Pulsed resources and community dynamics of consumers in terrestrial ecosystems

Richard S. Ostfeld and Felicia Keesing

Recently, the field of community ecology has integrated the notions of ‘top-down’ and ‘bottom-up’ influences on community organization. According to this framework, populations occupy positions in a food web and their abundance or biomass can be controlled by populations at higher trophic levels (e.g. top-down effects of predators on prey), lower trophic levels (e.g. bottom-up effects of biotic resources on consumers) or the same level (more traditional competitive interactions). The top-down bottom-up approach is sympathetic to the notion that interactions between populations might be either direct (e.g. a predator controlling prey density) or indirect (e.g. a primary producer enhancing a parasitoid population by increasing population growth of a herbivore host). Recently, temporal fluctuations in the strengths of interactions among species have been of great interest to ecologists, but these fluctuations have not been integrated into the top-down bottom-up paradigm.

Many terrestrial (and aquatic) ecosystems are characterized by intermittent production of abundant resources for consumers, such as mast seeding and pulses of primary production following unusually heavy rains. Recent research is revealing patterns in the ways that consumer communities respond to these pulsed resources. Studies of the ramifying effects of pulsed resources on consumer communities integrate ‘top-down’ and ‘bottom-up’ approaches to community dynamics, and illustrate how the strength of species interactions can change dramatically through time.

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Many terrestrial ecosystems are characterized by intermittent production of abundant resources for consumers, such as mast seeding and pulses of primary production following unusually heavy rains. Recent research is revealing patterns in the ways that consumer communities respond to these pulsed resources. Studies of the ramifying effects of pulsed resources on consumer communities integrate ‘top-down’ and ‘bottom-up’ approaches to community dynamics, and illustrate how the strength of species interactions can change dramatically through time.
Because, by definition, resource pulses occur as episodic events with long interpulse intervals, few consumers are expected to specialize on such an ephemeral food supply as mast. Instead, we expect that the species most likely to respond to a masting event are trophic generalists. Generalists can be supported by nonmast resources during periods of low mast availability and can then switch to mast during the resource pulse. Owing to a superabundance of food, masting is expected to cause rapid population growth of these generalist consumers, but positive rates of growth and consequent high population density are expected to decline rapidly once the pulsed resource has been depleted. Similarly, because generalist mast consumers are expected to fluctuate dramatically in numbers, the predators of these mast consumers might be expected to be generalists as well, specializing on the mast consumers only when the latter are abundant.

Numerical responses of generalist consumers to pulsed resources, followed by depletion of the pulsed resource, are likely to cause situations in which, because of a delayed response to the resource, population density of the consumer is high but the pulsed resource is largely depleted. Such dramatic population fluctuations, which include high variability in consumer-resource ratios, are expected to lead to strong interactions between the mast consumer and its alternative prey, its predators, its competitors and its lead to strong interactions between the mast consumer and its alternative prey, its predators, its competitors and its

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\(N\), indicates that the abiotic resource or signal is unknown; \(N\), nitrogen.
Studied of pulsed seed production

Temperate tree masting

In Białowieża Primeval Forest of eastern Poland and western Belarus, oak (Quercus robur) and hornbeam (Carpinus betulus) are the most abundant tree species. Both are characterized by dramatic interannual fluctuations in the production of large, nutritious seeds. Over the past few decades, oak and hornbeam have synchronously produced especially heavy seed crops at intervals of four to eight years, resulting in a dramatic flush of resources. In years of mast production, populations of yellow-necked mice (Apodemus flavicollis), wood mice (Apodemus sylvaticus), and bank voles (Clethrionomys glareolus) and wild boar (Sus scrofa) exhibit high overwinter survival and begin to grow rapidly the following spring. All these species are generalists that consume items such as insects, nonmast fruits, fungi, and plant shoots when mast is unavailable. All four species reach population peaks in the summer or autumn following heavy mast production and then crash to particularly low levels in the next year.

Several mammalian and avian predators respond to these population peaks in a synchronized manner. A generalist predator, the pine marten (Martes martes), responds to the rodents by reaching its own peak one year after the rodents’ population peak. Another generalist predator, the tawny owl (Strix aluco), responds numerically to rodents by reaching a peak a few months after the rodent peak, owing to unusually successful fledging of large clutches. However, having achieved high population density only during or after the rodent crash, martens and tawny owls then switch to other prey (such as birds, their eggs and nestlings) and cause substantial declines in the breeding success of birds that nest on the ground, in shrubs or in large tree holes.

Some birds, such as the ground-nesting wood warbler (Phylloscopus sibilatrix), experience high nest predation by rodents in the summer following mast production and then again the next year, when martens and other predators are abundant.

These bottom-up effects of mast on rodents, mammalian carnivores, and raptors, followed by a top-down effect of predators on rodents and on birds and their predators on songbirds, can be superimposed on another pulsed resource: outbreaks of forest lepidopterans, such as the winter moth (Operophtera brumata). In years of high caterpillar abundance, rates of predation on songbird nests are reduced via two pathways. First, nesting birds with a good food supply spend less time foraging away from the nest, and are therefore better at defending eggs and nestlings. Second, when caterpillars are superabundant, generalist predators, such as rodents and corvids, switch from songbird nests to caterpillars, thus relaxing predation on the nests.

Production and survival of wild boar piglets in the spring and summer following heavy mast production cause rapid population growth in this species, but burgeoning wild boar populations suffer mass mortality when poor acorn crops follow a mast year. Boar carcasses provide a crucial winter resource for raccoon dogs (Nyctereutes procyonoides), which specialize on carrion during these starvation events but switch to rodents, shrews, amphibians and invertebrates in winters when carrion is scarce.

Similar patterns of community response to masting appear to occur in temperate forests throughout the world. In beech (Fagus spp.) forests of New Zealand, mast production stimulates high overwinter survival and subsequent summer peaks in the population density of introduced house mice (Mus musculus) and rats (Rattus rattus). High density of mice leads to population growth of introduced stoats (Mustela erminea), which prey heavily on mice during rodent peaks. Because of their high potential for population increase, peaks in the abundance of stoats are delayed behind those of rodent prey by only a few weeks to months; consequently, both rodents and stoats reach population peaks during the summer following heavy mast production. High densities of stoats, possibly combined with the declining abundance of rodents, are correlated with high rates of predation on endemic birds, including mohua (Mohoua ochrocephala) and kaka (Nestor meridionalis), both of which are rare or endangered. Both species are vulnerable to mammalian predators owing to the use of large tree holes for nesting sites.
In the case of the mohua, predation on adults and nests is heaviest in the summer following mast production and relieves in summers following poor mast production. In kaka, breeding is attempted (and successful) only in summers preceding heavy mast production; during this time population densities of rodents and stoats are low as a result of declines following the previous masting event. Trees are thought to have evolved masting behavior as a means of increasing reproduction by producing long intervals between mast events, populations of most consumers are likely to have crashed by the time the next mast crop is produced. By satiating the generalist seed predator, a mast crop might also promote simultaneous escape of other prey, including nestlings, seeds of other trees and insects.

A similar relationship between mast, rodent consumers, rodent predators and songbird victims exists in the oak forests of Virginia (USA). Heavy acorn production causes population growth of white-footed mice (Peromyscus leucopus), chipmunks (Tamias striatus) and grey squirrels (Sciurus carolinensis)23–25. White-footed mice attack ground nests of songbirds in a density-dependent manner26, such that nesting success is reduced in the summer following heavy acorn production. In addition, analysis of temporal patterns in abundance of breeding birds suggests that inhibitory effects of acorn production on songbird abundance can be heaviest two years after the masting event. Apparently, small carnivores respond numerically to abundant rodents, reach high densities two summers following mast production, and reduce the density of ground- and shrub-nesting songbirds27.

Trophic responses to acorn masting in forests of New York and New England (USA) have been implicated in the population dynamics of a defoliating insect, the gypsy moth (Lymantria dispar)28–30, and in the risk of exposure to tick-borne Lyme disease31–33. As in Virginia, populations of white-footed mice grow and shrink with fluctuating acorn production. In turn, mice are predators on the pupal stage of gypsy moths and are capable of regulating the population size of gypsy moths, at least when moth densities are at low to moderate density. In summers following poor acorn production, mouse populations tend to be sparse, and such crashes in the mouse population, if they occur during the low phase of the gypsy-moth cycle, might release moths from regulation and allow rapid growth to a peak34. Because defoliation of oaks by gypsy moths is known to delay or prevent masting, a self-perpetuating positive feedback loop might exist in these systems35.

**Desert ephemerals**

Heavy ENSO-induced rainfall in arid communities of Chile causes increased growth and seed production by desert ephemerals, which, in turn, causes population growth by pulvivorous, granivorous and omnivorous rodents. The length of time lags by rodents in response to increased availability of resources ranges from a few weeks to one year, depending on the life history characteristics of the rodent species. Both mammalian and avian predators of rodents, primarily foxes (Vulpes vulpes) and several species of owl, respond to rodent increases with population increases of their own. In addition to numerical responses to small mammal outbreaks, the avian and mammalian predators change their functional responses (proportion of each prey species in the diet) and their guild structure (size, membership and dietary similarity of groups of predators) with the fluctuating abundance of rodent prey. Changes in functional response and guild structure of these generalist predators implies that their effects on various prey species, both vertebrate and invertebrate, might change considerably with changing rodent abundance36.

**Pulsed resources and zoonotic diseases**

Population responses by rodents to pulsed resources have consequences for the epidemiology of zoonotic diseases for which the rodents are reservoirs. In eastern North America, white-footed mice and, to a lesser extent, chipmunks are natural reservoirs for the spirochete (Borrelia burgdorferi) that causes Lyme disease. A common vector of this disease, the black-legged tick (Ixodes scapularis), acquires the spirochete in early instars more efficiently when feeding on white-footed mice than on other species of vertebrate host. The greater the population density of mice in summer, when larval ticks seek hosts, the greater the opportunities for ticks to acquire the Lyme disease agent and the higher the density of infected ticks the following summer. Epidemiological evidence suggests that the incidence of Lyme disease in the human population is correlated with mouse density one year previously and with acorn production two years previously (R.S. Ostfeld, unpublished). A similar epidemiological impact of pulsed resources on the incidence of zoonotic diseases might exist in the American southwest and South America. In the deserts of New Mexico and Arizona, heavy rainfall causes flushes in the productivity of desert annuals, resulting in heavy seed production and consequent growth in populations of deer mice (Peromyscus maniculatus), which are the main reservoirs for the viral agent of hantavirus pulmonary syndrome in humans, in the Argentine pampas, heavy summer rainfall in 1990 and an associated pulse in green vegetation resulted in population outbreaks of corn mice (Calomys musculinus), which are reservoirs for Argentine hemorrhagic fever virus. The rodent outbreak coincided with an unusually severe epidemic of this disease in associated human populations.

**Other types of pulsed resources**

Consumer communities can respond to pulses of resources other than mast seeding. On islands in the Gulf of California, Mexico, dynamics of an invertebrate food web are profoundly influenced by periodically heavy rains37–39. Following ENSO

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**Fig. 3.** Percentage change in nesting bird density from years of moderate to high rodent densities (when predation pressure by mammalian carnivores and raptors on nesting birds is presumed to be low) to years of low rodent densities (when mammalian and avian predators on birds are presumed to be high). High predator densities, combined with low densities of their primary prey (rodents), are postulated to inflict heavy losses on nesting birds and their offspring. Bird species (the number of species sampled is written above the bar) are categorized according to the locations of nests: those nesting on the ground, on shrubs and in large tree holes are more vulnerable to predators, whereas those nesting in small holes and tree crowns are less vulnerable. Redrawn, with permission, from Ref. 21.
rains, the biomass of desert ephemerals increases, causing population growth in several species of herbivorous insects. In response to increases in their insect prey, biomass of a guild of web-building spiders doubles following the rains but then crashes one year later in spite of continued high prey availability. The crash in spider populations is caused by another group of generalist consumers, the pompilid wasps, the juveniles of which are obligate parasites to the pulsed resource; and mobility in response to the resource.

The rate of population response to the pulsed resource; the degree of specialization on the pulsed resource might be predictable as a function of three interrelated features of the terrestrial consumer community to respond to fluctuating resource levels. Pulsed resources are also known to focus the attention of community ecologists on biotic interactions within the context of chaotic processes (e.g. climate fluctuations), which might cause the effects of mast to be experienced in adjacent habitat types that do not themselves experience masting (e.g. coyotes moving from subsidized coastal areas to inland sites and bearded pigs or long-tailed parakeets migrating out of mast areas).

Generalities and predictions
Pulses of heavy seed production by forest trees and ENSO-induced rainfall in arid systems appear to be widespread phenomena (Table 1). In spite of strong variation in the taxonomic composition of consumer communities, in the various ecosystems subjected to pulsed resources, several generalities in the responses of these communities emerge. The consumers of pulsed resources are often generalists that respond numerically, but with a time lag, to fluctuating resource levels. By the time the generalist consumer has increased in density, the pulsed resource has begun to decline, in part as a result of depletion during population growth of the consumer. This sets the stage for temporal switching by the generalist consumer to alternative prey once the generalist consumer has been depleted. In some cases, the alternative resource is heavily exploited owing simply to high consumer density, in the absence of switching. In temperate forests on at least three continents, both the generalist consumers (rodents) and their predators (small carnivores and raptors) increase predation rates on the same alternative prey – nesting birds.

Community responses to pulsed resources should vary predictably as a function of three interrelated features of the generalist consumers: the degree of specialization on the pulsed resource; the rate of population response to the pulsed resource; and mobility in response to the resource. Consumers that specialize on the pulsed resource might respond numerically and influence their predators or parasites, but they are not expected to influence alternative prey (e.g. weevils that specialize on mast).

Those consumers that respond with moderately rapid population growth (e.g. small rodents) are likely to introduce modest time lags into the system. Their heaviest impact on alternative prey species is likely to be delayed several months to a year. Similarly, predators that consume these small rodents are likely to exhibit delayed responses in their prey. In a few species, the alternative resource is heavily exploited simply to high consumer density, in the absence of switching. In temperate forests on at least three continents, both the generalist consumers (rodents) and their predators (small carnivores and raptors) increase predation rates on the same alternative prey – nesting birds.

Conclusions
Pulsed resources appear to elicit bottom-up effects that are accompanied by top-down trophic cascades. A focus on the pulsed nature of many resources facilitates the integration of temporally varying top-down and bottom-up forces in terrestrial communities. The concept of pulsed resources also focuses the attention of community ecologists on biotic interactions within the context of chaotic processes (e.g. climate fluctuations), which might cause the effects of mast to be experienced in adjacent habitat types that do not themselves experience masting (e.g. coyotes moving from subsidized coastal areas to inland sites and bearded pigs or long-tailed parakeets migrating out of mast areas).

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