11

Insect Outbreaks in Tropical Forests: Patterns, Mechanisms, and Consequences

Lee A. Dyer, Walter P. Carson, and Egbert G. Leigh Jr.

11.1 Introduction

"First of all, the statement that there are no outbreaks in tropical forests (Elton 1958) is wrong." Wolda (1983) issued this verdict when he demonstrated that over six-year periods, tropical insect populations fluctuated as strongly as temperate ones. Nevertheless, the paradigm that tropical forests are free of outbreaks (Elton 1958) has persisted in the face of strong evidence to the contrary (Nair 2007). In fact, the term "tropical outbreaks" is usually associated with disease outbreak literature or, to a lesser extent, with insect outbreaks in agricultural ecosystems or tree plantations (Nair 2007). However, as studies of insect natural history and population dynamics in the tropics accumulate, it is clear that insect outbreaks occur in most natural tropical terrestrial ecosystems and that these outbreaks may occur moderately frequently (Table 11.1). Our goal is to review what is currently known about the frequency, causes, and consequences of outbreaks both within and among tropical forests worldwide.

In this chapter, we do the following: (1) define an outbreak, identify different general types of outbreaks, and outline challenges associated with quantifying and detecting outbreaks in tropical forests; (2) point out potential biotic linkages between outbreaks in managed landscapes and those in more natural forests; (3) identify taxa that are known to outbreak and traits that make species prone to outbreak; (4) predict where outbreaks are likely to occur both within a stand and across gradients from dry to wet forests; (5) discuss the consequences of outbreaks for plant communities and species coexistence; (6) make predictions about how global climate change will alter the frequency and severity of outbreaks; and, finally, (7) propose a series of testable hypotheses concerning outbreaks in the tropics to serve as a guide for future research. We focus mostly

Table 11.1 Examples of tropical insects for which outbreaks of native herbivores in natural ecosystems have been documented. The herbivores in these examples are assumed to be native, but natural history data for most tropical herbivores are so poor that it is difficult to determine the recent origin of most herbivores within a tropical forest. Additional references are provided for outbreaks of other species within the same broad taxonomic feeding guild. Diet breadth for guilds is categorized based on host family – generalists consume its diet breadth when outbreaking. Species categorized as "solitary" may be gregarious in earlier instars, or adults may oviposit large clutches. "Long-term" observational or experimental studies utilized at least 5 years of data; all others were short-term data sets. The Van Bael et al. (2004) and Torres (1992) references document one large outbreak in Panama and Puerto Rico, respectively. Only outbreaks recorded in tropical forests and measured or described as outbreaks or eruptions are included here. Other sources summarize outbreaks in tropical agriculture or of invasive insect species in the tropics (e.g., Nair 2007; Food and Agricultural Organization (FAO) 2011).

Order	Family	Example	Guild	Documentation	References	Outbreak damage
Coleoptera	Buprestidae	Agrilus kalshoveni in Indonesia	Specialist; wood borer	Long-term observational; tree mortality	Kalshoven 1953	Large-scale tree mortality
Coleoptera	Buprestidae	Sphenoptera aterrima in India	Specialist; wood borer	Observational; tree mortality	Singh et al. 2001	Large-scale tree mortality
Coleoptera	Cerambycidae	Hoplocerambyx spinicornis in India	Specialist; wood borer	Long-term observational; tree mortality	Roonwal 1978	3–7 million trees attacked
Coleoptera	Curculionidae	Ambates spp. in Costa Rica	Specialist; stem borer	Long-term observational, experimental; stem damage	Letourneau and Dyer 1998; Letourneau 1998	0.58±0.1% shrub mortality
Coleoptera	Curculionidae	Cryptorhynchus rufescens in India	Specialist; wood borer	Observational; tree mortality	Singh et al. 2001	Large-scale tree mortality
Coleoptera	Curculionidae	Dendroctonus frontalis in Central America	Specialist; wood borer	Long-term observational, experimental; tree mortality	Billings et al. 2004	1700–2 million ha
Coleoptera	Curculionidae	Platypus biformis in India	Specialist; wood borer	Observational; tree mortality	Singh et al. 2001	Large-scale tree mortality
Coleoptera	Curculionidae	Polygraphus longifolia in India	Specialist; wood borer	Observational; tree mortality	Singh et al. 2001	Large-scale tree mortality
Coleoptera	Various	Various species in Costa Rica	Generalist and specialist leaf chewers	Observational, leaf damage	Janzen 1981	Localized defoliation, >90% herbivory

Order	Family	Species/Location	Feeding type	Method	Reference	Effect
Hemiptera	Pentatomidae	*Udonga montana* in India	Generalist, seed predator, leaf chewer	Observational; adult numbers	Reviewed by Nair 2007	Millions of individuals
Hemiptera	Psyllidae	*Phytolyma* spp. In Africa	Specialist gall	Observational; gall numbers	Wagner et al. 1991	Large-scale mortality
Hymenoptera	Agridae	*Shizocera* spp. In Vietnam	Generalist; gregarious leaf chewer	Observational; leaf damage	Tin 1990	Severe leaf damage
Hymenoptera	Formicidae	*Atta* and *Acromymex* in the Neotropics	Generalist; leaf harvester	Long-term observational, experimental, leaf damage, nest density	Holldobler and Wilson 1990; Terborgh et al. 2001; Feeley and Terborgh 2008; Meyer et al. 2009	Doubled rates of colony growth; 5–11 times increases in density
Lepidoptera	Arctiidae	*Cosmosoma myrodora* in Puerto Rico	Specialist; gregarious leaf chewer	Observational; rough estimates of larval densities and leaf damage	Torres 1992	Herbivory per tree up to 99%
Lepidoptera	Arctiidae	*Eucereon tesselatum* in Panama	Generalist; solitary leaf chewer	Long-term observational; larval densities; leaf damage	Van Bael et al. 2004	0.32 larvae per young leaf
Lepidoptera	Arctiidae	*Munona iridescens* in Panana	Generalist; solitary leaf chewer	Long-term observational; larval densities; leaf damage	Van Bael et al. 2004	0.4 larvae per young leaf
Lepidoptera	Epiplemidae	*Syngria druidaria* in Panama	Specialist; solitary leaf chewer	Long-term observational; larval densities; leaf damage	Van Bael et al. 2004	1.09 larvae per young leaf
Lepidoptera	Geometridae	*Cleora injectaria* in Thailand	Specialist; solitary leaf chewer	Observational; larval densities; leaf damage	Piyakarnchana 1981	Up to 100% defoliation on trees in a large area
Lepidoptera	Geometridae	*Eois* spp. in Costa Rica	Specialist; solitary leaf chewer	Observational and experimental; larval densities and leaf damage	Letourneau and Dyer 1998; Letourneau 1998; Dyer and Gentry 2010	47±10% herbivory

Table 11.1 (Cont'd).

Order	Family	Example	Guild	Documentation	References	Outbreak damage
Lepidoptera	Geometridae	*Miliona basalis* in Indonesia	Specialist; solitary leaf chewer	Observational	Reviewed by Nair 2007	Repeated outbreaks
Lepidoptera	Geometridae	*Scotorythra paludicola* in Hawaii	Specialist; gregarious leaf chewer	Long-term observational; larval and adult densities; leaf damage	Haines et al. 2009	Repeated outbreaks; up to 16km^2 full defoliation
Lepidoptera	Hesperiidae	*Perichares philetes* in Puerto Rico	Specialist; solitary shelter builder	Observational; rough estimates of larval densities and leaf damage	Torres 1992	Herbivory per plant up to 75%
Lepidoptera	Hyblaeidae	*Hyblaea puera* across southern Asia	Specialist; shelter-building leaf chewer		Reviewed by Nair 2007	100% leaf herbivory, up to 100% herbivory per tree or shrub, large scale out breaks of up to 350 million larvae
Lepidoptera	Lasiocampidae	*Euglyphis* spp. in Panama	Generalist; gregarious leaf chewer	Long-term observational; larval densities; leaf damage	Van Bael et al. 2004	1.54 larvae per young leaf
Lepidoptera	Lasiocampidae	*Voracia casuariniphaga* in East Java.	Generalist; gregarious shelter builder	Observational; leaf damage	Kalshoven 1953	Up to 100% defoliation in 800ha of forest
Lepidoptera	Limacodidae	*Acharia hyperoche* in Costa Rica	Generalist; gregarious leaf chewer	Observational; larval densities, leaf damage	Dyer and Gentry 2010	90±12% herbivory per shrub
Lepidoptera	Lymantriidae	*Lymantria galinaria* in Indonesia	Generalist; gregarious leaf chewer	Observational; larval densities	Kalshoven 1953	100% of host trees attacked

Order	Family	Species and location	Feeding guild	Method	Reference	Outbreak measure
Lepidoptera	Noctuidae	*Condica cupentia* in Puerto Rico	Specialist; gregarious leaf chewer	Observational; rough estimates of larval densities and leaf damage	Torres 1992	Herbivory per vine up to 95%
Lepidoptera	Noctuidae	*Dyops dotata* in Panama	Specialist; solitary leaf chewer	Long-term observational; larval densities; leaf damage	Van Bael *et al.* 2004	5.07 larvae per young leaf
Lepidoptera	Noctuidae	*Eulepidotis* spp. in Panama	Generalist; gregarious leaf chewer	Long-term observational; larval densities; leaf damage	Wong *et al.* 1990; Pogue and Aiello 1999; Nascimento and Proctor 1994	95% trees with herbivory; herbivory per tree up to 100%
Lepidoptera	Noctuidae	*Ophiusa* spp. in Indonesia	Generalist; leaf chewer	Observational, leaf damage	Kalshoven 1953; Whitten and Damanik 1986	500–1000 ha
Lepidoptera	Noctuidae	*Spodoptera eridania* in Puerto Rico	Generalist; solitary leaf chewer	Observational; rough estimates of larval densities and leaf damage	Torres 1992	Herbivory per tree up to 100%
Lepidoptera	Notodontidae	*Anaphe venata* in Ghana	Specialist; gregarious leaf chewer	Long-term observational; leaf damage	Wagner *et al.* 1991	100% herbivory per host tree
Lepidoptera	Notodontidae	*Malocampa* spp. in Panama	Specialist; solitary leaf chewer	Long-term observational; larval densities; leaf damage	Van Bael *et al.* 2004	1.27 larvae per young leaf
Lepidoptera	Notodontidae	*Rifargia distinguenda* in Panama	Specialist; solitary leaf chewer	Long-term observational; larval densities; leaf damage	Van Bael *et al.* 2004	0.33 larvae per leaf
Lepidoptera	Notodontidae	*Zunacetha annulata* in Panama	Facultative generalist; gregarious leaf chewer	Long-term observational; adult and larval densities; leaf damage	Wolda and Foster 1978; Richards and Coley 2008	Up to 95% herbivory on 95% of host shrubs; over 10 000 larvae on 50 shrubs

Table 11.1 (Cont'd).

Order	Family	Example	Guild	Documentation	References	Outbreak damage
Lepidoptera	Nymphalidae	*Actinote* spp. in Ecuador	Specialist; gregarious leaf chewer	Observational; larval densities, leaf damage	Dyer et al. 2010	43±8% herbivory per shrub
Lepidoptera	Nymphalidae	*Antillea pelops* in Puerto Rico	Specialist; solitary leaf chewer	Observational; rough estimates of larval densities and leaf damage	Torres 1992	50% herbivory per plant
Lepidoptera	Nymphalidae	*Hypanartia paullus* in Puerto Rico	Specialist; solitary leaf chewer	Observational; rough estimates of larval densities and leaf damage	Torres 1992	100% herbivory on most host saplings
Lepidoptera	Psychidae	*Eumeta variegata* in Indonesia	Generalist; gregarious shelter builder	Observational	Reviewed by Nair 2007	Infrequent outbreaks
Lepidoptera	Psychidae	*Pteroma* spp. in Indonesia and Malaysia	Generalist; gregarious shelter builder	Long-term observational; shelter densities; leaf damage	Kalshoven 1953	Severe outbreaks
Lepidoptera	Pyralidae	*Deuterollyta nigripunctata* in Panama	Specialist; solitary shelter builder	Long-term observational; larval densities; leaf damage	Van Bael et al. 2004	0.05 larvae per leaf
Lepidoptera	Pyralidae	*Eutectona machaeralis* in India	Generalist; solitary shelter builder	Observational; larval densities; leaf damage	Reviewed by Nair 2007	100% of host trees with skeletonized leaves in a 32 mile forest transect

Order	Family	Species/Location	Feeding guild	Method	Reference	Impact
Lepidoptera	Pyralidae	*Pantographa expansalis* in Costa Rica	Generalist; solitary shelter builder	Observational; larval densities, leaf damage	Dyer and Gentry 2010	72% of trees attacked
Lepidoptera	Pyralidae	*Syllepte silicalis* in Puerto Rico	Generalist; solitary shelter builder	Observational; rough estimates of larval densities and leaf damage	Torres 1992	More than 50% damage on most host saplings
Lepidoptera	Saturniidae	*Hylesia* spp. throughout the Neotropics	Generalist; gregarious leaf chewer	Observational; larval and adult densities	Janzen 1984; Pescador 1993, 1995; Carrillo-Sanchez 2002	Up to 100% herbivory on multiple shrubs
Lepidoptera	Sphingidae	*Perigonia lusca* in Puerto Rico	Specialist; solitary leaf chewer	Observational; rough estimates of larval densities and leaf damage	Torres 1992	100% herbivory on most host shrubs
Orthoptera	Acrididae	*Anacridium malanorhodon* in Sudan	Generalist, gregarious leaf chewer	Long-term observational; adult densities, degree of defoliation	Food and Agricultural Organization (FAO) 2011	Up to 150 insects per tree

on natural systems and native herbivores. Nair (2007) provides a thorough review of outbreaks in tropical agriculture, and the Food and Agriculture Organization (FAO 2011) of the United Nations provides an extensive review and database of introduced and indigenous pest outbreaks in natural and planted forests throughout the tropics (http://www.fao.org/forestry/pests/en/).

11.2 Defining, categorizing, and detecting tropical insect outbreaks

11.2.1 Definitions and types of insect outbreaks

We define a tropical insect outbreak the same as a temperate outbreak, specifically a high-population density relative to long-term mean densities or ecosystem-wide densities (Berryman 1999, Nair 2007, Singh and Satyanarayana 2009). Here we focus on differences in the patterns and scales of tropical versus temperate outbreaks and examine mechanisms that cause population changes leading to outbreaks. We utilize the definitions provided by Berryman (1999) for two major categories of tropical outbreaks: (1) eruptive outbreaks are population explosions that re-occur in time and space because they are regulated by positive feedback or density-dependent processes (these outbreaks often spread to adjacent patches or ecosystems), and (2) gradient outbreaks are driven by local environmental conditions (e.g., temperature, precipitation, host plant availability, and quality) and track changes in these conditions in time or space. These outbreaks are typically confined to patches within an ecosystem.

Density-dependent processes with time lags are typically responsible for predictable cycles between herbivore outbreaks and low population densities, thus outbreaks can be characterized either by the presence of cycles or by pulses, which are short-lived increases in insect abundances. The eruptive-gradient and the pulse-cycle dichotomies are often combined to characterize different types of outbreaks throughout the outbreak literature (reviewed by Singh and Satyanarayana 2009, Nair 2007), and yield these main classes of outbreaks: pulse eruptive, cyclical eruptive, pulse gradient, and cyclical gradient. Other classifications consider the length of the cycle or the persistence of the outbreak (Berryman 1999, Singh and Satyanarayana 2009), thus terms such as "sustained gradient outbreak" refer to sites within an ecosystem that experience persistently high levels of herbivory compared to other sites. There is a perception that most outbreaks in tropical forests are pulse gradient. This suggests that disturbances or clear changes in resource availability are putatively responsible for tropical outbreaks that are ephemeral, unpredictable, and occurring unseen during a short-term nutrient flux or high up in forest canopies (Wolda 1978, Wolda and Foster 1978, Lowman 1997, Singh and Satyanarayana 2009).

We argue that when considering outbreaks, it is critical to consider both the temporal and spatial scales of outbreaks and perhaps most importantly to take a phytocentric view. As Strong *et al.* (1984) made clear, rare events such as outbreaks cannot be ignored because they may greatly influence plant diversity and relative abundance. Indeed, an outbreak that occurs once every 40–50 years

and causes major defoliation might seem infrequent or rare, yet it would occur several times in the life span of an individual tree that has managed to reach the canopy (Carson *et al.* 2004). Outbreaking insects that cause major defoliation or mortality on abundant species can be keystone species in plant communities (e.g., Carson and Root 2000) and occur in nearly all biomes (Carson *et al.* 2004). Additionally outbreaks in tropical forests may be as frequent as in temperate regions but go unnoticed because they are highly localized on a subset of patches or individuals of a fairly common species (Janzen 1981), they occur on uncommon and sparsely distributed species (Nair 2007), or they are out of sight, high in the canopy (Lowman 1997). We note that some pulse gradient outbreaks can occur at very small spatial and temporal scales, and even eruptive outbreaks can involve rare insect species that increase substantially in abundance. However, these outbreaks may never cause major defoliation or seriously injure host populations. Thus, our focus below is primarily on outbreaks that lead to major defoliation, host mortality, or both (Table 11.1).

11.2.2   Quantifying and detecting insect outbreaks

Some authors have suggested that cyclical gradient and cyclical eruptive outbreaks do not exist in tropical ecosystems (Wolda 1978, Myers 1988, but see Bigger 1976). Long-term cyclical outbreaks are well documented in temperate ecosystems (e.g., the larch bud moth experienced dramatic outbreak cycles from 800 to 1980 CE; Johnson *et al.* 2010), thus it is premature to dismiss their importance. They are difficult to detect in tropical ecosystems for three reasons. First, detection of most natural outbreaks, cyclical or otherwise, is very difficult because on average tropical herbivores are more specialized (Dyer *et al.* 2007), resulting in more localized outbreaks on one or a few species (Janzen 1981). Consequently, dismissing cyclical outbreaks is not possible without consistent (e.g., weekly) monitoring of entire populations of host plant genera over a number of years. Second, detection of cyclical outbreaks in particular requires very detailed time series of population data (e.g., weekly) to reveal cycles (Haines *et al.* 2009) because most tropical insects are multivoltine. This means that the standard cycle periodicity common in temperate systems should be longer than in the tropics because both population changes and time lags take longer for univoltine populations that go through a long seasonal quiescent phase. Third, outbreak detection methods that utilize tree rings are less useful because only a few tropical trees have annual growth rings; this diminishes the possibility of recording cyclical histories of defoliation (e.g., Buntgen *et al.* 2009). Thus, quantifying cyclical population dynamics will require years of data (e.g., Roland 1993) on focal host genera or species, long time series that may require weekly censuses of marked plants, and selection of plant–herbivore study systems that might be more susceptible to outbreaks.

While documenting and verifying outbreaks in the tropics in some regards are more difficult than in temperate regions, they may also be easier under certain conditions. The diversity of plants and insects, and the increase in the number of insect generations per year, may improve a tropical ecologist's ability to detect outbreaks over shorter periods of time and for many species simultaneously.

Indeed, Wolda (1983) was able to monitor population fluctuations of numerous species of Auchenorrhyncha (formerly known as Homoptera) using a single light trap. Thus the task, although challenging, is not daunting.

11.2.3 Monitoring insect population dynamics versus defoliation

Overall, an outbreak can be quantified by monitoring either the population dynamics of the insects, or defoliation as an indicator of an outbreak, including percentage of leaf removal or percentage of tree or shrub mortality (reviewed by Nair 2007). However, while high levels of damage often occur during outbreaks, it is problematic to use the degree of damage as an indicator of outbreaks when testing hypotheses generated by mathematical models or other theory and it is problematic when attempting any comparison of tropical and temperate outbreaks. This is because there are many factors that decouple measures of herbivory from herbivore population dynamics, including difficulties in measuring herbivory at multiple scales, inability to measure defoliation by specific herbivores (particularly when entire leaves are removed), error variance introduced by compensatory growth, changes in damage associated with herbivore density, and rapid leaf growth which can obscure damage. All of these problems can prevent accurate parameter estimates in models and can make it difficult to compare tropical outbreaks with quantitative studies of temperate outbreaks that focus on insect populations rather than herbivory (e.g., larval counts in Johnson *et al*. 2010). Nevertheless, both metrics of quantifying outbreaks have value, and typically the most common measure is the degree of defoliation or host mortality associated with an outbreak (e.g., Janzen 1981). Indeed, the degree of defoliation and its timing with other stressful abiotic factors (e.g., drought) may be the best metricd for evaluating the impact of the outbreak on plant population and community dynamics.

Useful models have been developed for defining and characterizing outbreaks, and have yielded relevant hypotheses about the patterns and causes of outbreaks. For example, Johnson *et al*. (2010) utilized a tritrophic discrete-space, discrete-time model to examine population densities of larch bud moths, host plant quality, and parasitoid population densities. Their modeling approach revealed that the elevation of outbreak epicenters for larch bud moths has been increasing with mean winter temperatures since 1870 CE, yielding a clear hypothesis that the disruption of long-term cyclical eruptive outbreaks is caused by limits to how far the moth distribution can shift upslope in response to warming temperatures. However, most traditional models for insect outbreaks focus on such population cycles and delayed density dependence (Myers 1988, Logan 2003, Turchin 2003). These models may be useful for generating testable hypotheses for tropical insect herbivores that exhibit cyclical outbreaks linked with density dependence (Godfray and Hassell 1989, Ray and Hastings 1996, reviewed by Wallner 1987), but there are still very few documented examples of cyclical outbreaks in the tropics (Wolda 1983, 1992, reviewed by Wallner 1987). Outbreaks are characterized by large departures from equilibrium with considerable spatial variation, thus models that assume fluctuations around equilibrium (i.e., cyclic outbreaks) without spatial structure may not provide relevant insight

into the causes and consequences of outbreaks (Hastings 1999). Several spatial-modeling techniques explicitly incorporate the role of spatial structure, including metapopulation models, reaction–diffusion models, and cellular automata approaches. These models address important questions, such as the role of dispersal or resource patchiness in the spread of outbreaks (Hastings 1999). In a tropical forest, where many host plants are rare and resources can be very patchy, metapopulation models, which examine subpopulations at scales as small as a single tree, can be useful for examining determinants of tropical outbreaks. Thus, if local outbreaks are common in tropical forests, the metapopulation approach (e.g., Kondoh 2003) is best suited for examining the causes and consequences of dynamics such as an outbreak on a single tree or in one patch. Such outbreaks can spread to other patches, or, alternatively, dynamics across the entire ecosystem can remain stable (Hastings 1999).

11.2.4 Knowledge of outbreaks in the tropics is often anecdotal

Many examples of tropical forest outbreaks are only known through anecdote or personal observations (reviewed by Nair 2007; D. Janzen, D. Wagner, V. Novotny, H. Morais, H. Greeney, and G. Gentry, personal communication). For example, Grogan (2001) described his encounter in Brazilian Amazonia with an unidentified Thysanoptera that "appeared by the tens of millions during the 1997 dry season in a 500-m^2 patch of forest, which was completely defoliated." Torres (1992) qualitatively described an eruption of larvae of *Spodoptera eridania* (Lepidoptera, Noctuidae) in Puerto Rico, following Hurricane Hugo in 1989. The larvae erupted and invaded nearby human habitats, whereby they "crossed forest roads in the Luquillo Mountains when their food was exhausted. USDA Forest Service personnel assigned to the Luquillo Mountains observed larvae feeding on tomatoes, potato skins, and lettuce inside trashcans. Larvae entered houses in the forest and even fed on dog food." Beyond these types of descriptions, few studies of tropical outbreaks were designed to parameterize mathematical models or test hypotheses that underlie outbreaks. For example, outbreaking *Hylesia* spp. (Saturniidae) caterpillars are a common and noticeable feature of forests and managed landscapes across the Neotropics (Janzen 1981, 1984, Pescador 1995, Specht *et al*. 2006, Hernandez *et al*. 2009). These caterpillars have urticating spines as larvae and urticating scales as adults. Studies on this genus therefore have focused on the human impacts resulting from these outbreaks, particularly the widespread cases of painful dermatitis they cause (e.g., Iserhard *et al*. 2007, Moreira *et al*. 2007). We searched for *Hylesia* on ISI Web of Science in August 2010 and found that only 6 of 34 studies of this genus were ecological and none used quantitative data to examine causes and consequences of the outbreaks. Nevertheless, there are a growing number of observational and experimental studies that document outbreaks of tropical insect herbivores though the bulk of these come from managed ecosystems (reviewed by Nair 2007; Table 11.1). Consequently, while future research on tropical outbreaks should be hypothesis driven (see Section 11.8), we argue that the simple documentation of the occurrence of outbreaks remains important. Indeed, these occurrences need to make their way into the peer-reviewed literature as short

communications where the identity of the herbivore, its hosts, its location, and other salient aspects of the outbreak are reported.

11.3   Outbreaks in managed systems have biotic linkages to intact forests and vice versa

The best documented cases of outbreaks are in agricultural landscapes (e.g., Azerefegne *et al*. 2001), but these outbreaks are not isolated from natural ecosystems because the arthropod communities often have host plants in both places (e.g., arthropods on Heliconiaceae in forests near banana plantations, Matlock and de la Cruz 2002; see also Azerefegne and Solbreck 2009). Tropical forests are likely to affect outbreaks in nearby agroecosystems (and vice versa) by serving as sources of outbreaking insects or natural enemies, or by more complex pathways (Azerefegne and Solbreck 2009, Vandermeer *et al*. 2010). In fact, tropical forests act as reservoirs for many pests in tropical agriculture and vice versa, and it can sometimes be difficult to distinguish native forest herbivores from exotic pests that may have immigrated from adjacent agroecosystems (Nair 2007, Azerefegne and Solbreck 2009). For example, in Costa Rican banana plantations that were formerly lowland rainforest, frequent outbreaks by 53 native species of lepidopteran defoliators occurred for over twenty years (1950–1973). These outbreaks followed aerial applications of the insecticides dieldrin and carbaryl to the plantations (Lara 1970, Ostmark 1974, Stephens 1984). In 1973, these applications were stopped and lepidopteran larvae have rarely exceeded their economic thresholds since (Stephens 1984, Thrupp 1990), presumably due to control by parasitoids that were susceptible to insecticide treatments (Dyer *et al*. 2005). These caterpillars are all species that occur in nearby wet forest fragments (Stireman *et al*. 2004, Dyer *et al*. 2005, Dyer and Gentry 2010), but they have not been documented to outbreak in natural forests. Although speculative, it is likely that natural forests are the original source of these eruptions and that when they occur in plantations they probably spill back into natural forests.

Can outbreaks within managed landscapes cause smaller-scale outbreaks in nearby intact forests? Trophic relationships suggest this possibility. Specifically, experimental and observational studies (Stireman *et al*. 2004, Dyer *et al*. 2005, Dyer unpublished data) indicate that most interactions between these caterpillars and their host plants and enemies are similar in their natural and managed settings. For example, parasitism and predation rates in low-pesticide banana plantations and in wet tropical forest at the La Selva Biological Station were identical for two of the most common outbreak Lepidoptera, *Caligo memnon* and *Opsiphanes tamarindi* (both Nymphalidae) (Stireman *et al*. 2004). Thus, indirect evidence suggests that large-scale outbreaks of these banana pests may spill back and cause outbreaks at small scales, perhaps on relatively dense patches of host plants or under conditions when natural enemy populations are depressed by climatic events or disturbances (e.g., in response to flooding, droughts, strong El Niño weather, or other disturbances; van Bael *et al*. 2004, Stireman *et al*. 2005). If spill-back of insect outbreaks from agriculture to forest isn't a rare

phenomenon, then outbreaks may increase in intact forests as fragmentation becomes more and more widespread.

11.4 What taxa are likely to outbreak, and which traits predispose species to outbreak?

Lepidoptera accounted for 73% and Coleoptera for 19% of the outbreaks listed in Table 11.1; together they accounted for 92% of these outbreaks. Similarly, Carson *et al*. (2004) found that 94% of outbreaks of native insects in natural habitats worldwide were caused by species in these two orders (Lepidoptera 58% and Coleoptera 36%). This may simply represent the high diversity and abundance of herbivores within these two orders. Specialists (herbivores feeding on plants within one family) comprised 56% of these taxa whereas 44% were generalists. Leaf chewers, wood borers, and shelter builders were the most important guilds (58%, 17%, and 12.5% respectively). Outbreaks occurred in all major tropical forest areas including Asia (21%), India (15%), Africa (3%), and the mainland Neotropics (42%). Only two outbreaks were documented in South America (Ecuador and Brazil) whereas 17% of all outbreaks were recorded from Puerto Rico. Thirty one percent of all outbreaks were documented in Panama and Costa Rica. These results must be interpreted with a big grain of salt because of the small sample size and the various means used to documenting outbreaks. Still, they do show that outbreaks occur in nearly all tropical forest regions, are most often documented in areas where numerous researchers have been active for years (Panama, Costa Rica, and Puerto Rico) and that specialists cause rather more outbreaks than generalists, especially as generalist outbreaks are more likely to be noticed.

A number of authors have compiled key life history traits that may make certain temperate taxa prone to outbreak, including high mean densities, efficient dispersal, large size, high intrinsic rates of increase, and polyphagous diets (see citations in Table 11.2). These generalizations are generated primarily from temperate studies, and it is worth considering whether or not outbreaking tropical herbivores possess these traits. Among these attributes, high mean density is a trait that is the most consistent characteristic of outbreak species (Table 11.2) because insect populations that fluctuate around high mean abundances are also more likely to exhibit wide fluctuations. One might expect abundance and variability to be linked in some cases (Root and Capuccino 1992) because it is not unusual to observe data where the variance increases with the mean. Abundant species, however, can be stable whereas rare species can hardly be given to outbreaks because wide population fluctuation could cause their extinction (Root and Capuccino 1992). Common species, whether they have narrow or broad diet breadths, have the potential to reach outbreak levels whenever ecosystem parameters or microhabitats are favorable (Table 11.2).

Other putative outbreak traits are not as well supported by empirical data on tropical outbreaks and research here could help clarify the effects of these traits on propensity to outbreak. For example, Redfearn and Pimm (1988) conclude that diet breadth is not tightly linked to propensity to outbreak. Thus, just because

Table 11.2   Attributes of outbreaking insect populations and relevance to tropical ecosystems. Selected references have proposed these attributes as conducive to outbreaks or have provided empirical evidence demonstrating the roles of these attributes in creating outbreaks.

Life history trait of pest or ecosystem parameters	Relevance to tropical ecosystems
High density (Hunter 1991, but see Root and Cuppuccino 1992)	More common in dry forests (Janzen 1993)
Gregarious larvae (Nothnagle and Schultz 1987, Hunter 1991)	Common for many tropical insects (Dyer and Gentry 2010)
Large clutch size (Hunter 1991)	Present in many tropical herbivores (Nair 2007)
Single large egg mass (Hunter 1991)	Present in many tropical herbivores (Nair 2007)
High intrinsic rate of increase (Nothnagle and Schultz 1987, Root and Cappuccino 1992)	True for all tropical ecosystems
Large size (Hunter 1991)	Common for many tropical insects
High dispersal (Greenbank 1956)	Unknown for most outbreaking herbivores in tropical forests
Polyphagous (Nothnagle and Schultz 1987, Hunter 1991, but see Redfearn and Pimm 1988)	Tropical herbivores are more specialized, but highly polyphagous species are present (Dyer et al. 2007)
Well defended (Hunter 1991, Veldtman et al. 2007)	Tropical herbivores may be better defended (Gauld et al. 1992)
Overwinter as eggs (Hunter 1991)	Relevant to dry forests
Reduced wings (Hunter 1995)	Not true for most outbreaking herbivores in tropical forests (Nair 2007)
Capital breeders (Tammaru and Haukioja 1996)	The most damaging tropical herbivores feed as immatures (Nair 2007)
Disturbance (Schowalter and Lowman 1999, Torres 1992)	Common in gaps and fragmented tropical forests
Favorable climate for population growth (Greenbank 1956, Roland 1998, McCloskey et al. 2009)	True for all tropical ecosystems
Low diversity at all trophic levels (Pimentel 1961, Root 1973, Letourneau 2009)	Only true in tropical agroecosystems or in highly disturbed areas

temperate herbivores have higher mean diet breadth than tropical ones (Scriber 1973, Dyer *et al*. 2007), does not necessarily indicate that temperate herbivores are more likely to outbreak. In fact, the outbreaks reported by Janzen (1981) were mostly specialists and Janzen argues that most outbreaking tropical herbivores are either specialists or only consume a small proportion of available plant species. While this assertion is not supported by the documented cases of generalist outbreaks in Table 11.1, it is clear from those empirical examples that numerous tropical specialists do not abide by the temperate paradigm that polyphagous herbivores are more likely to outbreak.

11.5 Likelihood of outbreaks within a stand and across transitions from dry to wet forests

11.5.1 Patchiness and scale of insect outbreaks within tropical forests

A number of studies have examined determinants of high levels of herbivory or high arthropod abundances within a forest and most have concluded that high density of new leaves and high light availability are two key factors predicting higher herbivore abundance (Basset 1992, Itioka and Yamauti 2004, Richards and Coley 2008). Furthermore, Eveleigh *et al*. (2007) argue that diversity across trophic levels should be a potent stabilizing mechanism, preventing outbreaks, and they demonstrated that outbreaks were more likely in less diverse forest plots, which is likely due to resource concentration and other mechanisms that are responsible for higher herbivory in less diverse communities (Pimentel 1961, Root 1973, Letourneau *et al*. 2009, Long *et al*. 2003, Carson *et al*. 2004). There is compelling evidence that outbreaks, whether in temperate or tropical systems, are more likely when host species become aggregated or dense at either neighborhood or regional spatial scales (reviewed by Carson *et al*. 2004, Nair 2007). Nair (2001) found that in Indonesian forests outbreaks were generally restricted to tree species that occurred "gregariously" and that a high host density could precipitate outbreaks even in natural assemblages (see also Nair 2000). For example, an outbreak by a Noctuid moth (*Eulepidotis phrygionia*) in the Amazonian rainforest caused severe defoliation of a leguminous tree (*Peltogyne gracilipes*) within monodominant stands versus those in nearby mixed stands where this tree species was less frequent (Nascimento and Proctor 1994). Furthermore, the famous outbreak of a lepidopteran in Panama occurred on the most abundant woody species on Barro Colorado Island (Wolda and Foster 1978). In addition, high insect herbivore densities and outbreaks might be more frequent in gaps or edges, where new growth and light availability are greatest (Richards and Coley 2008) and where hosts are aggregated or relatively abundant. Localized outbreaks within the intact understory have been documented as well (Table 11.1), but it is likely that they are smaller in scale and shorter in duration, and only outbreaks on the commonest understory species attract attention. The relationship of most outbreaks to host concentration typically remains unknown but a recent meta-analysis found a significant reduction in herbivory in more diverse forests (Jactel and Brockerhoff 2007).

Local outbreaks could also occur if the impact of enemies on herbivores is interrupted. Experimental removal of ants from *Piper* ant-plants cause local outbreaks of both specialist and generalist herbivores on these plants; these outbreaks decrease *Piper* density in the understory and spill over onto plants of other species (Letourneau 2004).

11.5.2 Predicting outbreaks across broad gradients: the dry-to-wet forest transition

We predict that outbreaks will be more likely to occur in more seasonal tropical forests than in wet forests, with an increase in frequency as precipitation decreases and seasonality increases. As total annual rainfall increases and the length of the

dry season decreases, tropical forests generally have higher plant species richness (Hall and Swaine 1976, Huston 1980, Gentry 1982, 1988, Leigh *et al*. 2004), greater primary productivity (Philips *et al*. 1994), less seasonal production of new vegetation (Opler *et al*. 1980, van Schaik *et al*. 1993), higher levels of anti-herbivore defense (Coley and Aide 1991), higher levels of predation and parasitism (Stireman *et al*. 2005, Janzen, Coley, and Dyer, unpublished data), and lower herbivore densities. These changes will alter the nature of tritrophic interactions across these gradients for at least three reasons. First, plant investments in qualitative anti-herbivore defenses, such as alkaloids, often increase with nutrient availability, whereas quantitative defenses, such as polyphenols and fiber increase with leaf lifetime (reviewed by Massad *et al*. 2011); thus, plant defenses should increase with rainfall in tropical forests (Coley and Aide 1991). Second, enhanced plant defenses with increasing rainfall will lead to significantly lower leaf damage and herbivore densities in wet tropical forests (Janzen 1993; Coley and Barone 1996). Third, rates of parasitism tend to increase with rainfall and variance in precipitation (Stireman *et al*. 2005; Dyer, Coley, Janzen, unpublished data). Parasitoids may be less abundant in dry forests because the hotter, drier conditions often may make it difficult for small-bodied insects to survive, and increased seasonality of herbivore abundance in drier forests makes it harder for parasitoids to track them (e.g., Janzen 1983, 1993; Parry *et al*. 2003, Stireman *et al*. 2005). Overall, the top-down impact of natural enemies and the bottom-up effect of plant defenses increase with greater rainfall, both of which make for lower annual herbivore densities in wetter tropical forests. As higher densities are correlated with greater incidence of outbreak (Hunter 1991), outbreaks should be most common in dry forests. Though it remains untested, the frequency and severity of herbivore outbreaks should decrease from dry to wet tropical forests. In fact, Janzen (1981) found that insect herbivores caused greater than 90% damage on numerous individuals of 25 tree species during just two growing seasons in a dry tropical forest in Costa Rica. We are not aware of the same extent of defoliation occurring in any wet forest. Probably no one has bothered to look, because outbreaks may be so hard to detect in wetter forests!

11.6   The consequences of outbreaks for plant communities and species coexistence

The long-term effects of outbreaks are more intense than gradient or eruptive increases in mean levels of herbivory (Carson and Root 2000). The effects of outbreaks can be comparable to abiotic disturbances such as storms, fires, floods, droughts, or other disturbances (Schowalter and Lowman 1999). Because outbreaks rarely occur within the lifetime of a single research grant, the large number of studies examining tropical community structure, such as tests of the Janzen-Connell hypothesis (Carson *et al*. 2008), tests of trophic cascades hypotheses (Knight *et al*. 2005), or tests of niche hypotheses (Wiens *et al*. 2010), have not included the impact of outbreaks as part of theoretical considerations, observational methods, or experimental design. As Carson and Root (2000) point out, most hypotheses in community ecology assume that outbreaks are rare

or exceptional. An outbreak, however, can have long-lasting effects with profound impacts on its community. We suggest that the roles of outbreaks in tropical ecosystems could be particularly important for the maintenance of diversity. Outbreaks of insect herbivores in many systems worldwide commonly occur on dominant plant species that are widespread and reach high abundance both locally and regionally (Carson and Root 2000, Carson *et al*. 2004). These outbreaks tend to substantially reduce the abundance and performance of these species, thereby opening up forest canopies, promoting the growth of other species and plant species richness, making these insect herbivores classic keystone species (Carson and Root 2000, Carson *et al*. 2004, Nair 2007). For example, in India, outbreaks of the wood borer *Hoplocerambyx spinicornis* (Cerambycidae) have been documented for more than a century in tropical deciduous Sal forests of India (Nair 2007, Ghimre and Dongre 2001). These wood borers prefer to attack the largest sal trees (*Shorea robusta*) and can kill millions of individuals over vast areas (500,000 ha); outbreaks are thought to be triggered at least in part by high host concentrations (Ghimre and Dongre 2001, Nair 2007). Overall, if outbreaks are more likely to occur when tree species in tropical forest become locally or regionally abundant or aggregated, then this will decrease the performance and competitive ability of the common trees and promote local species richness. This possibility deserves serious consideration at both small and large spatial scales.

11.7 Global change, disturbance, and outbreaks

Empirical studies and models predict intensified insect outbreaks in response to climate change, invasive species, habitat fragmentation, and other global changes (Roland 1993; Coley 1998; Logan *et al*. 2003; Stireman *et al*. 2005; Moreau *et al*. 2006). Insect populations respond rapidly to a wide variety of disturbances and environmental changes, and outbreaks are one common response to such changes (Schowalter and Lowman 1999). Massad and Dyer (2010) utilized meta-analysis to quantify increases in herbivory in response to major categories of global change and concluded that increases in temperature, CO_2, nutrient inputs, and decreases in diversity all create favorable conditions for herbivores, particularly for generalist insects, which can be important for outbreaks (Table 11.1). Fossil evidence suggests that global warming increases herbivory: might it also enhance the frequency or severity of outbreaks? For example, Currano *et al*. (2008) examined fossil records of herbivory and found that abrupt increases in the partial pressure of CO_2 and in temperature, comparable to current rates and levels of increase, were associated with distinct increases in herbivory.

For over a decade, models of global climate change have consistently predicted that temperature increases over the next century in the tropics will be relatively moderate, but extreme weather events, such as droughts and floods, will become more frequent (e.g., Hulme and Viner 1998, Easterling *et al*. 2000). These extreme weather events could trigger outbreaks in tropical forests via disrupting natural enemy control of herbivores and altering host plant abundance and quality. Stireman *et al*. (2005) found that parasitic wasps were particularly

vulnerable to extreme weather events; they concluded that increases in climatic variation could lead to higher frequencies and intensities of outbreaks via diminished control by parasitoids, possibly due to phenological asynchrony between the parasitoids and herbivores. Empirical studies in the tropics have demonstrated that outbreaks do increase with climatic changes associated with El Niño Southern Oscillation (ENSO) events (Van Bael *et al.* 2004, Srygley *et al.* 2010). For dry or moist tropical forests that are strongly seasonal, early onset of rainfall and increased precipitation in El Niño years can cause outbreaks via increased leaf flushing early in the season (Jaksic 2001). Srygley *et al.* (2010) documented such outbreaks for *Aphrissa statira* (Pieridae) butterflies in Panama in response to an increase in dry season rainfall and greater leaf flushing due to ENSO.

In addition to these global changes, increases in fragmentation are likely to enhance conditions for outbreaks via creating patches of high herbivore density, limiting movement of natural enemies (Schowalter and Lowman 1999) and increasing the abundance of well-lit edge habitats that favor more edible pioneers. Tropical ecosystems are subject to all of these changes and are likely to experience more outbreaks. Furthermore, in the tropics, the projected increases in extreme weather events due to climate change are potentially more important for plant insect interactions because outbreaks are also predicted as a result of disruption of parasitism (Stireman *et al.* 2005).

11.8   Critical hypotheses need to be tested: A guide for future research on outbreaks

Tropical insect outbreak research has been limited mainly to applied research in agricultural (Nair 2007) or reforested (Massad 2009) ecosystems and observational studies in natural forests. Future research in natural systems should incorporate careful models, a strong experimental approach, a focus on multiple mechanisms that cause outbreaks, and details of how key herbivore populations change throughout a forest (Myers 1988). The modeling approach used for tropical outbreaks should not always mirror approaches used for outbreaks in temperate forests (Turchin 2003). In particular, a focus on metapopulation models or spatially explicit models may be more useful for examining the potential dynamics and consequences of outbreaks at small spatial and temporal scales across a heterogeneous forest landscape. It is likely that low-density specialists on patches of host plants within a forest that have the appropriate population fluctuations necessary for local outbreaks will also experience local extinctions (Hunter 1991). Such dynamics, combined with dispersal from patch to patch, are perfectly suited for metapopulation models. On the other hand, for generalist herbivores, whose dynamics may mimic temperate outbreaks but with shorter periodicity, traditional models may be most appropriate.

While mathematical models will be useful for exploring theoretical possibilities and posing additional hypotheses, the existing literature, reviewed here, is also rich enough to provide hypotheses to drive observational and experimental research approaches to tropical forest outbreaks. Here we provide a series of

hypotheses that can be addressed via quantitative observational or careful experimental approaches. The first four hypotheses focus on where outbreaks are hypothesized to occur and assume that plant chemistry and natural enemies are important factors in preventing outbreaks. These are followed by several hypotheses about the impacts of outbreaks on tropical ecosystems.

Hypothesis 1. Outbreaks that are more localized and shorter in duration will occur in tropical wet forests (compared to dry forests and temperate forests) due to greater levels of plant defense.

Leaf quality declines with leaf lifetime, which is longer in wet forests. There is considerable preliminary evidence that a gradient of increasing chemical defense from dry to wet forests exists, which could lower frequency and amplitude of outbreaks. Testing this hypothesis will require appropriate methods for quantifying particular defensive compounds and their efficacy, long-term field experiments that manipulate leaf age and levels of chemical defenses, and assessment of effects on herbivore densities or incidence of outbreaks.

Hypothesis 2. Lower incidence of outbreaks in wet forests is the result of higher rates of parasitism or predation, which may interact with plant defenses.

If parasitism is higher in wet forests than in dry forests, this may lower the density of herbivores. The following approaches could help assess how predation or parasitism rates vary among forest types: (1) analyze life table data derived from following cohorts of insect herbivores over their larval lifetimes at multiple sites; (2) manipulate leaf age, defenses, and exposure to natural enemies and evaluate herbivore responses or outbreak incidence; and (3) model the dynamics of the focal outbreak system with parameters from rearing data and field experiments.

Hypothesis 3. Lower incidence of outbreaks in wet forests is the result of reduced tree species aggregation and higher tree species diversity.

Long-term monitoring studies of herbivore population abundance would be a first step in testing this hypothesis. It would be especially valuable to examine incidences of defoliation of individuals within a species that vary in abundance at multiple spatial scales both within a region and across rainfall gradients. Multivariate techniques that can distinguish the effects of the degree of host concentration from other explanations (enemies and defenses) would be required. We note here that theories that predict outbreaks based upon host concentration are more parsimonious than those based upon enemies or plant defenses because only aggregation predisposes a population to an herbivore outbreak whether it be on a local or regional scale.

Hypothesis 4. The absence of a distinct and forest-wide pulse in new leaf production in wet forests reduces food quantity and quality, thus limiting herbivore density and outbreaks.

In dry forests new leaf production is concentrated forest-wide at the beginning of the wet season, whereas in wet forests new leaves are produced at much lower rates throughout the year. This minimizes large, high-quality food pulses and hence outbreaks. Seasonality of new leaf production is intermediate in moist forests. Leaf quality parallels patterns in food quantity. Both the seasonal abundance and high quality of food in dry forests should work together to generate seasonal peaks in herbivore population densities, some of which may reach outbreak levels. This hypothesis can be tested via documenting the seasonality of new leaf production for selected plant species and examining correlations and partial correlations between the number of new leaves, leaf quality, the relative density of herbivores per host plant, and the incidence of outbreaks in sites that vary in precipitation and seasonality.

Hypothesis 5. In dry tropical forests, the short, sharp peaks in larval densities at the beginning of the wet season are difficult for parasitoids to track and regulate, resulting in lower parasitism rates in dry forests than wet forests.

This is best addressed via observational data (long-term rearing and population studies on focal plants), simulation models, and analytical models followed by careful long-term experiments designed to determine the population-level consequences of leaf quality and abundance, and parasitoid density on herbivore population dynamics.

Hypothesis 6: Outbreaks in tropical forests represent significant nutrient inputs, affecting plant physiology and growth and enemy dynamics.

Resource pulses are not commonly reported for tropical forests (Yang *et al.* 2010), presumably for the same reasons that outbreaks are not commonly reported – small spatial and temporal scales. Nevertheless, the resource pulse created by outbreaks, including greater nutrient availability from insect feces and mortality as well as greater prey availability for predators, is likely to have measurable effects on plant and natural enemy communities (reviewed by Yang *et al.* 2010).

Hypothesis 7. Outbreaks in managed habitats (e.g., plantations) will spill over into intact forests, cause localized outbreaks on shared hosts, and increase with fragmentation.

As deforestation and fragmentation continue to increase, outbreaks in these managed landscapes are also likely to increase and these herbivores may colonize shared hosts within intact forests. Thus the frequency of outbreaks in natural forest stands nearby may also increase, particularly at the scale of individual and patches of host plants.

Hypothesis 8. Outbreaking insects can function as keystone species and thereby increase plant diversity at many scales.

We need to go beyond studies that only documented the occurrence of outbreaks (though this remains important) and document the consequences of outbreaks for forest regeneration and the maintenance of diversity (Carson *et al*. 2008). As Schowalter (1996) concluded, outbreaks of insect herbivores that attack abundant trees in many temperate systems reduce dominance, thereby enhancing diversity. They likely do the same thing in tropical forests though at much smaller spatial scales of local tree species aggregation. Nonetheless, the relevant studies remain to be done. A first and basic step would be to evaluate whether the host plants attacked are relatively common forest-wide and then evaluate patterns of regeneration in the understory following these events.

11.9 Conclusions

Outbreaks of herbivorous insects do occur in tropical forests and may be far more frequent than previously thought. Nonetheless, documentation of outbreaks in the tropics remains scant and it remains important that such events find their way into the peer-reviewed literature. Outbreaks usually occur in restricted areas on sets of a few related plant species, but sometimes spread to other species. Outbreaks often follow disturbances. These disturbances typically increase light ability, abundance of new leaves, or the abundance of pioneers with tastier leaves, all of which may precipitate outbreaks, particularly at smaller spatial scales.

Outbreaks appear to attack the commonest species or uncommonly large aggregations of individual species. Whatever the scale and duration of such outbreaks, they may act as keystone species by influencing the diversity and relative abundance of species by opening space for rarer, or better defended, less competitive species. A variety of global changes, including global warming, increases in extreme weather events, and habitat fragmentation will likely enhance the frequency and magnitude of outbreaks in natural forests by opening abundant opportunities for pioneers.

We know little about the relationship between tropical climate and insect outbreaks. Wetter forests, however, are more diverse, and have longer lived, better defended leaves and parasitoids that are better able to track their herbivore prey. This suggests that insect outbreaks will be more frequent in dry forest, where new leaves flush in overwhelming abundance early in the rainy season. We ended this chapter by outlining a series of testable hypotheses to address the large number of unknowns that currently surround the prevalence and impact of insect outbreaks in tropical forests.

Acknowledgments

References

Aiello, A. 1992. Dry season strategies of two Panamanian butterfly species, *Anartia fatima* (Nymphalinae) and *Pierella luna luna* (Satyrinae) (Lepidoptera: Nymphalidae). Pages 573–575 *in* D. Quintero and A. Aiello (editors), *Insects of Panama and Mesoamerica: Selected Studies*. Oxford University Press, New York.

Azerefegne, F., C. Solbreck, and A. R. Ives. 2001. Environmental forcing and high amplitude fluctuations in the population dynamics of the tropical butterfly *Acraea acerata* (Lepidoptera: Nymphalidae). *Journal of Animal Ecology* 70:1032–1045.

Azerefegne, F., and C. Solbreck. 2009. Oviposition preference and larval performance of the sweet potato butterfly *Acraea acerata* on *Ipomoea* species in Ethiopia. *Agricultural and Forest Entomology* 12:161–168.

Basset, Y. 1992. Influence of leaf traits on the spatial-distribution of arboreal arthropods within an over-story rain-forest tree. *Ecological Entomology* 17:8–16.

Berryman A. A. 1999. *Principles of Population Dynamics and Their Application*. Stanley Thornes Publishers, Glasgow.

Bigger, M. 1976. Oscillations of tropical insect populations. *Nature* 259:207–209.

Billings, R. F., S. R. Clarke, V. Espino Mendoza, P. Cordon Cabrera, B. Melendez Figueroa, J. Ramon Campos, and G. Baeza. 2004. Bark beetle outbreaks and fire: a devastating combination for Central America's pine forests. *Unasylva* 55:15–21.

Buntgen, U., D. Frank, A. Liebhold, D. Johnson, M. Carrer, C. Urbinati, M. Grabner, K. Nicolussi, T. Levanic, and J. Esper. 2009. Three centuries of insect outbreaks across the European Alps. *New Phytologist* 182:929–941.

Carson, W. P., J. T. Anderson, E. G. Leigh Jr., and S. A. Schnitzer. 2008. Challenges associated with testing and falsifying the Janzen–Connell hypothesis: a review and critique. Pages 210–241 *in* W. P. Carson, and S. A. Schnitzer (editors), *Tropical Forest Community Ecology*. Wiley-Blackwell, Oxford.

Carson, W. P., and R. B. Root. 2000. Herbivory and plant species coexistence: community regulation by an outbreaking phytophagous insect. *Ecological Monographs* 70:73–99.

Carson, W. P., J. P. Cronin, and Z. T. Long. 2004. A general rule for predicting when insects will have strong top-down effects on plant communities: on the relationship between insect outbreaks and host concentration. Pages 193–212 *in* W. W. Weisser and E. Siemann (editors), *Insects and Ecosystem Functions*. Springer-Verlag, Berlin.

Coley, P. D. 1998. The effects of climate change on plant–herbivore interactions in moist tropical rainforests. *Climate Change* 39:455–472.

Coley, P. D., and T. M. Aide. 1991. Comparison of herbivory and plant defenses in temperate and tropical broad-leaved forests. Pages 25–49 *in* P. W. Price, T. M. Lewinsohn, G. W. Fernandes, and W. W. Benson (editors), *Plant–Animal Interactions: Evolutionary Ecology in Tropical and Temperate Regions*. John Wiley & Sons, Inc., New York.

Coley, P. D., and J. A. Barone. 1996. Herbivory and plant defenses in tropical forests. *Annual Review of Ecology and Systematics* 27:305–335.

Currano, E. D., P. Wilf, S. L. Wing, C. C. Labandeira, E. C. Lovelock, and D. L. Royer. 2008. Sharply increased insect herbivory during the Paleocene-Eocene thermal maximum. *Proceedings of the National Academy of Sciences of the USA* 105:1960–1964.

Dyer, L. A., and Gentry G. L. 2010. Caterpillars and parasitoids of a Costa Rican tropical wet forest. http://www.caterpillars.org

Dyer, L. A., R. B. Matlock, D. Chehrezad, and R. O'Malley. 2005. Predicting caterpillar parasitism in banana plantations. *Environmental Entomology* 34:403–409.

Dyer, L. A., M. S. Singer, J. T. Lill, J. O. Stireman, G. L. Gentry, R. J. Marquis, R. E. Ricklefs, H. F. Greeney, D. L. Wagner, H. C. Morais, I. R. Diniz, T. A. Kursar, and P. D. Coley. 2007. Host specificity of Lepidoptera in tropical and temperate forests. *Nature* 448:696–699.

Easterling, D. R., G. A. Meehl, C. Parmesan, S. A. Changnon, T. R. Karl, and L. O. Mearns. 2000. Climate extremes: observations, modeling, and impacts. *Science* 289:2068–2074.

Elton, C. S. 1958. *The Ecology of Invasions by Animals and Plants*. Chapman & Hall, London.

Eveleigh, E. S., K. S. McCann, P. C. McCarthy, S. J. Pollock, C. J. Lucarotti, B. Morin, G. A. McDougall, D. B. Strongman, J. T. Huber, J. Umbanhowar, and L. D. B. Faria. 2007. Fluctuations in density of an

outbreak species drive diversity cascades in food webs. *Proceedings of the National Academy of Sciences of the USA* 104:16976–16981.

Feeley, K. J., and J. W. Terborgh. 2008. Direct versus indirect effects of habitat reduction on the loss of avian species from tropical forest fragments. *Animal Conservation* 11:353–360.

Food and Agricultural Organization (FAO). 2011. Forest health. http://www.fao.org/forestry/pests/en/

Gauld, I. D., K. J. Gaston, and D. H. Janzen. 1992. Plant allelochemicals, tritrophic interactions and the anomalous diversity of tropical parasitoids: the "nasty" host hypothesis. *Oikos* 65:353–357.

Gentry, A. H. 1982. Patterns of neotropical plant-species diversity. *Evolutionary Biology* 15:1–85.

Gentry, A. H. 1988. Changes in plant community diversity and floristic composition on environmental and geographical gradients. *Annals of the Missouri Botanical Garden* 75:1–34.

Gerhardt, K. 1998. Leaf defoliation of tropical dry forest tree seedlings – implications for survival and growth. *Trees – Structure and Function* 13:88–95.

Ghimre, K., and A. Dongre. 2001. Sal borer problem in Indian Sal Forests: a serious threat to *Shorea robusta* forests ecosystems of India. http://www.iifm.ac.in/databank/problems/salborer.html

Gilman, S. E., M. C. Urban, J. Tewksbury, G. W. Gilchrist, and R. D. Holt. 2010. A framework for community interactions under climate change. *Trends in Ecology and Evolution* 25:325–331.

Godfray, H. C. J., and M. P. Hassell. 1989. Discrete and continuous insect populations in tropical environments. *Journal of Animal Ecology* 58:153–174.

Gray, B. 1972. Economic tropical forest entomology. *Annual Review of Entomology* 17:313–354.

Greenbank, D. O. 1956. The role of climate and dispersal in the initiation of outbreaks of the spruce budworm in New Brunswick. *Canadian Journal of Zoology* 34:453–476.

Grogan, J. 2001. Bigleaf mahogany (*Swietenia macrophylla* King) in southeast Pará, Brazil: a life history study with management guidelines for sustained production from natural forests. PhD dissertation, Yale University.

Haines, W. P., M. L. Heddle, P. Welton, and D. Rubinoff. 2009. A recent outbreak of the hawaiian koa moth, *Scotorythra paludicola* (Lepidoptera: Geometridae), and a review of outbreaks between 1892 and 2003. *Pacific Science* 63:349–369.

Hall, J. B., and M. D. Swaine. 1976. Classification and ecology of closed-canopy forest in Ghana. *Journal of Ecology* 64:913–951.

Hastings, A. 1999. Outbreaks of insects: a dynamic approach. Pages 206–215 *in* B.A. Hawkins and H.V. Cornell (editors), *Theoretical Approaches to Biological Control*. Cambridge University Press, Cambridge.

Hernandez, J. V., F. Osborn, B. Herrera, C. V. Liendo-Barandiaran, J. Perozo, and D. Velasquez. 2009. Larvae–pupae parasitoids of *Hylesia metabus* Cramer (Lepidoptera: Saturniidae) in northeastern Venezuela: a case of natural biological control. *Neotropical Entomology* 38:243–250.

Hölldobler B., and E. O. Wilson. 1990. *The Ants*. Harvard University Press, Cambridge, MA.

Hulme, M., and D. Viner. 1998. A climate change scenario for the tropics. *Climatic Change* 39:145–177.

Hunter, A. F. 1991. Traits that distinguish outbreaking and nonoutbreaking Macrolepidoptera feeding on northern hardwood trees. *Oikos* 60:275–282.

Hunter, A. F. 1995. Ecology, life history, and phylogeny of outbreak and nonoutbreak species. Pages 41–64 *in* N. Cappuccino and P. W. Price (editors), *Population Dynamics: New Approaches and Synthesis*. Oxford University Press, New York.

Hunter, M. D. 2001. Multiple approaches to estimating the relative importance of top-down and bottom-up forces on insect populations: experiments, life tables, and time-series analysis. *Basic and Applied Ecology* 2:295–309.

Huston, M. 1980. Soil nutrients and tree species richness in Costa Rican forests. *Journal of Biogeography* 7:147–157.

Iserhard, C. A., L. A. Kaminski, M. O. Marchiori, E. C. Teixeira, and H. P. Romanowski. 2007. Occurrence of lepidopterism caused by the moth *Hylesia nigricans* (Berg) (Lepidoptera: Saturniidae) in Rio Grande do Sul State, Brazil. *Neotropical Entomology* 36:612–615.

Itkao, T., and M. Yamauti. 2004. Severe drought, leafing phenology, leaf damage and lepidopteran abundance in the canopy of a Bornean aseasonal tropical rain forest. *Journal of Tropical Ecology* 20:479–482.

Jactel, H., and E. G. Brockerhoff. 2007. Tree diversity reduces herbivory by forest insects. *Ecology Letters* 10:835–848.

Jaksic, F. M. 2001. Ecological effects of El Niño in terrestrial ecosystems of western South America. *Ecography* 24:241–250.

Janzen, D. H. 1981. Patterns of herbivory in a tropical deciduous forest. *Biotropica* 13:271–282.

Janzen D. H. 1983. *Costa Rican Natural History*. University of Chicago Press, Chicago.

Janzen, D. H. 1984. Natural history of *Hylesia lineata* (Saturniidae, Hemileucinae) in Santa Rosa National Park, Costa Rica. *Journal of the Kansas Entomological Society* 57:490–514.

Janzen, D. H. 1993. Caterpillar seasonality in a Costa Rican dry forest. Pages 448–477 *in* N. E. Stamp, and T. M. Casey (editors), *Caterpillars: Ecological and Evolutionary Constraints on Foraging*. Chapman & Hall, New York.

Johnson, D. M., U. Buntgen, D. C. Frank, K. Kausrud, K. J. Haynes, A. M. Liebhold, J. Esper, and N. C. Stenseth. 2010. Climatic warming disrupts recurrent alpine insect outbreaks. *Proceedings of the National Academy of Sciences of the USA* 107:20576–20581.

Kalshoven, L. G. E. 1953. Important outbreaks of insect pests in the forests of Indonesia. *Transactions of the 9th International Congress of Entomology* 2:229–234.

Knight, T. M., M. W. McCoy, J. M. Chase, K. A. McCoy, and R. D. Holt. 2005. Trophic cascades across ecosystems. *Nature* 437:880–883.

Kondoh, M. 2003. Habitat fragmentation resulting in overgrazing by herbivores. *Journal of Theoretical Biology* 225:453–460.

Lara E. F. 1970. *Problemas y procedimientos bananeros en la zona Atlántica de Costa Rica*. Imprenta Trejos Anos, San Jose, Costa Rica.

Leigh, E. G., Jr., P. Davidar, C. W. Dick, J-P. Puyravaud, J. Terborgh, H. ter Steege, and S. J. Wright. 2004. Why do some tropical forests have so many species of trees? *Biotropica* 36:447–473.

Leigh, E. G., Jr., G. J. Vermeij, and M. Wikelski. 2009. What do human economies, large islands and forest fragments reveal about the factors limiting ecosystem evolution? *Journal of Evolutionary Biology* 22:1–12.

Letourneau, D. K. 1998. Ants, stem-borers, and fungal pathogens: experimental tests of a fitness advantage in *Piper* ant-plants. *Ecology* 79:593–603.

Letourneau, D. K. 2004. Mutualism, antiherbivore defense, and trophic cascades: *Piper* ant-plants as a mesocosm for experimentation. Pages 5–33 *in* L. A. Dyer and A. P. N. Palmer (editors), *Piper: A Model Genus for Studies of Phytochemistry, Ecology, and Evolution*. Kluwer Academic, New York.

Letourneau, D. K., and L. A. Dyer. 1998. Density patterns of *Piper* ant-plants and associated arthropods: top predator cascades in a terrestrial system? *Biotropica* 30:162–169.

Letourneau, D. K., J. A. Jedlicka, S. G. Bothwell, and C. R. Moreno. 2009. Effects of natural enemy biodiversity on the suppression of arthropod herbivores in terrestrial ecosystems. *Annual Review of Ecology Evolution and Systematics* 40:573–592.

Logan, J. A., J. Regniere, and J. A. Powell. 2003. Assessing the impacts of global warming on forest pest dynamics. *Frontiers in Ecology and the Environment* 1:130–137.

Long, Z., C. Mohler, and W. P. Carson. 2003. Herbivory, litter accumulation, and plant diversity: applying the resource concentration hypothesis to plant communities. *Ecology* 84:652–665.

Lowman, M. D. 1997. Herbivory in forests: from centimeters to megameters. Pages 135–149 *in* A. D. Watt, N. E. Stork, and M. D. Hunter (editors), *Forests and Insects*. Chapman & Hall, New York.

Maron, J. L., and S. Harrison. 1997. Spatial pattern formation in an insect host–parasitoid system. *Science* 278:1619–1621.

Massad, T. J. 2009. The efficacy and environmental controls of plant defenses and their application to tropical reforestation. PhD dissertation, Tulane University.

Massad, T. J., and L. A. Dyer. 2010. A meta-analysis of the effects of global environmental change on plant–herbivore interactions. *Arthropod–Plant Interactions* 4:181–188.

Massad, T. J., Fincher, R. M., Smilanich, A. M., and L. A. Dyer. 2011. A quantitative evaluation of major plant defense hypotheses, nature versus nurture, and chemistry versus ants. *Arthropod–Plant Interactions* 5:125–139.

Matlock, R. B., and R. de la Cruz. 2002. An inventory of parasitic Hymenoptera in banana plantations under two pesticide regimes. *Agriculture Ecosystems & Environment* 93:147–164.

McCloskey, S. P. J., L. D. Daniels, and J. A. Mclean. 2009. Potential impacts of climate change on western hemlock looper outbreaks. *Northwest Science* 83:225–238.

Meyer, S. T., I. R. Leal, and R. Wirth. 2009. Persisting hyper-abundance of leaf-cutting ants (*Atta* spp.) at the edge of an old Atlantic forest fragment. *Biotropica* 41:711–716.

Moreau, G., E. S. Eveleigh, C. J. Lucarotti, and D. T. Quiring. 2006. Ecosystem alteration modifies the relative strengths of bottom-up and top-down forces in a herbivore population. *Journal of Animal Ecology* 75:853–861.

Moreira, S. C., J. C. de Lima, L. Silva, and V. Haddad. 2007. Description of an outbreak of lepidopterism (dermatitis associated with contact with moths) among sailors in Salvador, State of Bahia. *Revista da Sociedade Brasileira de Medicina Tropical* 40:591–593.

Myers, J. H. 1988. Can a general hypothesis explain population-cycles of forest Lepidoptera? *Advances in Ecological Research* 18:179–242.

Nair, K. S. S. 2001. *Pest Outbreaks in Tropical Forest Plantations: Is There a Greater Risk for Exotic Tree Species?* Center for International Forestry Research, Bogor, Indonesia.

Nair, K. S. S. 2000. *Insect Pests and Diseases in Indonesian Forests: An Assessment of the Major Threats, Research Efforts and Literature.* Center for International Forestry Research, Bogor, Indonesia.

Nair, K. S. S. 2007. *Tropical Forest Insect Pests.* Cambridge University Press, Cambridge.

Nascimento, M. T., and J. Proctor. 1994. Insect defoliation of a monodominant Amazonian rainforest. *Journal of Tropical Ecology* 10:633–636.

Nothnagle, P. J., and J. C. Schultz. 1987. What is a forest pest? Pages 59–80 *in* P. Barbosa and J. C. Schultz (editors), *Insect Outbreaks.* Academic Press, San Diego.

Novotny, V., and Y. Basset. 2000. Rare species in communities of tropical insect herbivores: pondering the mystery of singletons. *Oikos* 89:564–572.

Opler, P. A., G. W. Frankie, and H. G. Baker. 1980. Comparative phenological studies of treelet and shrub species in tropical wet and dry forests in the lowlands of Costa Rica. *Journal of Ecology* 68:167–188.

Ostmark, E. H. 1974. Economical insect pests of bananas. *Annual Review of Entomology* 19:161–175.

Parry, D., D. A. Herms, and W. J. Mattson. 2003. Responses of an insect folivore and its parasitoids to multiyear experimental defoliation of aspen. *Ecology* 84:1768–1783.

Perfecto, I., J. H. Vandermeer, G. L. Bautista, G. I. Nunez, R. Greenberg, P. Bichier, and S. Langridge. 2004. Greater predation in shaded coffee farms: the role of resident neotropical birds. *Ecology* 85:2677–2681.

Pescador, A. R. 1993. The effects of a multispecies sequential diet on the growth and survival of a tropical polyphagous caterpillar. *Entomologia Experimentalis et Applicata* 67:15–24.

Pescador, A. R. 1995. Distribution and abundance of *Hylesia ineata* egg masses in a tropical dry forest in western Mexico. *Southwestern Entomologist* 20:367–375.

Philips, O. L., P. Hall, A. H. Gentry, S. A. Sawyer, and R. Vasquez. 1994. Dynamics and species richness of tropical rain forests. *Proceedings of the National Academy of Sciences of the USA* 91:2805–2809.

Piyakarnchana, T. 1981. Severe defoliation of *Avicennia alba* BL. by larvae of *Cleora injectaria* Walker. *Journal of the Science Society of Thailand* 7:33–36.

Pogue, M. G., and A. Aiello. 1999. Description of the immature stages of three species of *Eulepidotis guenee* (Lepidoptera: Noctuidae) with notes on their natural history. *Proceedings of the Entomological Society of Washington* 101:300–311.

Ray, C., and A. Hastings. 1996. Density dependence: are we searching at the wrong spatial scale? *Journal of Animal Ecology* 65:556–566.

Redfearn, A., and S. L. Pimm. 1988. Population variability and polyphagy in herbivorous insect communities. *Ecological Monographs* 58:39–55.

Richards, L. A., and P. D. Coley. 2008. Combined effects of host plant quality and predation on a tropical lepidopteran: a comparison between treefall gaps and the understory in Panama. *Biotropica* 40:736–741.

Roland, J. 1993. Large-scale forest fragmentation increases the duration of tent caterpillar outbreak. *Oecologia* 93:25–30.

Roonwal, M. L. 1978. The biology, ecology and control of the sal heartwood borer, *Hoplocerambyx spinicornis*: a review of recent work. *Indian Journal of Entomology* 1:107–120.

Root, R. B. 1973. Organization of a plant–arthropod association in simple and diverse habitats: the fauna of collards (*Brassica oleracea*). *Ecological Monographs* 43:95–124.

Root, R. B., and N. Cappuccino. 1992. Patterns in population-change and the organization of the insect community associated with goldenrod. *Ecological Monographs* 62:393–420.

Schowalter, T. D. 1996. *Insect Ecology: An Ecosystem Approach.* Academic Press, San Diego.

Schowalter, T. D., and M. D. Lowman. 1999. Forest herbivory: insects. Pages 253–270 *in* L. R. Walker (editor), *Ecosystems of Disturbed Ground.* Elsevier, Amsterdam.

Scriber, J. M. 1973. Latitudinal gradients in larval feeding specialization of the world Papilionidae (Lepidoptera). *Psyche* 73:355–373.

Singh, R., G. S. Goraya, C. Singh, H. Kumar, and S. Kumar. 2001. Mortality of chir pine trees by insect borers in Morni Hills, Haryana: a case study. *Indian Forester* 127:1279–1286.

Singh, T. V. K., and J. Satyanarayana. 2009. Insect outbreaks and their management. Pages 331–350 *in* R. Peshin, and A. K. Dhawan (editors), *Integrated Pest Management: Innovation-Development Process*. Springer, New York.

Specht, A., A. C. Formentini, and E. Corseuil. 2006. Biology of *Hylesia nigricans* (Berg) (Lepidoptera, Saturniidae, Hemileucinae). *Revista Brasileira de Zoologia* 23:248–255.

Srygley, R. B., R. Dudley, E. G. Oliveira, R. Aizprua, N. Z. Pelaez, and A. J. Riveros. 2010. El Nino and dry season rainfall influence hostplant phenology and an annual butterfly migration from neotropical wet to dry forests. *Global Change Biology* 16:936–945.

Stephens, C. S. 1984. Ecological upset and recuperation of natural control of insect pests in some Costa Rican banana plantations. *Turrialba* 34:101–105.

Stireman, J. O., L. A. Dyer, D. H. Janzen, M. S. Singer, J. T. Li, R. J. Marquis, R. E. Ricklefs, G. L. Gentry, W. Hallwachs, P. D. Coley, J. A. Barone, H. F. Greeney, H. Connahs, P. Barbosa, H. C. Morais, and I. R. Diniz. 2005. Climatic unpredictability and parasitism of caterpillars: implications of global warming. *Proceedings of the National Academy of Sciences of the USA* 102:17384–17387.

Stireman, J. O., L. A. Dyer, and R. B. Matlock. 2004. Top-down forces in managed versus unmanaged habitats. Pages 303–323 *in* P. Barbosa, and I. Castellanos (editors), *Ecology of Predator–Prey Interactions*. Oxford University Press, Oxford.

Strong D. R., J. H. Lawton, and T. R. E. Southwood. 1984. *Insects on Plants: Community Patterns and Mechanisms*. Harvard University Press, Cambridge, MA.

Terborgh, J., L. Lopez, P. Nunez, M. Rao, G. Shahabuddin, G. Orihuela, M. Riveros, R. Ascanio, G. H. Adler, T. D. Lambert, and L. Balbas. 2001. Ecological meltdown in predator-free forest fragments. *Science* 294:1923–1926.

Thrupp, L. A. 1990. Entrapment and escape from fruitless insecticide use: lessons from the banana sector of Costa Rica. *International Journal of Environmental Studies* 36:173–189.

Tin, N. T. 1990. Biology of the sawfly *Schizocera* sp. (Hymenoptera: Agridae) in Northern Vietnam. Pages 194–197 *in* C. Hutacharern, K. G. MacDicken, M. H. Ivory, and K. S. S. Nair (editors). FAO, Regional Office for Asia and the Pacific, Bangkok.

Torres, J. A. 1992. Lepidoptera outbreaks in response to successional changes after the passage of Hurricane Hugo in Puerto Rico. *Journal of Tropical Ecology* 8:285–298.

Turchin, P. 2003. *Complex Population Dynmaics: A Theoretical/Empirical Synthesis*. Princeton University Press, Princeton.

Van Bael, S. A., A. Aiello, A. Valderrama, E. Medianero, M. Samaniego, and S. J. Wright. 2004. General herbivore outbreak following an El Niño–related drought in a lowland Panamanian forest. *Journal of Tropical Ecology* 20:625–633.

Vandermeer, J., I. Perfecto, and S. Philpott. 2010. Ecological complexity and pest control in organic coffee production: uncovering an autonomous ecosystem service. *Bioscience* 60:527–537.

van Schaik, C. P., J. W. Terborgh, and S. J. Wright. 1993. Phenology of tropical forests: adaptive signficance and consequences for primary consumers. *Annual Review of Ecology and Systematics* 24:353–377.

Veldtman, R., M. A. McGeoch, and C. H. Scholtz. 2007. Can life-history and defence traits predict the population dynamics and natural enemy responses of insect herbivores? *Ecological Entomology* 32:662–673.

Vilela, E. F. 1986. Status of leaf-cutting ant control in forest plantations in Brazil. Pages 399–408 *in* C. S. Lofgren and R. K. Vander Meer (editors), *Fire Ants and Leaf-Cutting Ants: Biology and Management*. Westview Press, Boulder, CO.

Wagner M. R., S. K. N. Atuahene, and J. R. Cobbinah. 1991. *Forest Entomology in West Tropical Africa: Forest Insects of Ghana*. Kluwer Academic, Dordrecht.

Wallner, W. E. 1987. Factors affecting insect population dynamics: differences between outbreak and non-outbreak species. *Annual Review of Entomology* 32:317–340.

Whitten, A. J., and S. J. Damanik. 1986. Mass defoliation of mangroves in Sumatra, Indonesia. *Biotropica* 18:176.

Wiens, J. J., D. D. Ackerly, A. P. Allen, B. L. Anacker, L. B. Buckley, H. V. Cornell, E. I. Damschen, T. J. Davies, J. A. Grytnes, S. P. Harrison, B. A. Hawkins, R. D. Holt, C. M. Mccain, and P. R. Stephens. 2010. Niche conservatism as an emerging principle in ecology and conservation biology. *Ecology Letters* 13:1310–1324.

Wolda, H. 1978. Fluctuations in abundance of tropical insects. *American Naturalist* 112:1017–1045.

Wolda, H. 1983. Long-term stability of tropical insect populations. *Researches on Population Ecology* 112–126.

Wolda, H., and R. Foster. 1978. *Zunacetha annulata* (Lepidoptera: Dioptidae): an outbreak insect in a neotropical forest. *Geo-Eco-Trop* 2:443–454.

Wolda, H. 1992. Trends in abundance of tropical forest insects. *Oecologia* 89:47–52.

Wong, M., S. J. Wright, S. P. Hubbell, and R. B. Foster. 1990. The spatial pattern and reproductive consequences of outbreak defoliation in *Quararibea asterolepis*, a tropical tree. *Journal of Ecology* 78:579–588.

Yang, L. H., K. F. Edwards, J. E. Byrnes, J. L. Bastow, A. N. Wright, and K. O. Spence. 2010. A meta-analysis of resource pulse–consumer interactions. *Ecological Monographs* 80:125–151.