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### Insect Herbivore Effects on Forest Ecosystem Services

T. D. Schowalter<sup>a</sup>

<sup>a</sup> Department of Entomology, Louisiana State University Agricultural Center, Baton Rouge, Louisiana, USA

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## **Insect Herbivore Effects on Forest Ecosystem Services**

T. D. SCHOWALTER

*Department of Entomology, Louisiana State University Agricultural  
Center, Baton Rouge, Louisiana, USA*

*Forests provide important ecosystem services—including provision of food, building materials, fresh water, as well as carbon sequestration and climate moderation. Outbreaks of herbivorous insects have negative effects on the provision of plant products in the short-term, which are easily measured in terms of lost revenue. Effects on cultural services also are generally negative. However, effects on supporting ecosystem services are complex and include benefits that may compensate for costs, to some extent. For instance, native insect herbivores may function as regulators of forest primary production, maintaining primary production and water and nutrient use within historically sustainable levels. Therefore, “pest” and ecosystem management decisions should consider long-term trade-offs in costs and benefits among ecosystem services.*

*KEYWORDS* biogeochemical cycling, compensatory effects, fiber, food, trade-off

### INTRODUCTION

Ecosystems provide a variety of services on which humans and other organisms depend for survival (Millennium Ecosystem Assessment, 2005). Ecosystem services include provisioning services (marketable products),

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Address correspondence to T. D. Schowalter, Department of Entomology, 404 Life Science Building, Louisiana State University Agricultural Center, Baton Rouge, LA 70803, USA. E-mail: tschowalter@agcenter.lsu.edu

cultural services (religious and recreational values), supporting services (primary production and soil formation), and regulatory services (that maintain consistent supply of other services through density dependent feedback). While these services are clearly important to human survival and quality of life, estimation of economic value is difficult because most noncommodity services do not have market trade values (Dasgupta, Levin, & Lubchenco, 2000).

Forests are particularly valued for food, building materials, fresh water, and recreational activities, but also sequester carbon and modify global climate (Christensen et al., 2000). Herbivorous insects affect these forest services, especially during outbreaks. Because short-term losses in food and fiber production are obvious and economic losses easily measured, herbivorous insects traditionally have been viewed as detrimental to resource management goals (i.e., "pests"). However, herbivory also can increase primary production over the long-term, through natural pruning and thinning, potentially offsetting short-term costs. Therefore, control of outbreaks does not always contribute to management goals and may even be counterproductive over the long-term.

This article focuses on effects of native insect herbivores on forest ecosystem services. Evaluation of native insect herbivore effects on forest ecosystem services is complicated by two major issues. First, forests provide multiple services that reflect integration of many environmental factors, including insects—over long-time periods, requiring consideration of indirect, cumulative, and compensatory effects (Haynes & Weigand, 1997). Although stagnation and mortality of trees may be undesirable in intensively managed forests, tree loss in public forests managed for multiple uses provides space and other resources for new trees that increase diversity of age classes and species composition, ensuring continuity of ecosystem functions and services (Hooper et al., 2005) and making losses to insects less negative and subject to compensatory benefits. Second, accumulating evidence suggests that herbivorous insects may regulate primary production, which supports other ecosystem services. If herbivorous insects contribute to sustained (long-term), rather than maximum (short-term), primary production, within historic ranges of variation consistent with site condition, then control of outbreaks will not always benefit ecosystem services. Since we depend on a relatively constant flow of ecosystem services (sustained yield), pest management decisions need to address trade-offs among costs and benefits of insect effects for various ecosystem services over long-time periods.

## PROVISIONING SERVICES

Forest ecosystems provide food, water, building materials, biofuels, and medical and industrial resources for humans. Many plants produce edible

fruits, seeds, leaves, or tubers. Woody tissues are used for construction of homes, furnishings and fences, and for firewood. A large number of plant compounds provide pharmaceutical or industrial products such as salicylic acid, quinine, camphor, tannic acid, resins, and lacquer. Herbivorous insects obviously reduce forest production of these resources, especially during outbreaks. The costs of these effects are well-known and are used to develop economic thresholds for pest control (Pedigo, Hutchins, & Higley, 1986).

Wildlife and fish also represent important food sources provided by forests, and maintenance of their populations often is a primary forest management goal. Many mammal, bird, reptile, amphibian, and fish species feed primarily or exclusively on insects, and populations of these predators may increase when abundance of their insect prey increases (e.g., Koenig & Liebhold, 2005). Insects falling into forest streams comprise 30–80% of the diets of young salmon, with herbivores composing at least 20–25% (e.g., Allan, Wipfli, Caouette, Prussian, & Rodgers, 2003; Baxter, Fausch, & Saunders, 2005). Carbohydrate-rich honeydew from aphids, scale insects, and other Hemiptera provides an important food resource for hummingbirds and other animals, as well as many ant species and honey bees, *Apis mellifera* L. (Figure 1, Edwards 1982). In addition, canopy opening by herbivorous insects increases light availability for understory plants, which



**FIGURE 1** Honey bee collecting aphid honeydew dripping from red oak leaf.

provide primary floral resources for bees and other pollinators, especially in temperate forests (Collins, 1961; Regal, 1982). Pollination by insects is necessary for 35% of global crop production, but in many areas depends on proximity of crops requiring pollination to forest refuges with sufficient abundance of flowering plants to support wild bees or other pollinators (Kremen, Williams, & Thorp, 2002). Therefore, herbivorous insects are generally beneficial for wildlife, fish, and pollinators and potentially reduce the need for augmenting or stocking of these resources.

Forest ecosystems are valued sources of fresh water, and this often is the primary management goal for forested watersheds. Insect outbreaks increase water yields, as a result of reduced foliage area and evapotranspiration, but may temporarily increase streamwater concentrations of nitrogen and other elements leached from plant tissues and soil (Hunter, Linnen, & Reynolds, 2003; Lovett et al., 2002). Increased numbers of insects falling into streams draining forests also add substantial amounts of carbon, nitrogen, and phosphorus, contributing to the food base of aquatic food webs (Menninger, Palmer, Craig, & Richardson, 2008; Pray, Nowlin, & Vanni, 2009). Insect-induced increases in nutrient export generally are negligible and should have little effect on the quality of municipal water supplies (Lovett et al., 2002). The extent to which changes in water yield and quality are positive or negative depends on the needs of downstream communities. For example, increased water yield during a drought, a typical trigger for outbreaks (Mattson & Haack, 1987; Schowalter, 2011; Van Bael et al., 2004), would maintain relatively constant supply of water to municipalities and be seen as a benefit, whereas excess yield in some cases could flood downstream communities.

Herbivorous insect themselves represent valuable resources in many parts of the world, and outbreaks increase availability of these resources. Although insects currently are not valued as food in Europe or North America, cicadas, crickets, caterpillars, beetles, and other herbivorous insects make up 5–10% of dietary protein in many cultures (Ramos-Elorduy, 2009; Yen, 2009). For example, pandora moth, *Coloradia pandora* Blake, larvae and pupae were harvested by Native Americans in Oregon and northern California (Furniss & Carolin, 1977). Increased abundance of edible caterpillars (primarily two saturniids, *Gynanisa maja* Strand and *Gonimbrasia zambesina* Walker) in Zambian forests is of great value to indigenous cultures, and caterpillar harvest is ritually regulated (Mbata, Chidumayo, & Lwatula, 2002) demonstrating the importance of this provisioning service. In a unique study of the complementary costs and benefits of insect harvest versus control, Cerritos and Cano-Santana (2008) reported that harvesting grasshoppers for sale as food during an outbreak in Mexico substantially reduced grasshopper abundance and reproduction and provided \$3,000 revenue per family, compared to \$150 cost for insecticide treatment.

Silkworms, *Bombyx mori* (L.), provide the only source of commercial silk, and silkworms and other insects provide a variety of medically useful compounds (Singh & Jayasomu, 2002). Scale insects remain an important source of some commercial shellac. Gypsy moth, *Lymantria dispar* (L.), and other silk-producing species were introduced into North America as unsuccessful efforts to establish silk industries in the West (Andrews, 1868; Anelli & Prischman-Voldseth, 2009; Forbush & Fernald, 1896). Furthermore, insects can be used to identify plants with pharmaceutically active compounds (Helson, Capson, Johns, Aiello, & Windsor, 2009). Increased abundance of insects as a provisioning service, where recognized, requires consideration of trade-offs among various provisioning services in deciding whether or not to control an outbreak.

### CULTURAL SERVICES

Forest ecosystems provide various religious, recreational, and other cultural services—including hunting and fishing, extended backpacking ventures in wilderness areas, educational and scientific pursuits, and spiritual renewal. For example, most remnant forests in Ghana are sacred sites set aside by indigenous groups centuries ago and protected by religious sanctions and taboos (Bossart, Opuni-Frimpong, Kuudaar, & Nkrumah, 2006). The global value of recreational services alone (which can be calculated in part from usage fees) has been estimated at \$815 billion by Costanza et al. (1997), most of this in forest ecosystems.

Insect effects on cultural services appear to be primarily negative, depending on the extent and public perception of plant injury. Trees killed by insects can create safety hazards in camping or hiking areas. Defoliation reduces shade and may be perceived as unsightly. Insect tissues and feces falling on people or eating surfaces are largely considered a nuisance and may be allergenic to some (Perlman, Press, Googins, Malley, & Poarea, 1976). These features may cause reduced visitation to cultural or recreational sites experiencing outbreaks.

However, few studies have measured effects of insects on aesthetic or recreational values. Sheppard and Picard (2006) reviewed studies of public perception of forest insect damage, measured as visual-quality rating of landscapes with varying degrees of tree defoliation or mortality caused by insects, in North America. They found that visual-quality rating generally shows relatively low thresholds (e.g., at 10–20% defoliation or mortality) above which visual-quality rating declines more steeply than at lower levels. Visual-quality rating may or may not be affected by viewer knowledge of the natural interactions involved, indicating that educational efforts will not always be sufficient to reduce public demand for pest control.

## SUPPORTING SERVICES

Primary production and soil formation are major supporting services that underlie maintenance of other ecosystem services—including food production, water yield, and climate moderation (Foley, Costa, Delire, Ramankutty, & Snyder, 2003). Herbivory affects plant production and soil formation in complex direct and indirect ways that are not easily evaluated.

Herbivory conspicuously removes foliage or other plant parts, and often kills trees at foliage losses >90% for conifers and after multiple complete defoliation for deciduous trees (Schowalter, 2011). Such losses clearly reduce yields of important forest products during outbreaks. However, many plants are capable of replacing lost tissues (compensatory growth) and often overcompensate for losses (Alfaro & Shepherd, 1991; Gutschick & Wiegell, 1988; Trumble, Kolodny-Hirsch, & Ting, 1993). Low-to-moderate levels of herbivory can increase long-term plant production in forests, compared to production in the absence of herbivory (e.g., Alfaro & Shepherd, 1991; Kolb, Dodds, & Clancy, 1999; Lovett & Tobiessen, 1993; Trumble et al., 1993). Herbivory typically is focused on less-efficient and/or less-defended foliage, often resulting from superfluous foliage production, allowing plants to reallocate resources to more productive foliage (Gutschick & Wiegell, 1988; Trumble et al., 1993). Lovett and Tobiessen (1993) documented a significant 50% increase in photosynthetic rate by remaining leaves of red oak, *Quercus rubra* L., seedlings from which 80% foliage area was clipped, relative to leaves of unclipped seedlings. Even at high levels of herbivory, primary production over periods of 10–30 yr may largely replace short-term losses to insect herbivores (Alfaro & Shepherd, 1991; Romme, Knight, & Yavitt, 1986). Alfaro and Shepherd (1991) reported that short-term growth losses by individual defoliated conifers were followed by several years of growth rates, that exceeded predefoliation rates inversely proportional to their reduction during the outbreak; in other words, trees that suffered the highest rate of defoliation showed the highest rate of long-term recovery. Romme et al. (1986) reported that at least one pine forest suffering from mortality to mountain pine beetle, *Dendroctonus ponderosae* Hopkins, recovered preoutbreak levels of wood production within 10–15 yr. Although biomass reduction during outbreaks may not always be desirable, pruning and thinning are silvicultural tools used to increase timber production (Belle-Isle & Kneeshaw, 2007; DeBell, Curtis, Harrington, & Tappeiner, 1997; Schowalter & Turchin, 1993).

Defoliation in some cases improves plant survival during periods of adverse environmental conditions (Trumble et al., 1993). Kolb et al. (1999) reported that experimental defoliation of potted Douglas-fir, *Pseudotsuga menziesii* (Mirb.) Franco, seedlings by western spruce budworm, *Choristoneura occidentalis* Freeman, reduced seedling biomass but increased photosynthetic rate; stomatal conductance; foliar concentrations of N, Ca, and Mg; soil water potential; and seedling survival. Survival of

defoliated seedlings reflected reduced water use, hence lower moisture stress. Sthultz, Gehring, and Whitham (2009) reported that susceptible genotypes of mature *Pinus edulis* Engelman that were defoliated by *Dioryctria albovittella* Hulst had lower mortality during drought than did trees that were genetically resistant to defoliation. Given that drought is a common trigger for outbreaks (Allen & Breshears, 1998; Allen et al., 2010; Breshears et al., 2005; Mattson & Haack, 1987; McDowell et al., 2008; Van Bael et al., 2004), improved survival of defoliated plants warrants greater attention. Plant ability to compensate for losses to herbivores in the long-term depends on availability of water and nutrient resources (Frost & Hunter, 2007; Lovett & Tobiessen, 1993; Trumble et al., 1993). Nevertheless, if immediate salvage harvest is not required to meet yield goals, delaying harvest for 10–30 yr avoids costs of unscheduled salvage harvest and allows time for recovery of at least some lost production.

Severe outbreaks may increase vulnerability of weakened plants to other insect species. The Douglas-fir beetle, *Dendroctonus pseudotsugae* Hopkins, and fir engraver beetle, *Scolytus ventralis* LeConte, preferentially colonized Douglas-fir trees that had lost >90% of foliage to Douglas-fir tussock moth, *Orgyia pseudotsugata* (McDunnough), although larval survival was greater in nondefoliated than in defoliated trees (Wright et al., 1986). However, as noted above, intense defoliation also can reduce moisture stress during dry periods (Kolb et al., 1999; Sthultz et al., 2009).

Selective feeding by herbivorous insects alters the relative abundances of host and nonhost plant species (Allen & Breshears, 1998; Belle-Isle & Kneeshaw, 2007). Geographic patterns of distribution for many plant species can be explained by elevated herbivory on stressed plants at the edges of their ranges (Allen & Breshears, 1998; Schowalter, 2011). Outbreaks dramatically reduce the abundance of preferred host species and accelerate changes in vegetation structure and diversity (Figures 2 and 3; Belle-Isle & Kneeshaw, 2007; Romme et al. 1986; Schowalter, 2008). Outbreaks focused on abundant and/or stressed hosts tend to increase the abundance of nonhost species that are more tolerant of altered environmental conditions.

Outbreak-induced changes in vegetation structure and composition alter patterns of water and nutrient use by forests and affect rates of water and nutrient export and carbon sequestration (Allen et al., 2010; Lovett et al., 2002). Ritchie, Tilman, and Knops (1998) reported that herbivore-induced replacement of N-rich plant species by low-N species reduced overall use of N by vegetation. Large-scale pine mortality during outbreaks of the mountain pine beetle and defoliation by gypsy moth can reduce carbon uptake and increase carbon emission from decaying trees, contributing to increased atmospheric CO<sub>2</sub> loss from forests (Clark, Skowronski, & Hom, 2010; Kurz et al., 2008). However, Brown et al. (2010) noted that forests recovering from mortality to mountain pine beetle remained growing-season carbon sinks as a result of increased photosynthesis by remaining healthy trees and



**FIGURE 2** Hardwood trees, released by canopy opening, replacing pines killed by southern pine beetle, *Dendroctonus frontalis* Zimmerman, in the forest canopy (color figure available online).

understory vegetation, whereas nearby harvested stands remained carbon sources 10 yr after harvest. They suggested that deferred harvest of insect-attacked stands with secondary structure would prevent such stands from becoming carbon sources over extended periods.

Herbivorous insects affect soil formation directly (in ways that also affect primary production) by changing the amount, seasonal pattern, and form of organic matter and nutrients transferred from plants to the forest floor. Fresh foliage typically has higher nitrogen concentration and decomposes more rapidly than does senescent foliage from the same tree species, because plants retrieve up to 50% of N from senescing foliage for reallocation to other plant tissues (Gutschick, 1999; Marschner, 1995). In the absence of herbivory, litterfall is highly seasonal, concentrated at the onset of cold or dry conditions, and has low nutrient content. Insects increase litter mass and nutrient turnover during the growing season (as fragmented plant material, insect tissues, and insect feces), thereby maintaining a more consistent flux of litter and nutrients from vegetation to litter during the growing season and stimulating decomposition (Chapman, Hart, Cobb, Whitham, & Koch, 2003; Christenson, Lovett, Mitchell, & Groffman, 2002; Fonte & Schowalter,



**FIGURE 3** Herbivore modification of succession in central Sierran mixed conifer forest during 1998. White fir, *Abies concolor* (Gord. & Glend.) Lindl., increases in abundance in the absence of fire but becomes increasingly stressed by competition for water in this arid forest type. An outbreak of Douglas-fir tussock moth, completely defoliated white fir (brown trees), reducing the abundance of this tree species to historic levels and restoring the forest to a more stable condition dominated by drought- and fire-tolerant, Jeffrey and sugar pines, *Pinus jeffreyi* Grev. & Balf. and *P. lambertiana* Dougl., respectively; incense cedar, *Calocedrus decurrens* (Torr.) Florin; and sequoia, *Sequoiadendron giganteum* (Lindl.) J. Buchh. (green trees). Reprinted from Schowalter (2011), Figure 15.10, p. 475, with permission from Elsevier (color figure available online).

2005; Frost & Hunter, 2007, 2008; Gutschick, 1999; Hunter et al., 2003). A major effect of folivory is increased flux of nutrients in the form of nutrient-enriched precipitation percolating through the canopy (i.e., throughfall; Schowalter, Sabin, Stafford, & Sexton, 1991; Seastedt, Crossley, & Hargrove, 1983). However, Hunter et al. (2003) found that deposition of insect feces (Figure 4), even at low population levels, explained 62% of the variation in soil nitrate availability. Christenson et al. (2002) and Frost and Hunter (2007) demonstrated, using  $^{15}\text{N}$ , that herbivore feces decomposed rapidly, and feces-N was quickly incorporated into plant tissues and, subsequently, into herbivores during the same growing season. Alternatively, feces-N may be immobilized in microbial biomass (Lovett & Ruesink, 1995).

Herbivory reduces vegetation cover and increases penetration of sunlight, precipitation, and wind through the vegetation, thereby potentially modifying local climate. The effect of increased soil warming due to solar exposure may be offset to some extent by increased penetration of precipitation to the ground and water retention in litter. Experimental removal of 20% foliage mass by silver-spotted tiger moth, *Lophocampa argentata* (Packard),



**FIGURE 4** Feces from forest tent caterpillar, *Malacosoma disstria* Hübner, outbreak on water tupelo, *Nyssa aquatica* L., collected on understory vegetation. Reprinted from Schowalter (2011), Figure 12.1, p. 363, with permission from Elsevier (color figure available online).

caterpillars doubled the amount of water and litterfall reaching the soil surface under experimental trees, compared to untreated trees (Schowalter et al., 1991). Classen, Hart, Whitham, Cobb, and Koch (2005) found that foliage loss resulting from scale insect feeding increased soil temperature and moisture by 26 and 35%, respectively, similar to global change scenarios and enough to affect ecosystem processes.

Clearly, herbivorous insects affect supporting services in complex ways and require integration of multiple short- and long-term direct and indirect effects for proper evaluation and decisions regarding pest suppression. Pruning, thinning, and fertilization effects of herbivores potentially reduce the need for exogenous fertilizers in plantation forests. However, reduced primary production or vegetation cover in the short-term may cause serious economic losses and affect habitat conditions for associated organisms that affect ecosystem services.

## REGULATING SERVICES

Forests have considerable capacity to regulate ecosystem conditions, in the sense of reducing the extent of variation in environmental conditions. Forests regulate local and regional climate through shading; interception of precipitation and airflow; control of turbulence and condensation of moisture above the canopy, depending on canopy height and density (Foley et al. 2003); and water and nutrient availability through storage in biomass and control of factors affecting flux rates and decomposition (Whitford et al.,

1981). In some cases, herbivores indirectly affect primary production and vegetation cover in ways that could influence forest regulatory capability. By reducing variation in primary production via stimulating primary production at low rates of herbivory and suppressing primary production at high rates (Mattson & Addy, 1975), herbivores could maintain primary production at intermediate levels that may be most sustainable under prevailing environmental conditions (i.e., carrying capacity).

Populations of native insect herbivores themselves are regulated at small sizes, and low rates of herbivory in forests are regulated as a result of limited availability of suitable plant tissues (bottom-up regulation) and of predators and parasites (top-down regulation). Although plant food resources may appear to be nonlimiting for herbivores (Hairston, Smith, & Slobodkin, 1960), not all plants are acceptable hosts for herbivorous insects. Most plants are protected by various physical and chemical defenses (Coley & Barone, 1996; Gutschick, 1999; Harborne, 1994) or are “hidden” among nonhosts in diverse vegetation (Barbosa et al., 2009). Insect herbivores must find suitable host plants whose defenses they can avoid or detoxify in order to survive and reproduce (Coley & Barone, 1996; Kessler, Halitschke, & Baldwin, 2004). Finding suitable hosts within the matrix of various plant genotypes and species is a challenge for small herbivores such as insects because of limited vision and mixing of attractive host odors with nonattractive (or even repellent) nonhost odors (Barbosa et al., 2009; Courtney, 1985; Hunter & Arssen, 1988). Consequently, host-seeking adults often lay eggs (and commit their offspring to feeding) on less suitable hosts, because of high expense (in terms of time and energy) of searching for more suitable hosts, supporting the “plant apparency hypothesis” (Courtney, 1985). Furthermore, plants respond to feeding by herbivores with more specific induced defenses, including volatile elicitors that attract predators (Turlings et al., 1995) and induce production of defenses in neighboring plants, even unrelated species, in advance of herbivory (Dolch & Tschardtke, 2000; Kessler et al., 2004). Consequently, insect population growth reflects changes in host abundance or defensive capability that facilitate finding or exploiting their resources.

Outbreaks generally are triggered by environmental changes—including anthropogenic activities that increase host density, inhibit production of host defenses, and/or reduce predator or parasite abundances (Schowalter, 2011). Increased density of host plant species can result from natural succession, planted monocultures, or fire suppression and facilitates discovery of hosts by dispersing insects, promoting insect population growth and elevated herbivory (Schowalter & Turchin, 1993). Tree growth during optimal periods can lead to biomass accumulation in excess of long-term carrying capacity, resulting in water or nutrient limitation (Gutschick, 1999; Gutschick & Wiegand, 1988). Trees stressed by competition, drought, or other environmental changes typically sacrifice defensive chemicals in favor of more critical survival needs, such as the maintenance of foliage and root tissue, and

thereby become more vulnerable to both generalist and specialist insect herbivores (Gutschick, 1999; Kessler et al., 2004; Mattson & Haack, 1987).

Drought and storm damage are particularly important triggers for outbreaks (Allen & Breshears, 1998; Allen et al., 2010; Breshears et al., 2005; Mattson & Haack, 1987; McDowell et al., 2008; Van Bael et al., 2004), which reduce biomass, water, and nutrient demand, and may improve survival and future growth of host trees (Alfaro & Shepherd, 1991; Kolb et al., 1999; Sthultz et al., 2009; see above). However, outbreaks also can favor replacement of host trees by nonhost tree species that may be better adapted to changing environmental conditions (Figures 2 and 3). Planted monocultures and fire suppression, interacting with drought and other climate changes, have greatly increased the frequency and scale of forest insect outbreaks by providing abundant hosts (often species or varieties selected for rapid growth in lieu of adaptation to environmental variation) over extensive areas (Schowalter, 2008). During outbreaks, native insects eventually become food-limited, as they deplete their host resources (Schowalter, 2011). Concurrently, predators and parasites responding to increased prey availability accelerate decline in herbivore abundance, allowing trees to recover, as described above. Mooney (2007) demonstrated that predation by birds reduced herbivore abundances and led to increased growth of experimental ponderosa pine, *Pinus ponderosa* Laws., compared to bird exclusion treatment. Invasive forest insects also respond to host density or stress, but are less subject to regulation by plant condition, predation, and parasitism, and may consume resources beyond tree ability to compensate.

Although outbreaks appear to be destructive, they may function in natural forests to reduce variation in primary production (Mattson & Addy, 1975). Alleviation of water and nutrient limitation, as described above, may improve plant survival (e.g., Kolb et al., 1999; Sthultz et al., 2009) and prevent more extensive plant mortality in cases of moderate host stress (McDowell et al., 2008). Pruning, thinning, and fertilization are management practices used in intensively managed forests to increase primary production and/or reduce probability of insect outbreaks (Belle-Isle & Kneeshaw, 2007; DeBell et al., 1997; Schowalter & Turchin, 1993). Whether herbivore-enhanced N flux becomes available for plant growth or is immobilized in microbial biomass apparently depends on overall N availability in the ecosystem (Treseder, 2008). When background N is limiting, added N is more likely to be incorporated rapidly in plant tissues. Furthermore, Wood, Lawrence, Clark, and Chazdon (2009) demonstrated that experimental addition of litter material increased foliage production via mobilized N and P. Hence, biomass and nutrients transferred to the forest floor during outbreaks can be incorporated quickly into new plant tissues, alleviating nutrient limitation and supporting compensatory growth.

In cases of severe plant stress, insect outbreaks function to facilitate replacement of stressed and declining vegetation by more tolerant plant

species (e.g., Allen & Breshears, 1998), perhaps tailoring overall biotic demand for water and nutrients to prevailing conditions at a site. Herbivore-induced replacement of N-rich plant species by low-N species reduced overall demand for N under increasingly N-limited conditions (Ritchie et al., 1998), potentially improving sustainability of primary production. Similarly, in the absence of fire in forests of interior western North America, mountain pine beetle populations responding to competitive stress of host pines in dense, high-elevation mixed-conifer forests facilitate pine replacement by shade-tolerant firs; whereas spruce budworm, Douglas-fir tussock moth, and fir bark beetles responding to increased abundance of drought-stressed firs in more arid lower elevation forests facilitate fir replacement by drought-tolerant pines (Figure 3; Schowalter, 2008). From an ecological perspective, these insects appear to facilitate replacement of less tolerant by more tolerant plant species as environmental conditions change (Allen & Breshears, 1998), maintaining a more consistent level of primary production.

Increased litter production and dead trees resulting from insect outbreaks have been thought to increase the likelihood and severity of fire, but this is not necessarily the case (Jenkins, Herbertson, Page, & Jorgensen, 2008). Fine litter accumulation, such as produced by defoliators, in relatively open forests supports low intensity ground fire that maintains production of widely spaced trees. Depending on how quickly dead trees fall, increased tree mortality, especially at densities that convey fire into the canopy, could increase fire severity and affect canopy-dependent ecosystem services, such as water supply and carbon sequestration.

The hypothesis that herbivory could reduce variation in ecosystem conditions and services, compared to variation in the absence of herbivory, is difficult to test, and test results depend on perspective. For example, the Douglas-fir tussock moth outbreak depicted in Figure 3 caused devastating losses in short-term timber production and required emergency salvage harvest to prevent premarket wood degradation. However, the high density of drought-stressed fir trees that supported the outbreak reflected a century of fire suppression and other forest management practices that favored maximum timber production in Sierran forests. The insect outbreak effectively reversed this trend, producing a more historic forest structure that is the recommended management goal for these forests (North, Innes, & Zald, 2007). Similarly, mountain pine beetle and other insects that thin increasingly dense pine forests in the absence of fire have helped to meet expected future conditions for these forests (Christensen et al., 2000). From this perspective, the outbreak contributed to the stability of this forest. To the extent that native insect herbivores maintain forest structure and function within historic ranges of variability, contributing to sustained (long-term) rather than maximum (short-term) primary production, control of outbreaks might not contribute to ecosystem services, but thinning or tree species selection can prevent outbreaks and accomplish the same desired forest condition.

## CONCLUSIONS AND RECOMMENDATIONS

Herbivorous insects have substantial and complex effects on ecosystem structure and function. These effects may affect ecosystem services positively or negatively, depending on management goals and perspectives. Unfortunately, no single study has integrated the benefits and costs of herbivorous insects for multiple ecosystem services over short and long time periods in any forest ecosystem. Outbreaks generally interfere with yield of plant products in the short-term, but may benefit other provisioning services such as wildlife, fish, and pollinator production and water yield. Outbreaks in regions other than North America also provide benefits in terms of insects as food for humans. Effects on cultural services may be largely negative. Insects have complex direct and indirect effects on primary production and soil formation that potentially regulate forest function and the sustainability of ecosystem services over the long-term. Evidence that herbivory can increase long-term forest primary production warrants forest stand-level research. Although biomass reduction by insects may not be desirable in industrial forests, it can accomplish the same purpose as pruning and thinning, recommended for improved timber production. Where expensive salvage harvest of forest products can be delayed, trees may largely replace short-term losses in as few as 10 yr following an outbreak. "Pest" and ecosystem management decisions should consider trade-offs among multiple short- and long-term effects on ecosystem services. Decisions should produce a balance or optimization of ecosystem services, given the costs and benefits of herbivory for multiple services. To the extent that native herbivorous insects in natural ecosystems function as regulators of primary production and thereby maintain more constant levels of ecosystem services than would occur in their absence, suppression would not be cost-effective and could be counterproductive.

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