

Woody Plant Invasion into the Freshwater Marl Prairie Habitat of the Cape Sable Seaside Sparrow

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Summary

In the fall of 2005, U.S. Fish and Wildlife Services (USFWS) contracted with Florida International University (FIU) to study the physical and biological drivers underlying the distribution of woody plant species in the marl prairie habitat of the Cape Sable Seaside Sparrow (CSSS). This report presents what we have learned about woody plant encroachment based on studies carried out during the period 2006-2008. The freshwater marl prairie habitat currently occupied by the Cape Sable seaside sparrow (CSSS; *Ammodramus maritimus mirabilis*) is a dynamic mosaic comprised of species-rich grassland communities and tree islands of various sizes, densities and compositions. Landscape heterogeneity and the scale of vegetative components across the marl prairie is primarily determined by hydrologic conditions, biological factors (e.g. dispersal and growth morphology), and disturbances such as fire. The woody component of the marl prairie landscape is subject to expansion through multiple positive feedback mechanisms, which may be initiated by recent land use change (e.g. drainage). Because sparrows are known to avoid areas where the woody component is too extensive, a better understanding of invasion dynamics is needed to ensure proper management.

Through an integrated ground-level and remote sensing approach, we investigated the effects of hydrology, seed source and (more indirectly) fire on the establishment, survival and recruitment of woody stems. Our ground-level analyses were conducted at two scales and levels of detail, which we term the *micro-scale* (i.e. single tree islands and their immediate surrounding environments) and the *meso-scale* (i.e. intermediately-sized prairie landscapes that include multiple tree islands). We also endeavored to relate our ground-level observations to remotely detected woody plant distributions assessed at the *macro-scale* (i.e. large landscapes that include a heterogeneous mosaic of high- and low-density patches of tree islands).

Species patterns of establishment, survival and recruitment within *micro*-scapes

We established six 1 ha tree island-centered *micro*-scape study areas, one within each of the major CSSS sub-populations (A-F). In each *micro*-scape, we identified, measured and mapped all adult trees, saplings and seedlings present outside the central tree island. Elevations and hydroperiods were quantified across each *micro*-scape and at each seedling. In 2007, the second year of the project, *micro*-scape plots were revisited and all tagged seedlings and saplings were re-measured to assess survival and growth.

We successfully generated logistic regression models predicting the establishment of four common woody species (i.e. *Annona glabra*, *Morella cerifera*, *Persea borbonia* and *Taxodium distichum*) in four of our six *micro*-scapes. In each of these models, the combined proximity and size of potential seed sources (i.e. source effect) was the most useful positive predictor of establishment. Increases in hydroperiod were also found to positively predict the establishment of *Morella cerifera*, *Persea borbonia* and *Taxodium distichum* in *micro*-scape D.

Woody plant establishment within *meso*-scapes

We established four 1 kilometer-long, E-W oriented transects across each 1 km² *meso*-scape, equally spaced at 200 m intervals. Individual woody plants within 10 m of each transect line were identified, mapped, and measured. Marsh vegetation types were also determined along each transect. Tree islands within each *meso*-scape were detected via remote sensing, and hydrologic conditions were inferred from marsh vegetation patterning.

We successfully generated logistic regression models predicting generalized (non-species-specific) woody plant establishment in each of our six *meso*-scapes. In each case, source effect positively influenced woody plant establishment, and in *meso*-scape D, increases in hydrology also enhanced establishment.

Tree island aggregation within *macro*-scapes

To analyzing the spatial patterning of tree islands within each 4 mile² *macro*-scape, we developed maps of kernel density and calculated Moran's I and O-ring statistics. All six *macro*-scapes can be described as mosaics of tree island patches woven into a mixed-species matrix of grasses, sedges, and herbs. Patch distribution varied in both density, and size across the six *macro*-scapes. Without exception, the Prairie vegetation category was the most abundant, while Bayhead Hardwood Forest was, in general, the dominant woody plant community within the six *macro*-scapes sampled. Mean tree island size significantly differed among *macro*-scapes. Moran's I analysis revealed a very strong clustering of tree islands within all *macro*-scapes. The O-ring function paralleled this result, revealing a significant spatial aggregation of Tree Islands at multiples scales.

Multi-scaled effects of fire

Fire histories for all three landscape scales (*macro*, *meso*, and *micro*) were constructed from a geodatabase populated with Everglades National Park 1980 to 2008 fire records. This spatial dataset allowed the identification and extraction of all fires that occurred within the boundaries of the study areas during the last 29 years. Fire frequencies were calculated for each landscape scale and directly related to woody plant density at the *meso*-scale.

Seventy-eight fires burned 36,951 ha of marl prairie habitat within our study area over the last 29 years. Fire occurrence was relatively frequent; approximately once every 9 years in all *micro*-scapes, except for A where fire has been extremely uncommon during the last three decades. Surprisingly, we found no significant relationship across *meso*-scapes between Total Stem Density and Fire Frequency.

Conclusion

Woody plant invasion into the marl prairies involves a chain of processes, which are subject to various constraints and/or interruptions. Evidence suggests that the most

successful early marsh invaders are hydrophilic species such as *A. glabra* and *T. distichum*, followed closely by *P. borbonia* and *M. cerifera*. In addition to producing their own seed shadows, wetland adults appear to act as magnets for new recruits, possibly by serving as perch sites for avian seed dispersers. The seed shadows and attraction generated by early invaders can produce fine-scaled aggregation, which sometimes result in larger-scale colonization of new habitat. Successful propagule dispersal, seedling colonization, survival, aggregation into tree islands and further aggregation into a landscape-scale woody mosaic requires a precise set of conditions at each stage in the process. As tree islands form and increase in size, they develop a more humid microclimate, and become more resistant to fire. Tree islands in the marl prairie landscape are numerous, mostly but not exclusively small in size. They are aggregated at scales of hundreds to thousands of meters, separated by large expanses in which tree islands are sparse or absent. Their range and distribution of sizes, as well as their tendency to aggregate, suggest that groups of tree islands, like the species that inhabit them, may be thought of as populations, with birth, growth, and death rates that are sensitive to disturbance, available seed sources, and the nature of the physical environment.

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1. Introduction

The freshwater marl prairie habitat currently occupied by the Cape Sable seaside sparrow (CSSS; *Ammodramus maritimus mirabilis*) is a dynamic mosaic comprised of species-rich grassland communities and tree islands of various sizes, densities and compositions. The woody component of the marl prairie landscape, historically limited by natural disturbance, is subject to expansion through multiple positive feedback mechanisms. Since sparrows are known to avoid areas where the woody component is too extensive (Jenkins et al. 2003; Pimm et al. 2002), a better understanding of invasion dynamics is needed to ensure proper management. Jenkins et al. (2003) summarized the influence of woody plants in the prairie landscape on the basis of coarse scale (pixel size = 30 x 30 m) satellite imagery, but the structure of these woody plant populations was not examined in detail. Here we aim to integrate remote sensing efforts with field investigations of woody plant population processes in order to better understand invasion dynamics within sparrow habitats.

The CSSS is almost entirely restricted to short-hydroperiod marl prairies located along the edges of Shark River and Taylor Sloughs. The habitat of the CSSS is limited to six separate regions or populations (A-F), isolated by areas of unsuitable vegetation and hydrology (Figure 1). The CSSS require specific habitat conditions, regulated primarily by hydrology and to a lesser extent fire (Browder & Ogden 2000). Jenkins et al. (2003a,b) found that CSSS generally avoid regions within 40 m of pine and/or hardwood stems. Furthermore, they require marsh habitat with a drydown period that corresponds with their peak breeding season, i.e., from early March through May (La Puma et al. 2007). Since CSSS have a natural aversion to extensive woody vegetation and deep surface water, a delicate balance between wet and dry periods is required (Browder & Ogden 2000; Pimm et al. 2002). The CSSS' marl prairie habitat is also prone to fire, which creates heterogeneous burn patterns through multiple plant-soil-water feedbacks (DeAngelis & White 1994; Lockwood et al. 2003). Though fires render localized habitat patches initially unsuitable for sparrow populations, they may help maintain longer-term suitability by setting back expansion of k-selected woody species. Suitable sparrow habitat is rapidly diminishing due to current and historical management practices such as compartmentalization and fire suppression (Nott et al. 1998).

Rates of woody plant invasion depend on colonization and patch expansion over time (Peters et al. 2006). Tree island development in the marl prairie likely occurs via multiple positive feedback mechanisms, initiated by the establishment of a single woody stem, then followed by a slow process of nucleation. Woody stems frequently provide sufficient roughness to influence deposition of water- and air-borne materials and facilitate soil accretion. A positive feedback between plant productivity and peat accumulation has further been proposed as one of the major mechanisms involved in the nucleation process in wetlands (Reitkerk et al. 2004; Swanson & Grigal 1988). Peat mounds enable woody establishment and survival by reducing flooding stress and providing mineral nutrients for growth and proliferation (Brady 1990). Soil accumulation mechanisms are likely occurring within the freshwater Everglades (Hanan & Ross 2009, Wetzel et al. 2005). In addition to altering the local topography, established individuals serve as magnets for seed dispersing animals, resulting in the development of small mixed species assemblages. As they grow in size, differential transpiration rates and faunal input may contribute to the concentration of nutrients below the developing canopies (Ross et al. 2006,

McCarthy et al. 1993, Givnish et al. 2007), thus increasing the competitiveness of woody plants over grasses. Meanwhile, disturbance in the form of periodic fire serves to slow and set back the nucleation process (Lockwood et al. 2003).

Invasion success requires a suitable environment for initial establishment. In this study we focused not on the nucleation process that follows, but on the processes that control the critical establishment and survival of the initial invading individual, which depend upon existing woody plant patterning within the landscape, spatial and temporal variation in seed vectors, and on ambient environmental conditions (Bazzaz 1991; Schupp 1995). The size and distribution of the existing forested area within the marl prairie landscape affects large-scale dispersal patterning. Larger trees will typically produce more seeds for dispersal, and landscape woody patch density will affect the size and distribution of germinant populations. Seed dispersal tends to be extremely heterogeneous, with several, few or no seeds falling in a given location (McDonnell & Stiles 1983; Schupp 1993). The seedfall mosaic is shaped by various physiological and environmental conditions including parental fecundity (Herrera et al. 1998), diaspore morphology (Howe & Smallwood 1982), disperser conditions and/or behavior (Nathan & Muller-Landau 2000), and substrate conditions (Fort & Richards 1998; Vander Wall & Joyner 1998). Although seedfall patterning can vary widely between species (Ribbens et al. 1994), the highest seed densities are typically found in close proximity to parent trees (Campbell et al. 1990; Clark et al. 1999; Hughes & Fahey 1988). Seeds distributed outward from parents, i.e. seed shadows, serve as the template on which subsequent environmental processes further constrain germination, establishment and survival. Such constraints include light, nutrient and water availability, seed predation, herbivory, competition and disease (Nathan & Muller-Landau 2000).

Each of the abovementioned filters alters the ultimate distribution of new recruits (i.e. germinated and established individuals). We consider proximity to parent to be a primary factor controlling landscape patterning in Everglades marshes. While some constraining processes (e.g. competition and seed predation) may be more intense near parents (Janzen 1970), proximity to conspecific adults is often associated with increased habitat suitability. Holl (2002) illustrated the complex effects of proximity to parents, finding that both seed predation and survival of established individuals increased near woody patches. Hubbell (1980) pointed out that even after post-dispersal seed predation, the density of new recruits is still typically highest adjacent to parents and declines with increasing distance. We therefore expect that the recruitment of new woody individuals will be clustered in close proximity to conspecific adults and/or tree islands, because of the patchiness of such seed sources in the marl prairie landscape, and because these source trees are likely rooted in the most suitable regions for woody plant growth (e.g. reduced flooding, sufficient nutrient availability etc.). We also expect that the size of potential source trees will be an important driver of seedling population densities, because large individuals generally produce more seed. In addition to proximity to parents, hydrology and fire are significant environmental variables controlling landscape patterning in Everglades marshes (Lockwood et al. 2003; White 1994; Gunderson 1994). We predict that hydrology and fire will have strong and species-specific influences on recruitment demographics.

Through an integrated ground-level and remote sensing approach, we investigated the effects of hydrology, seed source and (more indirectly) fire on the establishment, survival and recruitment

of woody stems. Our ground-level analyses were conducted at two scales and levels of detail, which we term the *micro-scale* (i.e. single tree islands and their immediate surrounding environments) and the *meso-scale* (i.e. intermediately-sized prairie landscapes that include multiple tree islands). We also endeavored to relate our ground-level observations to remotely detected woody plant distributions assessed at the *macro-scale* (i.e. large landscapes that include a heterogeneous mosaic of high- and low-density patches of tree islands).

2. Methods

2.1. Study site

The study was conducted within the short-hydroperiod wetlands located along the edges of Shark River and Taylor Sloughs. Sampling took place between 2006 and 2008 in six CSSS subpopulations (A-F), located in the marl prairie landscape (Figure 1). Soils range from calcitic marls classified as fluvaquents (in the open marsh) to histosols (organic soils found within tree islands and/or other densely vegetated patches). In comparison to wetter Everglades marshes, the marl prairies have characteristically high graminoid diversity maintained by relatively short flooding durations (inundated for approximately 3-7 months per year). Some of the most common marl prairie species include muhly grass (*Muhlenbergia capillaris* ssp. *filipes*), switch grass (*Panicum virgatum*), southern beaksedge (*Rhynchospora microcarpa*), Tracy's beaksedge (*Rhynchospora tracyi*), little bluestem (*Schizachyrium rhizomatum*), foxtail grass (*Setaria parviflora*), and black-top sedge (*Schoenus nigricans*) interspersed with sawgrass (*Cladium mariscus* ssp. *jamaicense*) in wetter depressions. Tree islands typically form in conjunction with topographic rises, which reduce flooding stress that might otherwise inhibit woody growth. According to Browder & Ogden (2000), ideal CSSS habitat within the marl prairie landscape is flooded long enough to aid in control of woody plant expansion, but generally experiences a sufficiently short hydroperiod (annual flooding duration) that surface water is absent during the nesting season.

Hydroperiods in the Everglades are influenced by climatic drivers, as modified by the operations of the South Florida Water Management District's (SFWMD) network of water control structures. The primary controls of water redistribution to the study area are channeled through the S12 structures, located along the Tamiami Trail, north of Shark Slough, and S332 located on the canal L31W (Figure 1). The South Florida wet season typically extends from May through the beginning of October, while the dry season occurs from the end of October through April. Mean annual precipitation ranges from 120 cm to 160 cm, and mean daily temperatures range from 17°C to 25°C (Obeysekera et al. 1999). A record-setting drought between 2006 and 2008 impacted hydroperiods across the southern Everglades (Meeker 2008), including CSSS habitats.

Extensive conflagrations (i.e. consuming more than 93 km² of vegetation) occur approximately every 10-15 years in the larger Everglades ecosystem, typically in late spring when conditions are still relatively dry (Gunderson & Snyder 1994). Smaller fires that occur more frequently tend to spark during wet season thunderstorms typical of June and July. The natural fire return interval is complicated by fire management practices, which both suppress large natural fires and ignite controlled burns to reduce fuels, maintain early successional stages, and inhibit the proliferation of invasive species (La Puma et al. 2007; Lockwood et al. 2003). The role of fire in

the maintenance of species composition and structure within CSSS habitat is not fully understood.

2.2. Sampling Design

Our study was designed to analyze the woody plant invasion process broadly across Cape Sable seaside sparrow subpopulations and more intensively at specific invasion fronts within each subpopulation. Six study areas were established, one within each CSSS subpopulation (A-F; Figure 1), and sampling followed a hierarchical design. One *macro*-scape (i.e. 2 x 2 mile cell; SFWMD cell grid) was selected at random within each subpopulation, then divided into nine 1 x 1 km plots. From these, one 1 km² *meso*-scape was randomly selected in each subpopulation (Figure 2). To examine the demography of individual woody species in the vicinity of tree islands, one 100 x 100 m (1 ha) *micro*-scape was centered on randomly selected tree island within each *meso*-scape (Figure 3).

2.2.1. *Micro*-scape

In each *micro*-scape, all adult (height >2 m) trees, saplings (height 0.5-2 m) and seedlings (height <0.5 m) present outside the central tree island were identified by species, mapped to nearest 0.5 m, tagged, and measured for height. Trees within the central tree islands were mapped and measured in similar fashion, but saplings and seedlings were not. In most plots, the census of seedlings and saplings outside the tree island was exhaustive, but in plots D and F, such stems were enumerated in regular subsets of the one hundred 10 x 10 m subplots within each plot. Specifically, in plot D all seedlings and saplings were counted, but only seedlings within a random set of 25 10 x 10 cells were tagged. In plot F, only the four corner 10 x 10 subplots were surveyed for seedlings, while saplings were surveyed exhaustively. Elevations and soil depths were determined at the corners of each 10 x 10 m subplot, by auto-level surveys from benchmarks of known elevation. Additional elevations were determined at random points within the central tree island, and at the base of each woody seedling and sapling in the marsh. Elevation surfaces were created via ordinary kriging in ESRI® ArcMap™ 9.3 (ESRI) using a spherical model, and elevations were extracted for 400 5 x 5 m quadrats within the 1 ha plot, based on the center of each quadrat's geometric axis. Radial distances between quadrat centroids and each adult tree were calculated and subsequently used to relate size and proximity of potential seed sources to the distribution of seedlings and saplings outside the tree island.

In 2007, the second year of the project, *micro*-scape plots were revisited and all tagged seedlings and saplings were re-measured to assess survival and growth. In *micro*-scapes D and F, the 2007 census of seedlings and saplings included individuals present in all 100 sub-plots. Plots were also searched for recruitment of new seedlings, which were identifiable as such in all plots.

Between January and March of 2008 140 m buffers were extended around the center points of each of the six 1 ha intensive study plots (Figure 3), in order to identify additional potential seed sources for tagged seedlings and saplings. All peripheral tree islands and individual woody plants located within these 140 m buffers were visited and species were identified, mapped and measured.

2.2.2. *Meso*-scape

Four 1 kilometer-long, E-W oriented transects were established across each *meso*-scape, equally spaced at 200 m intervals (Figure 2). Individual woody plants present within 10 m from the transect were identified by species, mapped, and measured (in height), and GPS coordinates were recorded every 100 m. For analytical purpose, transects were divided into ten 90 m long segments (with 20 m unsampled spaces between segments to prevent overlap), and each segment was divided into 2 rows of 10 x 10 m cells (one on either side of the transect; 18 total per segment). Presence/absence and counts of woody plants within each 10 x 10 m cell were determined. Radial distances between cell centroids and remotely digitized tree islands were calculated and subsequently used to relate size and proximity of potential seed sources to mapped individuals found along each transect. Also, marsh vegetation community types were determined every 20 m along each transect. *Meso*-scapes in subpopulations B and D, were sampled in 2006, and A, C, E, and F were sampled in 2007.

2.2.3. *Macro*-scape

All landscape features within the six *macro*-scapes were identified and mapped by soft-copy remote sensing techniques using a set of 2004 NAPP color infrared aerial photographs with a 1-meter spatial resolution (1 x 1 meter pixel). Because of the quality and spatial resolution of the imagery, a 5 m² minimum mapping unit (mmu) was determined to be the lowest resolution by which landscape features could be properly discerned and accurately classified. Features larger than the mmu were digitized on screen, using ESRI® ArcMap™ 9.3 (ESRI), and classified. Ten distinct cover types were described, including three associated with anthropogenic disturbance, and a fourth lacking emergent vegetation (Table 1). Landscape features that extended beyond the perimeter of the *macro*-scape were truncated at the *macro*-scape boundary.

2.3. Data Analysis

2.3.1. *Micro*-scape analysis

2.3.1.1. Establishment

To analyze seed source and hydrologic effects on the establishment of specific woody species within the *micro*-scapes, Species Source Factors (SSF) and hydroperiods were calculated for each transect cell. Species source factors were calculated as follows:

$$(1) \text{SSF}_{ij} = \Sigma(\text{adult tree height}_j / \text{distance}_{i-j})$$

where i represents each of the 400 5 x 5m quadrats, j represents the tree species present as seedlings and saplings in the *micro*-scape, and $i-j$ represents the distance from quadrat i to all potential source trees of species j within the 140 m buffer. Adult tree heights were normalized by calculating their percent of the maximum height for each species.

Table 1: Community types with description used to map the six short-hydroperiod freshwater marl prairie *macroscapes*.

Cover Type	Description
Wet Disturbed Forest	Closed canopy (>50%) wooded forest with extended hydroperiods. Maximum canopy height generally above 4 meters. This community is associated with anthropogenic disturbance. The dominant species include <i>Ilex cassine</i> , <i>Magnolia virginiana</i> , <i>Annona glabra</i> , <i>Persea borbonia</i> , <i>Chrysobalanus icaco</i> , and <i>Salix caroliniana</i> . Exotics species may be common as well.
Bayhead Swamp	Open canopy (< 50%) wooded shrubland with longer hydroperiods than bayheads. Canopy height generally below 4 meters. The dominant species include <i>Magnolia virginiana</i> , <i>Annona glabra</i> , <i>Chrysobalanus icaco</i> , and <i>Salix caroliniana</i> . This community is usually associated with sawgrass strands in the tail of many large tree islands.
Cypress	Open or closed canopy shrubland of <i>Taxodium distichum</i> . This class also represents scattered individuals or groups of individuals ranging from 2 to 8 meters in height found peppering the prairie.
Impervious Surface	Anthropogenically modified or created surfaces that do not allow, or minimally allow, the penetration and percolation of water into the soil.
Prairie	Mixed-species matrix of grasses, sedges, and herbs, which are tolerant to seasonal flooding. Marsh communities dominated by <i>Cladium mariscus</i> ssp. <i>jamaicense</i> , <i>Eleocharis cellulosa</i> , and <i>Rhynchospora</i> sp. are often important components of this grassland.
Pine Rockland	Open canopy monospecific stands of <i>Pinus elliottii</i> var <i>densa</i> that are underlain by a species-rich understory of shrubs and herbs that are of both tropical and temperate origins.
Scarified	An area that has been cleared of native vegetation, or topographically modified such that the land is not presently in a successional sequence leading to the establishment of the vegetative communities that were once cleared or disturbed.
Bayhead-Hammock Forest	Closed canopy wooded mixed-species shrubland or forest with short hydroperiods usually lasting a few months or less. These communities are sometimes associated with topographic highs resulting from rock outcrops or soil accretion. Species composition is diverse and includes many tropical hardwood species: <i>Eugenia axillaris</i> , <i>Bursera simaruba</i> , <i>Metopium toxiferum</i> , <i>Coccoloba diversifolia</i> , <i>Quercus virginiana</i> , <i>Sideroxylon salicifolium</i> , and as well as Bayhead species: <i>Ilex cassine</i> , <i>Magnolia virginiana</i> , <i>Annona glabra</i> , <i>Persea borbonia</i> , <i>Chrysobalanus icaco</i> , and <i>Salix caroliniana</i> . The exotic species <i>Schinus terebinthifolius</i> can co-occur as well. This community is described in detail by Armentano et al. (2002) & Hofstetter & Hilsenbeck (1980).
Typha	Dominant species is <i>Typha domingensis</i> with live vegetation cover > 25 % and canopy heights > 2 meters.
Water	Open deep-water areas within the prairie lacking vegetative cover.

Hydroperiod was calculated for each quadrat based on elevation estimates coupled with daily water stages at the *micro*-scale centroid over the six-year period 2000-2006, based on the EDEN (Everglades Depth Estimation Network) network (EDEN 2008).

Using presence/absence of woody plants within plot quadrats (outside tree islands), the effects of community source factor and hydroperiod were evaluated by stepwise logistic regression using the following model:

$$(2) P(m) = \frac{1}{1 + e^{-(\beta_0 + \beta_1 SSF_{ij} + \beta_k Hydroperiod_i)}}$$

where P(m) is the probability of species *j* establishment within quadrat *i*. Logistic regressions were carried out for all species present in at least 2 quadrats in 2007, that had at least one potential parent tree within the 140 m buffer.

In a stepwise logistic regression, variables are selected in the order in which their statically significant contribution to the model is maximized. If a variable does not contribute significance to the model, it is removed and a reduced model is (minus that term) is then run.

2.3.1.2. Survival and 1-year recruitment

Survival was evaluated for all seedlings present in the marsh. Stepwise logistic regression was used, according to the following model:

$$(3) P(m) = \frac{1}{1 + e^{-(\beta_0 + \beta_1 Height2006_i + \beta_k Hydroperiod_i)}}$$

where P(m) is the probability of species *i* survival. Logistic regressions were carried out for all species with a density of at least 18 individuals per ha in 2006.

Since 2007 recruits did not occur in large enough numbers to analyze using logistic regression, 1-year recruitment data are illustrated in tables and figures only.

2.3.2. *Meso*-scale analysis

Species-specific observations of seedlings and saplings were made along transects, but species-specific regressions were not possible in the *meso*-scale analysis because the species composition of all tree islands within the 1 km² was not known. Likewise, the precise hydrology associated with each stem could not be estimated, due to the lack of a detailed and comprehensive topography for the *meso*-scale. Therefore, in order to analyze seed source and hydrologic effects on the establishment of individual woody plants within the *meso*-scale, we calculated a non-specific Woody Plant Source Factor (WPSF) and a vegetation-based Prairie Wetness Index (PWI) for each transect cell. Woody Plant Source Factors were calculated as follows:

$$(4) WPSF_i = \Sigma(\text{tree island area}_j / \text{distance}_{i;j})$$

where $WPSF_i$ is the Woody Plant Source Factor for cell i and j is a tree island within 100 m of cell i .

PWI was calculated from vegetation community observations made at 20-meter intervals along each transect. For each herbaceous community observed, a relativized wetness index ranging from 1 to 10 was derived from vegetation-inferred hydroperiods outlined in Ross et al. (2006). Communities at the lower end of the scale where less flood tolerant than communities at the upper end of the scale; e.g. the PWI of *Muhlenbergia* Wet Prairie and *Eleocharis-Rhynchospora* Marsh were 1 and 10, respectively.

Using presence/absence of woody plants within transect cells (outside tree islands), the effects of WPSF and PWI were evaluated by stepwise logistic regression using the following model:

$$(5) P(m) = \frac{1}{1 + e^{-(\beta_0 + \beta_1 WPSF_{ij} + \beta_k PWI_i)}}$$

where $P(m)$ is the probability of species j establishment within cell i . Logistic regressions were carried out for all species present in at least 2 quadrats in 2007, that had at least one potential parent tree within the 140 m buffer.

2.3.3. Macro-scale analysis

For the purpose of analyzing the spatial patterning of tree islands within each *macro*-scape, we developed maps of kernel density (Silverman 1986), and calculated Moran's I (Muller-Warrant et al. 2008) and O-ring statistics (Wiegand & Moloney 2004). Bayhead-Hammock forest, and Bayhead Swamp units (Table 1) were pooled and reclassified as Tree Islands. If two or more of the pooled landscape features shared common boundaries, they were merged. A centroid was then calculated for each Tree Island. Because we were primarily interested in the spatial patterning of tree islands composed of broadleaved species, Wet Disturbed Forests in *macro*-scape C & D, Pine Rocklands *macro*-scape B, Cypress patches in D, and all tree islands truncated by the *macro*-scape border were excluded from the analysis.

Kernel estimation is a non-parametric geospatial technique that calculates the density of features within an area. Using the centroids of each island, the kernel estimation procedure provided Tree Island density maps or hotspots for all six *macro*-scapes. The kernel estimation analysis followed the quadratic kernel function described by Silverman (1986) and has a raster output.

Moran's I, on the other hand, measures the spatial autocorrelation between the location of a feature and an attribute. Based on these parameters, Moran's I evaluates whether the patterns observed in the landscape are clustered, dispersed, or randomly distributed based on a calculated index value and a Z-score. Index values near +1.0 indicate clustering while values near -1.0 indicate dispersion. The null hypothesis—that there is not spatial patterning of values—is

rejected based on the magnitude of the Z-score. For this analysis, the feature location is the Tree Island centroid and the attribute is the Kernel density estimate at that location.

The O-ring function is a second-order probability density function designed to detect aggregation or dispersion of landscape features, Tree Islands in this case, across a range of distances. It differs from Moran's I in that it determines the scale at which the features are aggregated. The O-ring function complements the more commonly used Ripley's K-function (Wiegand & Moloney 2004). However, the O-ring function uses annuli (or rings) instead of circles, and thus is able to isolate the level of aggregation/dispersion at specific distance classes. In contrast, the Ripley's K-function confounds the effects between larger and shorter distances (Wiegand & Moloney 2004) since it is a cumulative measure in which patterns at multiple scales may be averaged as the radius of the circle increases. Another advantage of the O-ring function is that it resolves some of the issues associated with edge correction. The O-ring function for each *macro*-scapes was calculated in Programita (Wiegand & Moloney 2004) using 100 replicates for each run; a ring width of three; and a grid cell size of 50 meters. This cell size reflects the maximum tree island density observed ($4.5 \text{ Tree Islands} \cdot \text{ha}^{-1}$) throughout the marl prairie ecotone.

The Kernel estimate and Moran's I were both calculated in ESRI® ArcMap™ 9.3 (ESRI). Intra-regional differences in mean Tree Island size and the Kernel density estimate were tested using one-way analysis of variance (ANOVA), followed by a multiple comparison test (Bonferroni test) in Statistica 7.0 (StatSoft, Inc).

2.3.5. Fire

Fire histories for all three landscape scales (*macro*, *meso*, and *micro*) were constructed from a geodatabase populated with Everglades National Park 1980 to 2008 fire records. This spatial dataset allowed for the identification and extraction of all fires that occurred within the boundaries of the study areas during the last 29 years. For each landscape scale, a fire occurrence interval was calculated based on the number of fires per unit time within a specified area. Fire occurrence is the reciprocal of mean fire interval—the arithmetic average of all fire intervals determined, in years, within a designated area and a specified period. In this case, the period was 29 years and the area was 1,036 ha, 100 ha, & 1 ha for the *macro*, *meso*, and *micro*-scapes respectively. The fire frequency for all *meso*-scapes was also calculated using these data. Fire frequency represents the fire return interval in a given area over a specific time.

Table 2. Density (stems/ha) of individuals within each species present in 2006/2007 in *micro*-scapes, adults (>2 m in height; within 140m buffer including central tree island) and recruits (<2 m in height within 1 ha plot). Recruit densities do not include those from inside tree island.

Species	A		B		C		D		E		F	
	adult	recruit	adult	recruit	adult	recruit	adult	recruit	adult	recruit	adult	recruit
<i>Annona glabra</i>	1.62	41					1			23		
<i>Baccharis halimifolia</i>			0.16	1							3	0.49
<i>Baccharis spp.</i>											4	0.65
<i>Bursera simaruba</i>											5	0.81
<i>Cephalanthus occidentalis</i>	0.16											
<i>Chiococca parvifolia</i>						1						
<i>Chrysobalanus icaco</i>	0.32	5							2			
<i>Coccoloba diversifolia</i>											1	0.16
<i>Conocarpus erectus</i>					0.16	1					1	0.16
<i>Eugenia axillaris</i>											7	1.14
<i>Ficus aurea</i>	0.16				0.16			6			11	1.79
<i>Ilex cassine</i>	0.16				0.32	3				3	5	0.81
<i>Magnolia virginiana</i>	0.16					1	1.95	59	0.32	3	10	1.62
<i>Melaleuca quinquenervia*</i>											1	0.16
<i>Morella cerifera</i>	3.90	2	0.81	11	2.11	4	4.06	34	1.62	6	115	18.68
<i>Myrsine floridana</i>			0.16	1	0.81						35	5.68
<i>Persea borbonia</i>	2.60	66	0.16	9	2.76	29	5.85	423	1.46	105	105	17.05
<i>Psychotria nervosa</i>											1	0.16
<i>Randia aculeata</i>						3						
<i>Sabal palmetto</i>	0.65				0.16				0.49	9	44	7.15
<i>Salix caroliniana</i>		2			0.32				0.16		44	7.15
<i>Schinus terebinthifolius*</i>											53	8.61
<i>Serenoa repens</i>			0.16			9						
<i>Sideroxylon reclinatum</i>						1					1	0.16
<i>Sideroxylon salicifolium</i>					0.16						7	1.14
<i>Solanum donianum</i>						1		1				
<i>Taxodium distichum</i>					0.32		21.44	391				
Subtotals	9.74	116	1.46	22	7.31	54	33.29	914	4.06	151	453	73.57

* Invasive exotic species.

Table 3. Density (stems/ha) of species within size classes observed along transects in *meso*-scapes in 2007.

Species	A			B			C			D			E			F			Total
	0.5-1	1-2	>2	0.5-1	1-2	>2	0.5-1	1-2	>2	0.5-1	1-2	>2	0.5-1	1-2	>2	0.5-1	1-2	>2	
<i>Acacia pinetorum</i>							1.1												1.1
<i>Annona glabra</i>	5.0	0.2		0.6	0.2		1.7						1.1	0.4		3.9	1.6		14.7
<i>Baccharis spp.</i>					0.0		2.8	1.8											4.6
<i>Casuarina equisetifolia</i> *								0.2								30.6	24.7	2.4	57.9
<i>Cephalanthus occidentalis</i>							6.7	5.8					0.2			3.9	1.6		18.1
<i>Conocarpus erectus</i>				1.1	0.7		3.3	6.2	2.4								0.4		14.2
<i>Eugenia axillaries</i>																1.7			1.7
<i>Ficus aurea</i>				2.8	1.3		0.6	0.4		2.2			3.9	0.4		1.1	2.0		14.8
<i>Ilex cassine</i>				0.6	0.4		16.7	1.8	0.2	0.6			2.8			1.1			24.1
<i>Magnolia virginiana</i>	1.1	0.9		16.7	18.4		5.0	6.4	0.2	0.6	0.2	1.6				1.1	0.9		53.1
<i>Melaleuca quinquenervia</i> *														0.2		5.0	3.3	0.2	8.8
<i>Metopium toxiferum</i>				2.2	2.7			0.2	0.9	0.6	0.9	0.4					0.7		8.6
<i>Morella cerifera</i>	4.4	3.3	1.6	7.8	4.4	2.7	8.3	4.4		5.0	0.7		1.1	3.6		2.8	3.1	1.1	54.3
<i>Myrsine floridana</i>		0.4		6.7	2.9		10.0	2.4			0.2		3.9			12.8	6.4		45.8
<i>Persea borbonia</i>	0.6	2.0		12.2	13.3	0.2	20.6	5.1	1.6	5.0	2.4	0.2	1.7	2.2		10.6	4.9		82.6
<i>Pinus elliotitii var. densa</i>				1.1	2.2														3.3
<i>Randia aculeate</i>				12.8	2.0								1.1						15.9
<i>Sabal palmetto</i>	0.6	0.4	0.7	3.9	2.4		7.2	14.0	1.3		1.3		3.3	1.8		15.0	10.9	2.9	65.8
<i>Salix caroliniana</i>							2.2	19.1	14.9							5.6	21.3	9.8	72.9
<i>Sideroxylon reclinatum</i>				10.6	0.4		5.0	8.2	3.1					0.2					27.6
<i>Sideroxylon salicifolium</i>				1.1	0.9			0.9											2.9
<i>Solanum donianum</i>				0.0			21.1	0.4								72.2	0.7		94.4
<i>Stillingia sylvatica</i>				0.6															0.6
<i>Swietenia mahogoni</i>					0.2														0.2
<i>Taxodium distichum</i>										56.1	77.3	82.9							216.3
Total	11.7	7.3	2.2	80.6	52.7	2.9	112.2	77.6	24.7	70.0	83.1	85.1	18.9	9.1		167.2	82.4	16.4	904.1

* Invasive exotic species.

Figure 4: Type and dispersal mechanisms for species found across our *micro* and *meso*-scapes. Dispersal for each species inferred from Wunderlin1998 and/or Tomlinson 2001.

Species	Type	Dispersal
<i>Acacia pinetorum</i>	Upland	Bird, mammal
<i>Annona glabra</i>	Wetland	Mammal, water
<i>Baccharis halimifolia</i>	Upland	Wind
<i>Baccharis spp.</i>	Upland	Wind
<i>Bursera simaruba</i>	Upland	Bird
<i>Casuarina equisetifolia</i> *	Exotic	Wind
<i>Cephalanthus occidentalis</i>	Wetland	Water
<i>Chiococca parvifolia</i>	Upland	Bird, mammal
<i>Chrysobalanus icaco</i>	Wetland	Mammal
<i>Coccoloba diversifolia</i>	Upland	Bird, mammal
<i>Conocarpus erectus</i>	Wetland	Water
<i>Eugenia axillaries</i>	Upland	Bird, mammal
<i>Ficus aurea</i>	Upland	Bird, mammal
<i>Ilex cassine</i>	Wetland	Bird, mammal
<i>Magnolia virginiana</i>	Wetland	Bird, mammal
<i>Melaleuca quinquenervia</i> *	Exotic	Wind, Water
<i>Metopium toxiferum</i>	Upland	Bird, mammal
<i>Morella cerifera</i>	Wetland	Bird, mammal, water
<i>Myrsine floridana</i>	Upland	Bird, mammal
<i>Persea borbonia</i>	Wetland	Bird, mammal
<i>Pinus elliotitii var. densa</i>	Upland	Wind
<i>Psychotria nervosa</i>	Upland	Bird, mammal
<i>Randia aculeate</i>	Upland	Bird, mammal
<i>Sabal palmetto</i>	Upland	Bird, mammal, water
<i>Salix caroliniana</i>	Wetland	Wind
<i>Schinus terebinthifolius</i> *	Exotic	Bird, mammal
<i>Serenoa repens</i>	Upland	Bird, mammal
<i>Sideroxylon reclinatum</i>	Upland	Bird, mammal
<i>Sideroxylon salicifolium</i>	Upland	Bird, mammal
<i>Solanum donianum</i>	Upland	Bird, mammal
<i>Taxodium distichum</i>	Wetland	Water

3. Results

Thirty-five woody plant species were identified within the CSSS habitat, and total and species-specific stem densities varied between *meso*- and *micro*-scapes (Tables 2 & 3). Woody species varied in type and primary dispersal mechanism (Table 4). We found source factors (SSF and WPSF) to positively influence woody plant establishment ubiquitously across our *micro* and *meso*-scapes. Also hydroperiod and PWI were found to positively influence woody plant establishment in *micro* and *meso*-scape D only. *Micro* and *meso*-scale clustering around source trees and in regions of optimal hydroperiod contributes to the multi-scaled aggregation found within our *macro*-scapes. Results at each level of organization are described in greater detail below.

3.1. *Micro*-scape observations

Micro-scapes varied in the composition and structure of the woody plant assemblages invading into the marsh, the abundance of seed sources in nearby tree islands, and the hydrologic conditions that impact the invasion process (Tables 2, 5 & 6). The effects of the Species Source Factor and Hydroperiod on woody plant establishment are displayed in Table 7. A source effect was identified for 7 of the 8 species x site combinations with enough individuals to justify the logistic regression analysis, but a significant (positive) effect of hydroperiod was observed in only 3 cases, all in *micro*-scape D (see descriptions below). Highest seedling densities generally occurred immediately adjacent to the central tree island (Figure 4). While most species densities declined exponentially with distance from the main seed source (i.e. central tree island), some species such as *A. glabra* and *S. caroliniana* were well distributed throughout the *micro*-scapes (Figure 5). Also, seedling densities were maximum in quadrats flooded 120 to 210 days per year (Figure 6), and trailed off at higher and lower hydroperiods.

Table 5: Tree Island density and total area, and Center tree island size in each of the six *micro*-scapes.

	<i>micro</i> -scape					
	A	B	C	D	E	F
Number of Neighboring Tree Islands (radius = 140 m)	3	2	3	2	1	12
Tree Island Area (ha)	0.034	0.032	0.012	0.028	0.009	0.250
Center Tree Island Size (m ²)	192.701	173.235	63.756	243.489	86.907	147.651

Table 6: Mean hydroperiod (\pm 1 SD; days) in tree island and marsh areas in six *micro*-scapes.

Plot	Average Center Tree Island Hydroperiod \pm S.D.	Average Marsh Hydroperiod \pm S.D.	Marsh Range	Difference (days/year)
A	173.25 \pm 11.20	219.73 \pm 8.82	84.57	46.48
B	47.39 \pm 3.59	78.78 \pm 13.75	79.29	31.99
C	126.71 \pm 5.25	171.43 \pm 23.99	111.43	44.72
D	90.18 \pm 9.97	164.35 \pm 23.72	112	74.17
E	168.25 \pm 18.58	179.22 \pm 12.41	72.43	10.97
F	166.29 \pm 15.50	180.04 \pm 16.41	97	13.75

Table7: Results - logistic regression for source and hydroperiod effects on dispersal within *micro*-scapes. All significant effects were positive. (-) indicates term was removed from model.

Plot	Species	Model P	Source Effect (B1)	S.E.	Wald	P	Exp(B1)	Hydroperiod (B2)	S.E.	Wald	P	Exp(B2)	Occupied Cells	Adults
A	<i>A. glabra</i>	0.00*	44.82	8.54	27.55	0.00*	2.90E+19	(-)	(-)	(-)	(-)	(-)	36	10
A	<i>P. borbonia</i>	0.00*	5.61	1.07	27.46	0.00*	273.46	(-)	(-)	(-)	(-)	(-)	41	16
B	<i>M. cerifera</i>	0.01*	4.72	1.54	9.45	0.00*	112.03	(-)	(-)	(-)	(-)	(-)	6	27
D	<i>M. cerifera</i>	0.01*	(-)	(-)	(-)	(-)	(-)	0.03	0.01	6.97	0.01*	1.03	24	25
D	<i>P. borbonia</i>	0.01*	0.70	0.22	9.69	0.00*	2.01	0.02	0.01	7.09	0.01*	1.02	73	36
D	<i>T. distichum</i>	0.00*	0.29	0.10	9.13	0.00*	1.33	0.03	0.01	27.17	0.00*	1.03	97	132
E	<i>M. cerifera</i>	0.03*	4.36	1.66	6.91	0.01*	78.07	(-)	(-)	(-)	(-)	(-)	5	10
E	<i>P. borbonia</i>	0.00*	5.57	1.85	9.08	0.00*	262.56	(-)	(-)	(-)	(-)	(-)	34	9

*Significant at $\alpha=0.05$

Table 8. Results – logistic regression for parent height and hydroperiod effects on survival within *micro*-scapes.

<i>Plot</i>	<i>Species</i>	<i>Model P</i>	<i>Height 2006 B</i>	<i>S.E.</i>	<i>Wald</i>	<i>P</i>	<i>Exp(B)</i>	<i>Hydroperiod B</i>	<i>S.E.</i>	<i>Wald</i>	<i>P</i>	<i>Exp(B)</i>	<i># Survived</i>	<i># Dead</i>
A	<i>Annona glabra</i>	0.33	0.08	0.06	1.64	0.20	1.08	-0.01	0.04	0.02	0.88	0.99	23	7
C	<i>Persea borbonia</i>	0.02*	0.47	0.35	1.75	0.19	1.59	0.04	0.07	0.26	0.61	1.04	14	2
D	<i>Persea borbonia</i>	0.12	-0.16	0.13	1.57	0.21	0.85	0.03	0.02	1.40	0.24	1.03	16	2
D	<i>Taxodium distichum</i>	0.31	-0.07	0.08	0.77	0.38	0.94	-0.02	0.03	0.30	0.58	0.98	25	1
E	<i>Annona glabra</i>	0.02*	0.48	0.45	1.17	0.28	1.62	0.05	0.18	0.06	0.80	1.05	17	2

*Significant at $\alpha=0.05$

Regressions on species 2006-07 survival did not produce significant results, in part due to low mortality across *micro*-scares; for species that occurred in at least fifteen 5 x 5 m quadrats per *micro*-scape, survival ranged from 96% (*T. distichum* in *micro*-scape D) to 77% (*A. glabra* in *micro*-scape A; Table 8).

The central tree island in *micro*-scape A contained 43 adult trees of 7 species, the most abundant of which were *A. glabra*, *M. cerifera* and *P. borbonia* (Table 2). *P. borbonia* represented more than half of seedlings and saplings within the *micro*-scape, however stems were tightly clumped and therefore only present within five quadrats. *P. borbonia* establishment was positively influenced by Species Source Factor, but not by Hydroperiod (reduced model; Table 7, Figure 7). *A. glabra* was second in seedling abundance (Table 2), though it was much more evenly distributed throughout the plot (present within 30 quadrats). *A. glabra* establishment was also positively influenced by the Species Source Factor, but again there was no effect of hydrology. In 2007, 23 *A. glabra* seedlings were found to have survived, while 7 had died (Table 8) (reduced model; Table 7, Figure 7). Although adult *M. cerifera* individuals were common, no seedlings or saplings were found within the plot. In 2007, 86 new seedlings were found, most *P. borbonia* and *A. glabra* (Table 9).

Table 9. 2007 recruitment within 1 ha micro-scares. D and F are excluded since their 2006 seedling censuses were not exhaustive.

Species	A	B	C	E	Total
<i>Annona glabra</i>	18			6	24
<i>Baccharis halimifolia</i>		1			1
<i>Chiococca parvifolia</i>			1		1
<i>Chrysobalanus icaco</i>	3			1	4
<i>Ficus aurea</i>					0
<i>Ilex cassine</i>			1	3	4
<i>Magnolia virginiana</i>			1		1
<i>Myrica cerifera</i>		2		2	4
<i>Myrsine floridana</i>		1			1
<i>Persea borbonia</i>	65		13	106	184
<i>Sabal palmetto</i>				6	6
<i>Salix caroliniana</i>			1		1
<i>Serenoa repens</i>			3		3
<i>Taxodium distichum</i>					0
Total	86	4	20	124	234

Micro-scape B burned intensively in 2005 (Plate 1), followed immediately by flooding associated with Hurricane Katrina. As a result, only 22 seedlings and saplings were present in the marsh in the spring of 2006. Stems occupying the central tree island were predominantly *M. cerifera* and *P. borbonia*. *M. cerifera* seedling establishment exhibited a positive influence of Species Source Factor (reduced model; Table 7, Figure 8), but no Hydroperiod effect. The spring 2006 survey revealed that most woody plants measured in the *micro*-scape were damaged or dead. In 2007, four new recruits were found (Table 9), and the tree island was well on its way to recovery from the 2005 fire (Plate 1).

Sixteen different species were identified in *micro*-scape C, though only *P. borbonia* seedlings were present at densities higher than 10 individuals per hectare (Table 2). In 2007, 14 *P. borbonia* seedlings were found to have survived, while 2 had died (Table 8). Also in 2007, 20 new seedlings were found, most of which were *P. borbonia* (Table 9).

The central tree island in *micro*-scape D was larger and had more trees than those in other plots, with 155 adults (including *T. distichum*, *M. cerifera*, *P. borbonia*, and *Magnolia virginiana*). Several individual adult stems, mostly *T. distichum*, were also present in the surrounding prairie. *T. distichum*, *P. borbonia*, *M. virginiana* and *M. cerifera* were the most abundant seedlings (Table 2). Species Source Factor positively influenced establishment of both *P. borbonia* and *T. distichum* (Table 7, Figure 9). Somewhat surprisingly, increases in hydroperiod had a positive influence on the establishment of *P. borbonia*, *T. distichum* and *M. cerifera* within the context of *micro*-scape D (reduced model for *M. cerifera*; all water dispersed species; Figure 10). In 2007, 16 *P. borbonia* seedlings were found to have survived since the previous year, while 2 had died (Table 8). Also, 25 of 26 *T. distichum* seedlings survived through the annual cycle.

The central tree island in *micro*-scape E contained mostly *M. cerifera* and *P. borbonia* stems. Species Source Factor (but not Hydroperiod) positively influenced seedling establishment in both species (reduced models; Table 7, Figure 11). In 2007, 17 *A. glabra* seedlings were found to have survived, while 2 had died (Table 8). Also, in one year after the first survey in 2006, 124 new seedlings were found, most of which were *P. borbonia* (Table 9).

Although *M. cerifera* was the most common adult tree in *micro*-scape F, most seedlings were *P. borbonia*. Survival and 2007 recruitment could not be analyzed within *micro*-scape F, since the seedling census undertaken in 2006 did not include all quadrats. *Micro*-scape F was nearest to developed areas at the edge of the park and, not surprisingly, was the only *micro*-scape where exotic woody species were found (*S. terebinthifolius* and *M. quinquenervia*; Table 2).

3.2. *Meso*-scape observations

Meso-scapes varied in hydrology and woody plant composition and density (Table 3; Figure 12). With only six replicate landscapes, we found no significant relationship between prairie woody stem density and the total forested area present in each *meso*-scape (Figure 13a). Mean PWI decreased in the order *meso*-scape A ($\bar{x} = 8.35$) > D ($\bar{x} = 6.12$) > E ($\bar{x} = 3.38$) > B ($\bar{x} = 2.91$) > F ($\bar{x} = 2.80$) > C ($\bar{x} = 2.49$; Figure 12a). Analysis of variance indicated a significant difference in the PWI among *meso*-scapes at $p = 0.01$ (ANOVA $F = 1446.47$; $p = 0.00$), with only *meso*-scapes B and F not differing from each other at $p = 0.01$ (Bonferroni test; $MS = 2.719$, $df = 4098.0$). Although we did not find a relationship between total woody stem density and PWI across *meso*-scapes (Figure 13b: $n=6$), we did find a relationship between woody stem density and PWI within *meso*-scape D. This relationship is discussed in further detail below.

3.2.1. Species-specific observations

The number, size and density of propagule sources varied across the *meso*-scapes; with the fewest tree islands occurring in Populations A and D, and the most occurring in Population C

and B (Table 10). Woody stem density increased as a function of WPSF (source effect), up to an optimal value and then tapered off due to the increasing rarity of source effects > 125 that were still outside tree islands (Figure 14). Woody plant seedlings and saplings were rarely found far from assumed source islands and individuals, except in the case of *T. distichum* and pond apple (*Annona glabra*), which are frequently water dispersed. *T. distichum* individuals, which are almost exclusively water dispersed, were abundant and well-dispersed within subpopulation D (a relatively wet site), but were essentially non-existent in other plots. On the other hand, individuals of *A. glabra*, which are likely dispersed by animals as well as water, were present in most other plots. *Persea borbonia*, *Morella cerifera* and *Sabal palmetto* were fairly abundant along all transects, but most abundant near tree islands and individual adults. Seedlings of *P. borbonia* were frequently observed below adult *T. distichum* and *S. palmetto* individuals. Invasive exotic species were rare or absent from most subpopulations, though Australian pine (*Casuarina glauca*), cajeput (*Melaleuca quinquenervia*) and Brazilian pepper (*Schinus terebinthifolius*) were fairly common in subpopulation F, which is the driest *meso*-scape and closest to development. Combined species results from the remote and ground analyses are described in further detail below.

Table 10: Tree Island density, area, and *minimum*, *maximum*, and *mean* tree island size in each of the six *meso*-scapes. Minimum tree island size reflects the minimum mapping unit (mmu) used, 5 m², to identify and map the landscape features within each of the *meso*- and *macro*-scapes.

	<i>meso</i> -scape					
	A	B	C	D	E	F
Tree Island Density (TI • km ⁻²)	15	64	65	10	27	36
Total Tree Island Area (ha)	0.56	0.59	4.96	0.92	0.63	1.13
Tree Island Size (m ²)						
<i>Minimum</i>	12.5	5.3	5.2	9.8	11.6	5.2
<i>Maximum</i>	854.5	1,044.5	26,754.4	3,817.2	1,597.4	3,278.8
<i>Mean</i>	373.1	91.6	763.8	918.9	233.9	313.1

3.2.2. Cross-species Establishment

In *meso*-scapes A, B, C, E and F, a reduced model including only the Woody Plant Source Factor produced the strongest result (Table 11, Figures 15-19). In each case, the probability of establishment increased significantly with WPSF, i.e., the area and proximity of tree islands. In *meso*-scape D, the probability of establishment increased with both WPSF and PWI, i.e., in wet locations near tree islands (Table 11, Figure 20).

Overall, evidence suggests that woody plant establishment is most probable close to adult individuals, particularly groups of adults (i.e. tree islands), where conditions are also most suitable for survival. Seedlings of abiotically dispersed species (e.g. baldcypress [*Taxodium distichum*]) tend to be less concentrated adjacent to tree islands, though when concentrated, they were typically found below conspecific trees. Bird and animal-dispersed seedlings on the other hand (e.g. red bay [*Persea borbonia*]), were found in high concentration below various adult tree species utilized by seed dispersers (e.g. *T. distichum* and cabbage palm [*Sabal palmetto*]).

Table 11: Results - stepwise logistic regression for source and hydrology effects on dispersal within *meso*-scapes. Plots A, B, C, E and F employ a reduced model, Plot D employs a complete model. (-) indicates term was removed from model.

Plot	Model P	Source Effect	S.E.	Wald	P	Exp(B)	Hydroperiod	S.E.	Wald	P	Exp(B)	Occupied Cells	Islands
A	0.00*	0.08	0.01	42.97	0.00*	1.09	(-)	(-)	(-)	(-)	(-)	15	19
B	0.00*	0.02	0.00	25.55	0.00*	1.02	(-)	(-)	(-)	(-)	(-)	38	69
C	0.00*	0.05	0.01	30.25	0.00*	1.05	(-)	(-)	(-)	(-)	(-)	117	50
D	0.00*	0.31	0.00	49.72	0.00*	1.03	0.29	0.08	12.25	0.00*	1.34	105	18
E	0.03*	0.06	0.02	6.39	0.00*	1.06	(-)	(-)	(-)	(-)	(-)	15	27
F	0.00*	0.03	0.01	19.80	0.00*	1.04	(-)	(-)	(-)	(-)	(-)	92	33

*Significant at $\alpha=0.05$

Dispersal distances and survival in those locations differed among species, apparently reflecting their dispersal mechanisms. Bird and animal-dispersed *P. borbonia* seedlings and saplings, abundant across all sites, were found at the greatest distances from assumed sources in high elevation (relatively dry) sites. Water dispersed *T. distichum* seedlings and saplings, were found only in low elevation (relatively wet) areas.

3.3. Macro-scape observations

The six representative *macro-scape* vegetation maps are presented in Figure 21. Without exception, the Prairie category was the most abundant. Coverage exceeded 97% within all *macro-scapes* except B, where prairie coverage was only 90% due to extensive (~9%) Pine Rocklands (Table 12). Despite their ecological importance as wildlife habitat, seed source, nutrient sinks, etc., the combined Wet Disturbed Forest, Bayhead Swamp and Bayhead-Hammock Forest classes never exceeded 3.2% of total *macro-scape* area (Table 12). Except for *macro-scape* A, the percentage of the Bayhead-Hammock Forest was always higher than that of the Wet Disturbed Forest or Bayhead Swamp and ranged from a low of 0.9% in *macro-scape* E to a high of 2.1% in *macro-scape* C (Table 12). The Cypress, another important woody plant seed source and recruitment site, was present only in *macro-scape* D, and was limited in cover to about 0.5% of the total area. The two anthropogenic disturbed land cover types, Impervious Surface and Scarified, were restricted to *macro-scape* B and D, where they each account for < 0.5% of the total area mapped (Table 12).

Table 12: Percentage of total area (1,036 ha) represented by the ten landscape feature classes identified within the six *macro-scapes* associated with the habitat of the CSSS. See Table 1 for class descriptions.

Landscape Feature Classes	<i>macro-scape</i>					
	A	B	C	D	E	F
Wet Disturbed Forest			< 0.5	< 0.5		
Bayhead Swamp	2.0		< 0.5		< 0.5	< 0.5
Cypress				0.5		
Impervious Surface		< 0.5		< 0.5		
Prairie	96.7	89.8	97.2	97.6	99.1	98.0
Pine Rockland		8.5				
Scarified				< 0.5		
Bayhead-Hardwood Forest	1.2	1.7	2.1	1.1	0.9	2.0
Typha	< 0.5					
Water			< 0.5	< 0.5		

All six *macro-scapes* can be described as mosaics of patches woven into a mixed-species matrix of grasses, sedges, and herbs (Figure 21). Patch distribution varied in both density, and size across the six *macro-scapes* (Table 13), though more than 99% of non-anthropogenic patches were small (< 1 ha). At nearly 80 patches • km⁻², *macro-scape* B had the highest patch density of all the *macro-scapes* analyzed (Table 13). This high density is the result of the many small Pine Rockland fragments that pepper the Prairie south of Long Pine Key (Figure 21). Because of these pine fragments, maximum patch size was also greatest in *macro-scape* B (Table 13). The lowest patch density, 18.2 patches • km⁻², was observed in *macro-scape* D while the lowest maximum

and mean patch size, 0.34 ha and 0.02 ha, respectively, were observed in *macro*-scape E (Table 13). Because of the minimum mapping unit used, the *minimum* patch size for all *macro*-scapes was of course 0.0005 ha (Table 13).

Except for *macro*-scape B, where Pine Rocklands dominated the landscape, Bayhead Hardwood Forest was, in general, the dominant woody plant community within the six *macro*-scapes sampled (Table 12). Tree island density was highest in *macro*-scape C (49.9 TI • km⁻²) and lowest in D (12.6 TI • km⁻²; Table 14). Total tree island area (ha) was also highest in *macro*-scape C and decreased below that in the order A (20.4) > F (20.2) > B (15.9) > D (11.0) > E (8.9; Table 14). In contrast, Maximum tree island size (m²) was highest in *macro*-scape F (29,107) and decreased in the order B (26,872) > C (26,754) > A (24,802) > D (8,405) > E (3,373; Table 14). Mean tree island size significantly differed among *macro*-scapes (ANOVA: F = 12.188, *p* = 0.00), being highest in *macro*-scape A and lowest in E (mean Tree Island size 1,334 m² and 281 m², respectively; Table 14; Figure 22). Figure 23 indicates a significant overlap in tree island size across all *macro*-scapes, resulting from the overwhelming proportion of small (5 – 100 m²) and medium (100 – 1000 m²) size Tree Islands.

Table 13: Patch density and *minimum*, *maximum*, and *mean* patch size for all non-anthropogenic landscape features within six *macro*-scapes associated with the habitat of the CSSS. Minimum patch size reflects the minimum mapping unit (mmu) used to identify and map the landscape features within each of the *macro*-scapes.

	<i>macro</i> -scape					
	A	B	C	D	E	F
Patch Density (patches • km ⁻²)	19.7	78.7	53.1	18.2	31.9	51.1
Patch Size (ha)						
<i>Minimum</i>			0.0005			
<i>Maximum</i>	7.09	28.16	2.68	0.84	0.34	2.91
<i>Mean</i>	0.04	0.14	0.22	0.37	0.02	0.04

Table 14: Tree Island density, area, and *minimum*, *maximum*, and *mean* tree island size in each of the six *macro*-scapes. Minimum tree island size reflects the minimum mapping unit (mmu) used, 5 m², to identify and map the landscape features within each of the *macro*-scapes.

	<i>macro</i> -scape					
	A	B	C	D	E	F
Tree Island Density (TI • km ⁻²)	14.8	47.1	49.9	12.6	30.6	45.2
Total Tree Island Area (ha)	20.4	15.9	21.2	11.0	8.9	20.2
Tree Island Size (m ²)						
<i>Minimum</i>	5	5	5	8	6	5
<i>Maximum</i>	24,802	26,872	26,754	8,405	3,373	29,107
<i>Mean</i>	1,334	327	410	842	281	431

Table 15: Moran’s I, Z and P values for Tree Island Kernel estimates within the six *macro-scapes* chosen.

<i>macro-scape</i>	Moran’s I	Z	P
A	0.680	30.320	0.001
B	0.392	56.846	0.001
C	0.268	55.093	0.001
D	0.549	18.462	0.001
E	0.319	37.754	0.001
F	0.461	58.025	0.001

The Kernel density maps for tree islands in each *macro-scape* are shown in Figure 24. At a glance, Figure 24 suggests a significant spatial autocorrelation in Tree Island density. This observation is validated based on the results of the Moran’s I analysis, in which high Z-scores indicate very strong clustering of tree islands (Table 15).

The O-ring function revealed a significant spatial aggregation of Tree Islands at multiples scales within the six *macro-scapes* (Figure 25) and it parallels the results obtained from Moran’s I (Table 15). The scale (r) of spatial aggregation of Tree Islands was restricted to the shortest distances in *macro-scapes* D & F (significant aggregation through 600 m, but not beyond) and was larger in scale in *macro-scape* C, where it extended to 1350 m (Figure 25). *Macro-scape* E showed multiple scales of tree Island aggregation: all distances up to 400 m, then again between 650 and 1,100 m (Figure 25).

3.4. Fire

Seventy-eight fires burned 36,951 ha of marl prairie habitat within our study area over the last 29 years. The fire occurrence interval varied within and across the six landscapes and was scale dependent (Table 16). *Macro-scape* A had the longest fire occurrence interval at one fire every 366.3 years, which resulted in undetectable fire occurrence within the *meso-* and *micro-scale* plots (at least over the last 400 years; Table 16). Of course, our estimates are based on a 29-year record, and it seems inconceivable that the “natural” fire occurrence interval in this area could be so long. In contrast, *macro-scapes* B-F had an average fire occurrence interval of about one fire every 14.5 years. By chance, fire occurrences across *meso-scapes* were slightly more frequent than across *macro-scapes* (average approximate occurrence of one every 12 years; Table 16). Surprisingly, we found no significant relationship across *meso-scapes* between Total Stem Density and Fire Frequency (Figure 26). For the most part, fire frequency was consistent across *micro-scape*, *meso-scape*, and *macro-scape* levels (Table 16), suggesting that the processes we observed at the smallest scales were representative of the general landscape.

Table 16: Fire occurrence interval for all three landscape scales (*macro*, *meso*, and *micro*) associated with the habitat of the CSSS.

CSSS subpopulations	Fire Occurrence interval (years)		
	<i>macro</i> -scape	<i>meso</i> -scape	<i>micro</i> -scape
A	366.3	> 400	> 400
B	10.5	17.9	14.5
C	8.3	10.9	9.7
D	21.5	11.0	7.3
E	16.9	11.2	9.7
F	15.5	7.3	4.9

4. Discussion

Change is a defining constant across the southern Everglades woody plant-grassland mosaic. Landscape patches, woven together through intertwining biological and physical feedback mechanisms, are perpetually subject to expansion, contraction, or replacement. Local biota survive such flux via individual adaptations such as flood and/or fire tolerance, long- and short-distance dispersal, and phenological patterns. Despite these adaptations, some degree of equilibrium between constraining processes (particularly hydrology and fire) is required to maintain a landscape mosaic suitable to the diverse requirements of its many component species, including the Cape Sable seaside sparrow.

This study assessed the multi-scale process of woody plant establishment among several species under diverse hydrologic and topographic circumstances. We successfully generated logistic regression models predicting the establishment of four common woody species in four of our six *micro*-scapes (eight models total; see Table 7). In each of these models, source effect was a useful predictor of establishment. In each case source size and proximity increased the likelihood of establishment within the prairie. Furthermore, source effects were found to positively influence generalized woody plant establishment in all six *meso*-scapes. The singularity of results confirms a strong relationship between the recruitment of new seedlings and the strength of local seed sources. Successful woody plant invasion also requires long-distance dispersal in addition to germination, establishment and survival outside the zone of parental influence (Clark et al. 1999). The multiplicity of establishment pathways and constraints found within the marl prairies stems from the co-evolution of competing vegetation types (i.e. grasses and trees), whose relative cover has been maintained through historical disturbance patterns.

Under a natural disturbance regime, invasion into the prairie is likely aided by the dispersal mechanisms of individual woody species. In early successional communities bird dispersed species are said to exhibit much stronger clustering than wind dispersed species (Bazzaz 1996), since perch trees often act as recruitment foci for new seedlings (Duarte et al. 2006; Slocum 2001). Diaspore morphology (i.e. fruit and seed characteristics) usually indicates a species' typical dispersal mechanism (Howe & Smallwood 1982; van der Pijl 1972; Ridley 1930). For example, fleshy fruits attract birds and small mammals, while winged and plumed seeds are more

likely to be captured and dispersed by wind. Buoyant fruits and seeds can attract animal dispersers and also travel long distances in water. Among early marsh invaders in *macro*- and *micro*-scapes, small-seeded, bird and mammal dispersed species such as *P. borbonia* established in scattered patches, whereas wind dispersed species such as swamp willow (*Salix caroliniana*) were more widely dispersed, but frequently occurred in close proximity to assumed parent trees. Water dispersed species such as *T. distichum* exhibited minimal clustering, and were limited to specific regions that were relatively wet and in the general vicinity of an established parent population. Approximately one-third of the woody species found in our *micro*-scapes are thought to employ some sort of abiotic dispersal mechanism (see Table 4). Interestingly, this proportion is doubled among recruit species that were found to exist at distances greater than 140 m from potential parent trees (i.e. no adults present within the plot or buffer). Since more than three quarters of the woody species found within *micro*-scapes were at least in part dispersed by birds and/or mammals, it is not surprising that the woody component of the freshwater marl prairie tends to exist in scattered clumps.

Another influence on establishment and survival is mid- to long-term disturbance patterns. Potentially, one of these is hydrology, but in this study hydroperiod and Plant Wetness Index showed weak and non-significant correlations with establishment within most *micro*- and *meso*-scapes. The lack of evidence for hydrologic impacts may have been the result of a mismatch of scale between species response and sample plot size (5 x 5 or 10 x 10 m for *micro*-scape and *meso*-scape, respectively), and/or a lack of statistical power brought on by the low density and aggregated distributions of even the most abundant woody species. However, other evidence confirms that hydrology is an important driver of woody plant invasion. For example, *A. glabra* was found to be a highly successful invader within the very wet *meso*-scape A, which is not surprising considering that the species has been identified as the most flood-tolerant local wetland tree species (Gunderson et al 1988, Jones et al 2006, Reed 2007). *A. glabra* grows rapidly and exhibits apical dominance until it reaches statures of up to 30-40 cm as an early germinant (Reed 2007). *M. cerifera* is also shown to be flood-tolerant in its seedling and juvenile stage in part because of its growth of adventitious roots (Gunderson et al 1988, Reed 2007). However, Reed (2007) showed that the slow growth of *M. cerifera* could result in high mortality in areas where early-seasonal inundation of only a few inches coincided with mid-spring germination. This might explain the complete absence of *M. cerifera* seedlings (despite the large adult population) within *micro*-scape A. It is likely that an investigation targeted more narrowly at individual species would yield some evidence of niche partitioning by species according to their hydrologic tolerances.

Hydroperiods across *micro*-scape D were short relative to the surrounding *meso*-scape (see Table 6 & Figure 12), though the plot had a relatively wide range of hydrologic conditions, including several wet microsites (see table 6). Flooding duration in both *micro*- and *meso*-scapes positively influenced species-specific and generalized woody plant establishment within population D. The positive relationship between hydroperiod and establishment of *P. borbonia*, *T. distichum*, and *M. cerifera* in *micro*-scape D may in part relate to the species' competitive advantage in wetter microsites, and/or the possibility that hydrologic timing within *micro*-scape D was more suitable to the species' dispersal, germination, establishment and survival. The positive influence of PWI on generalized establishment within *meso*-scape D most likely relates to the high relative abundance of hydrophilic species such as *T. distichum* and *P. borbonia* within the region (see

table 3). While seedling growth morphology (e.g. apical dominance, advantageous roots, etc.) may favor certain wetland tree species over others under average hydrologic conditions, it may not explain seedling population responses under more extended periods of flooding or drought.

During wet years anoxic conditions often stunt growth and stress plants such that recovery is inhibited until the next growing season. As a result, individuals of low stature but relatively advanced lignification sometimes occur in aggregates of seedlings one or more years of age. Many of the individuals in these stunted/low-stature groups may be more sensitive to flooding than they otherwise would have been under drier hydrologic conditions. Even during dry years woody seedlings are vulnerable to mortality via several physical and biological mechanisms including lack of available resources, herbivory, competition and disease. Although we did not find strong relationships between seedling survival and either source effects or hydroperiod, such relationships are still likely to exist. Survival between 2006 and 2007 was quite high, possibly due (at least in part) to drought conditions, and as a result, our logistic regressions were weak (see Table 8). We suspect that during a wetter year, much-stronger survival trends would be detectable.

Intermediate disturbance mechanisms such as fire may also play an important role in the dynamics of marsh/prairie composition. R-strategists and species with clonal and vegetative growth patterns recover quickly, while woody species that may have invaded during a dry cycle (e.g. 2006-2008) may be removed from the area more permanently. This appears to be the case in *micro*-scape B, which burned intensively in 2005, followed by flooding associated with hurricane Katrina. In 2006 most woody plants were damaged or dead, and in 2007, only four new recruits were found. While the burned tree island in the *micro*-scape appears to be slowly recovering (see Plate 1), the fire and subsequent flood certainly reset marsh conditions surrounding the small tree island.

Woody plant invasion into the marl prairies involves a chain of processes, which are subject to various constraints and/or interruptions. Evidence suggests that the most successful early marsh invaders are hydrophilic species such as *A. glabra* and *T. distichum*, followed closely by *P. borbonia* and *M. cerifera*. In addition to producing their own seed shadows, wetland adults appear to act as magnets for new recruits, possibly by serving as perch sites for avian seed dispersers. The seed shadows and attraction generated by early invaders can produce fine-scaled aggregation, which sometimes result in larger-scale colonization of new habitat. Such expansion appears to be most probable adjacent to woody patch edges, where seedfall is most intense (Duarte et al. 2006; Clark et al. 1999). Successful propagule dispersal, seedling colonization, survival, aggregation into tree islands and further aggregation into a landscape-scale woody mosaic requires a precise set of conditions at each stage in the process (Figure 27).

The *macro*-scape analysis showed that tree islands in the marl prairie landscape are numerous, mostly but not exclusively small in size. They are aggregated at scales of hundreds to thousands of meters, separated by large expanses in which tree islands are sparse or absent. The range and distribution of their sizes, as well as their tendency to aggregate, suggest that groups of tree islands, like the species that inhabit them, may be thought of as populations, with birth, growth, and death at rates that respond to disturbance, available seed sources, and the nature of the physical environment (Figure 27). Gumbrecht et al. (2004) made a convincing case that such

population-like dynamics characterize the multitude of tree islands in the Okavango delta of Botswana. Like ours, tree islands in the Okavango were spatially aggregated, sometimes at very large scales. The islands formed by nucleation around termite mounds, followed by growth and decay over millennia under the influence of tree-induced geochemical changes, particularly the precipitation of calcite and eventually the buildup of salts in the island interiors (McCarthy et al. 1993, 1995, 1998). In our marl prairie study area, we have not yet isolated similar biogeochemical mechanisms, though we have limited evidence that a transpiration-driven process might be affecting tree island substrates in the long hydroperiod marshes of the interior Everglades (Graf et al. 2008). However, our examination of tree island:sapling associations in Everglades *meso*- and *micro*-scapes, do illuminate several factors that may affect tree island growth and establishment, i.e., the effects of seed source and local hydrology.

While one can only speculate on the mechanisms that caused tree islands in our study area to show close spatial association, at least one of its effects seem quite clear: aggregation tends to create further aggregation. Data presented earlier indicate that seedlings are far more likely to be established near an existing tree island than at more isolated locations in the prairie. Seedlings established near an island may eventually contribute to its growth, or serve as a nucleation point for a new, neighboring community. Moreover, as tree islands form and increase in size, they develop a more humid microclimate, and become more resistant to fire. This is even truer for large aggregates of tree islands, which are known to deflect fires, and interfere with their movement through the prairie (personal communication, Rick Anderson, ENP Fire Management Officer). However, this resistance to fire is not universal, and Everglades tree islands of any size do burn under extreme conditions (e.g. Plate 2). When this happens, all biological resources may be consumed, including the peat soils themselves. Under these circumstances, the presence of nearby tree islands which by chance have escaped the fire can serve as seed sources for vegetation recovery.

Tree island spatial patterns add to the overall heterogeneity of the marl prairie landscape by adding structure and bio-topographic relief to an extensive grassland matrix. As illustrated by the six *macro*-scapes we studied, the size, number and distribution of tree islands vary greatly from one part of the Everglades to another. The reasons for this variability are obscure and may never be fully known; in all likelihood, they result from the interactions of three underlying dominant physical and environmental factors: topography, hydrology, and fire. In any case, these *macro*-scapes create different environments for animals that range widely in mobility and habitat preferences. Some, like the Cape Sable seaside sparrow (CSSS), avoid tree islands altogether. Others depend on them as critical refuges during flood stages, or as roosting and foraging sites. Since there is no single distribution of tree islands that suit all conditions or objectives, it is difficult to assign restoration objectives in areas in which the pre-development distributions are no longer present. In the marl prairies, we do not know whether or not this is the case. Nevertheless, our study provides a reasonable survey of the types, densities, distributions, and sizes present in CSSS habitat, and an inkling of the processes that may cause them to grow, dwindle, or become transformed.

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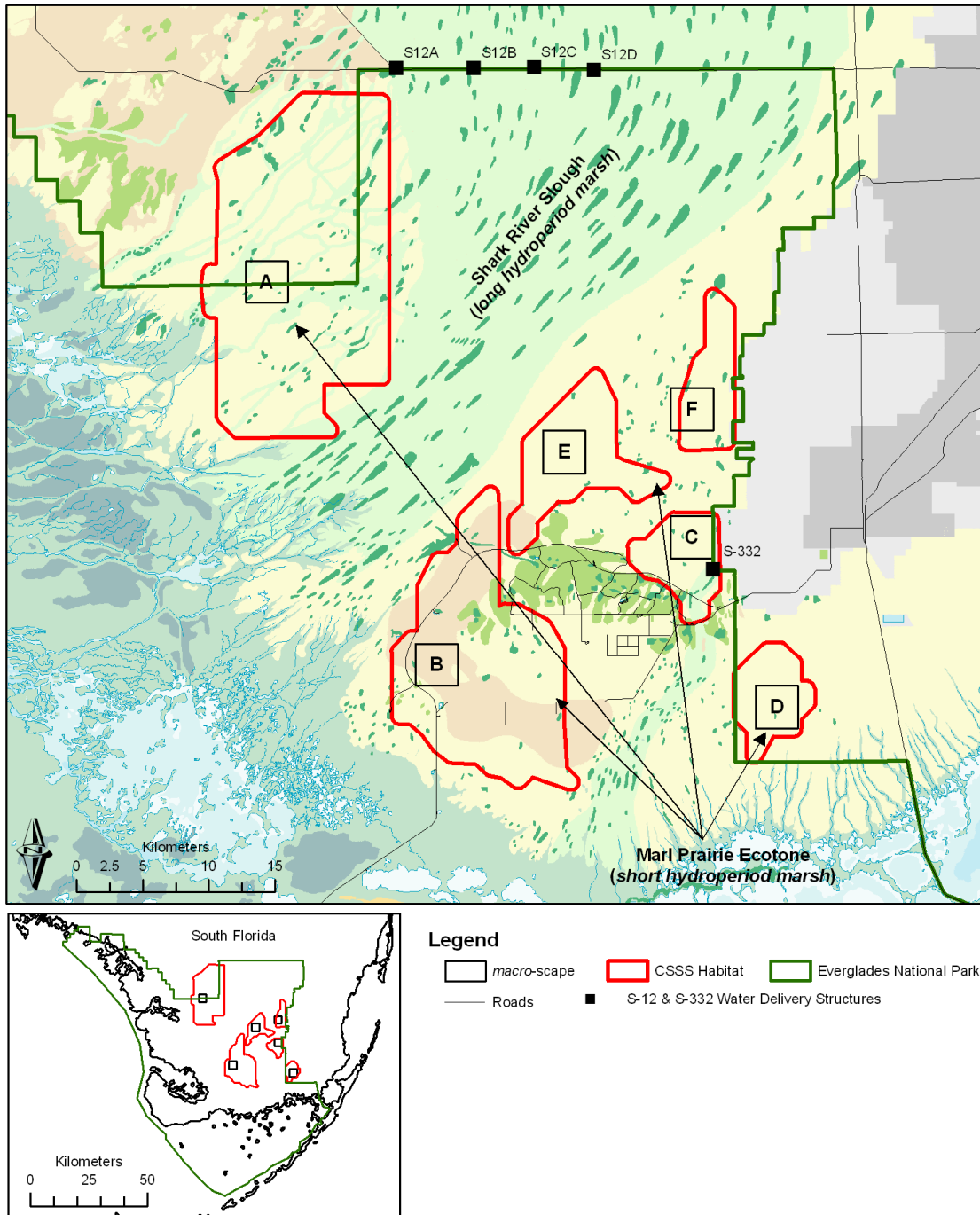


Figure 1: Location of the six *macro*-scope plots within the habitat of the Cape Sable Seaside Sparrow (CSSS) in Everglades National Park, FL.

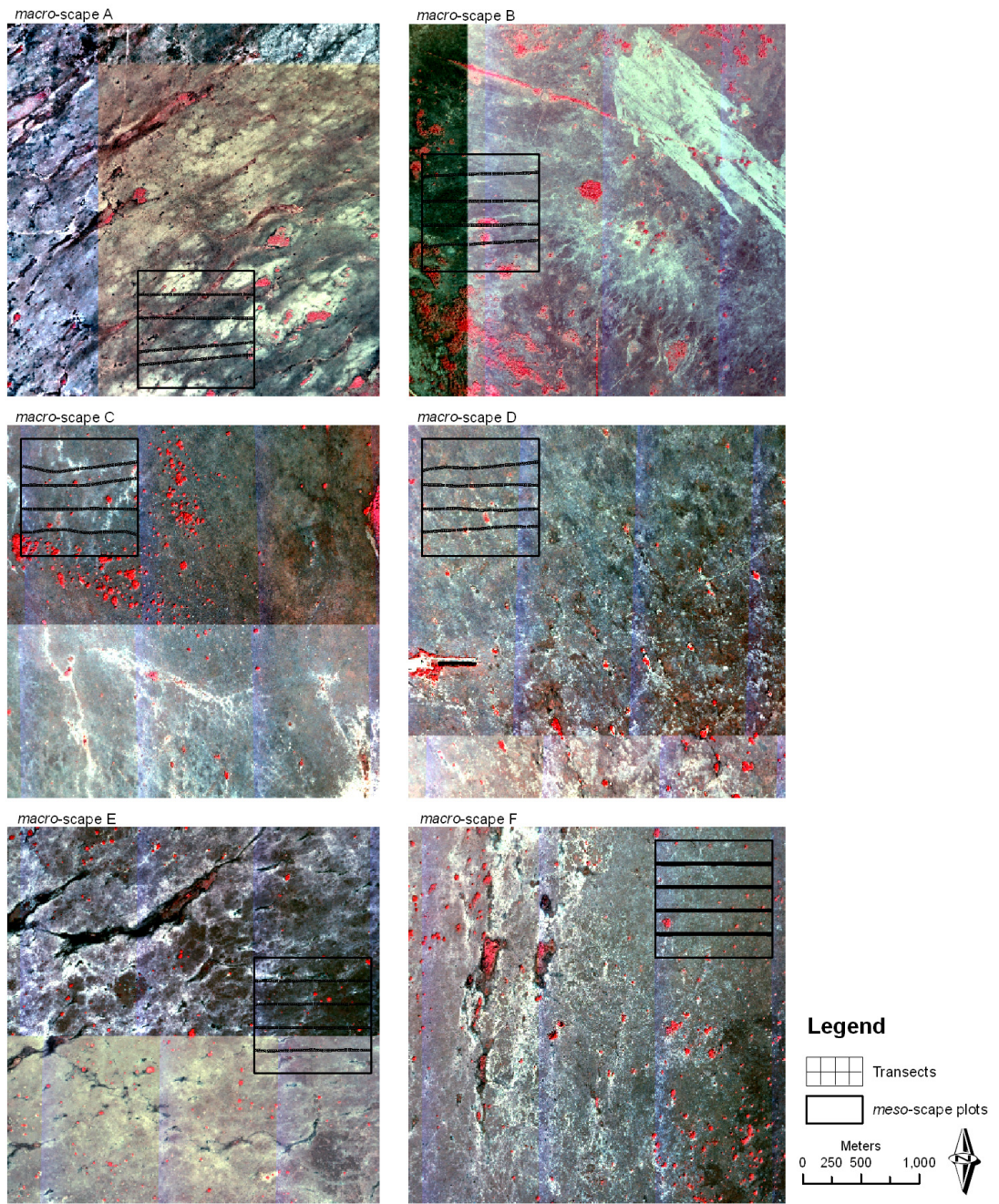


Figure 2: Location of *meso-scale* plot and transects within each of the six *macro-scapes*. Imagery source 2000 1m resolution NAPP CIR aerial photography. Imagery not spectrally calibrated.

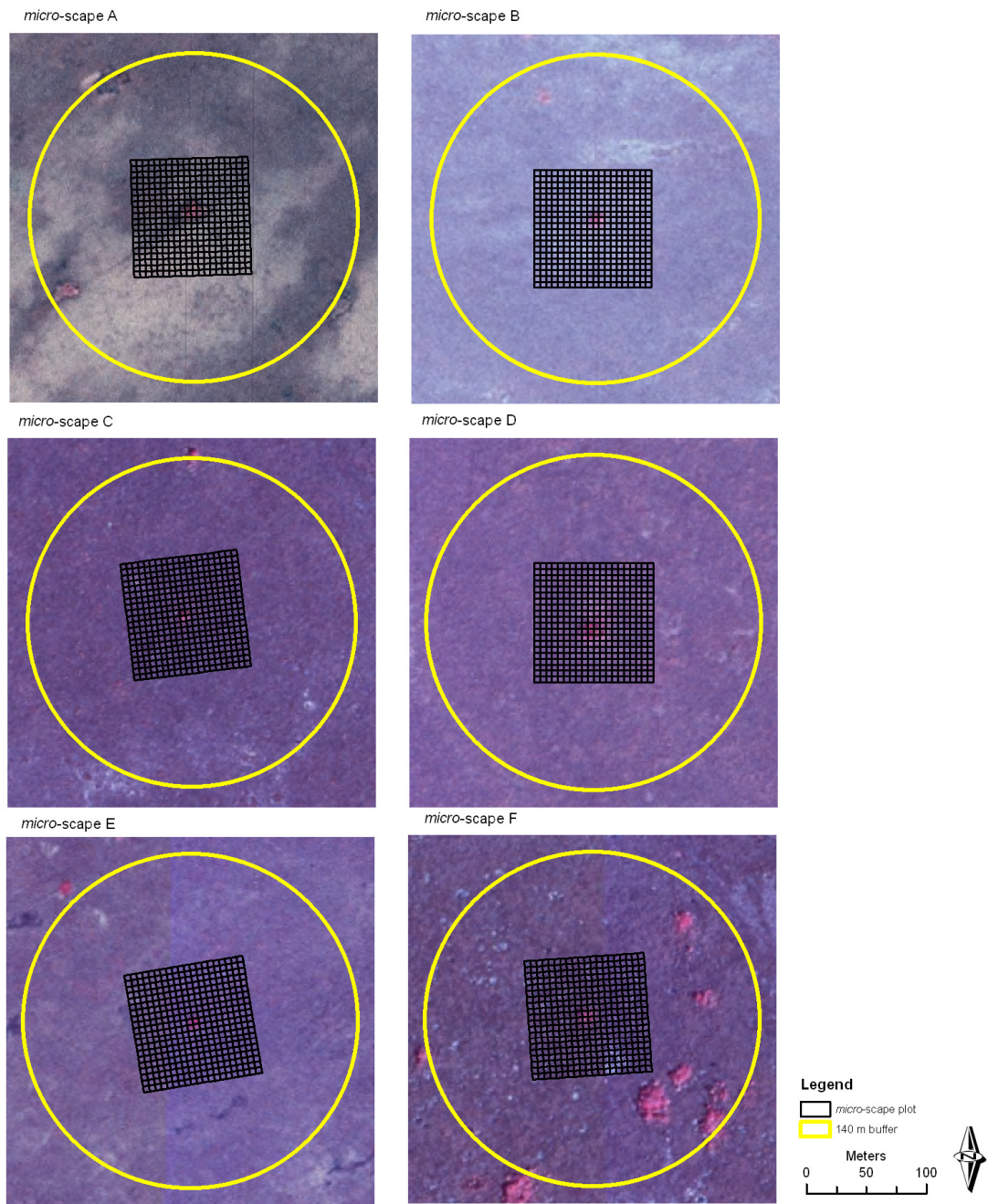


Figure 3: *Micro-scape* site layout with 140 m neighborhood buffer. Imagery source 2000 1m resolution NAPP CIR aerial photography. Imagery not spectrally calibrated.

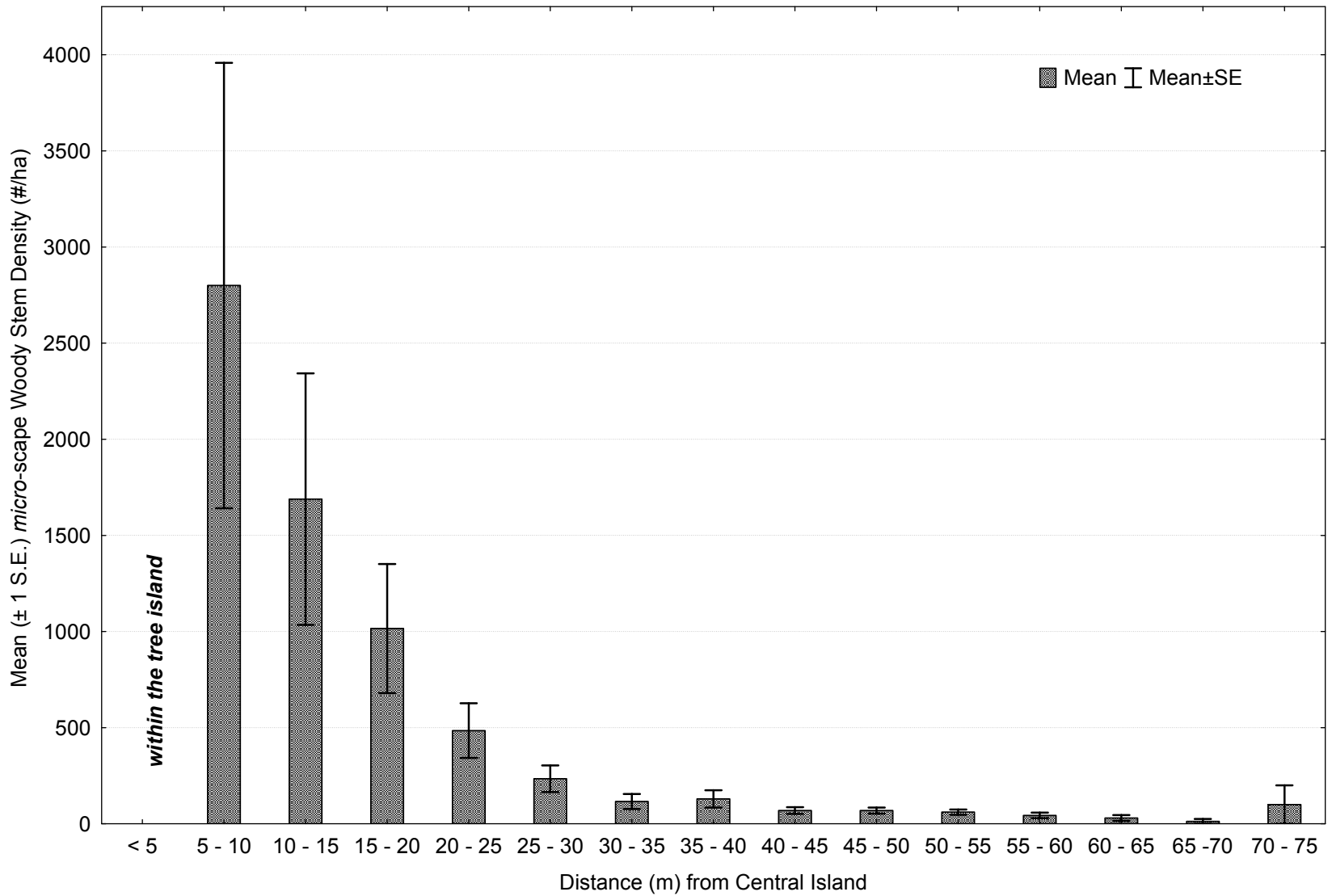


Figure 4: Mean (± 1 S.E.) woody stem densities (#/ha) as a function of distance from tree island centroid. Seedlings were not sampled within 5 m of the tree island centroid. Density and distance are average across all *micro*-scapes.

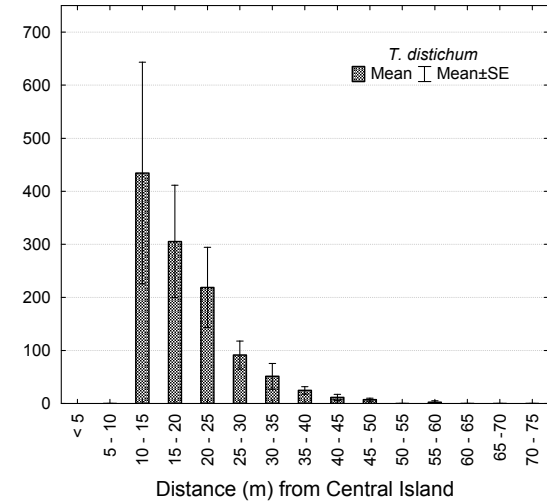
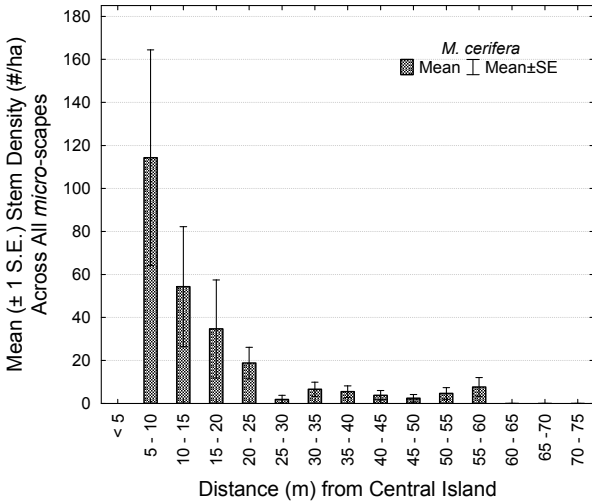
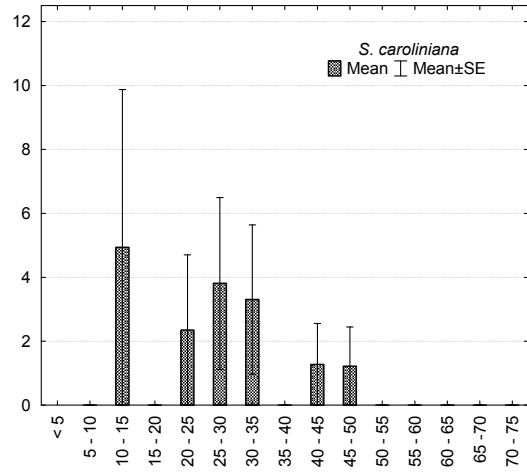
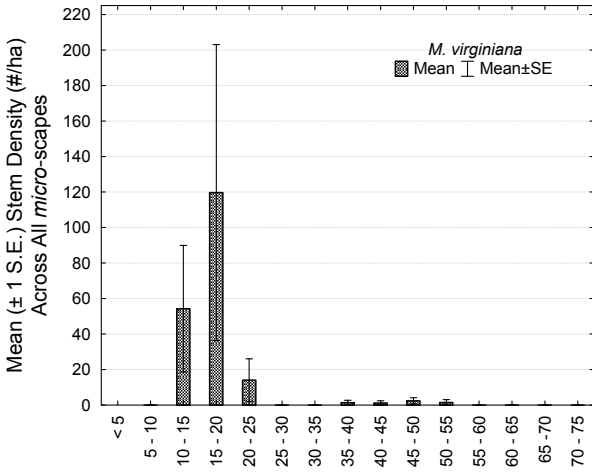
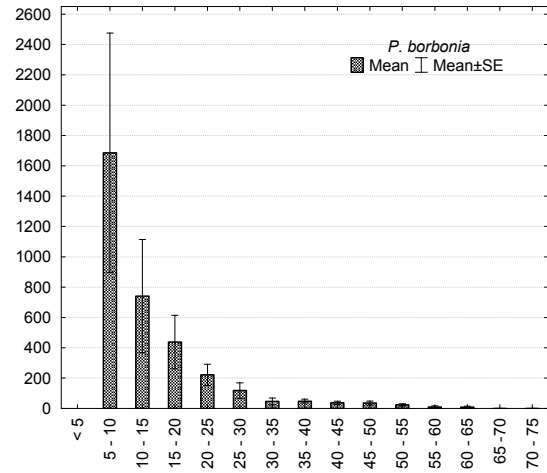
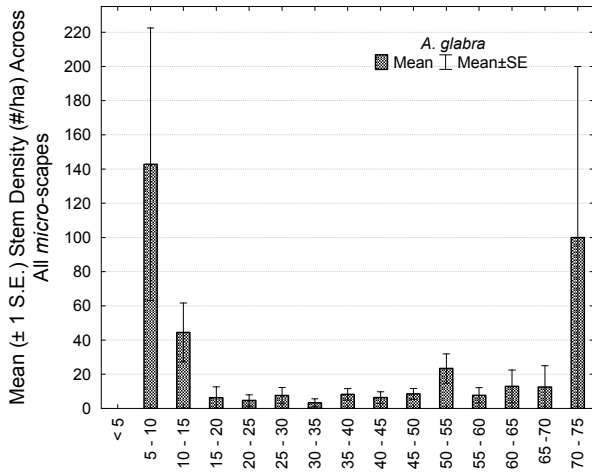


Figure 5: Mean (± 1 S.E.) *A. glabra*, *M. virginiana*, *M. cerifera*, *P. borbonia*, *S. caroliniana*, and *T. distichum* stem densities (#/ha) as a function of distance from tree island centroid. Seedlings were not sampled within 5 m of the tree island centroid. Density and distance are average across all *micro-scapes*.

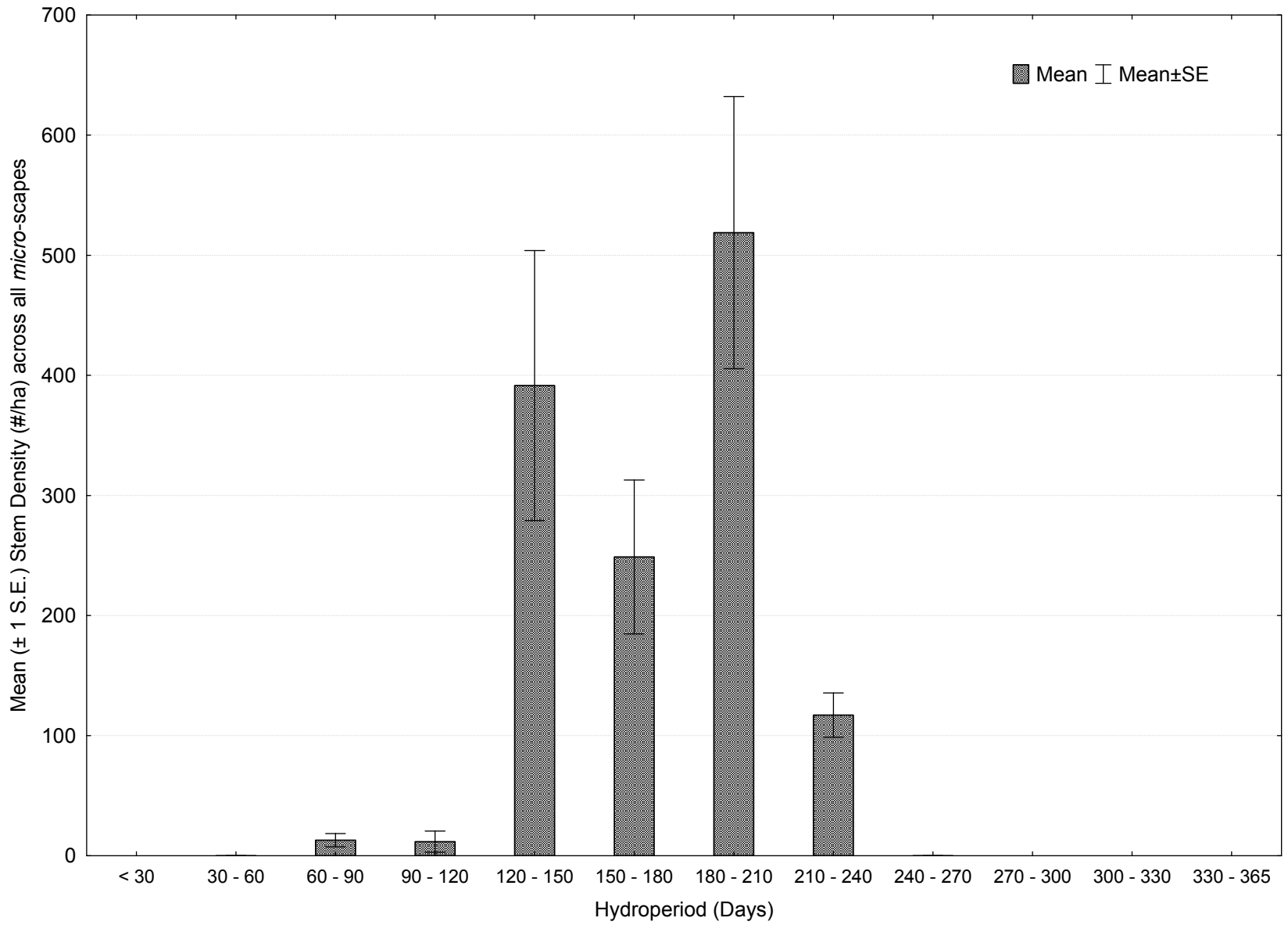


Figure 6: Mean (\pm 1 S.E.) woody plant density in relation to mean *micro*-scape hydroperiod.

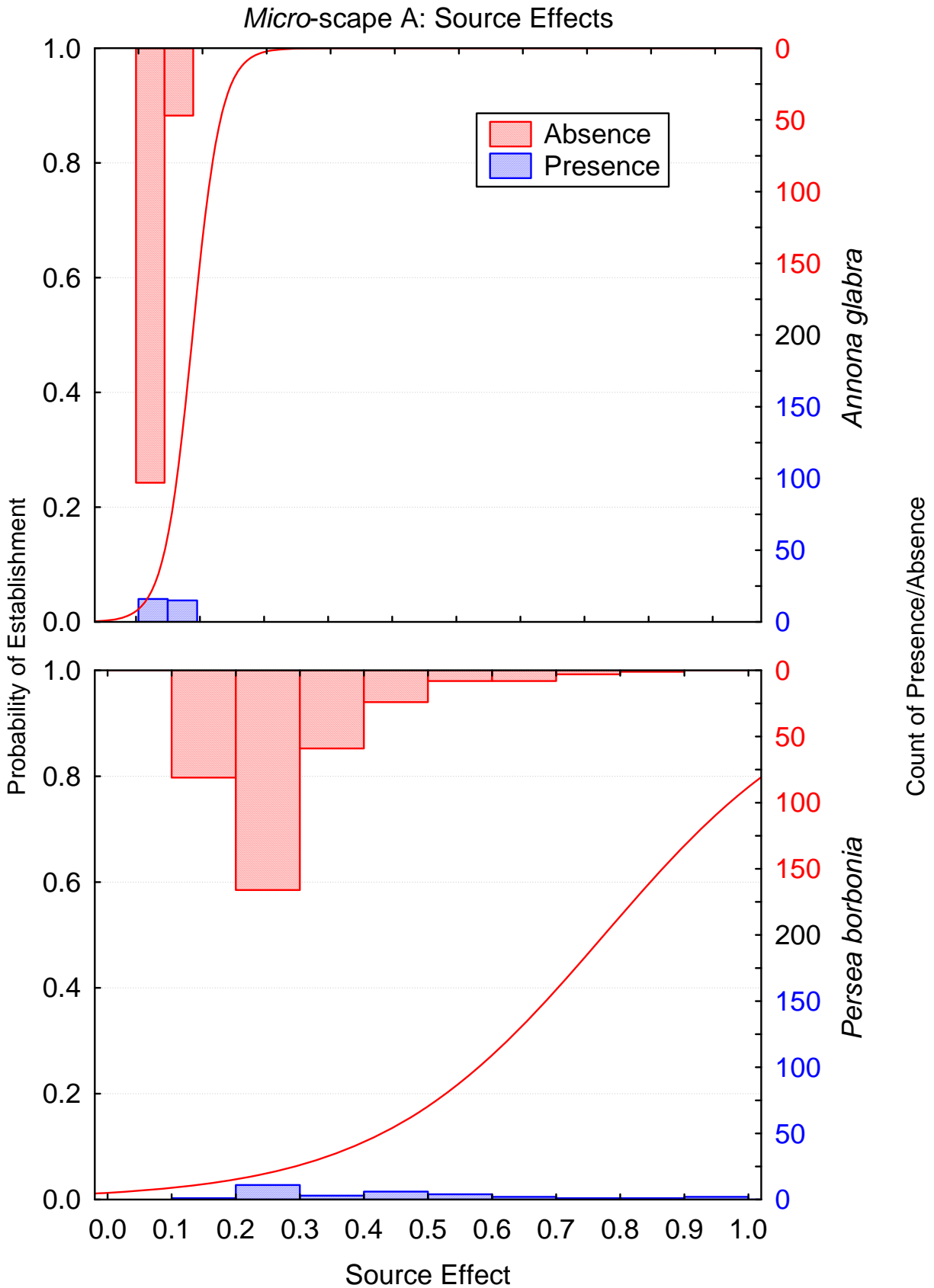


Figure 7: Source effects on the establishment of *A. glabra* and *P. borbonia* within *micro-scape* A. Bars represent the number of quadrats with individuals present or absent.

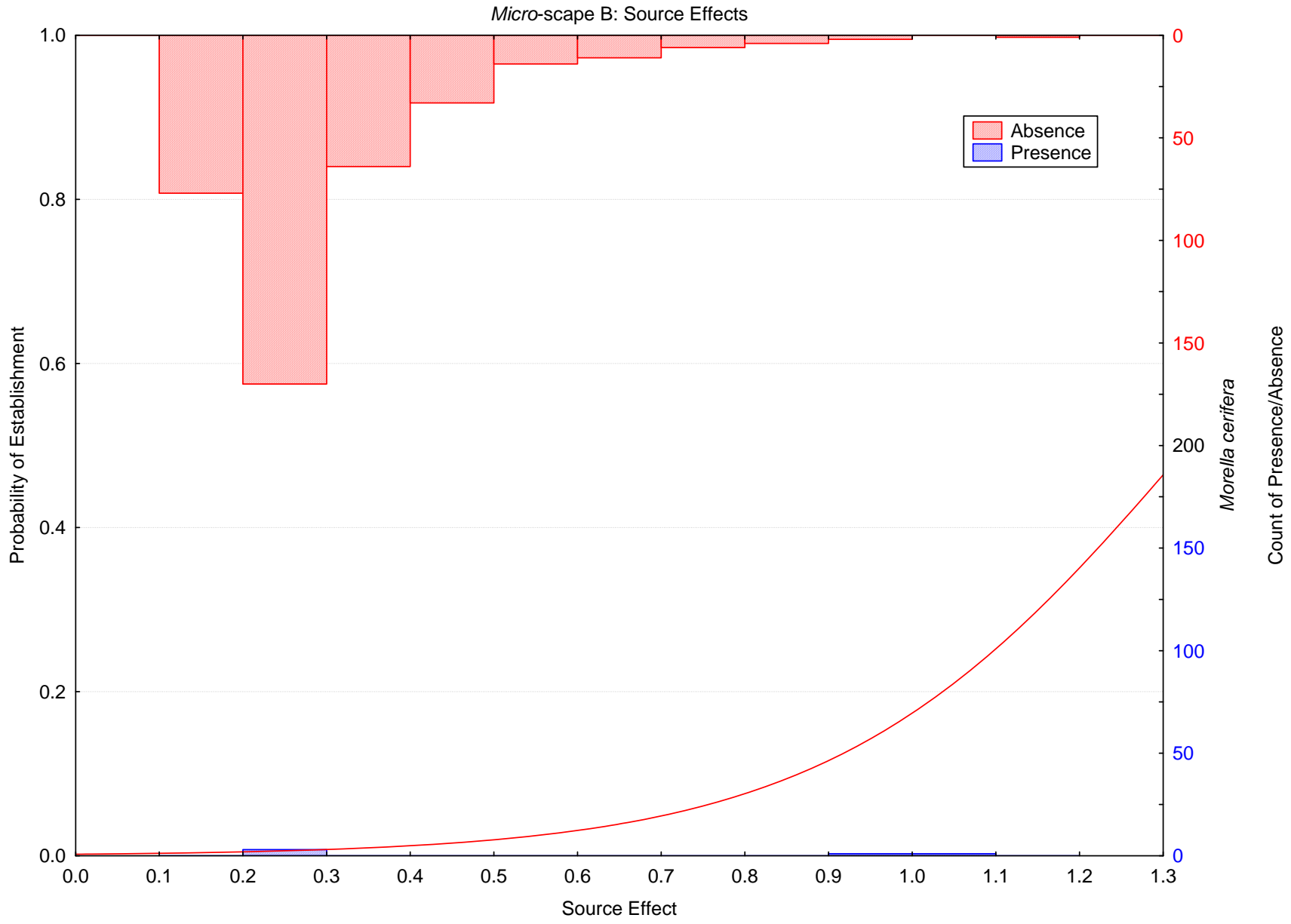


Figure 8: Source effects on the establishment of *M. cerifera* within *micro-scape* B. Bars represent the number of quadrats with individuals present or absent.

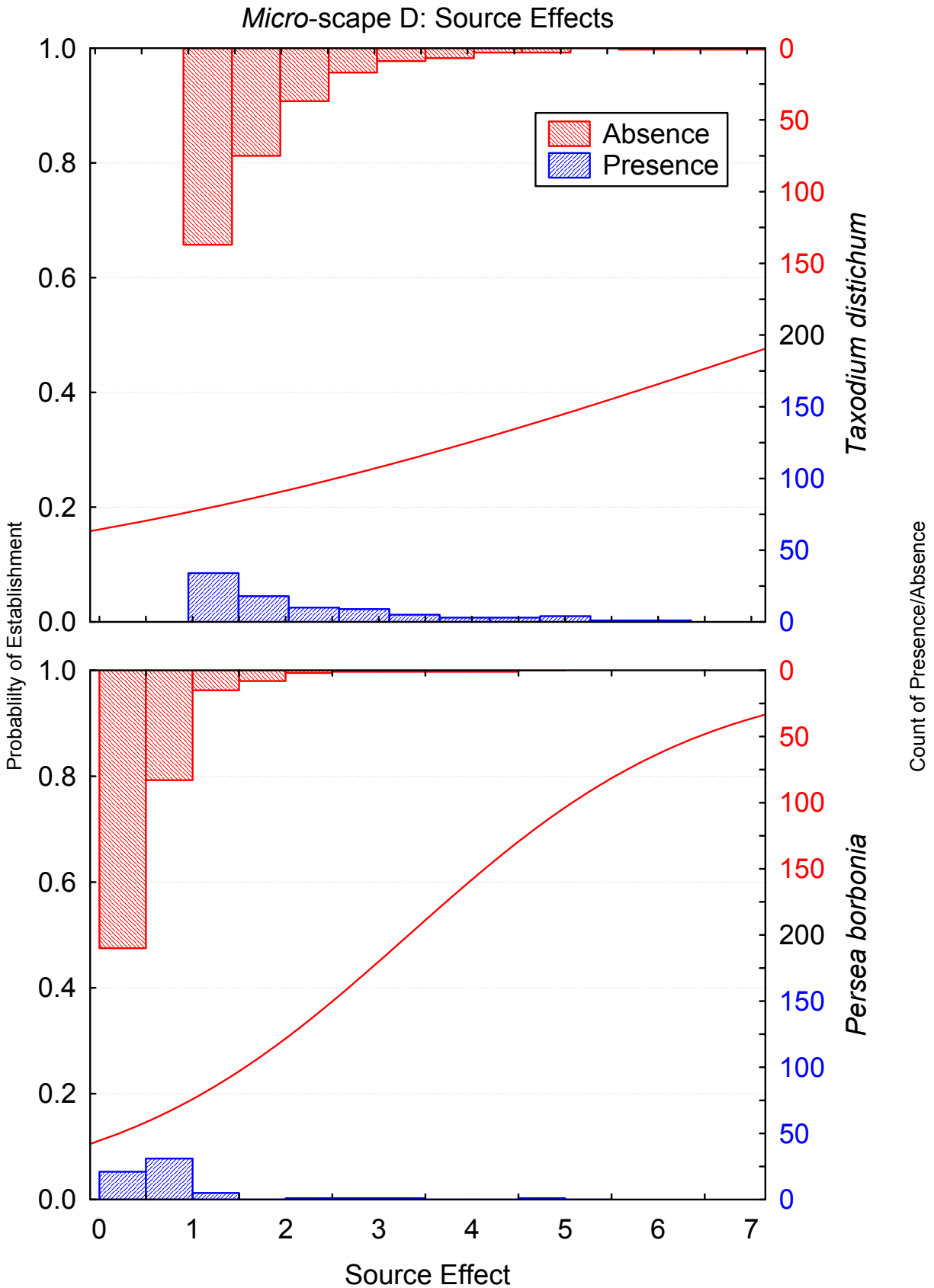


Figure 9: Source effects on the establishment of *T. distichum* and *P. borbonia* within *micro-scape* D. Bars represent the number of quadrats with individuals present or absent.

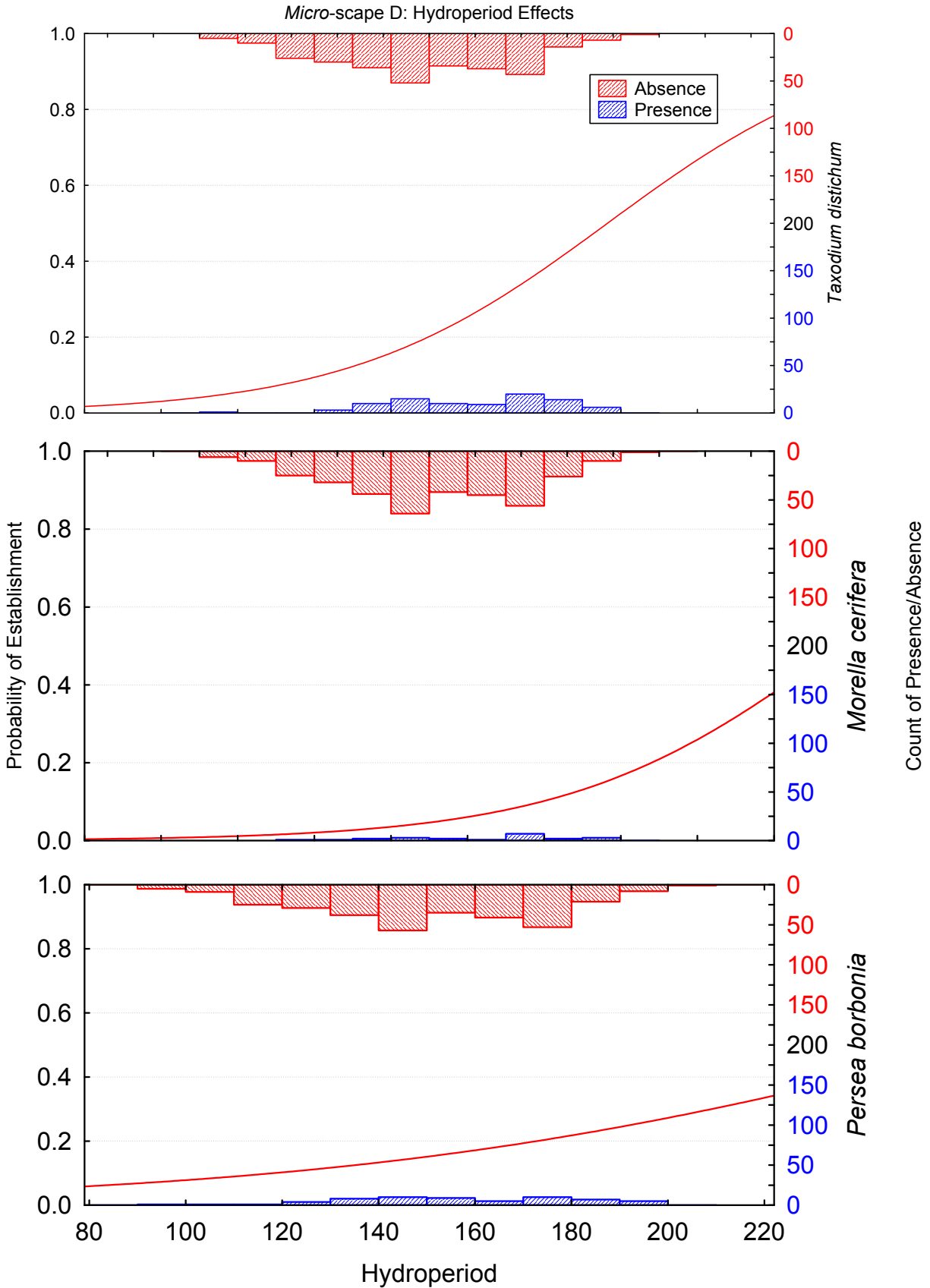


Figure 10: Hydroperiod effects on the establishment of *T. distichum*, *M. cerifera* and *P. borbonia* within *micro*-scape D. Bars represent the number of quadrats with individuals present or absent.

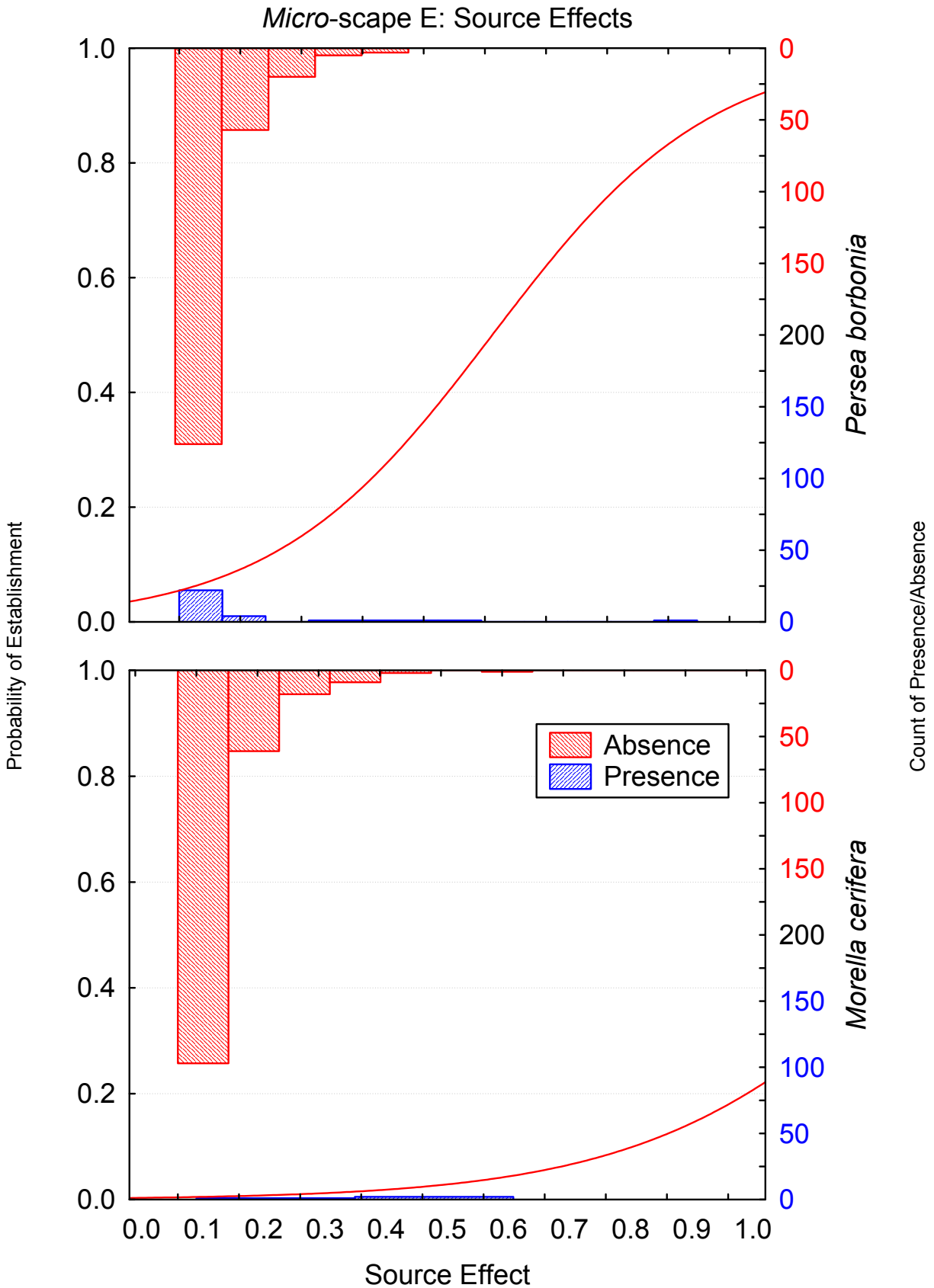


Figure 11: Source effects on the establishment of *P. borbonia* and *M. cerifera* within *micro-scape* E. Bars represent the number of quadrats with individuals present or absent.

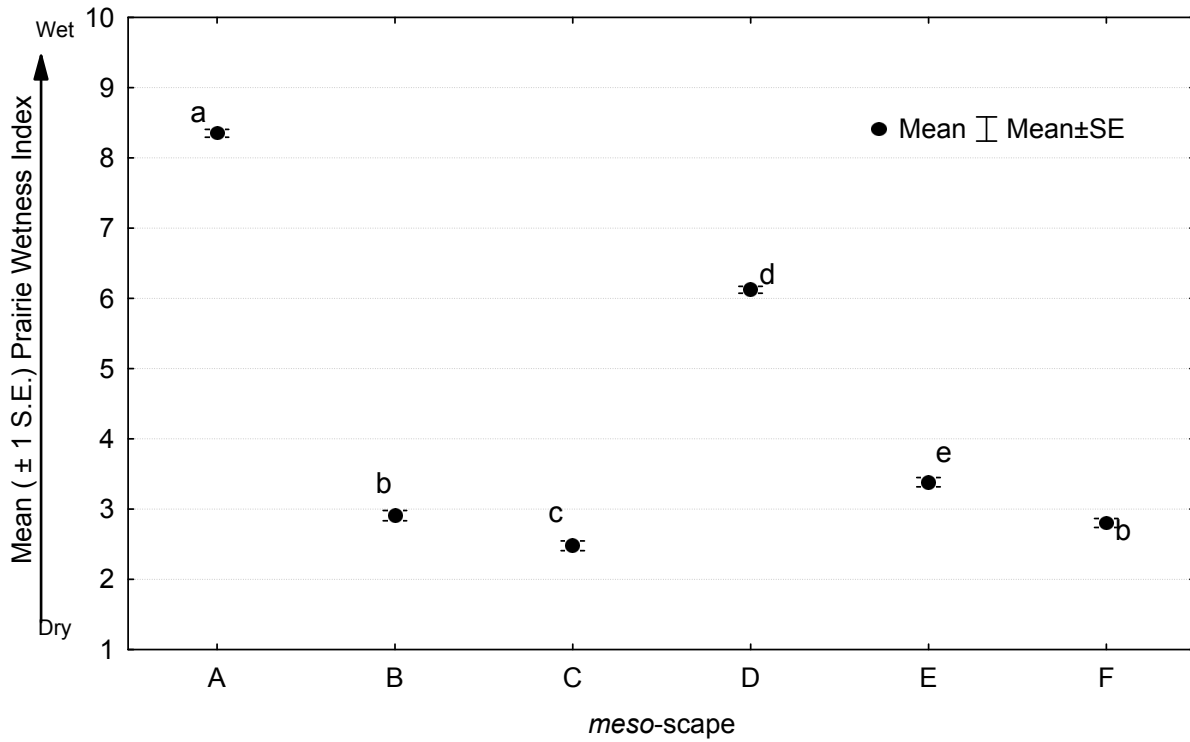


Figure 12a: Meso-scape differences in mean (± 1 S.E.) Prairie Wetness Index. Meso-scapes with same superscript do not differ at $p > 0.01$ (Bonferroni test).

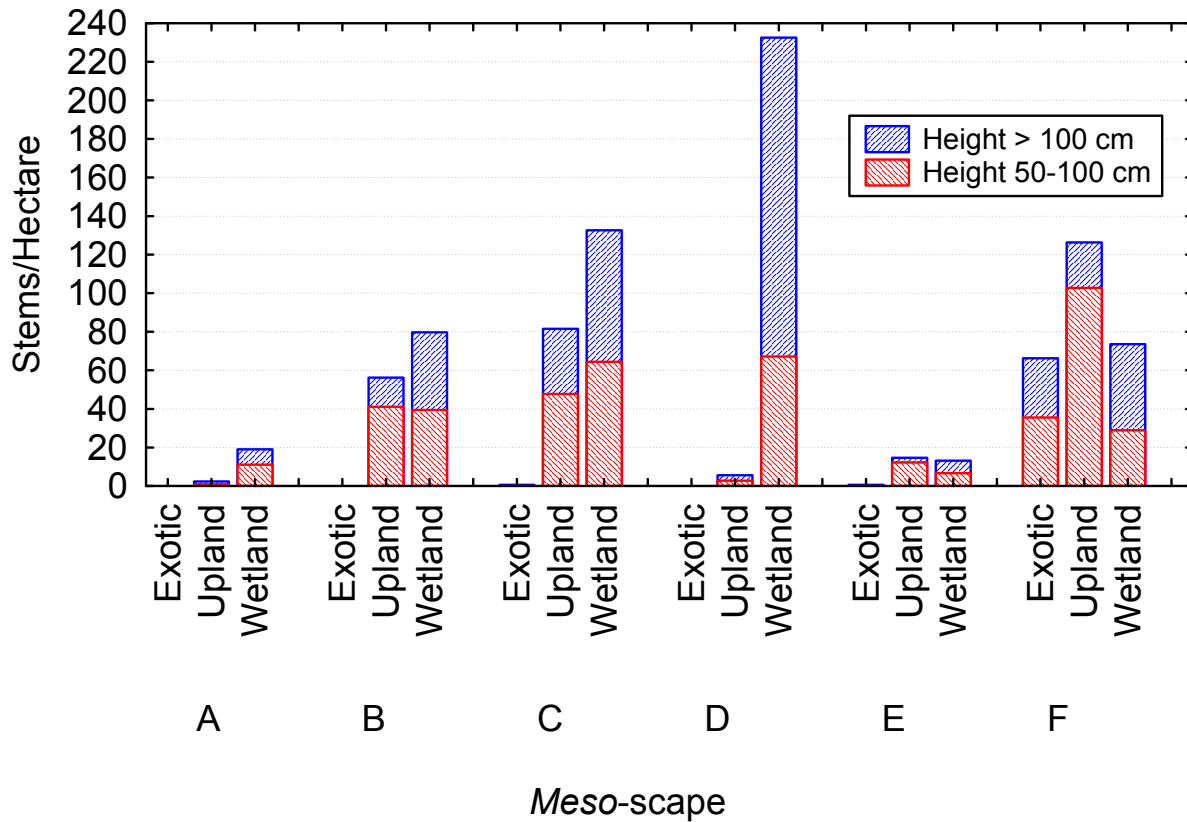


Figure 12b: Stem densities of upland/wetland/exotic species by height within meso-scapes.

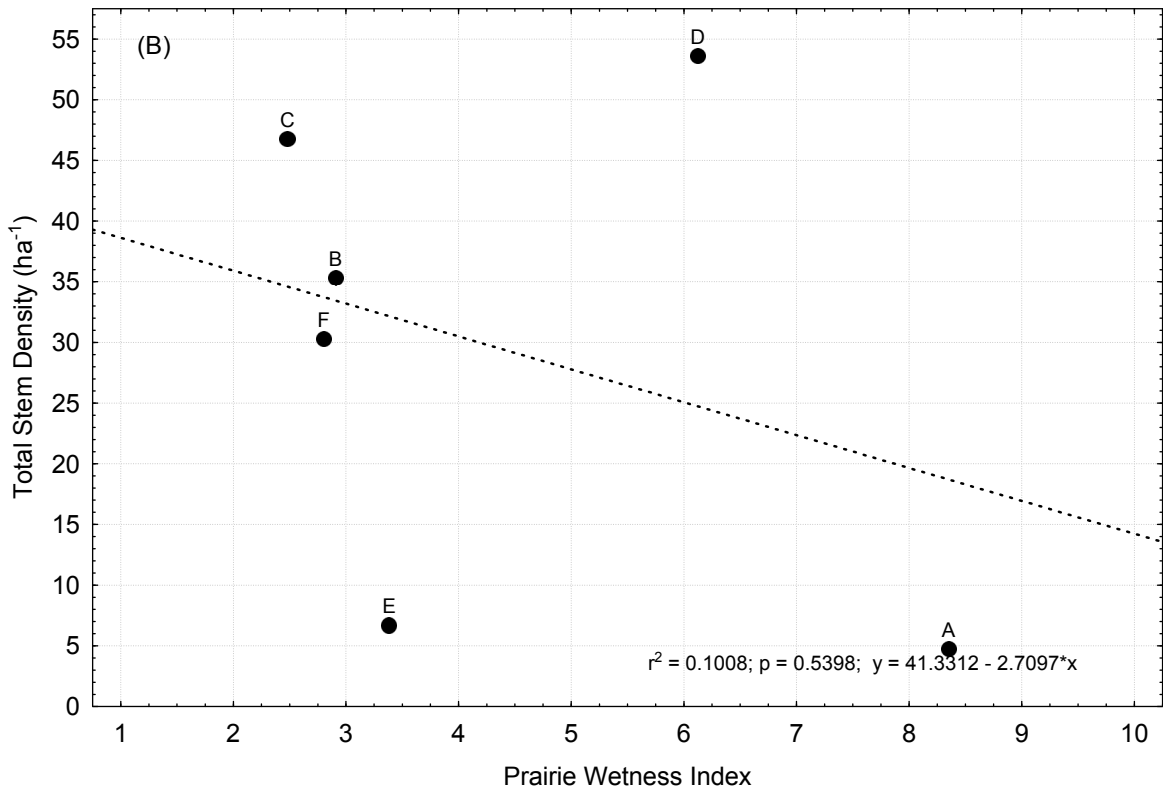
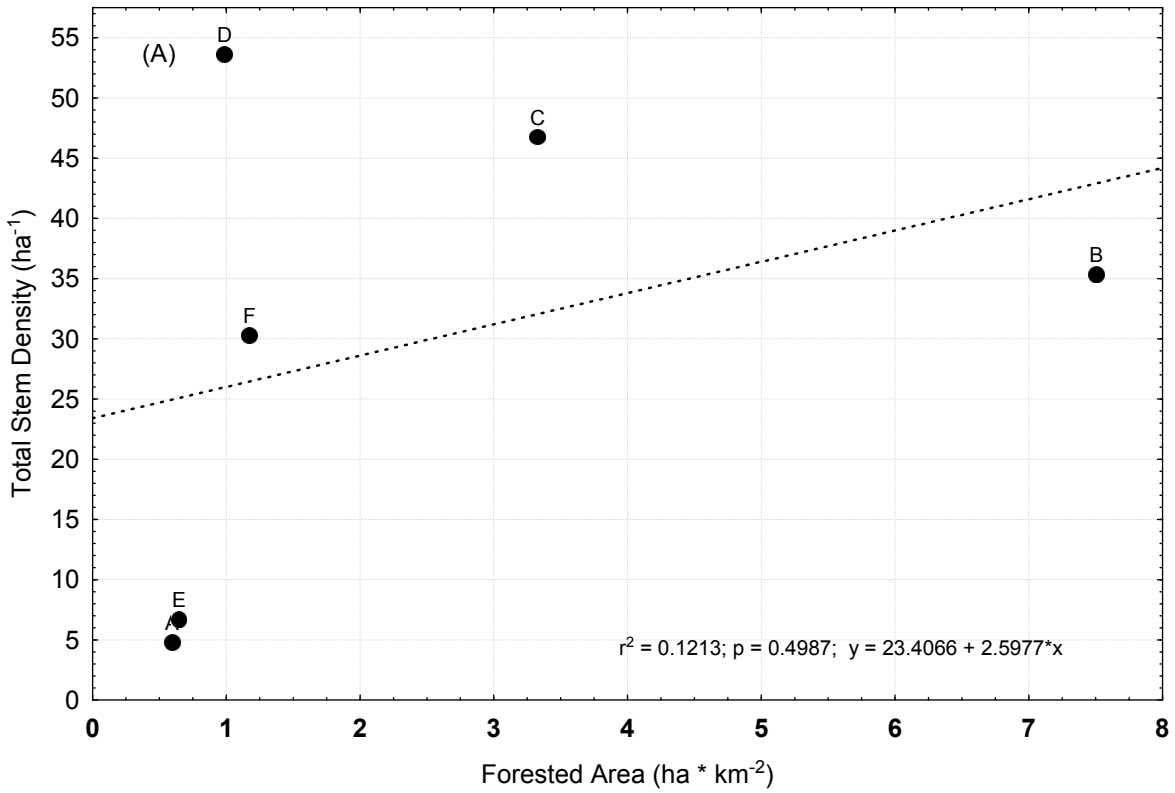


Figure 13a,b: Relationship between total stem density ($\# / \text{ha}$) and (A) total forested Area (ha / km^2) and (B) prairie wetness index within the *meso*-scape.

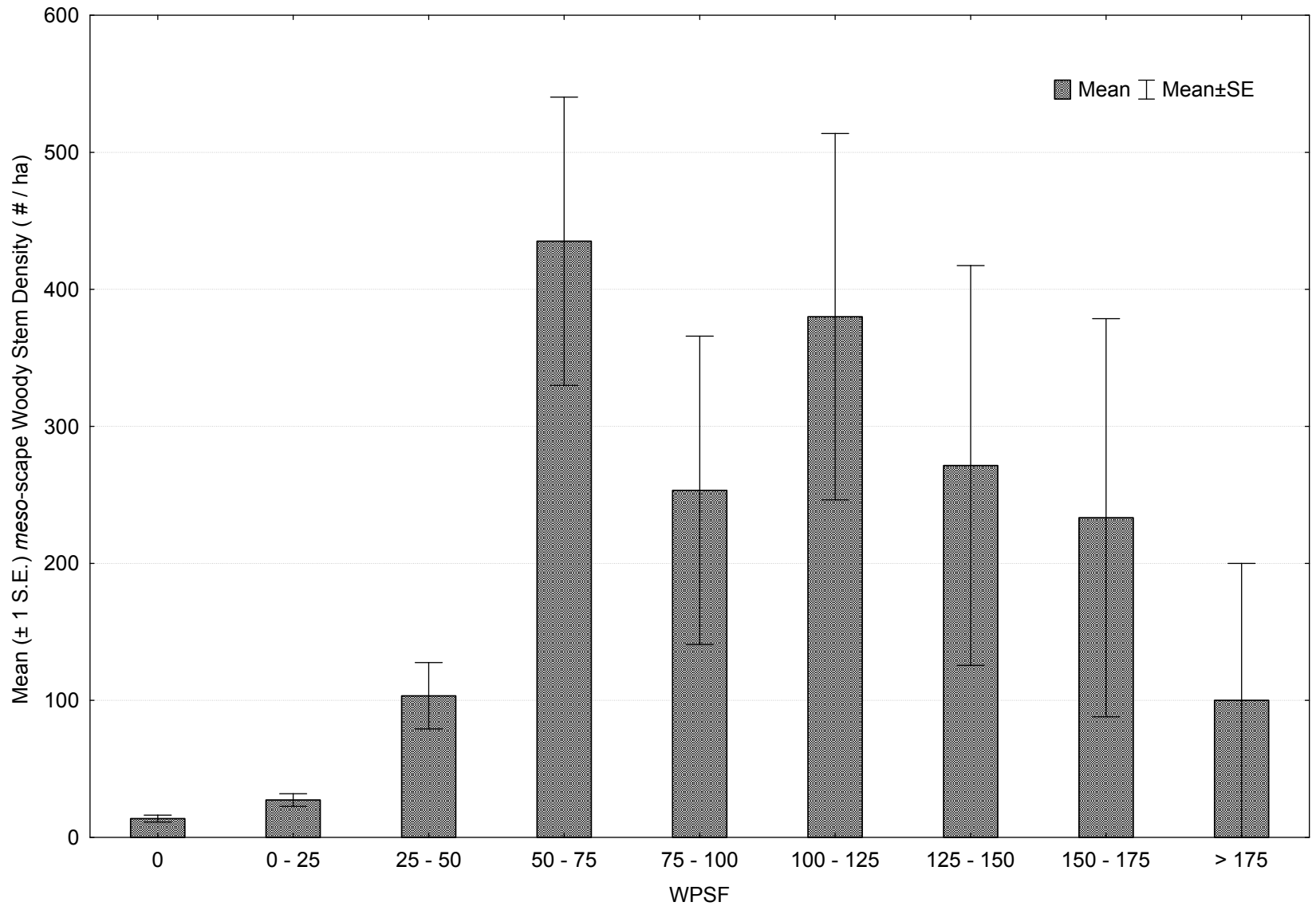


Figure 14: Mean (± 1 S.E.) *meso-scape* stem density (#/ha) as a function of WPSF (i.e size, number, & proximity of potential source islands).

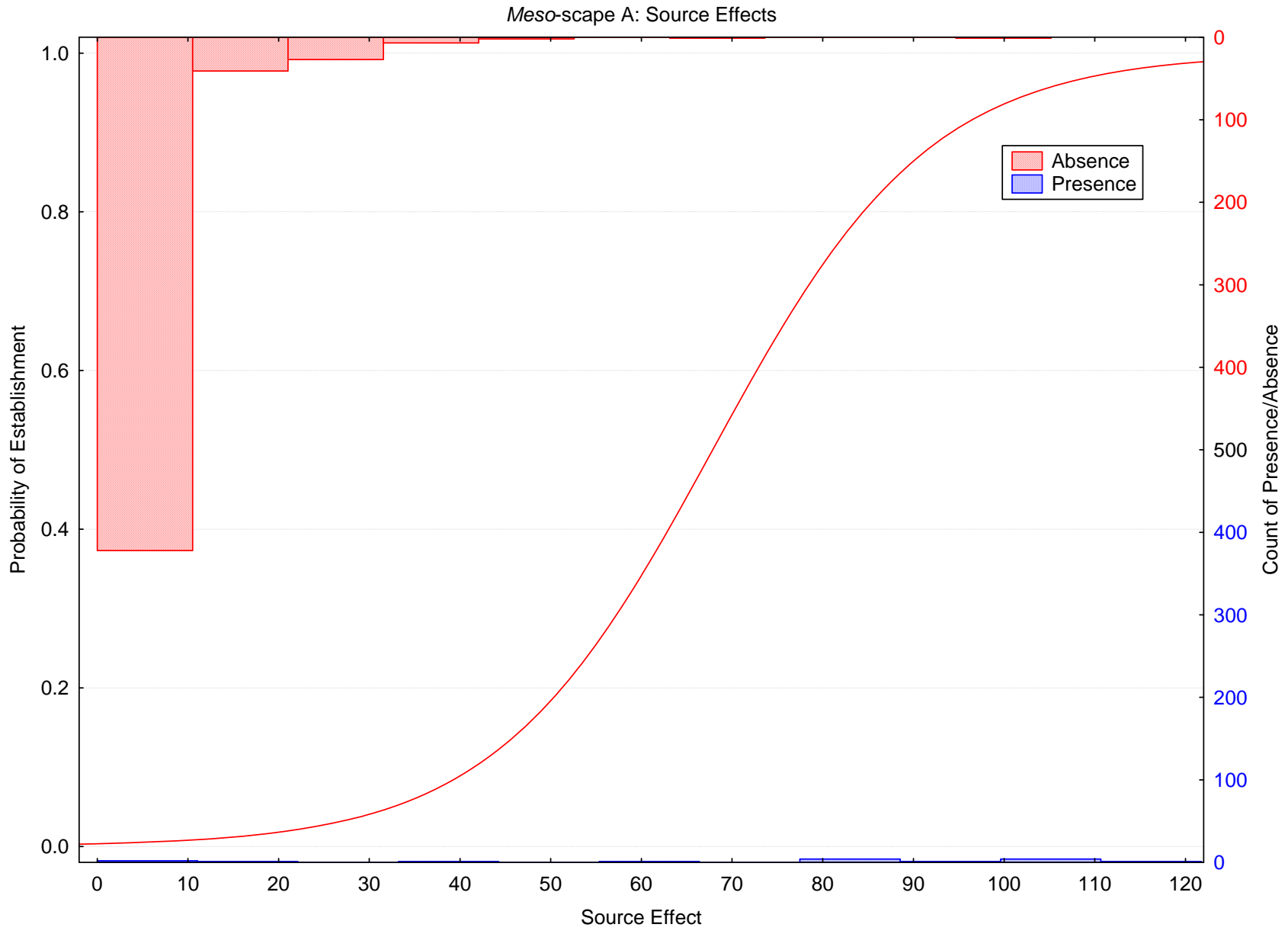


Figure 15: Source effects on non-species-specific establishment within *meso-scape* A. Bars represent the number of cells with individuals present or absent.

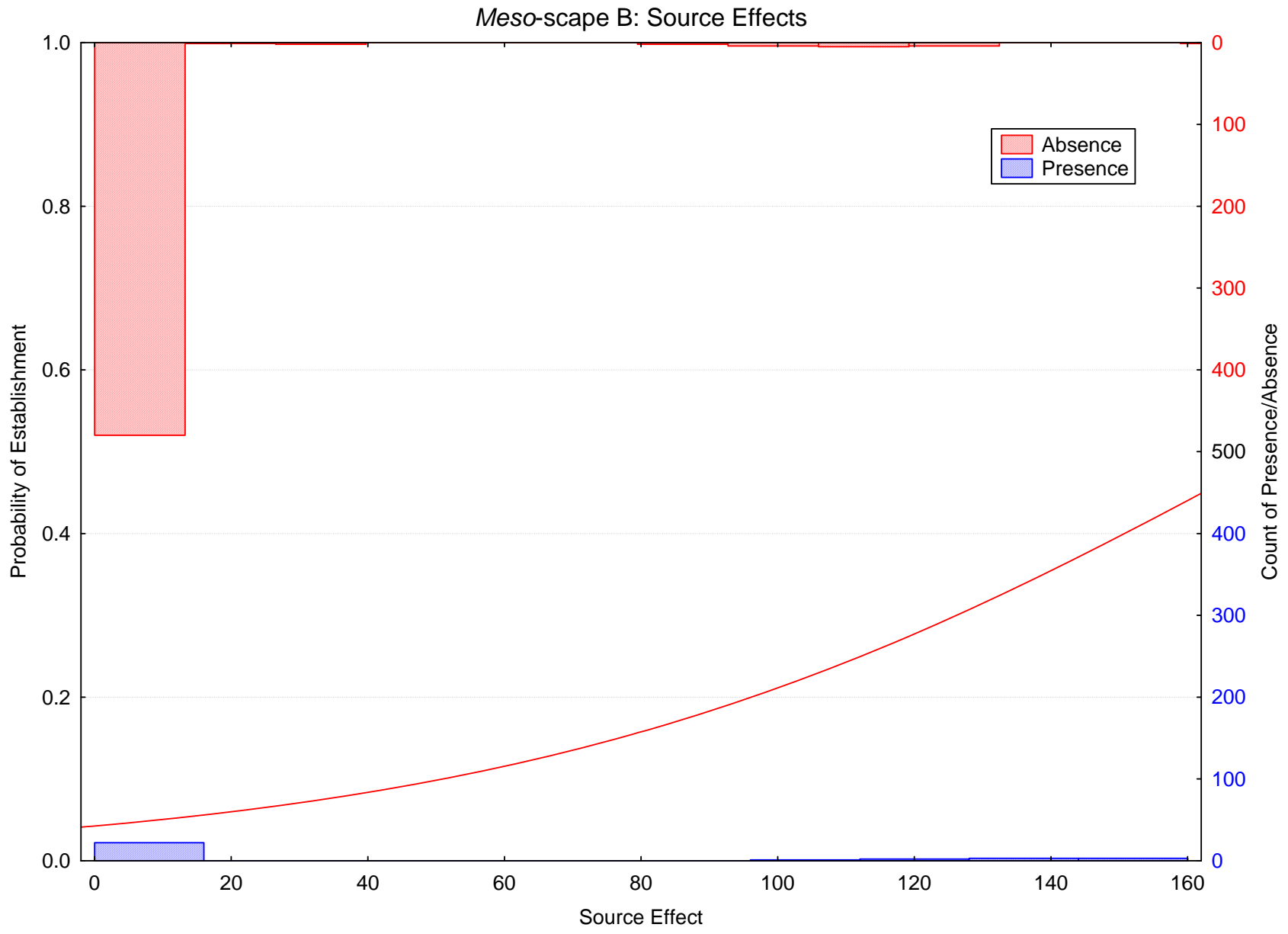


Figure 16: Source effects on non-species-specific woody plant establishment within *meso-scape* B. Bars represent number of cells with individuals present or absent.

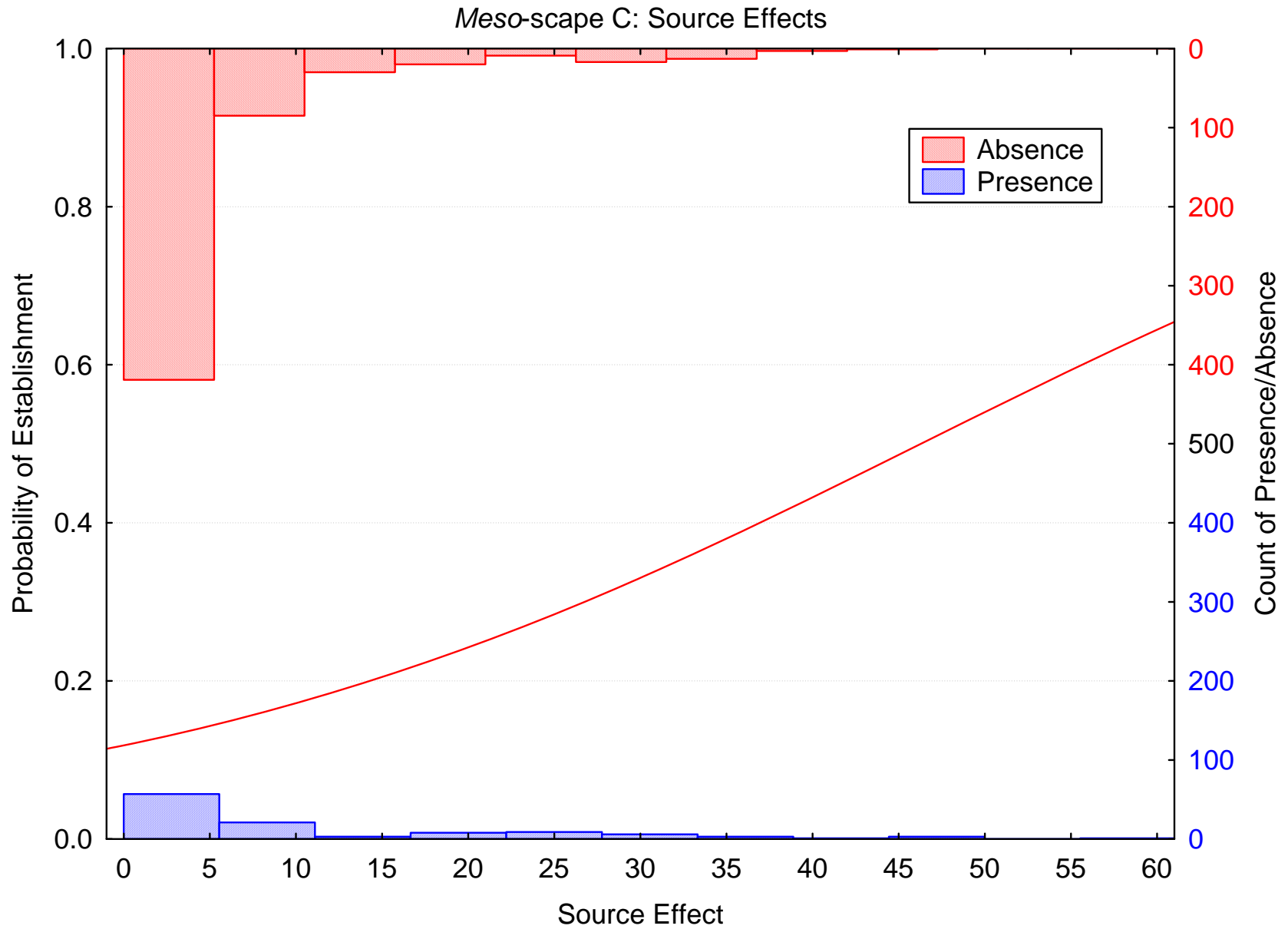


Figure 17: Source effects on non-species-specific establishment within *meso-scape* C. Bars represent number of cells with individuals present or absent.

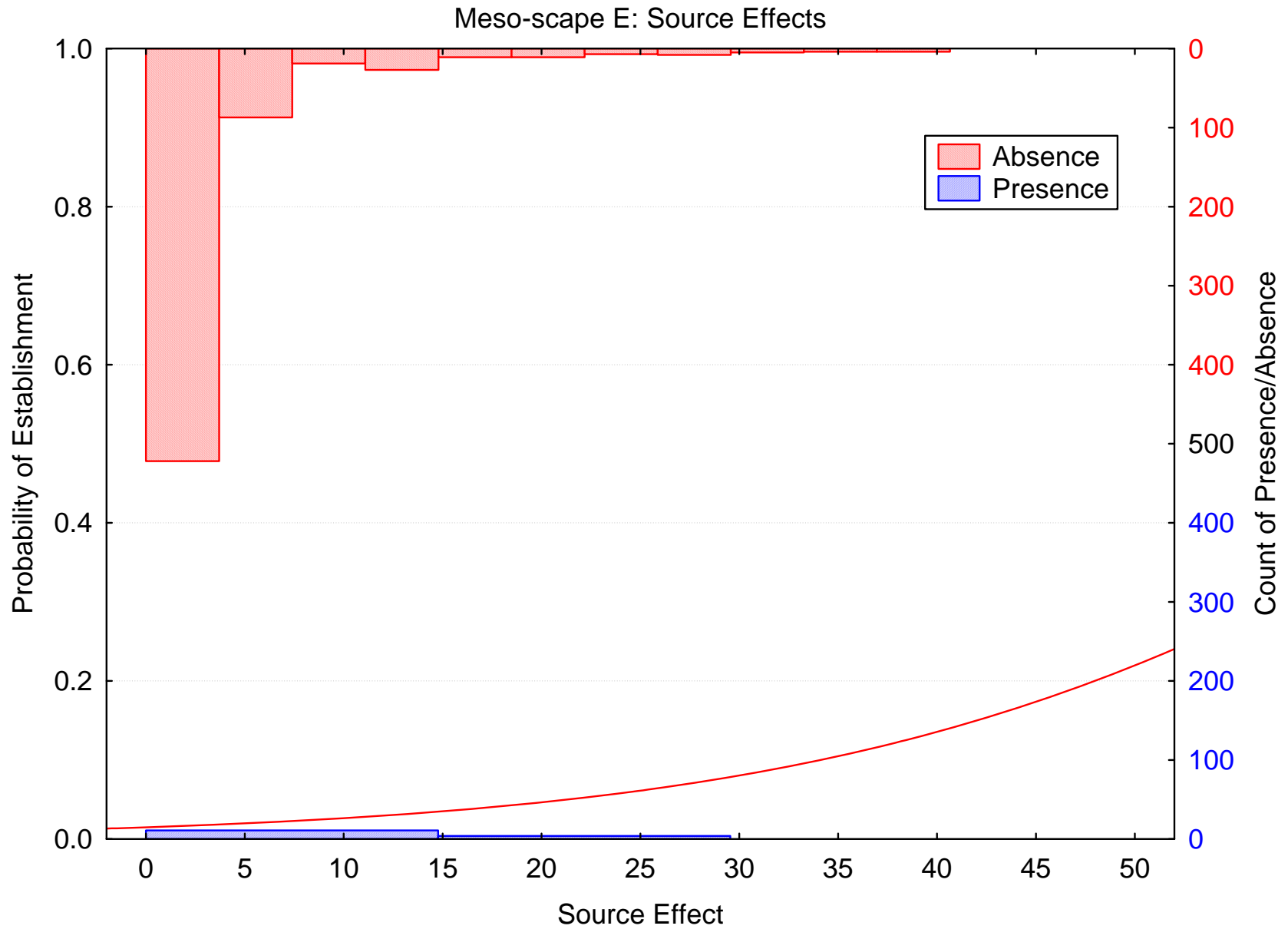


Figure 18: Source effects on non-species-specific woody plant establishment within *meso-scape* E. Bars represent number of cells with individuals present or absent.

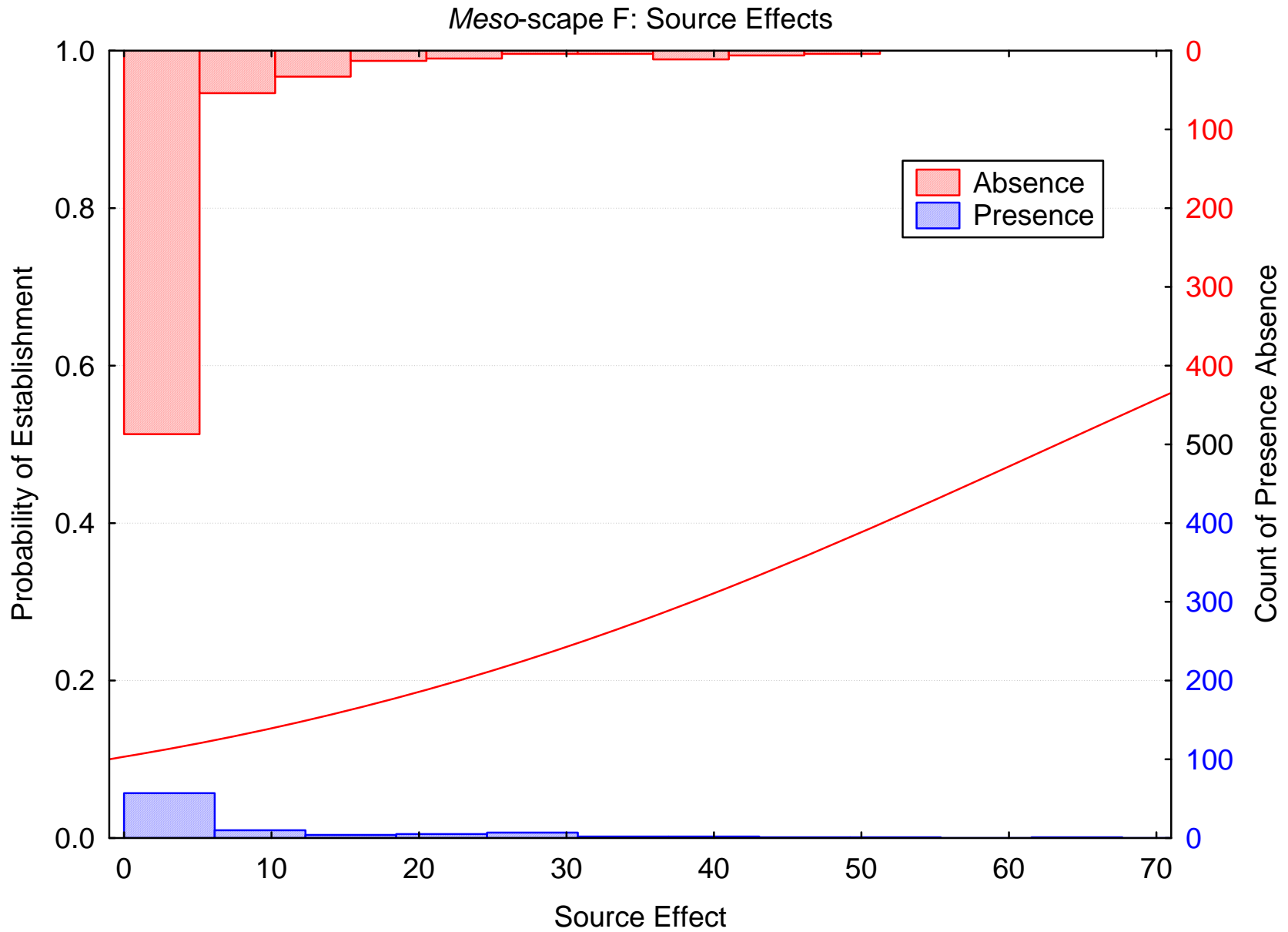


Figure 19: Source effects on non-species-specific woody plant establishment within *meso-scape* F. Bars represent the number of cells with individuals present or absent.

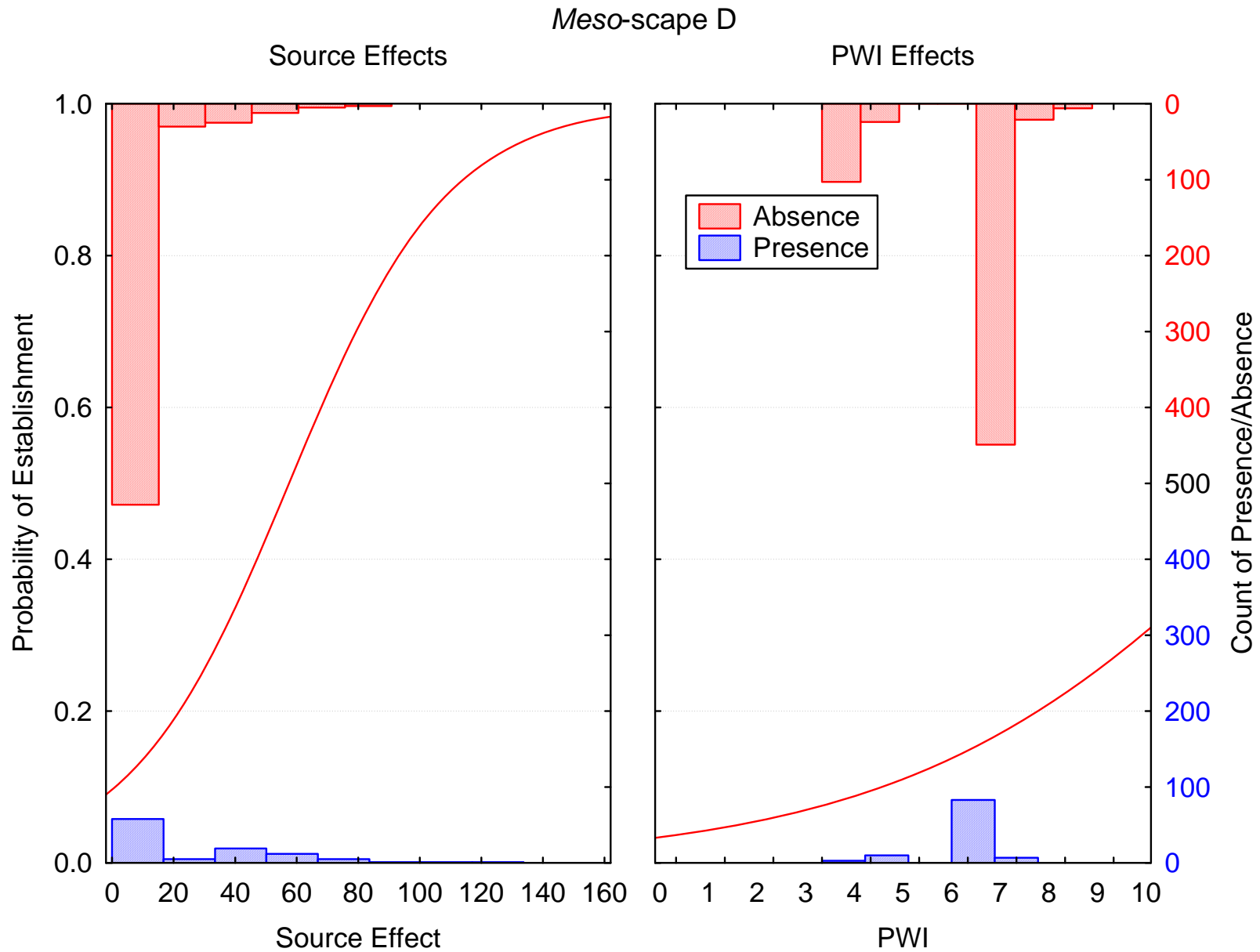


Figure 20: Source and PWI effects on non-species-specific woody plant establishment within *meso-scape D*. Bars represent the number of cells with individuals present or absent.

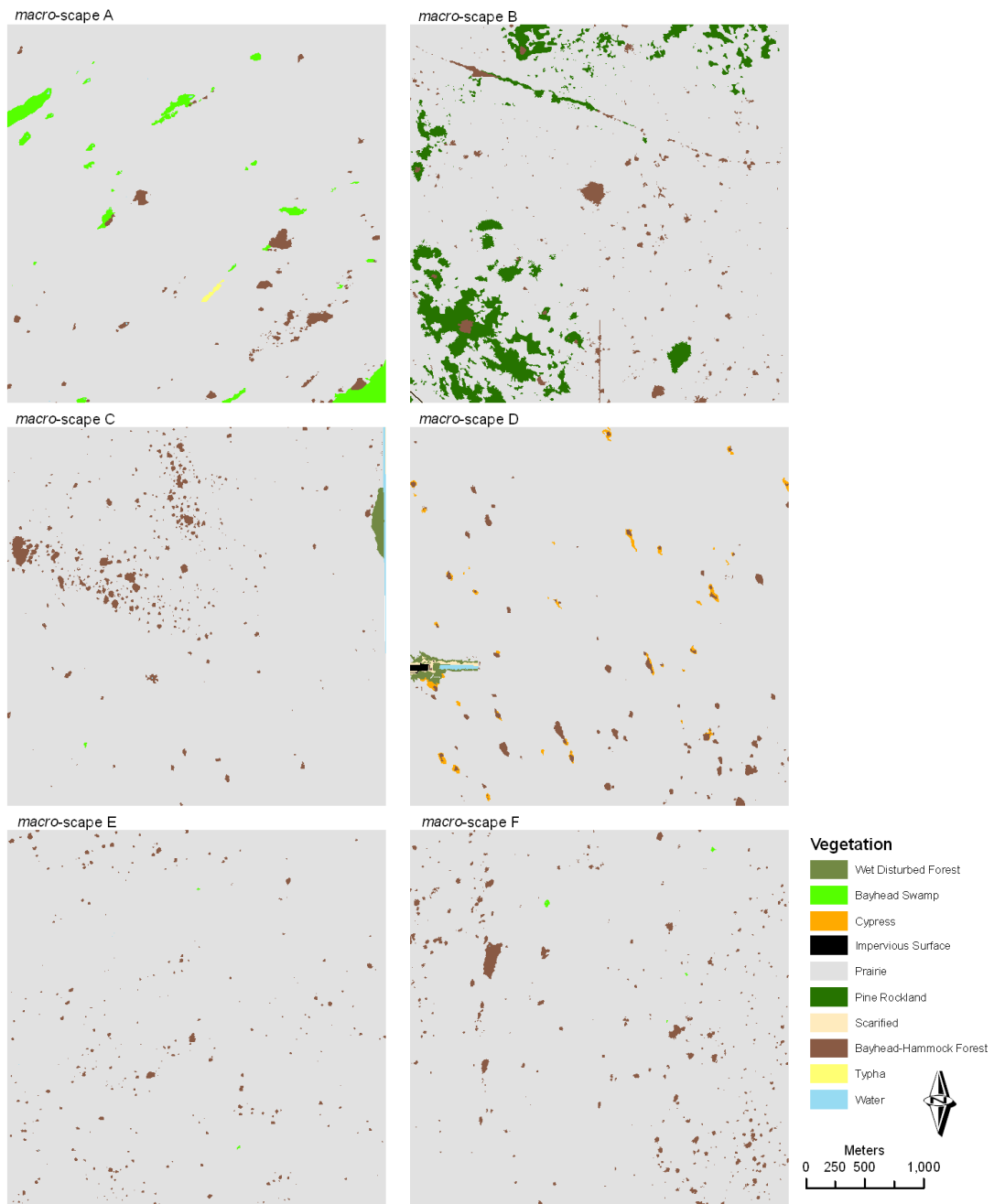


Figure 21: Vegetation maps for the six macro-scape plots within the habitat of the Cape Sable Seaside Sparrow in Everglades National Park, FL.

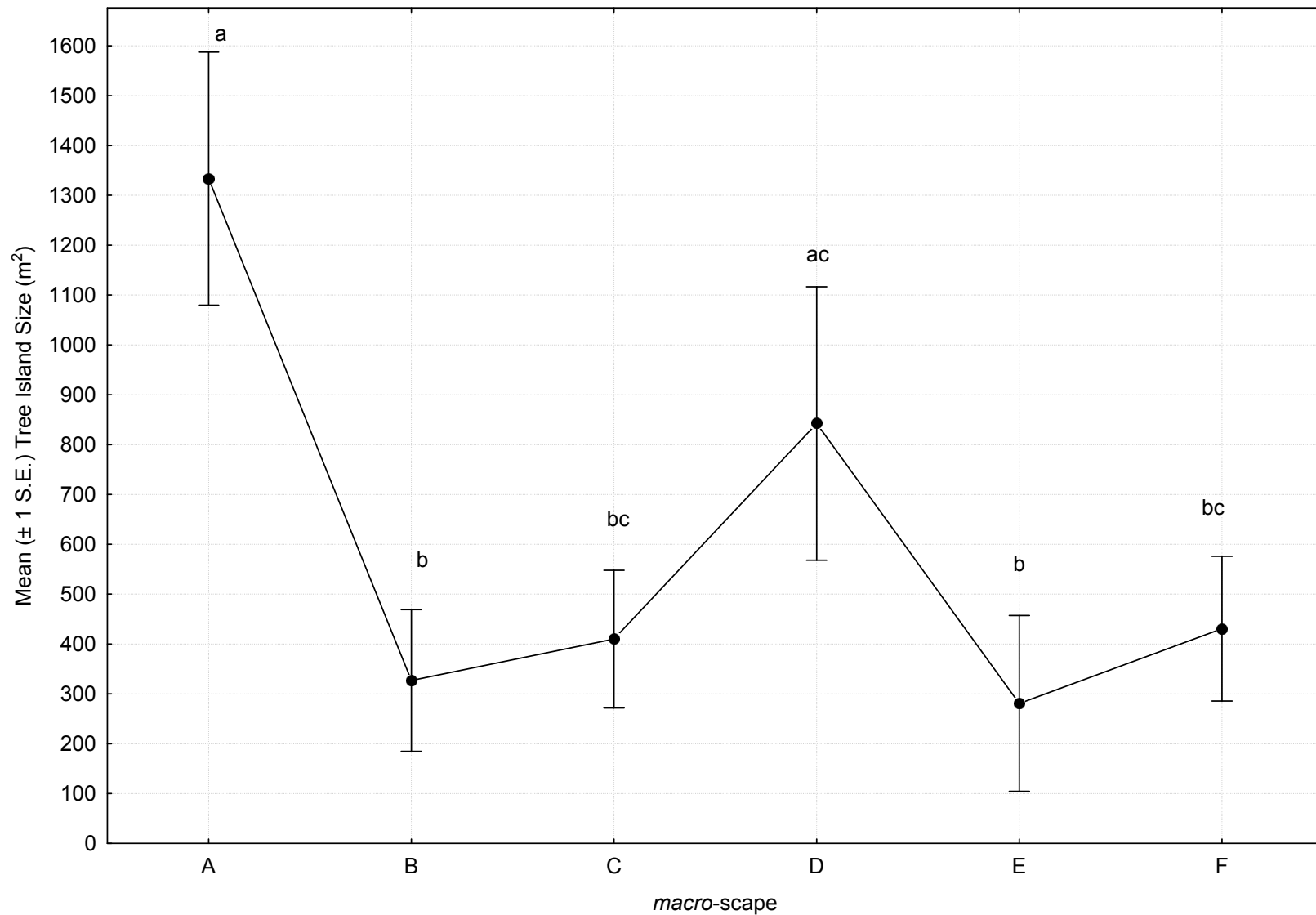


Figure 22: *Macro-scape* difference in mean (± 1 S.E.) tree island size (m²). *Macro-scapes* with same superscript do not differ at $p > 0.05$ (Bonferroni test).

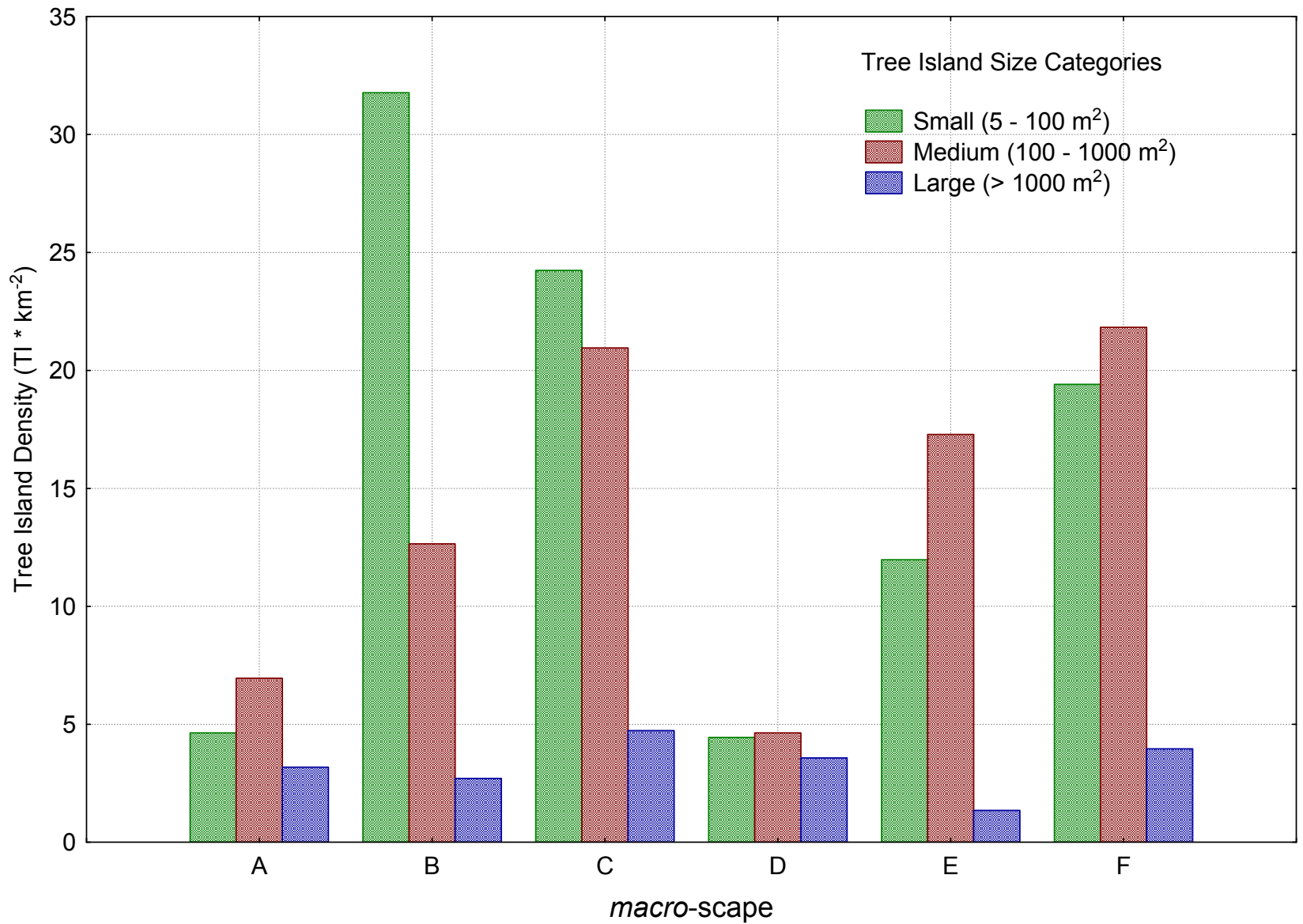


Figure 23: Distribution of Tree Island size by categories across all *macro-scapes*

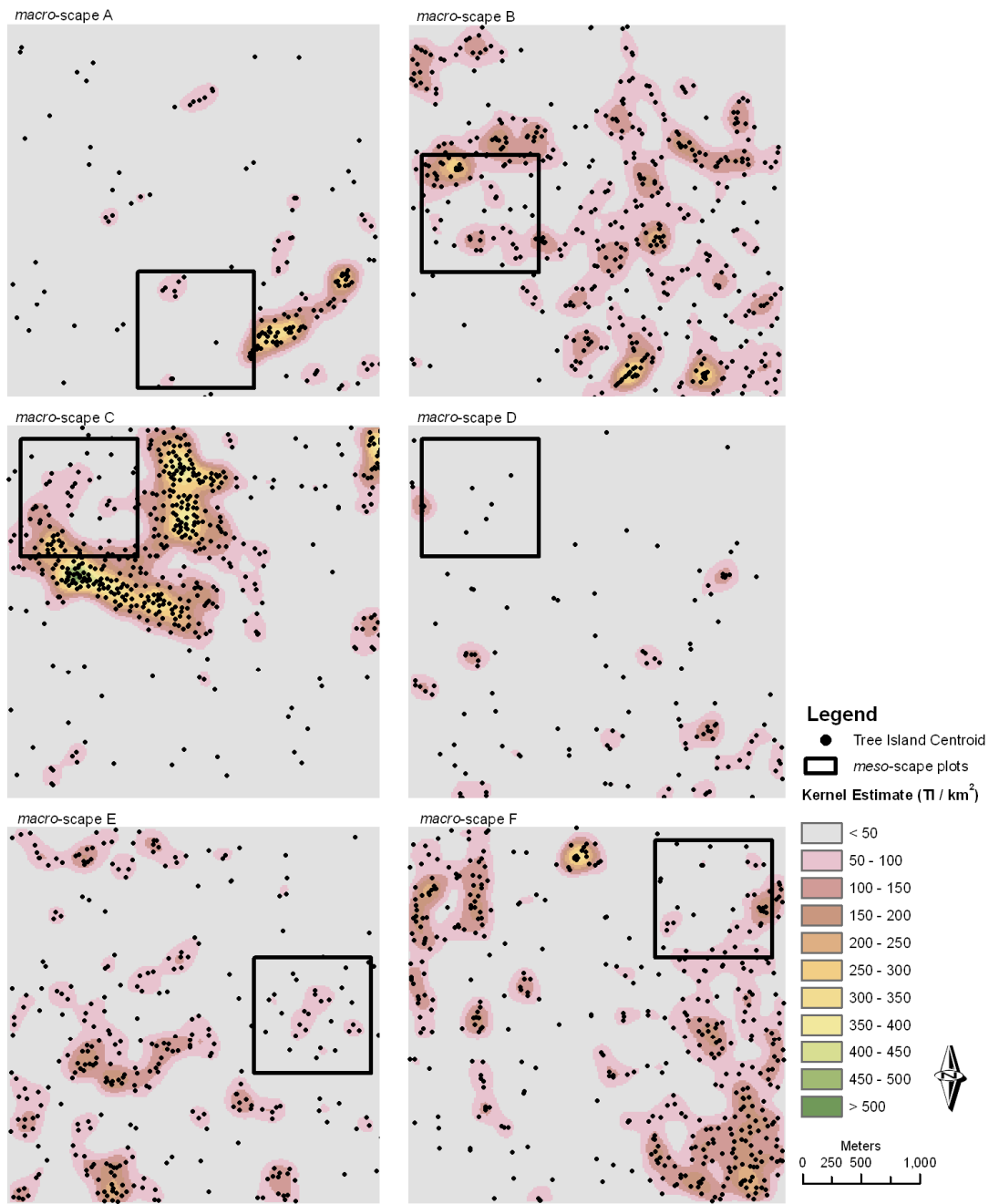


Figure 24: Kernel estimate of tree island density (Tree Island / km²) for all six macro-scapes.

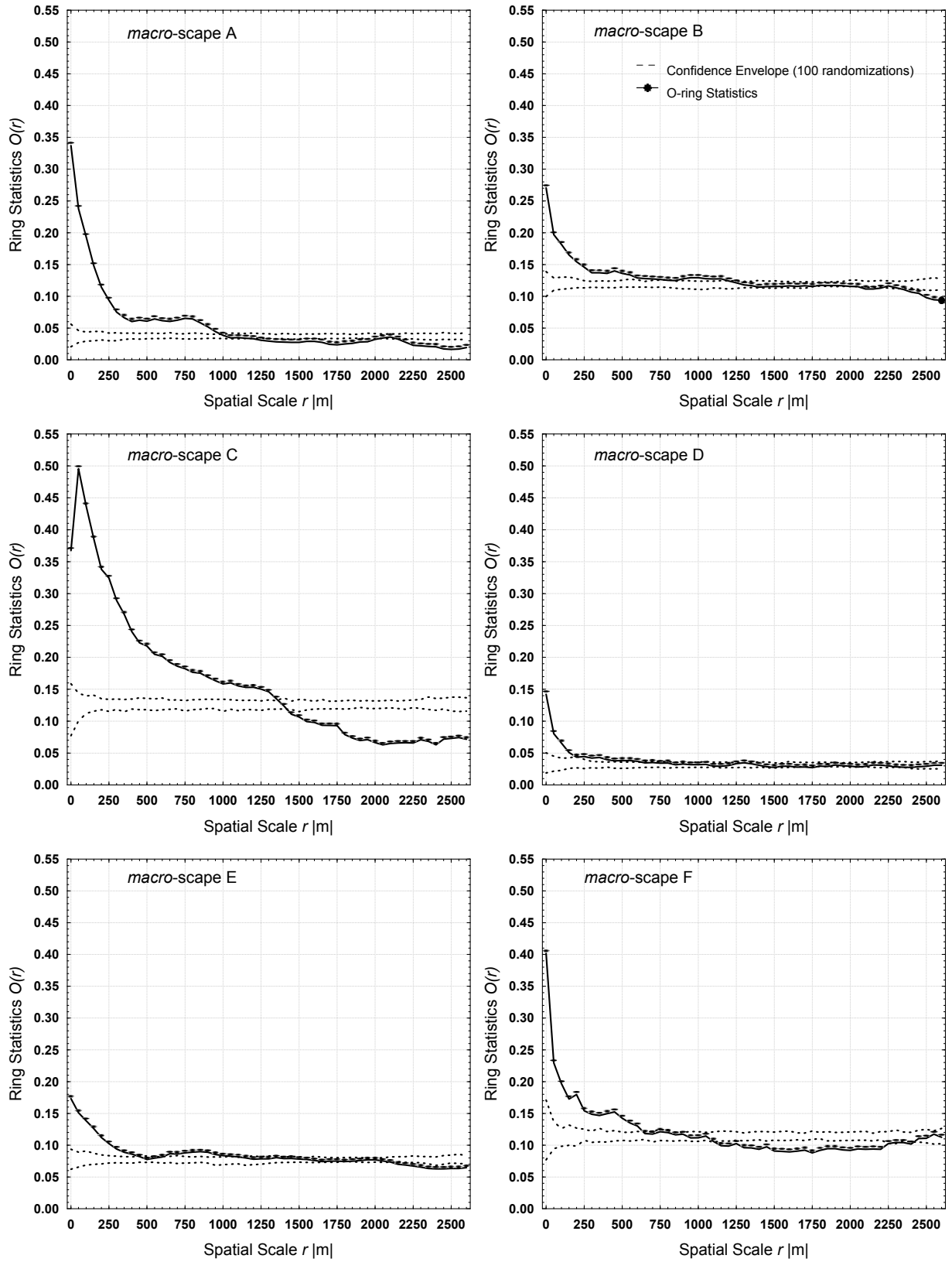


Figure 25: Univariate analysis of tree island aggregation within each of the six *macro-scapes* using the O-ring function (see methods section).

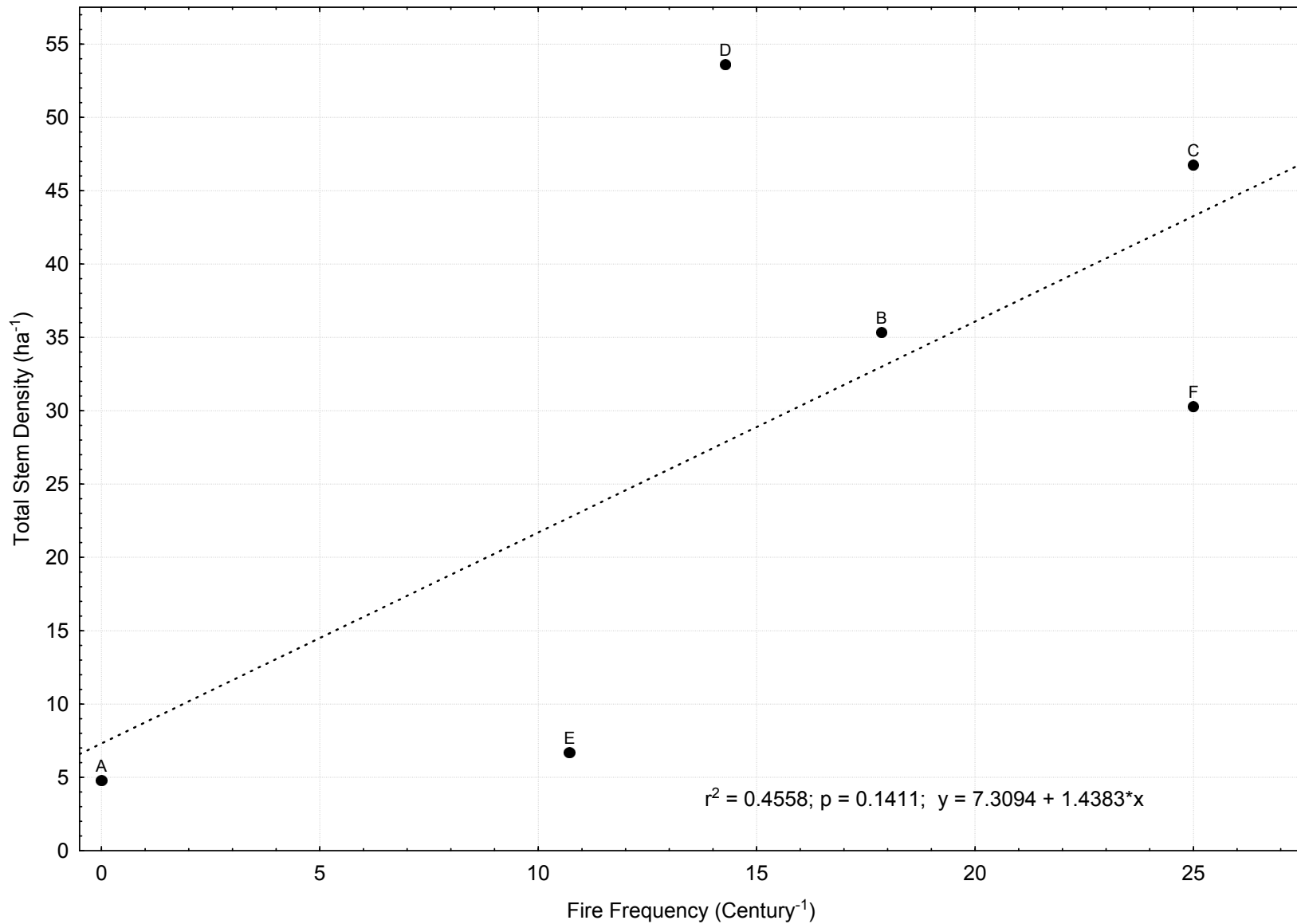


Figure 26: Relationship between total woody plant density and fire frequency within each of the *macro*-scapes.

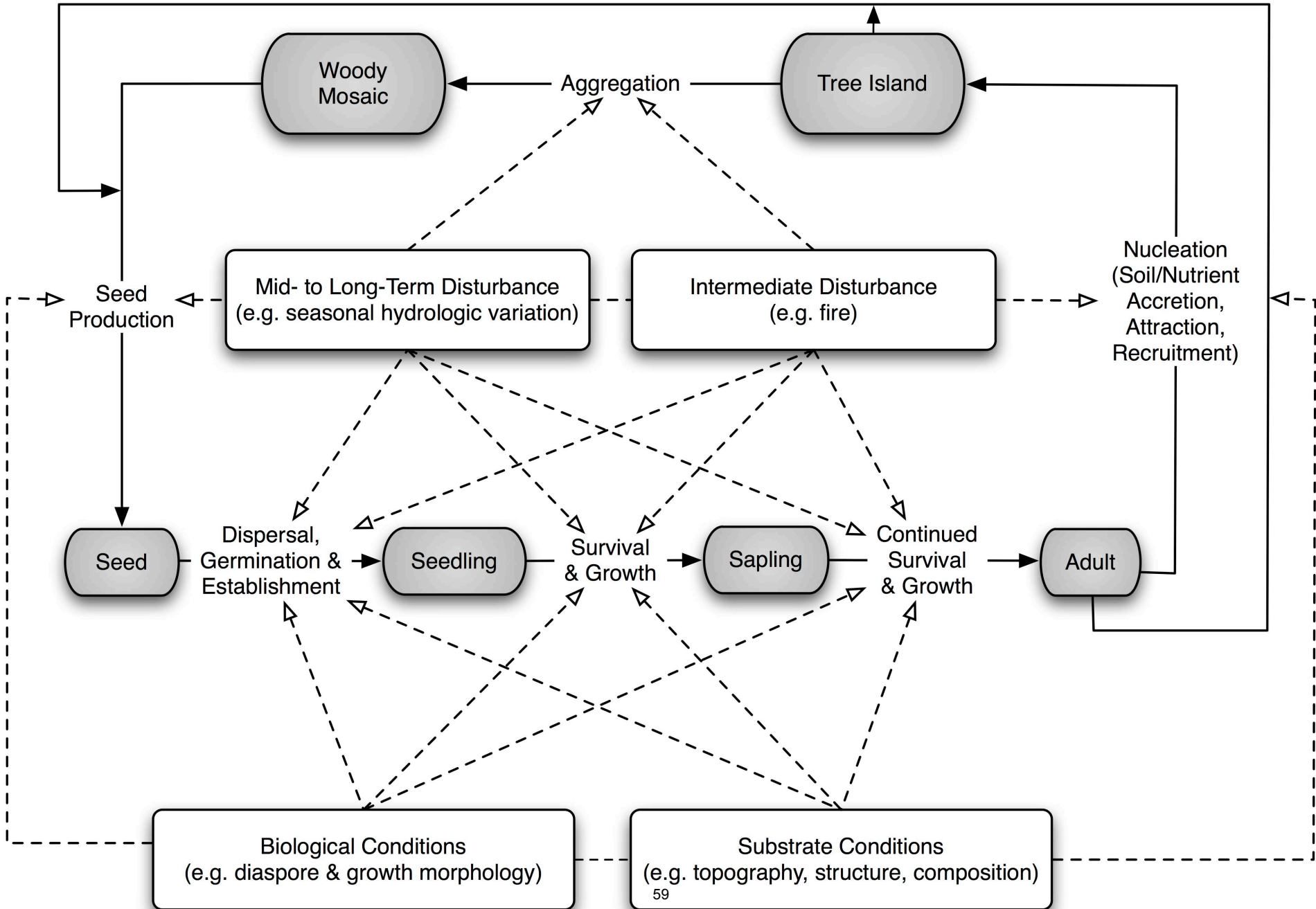




Plate 1: *Micro-scape B* central tree island approximately (A) 3 months and (B) 2 years after 2005 fire.

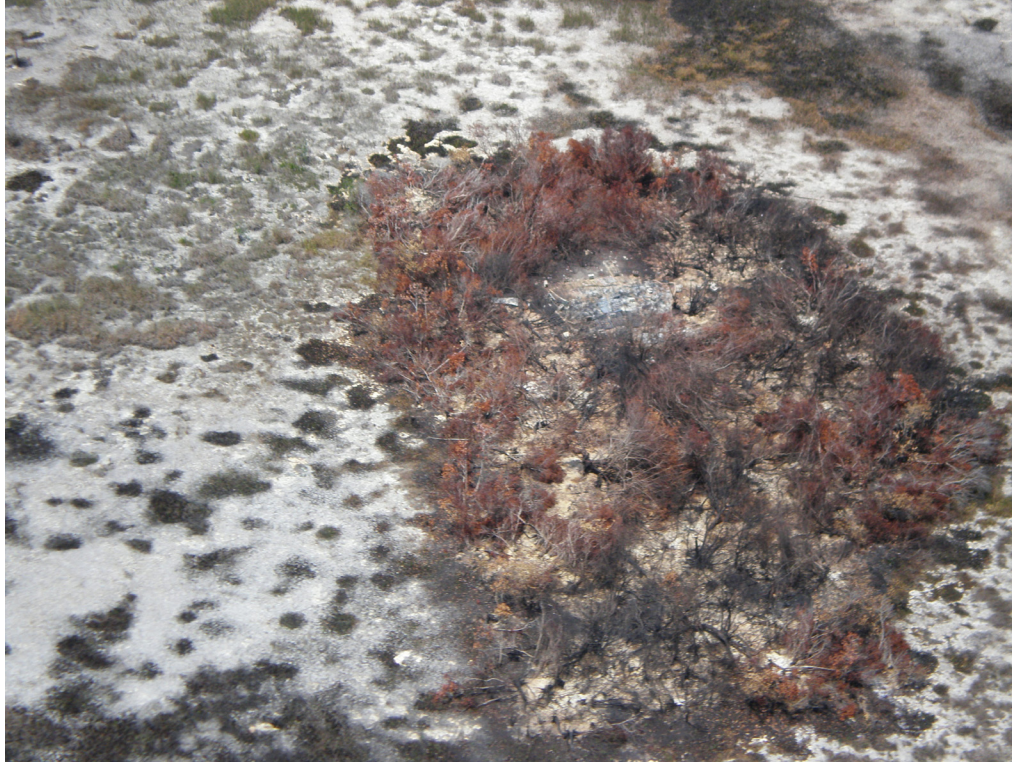


Plate 2: Tree island burn-out conditions resulting from the Mustang Corner Fire (May 2008) in Everglades National Park.