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The current status of forest Macrolepidoptera in northern New Jersey: evidence for the decline of understory specialists

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Abstract We compared most taxa of the forest Macrolepidoptera fauna of the northwestern corner of New Jersey documented from the late 1800s through the 1970s with that documented in 2003–2013. Over 95 % of documented species whose caterpillars feed on trees (n = 307) and forest litter (n = 27) were found. Among understory specialists, all eight specialists on ferns, which deer generally avoid, were found, as were all 12 specialists or oligophages on browse-tolerant lowbush blueberries. In contrast, only 11 of 20 specialists on non-ericaceous shrubs and 16 of 25 specialists on forest forbs were found, despite the bias of targeted sampling for most undetected forb feeders. Non-detections of understory species are highly consistent with deer impacts and most of those we did not find were still being found in the 1970s or 1980s. Most of the 13 undetected tree-feeders have last known collection dates in the 1950s or 1960s locally, and seven have reportedly declined more widely to the east. However, detection success for tree feeders was at least 90 % of all families.

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Introduction

Among the most diverse components of forest ecosystems are the Lepidoptera. They are a foundation of food webs (Schweitzer et al. 2011; Wagner et al. 2011; Fox et al. 2012) and play important roles as hosts, prey, herbivores, pollinators (National Research Council 2007), and detritivores in forest ecosystems (Hohn and Wagner 2000). While most species of caterpillars in eastern US forests feed on trees (Wagner 2005; Wagner et al. 2001, 2011), Appendix 1 of Schweitzer et al. (2011) lists 65 specialists on understory forbs and grasses. Some understory shrubs such as blueberries (*Vaccinium* spp.), and *Corylus* spp. support dozens of species, including specialists (Robinson 2002; Tallamy and Shropshire 2009) while others support very few caterpillars. Well over 30 Herminiinae and a few others specialize on leaf litter (Hohn and Wagner 2000; Wagner et al. 2011).

This stratified specialization allows for an examination of the patterns of change in Lepidoptera diversity across strata. The forest understory stratum is of particular interest because of competition with white-tailed deer for food plants in eastern forests (Wheatall et al. 2013). Overabundance of deer and other ungulates (Côté et al. 2004; Rawinski 2008) has brought dramatic changes to the structure and composition of forests throughout many parts of the world (Schreiner et al. 1996; Motta 2003; Takatsuki 2009). Given the dramatic impacts that deer can have on the forest understory (Russell et al. 2001), impacts on understory-dependent Lepidoptera would be expected

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(Hirao et al. 2009) and have been reported near our study area (O'Donnell et al. 2007; Schweitzer et al. 2011).

To examine changes in faunal composition over time across host plant feeding guilds corresponding to different forest strata, we compiled a list of forest Macrolepidoptera species documented from slightly before 1900 into the 1980s, but mostly 1954–1977, in northwestern New Jersey, USA and compared it to an inventory we conducted in the same area between 2003 and 2013. We address two primary questions: (1) how similar is the current forest fauna of northwestern New Jersey to that which was documented in the early to mid-twentieth century, and (2) have changes been equally distributed among guilds feeding in the major strata of these forests? We hypothesized that contemporary detections of understory Lepidoptera species would be lower than for tree-dependent species.

Methods

Field sites

Our three primary sampling sites are in the Ridge and Valley region of northwest New Jersey. These were Stillwater (397 m, 41.114926°N, 74.861395°W, Sussex County), High Point State Park (366–462 m, 41.2888°N, 74.6909°W, Sussex County) and Hardwick (149 m, 41.00143°N, 74.92083°W, Warren County). The Stillwater and High Point sites are contiguous with the Appalachian forest that covers millions of hectares and extends far beyond New Jersey.

All genera and virtually all species of frequent to common forest trees found in Sussex County (Hough 1983) occur within 1 km of the Stillwater site, including three native conifers (Pinaceae) which are nearly absent at the other sites. Among shrubs and two vines in Table 1, *Corylus*, *Physocarpus*, *Hydrangea*, and native *Lonicera* are not known to occur there. At High Point we sampled primarily six locations in relatively rich mesic forest where Niering (1953) had previously studied the vegetation. More acidic oak-Ericaceae woods were within a few 100 m of these sites. The sampling site at Hardwick consists mainly of successional habitats on fertile, limestone-based soils, with more mature forests <2 km away. Black walnut (*Juglans nigra*), and red cedar (*Juniperus virginiana*) are notably common, Prickly ash (*Zanthoxylum americanum*) is frequent on edges and to some extent in the understory. Ericaceae and native pines are virtually absent on these rich soils. Forbs are more abundant than at the other sites.

The deer population in this part of New Jersey rose throughout the mid to late twentieth century, reaching a peak of 40–50 per square mile in the mid-1990s (NJ Division of Fish, Game and Wildlife 1999) and has likely decreased since then due to more liberal deer hunting regulations. High point was closed to deer hunting until 1997 and some understory shrubs, notably azaleas, *Corylus*, and viburnums, occur mostly as sprouts that were under 30 cm tall in 2010. The supposedly common (Robichaud and Buell 1973; Hough 1983) genus *Corylus* was not seen at our other two sites.

Table 1 Detection success for understory shrub and vine specialists

Plant taxon	Plant frequency	Found	Not found
Ericaceae, including lowbush *Vaccinium*	Common	12	0
Ericaceae, highbush *Vaccinium* etc.	Frequent	3	0
Ericaceae, *Lyonia ligustrina*	Frequent	1	0
Subtotal, ericales feeders		16	0
Aquifoliaceae, *Ilex verticillata*	Common	1	0
Corylaceae, *Corylus*	Common	0	1
Menispermaceae, *Menispermum*	Common	1	0
Caprifoliaceae, shrub *Viburnum*	Common	3	0
Caprifoliaceae, native *Lonicera*	Frequent	0	1
Cornaceae, *Cornus* (*Cornus*)	Common	2	1
Grossulariaceae, *Ribes*	Frequent	2	1
Rhamnaceae, *Ceanothus*	Frequent	0	3
Rosaceae (Maloideae), *Photinia* (=*Aronia*)	Common	1	0
Rosaceae, *Physocarpus*	Infrequent	1	1
Saxifragaceae, *Hydrangea*	Infrequent	0	1
Subtotal non-ericaceous shrubs		11	9
Grand total all shrubs		27	9

If only a genus is listed, frequency is for the most numerous or only species according to Hough (1983). See Supplementary Appendices A and C for lepidopteran species

Moth sampling

At Stillwater moths were sampled by Garris (JRG) with lights almost every night from early spring until early or mid-October from July 2005 through 2013. Three stations, each with a 30 or 40-W blacklight, were used, except a mercury vapor light or, prior to 2008, "grow lights" were occasionally substituted at one site. One station was discontinued after 2011. White sheets were fastened to a wall behind each light. Lights were typically checked one or more times before midnight and again around dawn. At Hardwick a single mercury vapor light was operated by McBride (AEM), and was usually checked a few times before midnight and again around dawn. Diurnal collecting and observations were extensive at Stillwater and Hardwick, and we include a few from the adjacent White Lake Natural Resource Area.

All moths included from High Point were from 44 efforts with 15-W blacklights including 39 overnight bucket trap samples, usually three on each of two nights per sample period in June, July and September of both 2009 and 2010, and on one night in August 2011, at or within 100 m of Niering's (1953) six mesic forest sites.

Targeted sampling

Targeted efforts were made by McBride (2009) for *Papaipema* and other herb-feeding Apameini usually including both operation of blacklights and looking for larvae in patches of the food plants. There were occasional targeted efforts with blacklights in patches of *Helianthus*, *Lysimachia,* and bracken fern at High Point as well as DFS checking the former for *Papaipmea* and *Chlosyne* larvae. Seed pods and flowers on the few dozen stems of *Aureolaria* we encountered where checked for feeding signs of *Pyrrhia aurantiago*. *Psectrotarsia hebardi*, which apparently does not come well to lights, was sought as larvae at night on flowers of *Collinsonia canadensis* (AEM has since discovered that they can also be found in the daytime). Finding two butterflies, *Celastrina negelctamajor* and *Calephelis borealis*, also requires checking the immediate vicinity of the foodplants, which we consider targeted sampling even though the latter occurs within a km of our Hardwick site. Table 2 indicates which forbs were targeted and the results. We regard David Wright's searches for *Celastrina lucia* as the only targeted sampling for a shrub feeder.

Table 2 Detection success for understory forb specialists

Plant family and genus	Frequency	Found	Not found
Asteraceae, *Helianthus divaricatus* and H. strumosus**	Common	0	2
Asteraceae, *Helianthus decapetalus**	Frequent	1◆	0
Asteraceae, *Parkera obovatus**	Infrequent	1	0
Balsaminaceae, *Impatiens* spp.	Common	1	0
Berberidacae, *Podophyllum peltatum**	Common	1	0
Caryophllaceae, *Silene stellata*	Frequent	0	1
Cruciferae, *Arabis* spp.	Frequent	1	0
Cruciferae, *Cardamine (=Dentaria)*	Frequent	0	1
Labiatae, *Collinsonia**	Common	2	1
Primulaceae, *Lysimachia**	Common	1	0
Ranunculaceae, *Actaea*(=Cimicifuga)*	Frequent	1	0
Ranunculaceae, *Aquilegia**	Frequent	0	2
Rubiaceae, *Galium* spp.	Common	1	0
Saururaceae, *Saururus cernuus**	Infrequent	1	0
Scrophulariaceae, *Aureolaria flava**	Infrequent	0	1
Scrophulariaceae, *Scrophularia**	Frequent	0	1
Urticaceae, *Boehmeria cylindrica*	Common	1	0
Urticaceae, *Pilea pumila*	Frequent	1	0
Urticaceae, *Urtica* all taxa	Frequent	3	0
All forbs		16	9

Asterisks refer to genera on which targeted effort was made for all expected species. Frequency is based on the most frequent foodplant within the taxon according to Hough (1983). Details for detections and non-dectections are in Appendices A and C

◆ *Papaipema rigida*, besides Helianthus decapetalus, may have an additional foodplant locally (see Weiss 1915, McBride 2009)

Sources for historic records

Unlike in parts of Europe (Conrad et al. 2006; Mattila et al. 2009) no complete list of moths for New Jersey has been published, therefore we compiled our own. The following literature was useful in formulating an initial list of expected moth species for Sussex and Warren Counties, Smith (1910), Weiss (1915), Muller (1965, 1968, 1973, 1976, 1979, 1981), Moulding and Madenjian (1979), but no species are included as previously documented based solely on the literature. Historic moth records (Appendix A) are primarily from The American Museum of Natural History (AMNH) and the collection of the Rutgers University Department of Entomology. For *Catocala* we used currently unpublished distribution maps from Lawrence F. Gall. The AMNH collection was consulted primarily for species of Apameini (McBride 2009) and about 50 other expected moths for which we did not have Sussex or Warren County records as of 2009. All identifications for records we used from the Rutgers collection were verified by DFS. We did not make exhaustive efforts to document species that we had already encountered by 2009. David Iftner shared his extensive compilation of specimen records for butterflies and skippers which are the basis for Iftner and Wright (1996). This includes all records from AMNH, Rutgers, and the Yale University Peabody Museum, among other collections. Historic records for nocturnal moths essentially ceased soon after 1977, by which time Muller (1976, 1979), the source for many AMNH records that we used, had shifted his collecting to southernmost New Jersey due to declining results northward. *Hadena ectypa* (a forb specialist), with collections in 1979 and 1980 (now at AMNH via Muller), is our only undetected species with a date later than 1977 from the Rutgers light traps. The other records during the 1980s (Appendix A) were diurnally.

Comparison of ours and previous methods

Records of nocturnal moths from 1954 to 2013 were collected mostly at blacklights (Muller 1965) similar to those we used at Stillwater, those in the Rutgers collection are almost entirely from 15 W pest survey traps comparable to those we used at High Point. Methodology for collecting larvae or pupae of *Papaipema* and related borers (Wagner et al. 2011; McBride 2009) and butterflies is virtually unchanged in the last 100 years.

Documentation criteria

All species documented in Sussex or Warren County by any person or method from 2003 to 2013 are considered detected. We also consider *Celastrina neglectamajor* as detected based on two well-known extant populations within 300 and 460 m (estimated by AEM) of the Warren County border in Hunterdon and Morris Counties. Doing so is consistent with our criteria for previously documented species which we define as specimens examined by us or Iftner and Wright (1996) from either (1) Sussex or Warren County, or (2) from at least two of the six adjacent tri-state counties. We also accept the vagile northern *Polygonia progne* as detected based on a population (as of 2012–2013) slightly to the south in Hunterdon County as well as occasional reports (e.g. Gochfeld and Burger 1997) of singletons.

Species inclusion and reporting

Only potentially year-round resident forest Macrolepidoptera and Zygaenoidea with native foodplants are considered. Specifically six Urticales feeders, five nymphaloid butterflies and the moth *Hypena humuli* (Wagner et al. 2011), as well as the polyphagous *Zale lunata* are excluded as non-resident. Because we did very little baiting, and little sampling of any kind from mid October through March, the entire noctuid tribe Xylenini is excluded from this study, as was the genus *Eupithecia* because they are too difficult to identify. Lepidoptera nomenclature follows Pelham (2008) for butterflies and skippers, Lafontaine and Schmidt (2010) and Wagner et al. (2011) for Noctuoidea, Wagner et al. (2011) and Wagner (2005) for nearly all others. Plant scientific names follow the online USDA Plants Profiles. See supplemental Appendices A–D, and F for detailed lists of included and excluded species, and Appendix E regarding a few operational taxonomic units that might have been two species.

Defining foodplant guilds

Caterpillar foodplants are based heavily on McGuffin (1972, 1977, 1981), Wagner (2005), Wagner et al. (2001, 2011), but also (Butler 1992; Butler et al. 1995a, b), as well as the senior author's field and rearing experience, with several from Ferguson (1975), Rings and Lepidopterists (1992), Cech and Tudor (2005), and Maier (2004). The extensive literature searches by Handfield (1999) and Robinson (2002)were consulted for species level

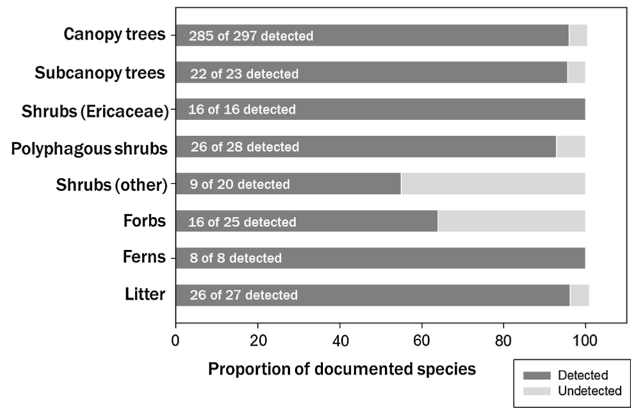

Fig. 1 Summary of detection success of forest-dependent Lepidopteran species diversity in northern New Jersey by larval feeding guild

identifications of foodplants, e.g. *Vaccinium* and *Viburnum*, that are commonly reported to genus only. If a caterpillar normally feeds in more than one stratum, it is included with the taller one (usually canopy trees). Appendices B–D list all species in each guild. Tables 1 and 2 list all understory plant genera included in Fig. 1 except for ferns.

Trees versus shrubs

We follow Sibley (2009), and the online USDA Plants Profiles Guides (plants.usda.gov) in defining trees, except we exclude *Rhus* spp. and *Salix* (see Appendix F) which are seldom forest trees in our area, We treat other woody plants as shrubs, or in a few cases vines. We include two vines that are (or were) strongly associated with that stratum with the understory shrubs (Table 1). Subfamily Maloideae (Rosaceae) specialists or oligophages that do not normally use *Prunus serotina*, which we treat as a canopy tree, but do use *Amelanchier* or *Sorbus americana* are included as subcanopy tree feeders. See Appendix F regarding Rosaceae feeders.

Herb feeders

While the above foodplant guilds essentially correspond to forest strata (canopy, subcanopy, shrubs), we discuss two guilds within the understory herb stratum. The term fern specialist is self explanatory and nearly all local ferns grow in more or less wooded habitats, although several not exclusively so. The foodplant range of some of the eight fern specialists is poorly known, but three appear to specialize on bracken (*Pteridium*) and one each on *Onoclea* and *Osmunda*. Forest understory forbs are not as easy to define because some also occur in meadows. For example violets (*Viola* spp.) grow in many habitats and the small *Thalictrum dioicum* is a forest species, while the larger *T. polygamum* also commonly grows in meadows and relatively open wetlands (Niering 1953; McBride 2009). We exclude both genera. Tables 1 and 2 include all plants we considered to be forest understory forbs or shrubs that have or had any specialized Lepidoptera in northwestern New Jersey No Fabaceae or gramminoid feeders are included because most of the former now commonly use non-native species (Gochfeld and Burger 1997; Schweitzer 2006; Wagner et al. 2011) and exact foodplants of grass feeders are poorly documented, and most are not tied to forests.

Polyphagous understory feeders

Based on the general habits of the caterpillars, scarcity or absence of the species in canopy caterpillar sampling (Butler 1992; Butler et al. 1995a, b), and shrubs included as foodplants by Ferguson (1975), Handfield (1999), McGuffin (1972, 1977, 1981), Robinson (2002), Rockburne and Lafontaine (1976), Wagner (2005), Wagner et al. (2001, 2011) and personal communication with David Wagner in 2010–2013, we treat 28 species (Appendix C) as polyphagous woody understory feeders. All of these share foodplants with more specialized shrub, especially *Vaccinium*, and/or subcanopy specialists.

Litter feeders

This guild includes only one noctuid, one zyagaenid, and 25 Herminiinae (Erebidae) (Appendix D) whose caterpillars can develop through all instars primarily to exclusively on non-graminoid forest litter or fungi growing on such litter (Hohn and Wagner 2000; Wagner et al. 2011), Some *Zanclognatha* species appear to use leaf litter and also ascend trees and shrubs (Wagner et al. 2011) where they presumably eat leaves. This guild does not include polyphagous Noctuidae (Wagner et al. 2011) that use dead leaves as food resources in their early instars or over the winter but switch to new growth of trees or shrubs or in spring.

Analyses

Most statistical tests are by Fisher's exact test, one Mann–Whitney U test was used. Although one-tailed procedures could be justified in some cases, we always report two-tailed results. Canopy and subcanopy trees were combined in most analyses. We considered limiting statistical analyses to moths collected at light from the three main sites, that is eliminating detections from targeted efforts and incidental observations, as well as all butterflies and skippers. However, we rejected this approach because treating understory species that were found solely by targeted or incidental observations as undetected disproportionally inflates the number of undetected forb specialists from nine to 16, and shrub specialists from nine to 11, and affects only 2 % of tree feeders, which would be a bias against the null hypothesis.

Results

Species detected

We detected 394 species of Macrolepidoptera and all of 16 expected Zygaenoidea, 410 total, and failed to find 34 macros (8.3 %) meeting our criteria for previously documented species, as summarized in Appendix A. All but four species that were collected only once were found from 2006 to 2013. We emphasize that 394 is far from the total Macrolepidoptera fauna at our sites. We had to exclude a major noctuid tribe Xylenini (ca. 40 species) and over 200 species do not fit any of our forest guilds, including over 50 polyphagous forb or grass-feeding Noctuidae, most Arctiinae, most butterflies and skippers, as well as legume and gramminoid specialists. Of the 307 detected tree-dependent species (Appendix B), 289 (94 %) were found at a single site-Stillwater.

Comparison of feeding guilds

Non-detections were not randomly distributed among the feeding guilds (Fig. 1). Detections were significantly higher ($p < 0.0001$) for tree (canopy and subcanopy) feeders, of which 307 were detected and 13 were not, compared with understory feeders. This significant difference holds when understory species are defined as any of these combinations: (1) forb or shrub specialists separately, (2) same pooled; (3) forb, shrub, and fern specialists plus polyphagous understory feeders pooled. The difference is driven entirely by forb and non-ericaceous shrub specialists, of which 27 were found and 18 were not.

Forest tree feeders

Except that only three out of four *Hamamelis* specialists were found, detection success was 92–100 % for specialists on all genera of trees (Appendix B), as well as for polyphagous species. Specialists and polyphagous tree-feeding species are pooled in all analyses. No non-detections involve specialists on *Ulmus americana* or *Castanea dentata*, which no longer occur as canopy trees, or on *Tsuga canadensis, Juglans cinerea*, or the distinctive subcanopy *Cornus (Benthamidia) florida* (Redlin, 1991) which have also declined.[1] All of nine described Macrolepidoptera meeting our criteria for previously documented that specialize on Oleaceae (Wagner 2007), i.e. ash trees (*Fraxinus* spp.) in our study area, were found at least at

[1] *Macaria fissinotata* probably is a *Tsuga* specialist. *Hydriomena divisaria*, *Feralia jocosa*, and *Caripeta divisata* are essentially hemlock specialists in New Jersey, but use spruces and fir farther north.

Stillwater. These species and about nine Microlepidoptera, will likely disappear from northern New Jersey forests soon after the Emerald Ash Borer becomes established (Wagner 2007).

Litter specialists

Herminiinae (Appendix D) were not extensively sampled at either Stillwater or Hardwick, or historically, so our list may be incomplete, but we found 24 L feeding species at High Point and one more, *Bleptina caradrinalis,* at Stillwater. We can document only one other, *Renia sobrialis* (AMNH, DFS collection), from the area. Counting the two from other families, we encountered 26 of 27 (96 %) of documented, forest litter-feeders.

Understory shrub specialists (Appendix C)

All of 16 Ericaceae feeders, but only 55 % of 20 specialists on non-ericaceous shrubs were found (Tables 1, 2). At least 12 of the Ericaceae feeders commonly use lowbush blueberries (*Vaccinium pallidum*, *V. angustifolium*), which persist, but produce few berries (Rawinski 2008), with heavy browsing. The results for *Viburnum* specialists may be incorrect. If the three we treated as shrub specialists also feed on the subcanopy tree species (*V. prunifolium, V. lentago*), treating them as shrub specialists inflated the low detection success for that guild, favoring the null hypothesis. Other than *Viburnum* and Ericacae feeders, only eight of 17 shrub specialists were found. Non-detections of shrub feeders include specialists on seven of eleven plant families.

The 93 % detection success for polyphagous woody understory feeders is much higher than for shrub feeders overall ($p = 0.0040$), but similar to that for Ericaceae (100 %) and subcanopy tree feeders (96 %), as would be expected since over 70 % (probably 100 %) will feed on Ericaceae and some subcanopy species. Both of the undetected species are univoltine northern and high elevation Noctuidae near their southern low-elevation limits, i.e. *Polia pupurissata* and *Autographa ampla*. *A. ampla* may not have really been established.

Subcanopy versus shrub specialists

We include 23 subcanopy specialists (Appendix B) among our forest tree feeders, of which 22 were found, a detection success significantly higher than for non-ericaceous shrub specialists ($p = 0.0027$, 0.072 with Ericaceae feeders included).

Herb feeders

All eight forest fern specialists were found (Supplemental Appendix C). Although the difference in detection success for fern and forb specialists is not statistically significant ($p = 0.0731$ two tailed, $p = 0.0530$ one-tailed), we discuss them separately. We note the difference would be significant if we really did encounter two species of the fern-feeding *Homochlodes* (Appendix E). The nine undetected forb specialists include species using seven of eleven plant families (Table 2). Of the 16 detected forb feeders, 13 are nocturnal moths 11 of which came to collecting lights at our standard sites, i.e. eight at Hardwick, five at Stillwater, and five at High Point. However, four of them did so only once; the foodplants of of two of these, *Papaipema rigida* and *Parapamea buffaloensis*, are not known to grow within 2 km of these detection sites. All eight fern feeders came to lights at Stillwater, but *Papaipema speciosissima* did so only once.

Results of targeted efforts for herb feeders

Table 2 summarizes the results for forb specialists. We note that without targeted efforts detection success would have been 12 of 25 (48 %) for this guild, and eleven of 20 (55 %) for non-ericaeous shrub feeders. For forb or fern feeding moths that we did find in routine sampling with lights at Stillwater or Hardwick (Appendix C), targeted efforts elsewhere (including McBride 2009) were successful for all of six. However, among targeted forb-specialist moths that we did not find at those sites only two of seven species were found elsewhere. There was no targeted effort to sample *Silene stellata* because we never encountered that "frequent" (Hough 1983) plant. Ultimately only four forb specialists, two Noctuidae and two butterflies, and one highbush blueberry feeder, were found solely by targeted efforts.

If targeted efforts for 15 of 25 forb specialists are ignored, all of eight fern feeders were still detected and decreasing the already low detection success for other understory species would not affect any statistical comparisons to tree-feeders since p is already <0.0001. Thus targeted efforts provided useful information on forb feeders that are of conservation concern (Schweitzer et al. 2011), but did not significantly alter the outcomes of our analyses.

Abundance of foodplants and detection success

Detection success for understory species with "common" (Hough 1983) foodplants is significantly higher ($p = 0.023$) than for those whose foodplants were merely "frequent" or "infrequent", but this is driven by lowbush blueberries, and if these are excluded, 14 of 21 specialists on common shrubs and forbs were found, compared to 14 of 28 for those with merely frequent or infrequent foodplants which does not approach significance ($p = 0.23$).

Lepidoptera phylogeny and detection success

The 13 undetected tree feeders are from 11 genera in six moth families. Detection success among tree feeders was 90–100 % for all families. Our 15 genera with undetected understory species are from six families but two of the genera are notable for widespread declines in the Northeast (Schweitzer et al. 2011): *Erynnis* (Hesperiidae) of which three of eight species are probably extirpated from New Jersey, and *Papaipema* (Noctuidae) for which McBride's (2009) extensive targeted efforts produced only 19 of 32 species known from northern New Jersey. Neither forest understory *Erynnis* was found, but all three oak-feeders are still common in the state. Only four of seven forest forb-feeding *Papaipema* in Table 2 were detected (including McBride 2009), but we found all three fern feeders and the one tree feeder. Non-detections in *Erynnis* and *Papaipema* were consistent with other species in the same guilds. Phylogeny (or the co-variable size) is not driving our results. Overwintering stage is also linked to phylogeny and reportedly to extirpation risk (Conrad et al. 2006; Mattila et al. 2009). *Erynnis* overwinter as fully fed larvae, otherwise for all feeding guilds pooled three undetected species do so as partly grown caterpillars, eleven (including *Papaipema*) as eggs, 17 as pupae, and one is unknown to us.

Comparison of last collection years

Figure 2 summarizes last observation years for undetected species in each stratum from Sussex and Warren and the three adjacent New Jersey Counties, and one each from Essex and Somerset Counties slightly to the southeast. As noted in the introduction, cessation of nocturnal efforts by

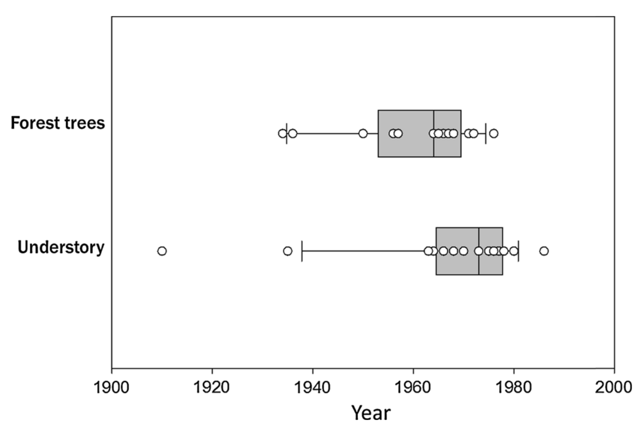

Fig. 2 *Box plots* illustrating the distribution of last known collection dates for forest tree and understory Lepidoptera species undetected in this study in northern New Jersey from 2003 to 2013. *Points* represent detection dates for each species. Understory species we did not detect were last collected significantly later than canopy species (Mann–Whitney *U* test U = 61.5, $p = 0.012$)

1980 is a factor in these dates. The dates for tree and understory feeders differ significantly (U = 61.5, $p = 0.012$) by Mann–Whitney *U* test, with undetected tree feeders having earlier last observation dates than undetected understory species. We note that Gochfeld and Burger (1997) reported no current localities for our four undetected understory forb or shrub-feeding butterflies or *Erynnis* skippers, nor did David Iftner encounter them during the 1990s and early 2000s.

Discussion

Thoroughness of historic information and our sampling

Several observations suggest that we detected almost the entire current fauna in most guilds. We detected 96–100 % of tree, Ericaceae, fern, and litter feeders ever documented in the region. Furthermore there was a strong diminishing returns effect, e. g. we added only five new species to our detected list at Stillwater from June 2010 through 2013 including two of 289 tree feeders, one of 24 shrub specialists, one of five forb specialists and one of eight fern specialists. The last three were taken there only once. One of the tree-feeders, *Eacles imperialis*, probably did not occur at Hardwick or Stillwater until late in our study.[2] In addition, we had a low incidence of singletons, including only three out of 289 tree feeders (0.7 %) at Stillwater. For the entire study area, 16 of 410 species (3.9 %) were documented only as single individuals, three of which were reliably reported once by local naturalists.

Additionally the early to mid twentieth century fauna was very well documented except for pine specialists. Our 11 year effort produced only one state record for New Jersey: *Brachionycha borealis*, collected at Stillwater, 11 April, 2008. Similarly, Moulding and Madenjian (1979) reported only one state record, an obvious stray or introduction, in their 5 year effort. About ten others that we encountered would not have met our criteria for previously documented. Of these *Eacles imperialis, Cleora sublunaria and Catocala nebulosa,* first documented in 2003, 2004, and 2013, are probably recent range extensions from the south and five of the other seven are localized pine feeders.

Undetected tree feeders in regional context

With 307 species that feed on trees detected from our study area, we failed to detect only 13 (4.1 %) but we note that seven of these, *Sphinx drupiferarum*, *Anisota senatoria*,

[2] Despite generalized range maps the Imperial Moth did not occur regularly inland at this latitude and would not have met our criteria for previously documented, See explanation in Appendix B.

Schizura concinna, *Datana contracta*, *Catocala robinsoni*, *Acronicta hamamelis*, and *Erannis tiliaria*, have also declined to the northeast of New Jersey in southern New England (Hessel 1976; Sargent 1976; Morrell 1979; Schweitzer 2004; Wagner 2012; Wagner et al. 2005, 2011). Five of the other six undetected species are rather common regionally, and two non-detections can be explained by the paucity of pines at our sample sites.

Understory species

Causes of declines

The significantly later last collection dates (mostly 1970s–1980s) for undetected shrub and forb specialists compared to tree feeders (mostly 1950s–1960s) (Fig. 2) suggest largely different factors affecting these guilds. Furthermore no undetected understory species are Sphingidae, Saturniidae, Notodontidae, or *Catocala* which account for seven of 13 undetected tree feeders.

Our detections appear to be in large part driven by three factors, (1) foodplant growth form (whether these include trees or not) and, if no foodplants are trees, then (2) whether the foodplants are ferns or (3) include lowbush blueberries. Over 95 % of species whose foodplants meet one of those criteria were found, compared to only 16 of 25 specialists on forbs and eleven of 20 specialists on non-ericaceous shrubs. Our detection of 26 of 27 litter specialists indicates that these have not been seriously impacted by exotic earthworms (Bohlen et al. 2004; Schweitzer et al. 2011), and Herminiinae were among the most abundant moths at light at High Point in early summer.

Factors that may explain patterns of change

Large-scale moth declines

Our findings do not provide evidence of large-scale multi-strata declines of macro-moths or butterflies such as those documented in Europe (Van Dyck et al. 2009; Mattila et al. 2009), especially Great Britain (Conrad et al. 2006; Fox et al. 2012), although results reported here are mostly at the presence/absence level, only for forest species, and mostly from three relatively high quality (but representative) localities. Nor do annual observations suggest on-going declines for those taxa for which we do have more complete data. For example, for both Saturniidae, of which over 100 were seen annually, and Sphinginae three of nine species had their highest annual catches per unit effort (number observed divided by the number of lights) since 2010 or 2011 at Stillwater in the last year of sampling (2013), as did the genus *Datana*. No tree-feeding Macrolepidoptera found in our study area are recognized as of global conservation concern by Schweitzer et al. (2011).

Changes in forest understory

Some major impact to understory species (except for litter, fern, and Ericaceae specialists) seems to have occurred during or soon after the late 1970s to early 1980s (Fig. 2) or possibly slightly later. Although circumstantial, the available evidence points to the increasing deer population in the late twentieth century as this key factor affecting understory species. We detected all of 22 specialists or narrowly oligophagous species that normally use lowbush blueberries, which persist vegetatively in heavily browsed forests (Rawinski 2008, Smith and Schweitzer unpublished data), or that feed on understory foodplants that he reports to be particularly unpalatable to deer (ferns and two forbs), compared to only 25 of 43 specialists on other understory shrubs and forbs ($p < 0.0001$). We also detected 26 of 28 polyphagous woody understory feeders, most or all of which can feed on lowbush blueberry.

We note that DFS and JAMS saw only two plants of *Ceanothus americanus*, which hosted three undetected and regionally now rare specialists (Schweitzer et al. 2011), and none of us encountered *Lonicera diocia* (or any native *Lonicera*) or *Silene stellata.* Hough (1983) listed all three plants as “frequent”. We encountered the “common” (see also Robichaud and Buell 1973) *Corylus* spp. mostly at High Point as sprouts under 30 cm tall. These four genera hosted one-third of our undetected understory species, and only three of the other twelve depended on “infrequent” foodplants. The proximate cause of most non-detections of understory specialists appears to be severe declines of “frequent” to “common” foodplants. If deer are in fact driving our non-detections of understory specialists, then results from the Hardwick-White Lake and Stillwater sites, which are in state wildlife management areas with a long history of hunting, may understate their declines.

Forest maturation

As discussed by Niering (1953), virtually all forests in New Jersey were clear cut, with deforestation peaking before 1850. Niering (1953) reported that one of our study sites, High Point State Park, regenerated in the 1850s to about 1880, making the forest at least 129 years old when we sampled it. Second growth forest covered 40 % of Sussex County and 26 % of Warren by 1899 and had increased to 58 and 44 % by 1970 (Robichaud and Buell 1973) by which time most of it was more than 80 years old, and so over 113 years old when our study began. Some understory shrubs and forbs probably decrease if the canopy becomes more closed in maturing forests, however forests are not necessarily less open now than 60 or even 100 years ago.

As Rawinski (2008) points out, chronically over-browsed stands can become more open because of a lack of young trees to compensate for canopy loss. Besides small-scale timber harvest and natural mortality, gypsy moth (*Lymantria dispar*) outbreaks starting in the 1960s killed millions of canopy trees (Robichaud and Buell 1973; Schweitzer 2004), especially oaks. Such outbreaks declined in frequency after about 1981 (Maier 2004; Schweitzer 2004). The abundance of dead standing or fallen trees (as of 2009–2011) attests to high (about 20 %) mortality at one of our High Point sites during the late twentieth century. Regardless of the cause, canopy thinning should benefit understory flora, especially forbs and those shrubs which gypsy moth caterpillars do not eat (Schweitzer 2004). One native herb that increased dramatically is hay-scented fern *(Dennstaedtia punctilobula)* which is generally diagnostic for impacts from overly abundant deer (Rawinski 2008; Royo et al. 2010; Nuttle et al. 2014). Niering (1953) does not report this fern at all from High Point, but we found it to be abundant (Smith and Schweitzer, unpublished).

Ten of 14 nocturnal understory moths that we did not encounter were collected at blacklights in the 1970s (Rutgers, AMNH) (Fig. 2, Appendix A), i.e. during the last decade of nocturnal efforts by which time most regional forests would probably have been about 90–120 years old. In addition *Papaipema duplicata* larvae were found in 1980 by Eric Quinter in Somerset County, bringing the total to 79 % detection in 1970–1980 (71 % for 1976–1980) for moths we could not find in 2003–2013. Similarly three of four undetected understory butterflies and skippers were last collected in 1975–1981, although for these groups there were later unsuccessful efforts (Gochfeld and Burger 1997), and one of the moths (*Erastria coloraria*) was collected again diurnally (DFS) in 1986. Of twelve undetected understory species documented since about 1900 from three or four of the five northwestern New Jersey counties, we found records from two or three such counties after 1970 for seven, plus additional concurrent northern New Jersey counties for six of these, which suggests they were still widespread in century-old forests.

Niering (1953) found *Corylus cornuta* present in several communities at up to 42 % of the shrub cover in some mesic stands. Both he and Robichaud and Buell (1973) also report shrub *Cornus* species, especially *C. racemosa*, to be characteristic of about 75 to over 100 year old mesic forests. We resampled several of Niering's sites and found no shrub *Cornus* species in or near them (Smith and Schweitzer, unpublished), and none of the three expected moths that specialize on these were taken in blacklight traps at these sites. In forests of similar canopy mix and age at Stillwater we encountered *Bomolocha bijugalis* once in about 23.5 trap-years with blacklights, and DFS verified a photograph of *Hydrelia albifera* from Warren County in 2013. However, in a 250 year old forest remnant, nearly twice as old as any we sampled, Moulding and Madenjian (1979) reported 11 individuals representing all three shrub *Cornus*-feeding moths (Appendix C) in the equivalent of 2.9 trap-years of effort with much smaller blacklights. Whether or not forest maturation is a factor in our observations regarding shrub *Cornus* apecialists, or in any of our 18 non-detections, it cannot explain the change in the typical stature of azaleas, viburnums, and *Corylus,* from 2 to 3 m tall shrubs to sprouts of <30 cm at High Point.

Invasive plants

The understories at High Point and around Stillwater are not dominated by invasive plants and several vines and shrubs now commonly regarded as invasive slightly to the south, including *Lonicera japonica*, *Celastrus orbiculatus*, and *Eunoymous alatus*, are still infrequently encountered in any abundance in most of Sussex County. We did not observe any of them at our High Point sites and *L. japonica* was not seen at our Stillwater site. *Berberis thunbergii*, garlic mustard *(Alliaria petiolata)*, and the invasive grass *Microstegium vimineum* are present at all three our sample sites, but these are still patchy at High Point and Stillwater. We note that while a toxic decoy effect from garlic mustard *(Alliaria petiolata)* is now a major threat to *Pieris virginiensis* (Schweitzer et al. 2011), this butterfly was last collected locally in 1935, decades before that plant became invasive.

Conclusions

We could document only 60 % of specialists on non-ericaceous understory shrubs and forest forbs, compared to 92–100 % of species in other guilds. Current scarcity of formerly frequent to common foodplants (Hough 1983) appears to account for most non-detections of understory species. Findings are consistent with deer as the key factor in these declines, but there have been other changes, such as forest maturation and increases in invasive plants which could negatively impact understory plants, while canopy thinning due to gypsy moth outbreaks should favor them.

Declines of understory species are not confined to New Jersey (Schweitzer et al. 2011). O'Donnell et al. (2007) listed deer as among the major threats to butterflies to the east in Connecticut, where *C. nycteis* also abruptly disappeared in the 1980s and *Papaipema astuta* is historic (Schweitzer et al. 2011). Targeted Lepidoptera inventories to the southwest on the Piedmont in 2004–2009 by the Delaware Natural Heritage Program with DFS as one of the investigators found none of five expected forest forb-feeding *Papaipema* but the expected fern feeder, the tree feeder, and all four old field species were found. We suggest that most non-ericaceous and non-fern feeding understory specialists are of regional conservation concern, especially those using the same genera as undetected species, such as *Physocarpus, Ribes, Collinsonia,* and *Helianthus*. Eight understory specialists from Tables 1, 2, three of them detected, are considered to be of global concern by Schweitzer et al. (2011).

Additional targeted efforts are needed to document the extent, magnitude, and causes, of declines in understory-dependent species especially west and south of eastern Pennsylvania. Future impacts from invasive plants may be especially important to monitor. Among tree feeders, we recommend monitoring of Saturniidae, Sphingidae, and other groups reported to be declining nearby, as citizen scientist projects. Understanding changes to Lepidoptera populations may ultimately offer insights into the mechanisms of population change of other forest-dependent species, such as birds, that have been linked to overabundant deer (DeCalesta 1996; Côté et al. 2004; Baiser et al. 2008; Chollet and Martin 2013).

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