1   ***Resources from another place and time: community responses to pulses in a***

2   ***spatially subsidized system***

3   ***(Special Feature)***

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19   ABSTRACT

20   As the theoretical bases for the dynamics of spatially subsidized communities emerge,

21   ecologists question whether spatially subsidized communities exhibit similar structure or

22   dynamics to communities that receive strongly pulsed resources. In both cases,

23   communities may be structured by responses to resources that are potentially absent at

24   any given point in time (pulsed communities) or space (subsidized communities), even if

25   pulsed resources are part of the *in situ* productivity of the system or the subsidies arrive

26   as a relatively constant input from a nearby system. The potential for significant spatial

27   or temporal resource limitation, therefore, may be a key factor influencing in similar

28   ways the persistence of populations, the structure and dynamics of communities, and

29   the evolution of specific life history traits. In most complex systems, however, multiple

30   resources may arrive for various trophic entities at various points in time and from

31   various points in space, and thus it may be difficult to separate or compare the

32   dynamics of spatially subsidized and pulsed systems. In this paper, we explore the

33   effects of interactions between pulses and subsidies in plant and animal populations

34   and communities on highly pulsed and variably subsidized islands in the Gulf of

35   California. While many of the plant and animal communities on the unsubsidized

36   islands in this system respond to pulses of rain in classic ways, responses to these rain

37   pulses on islands subsidized by seabird guano or other marine resources are quite

38   different and variable, and depend on a combination of life history characteristics,

39   physiology, competitive interactions, and trophic relationships. These variable

40   responses to rain pulses then translate into large differences in dynamics and

41   community structure of subsidized vs. unsubsidized islands. Indeed, most systems

42   experience both temporal pulses and spatial subsidies. When considered in tandem,

43   complementary or synergistic effects of the multiple, temporally and spatially variable

44   resources may emerge that help explain complex food web structure and dynamics.

45   Key Words: *community dynamics; deserts; Gulf of California; islands; lizards; nutrient*

46   *subsidies; plant physiology; population dynamics; primary productivity; rodents; spiders*

47   INTRODUCTION

48   As the theoretical bases for the dynamics of spatially subsidized communities

49   emerge, ecologists are examining whether spatially subsidized communities exhibit

50   similar structure or dynamics to communities that receive strongly pulsed resources

51   (Sears et al. 2004), and how subsidies and pulses interact or overlap to influence

52   communities (Polis et al. 1997b, Baxter et al. 2005, Yang et al., this volume). Spatial

53   subsidies are donor-controlled resources that originate in one habitat but move into

54   another habitat and alter the dynamics of recipient populations and communities (Polis

55   et al. 1997a). In some cases, spatial subsidies arrive continuously, and in other cases,

56   subsidies may arrive in pulses. Pulses are resources that occur episodically or rarely,

57   that briefly enhance resource availability above the baseline level, and that decay in

58   availability through time (Ostfeld and Keesing 2000; Yang et al., this volume). Pulses

59   may originate *in situ* or arrive from allochthonous sources, and often alter the dynamics

60   of recipient populations and communities (Polis et al. 1997, Polis et al. 1998, Yang et

61   al., this volume). Thus, if the impacts of subsidies and pulses interact or are

62   inseparable, as when subsidies are pulsed, well-understood theory for pulsed

63   communities may need to be modified to encompass the impacts of subsidies on

64   population and community structure and dynamics. Our goal in this paper is to examine

65   both plant and animal data from a pulsed and subsidized system to evaluate how spatial

66   subsidies may influence species and community responses to pulses.

67

68   GENERALIZATIONS ABOUT SUBSIDIZED COMMUNITIES

69   More than a decade of theoretical and empirical studies explicitly investigating

70   the dynamics of spatially subsidized systems have produced some generalities, but

71   have also opened up more questions. Most studies of spatially subsidized systems

72   indicate that resource subsidies produce a direct numerical response in recipient

73   populations (Polis and Hurd 1995, see Polis et al. 1997a for a review). A few long-term

74   studies and models (McCann et al. 1998) have provided evidence that subsidies may

75   help stabilize inter-annual fluctuations of populations and increase the probability of

76   long-term persistence by providing a minimum level of resource availability, particularly

77   for generalist consumers (Holt and Barfield 2004). The ability of resource subsidies to

78   stabilize populations may be particularly evident in unproductive or strongly pulsed

79   systems (Polis et al. 1997a).

80   In addition, only a few studies have emerged that document second-order or

81   higher responses to spatial subsidies in communities. The numerical response of the

82   direct or indirect consumers of the subsidy can spur apparent competition, intraguild

83   predation, trophic cascades, or other multi-trophic interactions within the recipient

84   community (Polis et al. 1998, Baxter et al. 2005, Croll et al. 2005, Schmidt and Ostfeld,

85   this volume). In some cases, a strong reciprocal flow of resources between two

86   systems may further complicate the predictions made for a simple donor-controlled

87   subsidy (Nakano and Murakami 2001, Baxter et al. 2005). Also, many subsidized

88   systems receive multiple subsidies to multiple trophic groups, which may or may not

89   arrive simultaneously, and which also shift dynamics in non-linear, and possibly

90   unpredictable ways (Huxel et al. 2002, Anderson and Polis 2004).

91   Very few studies have explored the influence of subsidies on species diversity

92   patterns (Anderson and Wait 2001; Barrett et al. 2003; Vidal et al. 2000). Shifts in

93   community interactions that result from direct and indirect population and community

94   responses to subsidies may cause shifts in species composition of particular groups,

95   but little is known about general impacts on richness and diversity. The ability to make

96   predictions about species diversity patterns may be complicated by the continuous vs.

97   pulsed availability of the subsidy, or the number of different subsidies occurring in a

98   particular system. Thus, the regularity, magnitude, and diversity of the subsidy may be

99   crucial in determining its impact on the recipient community, which highlights the need

100   to integrate studies of pulses and subsidies.

101

102   GENERALIZATIONS ABOUT PULSED COMMUNITIES

103   While our understanding of subsidized systems is still growing, theoretical and

104   empirical studies of pulsed systems are well developed and continue to become more

105   complex as ecologists investigate the effects of pulses on community dynamics

106   (Schmidt and Ostfeld, this volume), ecosystem type (Nowlin et al., this volume) and

107   subsidies (Yang et al., this volume).   Most studies of pulsed systems focus on either

108   plant responses or animal responses, but rarely both.

109   The majority of the pulse theory for plants was developed and tested in the

110   context of the effects of rain pulses on desert plant life histories, physiological

111   characteristics, community structure and dynamics, and ecosystem processes

112   (Chesson et al. 2004, Schwinning and Sala 2004). Indeed, pulses of rain are

113   considered the trigger for almost all biological activity in deserts, from microbial

114   decomposition to community succession (Schwinning and Sala 2004). Of course, the

115   frequency, magnitude, duration, and seasonality of the pulse are key determinants for

116   the scale of response, and specific responses of species or communities require that a

117   resource pulse reach a particular threshold (Schwinning et al. 2004, Schwinning and

118   Sala 2004).

119   Noy-Meir's (1973) classic pulse-reserve model (a.k.a. Bridges-Westoby model)

120   depicted "pulses" as the plant growth response to a trigger such as rain, which would

121   then contribute to a reserve (e.g., seeds, perennial vegetation, detritus) that would

122   slowly drain through the interpulse or drought period. Commonly, though, references to

123   this model refer to the trigger of rain as the pulse, and then use growth as the response

124   to the pulse (Reynolds et al 2004). A recent modification of the pulse-reserve model

125   added the role of antecedent soil conditions (e.g., nutrients, organic content, moisture)

126   and soil type in capturing and retaining water from a rain pulse and making it available

127   in appropriate amounts and for requisite lengths of time to influence various plant

128   species and communities of particular functional types (Reynolds et al. 2004). For

129   example, soil nutrients, organic content, pH, and particle size can all influence water

130   retention and evaporation rates with direct and indirect effects on plant physiological

131   adaptations and community structure (Wait et al. 2005).

132   Physiological adaptations of plant species to highly pulsed environments and the

133   consequential species composition (including seed bank reserves) of communities in

134   pulsed environments represent the "memory" of a system (*sensu* Schwinning et al.

135   2004) to a history of pulses. Indeed, only those species with life history characteristics

136   that allow rapid growth and/or storage during intermittent resource pulses followed by

137   periods of dependence on stored reserves will persist in strongly pulsed environments.

138   However, because numerous strategies exist for optimizing growth and storage during

139   pulses and for persisting through interpulse periods, Chesson and Huntly (1997) predict

140   that resource pulses will promote higher species diversity in communities via co-

141   existence of species with variable strategic responses to pulses. This prediction may

142   not apply, though, to pulsed communities that also receive resource subsidies such as

143   additional nutrients, particularly when nutrient subsidies directly or indirectly alter the

144   water retention capacity of soils, and hence the optimal physiological strategies and

145   resultant competitive interactions of plant species (Vidal et al. 2000). As predicted by

146   Goldberg and Novoplansky's (1997) Two-Phase Resource Dynamics Hypothesis,

147   strategies for persisting into interpulse periods may shift competitive outcomes towards

148   favoring those species with somewhat more conservative (in the plant growth sense) or

149   generalist (in the animal sense) strategies. Thus, species that can maximize growth

150   during the pulse but also keep growing upon return of the drought long enough to

151   complete reproduction, will emerge as superior competitors and possibly displace other

152   species. In systems that are both subsidized and pulsed, subsidies that amplify or

153   lengthen a pulse's effect are likely to influence competitive outcomes and species

154   composition or diversity.

155   In contrast to most of the studies of plant responses to seasonal or more

156   predictable resource pulses, recent studies of the effects of pulsed resources on

157   consumers have tended to emphasize rare, episodic events of extreme resource

158   abundance (Ostfeld and Keesing 2000). Such events might include periods of unusually

159   high primary productivity such as extreme climatic events (Holmgren et al. 2006),

160   synchronous emergences of arthropods such as periodical cicadas (e.g. Koenig and

161   Liebhold 2005, Yang 2004) or outbreaks of small mammals and insects (e.g., Singleton

162   et al. 2001, Peltonen et al. 2002). These types of rare and intense pulses are

163   distinguished from those that occur more predictably, such as seasonal litterfall of

164   detritus and invertebrates into forest streams (e.g., Sabo and Power 2002a, b, Nakano

165   and Murakami 2001, Vannote et al. 1980, Cummins et al. 1973) or regular inputs of

166   algal wrack to beaches (e.g. Orr et al. 2005, Kirkman and Kendrick 1997).

167   Ostfeld and Keesing (2000) proposed that the type of community response to

168   extreme pulses depends on the numerical response of consumer populations to pulses;

169   the degree to which consumers were specialists on pulsed resources; and the degree of

170   mobility of consumers relative to the spatial scale of the pulse. Consumers capable of

171   strong, immediate numerical response would show tight coupling between the timing of

172   the pulse and abundance, whereas others with lower intrinsic growth potential or

173   storage mechanisms might show a greater lag between the timing of the pulse and

174   increased population size. Moreover, generalist consumers would be expected to

175   demonstrate stronger responses to pulsed resources than specialist groups because of

176   their ability to switch from pulsed resources back to alternate prey as pulsed resources

177   were depleted, which could depress the alternate prey populations in a manner

178   equivalent to apparent competition (Holt and Barfield 2004). Likewise, more mobile

179   consumers can respond functionally and numerically to a spatially heterogeneous pulse

180   and thus connect adjacent habitats that receive either pulsed or spatially subsidized

181   resources (Polis et al. 1997a).

182   In summary, plant ecologists have focused on ecophysiological, life history, and

183   species diversity responses to pulses, while animal ecologists have been more

184   concerned with numerical and behavioral responses of consumer populations to pulses

185   and the consequent effects on food web structure and dynamics. Total plant

186   productivity representing *in situ* resource availability provides a measure for predicting

187   consumer responses, but rarely are more specific characteristics of plant species

188   composition, plant nutrient content, or plant life history (i.e., longevity) considered in

189   evaluating consumer responses to resource pulses transmitted through plants (but see

190   Sanchez-Piñero and Polis 2000). Moreover, few ecologists have examined the effects

191   of pulses on either plants or animals in both the presence and absence of spatial

192   subsidies. We will examine plant and animal data in concert from a strongly pulsed and

193   highly subsidized system to show how plants respond to pulses in subsidized vs.

194   unsubsidized conditions, and how various animal consumer groups respond to these

195   variable plant responses and other spatial subsidies.

196   PREDICTIONS FOR RESPONSES TO PULSES IN SUBSIDIZED VS. UNSUBSIDIZED

197   SYSTEMS

198   We propose general predictions for the responses of populations and

199   communities to interactions between pulses and subsidies that depend on whether or

200   not the pulsed resource and the subsidy are in phase or out of phase with each other. If

201   a subsidy becomes available or is mobilized primarily during pulse periods ("in phase"),

202 the subsidy will amplify the pulse, and thus recipients of those amplified resources may

203 experience stronger fluctuations in populations, unless the recipient can switch back to

204 more regularly available *in situ* resources between pulses. On the other hand, if a

205 subsidy is available continuously or primarily during interpulse periods ("out of phase"),

206 then total resource availability will be more constant, at least for generalist consumers

207 that can switch diets, and population fluctuations will be dampened and possibly

208 stabilized. If the subsidy and the pulse are one in the same (i.e, a pulsed subsidy), the

209 community will respond similarly as it would to a pulse of an *in situ* resource.

210   Using these general predictions for responses to both pulses and subsidies, we

211 show how plants, herbivores, and generalist consumers respond to pulses in the

212 presence and absence of subsidies in a strongly pulsed, hyperarid region. In the first

213 set of predictions, we examine the effects of intense precipitation pulses and nutrient

214 subsidies derived from seabird guano on plant physiology, life history, and community

215 structure, on herbivore abundance, and on granivorous rodent taxa. Since guano-

216 derived nutrient subsidies to plants are primarily available during precipitation pulses,

217 and likely amplify the pulse, we predict that, compared to unsubsidized islands, nutrient

218 subsidized islands would:

219   1) exhibit stronger population fluctuations and possibly higher risks of extinction

220 on a local scale;

221   2) be dominated by species with life histories and diets that maximize

222 assimilation of the subsidized resources during pulses; and

223   3) thus, exhibit lower species diversity at the local scale where the subsidy is

224   available. A caveat to the third prediction is that we would expect higher species

225   diversity at the regional scale that includes subsidized and unsubsidized areas via

226   spatial partitioning of species that utilize the subsidy from those that do not.

227   In the second set of predictions and examples, we predict that, compared to

228   unsubsidized systems, more generalized consumers in subsidized systems that can

229   switch between plant-based resources that are available during subsidy-amplified

230   pulses and other marine subsidies that are available more continuously would:

231   1) exhibit dampened population fluctuations and possibly lower risks of extinction

232   on a local scale;

233   2) be dominated by species with life histories and diets that allow for switching

234   diets or other behaviors in response to pulsed vs. continuously available resources,

235   subsidized or otherwise; and

236   3) thus, exhibit higher species diversity at the local scale where multiple

237   subsidies are available.

238

239   A MODEL SYSTEM FOR STRONG PULSES AND SPATIALLY VARIABLE

240   SUBSIDIES: DESERT ISLANDS IN THE GULF OF CALIFORNIA

241   Desert islands in the Gulf of California provide an interesting and well-studied

242   system to explore population and community dynamics that are strongly influenced by

243   both spatial subsidies and pulses. Mean annual precipitation in the region is 59 mm,

244   ranging from 0 mm to 215 mm per year over the past 53 years (Polis et al. 1997b,

245   Sanchez-Piñero and Polis 2000). The majority of this precipitation arrives in major storm

246   events associated with summer thunderstorms or arrhythmic El Niño Southern

247   Oscillation (ENSO) events. However, not all El Niño years produce greater-than-

248   average precipitation, and some years that have precipitation greater than the mean are

249   not officially recorded as El Niño years. Seasonality of precipitation is important in

250   determining plant and animal responses to rain. Winter rains that reach a minimum

251   threshold trigger strong plant-based responses while rains associated with summer

252   thunderstorms produce little or no response, probably due to the summer dormancy of

253   most plants and the high evaporation rate of summer precipitation (Polis et al. 1997b).

254   As a result of the extremely low precipitation rates, even in pulse years, these

255   hyperarid islands exhibit extremely low annual primary productivity that ranges from 0 g

256   m^{-2} yr^{-1} in dry years to 225 g m^{-2} yr^{-1} in wet years. The focal islands for these long term

257   studies lie within 20km of each other, and thus experience the same rain pulse events

258   to similar degrees. Large winter or spring precipitation events stimulate pulses of

259   annual productivity that trickle up to island consumer communities. Underlying this

260   pattern of pulses is a strong system of spatial subsidies that arrive from the ocean onto

261   the islands. The extremely productive marine system contributes macroalgae and

262   marine carrion to island shorelines (up to 27.9 kg m^{-1} shoreline yr^{-1}) and seabird

263   byproducts including guano, fish scraps, and chick and adult bodies and carcasses to

264   cliffs or areas further inland (Polis and Hurd 1996).

265   A high degree of spatial heterogeneity of quantity and quality of subsidies among

266   and within islands has lent itself to numerous studies of the impacts of various subsidies

267   on numerous recipient populations and communities. Islands vary in size (0.22 – 8.68

268   km^2) and perimeter-to-area ratio, which provides areas in the interior of larger islands

269   that are relatively disconnected from shore-based marine subsidies (Murphy et al.

270   2002). Moreover, seabirds do not use all islands or all areas of islands that they do use,

271   so it is easy to examine the impacts of seabird-based subsidies on plant and animal

272   communities inside and outside of seabird areas.

273   Some of these subsidies are available continuously or regularly, while others

274   arrive or become available with great irregularity. Seabird guano accumulates and

275   resides in the soil year-round, but is mobilized for plant uptake only during precipitation

276   events. Other inputs from seabirds, as well as coastal inputs, may also be strongly

277   pulsed: ENSO events often result in periods of massive breeding failure of seabirds

278   (Anderson et al. 1982), as well as widespread mortality of fishes and marine mammals

279   (Soto et al. 2004). Such events may increase the amount of carrion washing on shore

280   and remaining in seabird colonies, depending on the timing of mortality in relation to

281   nesting phenology; massive die-offs of adult birds prior to breeding may eliminate

282   sources of carrion for scavengers in colonies, whereas whole-scale abandonment of

283   eggs and chicks may actually briefly increase resource inputs to carrion and detritus

284   communities. Although such extreme temporal variation in these marine subsidies has

285   not been well-studied in this system, we expect that it could be very important. Thus,

286   with the combination of extreme spatial variation in marine subsidies and extreme pulse

287   events, both from rains and from marine inputs, this system provides an ideal natural

288   model for examining the population and community dynamics that arise in response to

289   precipitation pulses in the presence and absence of spatial subsidies.

290   Highly subsidized islands exhibit unique plant and animal patterns during

291   interpulse (drought) periods, and respond to pulses of rain in ways that are different

292   from responses on unsubsidized islands during pulse and interpulse periods. We will

293   begin by examining the effects of guano-derived nutrient subsidies that are taken up by

294   plants during precipitation pulses and used directly by herbivores and granivores.

295   However, in examining the subsequent, generalist consumer responses to pulses and

296   subsidies, we cannot and do not separate their responses to guano and rain-induced

297   plant growth from responses to other subsidies such as shoreline subsidies and other

298   seabird byproducts that consumers receive more directly than via plant pathways. (For

299   an example of a study that does separate those two conduits, see Sanchez-Piñero and

300   Polis 2000.)

301

302   *Soil and Plants*

303   To depict direct and indirect effects of pulses in the presence and absence of

304   subsidies in these island communities, we have modified the Reynolds et al. (2004)

305   'pulse-reserve' model to include the effects of spatial subsidies of seabird guano on soil,

306   plant species and communities, and animal populations and communities (Fig. 1). The

307   marriage of a pulse-reserve diagram with a food web diagram provides a context for

308   seeing soil and plant-mediated effects on animals. The Reynolds et al. (2004) model

309   and a related threshold-decay model (Ogle and Reynolds 2004) emphasize the

310   importance of antecedent soil conditions and plant functional types. Our 'temporal

311   pulse-spatial subsidy' model recognizes that antecedent soil conditions such as %N and

312   %P, % moisture, % organic matter, and pH differ substantially between areas with

313   subsidies (in the form of seabird guano inputs) and area without subsidies (see Wait et

314   al. 2005 for detailed results). Guano-enriched soils contain 7-fold greater N than

315   unsubsidized soils (0.22±0.03 vs. 0.03± 0.01%, respectively) and 4.9-fold greater P than

316   unsubsidized soils (1.30±0.24 vs. 0.35±0.17%, respectively), but those nutrients are

317   only available for plant growth primarily during pulsed periods of rain (Anderson and

318   Polis 1999). In addition, soil moisture is 3.1 times greater on subsidized islands in

319   pulsed years than in interpulse years, but only 1.1 times greater on unsubsidized

320   islands in pulsed years than in interpulse years (Fig. 2a), even though all islands receive

321   the same amount of rain. The higher moisture retention capacity and slower moisture

322   attenuation (data not shown) of subsidized island soils is probably due, in part, to the

323   higher organic matter content (6.1% vs. 1.4% on subsidized vs. unsubsidized islands),

324   which is a result of the greater primary productivity of these islands that contributes

325   slowly decomposing detritus to the upper soil horizons. As Reynolds et al. (2004)

326   explain, the primary productivity responses to soil water and nutrient availability feed

327   back directly and indirectly to antecedent soil conditions such as soil organic matter,

328   nutrient content, and moisture.

329   The combination of greater soil moisture and nutrient availability to plants on

330   subsidized islands compared to unsubsidized islands selects for species with different

331   physiological responses and subtly different life history traits. Thus, plant species

332   composition is vastly different in subsidized communities from that of unsubsidized

333   communities (Table 1). While both types of islands support communities of annuals in

334   their seed banks that will respond rapidly to rain pulses when they occur, communities

335   on subsidized islands typically only include three or four species, while communities on

336   unsubsidized islands may include 30 to 40 species, with as many as ten different

337   species found per square meter. These differences are not accounted for by traditional

338   species-area curves or other traditional biogeographic factors (Anderson and Wait

339   2001). Rather, a combination of physiological tolerance to the potentially toxic levels of

340   guano and the historical competitive exclusion of some species due to variability in

341   physiological responses to nutrient and moisture availability on subsidized islands likely

342   explains the large difference in species richness between subsidized and unsubsidized

343   islands.

344   The dominant species on subsidized islands exhibit physiological strategies for

345   responding to pulses that are very different from the dominant species on unsubsidized

346   islands. For example, even though nutrient subsidies lead to greater soil moisture

347   content in both pulse and interpulse years (Fig. 1a), *Amaranthus* spp. and

348   *Chenopodium* spp., which are only found on subsidized islands, have lower water

349   content during both pulse and interpulse periods, higher water potential (a measure of

350   moisture stress) during pulse periods, and greater instantaneous water use efficiency

351   (unit of growth/unit of water available) during pulse periods compared to *Cryptantha*

352   spp. and *Plantago* spp., which are common annuals on unsubsidized islands (Table 1).

353   These measurements indicate that while annual plants on subsidized islands contain

354   substantially higher foliar nutrient concentrations (Anderson and Polis 1999), they

355   exhibit more conservative strategies for using water, which probably allows these

356   species on subsidized islands to persist into subsequent drought periods longer than

357   the species that dominate on unsubsidized islands. Thus, the species on subsidized

358   islands are more likely to complete their life cycle when the pulse is small or short (e.g.,

359   1995, 2003 and 2005).

360   Interestingly, these differences in water use strategies are not associated with

361   differences in carbon assimilation rates (Table 1), as we might expect with enhanced

362   nutrient availability and higher foliar nutrient contents on subsidized islands (Anderson

363   and Polis 1999). Annual species photosynthesize at similar rates in both unsubsidized

364   and subsidized conditions, so growth rates are likely similar as well. However, because

365   species on subsidized islands live longer into interpulse periods, they ultimately achieve

366   greater biomass and reproductive output. In addition, ambient soil moisture is not great

367   enough on unsubsidized islands to initiate germination of most plant species in the

368   absence of a large pulse (Fig. 1b), but guano-enriched soils retain high enough soil

369   moisture during interpulse periods (either from persistent moisture from a large pulse, or

370   from major fog events, which are common in the area) for germination and growth of

371   some of the species on subsidized islands (Fig. 1b). Therefore, selection apparently

372   favors more conservative water use strategies over higher photosynthesis rates for

373   annual species growing in subsidized areas (Casper et al. 2005), but not for species

374   living in unsubsidized areas, which are more typical of this arid region. The rarity of this

375   strategy for annuals in this region may partially explain why the plant species richness

376   of subsidized areas is so low.

377   *Animals*

378   Larger amplitudes in plant quantity (Fig. 2b) and higher plant quality, as

379   demonstrated by 2.6 times greater % N and and 3.9 times greater % P in annual plant

380   tissues (Anderson and Polis 1999) translate into higher animal population densities on

381   islands with seabird-derived subsidies during and after pulses of rain. Invertebrate

382   herbivore communities respond directly and within the year of the rain and plant pulse to

383   increased resource availability (Fig. 2c), and the magnitude of their numerical response

384   is associated with the magnitude of the plant productivity (Linear regression, R^2 = 0.64,

385   p=0.007; also see Anderson and Polis 2004). Herbivore communities decline to

386   relatively low numbers during dry years on both subsidized and unsubsidized islands,

387   but during pulses, their abundance increases 3.3-4.8 times more on subsidized islands

388   than on unsubsidized islands. In addition to the greater biomass and nutrient mass

389   available in plants on subsidized islands, the increased longevity of available fresh plant

390   tissue on subsidized islands following a pulse may also contribute to the ability of

391   herbivores to respond numerically to plant pulses. In effect, the lag time of days or

392   weeks for herbivores to respond to a pulse of plant growth may be too long for the

393   herbivores to experience a full reproductive cycle before the drought returns. But, even

394   in the event of a short pulse, if plant responses are amplified and extended well into the

395   subsequent drought period, as they are on guano-subsidized islands, herbivores will be

396   able to complete their life cycles, and thus be more likely to persist on those islands.

397   One of the most common invertebrate detritivores, tenebrionid beetles on

398   seabird-subsidized islands exhibit positive numerical response to increased plant

399   detritus within one year following rain and plant pulses. Their response is primarily

400   behavioral in that they switch their diets from seabird carcasses in interpulse years to

401   plant detritus after pulses (Sanchez-Piñero and Polis 2000). Thus, beetle abundance

402   did not decline as availability of plant detritus declined on islands that receive seabird-

403   based subsidies. On unsubsidized islands and on the Baja California peninsula,

404   tenebrionids did not track increases or decreases in plant productivity either, but for

405   reasons that are less clear, but may be associated with greater amounts and more

406   regular availability of detritus from mainland perennials (Sanchez-Piñero and Polis

407   2000).

408   Except for the occasional raptor or snakes on a few islands, rodents represent

409   the top-level consumers on most small Gulf of California islands. Like tenebrionid

410   beetles, *Peromyscus* spp. are dietary generalists and inhabit many of the smallest

411   islands (<2 km^2; Lawlor et al. 2002; Stapp 2002), in part because they consume marine

412   subsidies, including algal wrack and marine carrion that arrive along shorelines (Stapp

413   and Polis 2003a; Stapp et al. 1999). The ability to use a broad range of terrestrial and

414   marine resources allows *Peromyscus* to persist and reach high densities on small

415   islands that receive multiple marine subsidies, even during interpulse periods of

416   extremely low terrestrial productivity. As a result, during pulse periods with high rainfall

417   and primary productivity, *Peromyscus* shows a strong numerical response, especially in

418   subsidized areas where densities are already high (Fig. 2d). This increase is relatively

419   short-lived, however, as most young produced during these periods are not alive by the

420   following year. The magnitude of the increase and decline is influenced by the

421   presence of marine subsidies, competitors and predators. On one small island (Flecha)

422   with large numbers of nesting cormorants but no terrestrial predators, *Peromyscus*

423   numbers increased approximately ten-fold following the 1997-98 ENSO, then declined

424   by 89% the following year, suggesting that mortality was due to terrestrial resource

425   scarcity (Stapp and Polis 2003b).

426   In contrast, granivorous rodents such as *Chaetodipus* spp. are found on fewer

427   islands, especially those with higher plant species diversity and presumably a larger

428   pallet of seed choices (Lawlor et al. 2002). They are not found on any small islands that

429   are covered in seabird guano. *Chaetodipus* rarely occurs in the absence of

430   *Peromyscus*, and competition from *Peromyscus* may affect the ability of *Chaetodipus* to

431   respond to pulsed seed production. The increase in *Chaetodipus* abundance on

432   unsubsidized islands in response to the 1997-98 ENSO was modest (Fig. 2d), which

433   may reflect the inherently low productivity of these small, nutrient poor islands as well as

434   the presence of *Peromyscus* and, on some islands, rattlesnakes (*Crotalus* spp.). As

435   with other rodents in the family Heteromyidae, many of which are specialized to live in

436   deserts, the reproductive potential of *Chaetodipus* is lower than that of species of

437   Muridae such as *Peromyscus*. Therefore, insular *Chaetodipus* may respond to pulses

438   not with a strong numerical response, but by storing seeds and maintaining lower

439   mortality rates.

440   *Chaetodipus* populations were much more stable over time than those of

441   *Peromyscus* (Fig. 2d), suggesting two different strategies for persisting on small islands

442   in the Gulf (Stapp and Polis 2003b). *Peromyscus* populations track plant resources

443   closely and therefore are more variable over time, but are prevented from extinction by

444   their ability to switch their diets to more constantly available marine subsidies during

445   interpulse periods. *Chaetodipus* appear to average out temporal variation in resources

446   by using storage mechanisms but are likely more vulnerable to extended periods of

447   extremely low terrestrial productivity, which explains their presence only on larger

448   islands or on islands with a higher diversity of seeds, such as islands without seabirds

449   (Stapp and Polis 2003a). On islands where these two taxa co-occur, they may affect

450   each other's response to pulsed resources, with *Peromyscus* briefly dominating by its

451   sheer numbers but *Chaetodipus* being behaviorally dominant and largely restricting the

452   spatial distribution of *Peromyscus* to areas near shore. Nonetheless, such spatial

453   segregation on islands receiving marine subsidies along the shoreline facilitates

454   coexistence of both groups. On larger islands that support rattlesnakes, the two

455   species may also interact indirectly via shared predation by rattlesnakes, which may

456   respond behaviorally and numerically to temporarily higher rodent densities during

457   pulses (P. Stapp, *unpublished data*).

458   Other generalist predators that inhabit these islands also show numerical

459   responses to pulses. Orb-web building spiders, predominantly *Metapeira arizonica*,

460   increase in density in response to rain and plant pulses within the year of the pulse.

461   The magnitude of their response is greater in subsidized areas and is associated with

462   increased productivity of plants (Linear regression, R^2 = 0.79, p=0.001) although not as

463   strongly with herbivore abundance (R^2 = 0.30, p=0.11; (Fig. 2e). However, predation on

464   spiders by scorpions, lizards and pompilid wasps also strongly influences spider

465   population dynamics (Polis and Hurd 1995, Polis et al. 1998). Like orb-web building

466   spiders, generalist lizards (mainly *Uta stansburiana*) respond to rain and plant pulses

467   more strongly in subsidized areas (including coastal areas of islands without seabirds)

468   than in unsubsidized areas (Fig. 2f). However, during interpulse periods, populations in

469   areas that receive multiple types of subsidies return to levels that are similar to

470   unsubsidized areas.   In general, subsidies such as algal wrack, marine carrion, and

471   seabird carcasses may be more constant than guano subsidies because they are

472   decoupled from pulses of precipitation. Therefore, the true subsidies for most generalist

473   predators may be the "temporal subsidies" (rather than spatial subsidies) of rare but *in*

474   *situ* plant and herbivore growth during rare rain pulses.

475   CONCLUSIONS

476   The presence of spatial subsidies substantially alters the structure and dynamics

477   of plant and animal populations and communities particularly as they respond to

478   resource pulses (Polis et al. 1998). Guano-derived nutrients amplify annual plant

479   productivity responses to rain pulses on islands with this type of subsidy, and this

480   response is driven by specific physiological and life history adaptations of a few annual

481   species to the soil nutrient and moisture conditions created by this subsidy.

482   Substantially lower plant species richness on the subsidized islands reflects both the

483   rarity of these strategies in the regional species pool, and the ability of these plants to

484   competitively exclude other species under such subsidized conditions. Invertebrate

485   herbivores also exhibit amplified responses to pulses of annual plant growth on nutrient

486   subsidized islands. It is unlikely, though, that they would be driven to local extinction

487   between pulses because a small number could persist on subsidized islands even

488   during drought periods when a few plants still germinate in the perpetually moist soils of

489   guano islands. Thus, the magnitude or the apparent duration of the pulse and the

490   reserve produced by the same amount of rain is substantially greater in subsidized

491   areas than in unsubsidized areas.

492   In contrast, granivorous rodents do not exist on nutrient subsidized islands, even

493   though they would have a consistent resource in these islands' extraordinary seed

494   banks. It is likely that the rapid numerical responses to rain pulses of omnivorous

495   rodents that are able to switch diets between plant-based resources and other forms of

496   marine subsidies that arrive along the shoreline have led to historical competitive

497   exclusion of the granivorous specialists. Thus, rodent diversity is lower on islands

498   receiving both seabird-derived and algal and carrion derived subsidies.

499   Similar to the omnivorous rodents, generalist detritivorous beetles respond to

500   pulses more strongly in subsidized areas, too, but do not experience severe population

501   declines during interpulse periods because the detrital reserves decay less rapidly than

502   availability of fresh plant tissue, and because they can shift their diets to other marine

503   based resources (Sanchez-Piñero and Polis 2000). The same pattern is true for

504   generalist predators like orb-web building spiders, but less so for lizards. Isotopic

505   studies of lizards (Barrett et al. 2005), spiders (Anderson and Polis 1998, Stapp et al.

506   1999), and rodents (Stapp et al. 1999, Stapp and Polis 2003b) have shown that,

507   compared to *in situ* terrestrial resources, marine resources make up a significantly

508   larger portion of these groups' diets in dry years than they do during either wet years or

509   in unsubsidized areas. Thus, if multiple forms of subsidies are available, generalist

510   consumer populations fluctuations can be dampened even in strongly pulsed systems

511   (Huxel et al. 2002), and will dominate in such systems, sometimes to the exclusion of

512   more specialized consumers.

513   Finally, the combination of widespread subsidies and strong pulses may tend to

514   reduce diversity within these islands, while perhaps enhancing regional diversity across

515   the archipelago by spatially partitioning species that maximize use of subsidies from

516   those that do not (Anderson and Wait 2001).   The low frequency but high intensity of

517   rain in this system is more extreme than what is seen in many desert systems, but is

518   relatively spatially homogeneous across all islands in the archipelago, so we can expect

519   that the nature of the rain pulses does not directly drive differences between subsidized

520   and unsubsidized islands. Rather it is the presence or absence of marine materials

521   entering island ecosystems (with or without the trigger of rain pulses) that determines

522   life history and physiological traits, population dynamics, species interactions, and,

523   consequently, diversity patterns. Thus, while most plant ecologists would agree that

524   pulses promote greater diversity through co-existence of species with different

525   responses to pulses (Chesson and Huntly 1997), the presence of nutrient subsidies

526   alters that prediction by strongly favoring the few species that can optimize the condition

527   of limited water with unlimited nutrients, which may represent a different form of stress

528   toleration (*sensu* Grime 1977).

529   The examination of our proposed predictions for subsidies to amplify or dampen

530   the effects of pulses on life history traits of species, population dynamics and

531   community structure should extend beyond the context of the temporally and spatially

532   variable system of the Gulf of California islands. The numerous studies of temporally

533   and spatially variable, multiple, reciprocal flows of detritus, invertebrates and mobile

534 consumers between streams and riparian zones may represent an equivalent context

535 for exploring the interactions between subsidies and pulses (Nakano and Murakami

536 2001, Sabo and Power 2002a, Baxter et al. 2005). However, in those circumstances,

537 most of the subsidies are also highly pulsed, such as the seasonal litterfall into streams,

538 terrestrial invertebrates dropping into streams, or aquatic insect emergences into the

539 riparian zone (Baxter et al. 2005). In such cases, then, the questions and predictions

540 would have to be adjusted to examine the potential for amplification or dampening of

541 population responses to two or more overlain pulsed or subsidized resources.

542   In summary, ignoring the presence of spatial subsidies when investigating the

543 effects of pulses or, likewise, ignoring the inputs of pulsed resources when investigating

544 the effects of subsidies, leads to incomplete pictures of spatially and temporally variable

545 ecosystems. Indeed, most systems experience both kinds of resource inputs, and in

546 many cases, the subsidies and pulses are one in the same. When they are not the

547 same, complementary or even synergistic effects of pulsed resources and multiple

548 spatial subsidies may arise, and demand that both kinds of inputs be considered in

549 tandem. Because feedbacks between responses to pulses and subsidies may occur

550 within and among trophic entities, and may occur with some time lag between

551 consumer-resource pairs, both spatial and temporal scales must be considered when

552 investigating population and community responses to both subsidies and pulses, as well

553 as the direct effects on recipient species and indirect effects on other species in the

554 recipient food webs.

555

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722   Yang, L. H., J. L. Bastow, K. O. Spence, and A. N. Wright. (this volume) What can we

723   learn from resource pulses?

724   TABLE 1. Herbaceous plant richness and mean (±SE) responses of the

725   dominant species to seasonal precipitation pulses and nutrient subsidies on

726   islands in the Gulf of California. For productivity in un-pulsed and pulsed years

727   see Fig. 2b.

Plant Response (units, # islands, # plots or samples)	Between precipitation pulses		During precipitation pulses	
	Unsubsidized	Subsidized	Unsubsidized	Subsidized
Observed species richness (# m^{-2}, 6, 60)	4.1 (0.3)[a]	1.9 (0.7)[b]	10.3 (0.6)[c]	4.0 (0.5)[a]
Dominant species (>80% of cover)	*Cryptantha Plantago*	*Amaranthus Chenopodium*	*Cryptantha Plantago Lotus Aristida*	*Perityle Amaranthus Chenopodium*
Seed bank (seeds m^{-2}, 9, 270)	no data	no data	26,580[a] (3,500)	310,340[b] (70,226)
Plant water content (%, 4, 12)	74.6 (1.9)[a]	61.1 (1.2)[b]	74.4 (1.9)[a]	67.3 (1.7)[a,c]
Mid-day water potential (MPa, 4, 12)	-1.4 (0.2)[a]	-2.5 (0.3)[b]	-1.6 (0.2)[a]	-0.12 (0.05)[c]
Seasonal water use efficiency C$_3$ species only (δ^{13}C, 4, 20)	-25.6 (0.7)[a]	-23.7 (0.9)[b]	-26.4 (0.2)[a,c]	-24.6 (0.4)[b,c]
Net assimilation rate	no data	no data	11.9 (2.1)[a]	8.9 (1.9)[a]

(μmol CO_2 m^{-2} s^{-1}, 4, 26)				
Instantaneous water use efficiency (A/g, 4, 26)	no data	no data	14.7 (2.1)[a]	35.1 (7.1)[b]

729

730 *Notes:* Letters within a row indicate significant differences in means between and during

731 pulses and unsubsidized and subsidized islands ($p < 0.05$, nested ANOVA's with island

732 type treated as sampling units and individual measures within an island type treated as

733 subsampling units; post-hoc comparisons were made using Tukey's test). Species

734 richness data collected from cleared productivity plots (see Fig. 1b for methods). Mid-

735 day water potential measured using a pressure bomb (PMS, Corvallis, Oregon, USA),

736 methods as in Casper et al. (2006). The $\delta^{13}C$ is based on the PeeDee limestone

737 standard for carbon isotope ratio, methods as in Wait et al. (2005). Instantaneous gas

738 exchange (A, net assimilation rate; g, stomatal conductance) determined between 10-11

739 AM using a LiCor 6400 (LiCor, Lincoln, Nebraska, USA). Plant water content is for

740 shoots only. Seed banks measured from 30 10 x 10 x 3 cm areas per island; seeds

741 were filtered with a soapy water solution and counted directly.

742 FIGURE LEGENDS

743 Figure. 1.   An integrated 'pulse-reserve' and food web model for a temporally pulsed

744 and spatially subsidized system. Original model was provided with permission to modify

745 by Reynolds et al. (2004). The original model depicted pulses of precipitation, the role of

746 antecedent soil conditions, and plant functional types and was explored using a

747 physiologically based ecosystem model developed for arid lands. We have modified the

748 model to include subsidy effects on antecedent soil conditions and detritivores, replaced

749 plant functional types with plant species assemblages associated with unsubsidized and

750 subsidized areas, and included higher trophic interactions. We examine our model using

751 data collected between 1992 and 2005 from a temporally pulsed and spatially

752 subsidized arid system (see text). Data illustrating how each of the components of the

753 model responds to below average (interpulse, or no pulse years) and above average

754 (pulse) precipitation are provided in Table 1 and Figure 2 as indicated.

755 [1] Wait et al. (2005) describe in detail how spatial subsidies (guano) in the system affect

756 soil chemistry (e.g., N, C/N, soil respiration, and spatial patterns in salinity and pH).

757 [2] Numerous studies (see text) have described the importance of spatial subsidies (e.g.,

758 guano, shore wrack, seabird carcasses) in the system.

759 [3] Sanchez-Piñero and Polis (2000) describes the direct influence of spatial subsidizes
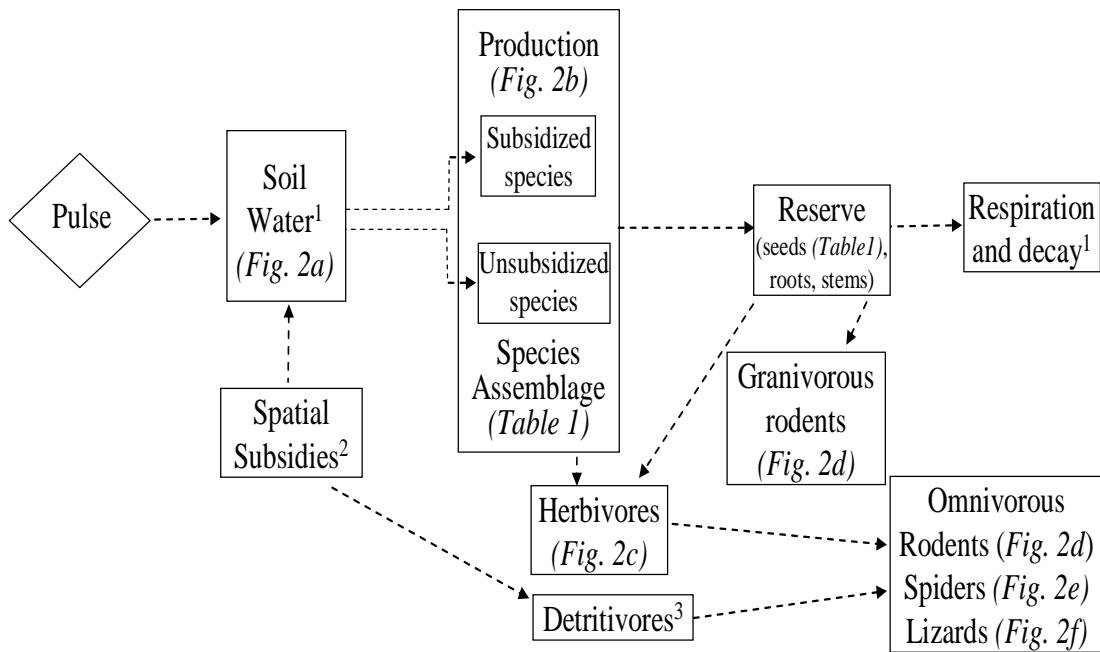
760 on detritivores.

761

762 Figure 2. Responses (mean ± SE) of soil, plants and animals to temporal pulses of

763 precipitation in the presence and absence of spatial subsidies. All data prior to 1999,

764 with the exception of soil moisture, comes from published work (see citations below).

765   Years within boxes experienced "significant" pulses, defined as precipitation during the

766   growing season 20% above the mean, and include 1992, 1993, 1995, 1998, 2003 and

767   2005. For figures a-c, "unsubsidized" refers to areas without seabird inputs, including

768   guano and carcasses. For graphs d-f, unsubsidized refers to areas without either

769   seabird or shoreline inputs. (a) Soil moisture was determined gravimetrically. Soil

770   moisture was significantly higher in subsidized than unsubsidized soils in all years (see

771   Wait et al. 2005 for methods, sample sizes, and analysis of 2001 and 2002 data). (b)

772   Plant productivity was determined from clearing 15 0.25m^2 plots per island according to

773   the methods of Polis et al. (1997b). Plant productivity was significantly greater on

774   subsidized than unsubsidized islands except in 1994, 1999, and 2001 ($p < 0.05$, ANOVA,

775   see Wait et al. (2005) for description of statistical analysis). (c) Herbivore population

776   size was estimated from sticky trap collections (see Polis et al. 1997b for methods). (d)

777   Rodent population sizes estimated from live trapping (see Stapp and Polis 2003a for

778   methods). (e) Orb-web building spider densities are estimated from counts on Cholla

779   spp. (see Polis and Hurd 1995 for methods). *Uta stansburiana* population sizes

780   estimated from timed searches (see Barrett et. al 2005). Regression analysis of

781   herbivores vs. productivity, spiders vs. productivity, and spiders vs. herbivores are

782   described in text.

783

784   Figure 1.

785

786   Figure 2.

787