PROC. ENTOMOL. SOC. WASH.
103(3), 2001, pp. 673–685

SPECIES TURNOVER IN THE LEAFROLLERS (LEPIDOPTERA: TORTRICIDAE) OF PLUMMERS ISLAND, MARYLAND: ASSESSING A CENTURY OF INVENTORY DATA

JOHN W. BROWN

Systematic Entomology Laboratory, PSI, Agricultural Research Service, U.S. Department of Agriculture, % National Museum of Natural History, Smithsonian Institution, Washington, DC 20560-0168 (e-mail: jbrown@sel.barc.usda.gov)

Abstract.—During the period 1900 through 1999, 119 species of tortricid moths (leafrollers) have been present at one time or another on Plummers Island and the adjacent northern shore of the Potomac River, Maryland. The number of species of leafrollers documented has declined over the last century from 71 in the decade 1900–1909 to 59 in the decade 1990–1999—a reduction of 17% in species richness. Of 71 species recorded from the turn of the century, only 30 are still present. With 41 apparent species extinctions and 29 apparent species colonizations, species turnover is 54%. Because of potential differences in sampling methods (e.g., equipment, diurnal vs. nocturnal, and frequency) between the two decades, "inventories" for the two decades are not strictly comparable. Hence these calculations do not represent precise measurements of changes in the fauna. Nonetheless, it is highly likely that they reflect the overall trend. Of six species described from Plummers Island just after the turn of the century, only one was detected during recent survey work. The most likely explanation for changes in the species composition of the site is faunal response to plant community succession. Since the turn of the last century, vegetation of the island has changed from an open juniper grassland to a submature hickory-maple-oak woodland. The adjacent northern shore, likewise, has undergone considerable succession. The hypothesis that changes in the fauna are the result of succession is consistent with the proposal that habitat maturation is the mechanism behind regional declines of several bird and mammal species that require early successional habitat in the northeastern United States.

Key Words: species inventory, species discovery curve, succession, local extinction, habitat management, conservation

The species composition of any site is dynamic, constantly changing in response to varying biotic and abiotic factors. Such changes may be driven by slow, long-term events, such as plate movements (hundreds of millions of years) or major shifts in regional or global climatic patterns (thousands of years), by more rapid processes such as community succession (tens to hundreds of years), or by short-term, localized environmental perturbation or ecological catastrophes (days to months). This concept of change is so fundamental to biogeography that it was a major, although rarely tested, component of MacArthur and Wilson's (1967) classic equilibrium theory of island biogeography, and it is referred to as species turnover. While species turnover can be estimated for some taxa at a coarse level (e.g., adjacent layers in fossil beds or

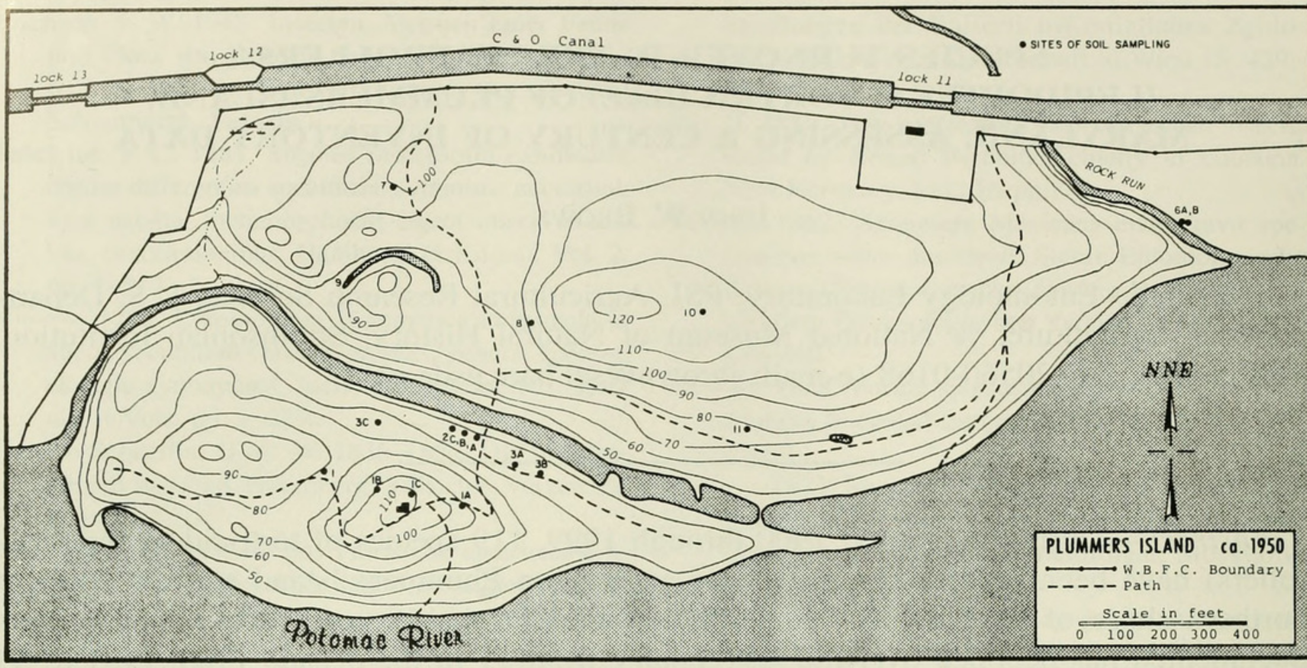

Fig. 1. Map of Plummers Island (from Erwin 1981).

changes in frequency of pollen of different plant species in core samples from lakes or shallow seas), contemporary or fine level turnover rates are unknown for most taxa. Obtaining such data typically requires long-term monitoring of the particular biotic element being evaluated.

Plummers Island, a small land feature situated along the northern shore of the Potomac River near Washington, D.C., has been a focal point of biological investigations for nearly a century. The natural history collections accumulated since 1900 represent a wealth of biological data. The moth family Tortricidae (leafrollers) is well represented in these collections, providing a unique opportunity to examine changes in the species composition of this family since 1900. I used historical specimens and data accumulated through field work in 1998–1999 to compile a cumulative species inventory of the site and examine species turnover and change in species richness, focusing on the decades 1900–1909 and 1990–1999. I also follow the fate of six species of Tortricidae described from Plummers Island during the first decade of the 20th century.

Materials and Methods

Study site.—The study site is Plummers Island (about 3.6 hectares) and a section of the immediately adjacent northern shore of the Potomac River (about 15.6 hectares) south of the C&O Canal, Montgomery County, Maryland (Fig. 1; also see TopoZone 2000), at 39.969°N, 77.177°W. The site is situated immediately east of Interstate Highway 495 (the Capitol Beltway) and approximately 14.5 km northwest of The Mall, Washington, D.C. Erwin (1981) describes the soils, topography, and vegetation of the area and presents a brief review of historical land use. In general, the flora of the island has changed from an open juniper grassland at the turn of the century, to a submature hickory-maple-oak woodland today. Portions of the adjacent northern shore were cleared either for agriculture or timber before the turn of the 20th century, and these areas now support a rather homogeneous subclimax woodland. The study site has existed in a protected state since about 1907, under the ownership of the Washington Biologists' Field Club.

Data sources.—Information on the leafrollers of Plummers Island was accumulated from three sources: (1) label data from specimens in the collection of the National Museum of Natural History (USNM), Smithsonian Institution, Washington, D.C.; (2) data from specimens accumulated during field work conducted in 1998–1999; and (3) historical literature on North American leafrollers. For each species of the family Tortricidae documented from the study area, the first year of capture was recorded; also, for each decade, the number of specimens examined and the number of species recorded were tallied.

The Lepidoptera collection at the USNM was examined thoroughly for specimens from Plummers Island. Owing to a longstanding interest in the site, the collection is rich in material gathered throughout the century, particularly during the first two decades.

During 1998, field work was conducted one night per week from early May through the end of September (n = 23 sampling nights) by the author and Michael G. Pogue (USDA, Systematic Entomology Laboratory), alternating weekly between collecting at a sheet and using a blacklight trap. Sheet collecting was conducted with a 15-watt UV (ultra-violet) light hung in front of a white sheet supported by a rope tied between two trees. On alternate weeks, a blacklight trap was deployed in the evening and retrieved the following morning. The blacklight trap consisted of an aluminum box, ca. 0.5 m × 0.5 m, with a large funnel and a baffle ca. 0.5 in height, using a 15-watt black light to attract insects. The trap was placed on the ground. In 1999, field work was conducted approximately one night per week from the first of April through the first of November (n = 30 sampling nights), using one or two blacklight traps (n = 38 samples). All specimens of Tortricidae were pinned, labeled, identified, and incorporated into the collection of the USNM.

It was impossible to determine the number of sampling dates for the first decade of the century because of the lack of precision in the data that accompanies the specimens (e.g., usually only the month and year are given, sometimes only the year), and because there is no way to determine how many sampling efforts resulted in no specimens. However, based on specimens with unambiguous label data, a minimum of 23 sampling dates can be determined with certainty: July 1902, August 1902, April 1903, May 1903 (three dates), June 1903, July 1903, August 1903, September 1903, March 1905, April 1905, May 1905, August 1905, September 1905, May 1906, June 1906, July 1907, September 1907, March 1908, May 1908, April 1909, and May 1909. Approximately 65% of the specimens from this decade are from the single year 1903. It is likely that samples included diurnal collecting (e.g., larvae from vegetation) as well as collecting with a lantern at night. A cursory review of the late August Busck's (USDA) field notes revealed no additional information (M. Epstein, pers. comm.).

Historical and contemporary sources of information on the family Tortricidae were reviewed for information regarding the Tortricidae of Plummers Island, including Heinrich's (1923, 1926) revisions of the Olethreutinae and taxonomic treatments by Kearfott (1907) and Busck (1906, 1907).

Data analyses.—The years of capture of each species were pooled by decade (i.e., 1900–1909, 1910–1919, 1920–1929, etc.), and a histogram was constructed using these data. A table of capture records for each species by decade was compiled, and the number of species and specimens recorded for each decade was tallied. Changes between the decades 1900–1909 and 1990–1999 were evaluated by comparing species richness and calculating species turnover. Percent change in species richness was calculated by the following equation: $R = b - d/b$, where "b" is the number of species documented from the first decade and "d" is the number of species documented from the last decade. When the number is negative, species richness has declined. Species turnover was calculated by the equation popularized by Diamond (1969): T = (e + c)/(b + d), where "e" is the number of apparent extinctions, "c" is the number of apparent colonizations, "b" is the number of species present at the first date, and "d" is the number of species present at the second date.

The first and last decade were chosen for comparison for two reasons: (1) they represent the greatest time interval and therefore provide the highest likelihood of detecting changes in the fauna; and (2) they are the two most thoroughly sampled decades.

The fate of six species of Tortricidae described around the turn of the century from material collected on Plummers Island was followed: *Ecdytolopha islandana* (Kearfott, 1907), *Proteoteras crescentana* Kearfott, 1907, *Saphenista foxcana* (Kearfott, 1907), *Saphenista plummeriana* (Busck, 1907), *Talponia plummeriana* (Busck, 1906), and *Thyralia gunniana* (Busck, 1907).

Results

A total of 1,095 specimens of Tortricidae from the study area was examined, including 595 historical specimens (pre-1990) in the USNM collection and 500 specimens acquired through field work in 1998–1999. Based on the specimen evidence, during the period 1900 through 1999, 119 species of Tortricidae have been present in the study area at one time or another (see Appendix). This number represents over 60% of the Tortricidae recorded from the entire state of Maryland (i.e., 195 species) (Brown unpubl.). The histogram of number of species by decade (Fig. 2) reflects relative collecting effort by decade. For example, in the first two decades of the century, several entomologists (e.g., C. Heinrich, A. Busck, E. Schwartz, W. Warren, and R. Shannon) were active on Plummers Island, followed by four decades of little activity. In the 1960s and 1970s Ronald W. Hodges and Donald R. Davis, respectively, repeatedly sampled microlepidoptera on Plummers Island, followed by little collecting in the 1980s.

A comparison of the decades 1900–1909 and 1990–1999 revealed that 71 species of leafrollers were present in the study area at the turn of the century (1900–1909) and only 59 today (1990–1999)—a reduction of 17% in species richness. Of the 71 species present at the turn of the century, only 30 are still there. With 41 apparent extinctions and 29 apparent colonizations, there is a species turnover of 54%. Actual species turnover is considerably higher than this value because between the two decades evaluated an additional 19 species were recorded and subsequently disappeared. Because of potential differences in sampling methods (e.g., equipment, diurnal vs. nocturnal, frequency) between the two decades, inventories for the two decades are not strictly comparable. Hence these calculations do not represent precise measurements of changes in the fauna. Nonetheless, it is highly likely that they reflect the overall trend. The status of the six species of leafrollers described from Plummers Island is detailed below.

Ecdytolopha islandana Kearfott (1907) was described from two worn males collected by August Busck in May, probably 1903; it has not been collected since. Although Heinrich (1926) indicated that "it [the only specimen of *E. islandana* he examined] looks like a runted specimen of [*E.*] *insiticiana*," both specimens lack the male secondary structures characteristic of *E. insiticiana* Zeller. The two specimens of *E. islandana* are nearly identical to *E. mana* (Kearfott), which occurs across the southern U.S. from Alabama to Arizona, and it is likely that the two are conspecific (*E. mana* has priority). *Ecdytolopha mana* has been reported to make galls on the leaves and petioles of *Celtis* sp. (Ulmaceae) in Texas (Brown et al. 1983).

Proteoteras crescentana Kearfott (1907) was described from seven specimens from Iowa, western Manitoba, Ohio, Illinois, and Maryland (Plummers Island). Its known

Fig. 2. Histogram of number of species documented (y-axis) by decade (x-axis).

range extends from Maryland west through the mid-western U.S., and north to Manitoba, Canada (Henirich 1923, USNM collection). Of the six species described from Plummers Island, it was the only one that we detected during recent survey work. With 19 specimens captured, it was among the most common species in 1998–1999. The recorded larval host plant is *Acer negundo* (Aceraceae) (Heinrich 1923).

Saphenista foxcana Kearfott (1907) was described from three specimens from Cincinnati, Ohio, and Plummers Island, Maryland. No additional specimens have been documented from the island or elsewhere. The larval host plant is unknown.

Saphenista plummeriana Busck (1907) was described from a single male from Plummers Island collected in May 1903. Two additional specimens were collected from the site in 1914, but it has not been recorded since. This species ranges throughout much of the central Atlantic States from Massachusetts to North Carolina, and west to Illinois and Wisconsin. The larval host plant is unknown, but related Cochylini utilize annual Asteraceae.

Talponia plummeriana Busck (1907) was described from a single male collected on Plummers Island in May 1906. Two additional specimens were collected in 1909, three in 1910, and 101 in 1914; all but the original male were collected as larvae on pawpaw (*Asimina triloba*; Annonaceae). Although the species is now known from Delaware, Kentucky, Maryland, Ohio, Alabama, and Mississippi, it has not been collected on Plummers Island since 1914. It is highly likely that this species is still present but that adults are not attracted to light (R. Brown, in litt.). Hence a thorough search of pawpaw, which is common in the area, is required to determine its presence/absence.

Thyralia gunniana Busck (1907) was described from a single specimen collected on Plummers Island in 1903. No subsequent specimens are known from Plummers Island or any other locality. The larval host plant is unknown, but it is suspected to be an herbaceous Asteraceae.

Of the six species discussed above, all but *P. crescentana* may to be locally extinct, although it is likely that *T. plummeriana* is present but not attracted to lights. While less than convincing, these observations suggests that leafrollers that utilize (or are suspected to utilize) herbs or shrubs as larval food plants have declined, while the only species that feeds on a tree species has not (but see discussion below regarding relative abundance).

Discussion

Explanations for the high species turnover and decline in species richness can be assigned to one of two major categories: sampling error or environmental change. Sampling error may include differences in study area boundaries or in sampling methodologies between the turn of the century and now. Alternatively, observed species turnover and decline may be a real phenomenon resulting from environmental change. Although there are virtually no "hard data" that reliably support arguments for or against these explanations, circumstantial evidence provides a context for briefly exploring each of the hypotheses below.

Shapiro (1998) concluded that species turnover in butterflies rarely can be evaluated using older species lists because of differences or ambiguities between the historical and current boundaries of study sites, and changing taxonomy. Using the example of the butterflies of Truckee, California, he showed that the historical study site of "Truckee" was clearly much larger than the city limits of the current town itself. In contrast, there is considerable evidence that the "Plummers Island" locality of early collectors is the same size as the current study area. Erwin (1981) discusses the history of early collecting and ownership of the area, and it is apparent that other field investigations defined the study area to include both the island and the adjacent shore. Additionally, the current work relied entirely on the examination of specimens, not on older species lists that may have been "biased" by the taxonomy of the era.

Another possible sampling error is that current survey methods may not have been as thorough or effective as those used at the turn of the century. However, one would expect the opposite to be true owing to improved collecting equipment (e.g., blacklight traps that run all night on portable batteries) and improved access to the site, the latter greatly facilitating frequent trips to the area. It is assumed that collecting around the turn of the century was accomplished both diurnally (e.g., larval collections) and nocturnally; the term "at light" on a few older specimen labels indicates that at least some collecting was conducted at night, presumably with kerosene lamps. It is possible that additional years of sampling, expanded seasonal work (i.e., sampling earlier in year), and searching for larvae would result in the documentation of a few additional species, but it seems unlikely that such increases would alter significantly the overall trends. The total of 59 species for 1990–1999 is the second highest decade, and the total of 500 specimens is over twice that of the next highest decade (see Appendix).

Because it is unlikely that observed changes in the fauna are entirely an artifact of sampling error, changes in the environment seem to provide the most likely explanation. The two most conspicuous changes in the landscape between 1900 and the present are the American Legion Memorial Bridge, spanning the Potomac River to the immediate west of the site (completed between 1963–1965), and the dramatic overall change in the plant community. Although the general area undoubtedly has suffered from habitat fragmentation through modest urbanization, an extensive national park that parallels the Potomac River has ensured the continued presence of at least a corridor of native vegetation for potential dispersal and colonization.

Traffic on the American Legion Memorial Bridge probably is responsible for some habitat degradation via air pollution (e.g., Lawrey and Hale 1979, Lawrey 1993), noise pollution, and light pollution, but the impacts of these perturbations are difficult or impossible to quantify because we have no data on these parameters prior to construction of the bridge. Because most leafrollers are nocturnal and attracted to lights, the large number of lights associated with the bridge may possibly interrupt dispersal. Potential leafroller colonists, particularly from the west, may be attracted to the nearby lights of the bridge, become disoriented, and never arrive on the site. However, in one of the few published reviews on the subject, Frank (1988) concluded that disruption of the dispersal of moths by lights is likely to have only a local affect (i.e., 10s of meters). I conclude that the bridge itself probably does not represent a significant barrier to the dispersal of moths, but features associated with the bridge, such as light pollution (potentially disrupting dispersal) and air pollution (potentially diminishing host plant quality in the vicinity) (e.g., Lawrey 1993) may exert a limited, localized affect.

More conspicuous than the bridge is the dramatic change in the vegetation of the study site as a result of plant community succession. When the Washington Biologists' Field Club first leased Plummers Island in 1901, the vegetation was described as an open juniper grassland (Erwin 1981). Approximately 3 hectares of the adjacent northern shore had been cleared for agriculture or timber. Owing to the protected status of the site over the last century, activities that degrade the habitat were ceased (starting in about 1907), and plant community succession has proceeded unabated. Today nearly the entire study area supports a rather homogeneous submature hickory-maple-oak woodland, with scattered tuliptrees (*Liriodendron tulipifera*; Magnoliaceae) and a moderately depauperate understory.

Because the larvae of all leafrollers are phytophagous (plant-feeding) and many are fairly host specific, it is logical to assume that changes in floral composition associated with plant community successional would lead to changes in leafroller species composition. Although succession represents the likely mechanism behind species turnover, the decline in species richness is more difficult to explain, given that the site continuously has supported native vegetation. It is possible that diminished habitat heterogeneity on the site, increased habitat fragmentation in the general area, and lowered habitat quality from pollution all have contributed to the overall decline in species numbers.

Changes in relative abundance of the most common species are summarized in Table 1. Of the 10 most common species in 1900–1909 (based on number of specimens), four are still among the most common (i.e., *Choristoneura rosaceana, Clepsis peritana, Platynota idaeusalis,* and *Coelostathma discopunctana*), five are still present but apparently in lower relative abundance, and two apparently are locally extinct. All four of the species that are still common are general feeders (polyphagous) as larvae; of the five still present but at lower relative abundance, two are general feeders and three specialists; and the two species that are extinct are both specialists—*Bactra furfurana* on *Cyperus* sp. (Cyperaceae) and *Ecdytolopha insiticiana* on *Robinia pseudoacacia* (Fabaceae). The most abundant species of the decade 1990–1999 (i.e., *Endothenia hebesana*) is highly polyphagous. Based on this small data set, there appears to be a positive correlation

Table 1. Most common species 1900–1909 and 1990–1999 (based on number of capture records).

1900–1909 (number of specimens 1900–1909—number of specimens 1990–1999)
1. *Clepis peritana* (15-77)
2. *Choristoneura rosaceana* (15-36)
3. *Coelostathma discopunctana* (14-14)
4. *Argyrotaenia velutinana* (13-3)
5. *Platynota idaeusalis* (10-14)
6. *Ecdytolopha insiticiana* (10-0)
7. *Eucosma derelicta* (9-2)
8. *Olethreutes concinnana* (8-2)
9. *Eucosma sombreana* (7-2)
10. *Bactra furfurana* (7-0)
1990–1999 (number of specimens 1990–1999—number of specimens 1900–1909)
1. *Endothenia hebesana* (95-5)
2. *Clepsis peritana* (77-15)
3. *Choristoneura rosaceana* (36-15)
4. *Notocelia trimaculana* (23-1)
5. *Proteoteras aesculana* (19-1)
6. *Proteoteras crescentana* (19-1)
7. *Acleris negundana* (16-1)
8. *Olethreutes fasciana* (16-4)
9. *Platynota idaeusalis* (14-10)
10. *Acleris semipurpurana* (14-0)
11. *Coelostathma discopunctana* (14-14)

between polyphagy and persistence. Additional support for this relationship can be found in the limacodid fauna (Lepidoptera: Limacodidae) of Plummers Island, which has changed very little over the past 100 years (M. Epstein, unpubl.); i.e., a species turnover of less than 10%. All of the resident limacodids are relatively polyphagous and are considered generalists.

Deviations from the pattern of "persistence by polyphagy" can be found. For example, although *Argyrotaenia velutinana* is a generalist, it has declined in relative abundance. While one might expect any species to persist as long as its larval host plant persists, *E. insiticiana* and *B. furfurana* apparently are locally extinct even though *Robinia* and *Cyperus* (their respective hosts) are still present in the study area.

In two other studies on insects, community succession or habitat change was implicated as the primary cause of changes in the fauna. In a study of the carabid beetles (Coleoptera: Carabidae) of Plummers Island, Erwin (1981) found records of 189 species from the turn of the century and 107 for the decade of 1971–1980, resulting in a turnover of about 45% and a reduction of species richness of about 43%. In a recent study on oecophorid moths (Jensen and Brown unpubl.), turnover was estimated to be about 34%, with a decline in species richness of only about 10%.

Similar patterns of declines in species richness or in populations of specific species as a result of succession or "habitat maturation" have been reported for a variety of bird species (e.g., Karr 1968, Morgan and Freedman 1987, Hunt 1998) and/or bird faunas (e.g., Willis 1974, Willis and Eisenmann 1979, Karr 1982). Litvaitis (1993) proposed that forest maturation was the mechanism behind regional declines of several bird and mammal species that require early successional habitat in the northeastern United States. The findings presented herein, together with those of Erwin (1981) and Jensen and Brown (unpubl.), suggest that this may be true for some invertebrates as well.

Potential implications of the findings of this study in a conservation or habitat management context are few, but include the following. First, caution must be exercised when compiling species inventories for comparing richness between or among sites for purposes of assigning or evaluating conservation priorities. That is, mixing historical and current data may present an extremely biased view of the actual species richness of a site. Although the cumulative data would lead one to believe that 119 species of leafrollers are present on Plummers Island, it is highly unlikely that the island has supported more than about 71 species at any given time over the past 100 years. The common practice of constructing species distribution maps based on cumulative specimen capture records likewise portrays data in a manner that does not reflect reality.

It generally is accepted that an asymptote in a species discovery curve provides a reasonable estimate of the number of species resident at a particular site being sampled (e.g., Caldwell and Coddington 1994). However, if the curve has been generated by sampling efforts spanning many years (e.g., Powell 1995), the asymptote may reflect the number of species that have been present over the sampling period, not the actual number of species present on the site at any given time. Hence, the asymptote may actually over-estimate the fauna. The longer the sampling time, the more likely the asymptote will over-estimate the fauna.

Finally, the "preservation" of Plummers Island (i.e., the interruption of activities that degrade the habitat or maintain some land in a state of early succession) has allowed the habitat to revert slowly to a homogeneous, subclimax community that supports considerably fewer species than were present prior to implementation of this policy. This and other studies (e.g., Morris and Web 1987, Bollinger 1995, Hunt 1998) suggest that the maintenance of at least some successional habitat may be critical for the maintenance of species richness, and that protection or management in the form of "benign neglect" may have significant, negative impacts on the species richness of a local site.

Acknowledgments

I thank Michael G. Pogue, Systematic Entomology Laboratory, USDA, National Museum of Natural History, Washington, D.C.; Melissa Jensen, Cornell University, Ithaca, New York; and John Brown, Jr., Fairfax, Virginia, for assistance with field work. I thank the Washington Biologists' Field Club and the Smithsonian Institution's Research Training Program for financial support. Terry L. Erwin, National Museum of Natural History, Washington, D.C., provided assistance interpreting his data on carabid beetles; Stan Shetler, National Museum of Natural History, shared information on the flora of Plummers Island; James Lawrey, George Mason University, Fairfax, Virginia, provided references on the affect of automobile exhaust; and Marc Epstein, Smithsonian Institution, provided data on the Limacodidae of Plummers Island and reviewed field notes compiled by the late August Busck. The following provided helpful reviews of the manuscript that enhanced its clarity and quality: Richard Brown, Mississippi State University, Mississippi State, Mississippi; Ronald Hodges, Eugene, Oregon; Manya Stoetzel and David Smith, USDA, Systematic Entomology Laboratory; and Marc Epstein, Department of Entomology, National Museum of Natural History, Smithsonian Institution, Washington, D.C.

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