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AVIAN COMMUNITIES OF CREATED AND NATURAL WETLANDS: BOTTOMLAND FORESTS IN VIRGINIA

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Abstract. The federal government requires those who destroy wetlands to preserve, restore, or create new ones with the goal of no net loss of wetlands. In the summer of 2000, we tested whether forested wetlands created an average of 8 years earlier had developed avian communities similar to natural wetlands of the same age in southeastern Virginia. We compared six created wetlands to five natural (reference) wetlands that had undergone ecological succession after clearcutting. We also created a trajectory of expected avian community development by comparing 20 reference wetlands, logged 1–25 years earlier, to mature forested wetlands that had not been logged for 50 years or more. Created wetlands had significantly lower avian richness and diversity, and a different community composition, than reference wetlands. These differences were likely due to the fact that created wetlands supported low numbers of the expected passerine species. In addition, natural wetlands supported species of higher conservation concern, as measured by Neotropical migratory status, trophic level, habitat specificity, and wetland dependency. The trajectory of avian community development indicated that the created wetlands were developmentally behind reference wetlands or were following a different developmental trajectory altogether. We hypothesize that the differences between created and reference forested wetlands were due to unnatural patterns of hydrology or retarded vegetation development on created wetlands. It should not be assumed that created forested wetlands can provide full ecosystem replacement for natural forested wetlands.

Key words: *created wetland, forested wetland, habitat restoration, wetland construction.*

Comunidades de Aves en Humedales Artificiales y Naturales: Bosques Ribereños en Virginia

Resumen. El gobierno federal requiere que tras destruir humedales, aquellos que lo hacen preserven, restauren o creen nuevos humedales con el objetivo de que no haya una pérdida neta de éstos. En el verano de 2000, probamos si los humedales arbolados creados en promedio 8 años atrás habían desarrollado comunidades de aves similares a las de humedales naturales de la misma edad en Virginia suroriental. Comparamos seis humedales artificiales con cinco naturales (de referencia) que habían sufrido sucesión ecológica luego de talas rasas. También creamos una trayectoria esperada del desarrollo de las comunidades de aves comparando 20 humedales de referencia donde se taló entre 1 y 25 años atrás, con humedales arbolados maduros que no habían sufrido talas por 50 años o más. Las comunidades de aves de los humedales artificiales presentaron una riqueza y diversidad significativamente menor y una composición diferente de las de los humedales de referencia. Estas diferencias probablemente se debieron al hecho de que los humedales creados presentaron un número de especies de paserinos menor que el esperado. Adicionalmente, los humedales naturales albergaron especies de mayor importancia para conservación, medida en términos de estatus migratorio neotropical, nivel trófico, especificidad de hábitat y dependencia de humedales. La trayectoria de desarrollo de las comunidades de aves indicó que los humedales artificiales se encontraban retrasados en su desarrollo con respecto a los naturales, o que estaban siguiendo trayectorias completamente diferentes. Hipotetizamos que las diferencias encontradas se debieron a patrones hidrológicos no naturales o a retrasos en el desarrollo de la vegetación en los humedales artificiales. No debería suponerse que los humedales arbolados creados representan un reemplazo completo del ecosistema natural.

INTRODUCTION

Bottomland hardwood forests (hereafter, "forested wetlands") make up over 70% of the total wetland area in the southeastern United States (>12 million ha, Cubbage and Flather 1993). The ecology of these forested wetlands is primarily determined by the flooding patterns of adjacent rivers, which drive water storage, nutrient flux, and sediment deposition (Gosselink et al. 1981) and ultimately determine characteristic vegetation communities (Hupp and Osterkamp 1985). Forested wetlands also support a diverse avifauna and critical populations of Neo-

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tropical migrants and area-sensitive species such as Prothonotary (*Protonotaria citrea*) and Swainson's Warblers (*Limnothlypis swainsonii*, Knutson et al. 1996, Kilgo et al. 1998, Sallabanks et al. 2000). These forests often support higher densities of breeding birds than adjacent uplands (Stauffer and Best 1980, Knutson et al. 1996) and, in the eastern United States, may have some of the highest densities of birds of any deciduous forests (Dickson 1978, Wharton et al. 1981). However, the area of forested wetlands has been reduced from 90 million ha (presettlement) to 41 million ha in 1985 (Kellison and Young 1997) and is expected to drop by another 15% before 2030 (USDA Forest Service 1988). The federal government recognizes the importance of wetland conservation in Section 404 of the Clean Water Act: in the event of wetland destruction, mitigation must be provided through preservation or enhancement of existing wetlands, restoration of drained wetlands, or creation of new wetlands (Beck 1994). For the first five years after wetland creation or restoration, the hydrology, soil, and vegetation of sites are sometimes monitored. Yet, despite the goal of no net loss of ecosystem function (National Wetlands Policy Forum 1988), the monitoring of upper trophic levels on mitigation sites is not required.

Because natural wetlands support over 65 avian families worldwide (Weller 1999), and 20% of North American bird species (Weller 1986), numerous studies have been conducted to assess the avian communities supported by mitigation wetlands. Restored and created wetlands can provide valuable avian habitat (Brown and Smith 1998), especially for waterfowl (Leschisin et al. 1992, VanRees-Siewert and Dinsmore 1996). However, to ensure that the ecosystem functions lost through wetland destruction are being replaced, the success of mitigation wetlands should be measured with specific reference to the natural wetlands they are intended to replace (Brinson and Rheinhardt 1996). In wetland types dominated by herbaceous vegetation, such as marshes, vegetation development occurs quickly (Noon 1996, Craft et al. 1999) and replacement success of mitigation wetlands can be measured with direct comparison to natural wetlands. Restored and created marshes often support bird abundances similar to natural marshes within a few years (LaGrange and Dinsmore 1989, Brown and Smith 1998, Melvin and Webb 1998). Sometimes restored marshes even have greater species richness and abundance than reference marshes (Brawley et al. 1998). However, more commonly, significant differences in avian community composition exist, often due to low species diversity on mitigation wetlands (Delphey and Dinsmore 1993, Brown and Smith 1998, Melvin and Webb 1998), calling into question whether such marshes can serve as replacement habitat for birds displaced from destroyed marshes.

In contrast to herbaceous wetland ecosystems, the vegetation and avian communities of forested wetlands take decades to mature (Mitchell and Lancia 1990, Kellison and Young 1997). Consequently, created wetlands must be evaluated with reference to a natural wetland in a comparable stage of ecological succession. It is probably due to the difficulties in establishing a suitable reference wetland that no studies exist comparing the avian communities of created forested wetlands to those of natural forested wetlands.

Our objective was to compare the avian communities of created forested wetlands to those on natural, early successional, forested wetlands regenerating from clearcut logging. The project was designed to produce a twofold evaluation of the ability of created forested wetlands to support the avian communities typical of natural forested wetlands. For our first set of comparisons we used as reference sites five regenerating natural wetlands that had been logged at approximately the same time that six created wetlands were constructed. Our second comparison was with 20 natural wetlands that had been regenerating for 1–25 years, which we used to establish an expected trajectory for the changes in avian communities of forested wetlands as they reach maturity. The trajectory was based on a comparison of the avian communities of each of the regenerating forests to that found in seven mature (>50 years since any logging) forested wetlands in the region.

METHODS

STUDY SITES

All reference and created sites were located in the portion of the Chowan River basin that extends into southeastern Virginia, including the Blackwater, Nottoway, and Meherrin Rivers (36°N, 76°W; Fig. 1). The Chowan River origi-

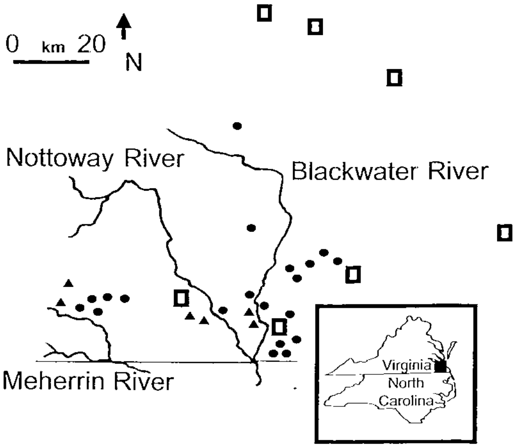

FIGURE 1. Location of forested wetland study sites in southeastern Virginia. Created wetlands ($n = 6$) are indicated with triangles, reference ($n = 20$) with circles, and mature ($n = 7$) with squares.

nates in the coastal plain and thus contains forested wetlands with consistent sediment deposition (Kellison and Young 1997). Four of our seven mature forested wetlands were located in other coastal plain watersheds, but were still <50 km away.

We studied forested wetlands that are flooded between 12.5% and 100% of the growing season with a 51–100% chance of annual flooding (Zone II, III, and IV wetlands, Wharton et al. 1982). Sites were chosen on the basis of vegetation typical of these habitats (e.g., bald cypress [*Taxodium distichum*] and water tupelo [*Nyssa aquatica*]; see Larson et al. 1981, Wharton et al. 1982).

Created wetlands. We evaluated six created forested wetlands, all built on upland sites 7–11 years prior to data collection to replace destroyed forested wetlands in the region. We are not aware of any other created forested wetlands, of comparable size and age, in the region. Hydrology of the sites had been established by grading the site to expose the local water table (one site), to allow periodic influx of water due to flooding of a nearby river (one site), or both (four sites). Hydrology was not regularly managed. In one case wetland soil had been imported; in all other cases the local upland soil had served as the substrate for wetland establishment. All sites had been planted with vegetation typical of forested wetlands in the study region: bald cypress, black gum (*Nyssa sylvatica*), water tupelo, oaks (*Quercus* spp.), black willow (*Salix nigra*), common buttonbush (*Cephalanthus occidentalis*), and river birch (*Betula nigra*). Additional species had invaded the sites after they were planted, such as red maple (*Acer rubrum*), green ash (*Fraxinus pennsylvanica*), and loblolly pine (*Pinus taeda*). Site size ranged from 3–8 ha. We estimated the percentage of each land cover type in the areas surrounding our wetland sites by estimating to the nearest 5% the amount of road, forest, and agriculture within a 5-km^2 area around the site. We used United States Geological Survey topographic maps (1:24 000) that had been drawn from aerial photographs taken after 1990.

Reference wetlands. Clearcut natural wetlands regenerating from stump and root sprouts or naturally dispersed seeds were used as natural reference sites. We excluded wetlands where replanting or spraying occurred after logging. We used only complete clearcuts, as retention of snags can affect species richness of regenerating clearcuts (Mitchell and Lancia 1990). In addition, we used sites harvested by ground-based, as opposed to helicopter, methods, as they have been shown to result in different successional processes (Lockaby et al. 1997).

Our set of created wetlands was matched to a set of clearcut reference wetlands such that the average values for percentages of each surrounding land cover did not differ. Average successional age (i.e., planting for created sites and logging for reference sites) was also the same. We chose the smallest sites available (5–15 ha) that closely matched the vegetation characteristics of created sites, but these sites were, on average, slightly larger than the created sites (see Results). In addition to the five matched reference wetlands, 15 other reference wetlands, aged 1–25 years, were used to produce a trajectory of avian community succession for the region. Reference wetlands were dominated by vegetation similar to intended communities of created wetlands (i.e., bald cypress, black gum, water tupelo, water oak [*Quercus nigra*], red maple, green ash, and many species of willow). We assumed that these reference sites would serve as adequate age-specific comparisons because regeneration of bottomland hardwood forests after clearcutting results in a composition of plant species similar to that present before disturbance (Messina et al. 1997, Rapp et al. 2001) despite temporary rises in wetland water tables and effects on other abiotic factors (Lockaby et al. 1997).

Mature wetlands. In order to determine what avian community should be replaced by created forested wetlands in this region we sampled the birds on seven wetlands that had not been logged for 50–100 years. These data were collected in 1999, one year before the data from reference and created sites (see below). Mature wetlands were typical bottomland hardwood forests of the type that the created wetlands were intended to replace.

AVIAN COMMUNITY SAMPLING

Fixed-radius point counts were used to assess the composition of each avian community on created and reference wetlands. The radius (50 m), number of count stations (two per site), number of visits (two per count station), and duration of each sample (10 min) were set to maximize sample size (Ralph et al. 1995, Smith et al. 1995). Our design allowed over 100 min of sampling in each treatment and age class of wetland.

Count stations were placed randomly within the sites under the condition they were more than 100 m from one another and more than 50 m from the edge of the site. The two visits to each site were made between 28 May–6 July 2000, one at dawn (04:30–05:30 EST) and the other no later than 08:30. The start date of the census was set to ensure that all singing birds on the site were breeding residents instead of migrants, and the end date was set so as to terminate sampling before singing declined. Order of site visits was determined randomly, but in a manner that assured each site was censused once early (28 May–15 June) and once late (16 June–6 July) in the season to balance any seasonal variation in detectability (Gibbons et al. 1996). Point counts were performed when the wind was <10 km per hr and precipitation was negligible (Ralph et al. 1995). The number of birds detected per point count was not significantly affected by remaining variation in weather, including temperature, wind, humidity, cloud cover, or precipitation (all $r^2 \leq 0.04$, all $F_{1,78} \leq 3.2$, all $P \geq 0.07$).

The senior author performed all 104 point counts and used a laser rangefinder to estimate distances. All birds using the site within the 50-m radius were recorded, including flying raptors and aerial feeders such as swifts (Ralph et al. 1995). Recounting was avoided by adding new individuals of a species only if previously counted individuals were still detectable and by continually mapping bird positions (Gibbons et al. 1996). Birds that were flushed while approaching a count station were recorded for an additional analysis on selected species (e.g., waterfowl, wading birds, and raptors; Ralph et al. 1995).

On mature sites, the avian community was measured using a 100-m variable-width transect (Emlen 1977) rather than point counts. Census methods differed between years due to the different purpose of each survey: in 1999 we sought to fully document the typical avian community of local mature forested wetlands, while in 2000 we sought to make standardized comparisons between created and reference sites with variable sizes and shapes. The combined data from the mature wetlands were used only as a single reference point to gauge the progress of younger reference sites used in our trajectory of wetland development. Data from the mature sites were not used in our comparison of created to reference sites, so the difference in census methods between 1999 and 2000 did not affect our conclusions.

VEGETATION AND HYDROLOGY SAMPLING

Methods of vegetation measurement were similar to James and Shugart (1970) except that we used smaller sampling areas (0.01 ha) for each site. Measurements were taken at six random points within each site. Vegetation density was measured by estimating percent coverage of a checkered board held 10 m from the observer at heights of 0, 1, and 2 m. Using a sighting tube, one observer estimated four measurements of canopy and ground cover to the nearest 5%. Heights of herbaceous and woody vegetation were estimated to the nearest 1 m (or 0.25 m if <1 m). Trees within 2 m of each vegetation sampling point were identified to species (or genus in case of willow) and diameter at breast height was measured to the nearest 1 cm. Water depth was measured to the nearest 1 cm. Water cover was estimated to the nearest 5% with a sighting tube.

STATISTICAL ANALYSIS

Avian species abundance was determined by taking the maximum number of detections for each count station (Gibbons et al. 1996), then averaging the two count stations at each site. Richness was defined as the total number of species detected. Diversity was calculated with the Shannon diversity index (MacArthur and MacArthur 1961). As a measure of successional stage we calculated percent similarity between avian communities of sites (Odum 1950) as $\Sigma(2A_i/A_{tot})$, where A_i is the lower abundance between two sites for a species i and A_{tot} is the sum of the abundances for that species at the two sites (Mueller-Dombois and Ellenburg 1974). The similarity of a created wetland to the set of reference wetlands was defined as the mean similarity index of that created wetland when compared to each reference wetland. These similarity values of created wetlands to reference wetlands were then compared to a standard: the mean similarity index for all reference wetlands compared to all other reference wetlands.

The abundances of regularly occurring species (i.e., those detected on more than 20% of the point counts) were examined individually. In addition, species were combined into guilds of wading birds, waterfowl, raptors, aerial feeders, woodpeckers, and passerines. Guilds detected infrequently or inconsistently (wading birds, waterfowl, and raptors) were analyzed using abundances that included flushed birds as well as those detected within 100 m of the count station. We ranked sites based on how rich they were in species with traits that make them of high interest for conservation: wetland dependency, habitat specificity, trophic level, and migratory status (Appendix, based on Croonquist and Brooks 1991). Each site was assigned a conservation-concern ranking in each of these categories that was the sum of ranks of all species present. Because passerines accounted for over 80% of the birds detected we reanalyzed the conservation-concern rankings for passerines, and modified the site values by weighting each species' ranking by its abundance at that site.

There are several types of forested wetlands, defined by their vegetation communities and resulting from patterns of flooding (Wharton et al. 1982). Although we chose reference sites that were similar to the created sites based on visual inspection, we performed an analysis to test whether there was any overall difference in wetland type between created and reference treatments. Trees were classified based on their highest tolerance of flooding (e.g., bald cypress = high tolerance [Zone II], loblolly pine = low tolerance [Zone V]; Larson et al. 1981, Wharton et al. 1982), and thus were indicators of not only patterns of hydrology, but also overall vegetation community. Vegetation community composition was analyzed based on importance values, which we calculated from the density, frequency, and basal area of all individuals of each tree species (Mueller-Dombois and Ellenburg 1974). We compared the total importance values for the created and reference sites within each category of flood tolerance to determine whether we had chosen comparable reference sites in terms of hydrology and vegetation community.

We used one-way ANOVA to test for differences in the avian community among treatments. We used O'Brien's test to confirm homogeneity of variance, and Shapiro-Wilks' test to detect deviations from normality (all proportions were arcsine transformed). In the event of heterogeneous variance a Welch ANOVA was used to test for differences. For data that were not distributed normally, a Wilcoxon two-sample test or Spearman rank-sum test was used. We performed linear regression to determine if an avian abundance or a measurement of the vegetation or hydrology was related to wetland age. As successional relationships are often parabolic in nature, a regression with second-degree polynomial was also performed. We report means ± SD in the text. All statistical tests were two-tailed with $\alpha = 0.05$. The adjusted Bonferroni correction (Rice 1989) was used within sets of multiple comparisons.

RESULTS

CREATED WETLANDS VS. MATCHED REFERENCE WETLANDS

Community composition. Total avian abundance did not differ between created and reference wetlands (Table 1). However, created wetlands had significantly lower diversity and species richness than reference wetlands of the same age (Table 1). The avian communities of the created wetlands were on average 36 ± 10% similar to matched reference wetlands, significantly lower than the similarity of reference wetlands to one another (Table 1).

Species and guilds. There were no significant differences between created and matched reference wetlands in the abundances of regularly occurring species (Appendix). Abundances were also analyzed according to guild. More passer-

TABLE 1. Comparison of the bird communities of created wetlands and reference wetlands of the same age in southeastern Virginia. "Similarity" is the proportion of species common to both created and reference wetlands, where each species' contribution to the index is weighted by its abundance.

Factor	Created ($n = 6$)	Reference ($n = 5$)	t[a]	P
Abundance (individuals per 1.57 ha)	11.3 ± 1.5	15.5 ± 1.6	1.9	0.09
Shannon-Weiner diversity index	2.2 ± 0.3	2.7 ± 0.2	3.6	<0.01
Species richness (no. of species)	10.5 ± 2.4	16.8 ± 3.7	3.4	<0.01
Similarity	0.36 ± 0.10	0.47 ± 0.03	2.9	<0.03

[a] df = 9 except for similarity, where df = 5.

ines were found on reference sites than on matched created sites (created: 7.3 ± 1.8 individuals, reference: 14.0 ± 2.2 individuals, $t_9 = 5.7$, $P < 0.001$). There were no differences between created and reference sites in numbers of wading birds, waterfowl, raptors, aerial feeders, or woodpeckers (all $P \geq 0.07$).

Conservation-concern rankings. Created wetlands had bird communities with significantly lower conservation value based on rankings for trophic level and migratory status (Table 2). The mean habitat specificity and wetland dependency of bird communities on created wetlands and reference wetlands of the same age did not differ (Table 2). Passerines accounted for 80% of the individuals detected in our study and were the only guild differing between created and reference wetlands. Therefore, we also compared conservation-concern rankings for passerines alone. Created wetlands had passerine communities with lower rankings for trophic level and migratory status (Table 2). In contrast to the analysis of rankings that included all species, the habitat specificity and wetland-dependency rankings were also lower for passerines on created wetlands (Table 2).

TRAJECTORY OF REFERENCE WETLAND DEVELOPMENT

In general, as reference wetlands matured they supported different densities of the regularly occurring species (Table 3). An overall trajectory of avian community development of the reference wetlands was established by calculating the similarity of each reference wetland to an idealized mature wetland community based on the average densities of each species found on the seven mature sites. Similarity of the avian community of reference wetlands to mature wetlands increased significantly with age ($r^2 = 0.40$, $F_{1,18} = 15.3$, $P < 0.01$; Fig. 2). The regression line predicts that a natural wetland would reach an avian community composition as similar to mature wetlands as the seven mature wetlands were to each other (51%) approximately 23 years after logging.

Given their age, created wetlands did not fall onto the predicted portion of the developmental trajectory (Fig. 2). Created wetlands were significantly less similar to mature sites than were reference wetlands of the same age (created: 0.18 ± 0.12, reference: 0.34 ± 0.14, $t_9 = 3.4$, $P < 0.01$). We calculated the theoretical age-

TABLE 2. Conservation-concern rankings for created and matched reference wetlands in southeastern Virginia. Rankings were calculated by summing rankings for all species found on reference or created sites (see Appendix for species rankings). For passerines, rankings were also weighted by abundance. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$ after Bonferroni correction for multiple tests.

	All birds			Passerines		
	Created	Reference	t_9	Created	Reference	t_9
Habitat specificity	19.2 ± 5.1	33.6 ± 13.9	2.4	11.3 ± 4.1	27.2 ± 7.6	4.4**
Wetland dependency	17.3 ± 3.5	24.1 ± 6.7	2.1	13.1 ± 2.9	18.6 ± 3.4	2.9*
Trophic level	27.5 ± 6.5	46.0 ± 10.5	3.6**	17.5 ± 5.6	36.0 ± 6.2	5.1***
Migratory status	44.2 ± 10.5	69.0 ± 13.2	3.5***	28.8 ± 7.9	56.9 ± 7.4	6.0***

TABLE 3. Species indicative of wetland community succession in southeastern Virginia, defined as those regularly occurring species whose presence was significantly related to reference wetland age. We used linear regression to identify three types of successional relationships: early successional (negative linear slope), late successional (positive linear slope), middle successional (concave-down, second-degree polynomial).

Species	r^2	$F_{1,18}$	P
Early successional			
Blue Grosbeak	0.27	6.6	<0.02
Chimney Swift	0.33	8.7	<0.01
Common Yellowthroat	0.47	15.8	<0.001
Indigo Bunting	0.34	9.1	<0.01
Northern Cardinal	0.24	5.7	<0.03
Orchard Oriole	0.26	6.3	<0.03
Yellow-breasted Chat	0.28	7.0	<0.02
Middle successional			
White-eyed Vireo	0.41	6.0	<0.01
Late successional			
Acadian Flycatcher	0.38	11.1	<0.01
Red-eyed Vireo	0.44	14.4	<0.01
Prothonotary Warbler	0.69	40.4	<0.001

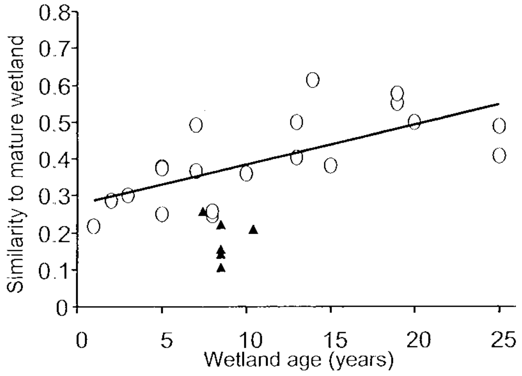

FIGURE 2. Trajectory of wetland development after clearcutting in southeastern Virginia. The successional stage of each reference wetland (circles) was measured with a similarity index comparing their avian community to the average avian community similarity of seven mature wetlands. The created wetlands (triangles) did not fall onto the expected trajectory given their age.

equivalence of the created wetlands by substituting their similarity values into the equation for the regression line predicting similarity of each wetland to the mature forests. The theoretical equivalent age for the average created wetland was −7.8 years. While a negative age is counterintuitive, it can be interpreted to mean that the avian community in created wetlands is far less similar to that of mature sites than that of reference wetlands of the same age (8.3 years), or any age. Interpreted strictly, it suggests that if created wetlands are to follow the same trajectory as reference sites they are already 16.1 years behind.

VEGETATION AND HYDROLOGY OF SITES

Created and matched reference sites did not differ in the proportion of tree species typical of highly saturated ($t_9 = 0.4$, $P < 0.70$), saturated ($t_9 = 0.6$, $P < 0.60$), semisaturated ($t_9 = 1.2$, $P < 0.30$), or partially saturated forested wetlands ($t_9 = 0.6$, $P < 0.60$). Thus, created wetlands and reference wetlands of the same age were not of different wetland types. Vegetation and hydrology variables were compared across all reference wetlands to test if they were related to wetland succession. Three factors significantly increased with wetland age: canopy cover ($r^2 = 0.46$, $F_{1,18} = 15.1$, $P < 0.001$), height of woody vegetation ($r^2 = 0.71$, $F_{1,18} = 44.8$, $P < 0.001$), and tree basal area ($r^2 = 0.43$, $F_{1,18} = 13.4$, $P < 0.01$). All 12 vegetation and hydrology variables were compared between created and matched reference wetlands. Created wetlands had significantly lower vegetation density at 1 m (created = 45.4 ± 20.5%, reference = 92.2 ± 5.3%, $t_9 = 4.9$, $P < 0.001$), and 2 m (created = 25.5 ± 15.1%, reference = 83.4 ± 8.2%, $t_9 = 7.6$, $P < 0.001$), woody vegetation height (created = 2.0 ± 0.9 m, reference = 4.4 ± 0.9 m, $t_9 = 4.4$, $P < 0.01$), and total basal area (created = 59.0 ± 48.6 cm^2, reference = 519 ± 159 cm^2, $t_9 = 6.8$, $P < 0.001$). Thus, two of three vegetation factors positively related to wetland age were different between created and matched reference wetlands. When the created wetlands were compared, instead, to a set of six of the youngest reference wetlands (age 1–5 years, all younger than the created wetlands), none of these vegetation factors differed (woody vegetation height: $t_{10} = 1.4$, $P > 0.1$; canopy cover: $t_{10} = 1.3$, $P > 0.2$; tree basal area: $t_{10} = 2.9$; $P = 0.02$ (not significant with Bonferroni correction).

POSSIBLE SITE BIASES

Created sites were on average smaller (4.0 ± 1.6 ha) than the matched reference sites (12.5 ± 1.7 ha, $t_9 = 3.7$, $P < 0.01$). While area can have important effects on avian communities (e.g., Kilgo et al. 1998), this is probably not an important difference because within the size range of the reference wetlands in this study, size did not have significant positive effects on any avian community measure (e.g., diversity: $r^2 = 0.16$, $F_{1,18} = 3.4$, $P = 0.09$; abundance, $r^2 = 0.02$, $F_{1,18} = 0.4$, $P = 0.56$).

There were no differences in the mean amount of surrounding forest (created: 74 ± 4%, reference: 72 ± 7%, $Z = 0.5$, $P = 0.64$) or open area (created: 14 ± 5%, reference: 24 ± 23%, $n = 11$, $Z = 0.5$, $P = 0.64$) between created and matched reference wetlands. The created wetlands had significantly more surrounding road, which produces noise and could reduce bird detectability (created: 5 ± 1%, reference: 1 ± 1%, $n = 11$, $Z = -2.8$, $P < 0.01$). However, we assumed that road effects on the composition or detection of avian communities were minimal, as proportion of surrounding road appeared to have no significant effects on the avian community of reference sites (e.g., diversity: $r^2 = 0.02$, $F_{1,18} = 0.3$, $P = 0.61$; abundance: $r^2 = 0.06$, $F_{1,18} = 1.1$, $P = 0.32$).

DISCUSSION

Creation and restoration of forested wetlands occurs frequently in the southern United States as a mitigation technique, under the assumption that created wetlands fully replace the ecosystem functions of destroyed natural wetlands. This assumption is largely untested, especially concerning replacement of populations of animals at high trophic levels, such as birds. Our results indicated that created wetlands had significantly fewer bird species, fewer passerines, and lower diversity than matched natural wetlands. In addition, they were significantly less similar to matched reference wetlands than the reference wetlands were among themselves. The cause of this lack of similarity was most likely the underrepresentation of the passerine community on the created sites. Created wetlands failed to support as many Neotropical migrant passerine species, and those passerines that are highly wetland dependent, highly habitat specific, or feed at the highest trophic levels.

A possible bias in our comparison of created and reference wetlands was uncertainty in our ability to match reference and created sites exactly for hydrology or vegetation community type. The hydrology and vegetation of forested wetlands are intimately connected and affect the avian community (Swift et al. 1984, Sallabanks et al. 2000). For instance, avian diversity, richness, and abundance have been related to degree of flooding (Gosselink et al. 1981, Wharton et al. 1981). We detected no systematic differences between our created and natural wetlands in vegetation typical of different forested wetland types, so we assumed that our reference sites were good matches.

Our predicted developmental trajectory revealed that the avian communities of reference wetlands normally take about 25 years to mature, similar to rates of avian community development in some other studies (e.g., Morgan and Freedman 1986, but see Buffington et al. 1997). The avian communities of created wetlands, in contrast, were either more than 10 years behind reference wetlands in maturation, or not on a developmental trajectory toward a mature forested wetland. Further evidence of retarded succession on created sites is that they had significantly lower avian diversity, fewer species with high habitat specificity, and an underrepresentation of breeding Neotropical migrants, three factors that increase with community succession (Odum 1950, Shugart and James 1973, Buffington et al. 1997).

Because patterns of vegetation succession have a major influence on the avian community, it is also possible that the differences we observed were due to fundamental characteristics of vegetation succession in clearcuts that make such wetlands inappropriate standards for created wetlands. Of several possible reference wetland types with differing rates of succession (e.g., clearcuts, strip mines, newly formed river islands), we used clearcuts because of their availability in the region and similarity in terms of landscape features. But even clearcut wetlands may differ in their rates of succession (e.g., results of this study versus Buffington et al. 1997). Spencer et al. (2001) found that secondary succession from root and stump ("coppice") sprouting on regenerating clearcut wetlands may be too rapid to warrant comparisons to succession on created wetlands where trees grow only from seeds and planted saplings. Indeed, the avian communities of cottonwood (*Populus deltoides*) plantations regenerating by coppice-sprouting have been reported to be different from those regenerating from planted stem cuttings (Twedt et al. 1999). Thus, it is possible that the differences we found in avian communities between reference and created wetlands are merely the result of comparing forests at different points in their succession. However, when we compared the birds of created wetlands to the youngest age class of reference wetlands, which did not differ significantly in those vegetation characteristics positively related to succession, they still had lower avian richness and diversity, and an incomplete passerine community, and our conclusions were the same (ECSR, unpubl. data). Thus, we conclude that differences in avian communities between created and reference wetlands of the same actual age are due to more than differences in successional stage of the vegetation.

WHY BIRDS DIFFER BETWEEN CREATED AND NATURAL WETLANDS

Wetland size. The created wetlands we studied were, out of necessity, small (mean 4.0 ± 1.6 ha); indeed, over 75% of the created forested wetlands in Virginia are less than 0.5 ha (Whittecar and Daniels 1999). We attempted to control for wetland size by choosing the largest created sites and smallest reference sites available. We found no area effects on the avian community within the size range of our reference wetlands, a size range greater than the size difference between our created and reference sites. Thus, we conclude that the small, but statistically significant, difference in size between treatments in our study was not the cause of the differences we found in the avian communities. But size has an undeniable influence on avian communities of forested wetlands (Knutson et al. 1996, Kilgo et al. 1998) and future created wetlands should be made larger or imbedded in areas of wetland habitat if they are to fully replace ecosystem functions of destroyed natural wetlands.

Inadequate vegetation development. Other possible contributions to retarded rates of avian and vegetation community succession on created forested wetlands are low recruitment of trees and slow growth of selected plantings. Only one of our six wetlands had natural wetland soil introduced during construction. Many studies have shown that by introducing a seed bank in this manner vegetation can be re-established much more quickly (Burke 1997). In addition, plantings of fast-growing early successional species (e.g., black willow, green ash) have been shown to result in canopy closure in less than 10 years (Twedt and Portwood 1997, Stanturf et al. 2000), shorter than at many of our reference sites, which had been planted with tree species that normally germinate later in the successional process. Efforts to increase vegetation growth in created forested wetlands by changes in construction methods may render the avian communities of created forested wetlands more comparable to natural forested wetlands.

Unnatural hydrology. The vegetation, and hence the higher-trophic-level communities, of forested wetlands are highly impacted by the hydrologic regime within which wetlands are found (Hupp and Osterkamp 1985, Weller 1999). An inability to reproduce natural patterns of hydrology on created forested wetlands could be the cause of the differences in the avian communities we observed. We made only limited measurements of hydrology (which did not differ between treatments) and we cannot determine the specific aspects of water flux that might have caused the differences between treatments. However, to aid direction of future study, we propose a hypothesis explaining these differences. We observed that four of our six created wetlands contained areas of deep, open water, a rare occurrence on reference wetlands. This property of created forested wetlands being "too wet" has been observed in other studies (Whittecar and Daniels 1999, Cole and Brooks 2000), where it results in long-term anaerobic conditions in the root zone. Unnatural permanent flooding can kill existing vegetation (Hunter et al. 1987) or hinder normal forest vegetation development, since periods of low water are necessary for seedling germination (Hodges 1997, Middleton 2000). As a result, avian community structure can change in response to permanent flooding (Hunter et al. 1987). For instance, these pondlike conditions are favorable for Red-winged Blackbirds (Oezesmi and Mitsch 1997), waterfowl, and wading birds, three groups well represented on the created wetlands. Further year-round study of how hydrologic regimes on created wetlands affect avian communities would be a productive next step.

The diverse avifauna of forested wetlands, coupled with the rapid rate of wetland destruction, make conservation of forested wetlands a priority. The avian communities of created forested wetlands, good indicators of ecosystem function (Croonquist and Brooks 1991), were not comparable to those of natural reference wetlands. We observed comparable abundances of birds, including some wetland-dependent species, on created wetlands, so they do provide wildlife habitat. However, until further evidence is available, it should not be assumed that forested wetland creation replaces the bird communities present on the destroyed natural wetlands. Preservation or restoration may be better mitigation options until research shows that created wetlands achieve the goal of no net loss of ecosystem function.

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APPENDIX. Ecological (conservation-concern) ranks of species. Ranks are according to Croonquist and Brooks (1991) and, where not available, author experience. Wetland dependency: 0 = upland, 1 = sometimes uses wetlands, 3 = usually lives in wetlands, 5 = found only in wetlands. Habitat specificity: 1 = generalist or edge species, 3 = dependent on a landscape (e.g., forest), although not a single habitat type, 5 = habitat specialist. Trophic level: 1 = omnivore, 2 = generalist herbivore, 3 = specialist herbivore, 4 = generalist carnivore, 5 = specialist carnivore. Migratory status: 0 = occasional, 1 = migratory transient, 2 = nonbreeding season resident only, 3 = year-round resident, 4 = short-distance migrant, 5 = Neotropical migrant. Regularly occurring species are those detected on more than 20% of the point counts.

Species	Wetland dependency	Habitat specificity	Trophic level	Migratory status
Regularly occurring species				
Great Blue Heron (*Ardea herodias*)	5	3	4	4
Chimney Swift (*Chaetura pelagica*)	0	1	4	5
Ruby-throated Hummingbird (*Archilochus colubris*)	1	1	3	5
Red-bellied Woodpecker (*Melanerpes carolinus*)	1	3	1	3
Downy Woodpecker (*Picoides pubescens*)	0	1	4	3
Acadian Flycatcher (*Empidonax virescens*)	3	3	4	5
Great Crested Flycatcher (*Myiarchus crinitus*)	0	3	4	5
Eastern Kingbird (*Tyrannus tyrannus*)	0	3	4	5
White-eyed Vireo (*Vireo griseus*)	3	3	4	5
Red-eyed Vireo (*Vireo olivaceus*)	0	1	4	5
Carolina Chickadee (*Poecile carolinensis*)	0	1	1	3
Tufted Titmouse (*Baeolophus bicolor*)	1	3	1	3
White-breasted Nuthatch (*Sitta carolinensis*)	0	5	1	3
Carolina Wren (*Thryothorus ludovicianus*)	0	1	4	3
Blue-gray Gnatcatcher (*Polioptila caerulea*)	1	3	4	5
Prairie Warbler (*Dendroica discolor*)	0	1	4	5
Prothonotary Warbler (*Protonotaria citrea*)	5	5	4	5
Common Yellowthroat (*Geothlypis trichas*)	3	2	4	4
Yellow-breasted Chat (*Icteria virens*)	1	3	4	5
Summer Tanager (*Piranga rubra*)	0	1	1	5
Eastern Towhee (*Pipilo erythrophthalmus*)	0	1	1	4
Northern Cardinal (*Cardinalis cardinalis*)	0	1	2	3
Blue Grosbeak (*Passerina caerulea*)	1	3	2	5
Indigo Bunting (*Passerina cyanea*)	1	1	1	5
Red-winged Blackbird (*Agelaius phoeniceus*)	3	1	1	3
Common Grackle (*Quiscalus quiscula*)	0	1	1	3
Orchard Oriole (*Icterus spurius*)	3	1	1	5
Uncommon species				
Great Egret (*Ardea alba*)	5	3	4	4
Green Heron (*Butorides virescens*)	5	3	4	4
Canada Goose (*Branta canadensis*)	5	3	2	4
Wood Duck (*Aix sponsa*)	5	5	3	4
Red-shouldered Hawk (*Buteo lineatus*)	3	3	4	3
Northern Bobwhite (*Colinus virginianus*)	0	3	1	3
Mourning Dove (*Zenaida macroura*)	0	1	2	3
Yellow-billed Cuckoo (*Coccyzus americanus*)	0	1	1	5
Hairy Woodpecker (*Picoides villosus*)	0	3	4	3

APPENDIX. Continued.

Species	Wetland dependency	Habitat specificity	Trophic level	Migratory status
Northern Flicker (*Colaptes auratus*)	0	3	1	3
Pileated Woodpecker (*Dryocopus pileatus*)	0	5	4	3
Eastern Wood-Pewee (*Contopus virens*)	0	1	4	5
Yellow-throated Vireo (*Vireo flavifrons*)	1	1	4	5
American Crow (*Corvus brachyrhynchos*)	0	1	1	3
Purple Martin (*Progne subis*)	3	3	4	5
Tree Swallow (*Tachycineta bicolor*)	1	5	4	5
Barn Swallow (*Hirundo rustica*)	0	1	4	5
Eastern Bluebird (*Sialia sialis*)	0	5	1	3
Wood Thrush (*Hylocichla mustelina*)	0	3	1	5
American Robin (*Turdus migratorius*)	0	1	1	3
Gray Catbird (*Dumetella carolinensis*)	1	1	1	3
Brown Thrasher (*Toxostoma rufum*)	0	1	1	3
Northern Parula (*Parula americana*)	3	3	4	5
Yellow-throated Warbler (*Dendroica dominica*)	3	3	4	5
Swainson's Warbler (*Limnothlypis swainsonii*)	5	5	4	5
Ovenbird (*Seiurus aurocapillus*)	0	3	4	5
Louisiana Waterthrush (*Seiurus motacilla*)	5	3	4	5
Hooded Warbler (*Wilsonia citrina*)	3	3	4	5
Field Sparrow (*Spizella pusilla*)	0	1	1	3
Brown-headed Cowbird (*Molothrus ater*)	0	1	1	3
American Goldfinch (*Carduelis tristis*)	0	1	2	3