Current Zoology 55(6): - , 2009

Micronutrient input into a mangrove ecosystem in Jobos Bay, Puerto Rico, by the exotic green iguana *Iguana iguana*

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Key words Detritus, Food web, Invasive species, Mangrove, Microorganisms, Reptile

Biological invasions are an important and growing component of global environmental change (Vitousek et al., 1996). Hundreds of billions of dollars are lost each year to invasive species damage and management (Pimentel et al., 2001). Scientists have responded by conducting research to understand the biology of the invasive species itself, in the hope that such information will allow effective control, and examining the impact of the invader on native taxa to determine the nature and magnitude of its effect. Introduced species can significantly impact native species, from altering their behavior, morphology and physiology (Phillips and Shine, 2006; Hoare et al., 2007; Greenless et al. 2007; Langkilde, 2009) to causing their extinction (Clavero and García-Berthou, 2005; Rodda and Savidge, 2007). These consequences can be especially severe in fragile island ecosystems (Case and Bolger, 1991; Reaser et al., 2003), and likely extend well-beyond individual species. However, we have limited understanding of the community-levels effects of biological invasions. This knowledge is useful if we are to adequately predict and manage the growing threat of invasive species (Park, 2004).

Examining the impact of invasive species on food webs can provide a useful approach for determining their community-level impact. Published research on this topic primarily considers the direct effect of invaders as novel consumers or prey species in their new environments (e.g. Pearson and Fletcher, 2008; McEwan et al., 2009; Wu et al., 2009). Incorporating studies on the impact of invaders on available energy and nutrient flow within an ecosystem, including analysis of changes in detrital input and nutrient load (Polis and Strong, 1996), will provide a more complete understanding of the nature and impact of invaders at the community-scale. In addition to the negative outcomes of invasion, such as habitat modification and homogenization (Holway and Suarez, 2006), invasive species may benefit some communities by providing new resources (Carroll et al. 2005; Maerz et al. 2005).

We test a potential impact of the invasive green iguana *Iguana iguana* by quantifying fecal microorganism input into a mangrove forest community at Jobos Bay in Puerto Rico. Green iguanas are relatively large herbivores (adult total length = 76 – 201 cm; Conant and Collins, 1998). They are primarily arboreal as adults and feed on the trees in which they live (Rand et al., 1990). Their high densities within invaded forests (– 33 iguanas per 100m edge), and strong site-fidelity, often results in the severe (> 70%) defoliation of individual mangrove trees over time (T. Carlo, unpub. data, collected in 2008 in San Juan Bay Estuary, Puerto Rico). A component of this material is then transferred to the forest floor as feces. As a result, the rate of nutrient input into iguana-invaded communities would likely be much faster, and nutritionally different, than would occur naturally though leaf fall or native animal defecation. Mangrove forests in Puerto Rico did not host large herbivores until the invasion of green iguanas, so these invaders appear to be filling a previously largely unoccupied niche.

Microorganisms represent an essential food source for many animals on the mangrove forest floor, including crabs, snails, and insect larvae, which forage directly on microorganisms within detritus or on microorganisms that grow in soil particles (Phillips, 1984). Such microorganisms may be a limiting resource within mangrove communities as they rarely comprise more than 1.2% of mangrove sediments (Blum et al., 1988). Iguana feces are a potential source of increased levels of microorganisms on the forest floor, either by directly inputting microorganisms that are found in the feces or by promoting their growth on soil particles. Fecal input by the green iguana may increase the carrying capacity of microphagous organisms, which in turn could have follow-on effects throughout the food web. Green iguanas can be very abundant within invaded areas, and so their impact on soil nutrients could be extensive (Meshaka et al., 2004; 2007). The relationship between the input of large

Received June 24, 2009; Accepted August 20, 2009

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volumes of fecal matter into mangrove ecosystems by this recent and successful exotic herbivore and its potential effect on the food web warrants investigation. This study is a preliminary investigation into the potential impact of green iguana fecal input on microorganism availability in mangrove forests.

1 Materials and Methods

This study was conducted in the mangrove forests of southern Puerto Rico at Jobos Bay National Estuarine Research Reserve (17° 7′ 22″ N, 66° 13′ 21″ W). We quantified the abundance of microorganisms in iguana feces, mangrove soil, and mangrove soil supplemented with iguana feces to represent the input experienced within iguana-invaded environments. We collected soil from the mangrove forest floor, and divided it in into two plastic bins so that each bin contained ~400 g soil. To one bin, we added ~40 g fresh iguana feces (less than 20 minutes old) obtained from a wild-caught iguana that was fed a natural diet of commonly occurring mangrove leaves (*Rhizopora mangle*, *Avicennia germinans*, and *Laguncularia racemosa*) over the previous 10 days. We gently disturbed the surface of the soil to mimic a natural defecation on the forest floor. We did not add feces to the second bin. Both bins were covered with a loose-fitting lid to allow air exchange but prevent contamination by other materials. Bins were kept at ambient temperature (24.7 ± 2.8℃). Three 15 g samples were obtained by taking a slice through the vertical plane of the soil from each bin twenty-four hours later, ensuring that all soil layers were equally represented in all samples. We took 2 subsamples from the feces immediately upon collection. We immediately froze the samples and held them at −20℃ until they were analyzed for lipid phosphate levels, which are directly proportional to the concentration of microbial biomass in a variety of soil types (White et al., 1979; Frostegard et al., 1991) using spectrophotometric analysis. Lipid phosphates were isolated from our samples by lipid extraction (as per Bligh and Dyer, 1959) followed by potassium persulfate digestion (as described by Findlay et al., 1989). Malachite green was added to the extractions and absorbance was measured at 610 nm (as per Van Veldhoven and Mannaerts, 1987). Known standards were run, and we calculated lipid phosphate concentration from a standard curve of absorbance versus concentration.

2 Results

Lipid phosphate levels, and therefore microbial biomass, varied among substrate types (ANOVA with lipid phosphate concentration as the dependent variable and substrate type- soil only, soil plus feces, or feces only- as a factor: $F = 126.89$, $df = 2$, $P < 0.0001$; Fig.1). Tukey's post-hoc test revealed that this difference was due to the iguana feces having a higher concentration of lipid phosphate than either the soil or the soil plus feces samples ($P < 0.0001$), and that this concentration did not differ between the soil-only and soil plus feces samples ($P = 0.57$).

3 Discussion

Iguana feces at Jobos Bay contain higher quantities of microorganisms than are found in mangrove mud. We predicted that the addition of feces to the substrate would boost productivity so that the microbial biomass of the soil with fecal input, as quantified by the concentration of lipid phosphate, would be greater than that of the soil without fecal input. A slight trend was detected in this direction (Fig.1), although this does not achieve statistical significance. This pattern is likely attributable

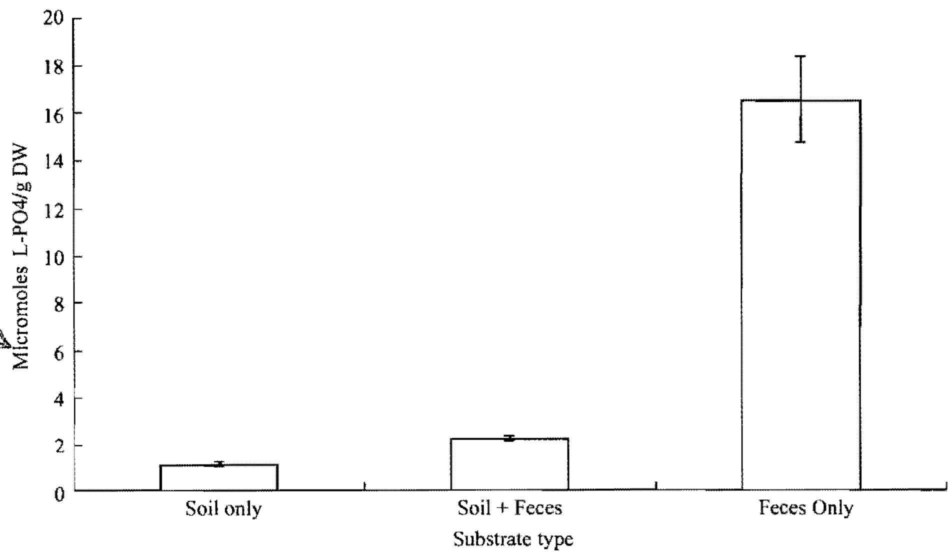

Fig.1 Micromoles of lipid phosphate (a direct proxy for microbial biomass) per gram dry weight of soil with and without the addition of iguana feces, and iguana feces

Error bars represent +/−1 standard error.

to the addition of microorganism-rich feces to the soil, or a slight increase in the growth of pre-existing soil microorganisms due to the input of the nutrient-rich feces. Although small, the input of fecal nutrients and microorganisms into this mangrove system through iguana feces is not necessarily negligible, particularly in heavily invaded areas. Additional research on the origin of microorganisms in mangrove soil after feces addition, and documentation of microorganism concentration in soil with fecal input over a longer time period, could provide valuable insight into the role of iguana feces in promoting mangrove soil microorganisms.

The fact that our study was conducted in the relatively cool and dry month of February suggests that our results may provide a conservative estimate of the input of nutrients into soil communities via iguana defecation. Iguanas prefer to defecate in the rain when possible (W. Meshaka, pers. comm.). As a result, in the wetter summer months more fecal matter will be washed to the forest floor to be mixed with soil and other organic debris. The increased availability of fecal matter, the warmer temperatures, and the pooling of water on the forest floor will likely create optimal conditions for a surge of microorganism growth during the summer months.

In light of its success as a colonizing species, populations of the green iguana are the subjects of removal programs in Florida and parts of the Caribbean (Engeman et al., 2005; Meshaka et al., 2004; Smith et al., 2007). Removing invaders can be argued to be ecologically necessary in certain cases, such as when they threaten at-risk species (e. g., McKie et al., 2005) or when they jeopardize human interests (Sementelli et al. 2008). This study reveals that green iguanas are contributing microorganism-rich fecal matter into mangrove ecosystems. Research that provides insight into how this nutrient input alters natural food webs, and how native communities respond to these changes, is important if we are to be able to predict and understand both the impact of this invader, and the consequences of its removal. Future research on a range of invaded mangrove forest communities, seasons, and mangrove soil types (with potentially different carrying capacities of microorganisms) would shed light on the effect of invasive iguanas on nutrient input across a range of native ecosystems.

Acknowledgements We thank T. Carlo-Joglar for insight into the system, H. Martínez for assistance in the field, and personnel at the Jobos Bay National Estuarine Research Reserve for permission and logistical support (especially A. Dieppa and L. Encarnación). We also thank W. Meshaka and two anonymous reviewers of this manuscript for their valuable comments. The research presented here adhered to Guidelines for the Use of Animals in Research, the legal requirements of the U. S. A. and the Institutional Guidelines of Penn State University (IACUC # 30329).

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