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Compositional Changes in Two Small Mammal Communities During Succession in Southeastern Virginia

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ABSTRACT

Changes in the composition of two small mammal communities were studied during 8 and 9 years of ecological succession in southern Chesapeake, Virginia. Using monthly live-trapping on grids of similar size and history since their abandonment as agricultural fields, we learned that house mice were early colonists on one grid but not the other. Two species of herbivorous rodent and the granivorous eastern harvest mouse were numerically dominant on both grids across the study. Some species disappeared early on one grid but persisted to the end at the other. The two arboreal small mammals, golden and white-footed mice, were most predictable between sites, showing up at year 8, after significant woody elements were present on the grids. The greatest abundances of small mammals (and probably greatest total biomass too) were seen between years 4 and 6 of ecological succession.

Key Words: community composition, small mammals, succession, Virginia

INTRODUCTION

Ecological succession, including of small mammals, begins immediately after an agricultural field is abandoned. In eastern North America, succession (as originally outlined by Clements, 1916, and best understood with plants) usually begins with the establishment of grasses and, to a lesser extent, herbaceous dicotyledonous plants (forbs); the seeds of these fast-growing plants are present in the soil seed bank. Later, woody elements such as shrubs and tree saplings are added, their composition being determined by proximity to seed sources, wind direction and intensity for carrying seeds to the field, seed transport and sometimes storage by seed-eating mammals such as squirrels or other rodents, among other factors. Eventually the shade provided by the leaves of woody plants eliminates the once-dominant herbaceous vegetation, and although some plant species able to live in low light do become established on the forest floor, the mature forest has much lower plant diversity than earlier stages of succession. As these changes in plant composition occur, the composition of almost every other

group of organisms in this dynamic habitat changes too, whether mycorrhizal fungi (e.g., Boerner et al., 1996; Hartnett and Wilson, 1999), insects (e.g., Martinko et al., 2006), spiders (e.g., Hurd and Fagan, 1992), or small mammals (e.g., Foster and Gaines, 1991; Kirkland, 1977; Larkin et al., 2008).

The speed with which an abandoned farm field becomes a mature forest depends on a number of factors, including the length of the growing season, the harshness of winters or duration of a drought, the amount and distribution within the year of rainfall, such physical factors as the water-holding capacity and richness of the soil, among others (Cramer and Hobbs, 2007). In southeastern Virginia, where our field studies of small mammals were conducted, many factors are particularly favorable for a rapid conversion from field to forest: a long growing season, hot summers, 1.3 m of rainfall uniformly distributed across the months of the year, a large number of cloud-free days, rich organic soils, and mild winters ([Southeast Regional Climate Center: www.sercc.com](http://www.sercc.com); see [Wallaceton-Lake Drummond site](#)).

The purpose of this research was to examine the changes in the numbers and kinds of small mammals present during the different stages of ecological succession, from habitats dominated by grasses to those with little herbaceous vegetation. We expected to see (1) dominance by herbivorous rodents early in succession, (2) gradual or sharp loss of herbivores when the grasses disappeared, and (3) the late appearance of arboreal small mammals when trees and shrubs came to dominance. To record these changes, we monitored the small mammals by monthly live trapping during which we caught, ear-tagged, and released small mammals on permanent grids of live traps. Thus, we were able to determine the abundance and residence periods of the several small mammal species across a range of years of study on two areas of similar history in their conversion from farm field to forest. Using this information, we hoped to be able to predict which small mammal species would be present in habitats of a particular stage of development along the grass-to-forest continuum in the coastal plain of our mid-Atlantic region.

MATERIALS AND METHODS

Descriptions of the two study sites

One study site was last used as a farm field in 2000, two growing seasons before we began our field studies. Now owned by The Nature Conservancy, the Su tract, named after its former owner, is located near Benefit Road in southern Chesapeake (36°37'N, 76°19'W), Virginia. In our first month of study at the Su tract, December 2002, the 11.5-ha field was dominated by 1.3-m tall little bluestem (*Schizachyrium scoparium*), other grasses, mostly panic grasses (*Panicum* spp.), and with some volunteer trees, mostly < 1-m loblolly pines (*Pinus taeda*) and with a few 1.5-m planted swamp chestnut oaks (*Quercus michauxii*). The field was bordered on two sides by mature hardwood forest, and by a freshwater marsh and a nearby mature (25-m) pine forest on the other sides. The small mammal study grid, placed about 30 m from the access road, was bisected by a meter-wide and 0.5-m-deep drainage ditch, typical of the ditching network of southern Chesapeake that makes agriculture possible in land formerly part of the Great Dismal Swamp, the distinctive geological feature of southeastern Virginia. The high water table of the region is due in part to moderate rainfall and low evapotranspiration during

winter. The Su tract lies about 4 km east of the 50,000-ha Great Dismal Swamp National Wildlife Refuge. Southern Chesapeake averages 247 frost-free days and 10 cm of snow annually, has 8-13 cm of rainfall each month, and the ground is rarely frozen for more than a few days in winter (www.sercc.com). In brief, the growing season is long and the winters are mild and wet.

The other study site, called the Stephens tract after its former owner, is also owned by The Nature Conservancy. Located north of Cornland Road at 36° 39' N, 76° 21' W, this 60-ha former corn field was removed from cultivation in 2002, two growing seasons before we established a similar grid of traps for studying small mammals. Our 1-ha study grid was placed in similar grass-dominated vegetation, with a row of about 8 planted 2.0-m sycamore (*Platanus occidentalis*) trees along its eastern margin and with about 10 planted 1.5-m bald cypress trees (*Taxodium distichum*) scattered throughout the grid. Later, other trees were volunteers, mostly sweet gum (*Liquidambar styraciflua*), bayberry (*Myrica cerifera*), and red maple (*Acer rubrum*), which later came to dominate the site.

Field methods

We trapped for 3 days each month from December 2002 through July 2005 on the Su grid, except for June 2003 when extreme predator disturbance required closing the traps. After the numbers of small mammals plummeted, we trapped intermittently to monitor the arrival times of forest species of small mammals and to document the disappearance of resident species. We trapped three days each month from April 2005 through September 2012 on the Stephens grid.

Our study grids were 8 by 8 with 12.5-m intervals, producing a grid with an effective trapping area of 1 ha (Stickel, 1954). At each grid coordinate we placed 1 Fitch live trap (Rose, 1994) baited with a mixture of wild bird seed and sunflower seeds, with fiberfill added in winter for insulation. We set traps in the late afternoon, usually during the new moon phase, and checked them early for the next 3 mornings. From April through October, we locked the traps open after checking them in the morning and reset them just before sundown to prevent heat-related mortality. Using this approach, mortality for rodents was nearly zero. At the Su tract, we used only one trap per coordinate because the modest densities of small mammals precluded the need for more traps. However, when the meadow vole population at the Stephens tract increased greatly in density (June 2006), we added a second trap at each coordinate; after the meadow vole density declined, we continued to use two traps per station there.

At its first capture, each rodent was given a right ear tag with unique number, which, if lost, was replaced with a tag in the left ear, and the animal was synonymized to avoid inflating numbers of individuals. Although we recorded detailed information on reproductive condition for both sexes, for this report we are interested primarily in the numbers of different tagged individuals (an estimate of relative abundance) and in the presence, persistence, and disappearance of a species in the community of small mammals, or later, in the appearance of forest-dwelling small mammals. Our goal was to individually mark all animals living on the grid and to monitor the changes in the composition of the small mammal community as ecological succession progressed.

We initiated our studies before the Old Dominion University Institutional Animal Care and Use Committee required their approval for field studies of wild mammals, and have had annual ODU IACUC approvals (#10-010, #11-012, #13-017, #16-003) since 2010. Our methods followed the guidelines for the use of mammals in research and education, as outlined by the American Society of Mammalogists (Sikes et al. (2016).

RESULTS

During the only month of trapping in 2002 at the Su grid, hispid cotton rats (*Sigmodon hispidus*) dominated the small mammal community (Table 1); large numbers of house mice (*Mus musculus*) were present too but these disappeared in 2003. Cotton rats increased in numbers, flourished, and then declined sharply in number from 2005 to 2006, and remained in low numbers as the pines came to dominate the site. Among the herbivorous rodents, meadow voles (*Microtus pennsylvanicus*) appeared early in 2003, increased greatly in numbers, and then disappeared after three good years. Marsh rice rats (*Oryzomys palustris*), another herbivorous rodent, disappeared the same year as meadow voles, and exactly when cotton rats numbers dropped sharply too. This was the time when herbaceous vegetation, especially grasses, had mostly disappeared. (A 10 m by 10 m depression, dug as a breeding pool for amphibians and located near the center of the grid, remained free of pines; the obligate wetland grasses, sedges, and soft rushes growing there provided some habitat and food, enabling cotton rats and eastern harvest mice [*Reithrodontomys humulis*] to persist.)

Colonizing eastern harvest mice, an 8-g seed-eating rodent, found the site early and increased substantially in numbers and then declined but persisted for years, longer than for most other rodents (Table 1). The two forest species, white-footed mouse (*Peromyscus leucopus*) and golden mouse (*Ochrotomys nuttalli*), appeared much later, in years 8 and 9 of succession, respectively. The only other small rodent of forests, the woodland vole (*Pitymys pinetorum*) was represented by one individual that appeared in year 9 of succession.

The pattern was different at the Stephens site where in the first year of trapping substantial numbers of the three dominant herbivores (meadow voles, rice rats, and cotton rats) already were present (Table 2). The same was true in the second year, when large numbers of harvest mice also were added to the community of small mammals. The next year, house mice, which had been totally absent, appeared and were numerous then and in 2008; then house mice declined in number and they almost disappeared after 10 years of succession. This pattern of appearance and disappearance for house mice was drastically different than at the Su site. Also different was the persistence of both meadow voles and rice rats on the Stephens grid; true, their numbers declined but even after 9 years of succession, 20 meadow voles and 15 rice rats were tagged in 2012. The one pattern similar to that observed on the Su site was the late appearance of both golden and white-footed mice: both first appeared in the 8th year of succession and seemed to increase slowly in abundance later.

Despite the between-grid differences in the speed of succession to forest, a correlation analysis, using the MNA totals for each year, revealed a significant correlation ($r = 0.72$, $n = 6$, P

< 0.05). The greatest numbers of small mammals were during years 4 to 6 (or 7), after which numbers declined, dramatically so on the Su grid.

DISCUSSION

We began our field studies of small mammals two growing seasons after the farm fields had been abandoned. During those early stages of ecological succession, grasses dominated the vegetation, and the common herbivorous rodents quickly found these sites and established populations there. In both fields, little bluestem and panic grasses were the dominant grasses, and goldenrods (*Solidago* spp.), asters (*Aster* spp.), and horse nettle (*Solanum carolinense*) were common dicots. We have detailed information on the diets of cotton rats and rice rats in southeastern Virginia. In winter and spring, monocots comprised the majority of the diet for cotton rats but dicots were dominant in summer and autumn (Walker and Rose, 2010). Dicots were present in all 103 rice rat stomachs and monocots in 82 percent of stomachs (Rose and McGurk, 2006). Meadow voles have even more exclusively plant diets where they have been studied (e.g., Zimmerman, 1965).

On the Su grid, house mice and rice rats colonized the site quickly (Table 1), but both were later replaced (or displaced) by other small mammals; house mice remained one more year and rice rats three more years, then disappeared. Hispid cotton rats, also early colonizers, quickly became numerically dominant for a few years and persisted as long as eastern harvest mice. Meadow voles were co-dominants with cotton rats and eastern harvest mice from 2003 to 2005, and then disappeared after 2005, a time when total numbers of all small mammals dropped sharply, by nearly 90 percent. (This was when shading by the maturing pines extinguished most of the grasses.) During years 8 and 9 of succession (2009, 2010), golden mice, absent for the first seven years, outnumbered all other species combined. By 2010, when the grid was a pine forest with only patches of herbaceous vegetation, the herbivorous rice rats and meadow voles had been absent for five and four years, respectively, but the equally herbivorous cotton rat persisted in small numbers almost to the end, as did the granivorous eastern harvest mouse. It is particularly noteworthy that the insectivorous shrew, *Blarina*, was never abundant and none was caught during the last five years. By contrast, in pine plantations of four different ages in nearby Isle of Wight County, *Blarina* was fifth in abundance among the nine small mammals collected with both pitfall and live traps (Dolan and Rose, 2007). (Southeastern Virginia has two species of short-tailed shrew: *Blarina carolinensis*, the 6-10 g southern short-tailed shrew averages 100 mm and lives mostly in open habitats, whereas *B. brevicauda telmalestes*, the Dismal Swamp [and largest] subspecies, is found mostly in forests. We have lumped these as *Blarina* spp.) Interestingly, no meadow vole or rice rat was trapped in the Dolan study, even in grassy 1-year-old pine plantations, in a multi-year study with 67,950 trap nights.

The pattern of change in composition was more erratic on the Stephens grid, where all 8 species still were present in small to moderate numbers in 2012, after 10 years of succession (Table 2). One of the surprises was that house mice were absent for the first two years of study, then had modest numbers for two years and lower numbers thereafter; but they persisted with the populations of native mammals, unlike in many studies (e.g., Lidicker, 1966; Stickel, 1979). House mice usually are among the first colonizers of abandoned fields (e.g., Gentry, 1966) but often they are displaced when native species establish populations (DeLong, 1966; Lidicker,

1966). The most numerous herbivore, the cyclical meadow vole, reached highest abundance in year 2 (2006), sustained relatively high numbers for three more years, and never disappeared; on the Su grid, meadow voles were absent for the last four years. Marsh rice rats and cotton rats also had their years of abundance, years of moderate numbers, but they too persisted to the end of study at the Stephens grid, when cotton rats were the most numerous of the 8 species. Unlike other species, the harvest mouse showed a similar pattern on both grids: it arrived early and thrived every year, showing an ability to tolerate a wide range of habitat types, and was present at the end of the field studies. At the Stephens grid, a few *Blarina* were present every year, also different from the pattern on the Su grid, where this shrew was absent for the last five years. On both grids, white-footed mice and golden mice first appeared after 7 years of succession, when the woody components of the plant community had become well established.

Thus, succession to forest went much more quickly on the Su grid than on the Stephens grid, mostly because of its proximity to a seed source: a mature pine forest with 25-m trees was located about 40 m west of the Su grid. Meter-high pine seedlings already were present in December 2002 when the trapping began. We measured and counted the pine trees on the grid in 2005, 2008, and 2010. Of the more than 15,000 seedlings/saplings we counted early in 2005, about 12 percent of mortality was due to girdling by cotton rats, mostly in late winter and spring of 2005 (Nadolny and Rose, 2015); consumption of bark was confirmed by Walker and Rose (2010). By 2008 and certainly by 2010, some pines were sufficiently mature, with diameters greater than 15 cm, to produce cones. In brief, succession to pine forest happened quickly due to the nearby source of pine seeds and to the innate rapid growth of loblolly pines, the dominant pine species in southeastern Virginia.

By contrast, we placed the grid at the Stephens tract more than 100 m from any forest edge and more than 200 m from the western edge of this much larger field. Pine seedlings and saplings were rare on the Stephens grid, where the majority of volunteer trees were sweet gum and red maple. Further, because the sycamores and cypresses planted by The Nature Conservancy grew relatively slowly, much more time was required before significant shading reduced the herbaceous ground cover. In addition, large patches of wool grass, *Scirpus cyperinus*, and soft rushes, *Juncus* spp., were present throughout the grid and these persisted until deciduous trees were sufficiently well established to lower the water table and shade out these obligate wetland plants. Thus, succession went much more slowly at the Stephens site than at the Su site, resulting in the much slower progression to forest there. Because grasses and forbs were present for several years, food was available to sustain all small mammal populations at modest densities on the Stephens grid. Even the shrews persisted to the end of the study on the Stephens grid.

Cotton rats were numerically dominant at the Su site with meadow voles second in total abundance of tagged animals; on the Stephens grid, their rank-order was reversed. Surprisingly, eastern harvest mice were third in abundance on both grids, the result of their modest but persistent annual populations. Their third-place status is due in part to the versatility of eastern harvest mice: in southeastern Virginia, it is the only species that might be trapped in any habitat, from the barest grassy habitat to the most mature deep-woods forest. In ecological terms, it has the broadest niche among the rodents in southeastern Virginia.

Perhaps the most consistent feature between grids was the timing of the appearance of the forest-dwelling species: the arboreal golden and white-footed mice. Vertical structure must be available before arboreal species can be accommodated and thus their late arrival on the grids was expected. Golden mice often are associated with forest edge, where shrubs and vines form the interface between forest and a more open habitat type, whether old field or crop field. Golden mice often build their spherical nests in thickets of brush and feed on invertebrates, fruits and seeds in these productive edge habitats (Rose, 2008), but they also nest in boxes placed on trees in a mature forest (Rose and Walke, 1988) and probably also in tree holes. Golden mice appeared on both Su and Stephens grids during the 8th year in succession. Golden mice were present only in the 8-year-old pine plantations (and absent in 18- and 24-year-old pines—Dolan and Rose, 2007), the same age as when they were present on both grids. The narrow habitat tolerances and low abundances of golden mice are best illustrated in the quote of Dueser and Shugart (1979): “The golden mouse [near Oak Ridge, Tennessee] has low variability in niche configuration, occurs in low abundance even in its optimal site, and is highly susceptible to influence by external and successional habitat alterations.”

In southeastern Virginia, *Peromyscus leucopus* seems to require older and larger trees, because it was never abundant even during the last year of study on either grid. Only 1 had been caught on the Su grid after 10 years of succession and 10 on the Stephens grid, the fewest of any species at both sites. Although regarded by some investigators as an arboreal species nesting in holes of large trees in maturing or mature forest (e.g., Linzey et al., 2012), some populations of white-footed mice are excellent colonizers, as seen in the study of small mammals on nine 1-ha grassy grids on reclaimed surface mines in eastern Kentucky (Larkin et al. 2008), where *P. leucopus* was overwhelmingly dominant ($n = 295$); only 5 individuals of other species were caught. By contrast, in a field study on the upper coastal plain of Virginia, *P. leucopus* was equally common in all five macrohabitats, ranging from old fields through pine forests and oak-hickory forests (Bellows et al., 2001). It is unclear why one species should show such varying results in its habitat affinities. Our results indicate that at least in southern Chesapeake, Virginia, *P. leucopus* is a forest mammal and definitely neither a good colonizer of newly created habitat nor versatile in occupying differing habitats along the grass-forest continuum.

In southeastern Virginia, the first small mammals to find a newly abandoned farm field often are house mice and eastern harvest mice (Cawthorn and Rose, 1989). In Cawthorn’s study, these two species comprised 90 percent of captures in a grassy oldfield. Numerous field studies (e.g., DeLong, 1966; Kaufman and Kaufman, 1990) report the early presence of house mice, including on disturbed sites with little covering vegetation. Later, house mice, an introduced species, often are replaced by native species of small mammals; Lidicker (1966) describes the extinction of a house mouse population as a population of California vole expanded and DeLong (1966) also reported house mice being displaced by *Microtus*. On a dredge spoil site in Portsmouth, Virginia, house mice and meadow voles coexisted for 13 months, during which time house mice dropped from 104 per ha to 37 per ha, while meadow voles increased from 8 to 41 per ha in a *Phragmites* marsh (Rose and Kratimenos, 2006). But sometimes house mice persist, as they did on the Stephens grid, and seemingly coexist with populations of native small mammals.

Our studies of small mammal communities in southeastern Virginia indicate that herbivorous rodents will find grassy sites quickly but can either disappear nearly as quickly when grasses are shaded out by canopy closure or persist longer if canopy closure proceeds more slowly. House mice quickly found one grid but not the other, and their responses differed too, for they abruptly disappeared on one grid when populations of native mammals had become established but coexisted for years with populations of the same native species on the other grid. The three herbivores showed similar differential responses, as did *Blarina*, disappearing in mid-succession on the Su grid but persisting to year 10 on the Stephens grid. Although white-footed mice are sometimes excellent colonizers or have similar abundances in a range of habitats, on our two study grids in southeastern Virginia, they were truly forest species, appearing only after 8 or 9 years of biological succession, when substantial trees and shrubs were present. The golden mouse also was predictable, appearing around year 8, and flourishing at least a year or two. In brief, although most information on small mammal communities is derived from inferences based on short-term trapping studies in a range of habitats in a region, such as those conducted across Wisconsin (Stephens and Anderson, 2014), our long-term studies at nearby locations with similar succession histories indicate that the composition of small mammal communities was less predictable and more variable than we expected.

Although the sites were not studied contemporaneously and thus cannot be considered to be replicates, the significant correlation of total MNA and years since abandonment from agriculture indicates that the patterns of greatest abundances of small mammals (from ages 4 to 6 [or 7]) were similar. The Su site transitioned so quickly to pine forest that the numbers of the three dominants dropped by nearly 90 percent from year 6 to year 7, whereas on the Stephens grid total numbers of these three dominants actually increased by about 20 percent from year 6 to year 7, and their numbers did not drop until year 8. Thus, a slow progression toward forest gives herbivorous rodents a longer residence time in southeastern Virginia and somewhat delays the appearance of the arboreal species of small mammals.

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Compositional Changes in Two Small Mammal Communities

Table 1. Numbers of individuals of small mammal species taken during monthly live trapping at the Su site in southern Chesapeake, Virginia, starting in year 3 of ecological succession after abandonment as a farm field. MNA refers to the number of individuals given uniquely numbered ear tags and mammals per trap night is the catch rate/100 traps.

Common Name	2002	2003	2004	2005	2006	2007	2008	2009	2010	Total
Short-tailed shrew	0	1	7	3	0	0	0	0	0	11
Eastern harvest mouse	1	51	73	63	12	0	8	2	1	211
Golden mouse	0	0	0	0	0	0	0	10	7	17
Hispid cotton rat	69	302	273	153	21	5	7	3	0	833
House mouse	22	30	0	0	0	0	0	0	0	52
Marsh rice rat	9	6	8	6	0	0	0	0	0	29
Meadow vole	0	50	87	95	2	0	0	0	0	234
Pine vole	0	0	0	0	0	0	1	0	0	1
White-footed mouse	0	0	0	0	0	0	1	0	0	1
Total mammal MNA	101	440	448	320	35	5	17	15	8	1389
Total number trap nights	256	1600	2432	1216	448	64	576	192	192	6976
Total mammals/trap night	0.39	0.28	0.18	0.26	0.08	0.08	0.03	0.08	0.04	.20

Compositional Changes in Two Small Mammal Communities

Table 2. Numbers of individuals of small mammal species taken during monthly live trapping at the Stephens site in southern Chesapeake, Virginia, starting in year 3 of ecological succession after abandonment as a farm field. MNA refers to the number of individuals given uniquely numbered ear tags and mammals per trap night is the catch rate/100 traps.

Common Name	2005	2006	2007	2008	2009	2010	2011	2012	Total
Short-tailed shrew	5	6	5	7	8	11	4	31	77
Eastern harvest mouse	9	37	59	71	67	56	43	29	371
Golden mouse	0	0	0	0	0	2	4	6	12
Hispid cotton rat	19	33	37	120	250	103	34	53	649
House mouse	0	0	57	62	11	5	0	2	137
Marsh rice rat	39	84	47	6	21	24	4	15	240
Meadow vole	109	516	206	136	129	27	25	20	1168
White-footed mouse	0	0	0	0	0	1	2	7	10
Total mammal MNA	181	676	411	402	486	229	116	163	2664
Total number trap nights	1280	4480	5504	4608	4736	4096	3456	3584	31744
Total mammals per trap night	0.14	0.15	0.07	0.09	0.1	0.06	0.03	0.05	0.08