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# Remarkable Amphibian Biomass and Abundance in an Isolated Wetland: Implications for Wetland Conservation

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**Abstract:** *Despite the continuing loss of wetland habitats and associated declines in amphibian populations, attempts to translate wetland losses into measurable losses to ecosystems have been lacking. We estimated the potential productivity from the amphibian community that would be compromised by the loss of a single isolated wetland that has been protected from most industrial, agricultural, and urban impacts for the past 54 years. We used a continuous drift fence at Ellenton Bay, a 10-ha freshwater wetland on the Savannah River Site, near Aiken, South Carolina (U.S.A.), to sample all amphibians for 1 year following a prolonged drought. Despite intensive agricultural use of the land surrounding Ellenton Bay prior to 1951, we documented 24 species and remarkably high numbers and biomass of juvenile amphibians (>360,000 individuals; >1,400 kg) produced during one breeding season. Anurans (17 species) were more abundant than salamanders (7 species), comprising 96.4% of individual captures. Most (95.9%) of the amphibian biomass came from 232095 individuals of a single species of anuran (southern leopard frog [*Rana sphenoccephala*]). Our results revealed the resilience of an amphibian community to natural stressors and historical habitat alteration and the potential magnitude of biomass and energy transfer from isolated wetlands to surrounding terrestrial habitat. We attributed the postdrought success of amphibians to a combination of adult longevity (often >5 years), a reduction in predator abundance, and an abundance of larval food resources. Likewise, the increase of forest cover around Ellenton Bay from <20% in 1951 to >60% in 2001 probably contributed to the long-term persistence of amphibians at this site. Our findings provide an optimistic counterpoint to the issue of the global decline of biological diversity by demonstrating that conservation efforts can mitigate historical habitat degradation.*

**Keywords:** amphibian decline, biodiversity, drought, land use, wetland recovery

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## Biomasa y Abundancia de Anfibios Extraordinaria en un Humedal Aislado: Implicaciones para la Conservación de Humedales

**Resumen:** *A pesar de la pérdida de hábitats de humedales y las declinaciones asociadas de poblaciones de anfibios, se han realizado pocos intentos para traducir las pérdidas de humedales en pérdidas mensurables en los ecosistemas. Estimamos la productividad potencial de la comunidad de anfibios que se afectaría por la pérdida de un humedal aislado que ha estado protegido de los impactos industriales, agrícolas y urbanos durante los últimos 54 años. Utilizamos un cerco de desvío en la Bahía Ellenton, un humedal dulceacuícola de 10 ha en el Río Savannah, cerca de Aiken, Carolina del Sur (E.U.A.), para muestrear todos los anfibios durante 1 año después de una sequía prolongada. A pesar del intensivo uso agrícola del suelo alrededor de la Bahía Ellenton antes de 1951, documentamos 24 especies y números y biomasa de anfibios juveniles notablemente altos (>360,000 individuos; >1,400 kg) en una temporada reproductiva. Los anuros (17 especies) fueron más abundantes que las salamandras (7 especies), y comprendieron 96.4% de las capturas individuales. La mayor parte (95.9%) de la biomasa provino de 232095 individuos de una sola especie de anuro (*Rana sphenoccephala*). Nuestros resultados revelaron que la resiliencia de la comunidad de anfibios a los estresantes naturales y a la alteración histórica del hábitat y la magnitud potencial de la transferencia de biomasa y energía desde los humedales aislados hacia el hábitat terrestre circundante. Atribuimos el éxito post-sequía de los anfibios a una combinación de longevidad de adultos (a menudo > 5 años), la reducción de la abundancia de depredadores y la abundancia de recursos alimenticios para las larvas. Asimismo, el incremento de la cobertura forestal alrededor de la Bahía Ellerton de < 20% en 1951 a > 60% en 2001 probablemente contribuyó a la persistencia de los anfibios a largo plazo en este sitio. Nuestros hallazgos proporcionan un contrapunto optimista al tema de la declinación global de la diversidad biológica al demostrar que los esfuerzos de conservación pueden mitigar a la degradación histórica del hábitat.*

**Palabras Clave:** biodiversidad, declinación de anfibios, recuperación de humedales sequía, uso de suelo

## Introduction

Isolated wetlands, which support high species diversities and serve as essential habitat for many groups of organisms, are under increased threat of destruction. In the United States, the ongoing decline in numbers of isolated and other palustrine wetlands due to agricultural and commercial development since European settlement is well documented (Dahl 1990, 2000). At least 87% of the original 1.2 million ha of shrub bog pocosins (see description in Sharitz & Gibbons 1982) in the southeastern United States have been destroyed or altered (Richardson 1983). Similarly, 69% of playas >4 ha in the Southern Great Plains have been modified by cultivation, grazing, and other activities (Guthery & Bryant 1982). The *Solid Waste Agency of Northern Cook County v. U.S. Army Corps of Engineers* (2000) decision by the U.S. Supreme Court has weakened federal jurisdiction over isolated wetlands, effectively leaving freshwater wetlands unprotected when they lack a permanent surface-water connection to navigable waterways and have no link to interstate commerce (Zedler et al. 2001; Downing et al. 2003). The loss and degradation of numerous wetlands have presumably resulted in a concomitant loss of species abundance and diversity, with ramifications for ecosystem functioning.

Despite the ecological value of isolated wetlands to regional biodiversity (Whigham 1999) and their importance for maintaining metapopulation connectivity for semi-aquatic species (Gibbs 1993; Semlitsch & Bodie 1998), few researchers have quantified the productivity achiev-

able within a taxonomic group from a single isolated wetland over a well-defined time frame. Moreover, although surrounding terrestrial habitats are critical for the integrity of wetland ecosystems (Gibbons 2003), few researchers have enumerated the potential transfer of biomass and energy from wetlands to surrounding terrestrial ecosystems.

Our study was undertaken to document the potential contribution of amphibians to secondary production and to the transfer of matter and energy between aquatic and terrestrial habitats. Although the global decline of amphibians has been confirmed repeatedly (Stokstad 2004; Stuart et al. 2004), attempts to translate wetland losses into tangible effects on ecosystems due to the loss of amphibian productivity have been lacking. Our results demonstrate the levels of amphibian abundance and diversity that contribute to habitat interconnectivity and that could potentially be lost by the elimination of a single isolated wetland. We also addressed the critical question of how rapidly and successfully amphibian populations inhabiting ephemeral wetlands in a historically agricultural landscape can recover from multiyear droughts.

## Methods

### Study Site

Ellenton Bay (Gibbons 1990) is an isolated freshwater wetland, typical of Carolina bays (see descriptions in Sharitz & Gibbons 1982; Sharitz 2003), and within a 202-ha

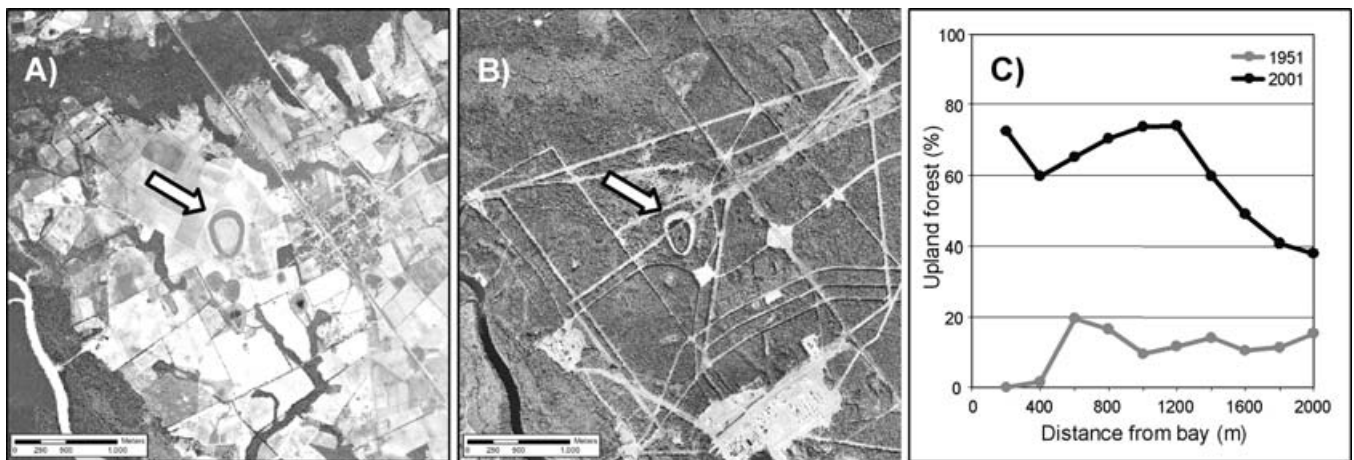


Figure 1. Aerial photos from (a) 1951 and (b) 2001 of land cover surrounding Ellenton Bay (arrows) and (c) relationship between distance from Ellenton Bay and the proportion of the landscape within 2 km of the periphery of Ellenton Bay classified as upland forest in 1951 and in 2001. In 1951 Ellenton Bay was within a 202-ha agricultural field planted in cotton and corn. By 2001 natural succession had restored the landscape to primarily pine and mixed pine-hardwood forest.

formerly agricultural field that was planted in cotton, peanuts, and corn from the 1870s through 1951 (Fig. 1; Davis & Janecek 1997). The fish-free wetland is in South Carolina on the U.S. Department of Energy's (DOE) Savannah River Site (SRS), a national environmental research park (Shearer & Frazer 1997). Wetlands on the SRS have been protected since 1951 from most of the environmental perturbations typically resulting from agricultural, urban, and industrial alterations in the region. Ellenton Bay and surrounding uplands have received special protection as part of the DOE Set-Aside Program, which was established to protect habitats and facilitate long-term research. No herpetofaunal diversity or population data are available for Ellenton Bay and surrounding areas before establishment of the SRS. Because of the historical emphasis on clearing and preparing lands for agricultural purposes, we presume that species diversity and abundance at the wetland in the first half of the twentieth century were reduced from historical levels. Nonetheless, long-term (since 1968) herpetological studies conducted at Ellenton Bay suggest that the amphibian species richness characteristic of the region (Gibbons & Semlitsch 1991) had recovered within 25 years. After 1951, Ellenton Bay and other wetlands on the SRS returned to more natural conditions as a consequence of secondary succession coupled with limited forest management activities.

The closest isolated wetland to Ellenton Bay is ~200 m away, and Ellenton Bay has the longest hydroperiod of the nonpermanent wetlands in the region. The only wetland within 1.4 km of Ellenton Bay that holds water during multiyear droughts is a small, human-made pond ~0.5 km from the bay. The areal extent of the Ellenton Bay basin when full is approximately 10 ha. A dike 5 to 6 m wide divides the bay completely and creates two distinct

aquatic areas when water depth is <1.5 m. Water surface area and depth are extremely variable, with a maximum depth of approximately 2 m. During periods of drought, subsurface moisture normally remains beneath the thick organic crust that covers the entire basin up to 0.5 m deep (Gibbons 1990). Parts of the basin remain mucky during some dry periods, with up to 1 ha of viscous mud surrounding small areas of open water, but no standing water remained during the 2000–2003 drought. Two major multiyear droughts have occurred at Ellenton Bay during the last 29 years (Willson et al., 2006), the first from October 1987 through August 1990, and the second from August 2000 to February 2003. We initiated the current study in February 2003 at the end of the second drought.

#### Historical Changes in Land Use

We used object-based classification of aerial photographs to quantify the change in land cover between 1951 and 2001. We classified groups of pixels, rather than individual pixels, which allowed us to incorporate both spectral (i.e., red-green-blue [RGB] values) and contextual information (i.e., spatial configuration) of objects (Walter 2004). To define our area of interest, we used a bounding rectangle that fully encompassed the 2-km radius from the edge of Ellenton Bay. Panchromatic aerial photographs, with an on-ground resolution of 2 m, were taken in 1951 in conjunction with the establishment of the DOE facility. False-color, infrared, aerial photographs were taken in 2001. We resampled from 0.3 to 2 m to provide a consistent on-ground resolution between time periods. We used filters and advanced learning algorithms incorporated in Feature Analyst (version 3.4, Visual Learning Systems, Missoula, Montana), an extension of ArcGIS (version 8.3,

Environmental Systems Research Institute [ESRI], Redlands, California), to conduct supervised classifications. We segmented images and extracted general types of land cover that were easily recognized (i.e., Anderson level 1 classes of urban, agricultural, forest, water, wetland, and barren) for both time periods. We generated summary statistics of classified maps for discrete 200-m-wide buffer intervals radiating out from the perimeter of Ellenton Bay.

### Collection Techniques

In February 2003, we re-erected a terrestrial drift fence (Gibbons & Semlitsch 1981; Semlitsch et al. 1996) that had been used in studies at Ellenton Bay for all or part of 19 of the 28 years from 1968 to 1994 (Gibbons 1990; Seigel et al. 1995). The continuous drift fence completely encircled the wetland and was equipped with pitfall and funnel traps, which allowed us to capture most of the amphibians entering and exiting the wetland. Serendipitously, we began monitoring the fence and traps 3 days before the start of a long period of rain that began to refill the wetland, after 2.5 years of drought. We monitored the fence from 1 February 2003 to 31 January 2004 and therefore were able to document the abundance and productivity of amphibians throughout the first wet year following the drought.

The drift fence was constructed of aluminum flashing (1230 m long, 40 cm high) and buried several cm into the soil (Gibbons & Semlitsch 1981). The distance of the fence from the margin of the water varied with water level but was <10 m in many places when the bay reached its maximum water level in August 2003. We placed 164 traps in pairs on opposite sides of the fence, with half of the traps on each side of the fence, allowing individual amphibians to be categorized as entering or leaving the bay (Gibbons & Semlitsch 1981). Of these, 41 pairs of 19-L pitfall traps (plastic buckets), spaced approximately every 30 m along the fence, were in place on 1 February 2003. On 24 February 2003, we installed 21 pairs of 2.3-L pitfall traps (metal coffee cans) between every other pair of buckets along the fence (60 m apart). On 27 February 2003, we installed 20 pairs of wooden box funnel traps (Himes 2000; Zappalorti & Torocco 2002) along the fence (60 m apart) between bucket pairs where cans had not been placed. Thus, bucket pairs were followed alternately by cans and funnel traps.

Pitfall and funnel traps were checked a minimum of once daily (0700–0900 hours). During warm months, traps were checked again in the late afternoon (1700–2000 hours). Sponges were placed in the bottom of buckets and cans, providing moisture during dry conditions or a “raft” if water collected in buckets between checks; however, standing water was bailed from buckets and cans daily as needed. We classified captured amphibians as recently metamorphosed individuals or adults (see

“Productivity and Biomass”) and released them approximately 10 m away on the opposite side of the fence.

During peak emigrations of recently metamorphosed amphibians (e.g., ~ 7,000 to 41,000 individuals per night), special procedures were needed to reduce mortality associated with predation and overcrowding in traps. Box traps were not deployed at night, and in addition to morning and afternoon checks, all other traps were checked multiple times during the night to aid emigration of recently metamorphosed individuals. On a few occasions, we did not use box traps during the day to reduce the possibility of heat-related mortality of amphibians. During peak emigrations involving thousands of animals, counting all individuals of some species would have resulted in unnecessary mortality due to prolonged retention of animals in traps. Consequently, we estimated the number of captured animals by counting the number of animals contained in a handful or one sweep of a dipnet and the number necessary to empty the trap. During mass emigrations, animals were released approximately 30 m on the outside of the fence to discourage immediate recapture. Recently metamorphosed amphibians captured entering the wetland during peak emigrations were assumed to have been emigrants that had been captured and released earlier, rather than being immigrants from other wetlands; therefore, they were re-released on the outside of the fence and not included in capture totals.

### Productivity and Biomass

To determine amphibian productivity at Ellenton Bay, we estimated the number of emigrating young of year of all species. Because the wetland was dry during the previous 2.5 years, recently metamorphosed amphibians captured leaving Ellenton Bay during this study could be categorized unambiguously as having been produced during the 2003 breeding season. One or more of three criteria were used to classify amphibians emigrating from the wetland as recently metamorphosed: (1) similar in size to published data on size at metamorphosis for the particular species from this region, (2) incomplete resorption of the tail in anurans or of the gills in salamanders, (3) species-specific attributes indicating recent metamorphosis (e.g., a distinct ventral stripe in *A. talpoideum*; scars at base of forearms in anurans).

To estimate body size at metamorphosis, we haphazardly collected subsamples of newly metamorphosed individuals ( $n = 1-148$ ) for focal species and measured snout-vent length (SVL;  $\pm 0.5$  mm) and wet body mass ( $\pm 0.01$  g). We used the mean wet mass to estimate the total biomass for each species produced at Ellenton Bay during 2003. Individuals that were part of the 2003 juvenile cohort but were older juveniles at the time of capture (i.e., likely had experienced significant postmetamorphic growth while still inside the fence) were not used for

estimates of body size at metamorphosis, but their counts were used in estimating total biomass.

At Ellenton Bay, the mole salamander (*A. talpoideum*) is the only species that undergoes facultative paedomorphosis (Patterson 1978; Semlitsch et al. 1990). Thus, we subsampled metamorphosed individuals of this species in two different seasons (spring and fall) to generate separate estimates of body size at metamorphosis and biomass. By January 2004 it became difficult to distinguish whether emigrating animals were large, newly metamorphosed individuals from breeding that occurred in 2003 (and therefore should have been tallied for the biomass estimate) or were postbreeding adults from the 2003–2004 season. Although some of these salamanders were no doubt part of the 2003 cohort, we did not count them as such. Consequently, our total biomass estimate for *A. talpoideum* is a highly conservative one.

To convert amphibian abundance to density estimates, we first had to calculate the maximum area of the wetland. We used global positioning system technology (Trimble Pro-XR, Sunnyvale, California, with submeter accuracy) to map the perimeter of the Ellenton Bay basin. We defined the perimeter of the maximum waterline as the boundary between emergent grasses (predominantly *Panicum* spp.) in the bay's basin and the surrounding pine (*Pinus* spp.) forest. We used ArcView (version 3.3, ESRI) to calculate the area of the resulting polygon.

## Results

### Historical Changes in Land Use

Historical accounts from inhabitants of the area suggest that intensive agriculture began in the 1800s, and agricultural alteration of the landscape was conspicuous in 1951, at which time forested habitat comprised <20% of the area within 1 km of Ellenton Bay (Fig. 1). The last row of crops—primarily corn, cotton, and peanuts—were harvested from fields adjacent to Ellenton Bay in 1951 (Davis & Janecek 1997). In 1957 pine trees were planted within 80 m of the south end of the wetland, and natural establishment of pines adjacent to the bay began to occur by the mid-1960s. Since that time, Ellenton Bay and most of the surrounding fields have undergone natural vegetation succession, with forest coverage within 1 km of the bay increasing to 60–75% by 2001 (Fig. 1).

### Productivity and Biomass

During the single year of drift-fence sampling at Ellenton Bay, we captured 408,220 amphibians representing 24 species. Of the individual captures, 96.4% were anurans (17 species) and the remainder were salamanders (7 species). Most ( $n = 21$ ) of the amphibian species at Ellenton Bay were captured by April 2003, and all had been captured by 19 August 2003. At least 362,956 recently

**Table 1.** Total number of young-of-year amphibian emigrants at a single isolated wetland, Ellenton Bay, in South Carolina (U.S.A.).<sup>a</sup>

Scientific name	Common name	Total biomass (kg)	Number of individuals	Mean mass (g)	Aquatic density (animals/ba)	Production (kg/ba/year)
<b>Salamanders</b>						
<i>Ambystoma opacum</i>	marbled salamander	0.35	104	3.33	11	0.04
<i>Ambystoma tigrinum</i>	tiger salamander	25	1,171	21.21	125	3
<i>Ambystoma talpoideum</i>	mole salamander—late summer metamorphosis	14	2,412	5.91	257	2
<i>Ambystoma talpoideum</i>	mole salamander—spring metamorphosis	29	6,046	4.87	643	3
total		68.35	9,733	—	1036	8.04
<b>Anurans</b>						
<i>Hyla chrysoscelis</i> <sup>b</sup>	gray treefrog	—	1	—	0.1	—
<i>Hyla squirella</i> <sup>b</sup>	squirrel treefrog	—	10	—	1	—
<i>Hyla cinerea</i> <sup>b</sup>	green treefrog	—	15	—	2	—
<i>Acris gryllus</i>	southern cricket frog	—	56	—	6	—
<i>Scaphiopus holbrookii</i>	eastern spadefoot toad	0.17	316	0.55	34	—
<i>Pseudacris crucifer</i>	spring peeper	0.89	1,970	0.45	210	0.09
<i>Rana clamitans</i>	green frog (bronze frog)	1	216	5.63	23	0.13
<i>Hyla gratiosa</i> <sup>b</sup>	barking treefrog	1	362	3.88	39	0.15
<i>Pseudacris ornata</i>	ornate chorus frog	4	3,126	1.20	333	0.40
<i>Bufo terrestris</i>	southern toad	48	115,056	0.42	12,240	5
<i>Rana sphenoccephala</i> <sup>b</sup>	southern leopard frog	1307	232,095	5.63	24,691	139
total		1421	353,223	—	37,577	151
Amphibian total		1490	362,956	—	38,612	159

<sup>a</sup>Secondary production during the 1-year study period was estimated as the number of young of year captured leaving the wetland, minus the number of young of year captured entering the wetland.

<sup>b</sup>Total captures were likely significantly underestimated due to the species' ability to climb or jump over the drift fence. Estimates of biomass are the number of young-of-year emigrants multiplied by the mean individual mass of 1–135 haphazardly selected individuals. The individual mass used for *R. clamitans* was estimated from the mass of similarly sized *R. sphenoccephala*.

metamorphosed amphibians produced at Ellenton Bay emigrated to the surrounding terrestrial habitat (Table 1). Most (95.9%) of the amphibian biomass came from 232095 individuals (1307 kg) of a single species of anuran (southern leopard frog [*R. sphenoccephala*]; Table 1). Two species of salamanders (mole salamander [*Ambystoma talpoideum*] and tiger salamander [*A. tigrinum*]) and one species of anuran (southern toad [*Bufo terrestris*]) each produced more than 24 kg of biomass during the year and collectively produced more than 115 kg (Table 1). Minimum estimates of larval amphibian density and biomass for the aquatic portion of Ellenton Bay were 38612 individuals/ha and 159 kg/ha/year, based on the maximum area inundated and numbers of emigrating young of year (Table 1). Productivity of *R. sphenoccephala* alone was at least 139 kg/ha/year (Table 1). Young-of-year densities (individuals per ha) for the two most abundant species were 24,691 (*R. sphenoccephala*) and 12240 (*B. terrestris*; Table 1). The productivity levels we observed for most amphibian species are likely substantial underestimates, because individuals were recorded only terrestrially when they departed from the aquatic area of the wetland.

## Discussion

Our findings on biomass and density demonstrate that amphibians are key components of wetland ecosystems and can potentially supply an appreciable portion of the energy transferred between aquatic and terrestrial habitats. Although high, our estimates of individual numbers and biomass of amphibians from a single natural wetland are conservative because of sampling protocols. For example, many individuals of some amphibian species did not leave the aquatic habitat during the study owing to delayed metamorphosis. Some species also tend to remain within or near aquatic areas following metamorphosis, making them less likely to emigrate as far as the drift fence. In addition, some climbing species of anurans (e.g., hylid treefrogs [Dodd 1991]; Table 1) are capable of surmounting drift fences, leading to an underestimation of abundance and young-of-year biomass for these species. Thus, the actual contribution of the amphibian community to secondary productivity at Ellenton Bay during a single year was appreciably higher than observed.

Previous estimates of wetland productivity have typically focused on primary production. Estimates of wetland primary productivity for vascular plants and algae (e.g., Barker & Fulton 1979; Neckles 1984; Hooper & Robinson 1976; Brinson et al. 1981) vary by an order of magnitude, depending on factors such as hydrology, timing and duration of inundation, latitude, and dominant plant species (Brinson et al. 1981). Net primary production of three depressional wetlands in South Carolina ranged from 564 to 774 g/m<sup>2</sup>/year as measured by stem production and litterfall (Busbee et al. 2003).

Secondary production in freshwater wetlands has been measured less often than primary production and most estimates are of invertebrate production (e.g., White 1985; Plante & Downing 1989; Leeper & Taylor 1998; Taylor et al. 1989). Information on productivity or biomass of vertebrates in aquatic systems, other than amphibians, is limited and includes studies on fish (e.g., Lawler et al. 1974), turtles (e.g., Iverson 1982; Congdon et al. 1986), and snakes (e.g., Godley 1980; Shine 1986). We did not determine terrestrial densities of the Ellenton Bay amphibian species. However, our density estimate of 38612 individuals/ha in the aquatic habitat is consistent with results of previous studies indicating that amphibians are among the most abundant vertebrates in aquatic and terrestrial systems. For example, terrestrial plethodontid salamanders reached densities of 2000–2500 individuals/ha in a New Hampshire forest (Burton & Likens 1975) and at least 18486 individuals/ha in a streamside habitat in the Southern Appalachians (Petranka & Murray 2001). Maximum biomass and numbers of larval tiger salamanders (*A. tigrinum*) were estimated to be 180 kg/ha and 5000 individuals/ha in prairie ponds of the western United States (Deutschman & Peterka 1988). Our productivity estimate (159 kg/ha/year) of amphibians that successfully emigrated from the aquatic habitat demonstrates that isolated wetlands contributed substantially to the overall productivity of the surrounding landscape.

The numbers of individuals and species of amphibians we observed, considering both the immediate drought and history of intensive agricultural use of the Ellenton Bay study site, demonstrate that wetland functions can recover from both natural and anthropogenic disturbances under some circumstances. During drought years in the Coastal Plain of the southeastern United States, when isolated wetlands either do not fill or have extremely short hydroperiods, amphibian populations can experience complete reproductive failure (i.e., zero recruitment). Ellenton Bay presumably had minimal amphibian productivity during the 3 years preceding the 2003 study, based on known responses of amphibians to drought and extrapolation from observations at Rainbow Bay, a Carolina bay wetland located 11.5 km from Ellenton Bay (Semlitsch et al. 1996). Continuous long-term data (1978–2004) for 13 amphibian species at Rainbow Bay indicate that all species suffered virtually complete reproductive failures for 4 of the first 16 years of study owing to shortened hydroperiods (Semlitsch et al. 1996). From 2000 to 2003, when both the Rainbow Bay and Ellenton Bay breeding sites remained dry for all or most of each year, limited or no juvenile recruitment occurred at Rainbow Bay (D.E.S., J.L.G. & B.S.M., unpublished data).

The continued presence and productivity of amphibians at Ellenton Bay in 2003–2004, despite prolonged drought, was due in part to an extensive storage component of long-lived individuals in habitats outside the wetland and a reduction in predators and increase in prey

within the wetland. Evidence suggests that most of the breeding adults that repopulated Ellenton Bay in 2003 were individuals that had persisted in the surrounding terrestrial habitat rather than being dispersers from other wetlands. A capture–recapture study at Rainbow Bay documented longevities of >5–10 years for individuals of at least seven of the species that occur at Ellenton Bay, and some of these species (e.g., *Ambystoma* spp., *B. terrestris*) are known to abide drought in terrestrial habitats adjacent to the wetland (D.E.S., unpublished data).

Although the persistence of many amphibian populations at the landscape level depends on dispersal and recolonization from other wetlands (Semlitsch 2000), most amphibians arriving at Ellenton Bay did not immigrate from the direction of the only nearby permanent water body, but instead arrived at the drift fence from all directions. All ephemeral wetlands within 2 km of Ellenton Bay have shorter hydroperiods and would not have served as a refuge for amphibians during the preceding drought. Following droughts, when adult amphibians return to Ellenton Bay to breed, their larvae benefit both from a reduced abundance of predators (e.g., aquatic snakes, turtles, and predatory insects; Gibbons et al. 1983; Seigel et al. 1995; Taylor et al. 1999; Willson et al. 2006) and from enhanced nutrient levels that support primary production (i.e., algae) and invertebrate prey (e.g., copepods and cladocerans; Taylor et al. 1988; Taylor & Mahoney 1990). Such years of strong recruitment are in effect “stored” in the population because the persistence and staggered reproduction of long-lived adults buffer against fluctuations in juvenile recruitment from the aquatic stage (Warner & Chesson 1985; Taylor et al. 2006).

Studies of the relationship between landscape characteristics and amphibian distribution patterns have generally found positive associations between amphibians and forested habitat (e.g., Hecnar & M'Closkey 1996; Gibbs 1998; Willson & Dorcas 2003; Porej et al. 2004). Assessing the effects of previous agricultural activities on amphibians is often equivocal, however, because of limited historical information and because associations between amphibians and agriculture vary regionally according to landscape context and species composition. Some researchers have detected decreases in amphibian diversity in landscapes with intensive agriculture (Bonin et al. 1997; Hecnar 1997). However, results of a study in Iowa and Wisconsin showed little effect or slightly positive effects of agriculture on amphibian richness and abundance in Wisconsin and more negative associations in Iowa (Knutson et al. 1999). Both the extent and proximity of forested lands to wetland breeding habitat influence amphibian species occurrence and abundance. Results of a study of forest extent and adjacency around 116 breeding ponds in Maine showed that five of nine amphibian species (three of which were woodland salamanders) were positively associated with forest area in

the surrounding landscape (Guerry & Hunter 2002). Similarly, Gibbs (1998) noted that two species of woodland salamanders do not persist once forest cover is reduced below a threshold level (30–50%).

In 1951 forest comprised <20% of the area within 1 km of Ellenton Bay, and it is likely that the salamander component of the amphibian fauna (*Ambystoma opacum* [marbled salamander], *A. talpoideum*, *A. tigrinum*) was reduced relative to current population sizes. In general, from 1951 to 2004, both the forest extent and adjacency increased dramatically (Fig. 1), which likely promoted increased salamander diversity and numbers. For anuran species, the impressive numbers of *B. terrestris* and *R. sphenoccephala* witnessed in 2003 as the wetland refilled after drought may have occurred under similar conditions prior to 1951, although no earlier records are available. Nonetheless, it is reasonable to assume that many of the amphibian species, particularly the forest-dependent salamanders, that use Ellenton Bay as a breeding site would not have persisted if the wetland had remained embedded in an agricultural landscape without forested peripheral habitats.

Our findings highlight the key role of small, isolated wetlands in amphibian productivity and in maintaining community dynamics by coupling aquatic habitats with adjacent terrestrial habitats via transfer of biomass and energy. Although the observed numbers and biomasses of amphibians we report are very high, we suspect these results are typical responses to postdrought conditions, rather than a one-time occurrence. Our findings offer hope that even moderate conservation efforts that protect wetlands and allow surrounding terrestrial habitat to recover from prior disturbance can promote a diverse amphibian community. Our results also suggest that current U.S. wetland regulations that do not offer protection to isolated wetlands will jeopardize conservation efforts to preserve the contribution of amphibian biodiversity to ecosystem productivity on a landscape level.

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