10 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

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10.1 Summary

We provide a new and general rule that predicts when native insect herbivores will have a major influence on dominant native plant species in communities and ecosystems worldwide. We argue that native insect herbivores will function as classic keystone species whenever their hosts become abundant and form large, persistent, dense stands. Specifically, our Host Concentration Model predicts that the impact of specialist insect herbivores will be more severe on a per individual basis as host species build up to form large and dense stands. The impact of these native insect herbivores, while important at non-outbreak levels, will be most important during major bouts of defoliation that occur during periodic insect outbreaks. Our review of the literature suggests that such outbreaks are common from a phytocentric perspective. Consequently, these insect outbreaks will have a major influence on ecosystem function via their ability to regulate and reduce the abundance of host species that may typically be the superior competitor across the landscape. Finally, we believe that this Host Concentration Model will predict when specialist insects will regulate plant communities and ecosystems better than resource supply models that rely on gradients in fertility or productivity.

10.2 Introduction

"The role of rare events, such as outbreaks … cannot be ignored as a force structuring ecological communities just because they are rare"

(Strong et al. 1984).

We propose a general rule that predicts when native insect herbivores will have very strong top-down effects on plant communities and ecosystems in

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any terrestrial or wetland habitat worldwide. Specifically, native specialist insect herbivores will function as a keystone species (sensu Paine 1969) whenever their hosts become abundant and form large, persistent, dense stands (see also Carson and Root 2000; Long et al. 2003). This Host Concentration Model results from a modification and extension of Root's resource concentration hypothesis (Root 1973), which states "...herbivores are more likely to find and remain on hosts that are growing in dense or nearly pure stands". There is ample empirical evidence to support this hypothesis for plant populations (see a review by Andow 1991; Joshi et al., Chap. 6, this Vol.), but its importance has only been recently extended to predict when insects will control vegetation dynamics (Carson and Root 2000; Long et al. 2003). This rule will operate whenever insect herbivores can track host plant abundance and should work in nearly any ecosystem at spatial scales from a few tens of meters to thousands of square kilometers. While outbreaks of native insects are not required for the rule to operate (see Long et al. 2003) or for insect herbivory to alter community dynamics (e.g. Bach 1994; Carson and Root 1999), the influence of insects will be most pronounced and important during outbreak events at both the community and ecosystem levels (e.g. Carson and Root 2000; Lovett et al. 2002). This rule leads to the conclusion that species-level trophic cascades will commonly lead to community-level trophic cascades in terrestrial communities whenever hosts are abundant, long-lived perennial plant species (cf. Polis and Strong 1996; Polis 1999). Furthermore, this rule means that as a superior plant competitor increases in density, becomes widespread and suppresses the abundance of subordinate plant species, it will not be long before it is found and attacked by its enemies. These attacks will decrease the abundance of the dominant plant so as to promote plant species coexistence, increase plant species diversity, lower standing crop biomass for potentially long periods of time and likely alter successional trajectories (e.g. Carson and Root 2000; Bach 2001).

10.3 The Significance of Insect Outbreaks

This general rule runs counter to much conventional wisdom and several theoretical lineages in ecology. First, outbreaks of native insects have often been considered rare and unusual events (Hairston et al. 1960; Strong et al. 1984; Faeth 1987; Owen 1987; Hartley and Jones 1997; Lowman 1997; Weisser and Siemann, Chap. 1, this Vol.; but see Matson and Addy 1975). Consequently, a prevailing view is that outbreaks are too infrequent and their effect too ephemeral to cause substantial and enduring top-down effects on plant communities. Consistent with this view, theories or discussions of trophic cascades rarely give outbreaks a place of importance (e.g. Polis 1999). We disagree with this perspective. Outbreaks of native insects appear to be nearly ubiquitous in ecosystems worldwide (Table 10.1). In addition, it is likely that these outbreaks result in strong and lasting top-down effects on these communities (e.g. Carson and Root 2000; Bach 2001). Also, these outbreaks appear to be much more common and more devastating in dense host stands (see below). Finally, outbreaks tend to occur repeatedly during the life span of long-lived perennial plant species; thus these events are not uncommon from a phytocentric perspective.

Second, outbreaks by their very nature are instances where plant defences, enemies, intra- or interspecific interactions among insects, and other processes (see Polis 1999) fail to prevent runaway consumption which results in major food depletion for the outbreaking insect (Berryman 1987). These bottom-up and top-down forces may 'kick in' during or following the outbreak and reduce herbivore numbers and their impact. By then, however, insect damage already will have had a strong top-down effect on the plant community. Consequently, theories regarding top-down control of insect herbivores by their enemies and bottom-up theories regarding plant defences or nutrition do not apply or only ameliorate or modify the effect of the outbreak. Below, we provide evidence for and explore the community- and ecosystem-level consequences of the following observations: (1) insect outbreaks occur in the vast majority of ecosystems and community types worldwide; (2) insect outbreaks are more common and more devastating per host in large, dense and continuous host stands; (3) outbreaking insects function as keystone species by reducing the abundance of the dominant species and increasing diversity; (4) insect outbreaks are common relative to host life span yet may often go unnoticed; (5) chrysomelid beetles and lepidoptera seem to be responsible for the majority of outbreaks. Finally, we briefly discuss and compare the Host Concentration Model with resource supply models.

10.3.1 Insect Outbreaks Are Common in Numerous Community Types Worldwide

Very few terrestrial communities and ecosystems are spared from outbreaks by native phytophagous insects (Carson and Root 2000; Table10. 1). Insect outbreaks appear to be common in numerous ecosystems including grasslands, mangroves, old-fields, heathlands, dry tropical forests, *Eucalyptus* forest and even in some wetland communities. Overall, we have identified more than 30 ecosystem and community types worldwide where outbreaks occur and cause major defoliation, often over vast areas, of the dominant plant species. Even relatively abundant species in diverse tropical forests may suffer from repeated insect outbreaks (Wolda 1978; Wolda and Foster 1978; Janzen 1981). Insect outbreaks appear to be particularly devastating in forest ecosystems. For example, numerous papers describe these outbreaks and their impact in northern and boreal forests (Table 10.1; see also Berryman 1987;

Table 10.1. Occurrence of insect outbreaks that caused major defoliation to dominant or very abundant species in communities and biomes throughout the world. We define an outbreak as an explosive increase in the abundance of a particular insect species that occurs over a relatively short period of time (Berryman 1987) and causes major defoliation on host species. This list, although extensive, is not meant to be comprehensive but rather to demonstrate the potential of these outbreaks to strongly influence a diverse array of community types. With a few exceptions, the vast majority of these insect and plant species are native and most of the insects are specialized on their associated host plants or cause the majority of their damage on the dominant species in the community with little damage to subordinate species. This table omits (with one Chrysomelidae exception) the 24 species of lowland dry forest trees that suffered total defoliation by insects (mostly Lepidoptera) described by Janzen (1981) and the numerous grasshopper defoliations occurring in US grasslands described by Joern (1989). Berryman (1987) and Schultz (1987) also describe some additional outbreaks in forested systems

Insect taxon	Dominant plant species attacked	Community type and geographic region	Source
Coleoptera			
Trirhabda nitidicollis (Chrysomelidaeae)	*Chrysothamnus nauseosus*	Rangeland (USA)	Massey and Pierce (1960); Dalen et al. (1986)
Trirhabda pilosa; *T. attenuata* (Chrysomelidae)	*Artemisia tridentata*, *A. tripartita*	Sagebrush-dominated rangeland (Canada and USA)	Pringle (1960); Banham (1961)
Trirhabda virgata, *Trirhabda canadensis* (Chrysomelidae)	*Solidago altissima*, *S canadensis*	Early successional old-field (USA)	McBrien et al. (1983); Root (1996); Morrow and Olfelt (2003)
Microrhopala vitata (Chrysomelidae)	*Solidago altissima*	Early successional old-field (USA)	Carson and Root (2000)
Pyrrhalta nymphaeae (Chrysomelidae)	*Nuphar luteum*	Wetlands (USA)	Wallace and O'Hop (1985)
Lochmaea suturalis (Chrysomelidae)	*Calluna*	Heathlands (Europe and Scotland)	Berdowski and Zeilinga (1987); Scandrett and Gimingham (1991)
Altica cordata[a] (Chrysomelidae)	*Salix cordata*	*Salix*-dominated early successional sand dunes (USA)	Bach (1994, 2001)
Chrysophtharta bimaculata (Chrysomelidae)	*Eucalyptus* spp.	*Eucalyptus* forest (Australia)	Ohmart (1996)
Chrysomela scripta (Chrysomelidae)	*Populus fremontii*	Cottonwood gallery forest (USA)	Anderson and Nelson (2002)
Chrysomela lapponica (Chrysomelidae)	*Salix borealis*	Not reported (Russia)	Zvereva et al. (1997); Zvereva (2002)
Altica spp.[b] (Chrysomelidae)	*Ludwigia leptocarpa*, L. *decurrens*	Wetlands (USA)	Scott and Haskins (1987)

Dorynota sp. (Chrysomelidae)	*Tabebuia impetiginosa*	Tropical lowland dry forest (Central America)	Janzen (1981)
Dendroctonus rufipennis (Scolytidae)	*Picea engelmannii*, *Abies lasiocarpa*	Subalpine spruce-fir forests (USA including Alaska and Canada)	Veblen et al. (1991); Parish et al. (1999); Matouska et al. (2001)
Dendroctonus ponderosae (Scolytidae)	*Pinus contorta*	Lodgepole pine forests (USA)	Romme et al. (1986)
Hadramphus spinipennis (Curculionidae)	*Aciphylla dieffenbachii*	Pasture (New Zealand)	Schops (2002)
Elaphidinoides spp (Cerambycidae)	*Rhizophora mangle*	Mangroves (Belize)	Feller (2002)
Lepidoptera			
Choristoneura pinus pinus (Tortricidae)	*Pinus banksiana*	Suboreal forests (USA and Canada	McCullough (2000)
Choristoneura fumiferana, *C. biennis* *C. occidentalis* among other *Choristoneura* species (Tortricidae)	*Abies balsamea*, *A. lasiocarpa*, *Picea glauca*, *P. engelmannii*	Spruce-fir forests (USA and Canada)	Filion et al. (1998); McCullough et al. (1998); Parish and Antos (2002)
Acleris variana (Tortricidae)	*Abies balsamea*	Balsam fir forests	Miller (1966)
Hypsidae[c]	*Shorea albida*	*Shorea albida* forest/peat swamps (Sarawak, Malaysia)	Anderson (1961)
Perthida glyphopha (Incurvariidae)	*Eucalyptus marginata*	*Eucalyptus* forest (Australia)	Abbott (1990)
Epirrita autumnata also called *Oporinia autumnata* (Geometridae)	*Betula pubescens*	Mountain birch forests (Europe)	Tenow (1972); Laine and Niemela (1980); Ruohomaki et al. (2000)
Voracia casuariniphaga	*Casuarina junghuhniana*	Ridge-top stands of *Voracia casuariniphaga* (Indonesia)	Nair (2000)
Eulepidotis phrygionia (Noctuidae)	*Peltogyne gracilipes*	Monodominant Amazonian rainforest (Brazil)	Nascimento and Proctor (1994)
Spodoptera eridania (Noctuidae)	*Phytolacca rivinoides*, *Impatiens wallerana*, *Ipomoea tiliacea*, *Cestrum macrophylum*	Early successional tropical forest[d] (Puerto Rico)	Torres (1992)
Spodoptera litura (Noctuidae)	*Pisonia grandis*	*Pisonia grandis* subtropical forest (Polynesia)	Brooke et al. (1996)
Cerapteryx graminis (Noctuidae)	Grasses including *Poa pratensis* and *Deschampsia cespitosa*	Meadow vegetation (Europe)	Danell and Ericson (1990)
Operophtera brumata (Geometridae)	*Calluna vulgaris*, *Prunus padus*	Heathlands (Scotland), *Prunus*-dominated secondary forest (Fennoscandia)	Kerslake et al. (1996); Tikkanen and Roininen (2001)
Malacosoma disstria (Lasiocampidae)	*Populus tremuloides*, *Liquidambar styraciflua*	Aspen stands (Canada), Bottomland hardwoods (USA)	Hildahl and Reeks (1960) Siemann and Rogers (2003)

Table 10.1. (*Continued*)

Insect taxon	Dominant plant species attacked	Community type and geographic region	Source
Eulepidotis sp. (Noctuidae)	*Quararibea asterolepis*	Seasonally moist tropical forest (Central America)	Wong et al. (1990)
Zunacetha annulata (Dioptidae)	*Hybanthus prunifolius*	Seasonally moist tropical forest (Central America)	Wolda and Foster (1978)
Ammalo sp. (Arctiidae)	*Ficus* sp.	Seasonally moist tropical forest (Central America)	Wolda and Foster (1978)
Orgyia vetusta (Lymantriidae)	*Lupinus arboreus*	Coastal grassland (USA)	Harrison and Maron (1995)
Hepialus californicus (Hepialidae)	*Lupinus arboreus*	Coastal grassland (USA)	Strong et al. (1995)
Aroga websteri (Gelechiidae)	*Artemisia tridentata*	Sagebrush-dominated rangeland (USA)	Andres (1971)
Cleora injectalia (Geometridae), *Ophiusa melicerta* (Noctuidae), *Nephopterix syntaractis* (Pyralidae), *Junonia evarete* (Nymphalidae), *Hyblaea purea* (Hyblaeidae) *Planotortrix avicenniae*, (Tortricidae), *Phocides pigmalion* (Hersperiidae)	*Avicennia alba*, *A marina*, *A. germinans*, *Rhizophora* spp., *Excoecaria agallocha*	Mangroves (Central America, Asia, Australia, New Zealand and Indonesia)	Piyakarnchana (1981); West and Thorogood (1985); Whitten and Damanik (1986); Anderson and Lee (1995); Ellison and Farnsworth (1996); Burns (1998); Saur et al. (1999)
Homoptera			
Magicicada spp. (Cicadidae)	*Cornus drummondii*	*Cornus*-dominated early successional shrubland (USA)	Cook et al. (2001); Cook and Holt (2002)
Magicicada septendecim (Cicadidae)	*Quercus ilicifolia*	Scrub oak communities (USA)	Karban (1980)
Orthoptera			
Didymuria violescens (Phasmatidae)	*Eucalyptus delegatensis*, *E. robertsoni*	Readshaw (1965); Mazanec (1968) *Eucalyptus* forest (Australia)	

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[a] Insects may not have been at outbreak levels but caused heaving defoliation.
[b] Insects did not reach outbreak levels but were very abundant.
[c] The insect species responsible remains unclear from the published report.
[d] These species became 'very abundant' following Hurricane Hugo in 1989.

Carson and Root 2000). Lowman (1997) has suggested that outbreaks in forests occur frequently but are overlooked because they are patchy and go unnoticed high in the canopy (see also Wolda and Foster 1978).

10.3.2 Insect Outbreaks Are More Common and More Devastating Per Host in Large, Dense and Continuous Host Stands

The Host Concentration Model provides a viable insect–plant feedback mechanism whereby insect impact and damage increases as dominant plant species or superior competitors become more and more dense or concentrated (e.g. Long et al. 2003). If insect damage and subsequent impact are greater (per capita) and insect outbreaks more common in larger and denser stands of hosts, then insect herbivory may commonly exert strong top-down effects on plant communities whenever superior competitors increase sufficiently in density and area (cf. Strong 1992; Polis and Strong 1996; Polis 1999). Indeed, there seems to be a growing consensus that outbreaks are more likely and insect impact greater in natural vegetation where one or a few plant species are dominant, abundant or aggregated, thereby forming large, continuous host stands (Whitmore 1975; Morrow and Fox 1989; Bach 1994; Morris et al. 1996; Schowalter 1996a; Bergeron and Leduc 1998; Cappucino et al. 1998; Carson and Root 2000; Dymerski et al. 2001; Nair 2000, 2001; Schops 2002; Long et al. 2003).

That insect outbreaks occur more frequently and do more damage per host plant in large, continuous host stands comes as no surprise to ecologists who study northern, boreal and subalpine ecosystems (see a review by McCullough et al. 1998; Table 10.1). Indeed, Bergeron and Leduc (1998) concluded that in balsam fir forests (*Abies balsamea*) "...mortality due to outbreaks appears to be more important in regions where *Abies balsamea* is dominant". They further concluded that there was "...a direct correlation between mortality and the abundance of the host species". This relationship between host concentration and insect outbreaks appears to hold for numerous community types. For example, insect outbreaks have defoliated hundreds of square kilometers of mangroves in locations worldwide (Table 10.1; Anderson 1961; Whitten and Damanik 1986). Mangroves are typically characterized by dense stands of one or a few dominant species. Similarly, Australian *Eucalyptus* forests are low-diversity forests dominated by the genus *Eucalyptus*. These forests suffer heavy insect damage and outbreaks are common relative to the life span of the hosts (Morrow and Fox 1989; Fox and Morrow 1992; Table 10.1). Morrow and Fox (1989) concluded that the primary factor that caused these forests to suffer heavy damage was host concentration. Likewise, Nair (2000) concluded that in tropical Indonesian forests "...most outbreaks have been recorded in tree species that occur gregariously....A high host density appears to be a key factor promoting pest outbreaks" (see also Nair 2001).

Indeed, Nascimento and Proctor (1994) documented an outbreak event that severely damaged a monodominant Amazonian rainforest and Wolda and Foster (1978) documented an outbreak of a lepidopteran that attacked what is by far the most abundant woody species – *Hybanthus prunifolius* – on Barro Colorado Island in Panama. There are now numerous examples of insect outbreaks attacking dominant or abundant species in natural vegetation (Table 10.1).

10.3.3 Native Outbreaking Insects Function as Keystone Species by Reducing the Abundance of the Dominant Species and Increasing Diversity

Insect outbreaks typically reduce the abundance or growth of the dominant species within the community, subsequently freeing resources for subordinate species and thereby increasing diversity (MacLean 1988; Bach 1994; De Grandpré and Bergeron 1997; Carson and Root 2000; Dery et al. 2000; Matouska et al. 2001; Parish and Antos 2002; Long et al. 2003). In this way, outbreaking insects function as classic keystone species (e.g. Carson and Root 2000). Matouska et al. (2001) described the strong top-down impact of the spruce beetle (*Dendroctonus rufipennis*) on boreal forest systems:

“Outbreaks varying in size and severity have occurred in the region at approximately 30- to 50-year intervals since 1920. During large outbreaks, spruce beetles can cause widespread changes to the structure of forests by selectively attacking and killing the large diameter spruce (*Picea* sp.)....After the canopy forming trees have died, understorey vegetation may be released from competition for light, nutrients and water; this may result in the rapid growth of the smaller, subordinate trees, shade-intolerant herbs and grasses. As a result, plant communities following a large outbreak may be quite different in structure and composition from those that dominated before the irruption”.

Unfortunately, with the exception of northern and boreal forests (e.g. MacLean 1988; Veblen et al. 1991; De Grandpré and Bergeron 1997; Dery et al. 2000; Matouska et al. 2001; Parish and Antos 2002) and sand dune and old-field successional communities in the USA and Canada (e.g. McBrien et al. 1983; Bach 1994; Carson and Root 2000), most studies have not considered the consequences of outbreaks for non-host species, for plant species composition or for diversity. Nonetheless, large-scale outbreaks of native insect herbivores often dramatically reduce the growth of their hosts and cause substantial mortality of the dominant plant species (e.g. Carson and Root 2000). If these outbreaks are common relative to host life span, then outbreaking insects may typically function as keystone species, causing strong top-down effects on plant communities. Indeed, Schowalter (1996a) concluded that when hosts become abundant, “...high intensities of herbivory represent a major mechanism for reversing site dominance ...and increasing diversity" in forest ecosystems.

10.3.4 Insect Outbreaks Are Common Relative to Host Life Span Yet May Often Go Unnoticed

There is a general perception that outbreaks of native insect species defoliating native plant species are uncommon or rare events (Hairston et al. 1960; Strong et al. 1984; Hartley and Jones 1997; Lowman 1997). Nonetheless, it is clear that in many cases outbreaks will occur repeatedly over the life span of long-lived hosts. For example, Root (1996) concluded that devastating outbreaks would occur on goldenrods in goldenrod-dominated fields in central New York, USA, every 5–15 years and goldenrod life span and period of dominance is 10–30+ years. These outbreaks dramatically reduce community biomass, increase plant diversity and alter successional trajectories for years following the outbreak (Carson and Root 2000). Outbreaks of insects in aspen stands in Canada, mountain birch forests in Europe, *Eucalyptus* forest in Australia, spruce-fir forests in North America and heathlands in Europe all experience outbreaks that occur at least once, if not repeatedly, during the life span of the dominant species in the stand (Table 10.1; Hildahl and Reeks 1960; Berdowski and Zeilinga 1987; Morrow and Fox 1989; Veblen et al. 1991; Fox and Morrow 1992; Carson and Root 2000; Ruohomaki et al. 2000; Matouska et al. 2001). For many community types, however, the frequency and scale of outbreaks remain unknown. If the probability of an outbreak is high for dominant or abundant plant species in a stand in any community type, then outbreaks may commonly have a strong top-down effect on plant communities. Unfortunately, in many community types, outbreaks are fairly short-term events that appear and then disappear relatively suddenly. In addition, in forests, outbreaks may occur high in the canopy and go unnoticed (e.g. Wolda and Foster 1978; Lowman 1997). Consequently, outbreaks may be poorly documented, dismissed or overlooked.

10.3.5 Chrysomelid Beetles and Lepidoptera Seem to Be Responsible for the Majority of Outbreaks

We found that Lepidoptera and Coleoptera accounted for approximately 58 and 36 % of outbreaking taxa respectively (Table 10.1). Thus, these two taxa accounted for more than 90 % of the outbreaks categorized in Table 10.1. Similarly, of the major defoliations described by Janzen (1981), Lepidoptera and Coleoptera accounted for 65 and 30 % respectively. These percentages among community types (Table 10.1) and within a community type (tropical dry forest, Janzen 1981) are strikingly similar and this may in part reflect the prominence of these two taxa among phytophagous insects (Strong et al. 1984) as well as reflecting the characteristics of these groups that make them more likely to outbreak (e.g. Schultz 1987).

Within the Lepidoptera, we found that 50 % of the outbreaks were caused by noctuids, tortricids and geometrids (Table 10.1). Janzen (1981) found that geometrids and noctuids accounted for 33 % of outbreaks in a dry tropical forest, but he did not describe any outbreaks by tortricids, which seem to be most important in northern and boreal forests (Table 10.1). Schultz (1987) concluded that geometrids were prone to being pests. We found that among the Coleoptera, a surprising 75 % of outbreaks were caused by chrysomelids. We suggest that chrysomelid beetles may frequently function as keystone species in plant communities (1) because they are a species-rich group, (2) owing to their tendency to break out (Table 10.1; Root 1996; White 1996; Carson and Root 2000), (3) owing to their tendency to aggregate on host plants or dense host patches (Bach and Carr 1990; Herzig 1995; Herzig and Root 1996; Morris et al. 1996; Long et al. 2003) and (4) because they cause strong top-down effects on biomass in plant communities (e.g. Carson and Root 2000). Thus, we suggest that it may be more than pure coincidence that three most 'spectacular cases' of biological control have used chrysomelid beetles to control abundant exotic perennial plants (*Hypericum perforatum*, *Senecio jacobaea* and *Alternanthera philoxeroids*; Huffaker 1964; Maddox et al. 1971; Crawley 1989; McEvoy et al. 1993; Buckingham 1996; Zwölfer and Zimmermann, Chap. 7, this Vol.). Overall, our findings lead us to the conclusion that chrysomelid beetles along with outbreaking species of Lepidoptera may commonly exert strong top-down effects on numerous community types worldwide. Lepidoptera appear to have their greatest impact on forest systems whereas chrysomelids appear to have their greatest impact on herbaceous or early successional systems, though exceptions to this generalization occur (Table 10.1).

10.4 The Host Concentration Model May Predict Insect Impact on Plant Communities at Multiple Spatial Scales Better Than Resource Supply Theory

10.4.1 Resource Supply Theory

The bottom-up, top-down debate has been dominated by a single and very important theoretical framework, called here Resource Supply Theory (RST; also called Resource Dependent Foodwebs by Grover 1997). RST encompasses a variety of models that are all fundamentally based on the premise that variation in the strength of top-down control by herbivores can be explained by changes in resource supply to primary producers (e.g. Oksanen et al. 1981, 1995; Leibold 1989, 1996; Schmitz 1992, 1993, Holt et al. 1994; Grover 1997). Much empirical work investigating top-down effects has taken its lead from these theories and has investigated how resource supply influences herbivore abundance (e.g. Siemann 1998; Ritchie 2000) and herbivore impact on communities (e.g. Fraser and Grime 1998). There is now a whole array of these models (see Chase et al. 2000) with varying degrees of empirical support.

We suggest that this theoretical framework may not accurately predict when *specialist insect herbivores* will have a strong top-down impact on a plant community. Specifically, RST models focus on how resource supply affects plant defences or net primary productivity or both, which then directly or indirectly (via predators) regulate herbivore control over primary producers. Alternatively, we suggest that insects will regulate vegetation dynamics whenever dominant host plants become concentrated and abundant and that this regulation will be most pronounced during outbreaks (but see Long et al. 2003 for a non-outbreak example). This means that to predict when specialist insect herbivores will have a strong top-down effect it may be more important to know the distribution and abundance of their hosts than to know how resource supply affects their enemies or plant traits (e.g. defences). Because the vast majority of insect herbivores are specialists (e.g. Fox and Morrow 1981; Thompson 1994; Janz et al. 2001; Nosil 2002), the Host Concentration Model may typically predict when insect herbivores in general will impact plant communities. We do not dispute the fact that resource supply and its relationship to productivity, plant defences and enemies have important consequences for insect herbivores. All we are suggesting is that host concentration may more accurately predict and determine when insect herbivores will have a strong top-down effect on a plant community.

10.4.2 The Host Concentration Model (HCM)

HCM predicts that specialist insect herbivores will have strong top-down effects on plant communities whenever their hosts form large, persistent dense stands (see also Long et al. 2003; Carson and Root 2000). This impact will be most pronounced and enduring following outbreaks. The host concentration model is more parsimonious than resource supply models (also see Polis 1999). It makes assumptions neither about predators, plant defences nor changes in resource supply. The only assumption of HCM is that the per stem impact of herbivores increases with host plant density or area sufficiently enough to have a top-down impact on plant communities. Furthermore, if native plants that are superior competitors are also widespread, which is typical, then these plants will have a substantially richer herbivorous insect fauna than inferior competitors that are more sparsely distributed

(Strong et al. 1984). Consequently, widespread, superior competitors may commonly have specialist insects that not only track their abundance but also periodically outbreak (Table 10.1), thereby reducing the impact of these dominant plant species on subordinate plant species within the community. Finally, insect herbivores appear to be able to track host plant abundance from spatial scales of a few tens of meters (e.g. Morrow et al. 1989; Herzig and Root 1996; Carson and Root 2000; Long et al. 2003) to tens of thousands of hectares (e.g. Bergeron and Leduc 1998; Cappucino et al. 1998; McCullough et al. 1998; Kruess et al., Chap. 8, this Vol.). Consequently, the host concentration model should apply across huge spatial scales depending upon the host finding behaviour of the specialist insect.

10.4.3 Distinguishing Between the Two Models

It is important to note that RST and the HCM can make very similar predictions about increasing regulation of plant communities with increasing resource supply when both the density and productivity of the dominant host plant increases with community productivity. If insect herbivores track host-plant abundance but host-plant abundance and productivity are positively correlated, then RST can make the correct prediction *based on the wrong mechanism*. Alternatively, if insect herbivores track host-plant abundance but host-plant abundance and resource supply are not correlated, RST *can make the wrong prediction*. It is only when measures of both host plant density, host plant productivity and host quality at both the population and community level are available that we can distinguish among the models.

10.5 Relationship to Other Related Processes Proposed to Promote Diversity

Our goal in this chapter was to provide a general rule to predict when *specialist insect herbivores* will have strong top-down effects on plant communities across multiple spatial scales and to argue that such effects may be pervasive and enduring from a phytocentric perspective. The current prevailing view is that top-down (e.g. predation and parasitism) and bottom-up forces (e.g. plant defences) in terrestrial food webs severely constrain the impact of insect herbivores on plant communities. We believe this focus may miss the brief but critical windows when insect herbivory will regulate plant communities: specifically when hosts form large dense stands and when insects outbreak in these stands. We recognize that the rule has many similarities to other general processes where enemies respond and suppress their prey or hosts in a density-dependent fashion. For example, our rule has many parallels to the

Janzen–Connell hypothesis that was originally proposed to explain the maintenance of tree diversity in tropical forests (Connell 1971; Janzen 1970). Our hypothesis, however, is focused specifically on the impact of specialist outbreaking phytophagous insects that attack large, dense concentrations of hosts. It is not focused on seed predation, the impact of predators on juveniles or the relationship between juvenile survivorship and distance to putative adult parents. Nonetheless, inherent within our rule and the Janzen-Connell hypothesis is that as host density increases the per host impact of predation (or herbivory) increases.

10.5.1 Does Pathogen Impact Increase with Host Concentration?

There is growing evidence that pathogens, like specialist insects, can have a strong top-down effect on plant communities (Dickman 1992; Van der Putten et al. 1993; Van der Putten and Peters 1997; Olff et al. 2000; Packer and Clay 2000; Rizzo et al. 2000; Joshi et al., Chap. 6, this Vol.; Kruess et al., Chap. 8, this Vol.). If the per host impact of these pathogens increases with host density (e.g. reviewed in Burdon and Chilvers 1982; Augspurger 1988; Burdon et al. 1989; Alexander 1992), then we believe the Host Concentration Model will also apply to many plant pathogens. Consequently, abundant plant species may have to contend with not only periodic insect outbreaks but also periodic pathogen outbreaks. Because of lack of empirical work at the community level, it remains unknown which is more important or how the combined impact of host-tracking insects and pathogens may interact to structure plant communities.

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