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Original article

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

Teresa M. Cooper [a,*], J. Howard Frank [a], Ronald D. Cave [b]

[a] Entomology and Nematology Dept., University of Florida, Bldg. 970, Natural Area Drive, Gainesville, FL 32611-0620, USA
[b] Indian River Research and Education Center, University of Florida, 2199 South Rock Road, Ft. Pierce, FL 34945-3138, USA

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A B S T R A C T

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 byproducts 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

* Corresponding author. Present address: 2199 South Rock Road, Ft. Pierce, FL 34945-3138, USA. Tel.: +1 772 468 3922x224; fax: +1 772 468 5668.
E-mail addresses: tmcooper@ufl.edu (T.M. Cooper), jhfrank@ufl.edu (J.H. Frank), rdcave@ufl.edu (R.D. Cave).

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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 survival curve for the *T. utriculata* population. Failure mode was death by weevil.

From previous observations of weevil-infested, large, dense *T. utriculata* populations, we expected the infestation rate to advance quickly. The bromeliad population would decline rapidly until it was devastated, and then the infestation rate would proceed more slowly (Cooper, 2006). We used the *T. utriculata* survival curve to determine when the *T. utriculata* population had been devastated and the rate of the weevil infestation changed from rapid to slow. We calculated the total maximum *T. utriculata*-contained water in the forest canopy at 3 time points: 1) the initial survey; 2) when the *T. utriculata* population was devastated; and 3) the end of study (27 months). To make these calculations, we needed an estimated total number of *T. utriculata* in EFS and the most frequent volumetric capacity of *T. utriculata* for the 3 time points. We estimated the total number of *T. utriculata* by dividing the number of living *T. utriculata* counted in the monitored areas by the area monitored, and then multiplied this by the area with *T. utriculata* growth. We calculated volumetric capacity by using a curvilinear relationship between the longest leaf length of a *T. utriculata* and its volumetric capacity (Frank and Curtis, 1981). This relationship is:

$$VC = 0.003251\ LL^{2.7799}$$

where VC = volumetric capacity (ml) and LL = longest leaf length (cm).

The longest leaf length that was used for calculating volumetric capacity was the mid-point of the size category that had the highest percentage of bromeliads for the 3 time points. Total water in the canopy was determined by multiplying the estimated total number of *T. utriculata* in EFS by the calculated volumetric capacity of *T. utriculata*. For subtractions used to calculate total water loss (due to weevil) between time points, we considered the problem of including water loss from plants that were not killed by the weevil, thus inflating the outcome. This did not become a problem, however, because 99% of the bromeliads that died were killed by the weevil, making the loss of water to other causes negligible.

3. Results

In March 2007, 2176 bromeliads were counted. The *T. utriculata* population declined rapidly during the first 6 months (Fig. 1). In September 2007, 286 *T. utriculata* were counted. The *T. utriculata* population, with an 87% loss, had been effectively devastated. For the remainder of the study, the *T. utriculata* population steadily declined, and at 27 months the population was less than 3% of the initial population; only 53 plants remained in the monitored areas.

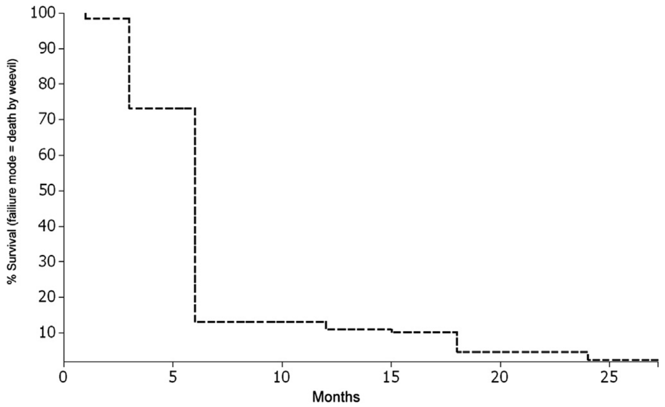

Fig. 1. Survival curve for *Tillandsia utriculata* in the Enchanted Forest Sanctuary. Failure mode = death by *Metamasius callizona*.

For the entire study, less than 1% of *T. utriculata* mortality was caused by something other than the weevil (dislodged from the canopy or seed production followed by senescence).

The estimated total number of *T. utriculata* was 46,552 at $t = 0$, 8835 at $t = 6$ months, and 1134 at $t = 27$ months. The medium-large size category was the most frequently represented category for each time point (Table 1), therefore 65 cm (the mid-point for the medium-large size category) was used as the longest leaf length for all water volume calculations. The estimated maximum total volume of *T. utriculata*-contained water in EFS's canopy was 16,758 L at $t = 0$, 3180 L at $t = 6$ months, and 408 L at $t = 27$ months. Plant mortality due to the weevil resulted in a loss of 13,577 L of water in the first 6 months of the study and 2772 L over the following 21 months, for a total of 16,350 L lost.

4. Discussion

T. utriculata was once an abundant species found from central to south Florida. Now, it is a rare and sparsely distributed species, because of *M. callizona*. The weevil infestation at the Enchanted Forest has demonstrated the weevil's ability to rapidly destroy *T. utriculata*: 87% of the population was gone in the first 6 months, and less than 3% remained after 2¼ years. With the loss of these plants, phytotelmata were lost, resulting in an estimated loss in the tens of thousands of liters of water in the first 6 months, and a few hundred more liters over the following 21 months.

When we began our study in March 2007, the weevil had already been present in EFS for 1–2 years. The weevil infestation at EFS was typical for an infestation on *T. utriculata*, with rapid, high mortality then slowing down once the population was devastated. The infestation before our arrival was likely just as aggressive and damaging as what we witnessed in the first 6 months of our study, so it would not be too conjectural to say that the pre-weevil *T. utriculata* population and amount of phytotelmata were at least 2 times greater than our initial estimation in March 2007.

When we ended our study, there were no longer any very large plants and only 53 medium to large plants scattered over a large area. There were several patches of very small and small plants, too small and several years away from being able to hold water. The weevil infestation died back with the loss of the medium and large plants, but the weevil will be able to persist in the forest at a lower rate as long as there are plants with a longest leaf length of 10 cm or more (Cooper, 2006). It is uncertain if *T. utriculata* will eventually be completely destroyed by the weevil or if it will persist at reduced levels, in EFS as well as in other parts of Florida. Pressure from weevil herbivory is unlikely to go away because smaller plants will continue to support weevils and because other bromeliad populations in Florida will support the weevil, primarily *T. fasciculata* Swartz, but also the other native bromeliads that can support the weevil as well as several species of ornamental bromeliads used in landscaping (there are no invasive bromeliads in Florida; Luther and Benzing, 2009; FLEPPC, 2011). Whether *T. utriculata* persists

Table 1
Percentages of medium, medium-large, large, and very large bromeliads in a population of *Tillandsia utriculata* at the Enchanted Forest Sanctuary at time = 0, time = 6 months, and time = 27 months.

Size category	Time = 0 months	Time = 6 months	Time = 27 months
Medium	21.2	16.4	15.1
Medium-large	42.4	50.3	47.2
Large	21.5	21.1	37.7
Very large	14.9	12.2	0.0

at reduced rates or is extirpated, *T. utriculata*'s importance as an ecosystem engineer has been diminished.

Sometimes, when an autogenic engineer is removed from an ecosystem, it can be replaced by another autogenic engineer that performs a similar function at like magnitude. When oak populations declined because of the gypsy moth, *Lymantria dispar* (L.), maples and ashes increased in abundance (Whitmire and Tobin, 2006); although ash trees were later attacked by the emerald ash borer, *Agrilus planipennis* Fairmaire (Poland and McCullough, 2006). When Carolinahemlock populations declined because of the hemlock woolly adelgid, *Adelges tsugae* Annand, several tree species filled in the vacancies (Gandhi and Herms, 2010). Are there epiphytes in Florida that could colonize the vacancies created by the removal of *T. utriculata*? Of the other 15 native species of bromeliads, only *Guzmania monostachia* (L.) Rusby ex Mez might come close to *T. utriculata* in size, phytotelm formation, and the habit of growing in large, dense populations (Luther and Benzing, 2009). However, *G. monostachia* is restricted to the extreme southern part of Florida, and could only have an effect in that region. Unfortunately, it is also susceptible to attack by *M. callizona*.

Tillandsia fasciculata shares habitat with and is similar in size (individually and collectively) to *T. utriculata* but does not impound enough water to form complex phytotelm ecosystems as *T. utriculata* does (ecosystems in phytotelmata increase in complexity with an increase in the volume of water contained; Richardson, 1999; Frank et al., 2004; Frank and Fish, 2008). The remaining tank bromeliads are restricted to the southern tip of Florida and/or too small and/or grow in populations that are too small and sparse to replace *T. utriculata*. As well, it must be remembered that these bromeliads, as well some of the non-tank bromeliads (which are also small and rare), are susceptible to attack by the weevil. Like *T. utriculata*, these other weevil-host bromeliads are creating vacancies in the canopy because of removal by *M. callizona*.

Other plants that might colonize canopy vacancies left by *T. utriculata* are the 4 species of bromeliads not susceptible to weevil attack, *Tillandsia bartramii* Elliot, *Tillandsia recurvata* (L.), *Tillandsia setacea* Swartz, and *Tillandsia usneoides* (L.), and other epiphytes. These 4 bromeliad species have wide ranges and often grow in large, dense populations in habitat with *T. utriculata*, particularly the last 3 listed (*T. bartramii* has a more northern distribution; Luther and Benzing, 2009), and it is possible that these species would colonize canopy vacancies left by *T. utriculata*. All of these species are small (which is why they are not attacked by the weevil – the plants cannot support weevil larval growth; Frank and Thomas, 1994; Sidoti and Frank, 2002; Cooper, 2006) and would not likely replace total phytomass or heterogeneity that were lost. As well, these 4 species of bromeliads do not support phytotelmata.

Other epiphytes include lycophytes (2 families, 2 species), pteridophytes (8 families, 23 species), and spermatophytes (7 families, 59 species) (Marie Selby Botanical Gardens, 2012). Some of these epiphytes, including *Pleopeltis polypodioides* (L.) Andrews and Windham (Polypodiaceae) and *Encyclia tampensis* (Lindl.) Small (Orchidaceae), might colonize vacancies. *Pleopeltis polypodioides* and *E. tampensis* are commonly found growing with *T. utriculata*. *Pleopeltis polypodioides* can grow in dense populations, but it is a small plant and creates a vegetative mat that is close to the branch it colonizes; as well, when conditions are dry, the plants become dry and the leaves curl, a habit from which they get the common name 'resurrection fern', because when the rains return, the leaves uncurl and turn green again (Kessler and Siorak, 2007). *Encyclia tampensis* is larger than *P. polypodioides* but smaller than *T. utriculata* and tends to grow as single plants and not in dense crowds. The other epiphytes are small and/or rare and/or restricted in range or growth habit, and/or do not share habitat with *T. utriculata*.

Loss of habitat caused by an invasive engineer may cause changes in species composition and abundance. For example, loss of Fraser firs caused the decline of several bird species in North American forests (Rabenold et al., 1998; Kenis et al., 2009) and the loss of hemlock trees attacked by *A. tsugae* altered bird composition, deer survival, and salamander populations (Tingley et al., 2002; Kenis et al., 2009). It is uncertain how species composition or abundance will change with the reduction or loss of *T. utriculata*. A decline in overall biodiversity is likely because facultative transient and resident organisms will lose total available habitat, both terrestrial and aquatic, and will therefore have less area for expansion. A wide variety of organisms, including mammals, birds, reptiles, amphibians, arthropods, and other invertebrates, use habitat created by epiphytic bromeliads as hunting grounds, nesting material, or refugia. Nadkarni and Matelson (1989) reported 58 species of birds using epiphytic bromeliads in Costa Rica for nesting material, as water sources, and as hunting grounds. Cypress swamps in south Florida flood during the wet season and animals can use the bromeliads as habitat to which they can retreat (Luther and Benzing, 2009).

Specialists of phytotelmata are more likely to face extinction because there would be no other habitat to which they could retreat. In Florida, a survey of *T. utriculata* populations by Frank and Fish (2008) showed there to be 9 to 19 invertebrates that are specialists of *T. utriculata* phytotelmata and, of these, 5 are precinctive ("endemic"; see Frank and McCoy, 1990). Included in possible extinctions are the host bromeliads, *T. utriculata* as well as 11 other native bromeliads. *Metamasius callizona* can grow in 12 of Florida's 16 native species of bromeliads, and 8 of these have been observed being attacked by the weevil in the wild, 1 of which (*Tillandsia simulata* Small) is precinctive (Frank and Cave, 2005). The 4 susceptible species not observed being attacked in the field include the very rare species *Tillandsia pruinosa* Swartz, *Catopsis berteroniana* (Schult. and Schult. f.) Mez, *Catopsis floribunda* L.B. Smith, and *Catopsis nutans* (Swartz) Grisebach. All are restricted to a very limited southern range, but *C. nutans* is the rarest, with just a few small patches over a few square kilometers in the most southern part of Florida (Luther and Benzing, 2009).

With the loss of *T. utriculata*, water sources are lost in the canopy, reducing available drinking sources and aquatic habitat. Moreover, nutrients are no longer biologically available to support complex food webs once supported by the phytotelmata and, instead, will be redirected to the forest floor because throughfall and leaf litter and other debris will no longer be intercepted by the bromeliads (Frank, 1983; Benzing, 2000). Throughfall and leaf litter that falls on the forest floor will increase the nutrients made available to forest floor ecosystems, understory vegetative growth, and the trees that once supported *T. utriculata*. Florida has sandy soils and it is also possible that much of the throughfall could leach into streams, ponds, lakes, or swamps that are often part of *T. utriculata* habitat (Myers and Ewel, 1990). Many trees that host *T. utriculata* grow in or over the water, in which case the throughfall and leaf litter would fall directly into the water.

Besides the nutrients captured in the phytotelmata and associated food webs, tank bromeliads hold nutrients in their phytomass (Benzing, 2000). Nutrients held in the phytomass will be transformed into weevil and weevil by-product and into decaying plant matter on the forest floor. After a *T. utriculata* population is devastated, the increased amount of throughfall and leaf litter will continue to fall and add nutrients to the forest floor. Weevil infestations on *T. utriculata* happen rapidly and the number of dead *T. utriculata* that fall on the forest floor can be substantial (Frank and Thomas, 1994; Frank and Cave, 2005). However, once the *T. utriculata* population is devastated, the transformation of phytomass into weevils and the input of dead plant material on the forest floor will slow down. Bromeliad leaves can take a long time

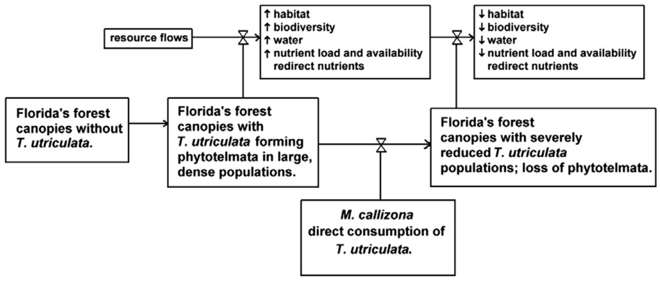

Fig. 2. Schematic of engineering by *Tillandsia utriculata* and *Metamasius callizona* based on Jones et al.'s (1994) 5 types of ecosystem engineering. The symbol indicates points of modulation.

to decompose, so the mass of dead plant material may cause short term changes in forest soil communities. It is difficult to predict what the long term outcomes will be with the loss and redirection of nutrients in Florida's forests, but there will likely be a decrease in overall productivity (Nadkarni, 1984, 1994; Benzing, 2000). Because *T. utriculata* grows in various habitats, it may be that outcomes will be locally variable (Benzing, 2000).

Jones et al. (1994) gave 5 types of ecosystem engineering. The invasion of *M. callizona* in Florida and its interactions with *T. utriculata* are a combination of case 3 (an autogenic engineer that physically modifies the habitat via its living or dead tissues, thereby altering resource flows) and case 4 (an allogenic engineer that physically transforms living or non-living materials by means of its activities with concomitant impacts on resource flows). Fig. 2 shows a schematic illustration, using Jones et al.'s (1994) scheme, of these 2 cases combined. Florida forest canopies are transformed by the growth and development of large, dense *T. utriculata* populations. *T. utriculata* forms phytotelmata, which creates habitat, increases biological diversity, increases water supplies in time and space, increases nutrient loads and availability, and captures and redirects nutrients. The arrival of *M. callizona* and the subsequent destruction of *T. utriculata*, by direct consumption, have transformed forest canopies from canopies with large, dense *T. utriculata* populations to canopies with severely reduced *T. utriculata* populations primarily composed of small to medium plants that are not large enough to form phytotelmata mixed with a few larger, scattered plants with phytotelmata. The remaining phytotelmata are not enough to have engineering effects of great magnitude and the results are loss of habitat, loss of biological diversity, a decrease in water and nutrients, and alterations in the water and nutrient cycles. *Metamasius callizona* is thus a destructive engineer that reverses the engineering performed by *T. utriculata*.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.actao.2013.01.016.

References

Anderson, C.B., Rosemond, A.D., 2007. Ecosystem engineering by invasive exotic beavers reduces in-stream diversity and enhances ecosystem function in Cape Horn, Chile. Oecologica 154, 141–153.

Benzing, D.H., 2000. Bromeliaceae Profile of an Adaptive Radiation. CambridgeUniversityPress, United Kingdom.

Carrias, J.F., Cussac, M.E., Corbara, B., 2001. A preliminary study of freshwater protozoa in tank bromeliads. J. Trop. Ecol. 17, 611–617.

Cooper, T.M., 2006. Ecological and demographic trends and patterns of *Metamasius callizona* (Chevrolat), an invasive bromeliad-eating weevil, and Florida's native bromeliads. Master's thesis. Gainesville, Florida, University of Florida, p. 69.

Cooper, T.M., 2008. Seasonality and abundance of *Metamasius callizona* (Coleoptera: Dryophthoridae), an invasive insect herbivore, on two species of *Tillandsia* (Bromeliaceae) in Florida. J. Nat. Hist. 42, 2721–2734.

FLEPPC, 2011. List of Invasive Plant Species. Florida Exotic Pest Plant Council. Internet. <http://www.fleppc.org/list/list.htm> (Last accessed: January 2013).

Food and Agriculture Organization, 2010. Global Forest Resources Assessment 2010 – Main Report. FAO Forestry Paper, 163 Rome, Italy. Available online at: <www.fao.org/forestry/fra/fra2010/en/>. Last accessed: January 2013.

Frank, J.H., 1983. Bromeliad phytotelmata and their biota, especially mosquitoes. In: Frank, J.H., Lounibos, L.P. (Eds.), Phytotelmata: Terrestrial Plants as Hosts for Aquatic Insect Communities. Plexus, Medford, New Jersey, pp. 101–128.

Frank, J.H., Cave, R.D., 2005. *Metamasius callizona* is destroying Florida's native bromeliads. In: Second International Symposium on Biological Control of Arthropods; 2005 Sep 12–16, vol. 1. USDA Forest Service Publication FHTET-2005-08, Davos, Switzerland, pp. 91–101.

Frank, J.H., Cooper, T.M., Larson, B.C., 2006. *Metamasius callizona* (Coleoptera: Dryophthoridae): longevity and fecundity in the laboratory. Fla. Entomol. 89, 208–211.

Frank, J.H., Curtis, G.A., 1981. Bionomics of the bromeliad-inhabiting mosquito *Wyeomyia vanduzeei* and its nursery plant *Tillandsia utriculata*. Fla. Entomol. 64, 491–506.

Frank, J.H., Curtis, G.A., O'Meara, G.F., 1984. On the bionomics of bromeliad-inhabiting mosquitoes. J. Med. Entomol. 21, 149–158.

Frank, J.H., Fish, D., 2008. Potential biodiversity loss in Florida bromeliad phytotelmata due to *Metamasius callizona* (Coleoptera: Dryophthoridae), an invasive species. Fla. Entomol. 91, 1–8.

Frank, J.H., Lounibos, L.P., 1987. Phytotelmata: swamps or islands? Fla. Entomol. 70, 14–20.

Frank, J.H., McCoy, E.D., 1990. Introduction to attack and defense: behavioral ecology of predators and prey; endemic and epidemics of shibboleths and other things causing chaos. Fla. Entomol. 73, 1–9.

Frank, J.H., Sreenivasan, S., Benshoff, P.J., Deyrup, M.A., Edwards, G.B., Halbert, S.E., Hamon, A.B., Lowman, M.D., Mockford, E.L., Scheffrahn, R.H., Steck, G.J., Thomas, M.C., Walker, T.J., Welbourn, W.C., 2004. Invertebrate animals extracted from native *Tillandsia* (Bromeliales: Bromeliaceae) in Sarasota County, Florida. Fla. Entomol. 87, 176–185.

Frank, J.H., Thomas, M.C., 1994. *Metamasius callizona* (Chevrolat) (Coleoptera: Curculionidae), an immigrant pest, destroys bromeliads in Florida. Can. Entomol. 126, 673–682.

Gandhi, J.K., Herms, D.A., 2010. Direct and indirect effects of alien insect herbivores on ecological processes and interactions in forests of eastern North America. Biol. Invasions 12, 389–405.

Greeney, H.F., 2001. The insects of plant-held waters; a review and bibliography. J. Trop. Ecol. 17, 241–260.

Isley, P.T., 1987. *Tillandsia* the World's Most Unusual Air Plants. Botanical Press, Gardena, California, USA.

Jones, C.G., Lawton, J.H., Shachak, M., 1994. Organisms as ecosystem engineers. Oikos 69, 373–386.

Jones, C.G., Lawton, J.H., Shachak, M., 1997. Positive and negative effects of organisms as physical ecosystem engineers. Ecology 78, 1946–1957.

Kaplan, E.L., Meier, P., 1958. Nonparametric estimation from incomplete observations. J. Am. Stat. Assoc. 53, 457–481.

Kenis, M., Auger-Rozenberg, M., Roques, A., Timms, L., Péré, C., Cock, M.J.W., Settele, J., Augustin, S., Lopez-Vaamonde, C., 2009. Ecological effects of invasive alien insects. Biol. Invasions 11, 21–45.

Kessler, M., Siorak, Y., 2007. Desiccation and rehydration experiments on leaves of 43 pteridophyte species. Am. Fern J. 97, 175–185.

Luther, H.E., Benzing, D.H., 2009. Native Bromeliads of Florida. Pineapple Press, Inc., Sarasota, Florida, USA.

Marie Selby Botanical Gardens, 2012. List of Vascular Plant Species Growing as Epiphytes in Florida. Available online at: <http://www.selby.org/learningandgrowing/articles/list-vascular-plant-species-growing-epiphytes-florida> (Last accessed: January 2013).

Mestre, L.A.M., Aranha, J.M.R., de Lourdes, P., Esper, M., 2001. Macroinvertebrate fauna associated to the bromeliad *Vriesia inflata* of the Atlantic forest (Paraná State, Southern Brazil). Braz. Arch. Biol. Techn. 44, 89–94.

Myers, R.L., Ewel, J.J., 1990. Ecosystems of Florida. University of Central Florida Press, Orlando, Florida, USA.

Nadkarni, N.M., 1984. Epiphyte biomass and nutrient capital of a Neotropical Elfin Forest. Biotropica 16, 249–256.

Nadkarni, N.M., 1994. Diversity of species and interactions in the upper tree canopy of forest ecosystems. Am. Zool. 34, 70–78.

Nadkarni, N.M., Matelson, T.J., 1989. Bird use of epiphyte resources in Neotropical trees. Condor 91, 891–907.

Nadkarni, N.M., Solano, R., 2002. Potential effects of climate change on canopy communities in a tropical cloud forest: an experimental approach. Oecologia 131, 580–586.

Naiman, R.J., 1988. Animal influences on ecosystem dynamics. BioScience 38, 750–752.

Paoletti, M.G., Taylor, R.A.J., Stinner, B.R., Stinner, D.H., Benzing, D.H., 1991. Diversity of soil fauna in the canopy and forest floor of a Venezuelan cloud forest. J. Trop. Ecol. 7, 373–383.
Poland, T.M., McCullough, D.G., 2006. Emerald ash borer: invasion of the urban forest and the threat to North America's ash resource. J. For. 104, 118–124.
Rabenold, K.N., Fauth, P.T., Goodner, B.W., Sadowski, J.A., Parker, P.G., 1998. Response of avian communities to disturbance by an exotic insect in spruce-fir forests of the southern Appalachians. Conserv. Biol. 12, 177–189.
Richardson, B.A., 1999. The bromeliad microcosm and the assessment of faunal diversity in a Neotropical forest. Biotropica 31, 321–336.
Sidoti, B.J., Frank, J.H., 2002. The effect of host plant (*Tillandsia utriculata*: Bromeliaceae) on development of *Metamasius callizona* (Dryophthoridae). Selbyana 23, 220–223.
Stuntz, S., Ziegler, C., Simon, U., Zotz, G., 2002. Diversity and structure of the arthropod fauna within three canopy epiphyte species in central Panama. J. Trop. Ecol. 18, 161–176.
Tingley, M.W., Orwig, D.A., Field, R., Motzkin, G., 2002. Avian response to removal of a forest dominant: consequences of hemlock woolly adelgid infestations. J. Biogeogr. 29, 1505–1516.
Whitmire, S.L., Tobin, P.C., 2006. Persistence of invading gypsy moth populations in the United States. Oecologica 147, 230–237.