

RESOURCES FROM ANOTHER PLACE AND TIME: RESPONSES TO PULSES IN A SPATIALLY SUBSIDIZED SYSTEM

WENDY B. ANDERSON,^{1,4} D. ALEXANDER WAIT,² AND PAUL STAPP³

¹*Department of Biology, Drury University, Springfield, Missouri 65802 USA*

²*Department of Biology, Missouri State University, Springfield, Missouri 65897 USA*

³*Department of Biology, California State University, Fullerton, California 92831 USA*

Abstract. As the theoretical bases for the dynamics of spatially subsidized communities emerge, ecologists question whether spatially subsidized communities exhibit similar structure or dynamics to communities that receive strongly pulsed resources. In both cases, communities may be structured by responses to resources that are potentially absent at any given point in time (pulsed communities) or space (subsidized communities), even if pulsed resources are part of the in situ productivity of the system or the subsidies arrive as a relatively constant input from a nearby system. The potential for significant spatial or temporal resource limitation, therefore, may be a key factor influencing in similar ways the persistence of populations, the structure and dynamics of communities, and the evolution of specific life history traits. In most complex systems, however, multiple resources may arrive for various trophic entities at various points in time and from various points in space, and thus it may be difficult to separate or compare the dynamics of spatially subsidized and pulsed systems. In this paper, we explore the effects of interactions between pulses and subsidies in plant and animal populations and communities on highly pulsed and variably subsidized islands in the Gulf of California. While many of the plant and animal communities on the unsubsidized islands in this system respond to pulses of rain in classic ways, responses to these rain pulses on islands subsidized by seabird guano or other marine resources are quite different and variable, and depend on a combination of life history characteristics, physiology, competitive interactions, and trophic relationships. These variable responses to rain pulses then translate into large differences in dynamics and community structure of subsidized vs. unsubsidized islands. Indeed, most systems experience both temporal pulses and spatial subsidies. When considered in tandem, complementary or synergistic effects of the multiple, temporally and spatially variable resources may emerge that help explain complex food web structure and dynamics.

Key words: *community dynamics; deserts; Gulf of California; islands; lizards; nutrient subsidies; plant physiology; population dynamics; primary productivity; rodents; spiders.*

INTRODUCTION

As the theoretical bases for the dynamics of spatially subsidized communities emerge, ecologists are examining whether spatially subsidized communities exhibit similar structure or dynamics to communities that receive strongly pulsed resources (Sears et al. 2004), and how subsidies and pulses interact or overlap to influence communities (Polis et al. 1997b, Baxter et al. 2005, Yang et al. 2008). Spatial subsidies are donor-controlled resources that originate in one habitat but move into another habitat and alter the dynamics of recipient populations and communities (Polis et al. 1997a). In some cases, spatial subsidies arrive continuously, and in other cases, subsidies may arrive in pulses. Pulses are resources that occur episodically or rarely, that briefly enhance resource availability above the

baseline level, and that decay in availability through time (Ostfeld and Keesing 2000, Yang et al. 2008). Pulses may originate in situ or arrive from allochthonous sources, and often alter the dynamics of recipient populations and communities (Polis et al. 1997, 1998, Yang et al. 2008). Thus, if the impacts of subsidies and pulses interact or are inseparable, as when subsidies are pulsed, well-understood theory for pulsed communities may need to be modified to encompass the impacts of subsidies on population and community structure and dynamics. Our goal in this paper is to examine both plant and animal data from a pulsed and subsidized system to evaluate how spatial subsidies may influence species and community responses to pulses.

GENERALIZATIONS ABOUT SUBSIDIZED COMMUNITIES

More than a decade of theoretical and empirical studies explicitly investigating the dynamics of spatially subsidized systems have produced some generalities, but have also opened up more questions. Most studies of spatially subsidized systems indicate that resource subsidies produce a direct numerical response in

Manuscript received 12 February 2007; revised 25 April 2007; accepted 21 June 2007. Corresponding Editor: L. H. Yang. For reprints of the Special Feature, see footnote 1, p. xxx.

⁴ E-mail: wanderso@drury.edu

recipient populations (Polis and Hurd 1995; see Polis et al. 1997a for a review). A few long-term studies and models (McCann et al. 1998) have provided evidence that subsidies may help stabilize interannual fluctuations of populations and increase the probability of long-term persistence by providing a minimum level of resource availability, particularly for generalist consumers (Holt and Barfield 2003). The ability of resource subsidies to stabilize populations may be particularly evident in unproductive or strongly pulsed systems (Polis et al. 1997a).

In addition, only a few studies have emerged that document second-order or higher responses to spatial subsidies in communities. The numerical response of the direct or indirect consumers of the subsidy can spur apparent competition, intraguild predation, trophic cascades, or other multi-trophic interactions within the recipient community (Polis et al. 1998, Baxter et al. 2005, Croll et al. 2005, Schmidt and Ostfeld 2008). In some cases, a strong reciprocal flow of resources between two systems may further complicate the predictions made for a simple donor-controlled subsidy (Nakano and Murakami 2001, Baxter et al. 2005). Also, many subsidized systems receive multiple subsidies to multiple trophic groups, which may or may not arrive simultaneously, and which also shift dynamics in nonlinear, and possibly unpredictable ways (Huxel et al. 2002, Anderson and Polis 2004).

Very few studies have explored the influence of subsidies on species diversity patterns (Vidal et al. 2000, Anderson and Wait 2001, Barrett et al. 2003). Shifts in community interactions that result from direct and indirect population and community responses to subsidies may cause shifts in species composition of particular groups, but little is known about general impacts on richness and diversity. The ability to make predictions about species diversity patterns may be complicated by the continuous vs. pulsed availability of the subsidy, or the number of different subsidies occurring in a particular system. Thus, the regularity, magnitude, and diversity of the subsidy may be crucial in determining its impact on the recipient community, which highlights the need to integrate studies of pulses and subsidies.

GENERALIZATIONS ABOUT PULSED COMMUNITIES

While our understanding of subsidized systems is still growing, theoretical and empirical studies of pulsed systems are well developed and continue to become more complex as ecologists investigate the effects of pulses on community dynamics (Schmidt and Ostfeld 2008), ecosystem type (Nowlin et al. 2008), and subsidies (Yang et al. 2008). Most studies of pulsed systems focus on either plant responses or animal responses, but rarely both.

The majority of the pulse theory for plants was developed and tested in the context of the effects of rain pulses on desert plant life histories, physiological

characteristics, community structure and dynamics, and ecosystem processes (Chesson et al. 2004, Schwinning and Sala 2004). Indeed, pulses of rain are considered the trigger for almost all biological activity in deserts, from microbial decomposition to community succession (Schwinning and Sala 2004). Of course, the frequency, magnitude, duration, and seasonality of the pulse are key determinants for the scale of response, and specific responses of species or communities require that a resource pulse reach a particular threshold (Schwinning and Sala 2004, Schwinning et al. 2004).

Noy-Meir's (1973) classic pulse-reserve model (also known as the Bridges-Westoby model) depicted "pulses" as the plant growth response to a trigger such as rain, which would then contribute to a reserve (e.g., seeds, perennial vegetation, detritus) that would slowly drain through the interpulse or drought period. Commonly, though, references to this model refer to the trigger of rain as the pulse, and then use growth as the response to the pulse (Reynolds et al. 2004). A recent modification of the pulse-reserve model added the role of antecedent soil conditions (e.g., nutrients, organic content, moisture) and soil type in capturing and retaining water from a rain pulse and making it available in appropriate amounts and for requisite lengths of time to influence various plant species and communities of particular functional types (Reynolds et al. 2004). For example, soil nutrients, organic content, pH, and particle size can all influence water retention and evaporation rates with direct and indirect effects on plant physiological adaptations and community structure (Wait et al. 2005).

Physiological adaptations of plant species to highly pulsed environments and the consequential species composition (including seed bank reserves) of communities in pulsed environments represent the "memory" of a system (sensu Schwinning et al. 2004) to a history of pulses. Indeed, only those species with life history characteristics that allow rapid growth and/or storage during intermittent resource pulses followed by periods of dependence on stored reserves will persist in strongly pulsed environments. However, because numerous strategies exist for optimizing growth and storage during pulses and for persisting through interpulse periods, Chesson and Huntly (1997) predict that resource pulses will promote higher species diversity in communities via coexistence of species with variable strategic responses to pulses. This prediction may not apply, though, to pulsed communities that also receive resource subsidies such as additional nutrients, particularly when nutrient subsidies directly or indirectly alter the water retention capacity of soils, and hence the optimal physiological strategies and resultant competitive interactions of plant species (Vidal et al. 2000). As predicted by Goldberg and Novoplansky's (1997) two-phase resource dynamics hypothesis, strategies for persisting into interpulse periods may shift competitive outcomes towards favoring those species with somewhat more conservative (in the plant growth sense) or generalist (in the animal

sense) strategies. Thus, species that can maximize growth during the pulse but also keep growing upon return of the drought long enough to complete reproduction, will emerge as superior competitors and possibly displace other species. In systems that are both subsidized and pulsed, subsidies that amplify or lengthen a pulse's effect are likely to influence competitive outcomes and species composition or diversity.

In contrast to most of the studies of plant responses to seasonal or more predictable resource pulses, recent studies of the effects of pulsed resources on consumers have tended to emphasize rare, episodic events of extreme resource abundance (Ostfeld and Keesing 2000). Such events might include periods of unusually high primary productivity such as extreme climatic events (Holmgren et al. 2006), synchronous emergences of arthropods such as periodical cicadas (e.g., Yang 2004, Koenig and Liebhold 2005) or outbreaks of small mammals and insects (e.g., Singleton et al. 2001, Peltonen et al. 2002). These types of rare and intense pulses are distinguished from those that occur more predictably, such as seasonal litterfall of detritus and invertebrates into forest streams (e.g., Cummins et al. 1973, Vannote et al. 1980, Nakano and Murakami 2001, Sabo and Power 2002*a, b*) or regular inputs of algal wrack to beaches (e.g., Kirkman and Kendrick 1997, Orr et al. 2005).

Ostfeld and Keesing (2000) proposed that the type of community response to extreme pulses depends on the numerical response of consumer populations to pulses; the degree to which consumers were specialists on pulsed resources; and the degree of mobility of consumers relative to the spatial scale of the pulse. Consumers capable of strong, immediate numerical response would show tight coupling between the timing of the pulse and abundance, whereas others with lower intrinsic growth potential or storage mechanisms might show a greater lag between the timing of the pulse and increased population size. Moreover, generalist consumers would be expected to demonstrate stronger responses to pulsed resources than specialist groups because of their ability to switch from pulsed resources back to alternate prey as pulsed resources were depleted, which could depress the alternate prey populations in a manner equivalent to apparent competition (Holt and Barfield 2004). Likewise, more mobile consumers can respond functionally and numerically to a spatially heterogeneous pulse and thus connect adjacent habitats that receive either pulsed or spatially subsidized resources (Polis et al. 1997*a*).

In summary, plant ecologists have focused on ecophysiological, life history, and species diversity responses to pulses, while animal ecologists have been more concerned with numerical and behavioral responses of consumer populations to pulses and the consequent effects on food web structure and dynamics. Total plant productivity representing in situ resource availability provides a measure for predicting consumer responses, but rarely are more specific characteristics of plant

species composition, plant nutrient content, or plant life history (i.e., longevity) considered in evaluating consumer responses to resource pulses transmitted through plants (but see Sanchez-Piñero and Polis 2000). Moreover, few ecologists have examined the effects of pulses on either plants or animals in both the presence and absence of spatial subsidies. We will examine plant and animal data in concert from a strongly pulsed and highly subsidized system to show how plants respond to pulses in subsidized vs. unsubsidized conditions, and how various animal consumer groups respond to these variable plant responses and other spatial subsidies.

PREDICTIONS FOR RESPONSES TO PULSES IN SUBSIDIZED VS. UNSUBSIDIZED SYSTEMS

We propose general predictions for the responses of populations and communities to interactions between pulses and subsidies that depend on whether or not the pulsed resource and the subsidy are in phase or out of phase with each other. If a subsidy becomes available or is mobilized primarily during pulse periods ("in phase"), the subsidy will amplify the pulse, and thus recipients of those amplified resources may experience stronger fluctuations in populations, unless the recipient can switch back to more regularly available in situ resources between pulses. On the other hand, if a subsidy is available continuously or primarily during interpulse periods ("out of phase"), then total resource availability will be more constant, at least for generalist consumers that can switch diets, and population fluctuations will be dampened and possibly stabilized. If the subsidy and the pulse are one in the same (i.e., a pulsed subsidy), the community will respond similarly as it would to a pulse of an in situ resource.

Using these general predictions for responses to both pulses and subsidies, we show how plants, herbivores, and generalist consumers respond to pulses in the presence and absence of subsidies in a strongly pulsed, hyperarid region. In the first set of predictions, we examine the effects of intense precipitation pulses and nutrient subsidies derived from seabird guano on plant physiology, life history, and community structure, on herbivore abundance, and on granivorous rodent taxa. Since guano-derived nutrient subsidies to plants are primarily available during precipitation pulses, and likely amplify the pulse, we predict that, compared to unsubsidized islands, nutrient subsidized islands would (1) exhibit stronger population fluctuations and possibly higher risks of extinction on a local scale; (2) be dominated by species with life histories and diets that maximize assimilation of the subsidized resources during pulses; and (3) thus, exhibit lower species diversity at the local scale where the subsidy is available. A caveat to the third prediction is that we would expect higher species diversity at the regional scale that includes subsidized and unsubsidized areas via spatial partitioning of species that utilize the subsidy from those that do not.

In the second set of predictions and examples, we predict that, compared to unsubsidized systems, more generalized consumers in subsidized systems that can switch between plant-based resources that are available during subsidy-amplified pulses and other marine subsidies that are available more continuously would (1) exhibit dampened population fluctuations and possibly lower risks of extinction on a local scale; (2) be dominated by species with life histories and diets that allow for switching diets or other behaviors in response to pulsed vs. continuously available resources, subsidized or otherwise; and (3) thus, exhibit higher species diversity at the local scale where multiple subsidies are available.

A MODEL SYSTEM FOR STRONG PULSES AND SPATIALLY VARIABLE SUBSIDIES: DESERT ISLANDS IN THE GULF OF CALIFORNIA

Desert islands in the Gulf of California provide an interesting and well-studied system to explore population and community dynamics that are strongly influenced by both spatial subsidies and pulses. Mean annual precipitation in the region is 59 mm, ranging from 0 mm to 215 mm per year over the past 53 years (Polis et al. 1997b, Sanchez-Piñero and Polis 2000). The majority of this precipitation arrives in major storm events associated with summer thunderstorms or arrhythmic El Niño Southern Oscillation (ENSO) events. However, not all El Niño years produce greater-than-average precipitation, and some years that have precipitation greater than the mean are not officially recorded as El Niño years. Seasonality of precipitation is important in determining plant and animal responses to rain. Winter rains that reach a minimum threshold trigger strong plant-based responses while rains associated with summer thunderstorms produce little or no response, probably due to the summer dormancy of most plants and the high evaporation rate of summer precipitation (Polis et al. 1997b).

As a result of the extremely low precipitation rates, even in pulse years, these hyperarid islands exhibit extremely low annual primary productivity that ranges from $0 \text{ g}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ in dry years to $225 \text{ g}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ in wet years. The focal islands for these long term studies lie within 20 km of each other, and thus experience the same rain pulse events to similar degrees. Large winter or spring precipitation events stimulate pulses of annual productivity that trickle up to island consumer communities. Underlying this pattern of pulses is a strong system of spatial subsidies that arrive from the ocean onto the islands. The extremely productive marine system contributes macroalgae and marine carrion to island shorelines (up to $27.9 \text{ kg}\cdot\text{m}^{-1}\cdot\text{yr}^{-1}$) and seabird byproducts including guano, fish scraps, and chick and adult bodies and carcasses to cliffs or areas farther inland (Polis and Hurd 1996).

A high degree of spatial heterogeneity of quantity and quality of subsidies among and within islands has lent

itself to numerous studies of the impacts of various subsidies on numerous recipient populations and communities. Islands vary in size ($0.22\text{--}8.68 \text{ km}^2$) and perimeter-to-area ratio, which provides areas in the interior of larger islands that are relatively disconnected from shore-based marine subsidies (Murphy et al. 2002). Moreover, seabirds do not use all islands or all areas of islands that they do use, so it is easy to examine the impacts of seabird-based subsidies on plant and animal communities inside and outside of seabird areas.

Some of these subsidies are available continuously or regularly, while others arrive or become available with great irregularity. Seabird guano accumulates and resides in the soil year-round, but is mobilized for plant uptake only during precipitation events. Other inputs from seabirds, as well as coastal inputs, may also be strongly pulsed: ENSO events often result in periods of massive breeding failure of seabirds (Anderson et al. 1982), as well as widespread mortality of fishes and marine mammals (Soto et al. 2004). Such events may increase the amount of carrion washing on shore and remaining in seabird colonies, depending on the timing of mortality in relation to nesting phenology; massive die-offs of adult birds prior to breeding may eliminate sources of carrion for scavengers in colonies, whereas whole-scale abandonment of eggs and chicks may actually briefly increase resource inputs to carrion and detritus communities. Although such extreme temporal variation in these marine subsidies has not been well-studied in this system, we expect that it could be very important. Thus, with the combination of extreme spatial variation in marine subsidies and extreme pulse events, both from rains and from marine inputs, this system provides an ideal natural model for examining the population and community dynamics that arise in response to precipitation pulses in the presence and absence of spatial subsidies.

Highly subsidized islands exhibit unique plant and animal patterns during interpulse (drought) periods, and respond to pulses of rain in ways that are different from responses on unsubsidized islands during pulse and interpulse periods. We will begin by examining the effects of guano-derived nutrient subsidies that are taken up by plants during precipitation pulses and used directly by herbivores and granivores. However, in examining the subsequent, generalist consumer responses to pulses and subsidies, we cannot and do not separate their responses to guano and rain-induced plant growth from responses to other subsidies such as shoreline subsidies and other seabird byproducts that consumers receive more directly than via plant pathways. (For an example of a study that does separate those two conduits, see Sanchez-Piñero and Polis [2000].)

Soil and plants

To depict direct and indirect effects of pulses in the presence and absence of subsidies in these island

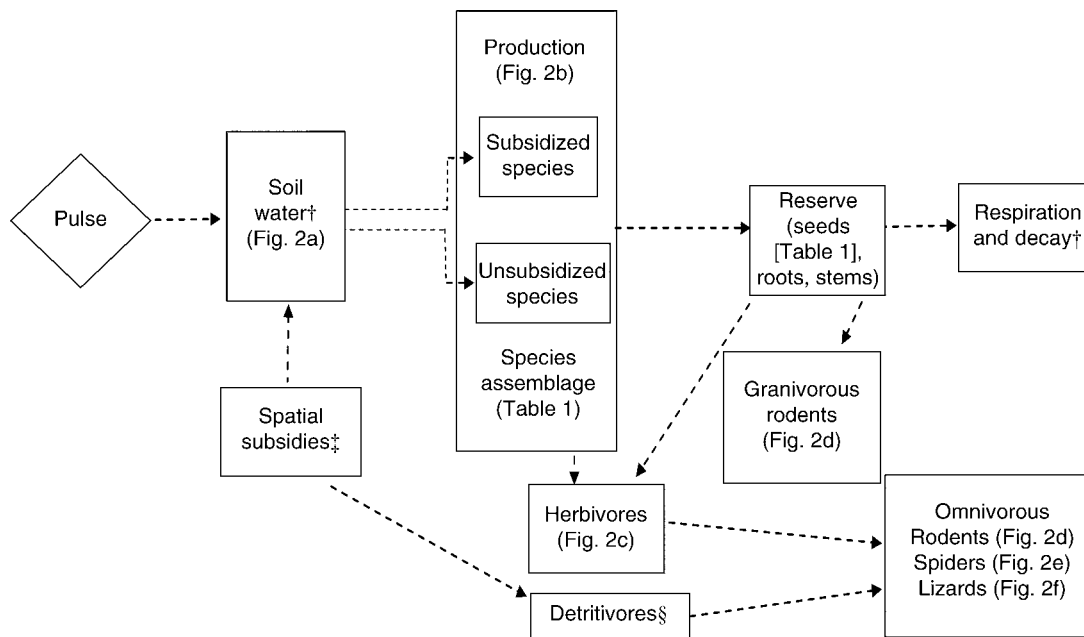


FIG. 1. An integrated “pulse–reserve” and food web model for a temporally pulsed and spatially subsidized system. The original model was provided, with permission to modify, by Reynolds et al. (2004). The original model depicted pulses of precipitation, the role of antecedent soil conditions, and plant functional types and was explored using a physiologically based ecosystem model developed for arid lands. We have modified the model to include subsidy effects on antecedent soil conditions and detritivores, replaced plant functional types with plant species assemblages associated with unsubsidized and subsidized areas, and included higher trophic interactions. We examine our model using data collected between 1992 and 2005 from a temporally pulsed and spatially subsidized arid system. Data illustrating how each of the components of the model responds to below average (interpulse, or no pulse years) and above average (pulse) precipitation are provided in Table 1 and Fig. 2 as indicated. Symbols: † Wait et al. (2005) describe in detail how spatial subsidies (guano) in the system affect soil chemistry (e.g., N, C:N, soil respiration, and spatial patterns in salinity and pH); ‡ numerous studies have described the importance of spatial subsidies (e.g., guano, shore wrack, seabird carcasses) in the system; § Sanchez-Piñero and Polis (2000) describe the direct influence of spatial subsidies on detritivores.

communities, we have modified the Reynolds et al. (2004) “pulse–reserve” model to include the effects of spatial subsidies of seabird guano on soil, plant species, and communities, and animal populations and communities (Fig. 1). The marriage of a pulse–reserve diagram with a food web diagram provides a context for seeing soil and plant-mediated effects on animals. The Reynolds et al. (2004) model and a related threshold-decay model (Ogle and Reynolds 2004) emphasize the importance of antecedent soil conditions and plant functional types. Our “temporal-pulse–spatial-subsidy” model recognizes that antecedent soil conditions such as N and P percentage, moisture percentage, organic matter percentage, and pH differ substantially between areas with subsidies (in the form of seabird guano inputs) and area without subsidies (see Wait et al. [2005] for detailed results). Guano-enriched soils contain sevenfold greater N than unsubsidized soils ($0.22\% \pm 0.03\%$ vs. $0.03\% \pm 0.01\%$, respectively [mean \pm SD]) and 4.9-fold greater P than unsubsidized soils ($1.30\% \pm 0.24\%$ vs. $0.35\% \pm 0.17\%$, respectively), but those nutrients are only available for plant growth primarily during pulsed periods of rain (Anderson and Polis 1999). In addition, soil moisture is 3.1 times greater on subsidized islands in

pulsed years than in interpulse years, but only 1.1 times greater on unsubsidized islands in pulsed years than in interpulse years (Fig. 2a), even though all islands receive the same amount of rain. The higher moisture retention capacity and slower moisture attenuation (data not shown) of subsidized island soils is probably due, in part, to the higher organic matter content (6.1% vs. 1.4% on subsidized vs. unsubsidized islands), which is a result of the greater primary productivity of these islands that contributes slowly decomposing detritus to the upper soil horizons. As Reynolds et al. (2004) explain, the primary productivity responses to soil water and nutrient availability feed back directly and indirectly to antecedent soil conditions such as soil organic matter, nutrient content, and moisture.

The combination of greater soil moisture and nutrient availability to plants on subsidized islands compared to unsubsidized islands selects for species with different physiological responses and subtly different life history traits. Thus, plant species composition is vastly different in subsidized communities from that of unsubsidized communities (Table 1). While both types of islands support communities of annuals in their seed banks that will respond rapidly to rain pulses when they occur,

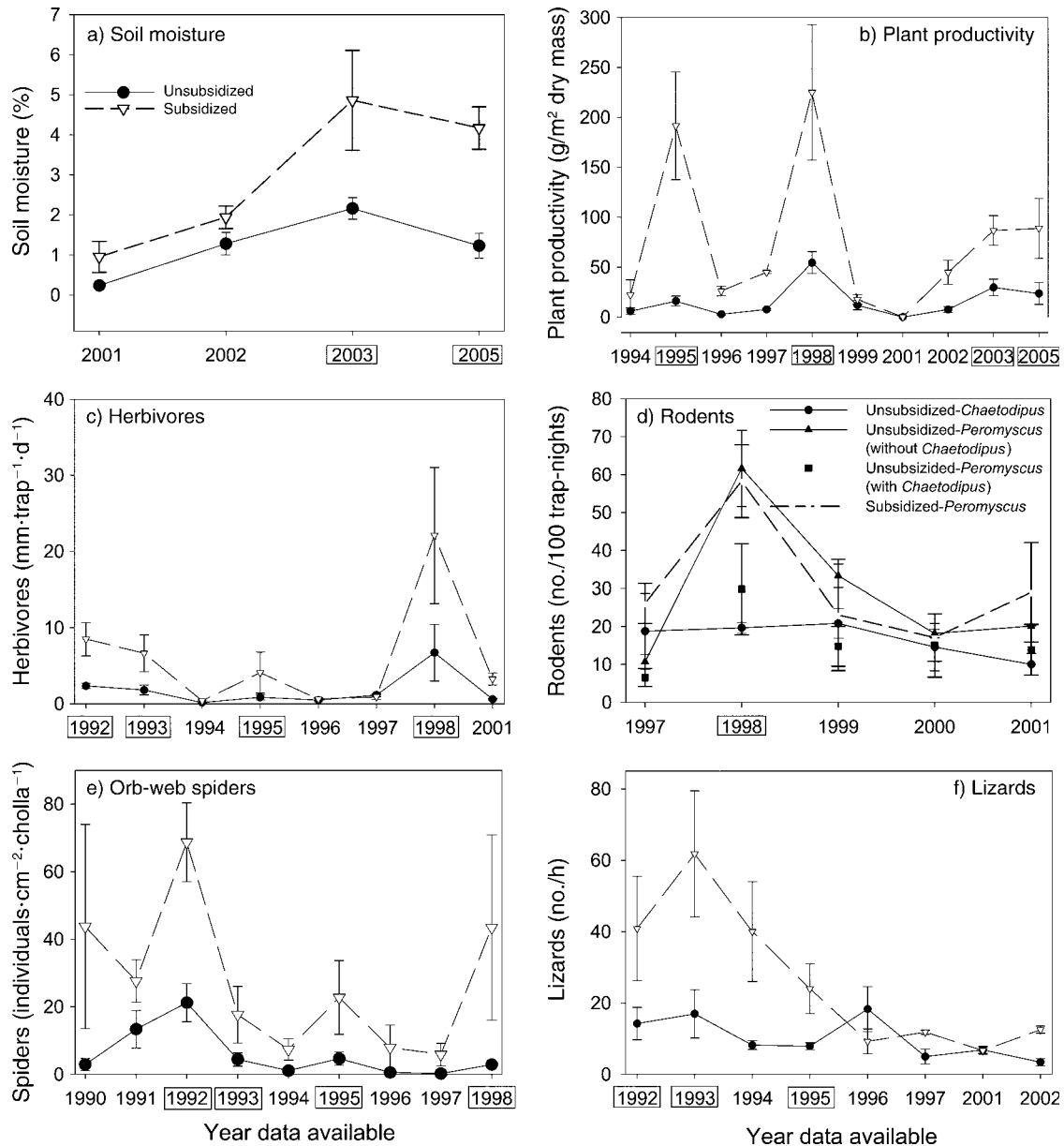


FIG. 2. Responses (mean \pm SE) of soil, plants, and animals to temporal pulses of precipitation in the presence and absence of spatial subsidies. All data prior to 1999, with the exception of soil moisture, come from published work (see citations below). Years within boxes experienced “significant” pulses, defined as precipitation during the growing season 20% above the mean, and include 1992, 1993, 1995, 1998, 2003, and 2005. For panels a–c, “unsubsidized” refers to areas without seabird inputs, including guano and carcasses. For panels d–f, unsubsidized refers to areas without either seabird or shoreline inputs. (a) Soil moisture was determined gravimetrically and was significantly higher in subsidized than unsubsidized soils in all years (see Wait et al. [2005] for methods, sample sizes, and analysis of 2001 and 2002 data). (b) Plant productivity was determined from clearing 15 0.25-m² plots per island according to the methods of Polis et al. (1997b), and was significantly greater on subsidized than unsubsidized islands except in 1994, 1999, and 2001 ($P < 0.05$, ANOVA; see Wait et al. [2005] for description of statistical analysis). (c) Herbivore population size (in this case, insect body length) was estimated from sticky-trap collections (see Polis et al. [1997b] for methods). (d) Rodent population sizes were estimated from live trapping (see Stapp and Polis [2003a] for methods). (e) Orb-web-building spider densities are estimated from counts on *Cholla* spp. (see Polis and Hurd [1995] for methods). (f) *Uta stansburiana* population sizes were estimated from timed searches (see Barrett et al. 2005).

communities on subsidized islands typically only include three or four species, while communities on unsubsidized islands may include 30 to 40 species, with as many as ten different species found per square meter. These

differences are not accounted for by traditional species-area curves or other traditional biogeographic factors (Anderson and Wait 2001). Rather, a combination of physiological tolerance to the potentially toxic levels of

TABLE 1. Herbaceous plant richness and responses of the dominant species to seasonal precipitation pulses and nutrient subsidies on islands in the Gulf of California.

| Plant response (units, no. islands, no. plots or samples) | Between precipitation pulses | | During precipitation pulses | |
|--|--|---|--|--|
| | Unsubsidized | Subsidized | Unsubsidized | Subsidized |
| Observed species richness (no./m ² , 6, 60) | 4.1 ^a (0.3) | 1.9 (0.7) | 10.3 (0.6) ^c | 4.0 (0.5) ^a |
| Dominant species (>80% of cover) | <i>Cryptantha</i> , <i>Plantago</i> | <i>Amaranthus</i> , <i>Chenopodium</i> | <i>Cryptantha</i> , <i>Plantago</i> , <i>Lotus</i> , <i>Aristida</i> | <i>Perityle</i> , <i>Amaranthus</i> , <i>Chenopodium</i> |
| Seed bank (no. seeds/m ² , 9, 270) | no data | no data | 26 580 ^a (3500) | 310 340 (70 226) |
| Plant water content (%; 4, 12) | 74.6 ^a (1.9) | 61.1 ^b (1.2) | 74.4 ^a (1.9) | 67.3 ^{a,c} (1.7) |
| Midday water potential (MPa; 4, 12) | -1.4 ^a (0.2) | -2.5 ^b (0.3) | -1.6 ^a (0.2) | -0.12 ^c (0.05) |
| Seasonal water use efficiency, C ₃ species only (δ ¹³ C, 4, 20) | -25.6 ^a (0.7) | -23.7 ^b (0.9) | -26.4 ^{a,c} (0.2) | -24.6 ^{b,c} (0.4) |
| Net assimilation rate (μmol CO ₂ ·m ⁻² ·s ⁻¹ , 4, 26) | no data | no data | 11.9 ^a (2.1) | 8.9 ^a (1.9) |
| Instantaneous water use efficiency (A/g, 4, 26) | no data | no data | 14.7 ^a (2.1) | 35.1 ^b (7.1) |

Notes: All values are means with SE in parentheses. For productivity in un-pulsed and pulsed years, see Fig. 2b. Different lowercase letters within a row indicate significant differences in means between and during pulses and unsubsidized and subsidized islands ($P < 0.05$, nested ANOVAs with island type treated as sampling units and individual measures within an island type treated as subsampling units; post hoc comparisons were made using Tukey's test). Species richness data were collected from cleared productivity plots (see Fig. 1b for methods). Midday water potential was measured using a pressure bomb (PMS, Corvallis, Oregon, USA); methods were as in Casper et al. (2006). The δ¹³C is based on the PeeDee limestone standard for carbon isotope ratio; methods were as in Wait et al. (2005). Instantaneous gas exchange (*A*, net assimilation rate; *g*, stomatal conductance) was determined between 10:00 and 11:00 hours using a LICOR 6400 (LICOR, Lincoln, Nebraska, USA). Plant water content is for shoots only. Seed banks were measured from 30 10 × 10 × 3 cm areas per island; seeds were filtered with a soapy water solution and counted directly.

guano and the historical competitive exclusion of some species due to variability in physiological responses to nutrient and moisture availability on subsidized islands likely explains the large difference in species richness between subsidized and unsubsidized islands.

The dominant species on subsidized islands exhibit physiological strategies for responding to pulses that are very different from the dominant species on unsubsidized islands. For example, even though nutrient subsidies lead to greater soil moisture content in both pulse and interpulse years (Fig. 2a), *Amaranthus* spp. and *Chenopodium* spp., which are only found on subsidized islands, have lower water content during both pulse and interpulse periods, higher water potential (a measure of moisture stress) during pulse periods, and greater instantaneous water use efficiency (unit of growth/unit of water available) during pulse periods compared to *Cryptantha* spp. and *Plantago* spp., which are common annuals on unsubsidized islands (Table 1). These measurements indicate that while annual plants on subsidized islands contain substantially higher foliar nutrient concentrations (Anderson and Polis 1999), they exhibit more conservative strategies for using water, which probably allows these species on subsidized islands to persist into subsequent drought periods longer than the species that dominate on unsubsidized islands. Thus, the species on subsidized islands are more likely to complete their life cycle when the pulse is small or short (e.g., 1995, 2003, and 2005).

Interestingly, these differences in water use strategies are not associated with differences in carbon assimilation rates (Table 1), as we might expect with enhanced nutrient availability and higher foliar nutrient contents on subsidized islands (Anderson and Polis 1999). Annual species photosynthesize at similar rates in both

unsubsidized and subsidized conditions, so growth rates are likely similar as well. However, because species on subsidized islands live longer into interpulse periods, they ultimately achieve greater biomass and reproductive output. In addition, ambient soil moisture is not great enough on unsubsidized islands to initiate germination of most plant species in the absence of a large pulse (Fig. 2b), but guano-enriched soils retain high enough soil moisture during interpulse periods (either from persistent moisture from a large pulse, or from major fog events, which are common in the area) for germination and growth of some of the species on subsidized islands (Fig. 2b). Therefore, selection apparently favors more conservative water use strategies over higher photosynthesis rates for annual species growing in subsidized areas (Casper et al. 2005), but not for species living in unsubsidized areas, which are more typical of this arid region. The rarity of this strategy for annuals in this region may partially explain why the plant species richness of subsidized areas is so low.

Animals

Larger amplitudes in plant quantity (Fig. 2b) and higher plant quality, as demonstrated by 2.6 times greater percentage of N and 3.9 times greater percentage of P in annual plant tissues (Anderson and Polis 1999) translate into higher animal population densities on islands with seabird-derived subsidies during and after pulses of rain. Invertebrate herbivore communities respond directly and within the year of the rain and plant pulse to increased resource availability (Fig. 2c), and the magnitude of their numerical response is associated with the magnitude of the plant productivity (linear regression, $R^2 = 0.64$, $P = 0.007$; also see Anderson and Polis 2004). Herbivore communities

decline to relatively low numbers during dry years on both subsidized and unsubsidized islands, but during pulses, their abundance increases 3.3–4.8 times more on subsidized islands than on unsubsidized islands. In addition to the greater biomass and nutrient mass available in plants on subsidized islands, the increased longevity of available fresh plant tissue on subsidized islands following a pulse may also contribute to the ability of herbivores to respond numerically to plant pulses. In effect, the lag time of days or weeks for herbivores to respond to a pulse of plant growth may be too long for the herbivores to experience a full reproductive cycle before the drought returns. But, even in the event of a short pulse, if plant responses are amplified and extended well into the subsequent drought period, as they are on guano-subsidized islands, herbivores will be able to complete their life cycles, and thus be more likely to persist on those islands.

One of the most common invertebrate detritivores, tenebrionid beetles on seabird-subsidized islands exhibit positive numerical response to increased plant detritus within one year following rain and plant pulses. Their response is primarily behavioral in that they switch their diets from seabird carcasses in interpulse years to plant detritus after pulses (Sanchez-Piñero and Polis 2000). Thus, beetle abundance did not decline as availability of plant detritus declined on islands that receive seabird-based subsidies. On unsubsidized islands and on the Baja California peninsula, tenebrionids did not track increases or decreases in plant productivity either, but for reasons that are less clear, but may be associated with greater amounts and more regular availability of detritus from mainland perennials (Sanchez-Piñero and Polis 2000).

Except for the occasional raptor or snakes on a few islands, rodents represent the top-level consumers on most small Gulf of California islands. Like tenebrionid beetles, *Peromyscus* spp. are dietary generalists and inhabit many of the smallest islands (<2 km²; Lawlor et al. 2002, Stapp 2002), in part because they consume marine subsidies, including algal wrack and marine carrion that arrive along shorelines (Stapp et al. 1999, Stapp and Polis 2003a). The ability to use a broad range of terrestrial and marine resources allows *Peromyscus* to persist and reach high densities on small islands that receive multiple marine subsidies, even during interpulse periods of extremely low terrestrial productivity. As a result, during pulse periods with high rainfall and primary productivity, *Peromyscus* shows a strong numerical response, especially in subsidized areas where densities are already high (Fig. 2d). This increase is relatively short-lived, however, as most young produced during these periods are not alive by the following year. The magnitude of the increase and decline is influenced by the presence of marine subsidies, competitors and predators. On one small island (Flecha) with large numbers of nesting cormorants but no terrestrial predators, *Peromyscus* numbers increased approximate-

ly 10-fold following the 1997–1998 ENSO, then declined by 89% the following year, suggesting that mortality was due to terrestrial resource scarcity (Stapp and Polis 2003b).

In contrast, granivorous rodents such as *Chaetodipus* spp. are found on fewer islands, especially those with higher plant species diversity and presumably a larger pallet of seed choices (Lawlor et al. 2002). They are not found on any small islands that are covered in seabird guano. *Chaetodipus* rarely occurs in the absence of *Peromyscus*, and competition from *Peromyscus* may affect the ability of *Chaetodipus* to respond to pulsed seed production. The increase in *Chaetodipus* abundance on unsubsidized islands in response to the 1997–1998 ENSO was modest (Fig. 2d), which may reflect the inherently low productivity of these small, nutrient-poor islands as well as the presence of *Peromyscus* and, on some islands, rattlesnakes (*Crotalus* spp.). As with other rodents in the family Heteromyidae, many of which are specialized to live in deserts, the reproductive potential of *Chaetodipus* is lower than that of species of Muridae such as *Peromyscus*. Therefore, insular *Chaetodipus* may respond to pulses not with a strong numerical response, but by storing seeds and maintaining lower mortality rates.

Chaetodipus populations were much more stable over time than those of *Peromyscus* (Fig. 2d), suggesting two different strategies for persisting on small islands in the Gulf (Stapp and Polis 2003b). *Peromyscus* populations track plant resources closely and therefore are more variable over time, but are prevented from extinction by their ability to switch their diets to more constantly available marine subsidies during interpulse periods. *Chaetodipus* appear to average out temporal variation in resources by using storage mechanisms but are likely more vulnerable to extended periods of extremely low terrestrial productivity, which explains their presence only on larger islands or on islands with a higher diversity of seeds, such as islands without seabirds (Stapp and Polis 2003a). On islands where these two taxa co-occur, they may affect each other's response to pulsed resources, with *Peromyscus* briefly dominating by its sheer numbers but *Chaetodipus* being behaviorally dominant and largely restricting the spatial distribution of *Peromyscus* to areas near shore. Nonetheless, such spatial segregation on islands receiving marine subsidies along the shoreline facilitates coexistence of both groups. On larger islands that support rattlesnakes, the two species may also interact indirectly via shared predation by rattlesnakes, which may respond behaviorally and numerically to temporarily higher rodent densities during pulses (P. Stapp, unpublished data).

Other generalist predators that inhabit these islands also show numerical responses to pulses. Orb-web building spiders, predominantly *Metapeira arizonica*, increase in density in response to rain and plant pulses within the year of the pulse. The magnitude of their response is greater in subsidized areas and is associated

with increased productivity of plants (linear regression, $R^2 = 0.79$, $P = 0.001$) although not as strongly with herbivore abundance ($R^2 = 0.30$, $P = 0.11$; Fig. 2e). However, predation on spiders by scorpions, lizards and pompilid wasps also strongly influences spider population dynamics (Polis and Hurd 1995, Polis et al. 1998). Like orb-web building spiders, generalist lizards (mainly *Uta stansburiana*) respond to rain and plant pulses more strongly in subsidized areas (including coastal areas of islands without seabirds) than in unsubsidized areas (Fig. 2f). However, during interpulse periods, populations in areas that receive multiple types of subsidies return to levels that are similar to unsubsidized areas. In general, subsidies such as algal wrack, marine carrion, and seabird carcasses may be more constant than guano subsidies because they are decoupled from pulses of precipitation. Therefore, the true subsidies for most generalist predators may be the “temporal subsidies” (rather than spatial subsidies) of rare but in situ plant and herbivore growth during rare rain pulses.

CONCLUSIONS

The presence of spatial subsidies substantially alters the structure and dynamics of plant and animal populations and communities particularly as they respond to resource pulses (Polis et al. 1998). Guano-derived nutrients amplify annual plant productivity responses to rain pulses on islands with this type of subsidy, and this response is driven by specific physiological and life history adaptations of a few annual species to the soil nutrient and moisture conditions created by this subsidy. Substantially lower plant species richness on the subsidized islands reflects both the rarity of these strategies in the regional species pool, and the ability of these plants to competitively exclude other species under such subsidized conditions. Invertebrate herbivores also exhibit amplified responses to pulses of annual plant growth on nutrient subsidized islands. It is unlikely, though, that they would be driven to local extinction between pulses because a small number could persist on subsidized islands even during drought periods when a few plants still germinate in the perpetually moist soils of guano islands. Thus, the magnitude or the apparent duration of the pulse and the reserve produced by the same amount of rain is substantially greater in subsidized areas than in unsubsidized areas.

In contrast, granivorous rodents do not exist on nutrient subsidized islands, even though they would have a consistent resource in these islands' extraordinary seed banks. It is likely that the rapid numerical responses to rain pulses of omnivorous rodents that are able to switch diets between plant-based resources and other forms of marine subsidies that arrive along the shoreline have led to historical competitive exclusion of the granivorous specialists. Thus, rodent diversity is lower on islands receiving both seabird-derived and algal and carrion derived subsidies.

Similar to the omnivorous rodents, generalist detritivorous beetles respond to pulses more strongly in subsidized areas, too, but do not experience severe population declines during interpulse periods because the detrital reserves decay less rapidly than availability of fresh plant tissue, and because they can shift their diets to other marine based resources (Sanchez-Piñero and Polis 2000). The same pattern is true for generalist predators like orb-web-building spiders, but less so for lizards. Isotopic studies of lizards (Barrett et al. 2005), spiders (Anderson and Polis 1998, Stapp et al. 1999), and rodents (Stapp et al. 1999, Stapp and Polis 2003b) have shown that, compared to in situ terrestrial resources, marine resources make up a significantly larger portion of these groups' diets in dry years than they do during either wet years or in unsubsidized areas. Thus, if multiple forms of subsidies are available, generalist consumer populations fluctuations can be dampened even in strongly pulsed systems (Huxel et al. 2002), and will dominate in such systems, sometimes to the exclusion of more specialized consumers.

Finally, the combination of widespread subsidies and strong pulses may tend to reduce diversity within these islands, while perhaps enhancing regional diversity across the archipelago by spatially partitioning species that maximize use of subsidies from those that do not (Anderson and Wait 2001). The low frequency but high intensity of rain in this system is more extreme than what is seen in many desert systems, but is relatively spatially homogeneous across all islands in the archipelago, so we can expect that the nature of the rain pulses does not directly drive differences between subsidized and unsubsidized islands. Rather it is the presence or absence of marine materials entering island ecosystems (with or without the trigger of rain pulses) that determines life history and physiological traits, population dynamics, species interactions, and, consequently, diversity patterns. Thus, while most plant ecologists would agree that pulses promote greater diversity through coexistence of species with different responses to pulses (Chesson and Huntly 1997), the presence of nutrient subsidies alters that prediction by strongly favoring the few species that can optimize the condition of limited water with unlimited nutrients, which may represent a different form of stress toleration (*sensu* Grime 1977).

The examination of our proposed predictions for subsidies to amplify or dampen the effects of pulses on life history traits of species, population dynamics and community structure should extend beyond the context of the temporally and spatially variable system of the Gulf of California islands. The numerous studies of temporally and spatially variable, multiple, reciprocal flows of detritus, invertebrates, and mobile consumers between streams and riparian zones may represent an equivalent context for exploring the interactions between subsidies and pulses (Nakano and Murakami 2001, Sabo and Power 2002a, Baxter et al. 2005). However, in those circumstances, most of the subsidies

are also highly pulsed, such as the seasonal litterfall into streams, terrestrial invertebrates dropping into streams, or aquatic insect emergences into the riparian zone (Baxter et al. 2005). In such cases, then, the questions and predictions would have to be adjusted to examine the potential for amplification or dampening of population responses to two or more overlain pulsed or subsidized resources.

In summary, ignoring the presence of spatial subsidies when investigating the effects of pulses or, likewise, ignoring the inputs of pulsed resources when investigating the effects of subsidies, leads to incomplete pictures of spatially and temporally variable ecosystems. Indeed, most systems experience both kinds of resource inputs, and in many cases, the subsidies and pulses are one in the same. When they are not the same, complementary or even synergistic effects of pulsed resources and multiple spatial subsidies may arise, and demand that both kinds of inputs be considered in tandem. Because feedbacks between responses to pulses and subsidies may occur within and among trophic entities, and may occur with some time lag between consumer-resource pairs, both spatial and temporal scales must be considered when investigating population and community responses to both subsidies and pulses, as well as the direct effects on recipient species and indirect effects on other species in the recipient food webs.

ACKNOWLEDGMENTS

We would like to thank M. Holmgren, L. Yang, and three anonymous reviewers for their comments, which substantially improved the manuscript. Field assistance was provided by D. Aubrey, K. Barrett, M. Cortez, K. Heckman, M. Rose, F. Sánchez Piñero, P. Smith, and A. Subalusky. We appreciate the help of our Mexican colleagues, M. L. Jiménez, A. Reséndiz, S. T. Alvarez Casteñada, A. Zavala, C. Godínez, and A. Narvaez. J. Reynolds kindly provided his model for modification. The Mexican government provided scientific, logistic and diplomatic support of our research (DAN-022201, -00722, -01529, -00963, -01542, -01909, -00865, and supporting documents). Our research was funded by grants from the National Science Foundation (DEB-9806657) to P. Stapp and from the Andrew Mellon Foundation to W. B. Anderson and D. A. Wait, and by support from the Missouri State University Graduate College, Drury University, and Vanderbilt University.

LITERATURE CITED

- Anderson, D., F. Gress, and K. F. Mais. 1982. Brown pelicans: influence of food supply on reproduction. *Oikos* 39:23–31.
- Anderson, W. B., and G. A. Polis. 1998. Marine subsidies of island communities in the Gulf of California: evidence from stable carbon and nitrogen isotopes. *Oikos* 81:75–80.
- Anderson, W. B., and G. A. Polis. 1999. Nutrient fluxes from water to land: Seabirds affect plant nutrient status on Gulf of California islands. *Oecologia* 118:324–332.
- Anderson, W. B., and G. A. Polis. 2004. Allochthonous nutrient and food inputs: consequences for temporal stability. Pages 82–95 in G. A. Polis, M. E. Power, and G. R. Huxel, editors. *Food webs at the landscape scale: the ecology of trophic flow across habitats*. University of Chicago Press, Chicago, Illinois, USA.
- Anderson, W. B., and D. A. Wait. 2001. Subsidized island biogeography theory: a new twist on an old theory. *Ecology Letters* 4:289–291.
- Barrett, R. K., W. B. Anderson, D. A. Wait, L. L. Grismer, G. A. Polis, and M. D. Rose. 2005. Marine subsidies alter diet and abundance of insular and coastal lizard populations. *Oikos* 109:145–153.
- Barrett, R. K., D. A. Wait, and W. B. Anderson. 2003. Small island biogeography in the Gulf of California: Lizards, the subsidized island biogeography hypothesis, and the small island effect. *Journal of Biogeography* 30:1575–1581.
- Baxter, C. V., K. D. Fausch, and W. C. Saunders. 2005. Tangled webs: reciprocal flows of invertebrate prey link streams and riparian zones. *Freshwater Biology* 50:201–220.
- Casper, B. B., I. N. Forseth, and D. A. Wait. 2005. Variation in carbon isotope discrimination in relation to plant performance in a natural population of *Cryptantha flava*. *Oecologia* 145:541–548.
- Casper, B. B., I. N. Forseth, and D. A. Wait. 2006. A stage-based study of drought response in *Cryptantha flava* (Boraginaceae): gas exchange, water use efficiency, and whole plant performance. *American Journal of Botany* 93:977–987.
- Chesson, P. L., R. L. E. Gebauer, S. Schwinning, N. Huntly, K. Wiegand, M. S. K. Ernest, A. Sher, A. Novoplansky, and J. F. Weltzin. 2004. Resource pulses, species interactions, and diversity maintenance in arid and semi-arid environments. *Oecologia* 141:236–253.
- Chesson, P. L., and N. Huntly. 1997. The roles of harsh and fluctuating conditions in the dynamics of ecological communities. *American Naturalist* 150:519–553.
- Croll, D. A., J. L. Maron, J. A. Estes, E. M. Danner, and G. V. Byrd. 2005. Introduced predators transform subarctic islands from grassland to tundra. *Science* 307:1959–1961.
- Cummins, K. W., R. C. Peterson, F. O. Howard, J. C. Wuycheck, and V. I. Holt. 1973. The utilization of leaf litter by stream detritivores. *Ecology* 54:336–345.
- Goldberg, D., and A. Novoplansky. 1997. On the relative importance of competition in unproductive environments. *Journal of Ecology* 85:409–418.
- Grime, J. P. 1977. Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *American Naturalist* 111:1169–1194.
- Holmgren, M., et al. 2006. Extreme climatic events shape arid and semiarid ecosystems. *Frontiers in Ecology and the Environment* 4:87–95.
- Holt, R. D., and M. Barfield. 2003. Impacts of temporal variation on apparent competition and coexistence in open ecosystems. *Oikos* 101:49–58.
- Huxel, G. R., K. McCann, and G. A. Polis. 2002. Effects of partitioning allochthonous and autochthonous resources on food web stability. *Ecological Research* 17:419–432.
- Kirkman, H., and G. A. Kendrick. 1997. Ecological significance and commercial harvesting of drifting and beach-cast macroalgae and seagrasses in Australia: a review. *Journal of Applied Phycology* 9:311–326.
- Koenig, W. D., and A. M. Liebhold. 2005. Effects of periodical cicada emergences on abundance and synchrony of avian populations. *Ecology* 86:1876–1882.
- Lawlor, T. E., D. J. Hafner, P. T. Stapp, B. R. Riddle, and S. T. Alvarez-Castaneda. 2002. Mammals. Pages 326–361 in T. J. Case, M. L. Cody, and E. Ezcurra, editors. *A new island biogeography of the Sea of Cortés*. Oxford University Press, Oxford, UK.
- McCann, K. S., A. Hastings, and G. R. Huxel. 1998. Weak trophic interactions and the balance of nature. *Nature* 395:794–798.
- Murphy, R. W., F. Sanchez-Piñero, G. A. Polis, and R. L. Aalbu. 2002. New measurements of area and distance for islands in the Sea of Cortés. Pages 447–466 in T. J. Case, M. L. Cody, and E. Ezcurra, editors. *A new island biogeography of the Sea of Cortés*. Oxford University Press, Oxford, UK.
- Nakano, S., and M. Murakami. 2001. Reciprocal subsidies: dynamic interdependence between terrestrial and aquatic

- food webs. *Proceedings of the National Academy of Science (USA)* 98:166–170.
- Nowlin, W. H., M. J. Vanni, and L. H. Yang. 2008. Comparing resource pulses in aquatic and terrestrial ecosystems. *Ecology* 89:xx–xx.
- Noy-Meir, I. 1973. Desert ecosystems: environment and predators. *Annual Review of Ecology and Systematics* 4: 25–51.
- Ogle, L., and J. F. Reynolds. 2004. Plant responses to precipitation in desert ecosystems: integrating functional types, pulses, thresholds, and delays. *Oecologia* 141:282–294.
- Orr, M., M. Zimmer, D. E. Jelinski, and M. Mews. 2005. Wrack deposition on different beach types: spatial and temporal variation in the pattern of subsidy. *Ecology* 86: 1496–1507.
- Ostfeld, R. S., and F. Keasing. 2000. Pulsed resources and community dynamics of consumers in terrestrial ecosystems. *Trends in Ecology and Evolution* 15:232–237.
- Peltonen, M., A. M. Liebhold, O. N. Bjørnstad, and D. W. Williams. 2002. Spatial synchrony in forest insect outbreaks: roles of regional stochasticity and dispersal. *Ecology* 83: 3120–3129.
- Polis, G. A., W. B. Anderson, and R. D. Holt. 1997a. Toward an integration of landscape and food web ecology: the dynamics of spatially subsidized food webs. *Annual Review of Ecology and Systematics* 28:289–316.
- Polis, G. A., and S. D. Hurd. 1995. Extraordinarily high spider densities on islands: flow of energy from the marine to terrestrial food webs and the absence of predation. *Proceedings of the National Academy of Science (USA)* 92:4382–4386.
- Polis, G. A., and S. D. Hurd. 1996. Linking marine and terrestrial food webs: allochthonous input from the ocean supports high secondary productivity on small islands and coastal communities. *American Naturalist* 147:396–423.
- Polis, G. A., S. D. Hurd, C. T. Jackson, and F. Sanchez-Piñero. 1997b. El Niño effects on the dynamics and control of an island ecosystem in the Gulf of California. *Ecology* 78:1884–1897.
- Polis, G. A., S. D. Hurd, C. T. Jackson, and F. Sanchez-Piñero. 1998. Multifactor population limitation: variable spatial and temporal control of spiders on Gulf of California islands. *Ecology* 79:490–502.
- Reynolds, J. F., P. R. Kemp, K. Ogle, and R. J. Fernández. 2004. Modifying the “pulse-reserve” paradigm for deserts of North America: precipitation pulses, soil water, and plant responses. *Oecologia* 141:194–210.
- Sabo, J. L., and M. E. Power. 2002a. River-watershed exchange: effects of riverine subsidies on riparian lizards and their terrestrial prey. *Ecology* 83:1860–1869.
- Sabo, J. L., and M. E. Power. 2002b. Numerical response of lizards to aquatic insects and short-term consequences for terrestrial prey. *Ecology* 83:3023–3036.
- Sanchez-Piñero, F., and G. A. Polis. 2000. Bottom-up dynamics of allochthonous input: direct and indirect effects of seabirds on islands. *Ecology* 81:3117–3132.
- Schmidt, K. A., and R. S. Ostfeld. 2008. Numerical and behavioral effects within a pulse-driven system: Consequences for shared prey. *Ecology* 89:xx–xx.
- Schwinning, S., and O. E. Sala. 2004. Hierarchy of responses to resource pulses in arid and semi-arid ecosystems. *Oecologia* 141:211–220.
- Schwinning, S., O. E. Sala, M. E. Loik, and J. R. Ehleringer. 2004. Thresholds, memory, and seasonality: understanding dynamics in arid/semi-arid ecosystems. *Oecologia* 141:191–193.
- Sears, A. L. W., R. D. Holt, and G. A. Polis. 2004. Feast and famine in food webs: the effects of pulsed productivity. Pages 359–386 in G. A. Polis, M. E. Power, and G. R. Huxel, editors. *Food webs at the landscape scale: the ecology of trophic flow across habitats*. University of Chicago Press, Chicago, Illinois, USA.
- Singleton, G., C. Krebs, S. Davis, L. Chambers, and P. Brown. 2001. Reproductive changes in fluctuating house mouse populations in Southeastern Australia. *Proceedings of the Royal Society of London B* 268:1741–1789.
- Soto, K. H., A. W. Trites, and M. Arias-Schreiber. 2004. The effects of prey availability on pup mortality and the timing of birth of South American sea lions (*Otaria flavescens*) in Peru. *Journal of Zoology* 264:419–428.
- Stapp, P. 2002. New records of mammals on small islands in the Gulf of California, México. *Bulletin of the Southern California Academy of Sciences* 101:131–136.
- Stapp, P., and G. A. Polis. 2003a. Marine resources subsidize insular rodent populations in the Gulf of California, Mexico. *Oecologia* 134:496–504.
- Stapp, P., and G. A. Polis. 2003b. Influence of pulsed resources and marine subsidies on insular rodent populations. *Oikos* 102:111–123.
- Stapp, P., G. A. Polis, and F. Sanchez-Piñero. 1999. Stable isotopes reveal strong marine and El Niño effects on island food webs. *Nature* 401:467–469.
- Vannote, R. L., G. W. Minshall, K. W. Cummins, J. R. Sedell, and C. E. Cushing. 1980. The river continuum concept. *Canadian Journal of Fisheries and Aquatic Science* 37:130–137.
- Vidal, E., F. Midail, T. Tatoni, and V. Bonnet. 2000. Seabirds drive plant species turnover on small Mediterranean islands at the expense of native taxa. *Oecologia* 122:427–434.
- Wait, D. A., D. P. Aubrey, and W. B. Anderson. 2005. Seabird guano influences on desert islands: soil chemistry and herbaceous species richness and productivity. *Journal of Arid Environments* 60:681–695.
- Yang, L. H. 2004. Periodical cicadas as resource pulses in North American forests. *Science* 306:1565–1567.
- Yang, L. H., J. L. Bastow, K. O. Spence, and A. N. Wright. 2008. What can we learn from resource pulses? *Ecology* 89: xx–xx.