

The effect of chronic seaweed subsidies on herbivory: plant-mediated fertilization pathway overshadows lizard-mediated predator pathways

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Abstract Flows of energy and materials link ecosystems worldwide and have important consequences for the structure of ecological communities. While these resource subsidies typically enter recipient food webs through multiple channels, most previous studies focussed on a single pathway of resource input. We used path analysis to evaluate multiple pathways connecting chronic marine resource inputs (in the form of seaweed deposits) and herbivory in a shoreline terrestrial ecosystem. We found statistical support for a fertilization effect (seaweed increased foliar nitrogen content, leading to greater herbivory) and a lizard numerical response effect (seaweed increased lizard densities, leading to reduced herbivory), but not for a lizard diet-shift effect (seaweed increased the proportion of marine-derived prey in lizard diets, but lizard diet was not strongly associated with herbivory). Greater seaweed abundance was associated with greater herbivory, and the fertilization effect was larger than the combined

lizard effects. Thus, the bottom-up, plant-mediated effect of fertilization on herbivory overshadowed the top-down effects of lizard predators. These results, from unmanipulated shoreline plots with persistent differences in chronic seaweed deposition, differ from those of a previous experimental study of the short-term effects of a pulse of seaweed deposition: while the increase in herbivory in response to chronic seaweed deposition was due to the fertilization effect, the short-term increase in herbivory in response to a pulse of seaweed deposition was due to the lizard diet-shift effect. This contrast highlights the importance of the temporal pattern of resource inputs in determining the mechanism of community response to resource subsidies.

Keywords Resource subsidy · Detritus · Stable isotope analysis · Path analysis · Aboveground–belowground linkage

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Introduction

The transport of energy and nutrients across habitat boundaries has important consequences for the structure of food webs in recipient ecosystems (Polis et al. 1997, 2004). Theoretical studies suggest that the food-web effects of these resource subsidies depend on the pathway of resource flux (Leroux and Loreau 2008) and the temporal signature of resource inputs (Sears et al. 2004; Holt 2008; Takimoto et al. 2009). However, empirical studies of resource subsidies tend to focus on a single pathway of resource transfer and a single temporal regime of subsidy inputs. Here, we examine how multiple pathways of resource transfer mediate the effect of both chronic and pulsed seaweed subsidies on herbivory in a shoreline ecosystem.

Most empirical studies of resource subsidies have focused on either predator-mediated or plant-mediated subsidy pathways (but see Dreyer et al. 2012; Hoekman et al. 2012). The presence of an alternate resource can lead to increased predator abundance, thereby enhancing the effect of predators on lower trophic levels (Polis and Hurd 1996; Henschel et al. 2001; Murakami and Nakano 2002). Predators may also shift their diet towards allochthonous prey, which can release autochthonous prey from predation pressure (Nakano et al. 1999; Sabo and Power 2002b; Baxter et al. 2004). In addition to these predator-mediated pathways, allochthonous resources can also lead to bottom-up effects in subsidized food webs by enhancing the growth and nutrient content of plants (Anderson and Polis 2004; Fukami et al. 2006). Theoretical studies that include both predator- and plant-mediated pathways suggest that subsidies enhance the long-term effects of predators on lower trophic levels (Leroux and Loreau 2008).

The relative importance of predator- and plant-mediated pathways may depend on the temporal pattern of subsidy inputs. For example, predator diet may change rapidly and dominate short-term community responses to an ephemeral, pulsed subsidy, while changes in plant growth and nutrient content may be more likely to emerge in response to chronic subsidy inputs and have longer-lasting effects on food webs. However, a complete understanding of the relationship between temporal subsidy regimes and the mechanisms of community response remains elusive because empirical studies tend to focus on either short-term responses to ephemeral resource inputs, such as the seasonal emergence of aquatic insects (e.g., Murakami and Nakano 2002; Sabo and Power 2002b), or long-term responses to chronic subsidy inputs, such as seabird guano (e.g., Croll et al. 2005; Fukami et al. 2006). In the current paper, we use an observational study to evaluate the long-term responses of a shoreline food web to chronic seaweed inputs, then compare the results to those from a previous experimental study evaluating the short-term effects of a pulsed seaweed subsidy in the same ecosystem.

We measured seaweed abundance, herbivory, plant nutrient content, lizard abundance, and lizard diet in shoreline plots encompassing a naturally-occurring gradient in seaweed deposition over the course of a year. Path analysis was used to evaluate the following effects: (1) *the fertilization effect*—higher seaweed abundance is associated with greater nutrient content in plants, which, in turn, is associated with greater herbivory; (2) *the lizard numerical response effect*—higher seaweed abundance is associated with greater lizard density, which, in turn, is associated with reduced herbivory; (3) *the lizard diet-shift effect*—higher seaweed abundance is associated with a greater proportion of marine-derived prey in lizard diets, which, in turn is associated with greater herbivory.

A previous study in this ecosystem demonstrated that a large, experimental pulse of seaweed deposition (1) increased plant nutrient content, (2) increased lizard density, (3) shifted lizard diets towards marine-derived prey, and (4) increased herbivory; the timing of these responses suggested that the lizard diet-shift effect was responsible for increased herbivory (Spiller et al. 2010). Our path analysis will allow us to determine whether chronic subsidy inputs influence herbivory via the lizard diet-shift effect (as in our short-term seaweed pulse experiment), the lizard numerical response effect (as predicted in Leroux and Loreau 2008), or the fertilization effect.

Materials and methods

Study system

This study was conducted on shorelines in the Exuma Cays, a chain of islands in the central Bahamas. We collected data on seaweed abundance, lizard density, lizard diet, leaf nitrogen, and herbivory in 29 plots on the windward (east) shoreline of three large islands. The shoreline side of the plot was formed by the high tide line, and the rectangular plots extended 5 m onto the land and 10 m along the shoreline. Plots were separated by at least 30 m of shoreline. Eighteen plots were located near Georgetown, Great Exuma, and the remaining 11 plots were located approximately 100 km northwest, on a large island near Staniel Cay (see Piovita-Scott 2009 for a map of the study area). Plots were selected with the goal of obtaining an even distribution of seaweed densities that spanned the range of natural variation while controlling for variation in other plot attributes (e.g., wind and wave exposure). We collected data for all measured variables between October 2007 and October 2008, and we continued to collect data on seaweed abundance until October 2010 (sampling dates for each variable are given in Online Resource 1). While some of the 2007 data from these plots were presented in Spiller et al. (2010), the current study presents data from a longer time period, contains stable isotope and leaf nitrogen data not presented in the previous analysis, and features an entirely new analytical approach (path analysis).

Hypothesized relationships between measured variables are shown in Fig. 1a. It is important to note that the causal paths depicted in Fig. 1a do not correspond to direct trophic exchanges. For example, lizards do not consume seaweed directly, but prey upon detritivores and other organisms that are derived from seaweed, and resources derived from seaweed are likely processed by decomposers prior to uptake by plants and incorporation into leaf tissue (figure 1C in Spiller et al. 2010 contains a more complete food-web diagram). Furthermore, while this path diagram

does not include all biologically feasible paths, it reflects our best understanding of causal relationships between the measured variables (see Online Resource 2 for supplementary analyses of two alternate path models). For example, while predators can regulate nutrient dynamics (Bardgett and Wardle 2010; Schmitz et al. 2010) and therefore might influence leaf nutrient content, allochthonous seaweed inputs likely have a much greater effect on the amount of plant-available nutrients in our shoreline plots than lizards and other predators.

Data collection

Wet seaweed biomass was estimated visually in each plot. Prior to conducting visual estimates, we calibrated ourselves by visually estimating the amount of seaweed present in plots outside of the study area, then collecting

and weighing the seaweed to get a measured biomass; visual biomass estimates were highly correlated with biomass measured by collecting and weighing seaweed (Spiller et al. 2010). Seaweed deposits consisted primarily of brown algae in the genus *Sargassum* and sea grasses (*Thalassia testudinum*, *Syringodium fuliforme*). For plant measurements, we focused on buttonwood (*Conocarpus erectus*), one of the most common shoreline plants in our study area (Correll and Correll 1982; Schoener 1988; Spiller et al. 2010). Two buttonwood trees were selected in each plot for measurements of herbivory and leaf nitrogen. We measured herbivory by analyzing digital images of leaves for the periods May–October 2007, October–December 2007, and May–October 2008. At the beginning of each time interval, we randomly selected four actively-growing stems and marked the most distal leaves. At the end of each time interval, we collected all leaves that had emerged since the stems had been marked (i.e., more distal than the marked ones). Twenty of these leaves were selected at random, then pressed and photographed. We measured total leaf and damaged area from the images using SigmaScan Pro Image Analysis System (Systat Software). Herbivory was calculated by summing the damaged areas of all leaves photographed and dividing by the sum of the total leaf area for each plant, giving an integrated measure of herbivore activity during each time interval. Leaf nitrogen content for each plant was measured with the mass spectrometer used for stable isotope analysis (described below).

Lizard density was estimated in each plot by counting the total number of lizards observed during exhaustive searches conducted on two consecutive days. The current study focuses on the density and diet of the brown anole (*Anolis sagrei*), which represented 92 % (1,117 out of 1,217) of all lizards observed. Counted lizards were marked with paint in order to avoid double-counting individuals. We measured the proportion of marine prey in *A. sagrei* diets by analyzing carbon stable isotope ratios. Marine sources of fixed carbon tend to have a higher proportion of ¹³C than terrestrial sources (Peterson and Fry 1987), and previous research in this system demonstrates that seaweed has a higher δ¹³C ($= [^{13}\text{C}/^{12}\text{C}_{\text{sample}}] / [^{13}\text{C}/^{12}\text{C}_{\text{standard}}] - 1$) than terrestrial leaf tissue (Spiller et al. 2010). In each plot, we captured 1–4 lizards (mean 3.01) by hand or with a noose and clipped ~2 cm from the end of each captured lizard’s tail. Tail tips were dried at 55 °C for 48 h and lipids were extracted using a methanol–chloroform mixture (2:1 by volume) prior to analysis. No significant difference in δ¹³C was found between the tail and whole body of *A. sagrei* (Takimoto et al. 2008). In order to establish a marine baseline, we analyzed seaweed collected from 5 of the 29 plots; in order to establish a terrestrial baseline, we analyzed buttonwood leaves from

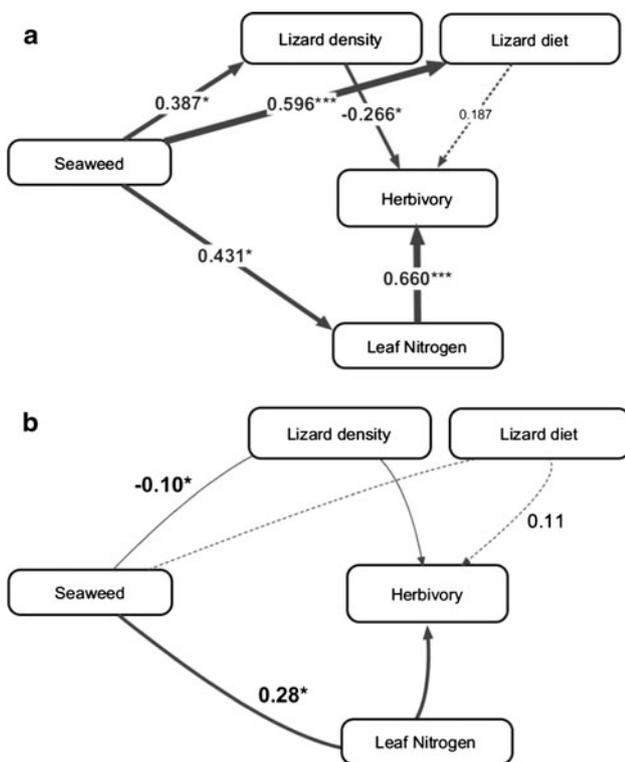


Fig. 1 **a** Path diagram depicting relationships between seaweed and terrestrial food web components. Standardized path coefficients are shown on top of corresponding paths. **b** Indirect path coefficients (calculated from standardized direct path coefficients) connecting seaweed and herbivory. Lizard density and diet were measured for the brown anole (*Anolis sagrei*); leaf nitrogen and herbivory were measured on buttonwood (*Conocarpus erectus*); seaweed deposits included both algae (*Sargassum* spp.) and sea grasses (*Thalassia testudinum*, *Syringodium fuliforme*). Solid lines denote statistically significant paths and dashed lines indicate paths that were not statistically significant (see Table 2), asterisks denote *P* values (**P* < 0.05, ***P* < 0.01, ****P* < 0.001), and line width is proportional to the magnitude of the path coefficient

each of the 29 plots. Seaweed and buttonwood leaves were dried at 55 °C for 48 h and ground to a fine powder prior to analysis. Preliminary analyses confirmed that seaweed had a higher $\delta^{13}\text{C}$ than buttonwood leaves in this study (t test: $P < 0.0001$). We used a simple mixing model to calculate the percentage of marine-based prey consumed by lizards in each plot: % marine prey = $100(\delta^{13}\text{C}_L - \delta^{13}\text{C}_T) / (\delta^{13}\text{C}_S - \delta^{13}\text{C}_T)$, where $\delta^{13}\text{C}_L$ is the mean carbon isotope ratio for lizards in a plot, $\delta^{13}\text{C}_T$ is the mean carbon isotope ratio for buttonwood leaves in a plot, and $\delta^{13}\text{C}_S$ is the mean carbon isotope ratio for seaweed averaged over the 5 plots from which it was collected, as data for individual plots were not available. Analyses of raw isotopic ratios for lizards ($\delta^{13}\text{C}_L$) in place of % marine diet produce the same qualitative results. Stable isotope samples were analyzed at the University of California, Davis, stable isotope facility.

Statistical analyses

We used a random effects model to assess the amount of variation in seaweed density explained by plot and sampling date between October 2007 and October 2010. We fit a model that included plot identity and sampling date as random effects and calculated the percent of total variation in seaweed density that could be uniquely attributed to spatial variation (i.e., between plots) and temporal variation (i.e., between dates). Seaweed density was log-transformed to meet assumptions of normality.

We used confirmatory path analysis to assess the strength of the pathways connecting seaweed and herbivory between October 2007 and October 2008. This analytical technique is well suited to our hypotheses, as it allows for the simultaneous assessment of the effects of multiple pathways between variables. We analyzed the a priori model shown in Fig. 1a. Since the goal of this study was to evaluate the long-term effects of consistent differences in seaweed inputs, we analyzed plot-level means, averaging the value of each measured variable across all sampling periods. In order to comply with assumptions of normality, plot averages of all variables were log-transformed to normalize their distributions. Since large differences in

variance between measured variables can adversely affect the estimation of path models (Kline 2005, pp. 57–58), we added a constant to the seaweed abundance and buttonwood leaf N variables (0.5 and -0.5 , respectively) prior to log transformation, in order to make their variances comparable to those of the other measured variables. Multivariate normality was confirmed graphically by comparing the squared Mahalanobis distance between observations for each plot and the centroid to a Chi-squared distribution in a quantile–quantile plot (Gnanadesikan 1977). Table 1 gives univariate statistics for all measured variables and the covariance matrix that formed the basis for our path analysis.

Because of the relatively low number of plots ($n = 29$), we used a methodology optimized for small sample sizes to assess model goodness-of-fit (Fisher's C statistic; Shipley 2000). This metric indicated adequate fit of our model to the data ($C = 9.25$, $df = 8$; $P = 0.32$); an asymptotic χ^2 goodness-of-fit metric, which may be inappropriate for such small sample sizes, also indicated adequate fit ($\chi^2 = 6.74$, $df = 4$; $P = 0.15$). Statistical significance of the three pathways connecting seaweed and herbivory was calculated based on the distribution of the product of two normally-distributed random variables (MacKinnon and Fritz 2007). Because there is strong evidence from previous studies that *A. sagrei* reduces herbivory on *C. erectus* (Schoener 1988; Spiller and Schoener 1996, 2007; Schoener and Spiller 1999), we used a one-tailed test to evaluate the effect of lizard density on herbivory and the indirect effect of seaweed on herbivory mediated by lizard density. Other tests of direct and indirect path coefficients were two-tailed. The total effect of seaweed on herbivory and other post hoc comparisons of indirect path coefficients were evaluated using bootstrapped parameter estimates ($n = 1,000$). Bootstrap P values were calculated by assessing the proportion of the appropriate combination of parameter values that were greater than or less than zero (depending on the direction of the effect). All hypothesis tests were based on models fit to unstandardized data. To facilitate comparisons of effect sizes we also fit our a priori path model to standardized data and present these results in

Table 1 Univariate statistics of plot-level means for measured variables and the covariance matrix used for path analysis

	Seaweed density (kg m ⁻²)	Lizard diet (% marine diet)	Leaf nitrogen (% mass)	Lizard density (lizards m ⁻²)	Herbivory (% damage)
Mean	0.205	53.446	0.815	0.156	4.938
Standard deviation	0.45	9.91	0.11	0.06	2.33
Range	0–2.17	33.21–76.19	0.64–1.05	0.07–0.39	1.82–11.18
Univariate statistics are based on untransformed values of measured variables, while the covariance matrix is based on log-transformed values (see “Materials and methods” for additional details)	Seaweed density	0.1717			
	Lizard diet	0.0441	0.0319		
	Leaf nitrogen	0.0659	–0.0047	0.1364	
	Lizard density	0.0582	0.0319	0.0160	0.1319
	Herbivory	0.0571	0.0060	0.1025	–0.0230

Fig. 1 and Table 2. Online Resource 2 contains additional information on our path model and supplementary path analyses.

All analyses were conducted in R (R Development Core Team 2012). Path models were fit using the ‘lavaan’ package (Rosseel et al. 2011), the goodness-of-fit statistic for small sample sizes was computed using the ‘ggm’ package (Marchetti et al. 2011), and significance of indirect path coefficients was assessed using the ‘RMediation’ package (Tofighi and MacKinnon 2011).

Results

Between October 2007 and October 2010, average seaweed densities in experimental plots ranged from 0 to 2.173 kg m⁻². The amount of variation in seaweed density attributable to space was much greater than the amount attributable to time, with plot identity explaining 82 % of the overall variation in seaweed density, compared with only 2.6 % for sampling date (the residual variation could not be uniquely attributed to space or time). Thus, although there was some temporal variation in seaweed density, there were substantial differences between study plots, with certain plots receiving consistently greater amounts of seaweed than others.

Between October 2007 and October 2008, plots with more seaweed had more lizards, and those lizards ate a greater proportion of marine prey (Table 2; Fig. 1a). Higher levels of seaweed were also associated with greater buttonwood leaf nitrogen. Plots with higher levels of leaf nitrogen had more herbivory, as did plots with lower lizard densities, but there was no significant relationship between lizard diet and herbivory (Table 2; Fig. 1a). There were significant indirect pathways between seaweed and herbivory mediated by leaf nitrogen ($P = 0.01$) and lizard abundance ($P = 0.04$), but

the indirect pathway connecting seaweed and herbivory via lizard diet was not significant ($P = 0.19$) (Fig. 1b). Bootstrapped parameter estimates indicated that there was a marginally significant difference in the magnitude of the leaf nitrogen-mediated pathway between seaweed and herbivory and the lizard density-mediated pathway ($P = 0.06$), indicating that increased herbivory due to fertilization did not completely offset the reduction due to higher lizard density. However, the indirect pathway between seaweed and herbivory mediated by leaf nitrogen was greater than the sum of the two (opposite-signed) lizard-mediated indirect pathways ($P = 0.01$), resulting in an overall positive effect of seaweed deposition on herbivory ($P = 0.04$).

Discussion

Allochthonous resources can enter food webs in recipient ecosystems through multiple pathways. We found that both top-down, lizard-mediated, and bottom-up, plant-mediated pathways contributed to the long-term effect of chronic seaweed deposition on herbivory. However, the bottom-up fertilization pathway overshadowed the effects of the top-down lizard-mediated pathways, resulting in a positive association between seaweed deposition and herbivory. In contrast, our previous experimental study indicated that a short-term increase in herbivory in response to a single, large pulse of seaweed deposition was due to the lizard diet-shift pathway. Thus, even though both chronic and pulsed subsidies increased herbivory, the mechanism underlying this response depended on the temporal pattern of subsidy inputs, with a predator-mediated pathway dominating short-term responses to pulsed subsidies and a plant-mediated pathway dominating long-term responses to chronic subsidy inputs.

Table 2 Parameter values and standard errors for the path analyses described in the text

Parameter	Unstandardized estimate	Standard error	Z	P	Standardized estimate
Direct effects					
Seaweed–Lizard diet	0.257	0.064	4.0	<0.0001	0.596
Seaweed–Lizard density	0.339	0.150	2.26	0.024	0.387
Seaweed–Leaf N	0.384	0.149	2.60	0.010	0.431
Lizard diet–Herbivory	0.473	0.364	1.30	0.194	0.187
Lizard density–Herbivory	−0.330	0.176	−1.88	0.030 ^a	−0.266
Leaf N–Herbivory	0.806	0.174	4.64	<0.0001	0.660
Variations					
Lizard diet	0.020	0.005			0.623
Lizard density	0.108	0.028			0.821
Leaf N	0.107	0.028			0.787
Herbivory	0.107	0.028			0.524

^a One-tailed P value

The current study provides evidence for a fertilization effect on herbivory, in which greater seaweed abundance leads to increased leaf nitrogen content, which, in turn, is associated with increased herbivory. Marine subsidies have been shown to also increase plant nutrient content in other systems (Anderson and Polis 1999; Helfield and Naiman 2002; Wilkinson et al. 2005; Fukami et al. 2006; Hocking and Reynolds 2011), and nitrogen fertilization is strongly linked to increased foliar nitrogen in many woody plant species (Koricheva et al. 1998). As the growth and reproduction of herbivores is often limited by the nitrogen content of their plant hosts (Mattson 1980), it is not surprising that fertilization-induced increases in leaf nitrogen content frequently lead to increased herbivory (Kyto et al. 1996; Herms 2002; Tripler et al. 2002; Denyer et al. 2007; Yang 2008). The strength of the indirect pathway between seaweed, leaf nitrogen, and herbivory in this system may be related to strong nitrogen limitation—leaf nitrogen is conspicuously low in buttonwood (Table 1) and other common shoreline plants in this ecosystem (Takimoto et al., unpublished data), roughly half of the estimated global mean for higher plants (Reich and Oleksyn 2004).

Our analyses provide evidence for a lizard numerical response effect on herbivory, in which greater seaweed deposition is associated with higher lizard density, which, in turn, reduces herbivory. Lizards have shown a numerical response to aquatic subsidies in another system (Sabo and Power 2002a), and the link between lizards and herbivory confirms previous research in this study system showing that *A. sagrei* are associated with lower herbivory on *C. erectus* (Schoener 1988; Spiller and Schoener 1996, 2007; Schoener and Spiller 1999). This enhanced indirect positive effect of predators on plants is consistent with theoretical studies of the long-term effects of resource subsidies (Leroux and Loreau 2008). We also found that seaweed deposition increases the proportion of marine-derived prey in lizard diets. However, while the sign of the relationship between lizard diet and herbivory was in the predicted direction (increased herbivory with a higher percentage of marine prey in lizard diet), our analysis indicated that this path coefficient was not statistically significant, and we did not find support for an indirect path in which the effect of seaweed on herbivory is mediated by lizard diet (i.e., the lizard diet-shift effect).

In the current study, the total effect of seaweed on herbivory was positive and the fertilization effect was stronger than the combined lizard effects. While other empirical studies have considered both plant- and predator-mediated subsidy pathways (Dreyer et al. 2012; Hoekman et al. 2012), the relative importance of these two pathways for food-web processes is unclear, and the only theoretical study that included both pathways focused on predator-mediated indirect effects (Leroux and Loreau 2008). Our

study suggests that plant-mediated effects of subsidies may be particularly important when the subsidy includes a significant detrital component. Interestingly, the combination of the lizard numerical response effect and the fertilization effect only had a marginally significant effect on herbivory, highlighting the fact that the top-down effect of subsidized predators is a combination of opposite-signed density-mediated and trait-mediated pathways (Sabo and Power 2002a; Leroux and Loreau 2008; Takimoto et al. 2009). Our results indicate that in the presence of plant-mediated bottom-up effects, predator diet shifts can tip the scales toward a positive overall effect of subsidies on herbivory. Thus, the below-ground fertilization effect appears to be stronger than the above-ground, top-down effect of lizards in part because lizard density-mediated and trait-mediated pathways have opposing effects.

In both the current study, which likely represents a system close to its equilibrium, and our previous experimental study (Spiller et al. 2010), which focused on transient dynamics after a single, large pulse of seaweed deposition, seaweed subsidies increased herbivory. However, the mechanistic pathway underlying this increase differed between the two studies. For long-term responses to chronic seaweed deposition, the fertilization effect overshadowed the two top-down lizard effects. In contrast, the timing of responses to a single, large pulse of seaweed suggests that the lizard-diet shift effect was responsible for increases in herbivory—in that experiment, we observed increased herbivory and a pronounced lizard diet shift 4 months before we observed increased leaf nitrogen content (Spiller et al. 2010). Thus, the relatively rapid response of predator diet to the increased availability of allochthonous resources explains why the predator diet-shift effect dominates short-term responses to subsidy, while the relatively slow response of plant nutrient content may explain why the effects of the fertilization pathway are only apparent in a more ‘equilibrium’ situation. These results highlight the importance of the relative rates of different ecological processes in determining how subsidized ecosystems respond to distinct temporal patterns of resource input.

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