Insect Responses to Major Landscape-Level Disturbance

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Abstract

Disturbances are abrupt events that dramatically alter habitat conditions and resource distribution for populations and communities. Terrestrial landscapes are subject to various disturbance events that create a matrix of patches with different histories of disturbance and recovery. Species tolerances to extreme conditions during disturbance or to altered habitat or resource conditions following disturbances determine responses to disturbance. Intolerant populations may become locally extinct, whereas other species respond positively to the creation of new habitat or resource conditions. Local extinction represents a challenge for conservation biologists. On the other hand, outbreaks of herbivorous species often are triggered by abundant or stressed hosts and relaxation of predation following disturbances. These insect responses can cause further changes in ecosystem conditions and predispose communities to future disturbances. Improved understanding of insect responses to disturbance will improve prediction of population and community dynamics, as well as ecosystem and global changes.

INTRODUCTION

Disturbances are relatively abrupt events in time and space that substantially alter habitat conditions and resource distribution across landscapes (130, 133, 142). The extreme change in conditions created by disturbances is among the most significant factors affecting populations and communities, leading to local extinction of susceptible species and elevated populations of others that can exploit postdisturbance resources or predator-free space.

Insects are affected directly and indirectly by conditions produced during and after disturbances, and some show life-history strategies that likely reflect adaptations to disturbances (e.g., 110). Insect responses affect their interactions with other species and the resulting pathways and rates of energy and nutrient fluxes (102). Furthermore, insect responses to natural disturbances determine their responses to anthropogenic changes, often with serious consequences for ecosystem services on which humans depend (103). In particular, outbreaks of herbivores and disease vectors often are triggered by management practices (particularly harvest, species replacement, and change in fire frequency or intensity) that create favorable resource or habitat conditions similar to those resulting from natural disturbances (103, 129, 144). Local extinction of susceptible species potentially threatens others that depend on them for food, pollination, or seed dispersal (120). In some cases, insect responses alter community and ecosystem conditions in ways that increase the likelihood of subsequent disturbances (e.g., 12, 90, 119).

This review emphasizes insect responses to landscape-level disturbances. Topics include disturbance characteristics and their direct and indirect effects on abiotic conditions and postdisturbance conditions that affect insect populations in disturbed landscapes. Given the breadth of this topic, some aspects cannot be addressed adequately. Responses of aquatic insects to aquatic disturbances are not addressed in this review, and effects of anthropogenic pollutants and climate change are addressed only to the extent that they relate to insect ability to tolerate toxic materials produced during disturbances. Insect responses to natural disturbances largely determine their responses to anthropogenic disturbances that may imitate natural disturbances to varying degrees. Finally, this review addresses consequences of disturbance-induced changes in insect abundances for community interactions, ecosystem processes, and ecosystem services.

Adaptation: increased tolerance to disturbance, or other environmental changes, as a result of shifts in gene frequencies in response to intense selection during or after a disturbance

Disturbance event: the occurrence of an abrupt and extreme departure from the normal range of variation in abiotic conditions, within a relatively short time period, sufficient to cause measurable change in abundance or distribution of resources, populations, and communities

Disturbance type: categorized by the physical variables that depart from normal ranges

Disturbance magnitude: the extent of departure from normal ranges in abiotic conditions (intensity) and in population and community structure (severity)

Disturbance frequency: the number of events per unit time or the average return time between events

Disturbance extent: the area affected by a disturbance

DISTURBANCE CHARACTERISTICS

Each disturbance event is characterized by a unique combination of type, magnitude, frequency, and extent that determines its effect on various organisms (130, 133). Superimposing a sequence of events on the landscape creates a mosaic of patches that differ in their disturbance histories (**Figure 1**). For example, over a 20-year period a rain forest in Puerto Rico experienced two major hurricanes (Hugo in 1989 and Georges in 1998) that broke or toppled trees on the windward sides of slopes over large areas and caused numerous landslides, several moderate hurricanes (Luis and Marilyn 1995, Bertha and Hortense in 1996, Erika in 1997, Jose in 1999, and Jeanne in 2004) that caused substantial defoliation and flooding, a number of minor hurricanes and tropical storms, a major drought (1994–1995, during which precipitation was only 41% of the annual mean), and several minor droughts (1991, 1996, 2001, and 2003), as well as an overall drying trend of 2 mm year^{-1} since 1988 (51). The particular sequence of disturbances affects insect species responses (7, 23, 109). A species adapted to poststorm conditions, but eliminated by a previous fire, would not be represented in the poststorm community. Responses of litter arthropod and canopy Lepidoptera to canopy-opening disturbances can reflect filtering of species composition by previous harvests as early as 60 years earlier (109, 118).

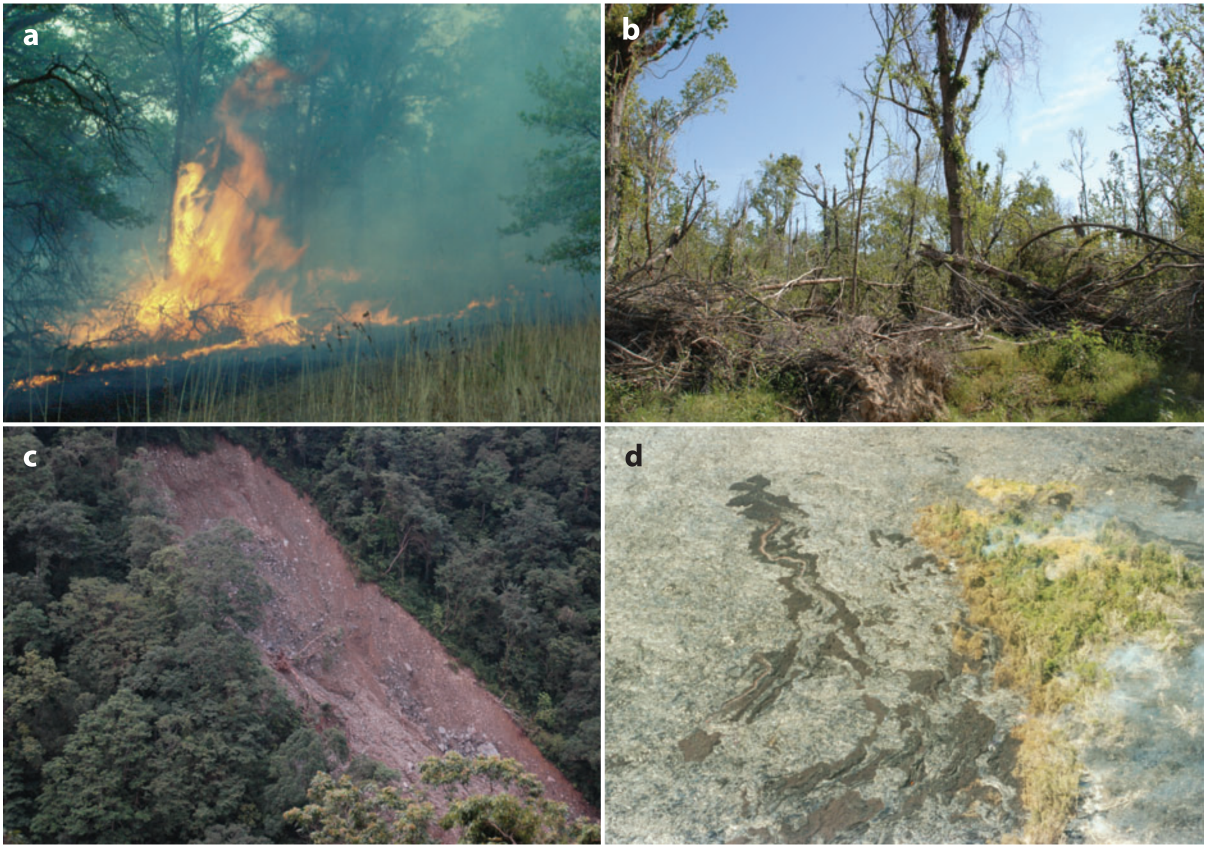

Figure 1

Examples of disturbances to illustrate variation in type, magnitude, extent, and contrast between disturbed and surrounding landscape patches. (*a*) Fire in oak savanna (note sites of high and low flame height and intensity). (*b*) Hurricane effect on coastal deciduous forest. (*c*) Landslide resulting from heavy rainfall. (*d*) Volcanic eruption (note fresh lava flow on left and zones of burning and exposure to fumes in vegetation fragment).

Type

Disturbance types vary in the conditions they impose on organisms, including insects. Severe storms, especially tropical cyclones, dislodge or injure insects and initiate landslides and flooding that redistribute sediments and bury organisms. Fires and volcanic eruptions impose extreme high temperatures, whereas ice storms impose extreme low temperatures. Fires and volcanic eruptions also fill the air with ash and caustic gases, and lava or ash deposition burns and buries organisms. The eruption of Mount St. Helens in 1980, for example, deposited up to 30 kg ash m^{-2} at depths of 1 to 8 cm over an area of 54,000 km^2 (27).

Insect outbreaks often are considered to be disturbances because they kill plants and alter distribution of biomass over large areas (16, 17, 73, 77). Outbreaks also can predispose ecosystems to subsequent abiotic or biotic disturbances (e.g., 90, 119). Although consideration of outbreaks as disturbances, rather than disturbance-induced changes in trophic interactions, remains a matter of perspective (100, 106), the significant interactions between insect outbreaks and abiotic disturbances require consideration in management of ecosystem resources and services (see below).

Magnitude

Disturbances vary in intensity and severity. Intensity often may be difficult to measure, e.g., actual temperature during a fire or velocity of wind gusts during a storm. Magnitude is measured more often by the severity of effects on species and ecosystems. A low-intensity ground fire affects primarily surface-dwelling organisms, many of which may be adapted to this level of disturbance, whereas the intense heat of a fire storm (created by convection during catastrophic wildfire) penetrates more deeply into soil and wood and kills a larger proportion of the community (124, 139). A minor flood slowly filling a floodplain for a few days affects fewer insects than does a major flood that scours and inundates the landscape for weeks (e.g., 132). Dead vegetation deprives many insects of food resources and alters microclimatic conditions that affect habitat quality (69, 141). However, some species thrive under the altered conditions (105, 125).

Frequency

Disturbances vary in their return interval. Fire intense enough to kill most vegetation occurred, on average, every 200 years since 1633 in a montane forest landscape in western North America (128), whereas hurricanes of this magnitude recur every 10 to 60 years at sites in the Caribbean region (51). Frequency, with respect to generation times, of a particular disturbance type affects the rate of selection for adaptive traits that confer tolerance (resistance) to disturbance. Infrequently disturbed ecosystems, such as tropical forests, may be affected most by disturbances because dominant species in these ecosystems experience too few disturbances to drive selection for tolerance. Long-lived organisms, especially perennial plants, are more likely to experience disturbances consistently among generations, leading to stronger selection for adaptive traits.

Insects with short life spans relative to disturbance return intervals experience less selective pressure for adaptation to disturbance than do longer-lived species. Nevertheless, some insect species show apparent adaptations to disturbance. Some wood-boring insects, which have life spans of 2 to 10 years, are attracted to sources of heat or smoke, indicative of dead wood resources in fire-killed trees (33, 110). Several ant species characteristic of floodplain habitats have adapted to periodic flooding by forming floating mats of ants and larvae that may be dispersed downstream (148). Avoidance of dense overstory and accumulated litter by ground-pupating larvae of the pandora moth, *Coloradia pandora* Blake (Saturniidae), may reflect adaptation to minimize mortality during fire, which occurs every five years, on average, compared to a two-year life cycle for this moth (85). Dispersal ability is an important adaptation for species exploiting temporary, unstable conditions (60). Many species (especially Lepidoptera and Coleoptera) that characterize infrequently disturbed forests are flightless, or at least weak dispersers, whereas species that characterize temporary, frequently disturbed habitats (such as many aphids) produce large numbers of strong dispersers.

Disturbances of greater severity typically occur at lower frequency. Increasing disturbance magnitude or frequency generally reduces species diversity (7, 44, 84), because fewer species are able to tolerate more extreme changes in habitat or resource conditions. Hanula & Wade (49) reported that most forest floor species decreased in abundance, but some species increased, with increasing fire frequency. De Mazancourt et al. (29) suggested that high biodiversity increases the likelihood that some species have genotypes that are adapted to altered conditions. Arrival of adapted colonists of various species from other areas augments community recovery (see below).

Timing of disturbances, relative to insect developmental stage, also affects insect responses. Winged adults may be able to escape as conditions become intolerable, whereas exposed pupae would be most vulnerable to disturbance. On the other hand, Martin-R. et al. (79) reported that experimental fires set during different developmental stages of spittlebug, *Aeneolamia albofasciata* (Lallemand) (Cercopidae), in buffelgrass, *Cenchrus ciliaris* L., grassland in Sonora, Mexico, eliminated spittlebugs for at least four years after burning, regardless of developmental stage at the time of burning.

Extent

Disturbances range in extent from a few hectares to continental, but the magnitude of particular disturbances varies across landscapes due to variation in topography, substrate condition, or vegetation, e.g., intervening hills, bedrock outcrops, bodies of water, or patches of vegetation that are resistant to particular disturbances. Veblen et al. (128) reported that fire has affected 59% and snow avalanches 9% of a montane forest landscape in western North America since 1633, compared to 39% by outbreaks of spruce beetle, *Dendroctonus rufipennis* (Kirby) (Curculionidae). The 1998 flood in Bangladesh inundated nearly 70% (about 100,000 km^2) of the country (72), leaving few refuges for insects intolerant of immersion. Heavy rains producing such floods typically saturate soils over a much larger area. Lava and ash from volcanic eruptions can cover thousands of square kilometers (27), but volcanic gases can affect atmospheric chemistry and climate globally (81). El Niño events in the southern Pacific Ocean also affect climate and insects globally (114, 125, 147). Insect outbreaks themselves are capable of consuming or killing most host plants over thousands of square kilometers (e.g., 91, 102, 104).

The extent of disturbed area affects insect responses. Populations restricted to areas smaller than the disturbed area are likely to disappear. This threat creates a challenge for conservation biologists, who must work to conserve large enough areas, or sufficient distribution of increasingly isolated refuges, to maintain adequate population sizes of target species vulnerable to large-scale disturbance (48). Colonization typically progresses inward from the edges of disturbed areas, as dispersing individuals from population sources find such "sinks," so smaller areas can be colonized more quickly than larger areas (6, 112). Insects with limited mobility may require considerable time to colonize large areas (66). More extensive disturbances, or disturbances that result in greater contrast between disturbed and undisturbed patches (e.g., **Figure 1*d***), create steeper gradients in postdisturbance temperature and relative humidity between disturbed and undisturbed patches, with sharper boundaries relative to insect tolerance ranges (112). However, edges of disturbed areas may provide unique resources for insects, e.g., species that exploit forest plants that are stressed by exposure or are favored by higher light available at the edge of a disturbed area (66, 97).

Source-sink relationship: colonization of disturbed sites (sink) through dispersal of individuals from population centers (source) in other parts of the landscape

Tolerance range: the range of values between lethal maxima and minima, for any environmental variable (or combination of variables), under which exposed organisms can survive

INSECT RESPONSES

Individual insects have specific tolerance ranges to abiotic conditions that dictate their ability to survive exposure to extreme temperatures, water availability, chemical concentrations, or other factors during and after a disturbance. Variable ecosystem conditions typically select for wider tolerance ranges than do more stable conditions. Although changes in abiotic conditions during disturbances can affect insects directly (e.g., burning, drowning, particle blocking of spiracles), disturbances also affect insects indirectly through changes in resource quality and availability and in exposure to predation or parasitism (e.g., 3, 59, 80, 85, 97, 113, 125). Population size and degree of genetic heterogeneity affect survival during disturbance (7). As habitat conditions change, intolerant individuals or species disappear, but tolerant species may be favored by reduced predation or improved resource conditions following disturbance (97, 101, 105). Because survival and reproduction of individual insects determine population size, distribution, and subsequent effects on community and ecosystem recovery, this section focuses on factors that affect insect responses directly and indirectly.

Direct Effects of Abiotic Changes

Disturbances alter abiotic conditions to varying degrees depending on disturbance type and severity. Insects are particularly vulnerable to changes in temperature, water availability, and air or water chemistry because of their relatively large surface area/volume ratio and limited homeostatic ability. Although some habitats may protect insects from disturbances, and some insects may be able to escape as conditions approach tolerance limits (62, 143), survival of many depends on physiological tolerance ranges relative to environmental extremes.

Temperature extremes. Fires and volcanic eruptions, in particular, create lethal temperatures for insects unable to escape. Disturbances that reduce vegetation cover subsequently expose surviving or colonizing insects to elevated surface temperatures. Ulyshen et al. (124) found that fire reduced abundances, but not species representation, of wood-boring beetles in coarse woody debris. Beetles were relatively protected in larger-diameter logs. Bark beetles (Curculionidae) in subcortical tissues, however, are vulnerable to heat mortality (139). Small, flightless litter species only need to move a few millimeters vertically within the soil profile to avoid lethal temperatures and desiccation during fire or canopy-opening disturbances (111). Nevertheless, Hanula & Wade (49) found that abundances of most forest floor species (especially predators) were reduced by prescribed burning and were reduced more by annual than by biennial or quadrennial burning, but a few species (especially detritivores) increased in abundance with more frequent burning.

Survival at high temperatures requires high body water content or access to water, because desiccation at low relative humidity causes death (45). Disturbances that reduce riparian canopy cover significantly increase water temperature, and reduce oxygen levels, of aquatic patches especially in the summer (64, 98). A distinct riparian fauna may be vulnerable to canopy-opening disturbance within 30 m of streams (98). However, stream grazers may respond positively to increased primary production resulting from higher light level when riparian canopies are opened (64).

Conversely, unseasonable ice storms or extreme cold periods also kill exposed insects. Ability to survive depends on prior preconditioning to sublethal temperatures (65) or physiological mechanisms, such as production of cryoprotectants to prevent intracellular ice formation and voiding the gut to prevent food particles from serving as nuclei for ice formation (45).

Precipitation extremes. Water availability becomes particularly limited during drought or excessive during floods, but high temperatures during fire or volcanic eruption may severely reduce relative humidity. Maintenance of water balance becomes a challenge for small organisms such as insects, but some insects are capable of minimizing water loss or tolerating dehydration (41). The exoskeleton is an important mechanism for control of water exchange. Larger, more heavily sclerotized arthropods are less susceptible to desiccation or waterlogging than are smaller, more delicate species (3, 63).

Extreme dehydration may trigger the onset of anhydrobiosis, a physiological state characterized by an absence of free water and of measurable metabolism (45, 137). Survival during anhydrobiosis requires stabilization of membranes and enzymes by compounds other than water, e.g., glycerol and trehalose, whose synthesis is stimulated by dehydration (45). Among insects only some larval Diptera and adult Collembola undergo anhydrobiosis (45). Hinton (54, 55) reported that the chironomid fly *Polypedilum vanderplanki* Hint., found in temporary pools in central Africa, withstands repeated dehydration to 8% of body water content. At 3% body water content, this midge is capable of surviving temperatures from −270°C to 100°C.

On the other hand, insects subjected to flooding must contend with excess water. Subterranean termites can survive short periods of inundation by entering a quiescent state; relative abilities of species to withstand periods of flooding correspond to their utilization of aboveground or belowground wood resources (35). Litter-dwelling ants are vulnerable to seasonal flooding in Amazonian forests (84). Specialist predators were virtually eliminated by flooding; one *Hypoponera* species (Formicidae) was adapted to a high degree of flooding, increasing in abundance with the frequency and duration of flooding. Webb & Pullin (132) found that pupae of the wetland butterfly *Lycaena dispar batavus* Oberthur (Lycaenidae) could tolerate 28 days of submergence, but survival was negatively correlated with duration of submergence between 28 and 84 days. However, inundation affects oxygen availability (see below), as well as water balance.

Wind speed and water flow. High wind speeds and water flow during storms dislodge and displace exposed insects, as well as sediment and organic debris, crushing or injuring many individuals. Some may survive and be able to move around and colonize new habitats to which they are relocated, but immature and sedentary insects most likely perish. Torres (122) documented several insect species, including a swarm of desert locusts, *Schistocerca gregaria* Forsskål (Acrididae), that were blown across the Atlantic Ocean from North Africa to Puerto Rico by hurricane winds. Although most species did not survive, such transport provides an opportunity to colonize habitats across major barriers and may explain the relative homogeneity of biotas among Caribbean islands (122).

Air and water quality. Some disturbances alter atmospheric and water quality. Fire and volcanic eruptions, in particular, release toxic abiotic and biotic gases and particulate materials, but high winds during storms and high river levels during flooding also increase the amount of dissolved and suspended materials that may affect exposed insects.

Oxygen supply is especially critical to survival but may become limiting during or after some disturbances, such as soil saturation during flooding or burial by sedimentation or ash fall. Many insects can tolerate short periods of anoxia, but prolonged periods result in reduced survival and developmental abnormalities (57). Adult alder leaf beetles, *Agelastica alni* (L.) (Chrysomelidae), which overwinter in frequently waterlogged or flooded riparian soil, showed a reduction in metabolic activity after 3 days to 2% of normal metabolic activity (68). Larval tiger beetles, *Phaeoxantha klugii* Chaudroir (Carabidae), found in central Amazonian floodplains tolerate anoxic conditions in flooded soils for up to 3.5 months at 29°C (146). This exceptional degree of anoxia tolerance appeared to require several days of induction as water levels rose, suggesting vulnerability to more rapid inundation. Brust & Hoback (18) found that tolerance to hypoxia among several tiger beetles (*Cicindela* spp.) was not related to likelihood of immersion.

Increased concentrations of atmospheric CO_2 that result from fire, volcanic eruption, or other causes appear to have little direct effect on insects or other arthropods. Fluorides, sulfur compounds, nitrogen oxides, ozone, and other toxic fumes affect many insect species directly, although the physiological mechanisms of toxicity are not well known (3, 52, 53). Disruption of epicuticular or spiracular tissues by these reactive chemicals may be involved.

Soil and water pH affects a variety of chemical reactions, including enzymatic activity. Changes in pH resulting from deposition of ash and release of caustic gases from fire or volcanic eruptions affect osmotic exchange, gill or spiracular surfaces, and digestive processes. Changes in pH often are correlated with other chemical changes, such as increased concentrations of nitrogen or sulfur compounds, and effects of pH change may be difficult to separate from other factors. Van Straalen & Verhoef (126) found that several species of soil collembolans and oribatid mites varied in their responses to acidic or alkaline soil conditions.

Dust and ash from volcanic eruptions or fires kill many insects, apparently because they absorb and abrade the thin epicuticular wax-lipid film that is the principal barrier to water loss, causing death by desiccation (3, 27, 78). Insects exposed to volcanic debris also can suffer gut epithelial stress from accumulation of heavy metals (96). Ash accumulation and retention by aquatic insects following the eruption of Mount St. Helens were affected by exoskeletal sculpturing, armature, and pubescence (40). Substantial accumulation was noted on respiratory structures, potentially interfering with respiration. Ash-covered insects showed increased activity and orientation upstream, which successfully washed off ash within 24 h. However, ash coating over cobbles, pebbles, and sand significantly inhibited colonization of these substrates (20).

Indirect Effects of Postdisturbance Changes

Insects that survive the direct effects of disturbance must contend with altered habitat conditions and resource availability. Disturbances destroy some habitats and resources and alter distribution or quality of others for a period, during which community and ecosystem conditions recover to a semblance of predisturbance conditions (ecological succession). Some insect species respond positively, others negatively, to these changes in community and ecosystem conditions owing to adaptive characteristics and trophic interactions (21, 26, 32, 36, 49, 56, 84, 88, 89, 105, 140). Species that increase in abundance following disturbance typically are favored by exposed conditions, stressed or rapidly growing plants, or detrital resources. In addition, some may be promoted by decoupling of predator-prey relationships in patches of enemy-free space.

Exposure. Disturbances that remove vegetation cover or litter expose insects to a wider range of ambient temperature and relative humidity (24, 98) and predators (14). Arboreal beetle responses to typhoon disturbance in tropical rain forest in Australia reflected species' adaptations to moisture, with more xerophilic species increasing in abundance and mesophilic species decreasing in abundance following canopy opening and general drying of the forest (42). Furthermore, reproduction, especially egg hatch, may be reduced at high temperature and low relative humidity (121).

Some ant species, e.g., *Solenopsis invicta* Buren and *Atta laevigata* F. Smith (Formicidae), preferentially colonize bare soil habitats to soil covered by vegetation or litter (117, 127). However, other species may be unable to survive the extreme temperatures of exposed sites. Meisel (83) reported that the army ant, *Eciton burchellii* Westwood (Formicidae), is restricted to forest fragments in Costa Rica, because workers survived less than 3 min at 51°C (the midday temperature of surrounding pastures) and only 18 min at 43°C.

Resource abundance and quality. Insects dependent on lost resources may disappear, but some insects flourish on surviving hosts that are stressed and less capable of defense or on new hosts that exploit reduced competition or predation. Sap-sucking hemipterans are favored by rapid growth of early-successional plants (101, 104, 108). Other species also respond to rapid growth of early-successional plants (13, 123). Carabid beetle abundance and species richness increased in riparian forests subject to periodic flooding, compared to nonflooded sites, indicating that flooding contributed to habitat suitability for these beetles (22, 74).

Disturbances that create large amounts of coarse woody debris (fires and storms) or stressed trees (droughts and storms) are typical triggers for bark beetle and wood borer outbreaks (16, 36, 80, 93). Acoustic cues from cavitating cell walls may attract bark beetles to water-stressed trees (80). Many wood-boring insects, such as wood wasps (Siricidae) and beetles (especially Buprestidae), are attracted to sources of smoke, infrared radiation, or volatile tree chemicals emitted from burned or injured trees over distances of up to 50 km (33, 39, 86, 94, 110, 138). These cues signal the availability of dead trees, typically rare in undisturbed forests, that are suitable sites for reproduction.

Plants stressed by disturbance, especially drought, frequently trigger outbreaks of some herbivorous insect species (80, 105, 125, 134–136). Defoliator outbreaks commonly reflect abundant water-stressed plants (102, 105, 125), perhaps reflecting changes in plant defensive chemistry, but this is not always the case (46). Interestingly, locust outbreaks appear to be triggered by either drought or flooding disturbances. A 1000-year record of locust outbreaks in China indicated that outbreaks typically originated in floodplain refuges, which are characterized by adequate vegetation and suitable oviposition sites, during drought years and years after flooding (116). Droughts increase the availability of suitable oviposition sites, as well as stressed vegetation, as water recedes, whereas similar conditions occur in formerly flooded areas in the year after flooding.

On the other hand, many herbivorous insects become less abundant on stressed host plants (92, 105, 131). A major drought in Pacific northwestern North America virtually eliminated the dominant folivore, a bud moth, *Zeiraphera hesperiana* Mutuura & Freeman (Tortricidae), and favored its replacement by the western spruce budworm, *Choristoneura occidentalis* Freeman (Tortricidae), and the balsam fir sawfly, *Neodiprion abietis* (Harris) (Diprionidae). Following the drought, *Z. hesperiana* recovered its dominance, and *C. occidentalis* and *N. abietis* disappeared (**Figure 2**) (101, 102). Schowalter et al. (105) reported that some herbivorous species increased, whereas others decreased, in abundance on creosote bushes, *Larrea tridentata* (DC) Coville, subjected to an experimental moisture gradient. Obviously, response to plant water status varies widely among herbivorous insects (71).

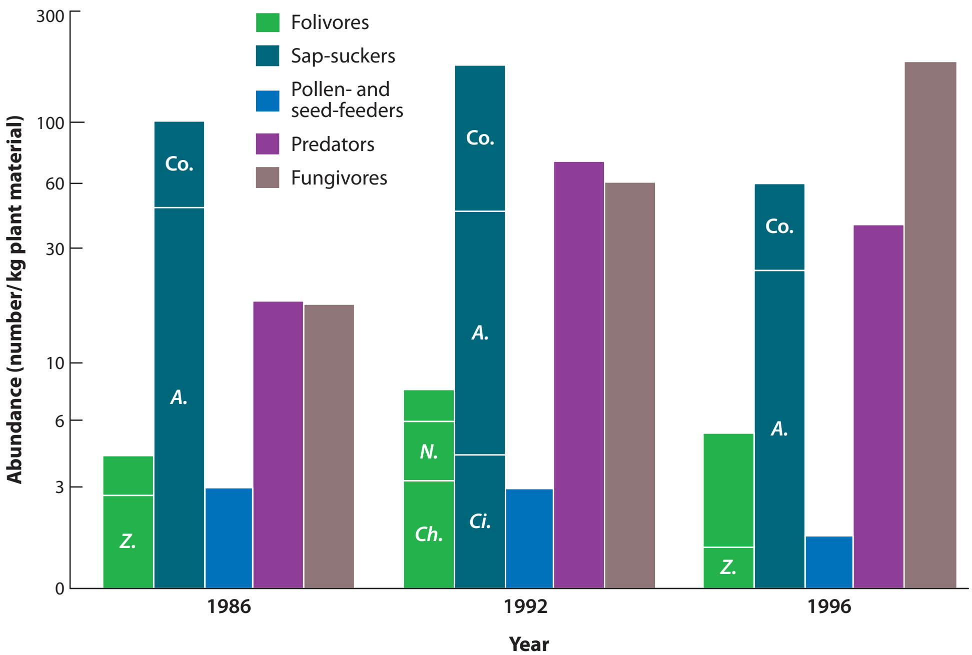

Figure 2

Drought-induced change in forest canopy insect species composition, followed by recovery in western Oregon. 1986 and 1996 were relatively normal wet years; 1992 was near the end of a drought period (1987–1993). Abbreviations: *Z.*, *Zeiraphera hesperiana*; *Ch.*, *Choristoneura occidentalis*; *N.*, *Neodiprion abietis*; *Ci.*, *Cinara* spp.; *A.*, *Adelges cooleyi*; Co., Coccoidea (four species). Note the log scale of abundance. From Reference 102 with permission from Elsevier.

Variation in response to plant stress is not clearly associated with changes in plant defensive chemistry. Hale et al. (46) reported that drought-stressed black poplar, *Populus nigra* L., increased phenolic glycoside concentrations, with differing effects on gypsy moth, *Lymantria dispar* (L.) (Lymantriidae), and whitemarked tussock moth, *Orgyia leucostigma* (J.E. Smith) (Lymantriidae). Forest canopy-opening disturbances often result in increased production of phenolics by early-successional plants growing under conditions of higher light availability (59, 113). However, despite higher foliar phenolic concentrations, many herbivores increased in abundance following Hurricane Opal in southeastern North America (59).

Even within families and genera, individual species respond quite differently to disturbances. Among Hemiptera, some scale insect species increased in abundance, and others decreased, during forest canopy recovery from hurricanes in Puerto Rico (104). Root bark beetles [e.g., *Hylastes nigrinus* (Mannerheim) (Curculionidae)] are attracted to chemicals emanating from exposed stump surfaces that advertise suitable conditions for brood development, and become more abundant following forest thinning (144), whereas stem-feeding bark beetles [e.g., *Dendroctonus* spp. (Curculionidae)] are sensitive to tree spacing and become less abundant in thinned forests (4, 99, 107).

Responses also vary among disturbance types. Paquin & Coderre (89) compared forest floor arthropod responses to forest clearing versus fire. Decomposers were less abundant, whereas predators were more abundant, in cleared plots than in undisturbed plots. Arthropod abundance overall was reduced 96% following experimental fire, but some organisms survived due to their occurrence in deeper soil levels or to the patchy effect of fire. Abundances of some species differed between cleared and burned plots.

Following disturbance, populations and ecosystems may recover to their predisturbance condition at rates that reflect the extent of change and the size of the disturbed area. Recovery can be as quick as a few months for rapidly reproducing species or assemblages, such as many insects, or for patches in landscape matrices that facilitate dispersal (36, 50). In contrast, recovery can be long, taking years to centuries for long-lived, slowly reproducing species or assemblages. Factors that delay recovery of plant communities also influence recovery of habitat conditions and rates of insect recovery. Insects often influence rates of community recovery. Herbivorous species can accelerate replacement of earlier successional host plant species by later successional nonhost plant species (28, 123). If the disturbance-free interval is shorter than the time needed for recovery, then earlier-successional communities may persist.

Predator/parasite abundance and foraging activity. Disturbances affect abundances and foraging activity of predators and their prey differently, creating areas of concentrated predation or of predator-free space (47, 75, 120). Insects at higher trophic levels appear to be particularly susceptible to disturbances (37, 47, 89, 104, 120), although some carabid beetle species increase in abundance in burned sites (37). Parasitoids commonly have a lower temperature tolerance than their hosts, and different thermal tolerances affect the temporal synchronization of parasitoid and host during the season (47). Beuzelin et al. (11) reported a threefold reduction in red imported fire ant (*S. invicta*) in areas inundated by storm surge during Hurricane Rita. Entomopathogen abundance may be reduced in disturbed areas by exposure to UV radiation (97). Reduced predation or parasitism in disturbed areas may permit prey species to increase in abundance.

RESPONSES TO ANTHROPOGENIC DISTURBANCES

Anthropogenic disturbances, including harvest, altered fire regimes, road construction, and release of toxic materials, such as oil spills and industrial effluents, have become a pervasive environmental factor. Insect responses to such disturbances reflect the degree to which direct and indirect effects resemble those of natural disturbances, e.g., forest harvest may elicit responses similar to other canopy-opening disturbances (21, 89). Gandhi et al. (38) compared forest floor beetle assemblages in remnant forest patches within harvested landscapes and burned landscapes and found that, whereas assemblages in remnant patches within harvested landscapes resembled those of uncut forest, they differed significantly from assemblages in remnant patches within burned forest, indicating that fire creates unique habitats within the landscape. Anthropogenic disturbances also introduce novel conditions, e.g., large numbers of cut stumps with exposed fresh surfaces and inground root systems that provide unique habitats for root-feeding insects (144) and sharp boundaries that alter the steepness of environmental gradients between disturbed and undisturbed patches and restrict dispersal of species intolerant of exposed conditions (24, 50). Catastrophic wildfires in western North America that have resulted from fuel accumulation during a century of fire suppression also may create conditions different from those of low-intensity ground fires to which species have adapted (2, 25).

Landscape matrix or mosaic: the patchwork of distinct communities on the landscape that represent different combinations and histories of disturbances and colonization

Anthropogenic disturbances differ from natural disturbances in their frequency, duration, and scale. Whereas the return frequency of stand-replacing fire in coniferous forests of the Pacific Northwest was about 500 years, harvest practices now restart forest recovery every 70 to 100 years (25). Ecosystem fragmentation and conversion to agricultural or urban uses have dramatic effects on survival and movement of various insects. Braschler et al. (15) found that many orthopterans avoided the mown matrix in a fragmented grassland, likely because of the lack of shelter. As a consequence, small populations became increasingly isolated in diminishing remnant patches of grassland, increasing their vulnerability to local extinction if large areas are mown simultaneously. Stream channelization and levee construction may threaten floodplain insects that depend on periodic flooding (22, 74). Extended periods of submersion resulting from dam operation may exceed the ability of many floodplain species to tolerate hypoxic conditions (19).

Anthropogenic changes also may exacerbate the effect of natural disturbances. Clearing land and impounding reservoirs have occurred simultaneously over large areas of the globe. These practices alter surface albedo in ways that increase regional warming, storm intensity (34, 58), runoff, and stream discharge. As a result, the average return time for floods of 100-year severity is likely to shrink to 30 years (72). Vegetation removal and smoke from fires that accompany forest conversion to agricultural or urban land use reduce cloud cover (from 38% in clean air to 0% in heavy smoke) and increase the altitude at which water condenses, leading to more violent thunderstorms and hail rather than warm rain (1, 5, 70). The increased frequency of extreme disturbances will affect insects and other organisms in ways that are difficult to predict (43).

CONSEQUENCES OF POPULATION CHANGES

Disturbance-induced changes in insect populations affect subsequent community and ecosystem processes. In some cases, insects respond in ways that substantially alter community recovery or predispose ecosystems to subsequent disturbances (28).

Community Recovery

Elderd (30) and Elderd & Doak (31) used manipulative experiments to demonstrate that increased herbivory by grasshoppers following flood events significantly reduced survival of a common riparian plant, *Mimulus guttatus* DC, that otherwise is favored by flooding. Bishop (13) found that several herbivorous insect species suppressed populations of lupine, *Lupinus lepidus* Douglas ex Lindl., an important early-successional, nitrogen-fixing plant, following the eruption of Mount

St. Helens, thereby affecting the rate of nutrient recovery and vegetative succession. Bark beetle populations increasing in injured or stressed conifers can reach sizes capable of killing surrounding uninjured trees over large areas (107).

Although outbreaks have been targets of pest management, they may alleviate stressful conditions and facilitate community and ecosystem development, at least in some cases. Drought-stressed plants may show higher survival when defoliated than when nondefoliated (67, 115). Canopy openings resulting from spruce budworm, *Choristoneura fumiferana* (Clemens) (Tortricidae), outbreaks had a greater diversity of saplings and trees and larger perimeter/area ratios than did canopy openings resulting from harvest practices, suggesting that stand recovery and contributions by the surrounding forest should be greater in budworm-generated openings than in harvest-generated openings (9). Alteration of vegetation composition by insects may tailor overall biotic demand for water and nutrients to prevailing conditions at a site, e.g., replacement of N-rich species by low-N species (10, 67, 95). Succession from pioneer pine forest to late-successional fir forest in western North America can be retarded or advanced by insects, depending primarily on moisture availability and the condition of the dominant vegetation (103). When moisture is adequate (e.g., in riparian corridors and at high elevations), mountain pine beetle, *Dendroctonus ponderosae* Hopkins (Curculionidae), advances succession by facilitating the replacement of host pines by more shade-tolerant, fire-intolerant understory firs. However, limited moisture and short fire return intervals at lower elevations favor pine dominance. In the absence of fire during drought periods, *C. occidentalis*, Douglas-fir tussock moth, *Orgyia pseudotsugata* (McDunnough) (Lymantriidae), and fir engraver beetle, *Scolytus ventralis* LeConte (Curculionidae), concentrate on the understory firs, truncating (or reversing) succession.

Some disturbance-induced changes in insect abundance and distribution increase the transmission rate of human and animal diseases (114, 129, 147). Flooding or canopy opening or both increase habitat for mosquitoes and other insect vectors. Vittor et al. (129) found that increased abundance and biting rate of the mosquito *Anopheles darlingi* Root (Culicidae), which is responsible for transmission of malaria to humans, in Peru were related to deforestation and road development. Stapp et al. (114) and Zhou et al. (147) reported increased incidence of human and wildlife diseases associated with El Niño–induced increases in abundances of insect vectors.

Promotion of Future Disturbances

Insect outbreaks can predispose ecosystems to subsequent disturbances. Severe defoliation can increase plant vulnerability to other mortality agents, e.g., bark beetles (145). Outbreaks also affect the probability or severity of abiotic disturbances, especially fire or storms (76).

Increased fuel accumulation generally has been considered to increase the likelihood and severity of fire (82), but this is not necessarily the case. Bebi et al. (8) concluded that mortality of spruce, *Picea engelmannii* Parry ex. Engelm., to the spruce beetle, *Dendroctonus rufipennis* (Kirby) (Curculionidae), did not increase the occurrence of subsequent fires. The probability of fire resulting from outbreaks depends on the amount and decomposition rate of increased litter. Grasshopper outbreaks that reduce grass biomass should reduce the severity of subsequent grassland fire. Outbreaks that increase only fine litter material (e.g., foliage fragments) increase the probability but reduce the intensity of fire, whereas outbreaks that increase coarse woody debris (especially of standing boles that increase the abundance of ladder fuels) are more likely to increase the risk of catastrophic fire (61).

Insect outbreaks that open the canopy increase penetration of high wind speeds but also reduce wind resistance of defoliated trees. Pruning at least 80% of the canopy can reduce wind stress significantly (87). Wind-related tree mortality following spruce budworm defoliation in eastern

Canada was related to outbreak severity and peaked 11 to 15 years after the outbreak, due to greater exposure of surviving trees to wind (119).

CONCLUSIONS

Insect responses to major landscape-level disturbance are dictated by disturbance characteristics, insect exposure to disturbance effects, and tolerance to altered conditions during and after the disturbance. Disturbances can eliminate populations of exposed or poorly adapted insects, but tolerant insects may survive or colonize the altered ecosystem. Postdisturbance responses include outbreaks of species that exploit abundant, stressed, or detrital resources.

Relatively few studies have documented insect responses to natural disturbances, compared to anthropogenic disturbances, largely because of unpredictability and statistical problems in comparing unreplicated disturbed and undisturbed patches. Some studies have fortuitously experienced superimposed disturbances that permitted comparison of pre- and postdisturbance abundances or activity. Other studies have employed experimental fire or canopy-opening manipulations to evaluate the effects of designed treatments on insects, but such manipulations may not reflect all conditions created by natural disturbances. Nevertheless, such experiments have provided the most useful data on insect responses to disturbances. Clearly, more research is needed on insect responses to natural disturbances and combinations of disturbances in order to improve prediction of responses that affect resource management goals and ecosystem services.

SUMMARY POINTS

1. Disturbances are relatively abrupt changes in environmental conditions that kill susceptible organisms and significantly alter the abundance and distribution of resources for surviving organisms.
2. Because of their small size and limited homeostatic ability, exposed insects are particularly sensitive to extreme temperatures and other variables that occur during or after disturbances.
3. Some species experience local extinction if habitat conditions exceed their tolerance ranges or if their resources disappear.
4. Disturbances often trigger outbreaks of herbivorous species favored by stressed or abundant hosts following disturbance.
5. Responses to anthropogenic disturbances depend on similarity between conditions created by anthropogenic disturbances and conditions created by natural disturbances that have shaped insect life-history adaptations.
6. Insect responses affect the rate or direction of community recovery from disturbance, affect the epidemiology of human or animal diseases, and may increase the likelihood of subsequent disturbances.
7. Additional studies on insect responses to multiple natural and anthropogenic changes are needed to improve prediction and management of outbreaks or endangered species.

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Errata

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