Moving beyond phenology: new directions in the study of temporal dynamics of tropical insect communities

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Understanding of temporal dynamics of tropical insect communities is hampered by the difficulty of disentangling population dynamics, timed phenology, migration and seasonal activity. Furthermore, there is a dearth of data on potential drivers of temporal dynamics, and on its consequences for ecosystem functioning. This article argues for collection of complementary data, and makes methodological recommendations.

Keywords: Activity, climate, longevity, migration, phenology, phenotypic plasticity, population dynamics.

LONG-term monitoring of tropical insect communities plays an important role in addressing key questions in ecology, evolution and conservation biology. Together with other types of data, information on phenology (temporal abundance fluctuations) is not only of descriptive value, but can also be used to test important hypotheses. Here I discuss recent studies that have moved beyond describing phenology, towards using these data to elucidate the drivers, the consequences for ecosystem functioning, evolution of species' traits, and for designing and interpreting biodiversity assessments. Communities consist of species; hence studies are ideally conducted at the species level, and cover most species in a community. It then becomes possible to compare the proportion of species that display certain dynamics, proportions of species that display certain sensitivities to climatic variation, and to test for density dependent interactions among species.

Distinguishing population dynamics, seasonal phenology and migrations

Biological interpretation of long-term data requires careful separation of sources of phenology of insect species. Observed temporal abundance fluctuations of tropical insects may be caused by population fluctuations, timed phenology of reproduction, migration and even seasonal behaviour[1].Therefore, it is useful to divide temporal abundance fluctuation into seasonal phenology (phenology in the strict sense, which represents only phenology of the life cycle), population dynamics, and migration (movements over long distances, not necessarily directional). Studies of tropical insect community dynamics tend to take adult abundance data as a surrogate for seasonal phenology or population dynamics, and ignore possible migrations. Hence none of them is addressed properly.

Seasonal variation in insect abundances can arise from phenological adaptations to seasonal environmental fluctuations. For example, species respond to environmental cues, which help them time their life-cycle optimally[2,3]. Diapausing insects may appear less abundant than they really are if activity determines observed abundance[4]. Many tropical insects have generation times that are shorter than the seasons; hence population dynamics can cause dramatic abundance fluctuations within a year[5,6]. Seasonal weather fluctuations may control population fluctuations of tropical insect populations either directly or via the amount of available resources or enemies[7]. For certain tropical insect species, seasonal variation in abundance is due to migrations[8]. However, insect migrations in the tropics are poorly documented. Therefore, care should be taken to separate timed phenology from population dynamics and migrations. However, this has hardly been attempted for tropical insects (Figure 1).

Species level analysis of temporal-abundance patterns of fruit-feeding butterflies in Uganda is shown in Figure 1. The length of the *r*-vector which can vary between 0 (evenly distributed amongst months) and 1 (all butterflies each year in one month) is shown on the *y*-axis, and variation in timing of peaks with years varying between 0 (always in the same month) and 81 degrees (in random months) is shown on the *x*-axis. I applied unimodal circular statistics[9] on the abundance of the most common species of fruit-feeding butterflies in 12-years of monthly sampling in Kibale Forest, Uganda[10]. I have reared a large proportion of the included species and never

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observed pupal diapause in these. Most species cluster in the bottom right corner of the graph. These species show a rather even distribution over the year and the variation among years in timing of abundance peaks is close to its maximum possible value. Even a known seasonal breeder, *Gnophodes chelys* (Fabricius, 1793), is found in this corner. This may be caused by long adult life spans[11] and equalizing dispersal. Some of the most seasonal species are migrants; three species of *Sevenia* (Kocak, 1996), and *Cymothoe herminia* (Grose-Smith, 1887). Some of the other species that show similarly distinct seasonal peaks (e.g. *Junonia temora* Felder 1867, *Charaxes candiope*, Godart, 1824 and *C. bipunctatus*, Rothschild, 1894) might also migrate, but these are not as common, and therefore, such migrations would be hard to notice.

Only after isolating population dynamics, can we confidently study inter-specific density dependence and interactions among species[12]. If interactions among species are important within ecological guilds, inter-specific density mediated interactions would play a significant role in population dynamics of species and affect patterns of species synchrony in communities. Synchrony has been identified in a general theoretical framework of ecosystem stability as an important trait of communities, which is affected by species interactions[13], however synchrony has not been formally addressed for tropical insect communities. To achieve such disentangling of different sources of temporal abundance variation, abundance time series need to be complemented with monitoring of early stages, age grading, mark-recapture data, or tracking studies.

Identifying drivers

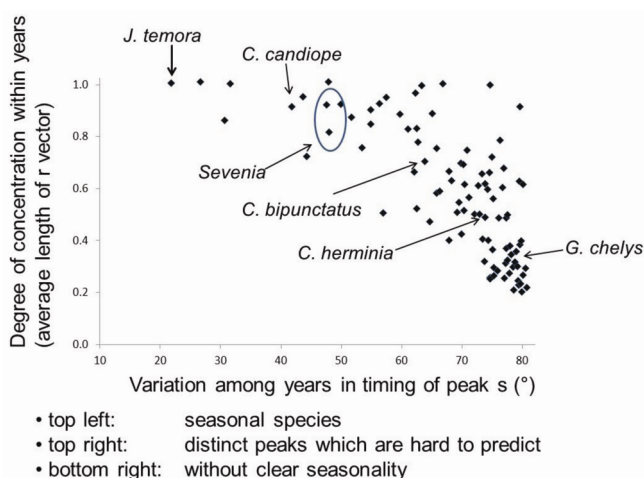When we isolate population dynamics from timed phenology, we may search for causes of population fluctuations by combining insect abundance time-series with information on potential drivers. Phenology of insect populations may be controlled by resources (bottom-up) or by mortality factors (top-down). Herbivorous insect populations can be expected to respond to vegetation growth, and this is often limited by rainfall[10]. Indeed, there are significant correlations between inter-annual variation in rainfall patterns and butterfly community abundance. However, only a small proportion of the variation in butterfly community abundance and community composition tends to be explained by variation in rainfall or vegetation greenness[10,14]. This suggests that bottom-up regulation only plays a small role. Thus, top-down regulation (natural enemies) plays an important role in determining tropical insect population dynamics.

Little is known about the regulation of insects by natural enemies in tropical forests. A one-year study in Uganda showed that attack rates on dummy caterpillars peaked during the two wet seasons, and appeared congruent with inferred peaks in caterpillar density[6]. This suggests a functional response (predators shifting to more abundant resource) or adaptive timed phenology (predators timing activity or breeding to coincide with seasonal peaks in prey abundance) of predators, rather than a numerical response (predator populations increasing following peaks in prey abundance). We do not know if this pattern is consistent among years, and how it varies among regions. Such predation would dampen abundance fluctuations and make fluctuations similar for different species within a community (synchronization). However, there are large temporal abundance fluctuations in most species, and a general lack of synchrony among species within the butterfly community[10,14]. Therefore, generalist predators are unlikely to drive temporal abundance patterns. Instead, it appears likely that specialist natural enemies such as parasitoids[15,16] play a dominant role in determining population fluctuations in tropical insect communities (Figure 2)[5].

Figure 2 shows a possible role parasitoids play in evolution of seasonal reproduction in a butterfly. In Kibale

Figure 1. Species level analysis of temporal-abundance patterns of fruit feeding butterflies in Uganda.
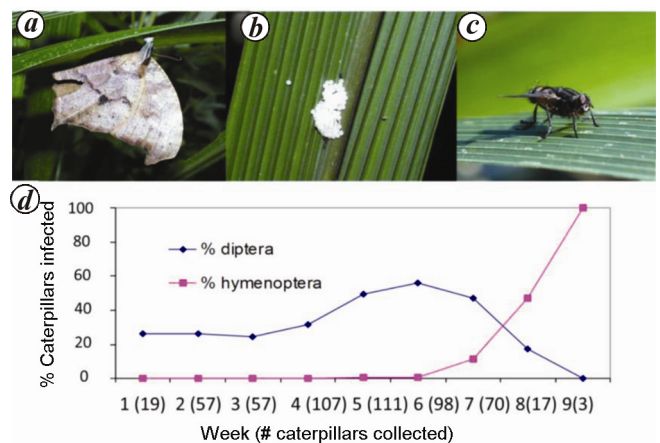

Figure 2. Parasitoids in evolution of seasonal reproduction in a butterfly.

forest, Uganda, I noticed that the butterfly *Gnophodes chelys* (female in Figure 2 *a*) lays large egg batches on large clusters of *Setaria megaphylla* (Steud.) T. Dur. & Schinz at the beginning of each rainy season (Figure 2 *b*, 200–350 eggs) and the outer eggs in each batch are almost invariably used by egg-parasitoids. Caterpillars are gregarious and change their stripy pattern with each instar until the last instar, matching the stripy effect of *Setaria* leaves. During the last instar, they often wander off individually and may feed on other grasses (e.g. elephant grass). I have only seen one exception, an egg batch on a sedge, where caterpillars were then very conspicuous. During the dry season, adults are present, but females remain unmated until the beginning of the rainy season[17], and therefore spend the dry seasons in reproductive diapause. Adults can live at least six months in the wild[11]. My student Peter Boons tried to collect at least 100 fourth instar larvae per week of the butterfly *Gnophodes chelys* throughout a breeding season in 2002. At the start and at the end of this period, this was not possible despite intense searches and help, but during the peak, they were easily collected in a few hours (Figure 2). He then reared the larvae and determined parasitation rates and parasitoid development time. While few larvae were parasitized during the first weeks, later in the season, parasitism soared (Figure 2 *d*). This corresponds to the six-week average development time of the hymenopterans (Braconidae pupating outside the host's larval stage) that were thus able to put in a second generation on the single generation of the host. Caterpillars that would be around even later, would be attacked by parasitoid flies (Tachinidae pupating inside the host pupa, Figure 2 *c*) that started emerging from the reared hosts during week nine. Note that parasitoids may delay larval development; hence caterpillars collected during the last week might be from eggs that were laid earlier than they appear. In conclusion, early laying females may expose their larvae to poor food quality and late laying females would expose their larvae to high population densities of parasitoids. Therefore, parasitoids may well be an important selective force in the evolution of seasonal and synchronous breeding. Therefore, to identify top-down control of temporal abundance patterns, time series of insect abundance should be combined with data on attack rates on (dummy) prey, temporal variation in beak-mark frequencies, or parasitation rates of sentinel prey.

Insight into effects of climatic variation on phenology of insect species helps predict how climate change may affect diversity of tropical communities[18]. This may include identifying species traits that are associated with sensitivities to climatic variation, including body size[19] and trophic position[6]. For example, one would expect specialist herbivores to show more pronounced temporal abundance fluctuation than generalist predators. To identify what species traits make them more vulnerable to climate change, time series of insect abundance can be combined with data on weather or vegetation greenness, to subsequently compare these correlations among species.

Ecosystem functioning

Invertebrates are 'the little things that run the world', and nowhere is this more evident than in tropical forests[20]. In rainforest ecosystems, invertebrates are dominant herbivores, predators of other invertebrates, pollinators, and are among the most important organisms for breaking down dead organic matter[21–23]. While a recent study demonstrated that logging in tropical forests decreases the relative contribution of insects to ecosystem functions[24], we know little about effects of climate change on ecosystem services provided by insects. Ecosystem functions may change on average, change in temporal pattern, or the relative contribution of insects to ecosystem services may change. These changes may differ among tropical climates and particulars of local climate change. Therefore, there is a need to monitor ecosystem functioning, for example phytophagy, decomposition rate, or pollen limitation.

Evolutionary questions

Drivers of populations can be expected to exert strong selection on insect traits. Therefore, long-term data can be used to address evolutionary questions on traits that affect performance under different climatic conditions, natural enemy pressure, and density-dependent interactions. Especially in seasonal tropical environments, many insect species exhibit dry and wet season phenotypes that are presumably fitting to their respective environments. This includes seasonal polyphenism in colour patterns that probably function in predator–prey interactions[25]. Therefore, there probably is seasonal variation in predator–prey interactions. Such seasonal polyphenism is a form of phenotypic plasticity, where during the immature stages, cues are used to predict the better fitting phenotype of the adult. Field data on such seasonal polymorphism may be used to derive indications on what cues may be used, and how such plasticity varies across species, and within species across environments[26,27]. Furthermore, stable isotopes in insects can be used to trace seasonal changes in host-plant use[28]. When polymorphism is genetically determined, long-term monitoring of multiple species in a community can document evolutionary change or stabilizing selection[29], or address questions on species interactions such as mimicry[30].

Informing design of biodiversity studies

An important methodological application of long-term data is their use as reference data for designing and interpreting rapid biodiversity assessments often used in

conservation biology[31]. For example, longer-term studies (several years) on tropical butterfly communities show temporal variation in community composition that is so extensive that at least a year of regular sampling is necessary to obtain a fair picture of the species diversity at a tropical site[10,14,32,33]. However, most long-term studies are from moist tropical forests. Hence temporal variation in community composition in other tropical climates is poorly represented[34,35]. Therefore, short-term studies remain difficult to interpret.

Practical considerations

Because one should not change methods during a long-term study, careful study design is paramount. If one intends to produce a time series of community diversity, it is important to select a system with at least 30 reasonably common species; otherwise the study will rather be on the population biology of the particular species than on a community. On the other hand, it is practical when the study community is manageable in terms of identification. Since long-term studies can rarely be sustained by one observer alone, it is best to avoid observer bias by using traps that can sample in a repeatable manner, such as fruit-baited traps, pitfall traps, or Malaise traps[36]. Given that collection of specimen is often an issue in tropical countries (e.g. India), it may be practical to pick a group that can be identified in the field. This has been my strategy in Uganda. However, field identification has important drawbacks. Some potential collaborators rejected the data because it is not possible to verify all identifications. Indeed, I have been pooling a recently reinstated cryptic species with its sister species, and I cannot go back now to correct the mistake. Photographing all specimens may help, but not all species can be identified reliably from photographs. Furthermore, photographs are not enough to describe new taxa and are not useful for any molecular, chemical, or isotopic studies. In any case, especially during the early stages of a study, an in-depth taxonomic inventory is essential. Especially with destructive sampling, there should be enough space between traps so that the trapping has little impact on local populations. Effects on local population dynamics can also be minimized by taking only male specimens. Furthermore, sampling regimes should be careful to include key micro-habitats such as canopy and understorey[31,37–39], and to record micro-habitats of sampling locations (e.g. tree-fall gaps)[40].

Performing long-term monitoring poses logistic, administrative and financial challenges. The physical distance between field sites and offices can make it especially challenging to carry out regular sampling, albeit less so for scientists based in the tropics. It is especially practical to work with people that live close to the field site. Some sampling regimes require very little training, e.g. replacing the collection jars of malaise traps. Also for other tasks, literacy is sufficient to acquire the needed expertise. A prime example of training of local people for entomological work is the New Guinea Binatang Research Center in Papua New Guinea[41]. In Uganda, I at first hired two local field assistants who had already worked with other researchers and trained them to identify fruit-feeding butterflies and then to carry out survey and experimental protocols. Over the years, I trained more people, and later many found jobs in other research projects. Such involvement of local people in research can also contribute to support conservation. Apart from fieldwork, time is required for administration. Data need to be entered and quality-checked. It is important to design a robust data entry system early on (e.g. database), rather than combine differently formatted data files, with the risk of mistakes.

Long-term studies often start as short-term studies that are then continued. They usually form a minor component of a larger research project. Thus, the project as a whole continuously generates tangible results, and the long-term monitoring takes up a minor proportion of resources in any given year. Long-term sampling may be aided by students that work in the study area on their own particular questions. Funding schemes dedicated to long-term studies usually require that at least a decade of data already exists.

Finally, long-term studies are a prime example of the need to integrate multiple specializations, which is most often achieved through collaboration. In particular, they require expert taxonomic knowledge, field ecology, logistics, and statistical prowess. Finally, papers about important topics can be published based on rich empirical data.

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