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Loss of phytotelmata due to an invasive bromeliad-eating weevil and its potential effects on faunal diversity and biogeochemical cycles

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ABSTRACT

Epiphytic tank bromeliads are important ecosystem engineers because they form phytotelmata that create habitat, increase species richness and abundance, create water sources and nutrient reservoirs in the canopy, and collect and redirect nutrients in forest ecosystems. Native bromeliad populations have been devastated in Florida (USA) because an invasive bromeliad-eating weevil (*Metamasius callizona*) has been destroying the plants. *Tillandsia utriculata* is a tank bromeliad that was once widespread from central to south Florida. Its populations have been hit hard by the weevil and are declining rapidly. This study quantifies the mortality rate caused by the weevil in a population of *T. utriculata* at the Enchanted Forest Sanctuary in central Florida and estimates the associated loss of phytotelmata. Estimations of phytotelmata were calculated for the *T. utriculata* baseline population, the population at 6 months into the study when 87% of the population was destroyed, and at the end of the study when less than 3% of the bromeliad population remained (99% of all deaths were caused by the weevil). The baseline population contained 16,758 L of water. At six months, there were 3180 L, and at the end of the study, there were 408 L. The loss of phytotelmata results in the loss of habitat, a decrease in biological diversity, and altered water and nutrient cycles and availability.

1. Introduction

Tank bromeliads grow as part of a canopy community which includes several other species of epiphytes, hemi-epiphytes, and lianas as well as non-tank bromeliads (Nadkarni, 1994). Together these plants create an arboreal landscape that provides habitat for plants, animals, and microbiota (Frank, 1983; Paoletti et al., 1991). The tank bromeliads dominate these communities in size, abundance, and species richness (Paoletti et al., 1991; Greeney, 2001; Luther and Benzing, 2009). Besides creating terrestrial-like habitat, the tank bromeliads also form phytotelmata, i.e., pools of water contained by plants or plant parts (Frank, 1983; Benzing, 2000). Tank bromeliads collect and contain water in tightly fitting, overlapping leaves that grow in the shape of a vase (Frank, 1983; Benzing, 2000). The amount of water a bromeliad can hold changes with age and size, and the actual amount held by the plant can vary in wet and dry seasons (Frank and Curtis, 1981). Measured volumes of bromeliad-contained water include 1.3 L for *Tillandsia utriculata* L. in Florida, 20 L for *Vriesia* sp. in Costa Rica, 27 L in *Brocchinia micrantha*(Baker) Mez in Guyana, and 45 L for *V. imperialis* Carrière, a bromeliad native to Brazil (Frank, 1983).

The fauna and flora of tank bromeliads consist of aquatic and amphibious organisms usually forming complex food webs. The total number of individuals and species collected in phytotelmata can be quite high (a single bromeliad may hold thousands of individuals and tens of species, many which are undescribed; see Frank et al., 1984; Paoletti et al., 1991; Carrias et al., 2001; Mestre et al., 2001; Stuntz et al., 2002; Frank et al., 2004). These numerous and diverse species are supported by and are part of the nutrients intercepted and cycled by the phytotelm bromeliads (Frank, 1983; Benzing, 2000). Debris, throughfall (rain that passes through the canopy and that leaches minerals), and organismal by-products collect in the tank water and are broken down by resident microbiota and other detritivores. Nutrients that are released become part of the soil that forms from the breaking down of the organic matter or suspended in the water (Paoletti et al., 1991; Nadkarni, 1994). These nutrients are used by the aquatic organisms, and by the bromeliads which absorb water and nutrients from the phytotelmata using special trichome cells on their leaves (Benzing, 2000). Tank bromeliads provide nutrient reservoirs in the canopy

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that are stable and biologically available (Frank, 1983; Nadkarni and Solano, 2002). Tank bromeliad phytotelmata have been likened to swamps, ponds, and lakes in size, colonization patterns, and biological activity (Frank and Lounibos, 1987; Carrias et al., 2001).

Because of the habitat they create and maintain and the resources they modulate, tank bromeliads can be identified as ecosystem engineers (Jones et al., 1994). Many organisms are ecosystem engineers, such as trees which form forests (Jones et al., 1997) or beavers that create dams (Naiman, 1988; Anderson and Rosemond, 2007). The tank bromeliads are autogenic engineers because, like trees but unlike beavers (which are allogenic engineers), the bromeliads create and maintain habitat that is formed by the engineer's body. Tank bromeliad communities are living engineers. When a plant dies, the phytotelmata are lost. If bromeliads are removed from the forest canopy, the significant portion that they add to the arboreal landscape is gone. Furthermore, not all epiphytic tank bromeliads are of equal importance as ecosystem engineers. Some are small, or have weak tank morphology, or are rare, or do not grow in dense populations (Benzing, 2000; Luther and Benzing, 2009). In Florida, there are 16 native species of bromeliads and 7 are classified as tank bromeliads, including *T. utriculata*. *T. utriculata* is an important ecosystem engineer because it is a long-lived, large plant (a body with a diameter of a meter or more and an inflorescence up to 2 m high) that grows in persistent, dense populations (several thousand plants) distributed over a wide range (central to south Florida), and that modulates many resources that are used by various organisms (Frank, 1983; Benzing, 2000; Luther and Benzing, 2009). *T. utriculata* grows in various habitats and, while it is able to tolerate some sun exposure, this species prefers shady habitat underneath forest canopies (Frank and Curtis, 1981; Frank, 1983; Luther and Benzing, 2009).

Epiphytic bromeliad communities throughout the Neotropics have suffered losses because of habitat loss (the forests in which they grow are being destroyed; Food and Agriculture Organization, 2010). In Florida, there is another grave danger facing the bromeliads: an invasive bromeliad-eating weevil, *Metamasius callizona* (Chevrolat), which is destroying native bromeliad populations (Frank and Thomas, 1994; Frank and Cave, 2005). The weevil is native to Mexico, Guatemala, and Belize and came to Florida on shipments of ornamental bromeliads shipped by a grower in Mexico. The weevil escaped and, in 1989, was found already established on native bromeliad populations in Florida. Since 1989, the weevil has spread to nearly fill its potential range in the state by its own movement as well as by humans moving infested ornamental bromeliads. The weevil is multivoltine, long-lived, and has high fertility (Frank et al., 2006). The larval stage mines the stems and leaves of the host bromeliad and kills the plant by chewing the meristematic tissue (Frank and Thomas, 1994; Frank and Cave, 2005). In so doing, the weevil is altering the environment by the direct consumption of autogenic engineers, which removes habitat and alters environmental processes.

T. utriculata is suffering more from the weevil compared to the other bromeliads native to Florida because of its relatively larger size and higher nutrient content, which also makes it susceptible to infestation by a large number of weevils (Frank and Thomas, 1994; Benzing, 2000; Sidoti and Frank, 2002; Cooper, 2006). *T. utriculata* also takes a long time to reach maturity and reproduces by monocarpy which limits its ability to recover after weevil attack (Isley, 1987; Benzing, 2000; Cooper, 2008).

T. utriculata populations devastated by the weevil were observed while surveying its spread (Frank and Cave, 2005). Because *T. utriculata* is declining so rapidly and because it is so ecologically important, we searched for a large *T. utriculata* population to monitor mortality caused by the weevil and to estimate the associated loss of phytotelmata. We found such a *T. utriculata* population at the Enchanted Forest Sanctuary (Brevard County). This paper summarizes the mortality rate caused by the weevil in this population of *T. utriculata* and estimates the associated loss of phytotelmata and the water held by them.

2. Method

A *T. utriculata* population in its first or second year of a weevil infestation was monitored every 3 months for bromeliad mortality from March 2007 to June 2009 at the Enchanted Forest Sanctuary (EFS), Brevard County, Florida. The Sanctuary has over 200 ha of land with various habitats, including mesic and hydric hammock, which are habitats supportive of *T. utriculata* (see Supplementary Map 1). We searched the mesic and hydric hammocks surrounding the public trails for medium to large, living *T. utriculata* plants, using unaided eyes and binoculars to scan the canopy. Using a Global Positioning System (GPS), we took longitude and latitude readings that broadly outlined the habitat in which we searched for *T. utriculata* growth; we also took readings of the perimeter surrounding the habitat that supported *T. utriculata* growth. Approximately 850,000 m^2 of habitat was searched for *T. utriculata* growth and about 240,000 m^2 within that area supported *T. utriculata* growth (see Supplementary Map 2). Searches were made in January and February 2007.

Within the area that supported *T. utriculata* growth, we walked the trails and scanned the canopy for the presence of *T. utriculata*. Those parts of the trails that passed under canopy that supported *T. utriculata* (medium size or larger) within 7.5 m of the center of the trail were mapped and monitored. The mapped area included all of the area parallel to the center of the trail at 7.5 m to either side that included *T. utriculata* growth. The monitoring sites were delineated using standard surveying flags and longitude and latitude points were taken of the perimeters (see Supplementary Map 3). There were 4 monitoring sites with a total area of 11,200 m^2. Supplementary Tables 1–3 list the longitude and latitude readings associated with the maps.

All bromeliads with a longest leaf length of 30 cm or more living in the monitored areas were counted at an initial survey and then every 3 months for 27 months. For each count, plants were classified according to size based on the estimated longest leaf length. We estimated the longest leaf length looking up from the ground to the canopy. Because this limited our accuracy, we used size categories rather than an estimate of length. The range for each category was 20 cm. From previous experiments, we assessed that bromeliads could be accurately sorted into these categories (Cooper, 2006). The categories were medium (30–50 cm), medium-large (50–70 cm), large (70–90 cm), and very large (90–110 cm). Plants with longest leaf lengths less than 30 cm were not counted because the smaller plants do not hold appreciable amounts of water (~0.04 L; Frank and Curtis, 1981) and are attacked much less frequently by the weevil (Cooper, 2006).

Each time we monitored, the dead plants were counted and examined for cause of death, which was determined by examining the dead plant bases in the canopy (looking from the ground) and by examining the cores of the dead plants that fell from the canopy and remained in the monitoring areas. Cause of death by weevil was determined by the presence of weevil damage (core of plant apparently chewed, base of plant remaining in the canopy, chew marks at the base of leaves, weevil larvae and/or pupal chambers in the plant remains). Weevil damage was easily differentiated from death by some other cause (rot, desiccation, cold damage, or seed production followed by senescence).

Right censored, non-parametric survival analysis using Kaplan–Meier Estimators (Kaplan and Meier, 1958) was used to create a