boundaries from the Omernik (A) and Bailey (B) classification schemes. Darker (greener) areas represent greater biomass as measured by the Normalized Difference Vegetation Index (NDVI).

Table 1
Temporal and spatial scales observed in the ecological and meteorological systems and sources of ecological variation in the timing of aerial movement of biota. Overlapping of the meteorological system with two or more ecological system scales occurs at the meso and macroscales

Temporal and spatial scales		
Meteorological System (Westbrook and Isard, 1999)	Ecological System	Biological Events and Processes
Macroscale (>weeks; $>10^3$ km^2; e.g., long waves in the westerlies, monsoon flows, trade-winds, migratory cyclones and anticyclones)	Continents (years-centuries; 10^7 km^2)	Evolution and movements of plants and animals that determine the distribution of life on Earth. Climate, landforms, and soils primarily determine the types of flora and fauna that inhabit the continents.
	Domains (weeks - months; 10^3–10^4 km^2)	Inter-annual variations in the seasonal phenology in biotic domains that are primarily governed by fluctuations in patterns of ocean circulation and climate.
	Divisions (regions) (days–weeks; 10^2–10^3 km^2)	Life histories (progression from one phenological stage to the next) of the assemblages of plants and animals in divisions that are influenced by the seasonal shifts in major atmospheric circulation features.
Meso (minutes–weeks; 1–10^3 km^2; e.g., hurricanes, fronts, low-level jets, sea-breezes, mountain-valley breezes, and thunderstorms)	Sections (subregions) (hours–days; 10 s–10^2 km^2)	Development within phenological stages of plants and animals in sections. The rate at which organisms within a particular phenological stage (e.g., egg or adult) develop is influenced by the daily weather.
	Landscapes (minutes–hours; 1–10 km^2)	Phenological development of plants and animals within landscapes as influenced by daily weather modified by the physical features and biota of the landscape.
Micro (seconds–minutes; 1 mm^2–1 km^2; e.g., thermals and turbulence)	Habitats (seconds–minutes; <1 km^2)	Physiological processes of plants and animals within habitats (e.g., respiration and cell growth). The physical and biological features of a habitat strongly influence air movement and horizontal and vertical gradients of atmospheric variables

black cutworm moth, monarch butterfly, cedar-rust fungus, and ragweed pollen represent organisms that use different movement strategies. The temporal scales of ecological phenomena that influence aerial movement of biota range from fractions of seconds to millennium. The spatial scales can range from leaf parts to continents. Because in aerobiology, the organisms of interest move in the atmosphere, the time and space scales associated with atmospheric motion systems (see Westbrook and Isard, 1999) are also important to the outcomes of the movement processes. The correspondence among geographical and meteorological scaling systems and the sources of ecological variation that impact the flow of organisms in the atmosphere are provided in Table 1.

Our approach to ecological scaling of long-distance biota movement is through developing the linkage between spatial ecoregion characteristics and temporal vegetation greenness which is correlated to temperature and moisture patterns and thus phenological events at landscape mosaic scales. This approach integrates the highly dynamic vegetation indices (e.g.,

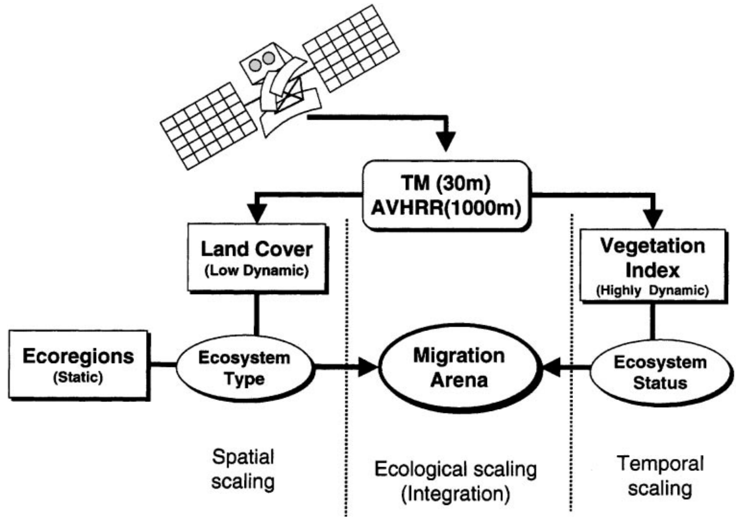

Fig. 2. Conceptual model of the ecological scaling process that integrates highly dynamic vegetation indices with less dynamic land cover-land use and relatively static ecoregion classification systems.

NDVI at bi-weekly resolution) derived from AVHRR or TM satellite data (representing temporal scaling) with the less dynamic land cover-land use (IGBP) classification and the relatively static ecoregion (e.g., Bailey or Omernik) boundaries (representing the spatial scaling) (Fig. 2**)**. The Ecoregion hierarchical classifications (Omernik or Bailey) can be used to define source and receptor areas in North America, whereas the IGBP land cover-land use classification can be used to refine the ecoregions to match aerobiota habitat preferences. A second step can include the dynamic characterization of source/receptor geographic units using phenological information at the landscape mosaic scale. Use of bi-weekly AVHRR imagery can establish the temporal phenological (greening) characteristics within each of the geographic units. The life history of target species can be linked to ecosystem phenology using meteorological-based variables and indices (e.g., degree days and moisture index). This will involve correlating life history data of organisms that move in the atmosphere with historical greening data sets characterizing source/receptor geographic units. To determine active source geographic units for target organisms, it will be necessary to estimate the time when a target organism initiates aerial movement based on knowledge about the biology of the organism in question including life stage relationships to degree-day accumulations, phenological estimates from ground weather observation stations (daily max, min), and bi-weekly AVHRR greening index for each ecoregion. Plate 3 (B and C) illustrates the high degree of correspondence between patterns of spring greening in the Mississippi River valley and the section (subregion) boundaries from the Omernik (Plate 3B) and Bailey (Plate 3C) ecoregion classifications. The correlation of life histories of aerobiota, especially the timing of take-off, to ecosystem phenology through meteorological-based variables and indices (e.g., degree days and moisture indices) allows dynamic characterization of source ecosystems. Phenological criteria can help define the set of habitats with suitable hosts in appropriate phenological stages for target organism utilization and colonization. In addition, this approach can be used to determine the receptivity of source/receptor geographic units for the aerobiota and the subsequent survivorship of the immigrants. The resulting information on source location and strength can be used to parameterize atmospheric flow models (e.g., HYSPLIT4 Model, 1997) to forecast the flow of biota in the air (e.g., Main et al., 1998; Levetin et al., 1998).

Maps of the seasonal breeding zones of black cutworm (*Agrotis ipsilon*) moths within the United States (Showers, 1997) illustrate the utility of using

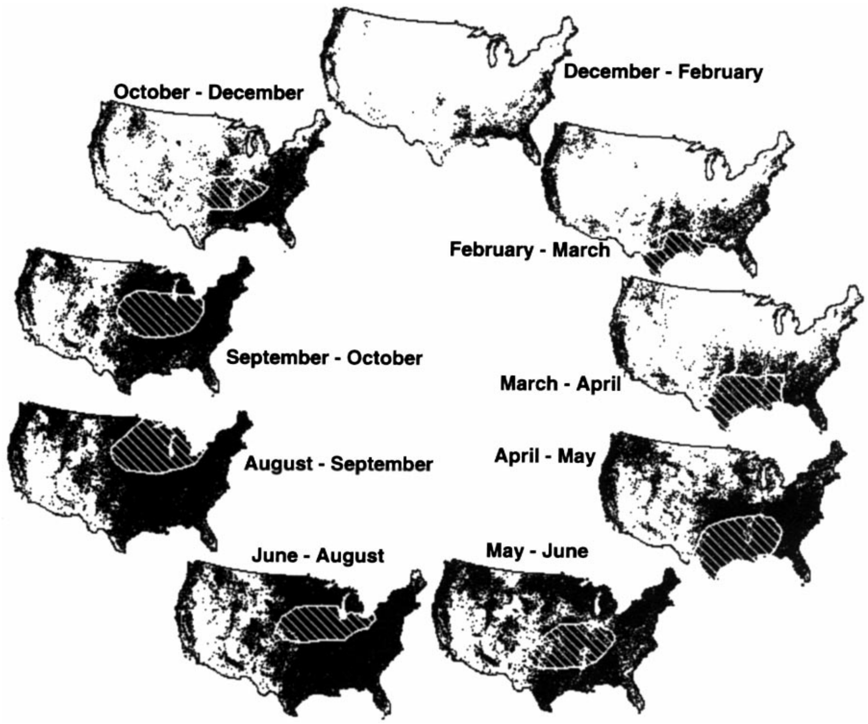

Fig. 3. Monthly distribution of black cutworm (*Agrotis ipsilon*) moth breeding areas (shaded area) in the continental United States from Shower 1997, overlain on the seasonal progression of greening (black areas) as measured by the Normalized Difference Vegetation Index (NDVI).

ecological scaling to understand the migration of organisms. In Fig. 3 the shaded areas on the maps show the monthly moth distribution of the black cutworm superimposed on temporal greening vegetation maps (NDVI) derived from AVHRR data. The change in geographical distribution of this insect from south to north during the spring and summer seasons closely matches the spread of vegetation greening. The return migration of the black cutworm to southern latitudes just precedes vegetation senescence. Mark-release-recapture studies have proven that this agriculturally significant, night-flying insect uses southerly airflows to move from the Gulf Coast states to the Corn Belt each spring (Showers et al., 1989) and northerly airflows behind cold fronts in autumn to return to their overwintering habitats (Showers et al., 1993). In this case, ecological scaling could be used for initiating sampling to assess crop loss in the impacted agricultural zones across the central United States and for 'turning on and off' black cutworm monitoring networks. Influence of plant phenology can also be observed on the long-range dispersal patterns of organisms with passive dispersal mechanisms. Aylor (1999) describes the case of the tobacco blue mold in which dispersal of the pathogen to higher latitudes can be constrained by cropping planting patterns determined by latitudinal heat gradients.

A wide range of aerobiota (ranging from allergens, fungi, and spores to insects and birds) use the same atmospheric motion systems to move long distances and thus follow similar pathways or atmospheric corridors. One such pathway, the Mississippi River valley, provides an uninterrupted topographic corridor for long-distance aerial movement between the subtropics and continental interior of North America (see Plate 3A). It has long been recognized that ducks and geese follow the same routes from their overwintering grounds to their breeding grounds and back each year (see Elphick, 1995). Waterfowl use a combination of visual and other cues to follow river corridors, topographic features, and landmarks during daytime as well as during night migrations (Hochbaum, 1960). Passively-transported organisms also use the Mississippi River valley to make similar migrations. Each year, spring-sown wheat in the northcentral United States and southcentral Canada receives spores from rusted autumn-sown wheat (*Puccinnia* spp.) in Mexico and Texas. In turn, winter wheat in the south becomes infected during autumn by spores from the north. In some years, the rust is spread gradually by anticyclones taking a succession of short trips with intervening stops where the inoculum multiplies locally. In other years, it may be transported from source to destination in a single day by a cyclone crossing the central United States (Stakman and Harrar, 1957).

5. Conclusions

The examination of phenomena such as the aerial movement of organisms over large geographic regions that are influenced by processes and events that occur at multiple scales requires a conceptual and operational framework. Phenology, in the broadest sense, is an important and valuable unifying theme for characterizing the flow of organisms at different spatial and temporal scales. Plant systems serve to integrate the effects of weather and climate and thus the stresses that induce long-distance movement of many organisms. Seasonal changes in weather serve to synchronize the phenology of many organisms within an ecosystem. A greening index derived from satellite measurements can provide a measure of phenological stage of vegetation communities and thus an indication of the timing of take-off by aerobiota that are synchronized with their hosts. The greening index can also provide a measure of the susceptibility of ecosystems for colonization by aerobiota upon descent from the atmosphere. The availability of: (1) satellite imagery on a weekly basis at multiple resolutions for large geographic areas, (2) ecoregion classification digital maps, and (3) increased data processing capabilities provide potential for new perspectives and opportunities for studying long-distance aerial movements of organisms and aerobiology. Further work is needed to collect observations and to investigate the interrelationships among meteorological systems, physical characteristics of geographical units, the phenology of ecoregions, and the long-distance movement of organisms that are important to human health, production systems, and the environment.

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