Habitats of *Dionaea muscipula* (Venus' Fly Trap), Droseraceae, Associated with Carolina Bays

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Abstract - *Dionaea muscipula* (Venus' fly trap) is endemic to a restricted area of the Carolina's Coastal Plain, including southeastern North Carolina and northeastern South Carolina. Our understanding of Venus' fly trap habitats is based largely on a single published study focused on plants associated with pocosins in North Carolina. Little is known about Venus' fly trap habitats or microhabitats in other parts of the endemic range. This paper presents data on Venus' fly traps at Lewis Ocean Bay Heritage Preserve, SC, an area where the species occurs at the ecotone between Carolina bays and adjacent plant communities. Complex microtopography including hummocks, hollows, and *Sphagnum* carpets, was common at this ecotone. Venus' fly trap seedlings were overrepresented in hollows; adult plants were overrepresented on *Sphagnum*. No vascular plant species were consistently associated with Venus' fly traps growing at the ecotone. However, areas downslope, relatively closer to bays, and areas upslope, relatively farther from bays, were associated with indicator species, presumably reflecting an underlying moisture gradient. Areas with Venus' fly traps were characterized by relatively high plant diversity, high *Sphagnum* cover, low total vascular plant cover, and soil disturbance associated with old vehicle tracks. Small, persistent openings in the shrub layer and soil disturbances that facilitate *Sphagnum* colonization may be important for maintaining populations of Venus' fly traps at the ecotone between Carolina bays and adjacent plant communities.

Introduction

Of the numerous carnivorous plants endemic to the Southeastern Coastal Plain, the *Dionaea muscipula* Ellis (Venus' fly trap), Droseraceae, is perhaps the species with greatest worldwide recognition. With leaves modified into snap traps, it is highly coveted as an ornamental and educational specimen and is a focal species for conservation efforts. Although the mechanism of the snap trap has long fascinated scientists (Stuhlman 1948), relatively little is known about the natural history of the Venus' fly trap when growing in the field. Indeed, the current understanding of Venus' fly trap ecology comes largely from observations of horticulturists (Schnell 2002) or from the classic paper published by Roberts and Oosting (1958).

Roberts and Oosting (1958) based their study on plants growing near the Duke University Marine Laboratory in Carteret County, NC. Here, the species occurred in association with frequently-burned pocosins (i.e., wet, evergreen shrub bogs). Herbarium specimens examined by Roberts and Oosting (1958) showed a historical Venus' fly trap endemic range with

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Beaufort County, NC, as the northern limit and the Santee River in South Carolina as the southern limit. This corresponds roughly to the Cape Fear Arch geologic area. The species is presently found in large numbers only in the Outer Coastal Plain of North Carolina and is nearly extirpated from more inland areas (Weakley 2004).

Roberts and Oosting (1958) presented a considerable amount of mostly qualitative data that can be summarized as follows: the Venus' fly trap grows at the ecotone of pocosin and pine savanna; no other plant species consistently occur in association with it; it grows on the St. Johns' soil series (sandy, acidic, low fertility, wet, with a hardpan); it is tolerant of inundation, while drought causes plants to go dormant; light availability is a strong determinant of leaf morphology and flower production; seed germination occurs immediately after seed release; and finally, it is fire resistant, and burning increases the vigor of surviving plants.

While it is clear that the Venus' fly trap evolved under a high-frequency fire regimen (Roberts and Oosting 1958), little is known about how fire affects various life history stages. Lack of frequent fire is considered the major threat to long-term viability of Venus' fly trap populations as a dense canopy of shrubs quickly forms, subjecting Venus' fly traps to both light and insect limitation (Schulze et al. 2001). However, the patchy distribution of the species, its relative rarity even under a prescribed fire regimen, and its G3 rank for endangerment throughout the native range suggest specialized habitat requirements.

Previous research in frequently burned ecosystems of the Southeast indicates that open soil microhabitats are critical for some relatively rare plant species (Brewer 1998, 1999a; Gray et al. 2003; Hawkes and Menges 1995, 1996; Menges and Kimmich 1996; Petru and Menges 2003; Quintana-Ascencio et al. 1998). These microhabitats occur as a result of heterogeneity in fire intensity or as a result of other types of historical disturbances (Menges and Hawkes 1998). Microhabitat factors may emerge as the dominant habitat factors for subordinate vegetation when the tree or shrub canopy is removed by fire or logging (Gilliam et al. 1995, Ramovs and Roberts 2003) and may also be critical for maintaining metapopulations in landscapes where rare species are limited to widely spaced patches (Quintana-Ascencio and Menges 1996).

This study focused on microhabitats and plant communities associated with the Venus' fly trap at Lewis Ocean Bay Heritage Preserve (LOBHP) in Horry County, SC. Here, numerous small populations of the species occur primarily at the ecotone between Carolina bays and adjacent plant communities. Carolina bays are considered unique geological formations with a characteristic shape and distinct boundaries. Pocosins, on the other hand, are considered unique plant communities that may or may not possess distinct boundaries (Sharitz and Gibbons 1982). Regardless of whether Venus' fly traps are associated with Carolina bays or pocosins, the species is threatened because habitats are being destroyed or modified at a rapid rate, a trend not predicted by Roberts and Oosting (1958) when they stated that "in many undisturbed areas, particularly in Brunswick, New Hanover, Bladen, Onslow, and Carteret Counties in North Carolina and in Horry County in South Carolina, great numbers of plants are present over wide stretches of land which are not likely to be used in development." Because of increasing rarity of Venus' fly traps, there is now much interest in enhancing populations in protected areas (Luken 2003). The goals of this study were twofold: to obtain basic information on Venus' fly trap habitats that can be used to guide population enhancement efforts, and to compare and contrast results with Roberts and Oosting (1958) to determine if pocosin habitats of Venus' fly trap are similar to Carolina bay habitats.

Methods

Study area

The study area was Lewis Ocean Bay Heritage Preserve (LOBHP) in Horry County, SC, a 3640-ha tract of land that includes 22 Carolina bays as well as extensive pine stands. Much of the preserve is occupied by pine plantations that were abandoned when the site was placed under protection beginning in 1989. Prior to protection in 1989, the area also served as a site for military training during World War II. Currently, the preserved is owned and managed by the State of South Carolina. Prescribed burning is attempted every 2–3 yrs.

Carolina bays at LOBHP support dense, impenetrable thickets of evergreen shrubs and a tree layer comprised of *Pinus serotina* Michaux (pond pine), *Persea palustris* (Rafinesque) Sargent (swamp red bay), and *Gordonia lasianthus* (L.) Ellis (loblolly bay). This community type is most similar to the loblolly-bay forest community (Identifier CEGL007044) as described by Southeast Ecology Working Group of Natureserve (SEWGNS) (n.d.). Abandoned *Pinus taeda* L. (loblolly pine) and *Pinus elliottii* Engelm. (slash pine) plantations and restored *Pinus palustris* Miller (longleaf pine) flatwoods surround the Carolina bays as do relatively dry sand rims that support stunted stands of *Quercus laevis* Walter (turkey oak). The most common types of communities surrounding Carolina bays at LOBHP are similar to the wet longleaf-pond pine flatwoods (Identifier CEGL004791) or mesic pine flatwoods (Identifier CEGL003648) as described by SEWGNS (n.d.). The ecotone between Carolina bays and other relatively dry plant communities at LOBHP is an important area for conservation of many rare carnivorous plants and orchids such as *Pogonia ophioglossoides* (L.) Ker-Gawl (rose pogonia), *Sarracenia flava* L. (yellow trumpet pitcher-plant), and *Sarracenia purpurea* L. (frog's breeches).

Microhabitats

In June 2003, twenty-four separate populations of Venus' fly traps were located at the ecotone between a single large Carolina bay and a pine flatwood. Populations were discovered as a result of a survey done during peak flowering. This area was last burned during early spring 2002. Each population was delimited by centering a 0.25-m^2 square frame over the plants and then permanently marking the corners with steel stakes. Four microhabitats were identified: hollows were defined as soil depressions not occupied by *Sphagnum* mosses; hummocks were small soil mounds or slightly elevated areas around shrub bases not occupied by *Sphagnum* mosses; and *Sphagnum* carpets of two types, one dominated by *Sphagnum tenerum* Sull. & Lesq. and the other dominated by *Sphagnum molle* Sull. Stems of *Sphagnum tenerum* formed relatively dense carpets, while *Sphagnum molle* stems formed relatively loose carpets. Microhabitats in each 0.25-m^2 area were mapped and the percent cover of each microhabitat was estimated. Adult Venus' fly trap plants (> 1 yr old) and seedlings (established in 2003) in each microhabitat were mapped and counted. Venus' fly trap densities, means ± SE, in the 24 plots were as follows: seedlings, 4 ± 1 plants/plot; adults, 12 ± 2 plants/plot. A distribution index (I) as described by Huenneke and Sharitz (1986) was calculated for each microhabitat across all 24 populations. This index expressed the presence of Venus' fly traps in a microhabitat, weighted by the abundance of that microhabitat. Values of I > 1.0 indicate overrepresentation of Venus' fly traps in a microhabitat while values of I < 1.0 indicate underrepresentation of Venus' fly traps in a microhabitat.

Plant community characteristics

In late summer 2003, 26 additional populations of Venus' fly traps were located at the ecotones associated with six Carolina bays. At each population, a 0.5-m^2 rectangular frame was centered on the Venus' fly trap plants. Cover values of ground layer species (< 1 m high and excluding *Sphagnum*) were estimated. *Sphagnum* ground cover was estimated separately from vascular species. Two additional samples of vegetation were taken. One sample was taken 5 m upslope of the Venus' fly trap population (i.e., towards the savanna) and another sample was taken 5 m downslope of the Venus' fly trap population (i.e., towards the bay). Relative cover values of individual species were calculated for each plot. Community composition at the three topographic positions was contrasted using the relative coverage values and detrended correspondence analysis (DCA). Default parameters suggested by McCune and Mefford (1999) were used. Association of Venus' fly traps with other plant species was tested with indicator species analysis. Differences in richness, diversity (H'), absolute *Sphagnum* cover, and total relative cover of vascular plants among the three topographic positions were examined with one-way analysis of variance followed by a Tukey's test. Nomenclature followed Radford et al. (1968), except for *Persea palustris* which followed Weakley (2004). Nomenclature for *Sphagnum* mosses followed Crum and Anderson (1981). Voucher specimens were deposited in the University of South Carolina Herbarium (USCH) and in the Northern Kentucky University Herbarium (KNK).

Results

Microhabitats

The coverage of different microhabitats was as follows: hollows, 38%; hummocks, 33%; *Sphagnum tenerum*, 18%; and *Sphagnum molle*, 11%. Seedlings and adult plants of the Venus' fly trap showed different patterns of microhabitat distribution. Seedlings were overrrepresented on hollows, but were underrepresented on the other three microhabitats (Fig. 1). In contrast,

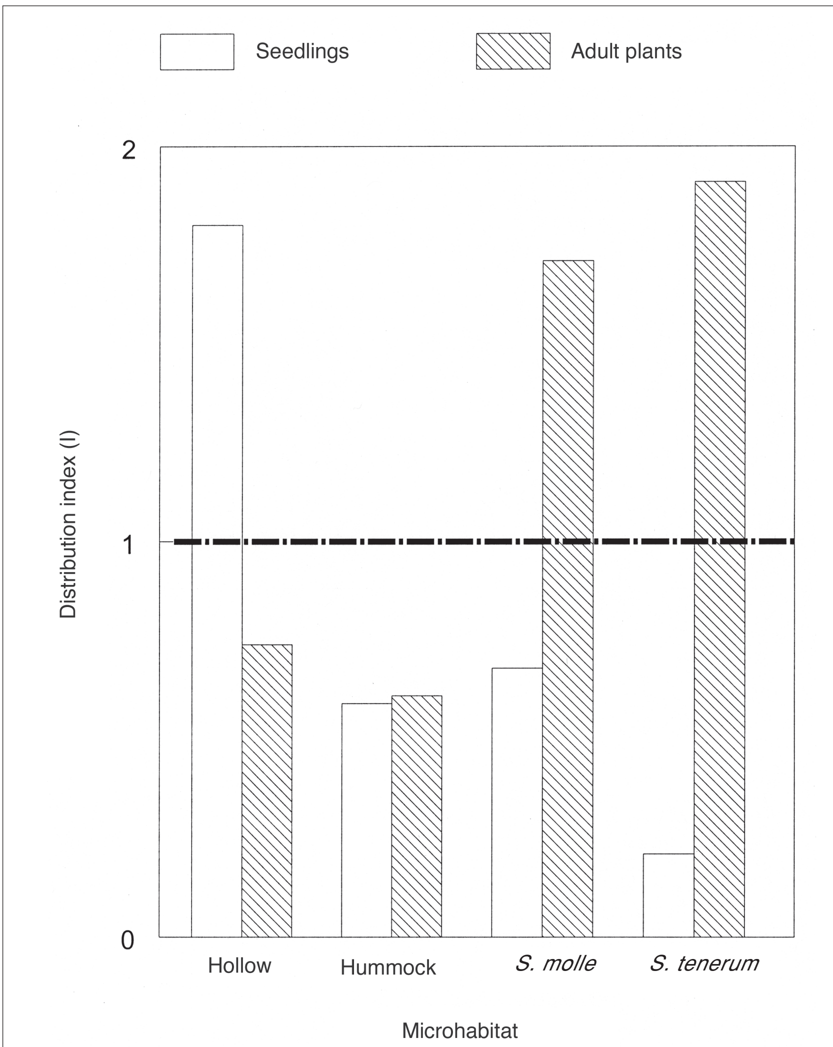

Figure 1. The distribution index (I) calculated for Venus' fly trap seedlings and adults growing in various microhabitats at Lewis Ocean Bay Heritage Preserve, SC. Values of I < 1 indicate underrepresentation in a microhabitat; values of I > 1 indicate overrepresentation in a microhabitat.

adult plants of Venus' fly trap were overrepresented on both species of *Sphagnum*, but were underrepresented on hummocks and hollows (Fig. 1).

Communities

The seventy-eight 0.25-m^2 plots distributed within the ecotone between Carolina bay and flatwoods or sand rims included 40 ground layer, vascular plant species. This ecotone supported a diverse assemblage of plant life-forms: shrubs (17 species), herbs (13 species), grasses and sedges (6 species), ferns (2 species) and vines (2 species). The three most frequently encountered species were *Vaccinium crassifolium* Andrews, *Lyonia lucida* (Lam.) K. Koch, and *Ilex coriacea* (Pursh) Chapman (Table 1).

The DCA ordination (total inertia = 4.23, 41% of variance in species' relative cover explained by axes 1 and 2) showed communities with Venus' fly traps as a poorly defined aggregation near the midpoints of axes 1 and 2 (Fig. 2). Vegetation samples taken downslope from the Venus' fly traps generally were at the lower end of axis 1; vegetation samples taken upslope from Venus' fly trap populations showed the most variation with roughly half of the samples clustered at the upper end of axis 1 (Fig. 2). There were weak negative correlations between total vascular plant cover and sample scores of both axes (Pearson r = -0.32, $P < 0.01$ for axis 1; r = -0.35, $P < 0.01$ for axis 2). No significant ($P > 0.05$) indicator species were found for positions on the ecotone that supported Venus' fly traps. However, three species were significant

Table 1. Vascular plant species at Lewis Ocean Bay Heritage Preserve, SC, observed in seventy-eight 0.25-m^2 plots placed on the ecotone of Carolina bays and adjacent communities. Only species with frequencies > 25% are shown[A]. Plots were placed in three topographic positions. Downslope = plots placed 5 m downslope toward the Carolina bay; *Dionaea* = plots placed on *Dionaea muscipula* populations; upslope = plots placed 5 m upslope away from the Carolina bay. Significant ($P < 0.05$) association with a topographic position on the ecotone (i.e., downslope, *Dionaeae,* upslope) was determined by Indicator Species Analysis. Ns = not significant.

Species	Life-form	Indicator	Frequency (%)
Vaccinium crassifolium Andrews	Evergreen trailing shrub	Upslope	65
Lyonia lucida (Lam.) K. Koch	Evergreen shrub	Ns	56
Ilex coriacea (Pursh) Chapman	Evergreen shrub	Ns	53
Gaylussacia frondosa (L.) T.&G.	Deciduous shrub	Upslope	51
Pteridium aquilinum (L.) Kuhn	Fern	Ns	46
Osmunda cinnamomea L.	Fern	Downslope	44
Rhynchospora glomerata (L.) Vahl	Tufted perennial sedge	Ns	44
Sorbus arbutifolia (L.) Heynhold[B]	Deciduous shrub	Ns	42
Clethra alnifolia L.	Deciduous shrub	Ns	37
Ilex glabra (L.) Gray	Evergreen shrub	Downslope	35
Xyris ambigua Beyrich	Perennial herb	Ns	33
Gaylussacia dumosa (Andrz.) T.&G.	Deciduous shrub	Ns	29
Aristida stricta Michaux	Tufted perennial grass	Upslope	27
Zenobia pulverulenta (Bartram) Pollard.	Deciduous shrub	Ns	26

[A]*Persea palustris* (Rafinesque) Sargent, an evergreen shrub with frequency of 17% was the only other significant indicator species. It was associated with positions downslope from *Dionaea muscipula*.

[B]var. *arbutifolia*

($P < 0.05$) indicators of each of the other two topographic positions (Table 1). Relative positions of indicator species on the community ordination suggest that axis 1 reflects an underlying moisture gradient (*Aristida stricta* Michaux and *Vaccinium crassifolium* at the upper end of axis 1; *Persea palustris* and *Osmunda cinnamomea* L. at the lower end of axis 1).

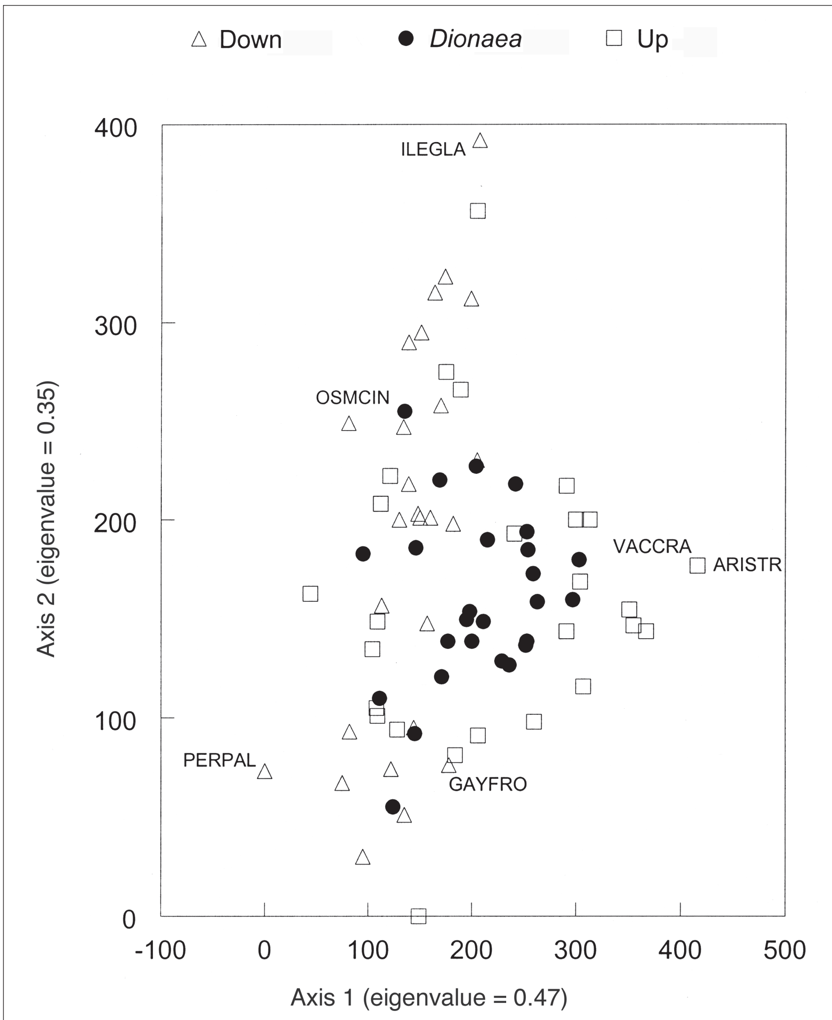

Figure 2. Detrended correspondence analysis (DCA) of plots and species sampled at the ecotone of Carolina bays and adjacent plant communities at Lewis Ocean Bay Heritage Preserve, SC. Down = plots placed 5m downslope toward the Carolina Bay; *Dionaea* = plots placed on Venus' fly trap populations; Up = plots placed 5 m upslope away from the Carolina bay. Only significant ($P < 0.05$) indicator species are shown. ARISTR = *Aristida stricta*; GAYLUS = *Gaylussacia frondosa;* ILEGLA = *Ilex glabra*; OSMCIN = *Osmunda cinnamomea*; PERPAL = *Persea palustris*; VACCRA = *Vaccinium crassifolim.*

Plant communities associated with Venus' fly traps had significantly ($P < 0.05$) higher richness, diversity (H'), and *Sphagnum* cover than communities located upslope or downslope from Venus' fly traps (Table 2). Total relative cover of vascular plants was lowest in communities associated with Venus' fly traps and highest at positions upslope from Venus' fly traps (Table 2).

Discussion

Roberts and Oosting (1958) focused their attention on understanding the distribution of Venus' fly traps along the moisture gradient associated with the pocosin to savanna ecotone. They presented a figure showing an "idealized" transect, roughly 10-m long, extending from the pocosin (wet) to the adjacent savanna (dry). This scale of observation assumed a gradual moisture gradient and corresponded to the scale used to assess variation of plant communities at the ecotone of Carolina bays and other plant communities at LOBHP. However, Roberts and Oosting (1958) repeatedly noted the occurrence of Venus' fly traps on flat areas lacking microtopography, with the conclusion that "hollows which have filled with *Sphagnum* … are not typical habitats." At this point, it cannot be determined if microtopographic variation at the scale of 0.25-m^2 plots, as assessed at LOBHP, was simply not present at the North Carolina study sites or whether Roberts and Oosting (1958) did not consider such variation as relevant to understanding Venus' fly trap habitats. They did, however, report that Venus' fly trap transplants grew more vigorously in hollows than on ridges.

Roberts and Oosting (1958) found that Venus' fly trap seed germination occurred soon after seed release, although they did not study seed germination in the field. This presumed pattern was confirmed at LOBHP. The positive association of Venus' fly trap seedlings with hollows at LOBHP likely reflects two characteristics of this microhabitat. Hollows remain consistently wet and this is important for seedling survival (Roberts and Oosting 1958). Hollows are largely devoid of litter and competing plants, factors considered important for successful seedling establishment of another small, rosette-forming carnivorous species, *Drosera capillaris* Poiret (Brewer 1999b).

Table 2. Richness of vascular plants (species/sample), diversity (H') of vascular plant communities, absolute *Sphagnum* cover (%), and total vascular plant relative cover in three topographic positions relative to *Dionaea muscipula* populations. Topographic positions are explained in Table (1). Means (± SE, n = 26) are presented. Means with different letters are significantly ($P < 0.05$) different.

	Relative topographic position		
Parameter	Downslope	*Dionaea*	Upslope
Richness	7.2 ± 0.4 a	9.9 ± 0.5 b	7.6 ± 0.4 a
Diversity	1.65 ± 0.06 a	2.00 ± 0.05 b	1.63 ± 0.06 a
Sphagnum cover	3 ± 2 a	32 ± 6 b	7 ± 3 a
Total relative cover	0.33 ± 0.01 ab	0.30 ± 0.01 a	0.36 ± 0.01 b

Although seedlings of Venus' fly traps were overrepresented in hollows lacking *Sphagnum*, adult Venus' fly traps were positively associated with *Sphagnum*; 75% of all Venus' fly trap-containing plots examined in this study had live *Sphagnum*. The close association between adult Venus' fly traps and *Sphagnum* may be due to similar moisture requirements of these species. It is also possible that Venus' fly trap seedling survival is higher when seedlings grow on *Sphagnum* carpets, that *Sphagnum* eventually colonizes hollows where Venus' fly trap seedlings have established, or that *Sphagnum* provides a suitable growth environment for Venus' fly traps. For example, Venus' fly traps transplanted to the New Jersey Pine Barrens showed long-term persistence when growing on *Sphagnum* (Smith 1972).

As a result of an ability to alter the moisture regimen and chemical characteristics of the substrate, *Sphagnum* mosses commonly *inhibit* both establishment and growth of vascular plants in some ecosystems (McVean 1963) and may even overgrow vascular plants when moisture conditions are appropriate (Santelmann 1991). Ecological interactions between *Sphagnum* mosses and vascular plants are largely unstudied in Carolina bays and could be quite different than such interactions in northern bogs. Instead of forming large, persistent hummocks as in northern bogs, *Sphagnum* mosses at LOBHP are subject to frequent diebacks due to desiccation. Peat accumulation is presumably also relatively low due to higher rates of decomposition.

Evergreen and deciduous shrubs dominated the vascular plant communities at the ecotone between Carolina bays and the drier upslope communities found at LOBHP. The distributions of some vascular plants (e.g., *Aristida stricta* and *Lyonia lucida* (Lam.) K. Koch) were identical to those described by Roberts and Oosting (1958) . Data collected within 0.25-m^2 plots at LOBHP confirmed that the Venus' fly trap was not consistently associated with any vascular plant species on the bay ecotone, although wetter habitats relatively closer to Carolina bays and drier habitats relatively farther from Carolina bays were associated with indicator species. Ordination results should be interpreted with caution as the ecotone considered in this study may not be a continuous moisture gradient as was assumed.

At LOBHP, communities with Venus' fly traps had relatively greater diversity of vascular plants, relatively greater coverage of *Sphagnum*, and relatively lower total cover of vascular plants. Association of the Venus' fly trap with "*Sphagnum* openings" was noted by Porcher and Rayner (2001), but it is not clear how all these openings at LOBHP were initially established or how the moisture regimen of the openings differs from other positions on the bay ecotone. Most of the openings at LOBHP can be explained by historical human disturbances: 76% of Venus' fly trap populations were associated with old vehicle tracks and shallow fire breaks. However, the remaining populations were in small, open depressions of unknown origin. Other plant communities subject to frequent fire often develop persistent gaps or openings as a result of variation in fire intensity, shrub allelopathy, or disturbances by animals (Menges and Hawkes 1998). Plant species that colonize these gaps do so via seeds, and the gaps tend to close quickly after fire (Hawkes and Menges 1996). Gap size and gap isolation affect seed arrival and seedling establishment and are thus important in determining probability of colonization and extinction (Quintana-Ascencio and Menges 1996).

Clearly, frequent fire is the dominant factor in maintaining populations of the Venus' fly trap (Gray et al. 2003). However, once the shrub layer is reduced by fire, small openings with high *Sphagnum* cover emerge as important habitats. Microtopographic variation within these *Sphagnum* openings provides opportunities for seedling establishment of Venus' fly traps, and the relatively high diversity of plants in Venus' fly trap habitats suggests that historical soil disturbances may also favor other plant species. Ramovs and Roberts (2003) concluded that microtopographic relief provided habitats for many species found in the understory of managed and natural forests. Efforts to cultivate new populations of Venus' fly trap (Luken 2003) are incorporating mechanical clearing, *Sphagnum* transplants, and soil disturbance to enhance Venus' fly trap seedling establishment and to ensure that restored habitats maintain the microtopography necessary for the various life history stages of Venus' fly traps.

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