SPACE, TIME AND THRIPS: BIOGEOGRAPHIC ISSUES IN THE EVOLUTIONARY ECOLOGY OF THYSANOPTERA

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Introduction

Most participants of this symposium will be concerned with understanding thrips ecology primarily in order to develop practical and effective control strategies. Questions dealing with historical aspects (evolution) may seem of only isolated "theoretical" interest with little significance for everyday pragmatic concerns. Evolutionary theory is widely presented, however, as a cornerstone of modern biology and this position implies that evolutionary considerations can and do provide a direct input into our understanding of both ecosystems and individual organisms. Most evolutionary perspectives on living organisms are derived from specialist studies such as ecological, genetic or developmental systems. Data from these studies are extrapolated to represent evolutionary processes in reference to some general theoretical or metaphorical framework (e.g., natural selection) that also has its source in the same kind of observations.

In evolutionary ecology the course of evolution is often separated out from the living present so that the historical "past" and the ecological "present" of evolution never seem to quite come together (Gray 1990). This arbitrary division between past and present may provide an implicit, and little recognized, barrier to effective synthesis between evolution and ecology in the study of modern-day organisms. I will address this problem with respect to the general biogeographic problem of incorporating space into evolution and the potential significance for future work on thysanopteran ecology.

Evolutionary Characters

An important component of evolutionary approaches to natural processes is the construction of a comparative framework for identifying information content. Comparative information is expressed by the establishment of a particular taxonomy representing what we understand of the real natural world through systematic analysis of characters (Nelson & Platnick 1981). There is unfortunately a dearth of comprehensive comparative phylogenetic and evolutionary information on the Thysanoptera (cf. Lewis this proceedings, Nakahara this proceedings) although the range of contributions in this symposium referring to many different situations suggests that this information could develop. However, systematics/taxonomy remains one of the most threatened of disciplines in the natural sciences suffering continuing attrition in funding, diminished emphasis in university courses and uncertainty about its scope and content from both systematists and non-systematists in the natural sciences (Whitehead 1990).

Understanding the role of systematics may represent the weakest link in establishing the discipline as a relevant component of general biological studies (Whitehead 1990). The systematic component most familiar to non-systematists is the taxonomy that provides an ordering of information within which organisms may be compared and specific issues identified. There is the danger, however, that this familiarity may degrade taxonomy as being nothing more than a convenient labelling system for the indifferent use of ecologists, environment managers etc. This perception overlooks the theoretical content of taxonomy that concerns the question of genealogy as shared evolutionary history (Fig. 1). Taxonomy is a direct representation of a natural process (evolution) and provides a summary, a statement about the current knowledge of that process (Nelson & Platnick 1981). It is through the process of evolution that systematics may be recognized as an indispensable component for any meaningful biological study whether phylogeny or ecology.

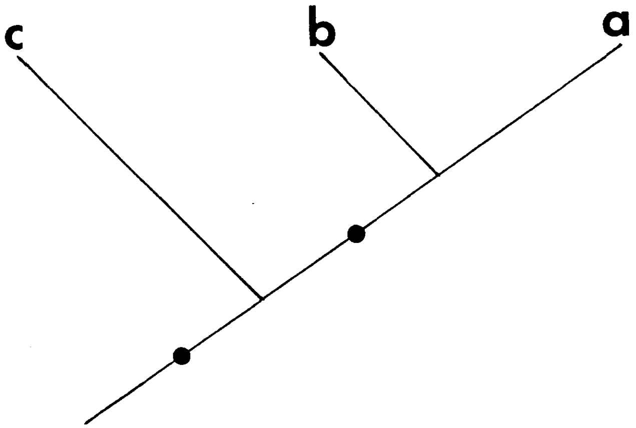

Figure 1. Simplified conceptual relationship between taxonomic category (taxa a, b, c) and phylogenetic evolution. Taxa are positioned according to inferred historical relationship. Taxa "a" and "b" are more closely related to each other than either taxon is to "c". Solid circles represent unique shared characters defining taxonomic and phylogenetic relationships (modified from Nelson & Platnick 1981).

At present there are insufficient detailed comparative studies on the ecology and phylogeny of Thysanoptera to establish an analytical approach for a narrative on thrips evolution. In optimistic anticipation of this future development I will briefly consider the important issue of space/time arising from systematic and biogeographic studies of evolution and examine the implication for understanding the evolutionary relationship between ecology and history.

Spatiotemporal Characters

The study of space/time in evolutionary biology is nominally the field of biogeography - the investigation of animal and plant distributions. Biological or evolutionary studies often give only tacit or implicit recognition to the existence of "space" and "time" and rarely does this concern receive critical appraisal outside biogeography. The implicit acceptance of space and time "as read" assumes a separate, discrete existence for each - a separate time (like an arrow of time) and a separate space (such as a defined area). While this "common sense" appreciation is based on an original separation, in practice we conceive of space in a temporal sense--a particular moment in time (this moment being the present, the "now" in which we think). Conversely time is thought in relation to a sequence or spacing of particular moments (Derrida 1982). Each, therefore, becomes a necessary counterpart to the other, and instead of referring to space *and* time in evolution it is be more appropriate to think of space/time (Craw 1988). This joining is significant for how we approach ecology and history which traditionally separates and isolates past (time) from present (place).

Distributions are explicitly spatiotemporal and show that organisms do not evolve only in their physical form, but have a real geographic existence with their evolutionary boundaries (ecological and historical limits) being determined or "defined" by space/time (Fig. 2). Biogeography has often assumed space and time to represent a separate stage or container that provided the environment in which organisms actively migrate and evolve so that organisms evolve, environments do not (Craw & Page 1988, Gray 1988). Migration stories were constructed largely on the belief that individual attributes of organisms (e.g., flying, walking, rafting etc.) are responsible for their different distributions (Darwin 1859, Wallace 1876). This evolutionary framework effectively exiled organic distributions from having any real existence in evolution. Instead of forming a data base in their own right, distributions were treated as an ephemeral manifestation of differing migratory abilities between of organisms. Without an explicit space/time dimension biogeography could not contribute anything much to evolution or ecology in general.

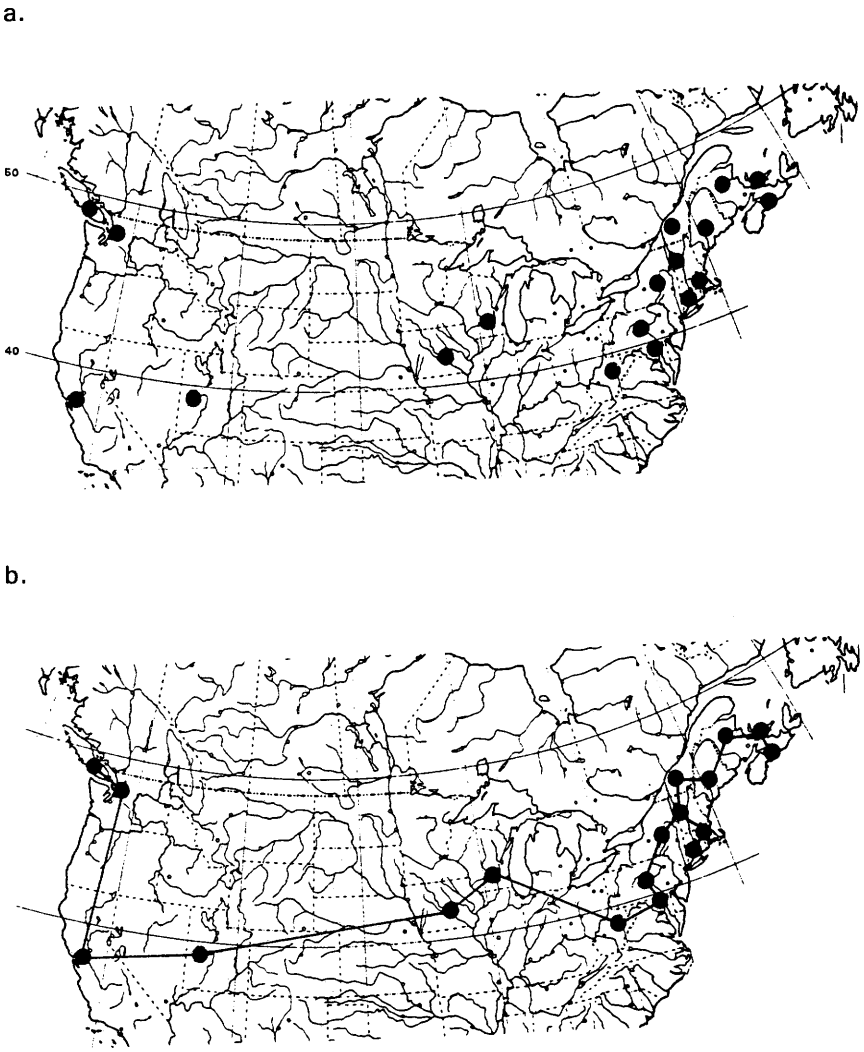

Figure 2. The biogeographic (space/time) evolution of organisms as represented in the range of the pear thrips (*Taeniothrips inconsequens*) in North America. (a) The range of pear thrips as a distribution emphasizing the general localities based on records of the insect. (b) The geographic localities represented as a biogeographic map of the space/time coordinates of the distribution filled in by lines. The lines connect the localities in the form of a minimal spanning tree. (distributional information from M. Skinner).

The treatment of space/time in evolutionary biogeography changed substantially in the 1950s through the establishment of panbiogeography (Croizat 1952, 1958). This form of biogeography examined distributions as providing a space/time data base - literally the "records of life" (Croizat 1964). Panbiogeography was concerned with developing an analytical framework for comparing the spatiotemporal characteristics of distribution patterns and deriving an understanding of the evolutionary relationship between historical events and the ecology of organisms with respect to present location. This geographic treatment of space/time provided an explicit role for evolutionary systematics by treating geographic information as characters amenable to analysis and interpretation (cf. Page 1987).

An important early finding in panbiogeography was that specific attributes of organisms, such as local means of survival (flying, walking, swimming, rafting etc.), were not general predictors of their present location on the globe. Just because an organism had the ability to fly did not mean that it was any more widely distributed than flightless beetle or worm. Croizat (1952, 1958) found that organisms with different migratory abilities could have the same pattern of distribution and suggested, therefore, that historical events were an important determinant of geographic range and the local ecology of organisms. Some organisms may appear to have greater freedom of movement and more expansive range than localized endemics, but their evolution in space/time was regarded as being fundamentally no different (Croizat 1964, Craw 1988). The common element of evolution for organisms with a "weedy" ecology (such as the pear thrips *Taeniothrips inconsequens* (Uzel)) and more specialized or localized forms concerns the role of actively changing ecological circumstances and their relationships with earth history. It is this interrelationship that concerns biogeography as a science investigating the space/time events that contribute to the evolutionary ecology of organisms.

Biogeographic Events

How may these very general biogeographic considerations bear on specific approaches to thrips ecology and "management?" With pear thrips, for example, the present ecology involves two major developments: (1) the presumed human mediated introduction of pear thrips into North America (Bailey 1944) and (2) the association of pear thrips with, and recent prevalence on, sugar maple (*Acer saccharum* Marsh.). Both events involve changing spatial and temporal boundaries in thrips evolution. Comparative inferences on the evolution of pear thrips host-plant relationships are limited by the lack of detailed information on host-plant relationships of pear thrips in the European range (see Mills, this proceedings) although it is known to feed on members of *Acer* and the sugar maple does not necessarily represent a major host-plant "departure." The host-range expansion has involved host plants that could not be previously exploited (because of their absence) in the Eurasian range of pear thrips. These geographic changes, occurring within the present historical record, could be visualized as an active "colonization" by an aggressive or assertive organism making use of new environmental opportunities. This view would assume space and time to be separate from the organism and it could, therefore, be argued that the thrips has actively entered a "new" passive environment.

In a static space and time model of evolution the pear thrips entry onto sugar maple may be treated as an "invasion" or "colonization" and in a *de facto* sense this appears to be true. It requires, however, the underlying assumption of discrete separateness between the insect and host-plant - that the thrips alone defines the host while the host has no active role through its own spatiotemporal characters. This one-sided dichotomy in favor of thrips presents the thrips as the sole "active" evolutionary partner establishing initial contact. The separation of insect (organism) and host-plant (environment) has been modelled by Janzen (1968) in terms of "island biogeography" formalized by McArthur & Wilson (1967). Janzen (1968) argues that a species of plant is an island in evolutionary time to the insect species that feeds on it, but the individual plant may also be analyzed in space and contemporary time to the individual insects that feed on it. The island concept presented by Janzen is explicitly based on space and time as containers (Fig. 3) and emphasized by the reference to McArthur & Wilson (1967) who view spatiotemporal evolution in the tradition of Darwin (1859) and Wallace (1876) where specific attributes of organisms are responsible for differential migration and colonization. Janzen (1968) extends this model to limit the plants role as the passive recipient to insect migration and affecting only the opportunity for establishment by character differences such as size, distance and chemical and structural composition.

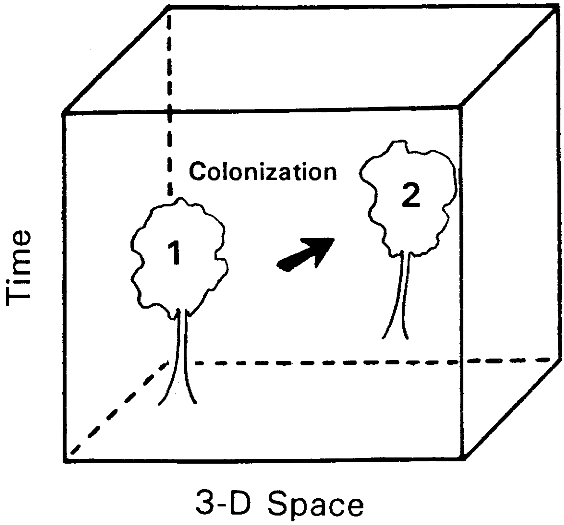

Figure 3. Host-plant relationships conceptualized for an organism/environment whereby evolution takes place within a container of absolute space and time. New host-plant relationships occur through the organism actively migrating from one environment location (1) to another (2) (modified from Craw & Page 1988).

If space/time is already present in the very existence of an organism (i.e., its ecological and developmental existence) the traditional division drawn between organism and environment is no more than an idealistic abstraction. Just as time may be thought of as space and space as time, a particular "ecology" has no meaningful existence without reference to "organism" and organisms do not come into existence without an ecology (i.e., environmental relations) (Gray 1988). If organisms and environments (ecology) are seen as having a reciprocal character, their individual boundaries are mutually contingent. When interpreting ecological changes such as that of the pear thrips, the evolutionary process involves reorganization of space/time boundaries (the North American extension) that includes both the thrips as an organism and the thrips as an ecology. Thus, it is not the pear thrips alone as a separate "organism" that has entered North America, but an evolving pear thrips ecology (since the thrips organism did not travel at any stage without an environment). In this perspective it is possible to look at the evolutionary history of thrips as a co-construction of organism and environment (cf. Gray 1988). This differs from some traditions in evolutionary ecology that look at organisms and environments as closely interacting, but only as separate, distinct entities. Here they have no prior separate existence. In a co-construction context the evolution of thrips could be seen to involve a process of development in a particular place/time where inheritance involves "organism" and "environment" components as the raw materials in each thrips generation (Fig. 4). Rather than treating either or both of the inherited characters as the determinants of thrips ecology, it is the process of mutual construction that takes place during development that defines the apparently distinct thrips "organism" as we see it, and the separate ecology that we associate with the insect. Neither of these aspects have come into existence pre-formed, they were involved in developmental (or successional) processes and these processes of co-construction are contingent upon the place/time in which they occur (cf. Gray 1990, Grehan 1988, Oyama 1982).

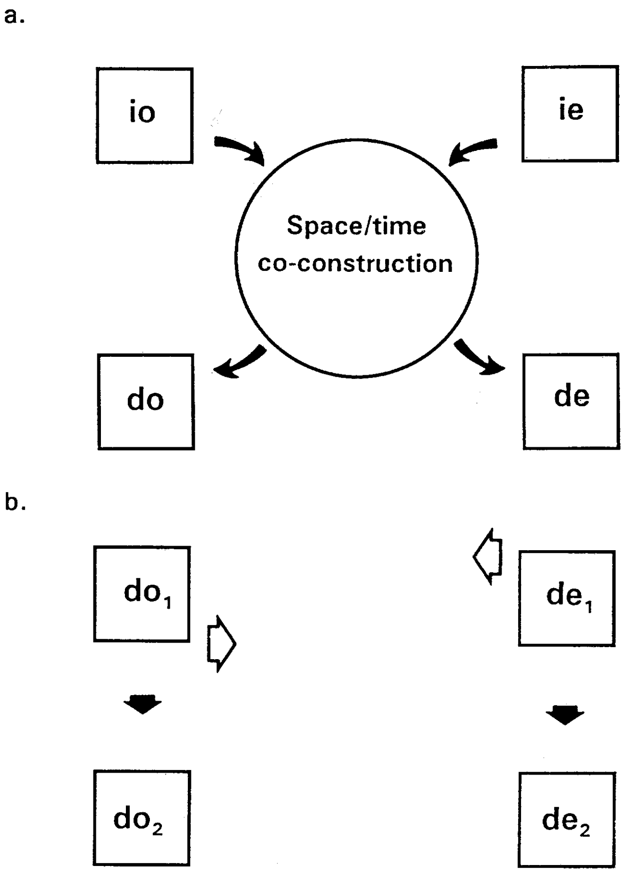

Figure 4. (a) A co-construction model of host-plant relationships. Evolution is contingent upon the interrelationship between space/time events (biogeography) and the initial "raw material" of inheritance in both its organism and environmental aspects (io = initial organic inheritance; ie = initial environmental inheritance). Through development there is a co-construction that results in the defined "organism" (do) and defined environment (de) which now may have the appearance of separate distinct entities. This can be contrasted to host-plant models (b) where evolution occurs through the interaction of separate organism (do1) and environment (de1) entities (here the host-plant is being treated as an environment with respect to a particular insect). The interaction may result in modification of either or both components (do2, de2).

The co-construction perspective has been recently formalized by Gray (1987, 1988, 1990) to help synthesize history and ecology in evolutionary studies. Co-construction is an important consideration because it places the historical context of evolution as being historically contingent upon when and where organisms and environments interact. Evolutionary systematics, through biogeography, is concerned with the spatiotemporal characters of evolution which may become important if not critical for understanding the present evolutionary ecology of organisms and how this may change in relation to the evolution of environments. Evolution in space/time may, therefore, be thought of as a process whereby ecology has history and history is mediated ecologically (Gray 1990).

In panbiogeography the incorporation of space/time in organism-environment relations leads to rejection of organisms as being representations of some kind of inner ideal that can be defined for all places/times (as in most approaches to species definitions). Instead organisms or natural taxa are seen as having a spatiotemporal existence whereby their individuality is diagnosable only with respect to particular places/times (Craw 1988). This contingency is developed as a general evolutionary framework whereby "earth" and "life" are seen to evolve together (Croizat 1964, Heads 1990) and biogeographic research is involved in the analytical and statistical ramifications (e.g., Craw & Page 1988, Craw 1988, Page 1987, Henderson 1990). The conceptual linking of space/time with the form of an organism allows the potential for interlocking the findings of different disciplines in evolutionary biology (Fig. 5) where ecology has for its immediate focus present spatial relations of an organism. These relations are, however, contingent upon spatiotemporal studies (biogeography), and developmental processes (which mediate organism-environment transactions). The conceptual model provides possibility for reciprocal insights to be developed between the disciplines.

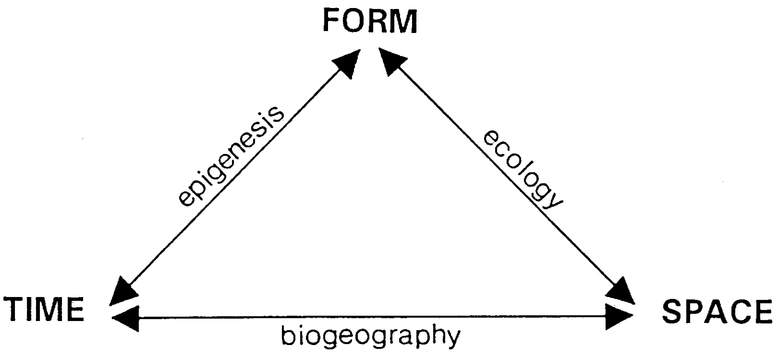

Figure 5. Model of the reciprocal relations between different evolutionary disciplines with respect to the contingent relationship of space/time with form. Biogeography may be regarded as having its primary focus with relative space/time and have a reciprocal relationship with ecology and developmental sciences (from Craw & Page 1988).

The *de facto* appearance of insects (or other animals) establishing relationships on plants and either maintaining a presence or not is not questioned here. The biogeographic problem concerns the metaphor of "island" which evokes a simplistic model of isolation and separation between entities that may be ecologically integrated. The establishment of pear thrips need not be interpreted as a lack or conquest of a barrier in the host-plant, but as a new ecological event contingent upon the mutual co-construction of evolutionary and ecological characters. In this sense the evolutionary "inheritance" of an insect concerns not just its genes or developmental characters, but also the environment characters. Each generation these characters do not appear already present and fully formed, but must be constructed in relation with each other through the development of the organism concerned. This interpretation involves a concept of space/time that is not only fluid, but totally contingent, a place where what is "organism" and what is "environment" is no longer quite as distinct as we might prefer from a pragmatic managerial standpoint.

Conclusion

Specialists may respond to this deconstruction approach of organism-environment relations by asking, "What practical difference does this make to my work?" My response is that it makes a difference only if a specialist is prepared to explore the foundations and implications that become apparent. Thus, it is not my purpose or intention to impose co-construction, but contribute an appreciation of space/time concerning concepts taken for granted in ecological studies that do have a bearing on our interpretation of the real, natural world and the solutions we construct for reaching practical solutions to ecological problems.

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