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Pulsed resources and community dynamics of consumers in terrestrial ecosystems

Richard S. Ostfeld and Felicia Keesing

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.

Richard Ostfeld is at the Institute of Ecosystem Studies, Millbrook, NY 12545, USA (rostfeld@ecostudies.org); Felicia Keesing is at Siena College, Loudonville, NY 12211, USA, and the Institute of Ecosystem Studies, Millbrook, NY 12545, USA (fkeesing@siena.edu).

Recently, the field of community ecology has integrated the notions of 'top-down' and 'bottom-up' influences on community organization[1–5]. 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[6], but these fluctuations have not been integrated into the top-down bottom-up paradigm[2].

Many terrestrial (and aquatic) ecosystems are characterized by pulsed resources – the temporary availability of dramatically higher than normal levels of resources, which then become depleted with time. Examples include mast fruiting by trees and herbs[7,8], periodic irruptions of palatable insects[9], and storm-induced transport of marine resources (e.g. whale carcasses) to terrestrial systems[10] or of terrestrial resources (organic nitrogen or phosphorus) to aquatic systems[11]. Determining how the effects of pulsed resources permeate through food webs is a major challenge for community ecology. Tracing the impacts of pulsed resources on communities incorporates both bottom-up and top-down influences, but requires ecologists to incorporate the concepts of disturbance, time delays and mobility of organisms into considerations of how populations affect one another.

Conceptual underpinnings

Recently, far-reaching effects of pulsed seed production have been documented in several terrestrial habitats. Mast seeding occurs in many terrestrial ecosystems, including boreal, temperate and tropical forests, as well as grasslands and deserts[7,12–14]. If the trees, shrubs or herbaceous plants that synchronously produce large fruit or seed crops (i.e. mast) are highly abundant, even dominant, members of their communities, the result is an extraordinary flush of nutritious foods for consumers (Box 1). Pulses of seed production can be elicited by regional or global climatic fluctuations, including El Niño southern-oscillation (ENSO) events, which can cause unusually high rainfall or solar radiation (potentially important abiotic resources). In arid ecosystems, plant communities typically respond to heavy rainfall with explosive production of seeds and vegetative tissues[15–17]. In moist, tropical forest systems, trees might respond to either unusually heavy rain or unusually dry, sunny conditions with heavy fruit production[18–20] (Table 1).

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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

Box 1. Mast seeding in plants

Perhaps the most common type of resource pulse in terrestrial ecosystems is mast seeding, defined as the intermittent, synchronous production of large seed crops by a population of plants (see Refs 7,44). Masting is best known in long-lived woody species, but also occurs in herbaceous plants[13,44]. Far more attention has been paid to the physiological and evolutionary causes of masting than to its consequences for communities of consumers. Masting is sometimes a consequence of plants tracking environmental variation in abiotic resources; this occurs when heavy seed and/or fruit production follows ENSO-induced rains[16] or ENSO-induced drought[18]. In other cases, populations of trees appear to respond to subtle signals (e.g. a modest drop in temperature) that probably have little effect on resource availability[45,46]. Masting also appears to have evolved in some species as a means of satiating predators or of facilitating pollination[7]. A recent model by Isagi *et al.*[47] postulated that plant species with a high physiological cost of producing seeds relative to that of producing flowers are likely to produce intermittent, synchronous seed crops owing to the time necessary for accumulating photosynthates. This mechanism might be responsible for the observed positive relationship between seed size and tendency to undergo masting behavior[14]. Larger seeds can be expected to be of greater food value for consumers, thus the same plant species that are most likely to undergo mast seeding might also be those that are most likely to influence dynamics of consumers.

Irrespective of the mechanisms involved in masting, synchronous, but episodic, production of heavy seed crops is geographically and taxonomically widespread, and can be quite spectacular. Mast seeding in boreal coniferous trees is synchronized over areas $>10^6$ km^2, suggesting that masting events can occur at regional to continental scales[48]. Moreover, mast seeding might occur synchronously in dozens of sympatric genera and hundreds of species, and might be compressed into a timespan as brief as two weeks[20].

Table 1. Recent studies of pulsed resources (primary producer), consumers, top-down effects and the abiotic resource or signal

Abiotic resource or signal[a]	Primary producer	Primary consumer	Secondary consumer	Tertiary consumer	No. of trophic levels	Top-down effects	Location	Refs
?	Forest tree seeds	Rodents and wild boar	Pine martens, weasels, owls and raccoon dogs	–	3	Owls and martens on birds, rodents on birds, avian and mammalian predators on amphibians	Poland and Belarus	21
Temperature	Forest tree seeds	House mice	Stoats	–	3	Stoats on mohua	New Zealand	23
Temperature	Forest tree seeds	House mice	Stoats	–	3	Stoats on kaka	New Zealand	24
?	Forest tree seeds	Rodents	Mammalian carnivores	–	3	Deer on acorns and carnivores on ground-nesting birds	USA	25
?	Forest tree seeds (acorns)	White-footed mice and white-tailed deer	Tick parasites	–	3	Mice on gypsy moths, mice on seeds, ticks on people and gypsy moths on trees	USA	28–31
?	Forest tree seeds	Bearded pigs and long-tailed parakeets	–	–	2	Seed predators on seed survival	Indonesia (Borneo)	19,20
Rainfall	Seeds of desert ephemerals	Granivorous rodents	Viral pathogens	–	3	Rodents on seed survival and plant regeneration	USA	17,35–37
Rainfall	Biomass and seed production of desert ephemerals	Folivorous and granivorous rodents	Owls and foxes	–	3	Owls and foxes on rodents and rodents on seeds?	Chile	15,16, 32,33
Rainfall	Desert ephemerals and plant biomass	Herbivorous insects	Spiders	Wasps	4	Wasps on spiders and spiders on insects?	Mexico	39,40
Solar radiation	Tropical forest trees and fruit production	Frugivorous mammals	–	–	2	Mammals on seed or fruit survival?	Panama	18
N fertilizer	Boreal forest trees	Phytophagous insects	Insectivorous birds	–	3	Birds on insects? Insects on 1° production	Canada	49
N fertilizer	Herbaceous plants	Phytophagous insects	Parasitoids	–	3	Parasitoids on insects	USA	50

[a] ?, indicates that the abiotic resource or signal is unknown; N, nitrogen.

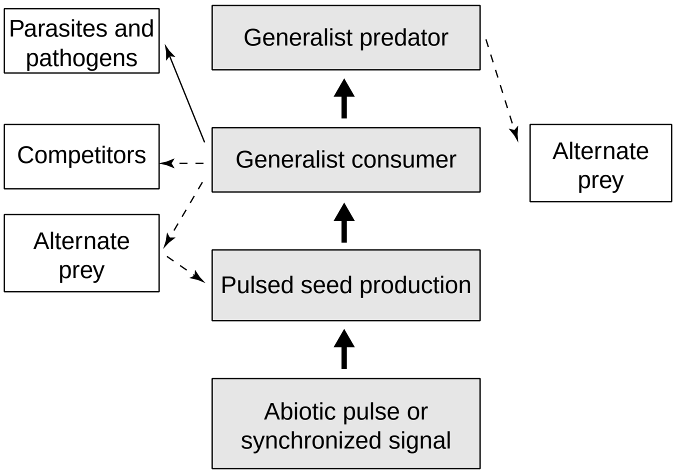

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Fig. 1. Conceptual model of the effects of pulsed resources permeating through a food web. The direction of arrows represents the direction of causal change in abundance or biomass. Solid lines indicate a positive effect and broken lines indicate a negative effect of one trophic group on another.

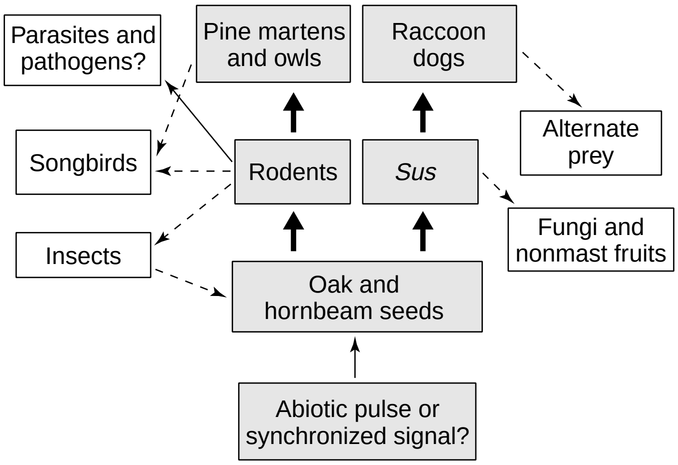

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Fig. 2. Conceptual model of the food web described by Jędrzejewska and Jędrzejewska[21] for Białowieża Primeval Forest in Poland and Belarus. The direction of arrows represents the direction of causal change in abundance or biomass. Unbroken lines indicate a positive effect and broken lines indicate a negative effect of one trophic group on another. Question marks in boxes indicate hypothesized, rather than demonstrated, effects.

parasites. These individuals might also fluctuate causing predictable changes in the abundance of species with which they interact (Fig. 1).

Studies 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 two most abundant tree species[21]. 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*), 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[21].

Several mammalian and avian predators respond to these population fluctuations of mast-consumers[21]. 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 (Fig. 2). 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 brooding success of birds that nest on the ground, in shrubs or in large tree holes (i.e. sites that are vulnerable to martens and owls) (Fig. 3). 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[21].

These bottom-up effects of mast on rodents, mammalian carnivores and raptors, followed by a top-down effect of predators on rodents and of rodents and their predators on songbirds, can be superimposed on another pulsed resource: outbreaks of forest lepidopterans, such as the winter moth (*Operophthera 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[21].

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[21].

Similar patterns of community response to masting appear to occur in temperate forests throughout the world. In beech (*Nothofagus* 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*)[22]. 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[22]. 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 relaxes in summers following poor mast production[23]. 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[24]. Trees are thought to have evolved masting behavior as a means of increasing seed survival; by maintaining long intervals between masting events, populations of mast 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*)[25,26]. White-footed mice attack ground nests of songbirds in a density-dependent manner[27], 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[25]. 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 songbirds[25].

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*)[28,29], and in the risk of exposure to tick-borne Lyme disease[30,31]. 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 moths 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 peak[28,31]. Because defoliation of oaks by gypsy moths is known to delay or prevent masting, a self-perpetuating positive feedback loop might exist in these systems[29].

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 folivorous, granivorous and omnivorous rodents[15,32]. 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 (*Pseudalopex culpaeus*) and several species of owl, respond to rodent increases with population increases of their own[33]. 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 abundance[33].

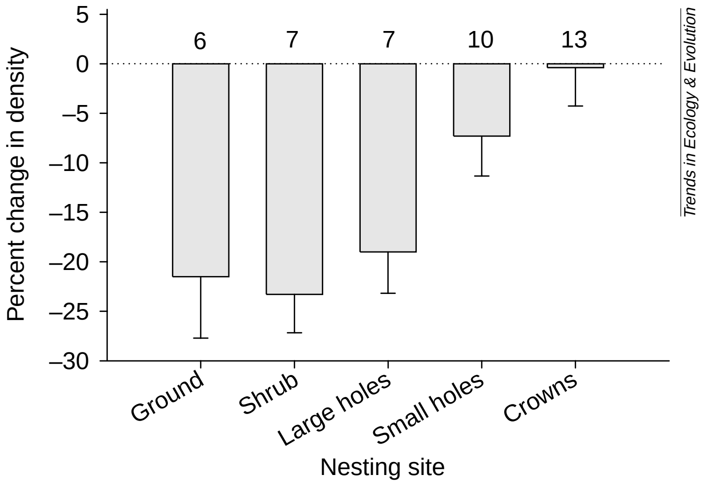

Fig. 3. Percentage change in nesting bird density from years of moderate to high rodent densities (when predation pressure by mammalian carnivores and raptors on nesting birds is presumed to be low) to years of low rodent densities (when mammalian and avian predators on birds are presumed to be high). 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, in 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.*

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[34]. A common vector of this disease, the blacklegged tick (*Ixodes scapularis*), acquires the spirochete in early instars more efficiently when feeding on white-footed mice than on other species of vertebrate host[34]. 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[30,31]. 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[17], resulting in heavy seed production and consequent growth in populations of deer mice (*Peromyscus maniculatus*)[35–37], 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[38].

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 rains[39,40]. Following ENSO 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 of spiders, but the adults of which are regulated by the availability of pollen and nectar. High survival and population density of nectarivorous adult wasps is stimulated by ENSO-induced plant productivity, and the wasp parasitoids then victimize populations of spiders that are burgeoning as an indirect result of ENSO rains[39]. The ability of the terrestrial consumer community to respond to fluctuating resource levels appears to be enhanced by the dominance of generalists, such as web-building spiders and rodents, which are able to respond opportunistically to pulses of different sources of food[39,40].

When allochthonous inputs from aquatic to terrestrial systems occur periodically, these ecotonal systems might also be understood in the light of pulsed resources and generalist consumers. For instance, the periodic importation of resource bonanzas, such as marine mammal carcasses from the sea to the coastal desert communities of Baja California, Mexico, might induce high rates of coyote (*Canis latrans*) recruitment within coastal zones[10]. Coyotes in these areas sustain higher population densities owing to increases in food supply. One possible consequence of elevated coyote density in areas subjected to allochthonous food inputs is the depression of alternative prey, such as rodents, to which the coyotes might turn when foods of marine origin are scarce[10].

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 resources, resulting in a strongly fluctuating impact on alternative resources. In turn, the generalist consumer itself can be considered a pulsed resource for its predators and parasites, who show an analogous increase in population density accompanied by switching 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[41]).

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 to their prey, often reaching a peak two years after the masting event. Consumers with a slow rate of increase are unlikely to show a numerical response to a pulse in resources because of a low intrinsic capacity to increase reproductive output (e.g. small litter size or single litter per year). These consumers are more likely to achieve their effects on the food web through mobility (e.g. immigration into areas with pulsed resources – deer[25], bearded pigs[19] and coyotes[10]) or a functional response.

Those consumers with poor mobility are likely to show a numerical response via reproduction, leading to a spatial coupling between the pulsed resource and the consequent effects in the local community. Those that are more highly mobile might exert strong temporary effects on the local community and then once the pulsed resource is depleted, disperse to other areas. This might cause the effects of masting to be experienced in adjacent habitat types that do not themselves experience masting (e.g. coyotes moving from subsidized coastal areas to inland sites[10] and bearded pigs or long-tailed parakeets migrating out of mast areas[19]).

Conclusions

Pulsed resources appear to elicit bottom-up effects that are accompanied by top-down trophic cascades[42]. 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 abiotic processes (e.g. climatic fluctuations), which might cause the resource pulse. Pulsed resources are also known to affect aquatic communities[42], although aquatic ecologists have tended to focus on seasonal, rather than super-annual, pulses. Studies of both chronic[43] and pulsed[11] inputs of nutrients into aquatic ecosystems strongly suggest that responses by primary producers and generalist consumers will cause predictable changes in community dynamics similar to those in terrestrial ecosystems.

Conceptual models of the ramifying effects of pulsed resources allow key aspects of the dynamics of highly complex systems, such as oak or beech forests, to be understood. Further explorations of this tentative understanding can be provided by testing specific predictions regarding the effects of a pulsed resource on population density, behavior or the interaction strength of species (or species pairs) removed by at least one trophic step from the resource itself. As has been found in the case of endangered birds in New Zealand and of Lyme disease in the United States, pulsed resources can provide predictive power relevant to practical issues in conservation and human health.

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