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A perfect storm: two ecosystem engineers interact to degrade deciduous forests of New Jersey

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Abstract Ecosystem engineers play a large role in physically structuring the ecosystem in which they are embedded. The focus of much of the research surrounding these species is to document the impacts of a single engineer on community composition and ecosystem processes. However, most ecosystems harbor multiple engineering species that interact in complex ways and rarely have the dynamics of such species been fully investigated. We look at how two ecosystem engineers, the white-tailed deer (*Odocoileus virginianus*) and the invasive plant Japanese stilt grass (*Microstegium vimineum*), interact to completely alter the structure and composition of the subcanopy within northern deciduous forests. This interaction has wide-ranging repercussions on forest food webs which we explore through a case study of breeding woodland birds in the state of New Jersey, USA. We show that the guilds of birds that rely on the subcanopy have experienced greater declines from 1980 to 2005 than birds that specialize on the intact upper canopy of impacted forests. This dynamic is not restricted to immediate temporal effects and may act to derail the long-term successional pathway of northern deciduous forests. It is no longer prudent to set aside tracts of forest and expect them to retain their native biodiversity without active management.

Introduction

Ecosystem engineers play a large role in physically structuring the ecosystem of which they are members (Jones et al. 1997). The focus of much of the research surrounding these species has been to document the direct and indirect impacts of a single engineer on community composition and ecosystem processes (Wright and Jones 2006). However, most ecosystems harbor multiple engineering species that interact in complex ways and rarely have the dynamics of such species been fully investigated especially in reference to their combined impacts on the ecological value of the ecosystem in which they are embedded (Jones et al. 1997; Wright and Jones 2006). In the temperate deciduous forests of North America, white-tailed deer (*Odocoileus virginianus*) exert a strong influence on the composition and structure of forest vegetation via direct trophic interactions and also through modification of abiotic resources (Wilby et al. 2001;

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Rooney and Waller 2003; Cote et al. 2004; Rooney et al. 2004). We review evidence that when deer abundance is very high in these forests, the invasion of non-native engineering plants can produce a profound and perhaps irreversible shift in forest structure and composition. This shift likely has several cascading effects that include causing rapid declines amongst birds that depend on forest mid-canopy and understory vegetation. We suggest that this scenario is far more likely to occur within urban and urbanizing ecosystems in part because the two engineering species are more likely to co-occur in large numbers.

Deer as ecosystem engineers

White-tailed deer have been described as keystone and engineer species (Cote et al. 2004) due to the very large impact they have on the forests they inhabit. Nearly every region of North America currently harbors larger numbers of white-tailed deer than at any time in the past century (McShea et al. 1997). The reason for this increase is multifaceted and includes an effect of reduced hunting pressure, loss of apex predators, and widespread changes in land use and cover. Ungulates across their ranges in North America have benefited from the extirpation of apex predators such as wolves (*Canis lupus*) and mountain lions (*Puma concolor*) (Cote et al. 2004). This is especially true in eastern North America where the white-tailed deer's historical main predator, the mountain lion, is completely extirpated (McCullough 1997). At the same time, the number of citizens participating in deer hunting has steadily declined over the last two decades in part because of an increase in the proportion of the US population that lives in urban areas (Zinn 2003; Adams et al. 2004). In addition, hunting opportunities have declined over the past decades as lands formerly in large forest tracts were fragmented and developed for housing and commercial purposes (Drake et al. 2002; Riley et al. 2003). These same land cover types are especially attractive to deer leading to a synergistic feedback whereby deer abundance increases in habitats that have the lowest hunting pressure (Riley et al. 2003; Cote et al. 2004).

Given their strong influence on forest structure and composition, it should not be surprising that when white-tailed deer reach very high abundances, their effects can be huge (Augustine and Frelich 1998;

Rooney and Waller 2003; Rooney et al. 2004). Overbrowsing by deer can extirpate browse-sensitive species, or drive them to very low densities (Rooney and Dress 1997; Griggs et al. 2006). The result is a large change in the physiognomy of a forest. Browse-resistant species are often structurally very different from browse-sensitive species that may have dominated previously (e.g., replacing native shrubs with grasses or leaf litter). This can alter the microclimate of forest floors and thus the abundance and distribution of species that sit at the base of the forest food web. For example, overbrowsing by deer reduced abundance and species diversity of forest-dwelling insects (Allombert et al. 2005a) as well as abundance and species richness of web spiders (Miyashita et al. 2004). Similarly, structural changes in forest understories due to deer overbrowsing caused a shift in avian communities, with birds dependent on understory vegetation for foraging and nesting decreasing in abundance within, or becoming absent from, heavily browsed forests (McShea et al. 1995; McShea and Rappole 2000; Allombert et al. 2005b).

When two ecosystem engineers meet

Invasive species are being introduced worldwide at increasingly high rates (Lockwood et al. 2007). They represent a major threat to native species and ecosystems across the globe (Elton 1958; Vitousek et al. 1996) especially when they act as ecosystem engineers (Crooks 2002). Engineering invasive plants show the ability to alter soil-based ecosystem processes, water availability, and vegetative structure of communities (Vitousek 1990; Sala et al. 1996; Ehrenfeld et al. 2001). The presence of engineering invasive plants can thus lead to drastic changes in the abundance or presence of native species or lead to losses of ecosystem services (Lockwood et al. 2007).

The same conditions that promote high white-tailed deer abundance in US northern deciduous forests can promote the spread of plant invaders into these forests. Both white-tailed deer and invasive plants benefit from the matrix of habitats dispersed between forest fragments (Janzen 1983; Alverson et al. 1988). In addition to foraging within forest interior, white-tailed deer regularly forage in row crops and early successional habitats (Alverson et al. 1988; Augustine and Jordan 1998). Non-native invasive plants are regularly found at high densities

in these same habitats, often spreading from these matrix lands into forest edges and interiors (Janzen 1983; Redman 1995).

Furthermore, Hobbs (2001) provides evidence that ungulates can serve to increase the prevalence of a co-occurring non-native invader. Invasive plants often readily disperse along roadsides and power line rights-of-way (Flory and Clay 2006) and into forest fragments via ungulates (Hodkinson and Thompson 1997). White-tailed deer disperse propagules of invasive plants into forest interiors via endozoochory and epizoochory (e.g., in hooves and fur) (Gill and Beardall 2001). Thus, when deer are present many invasive plants may enjoy increased opportunities for dispersal.

The positive effect of deer on invasive plants can at times extend to alteration of resources that favor the invasive. Deer browsing within forests may increase the likelihood of invader establishment and spread via browsing disturbance (e.g., thinning of shrub layer), thus providing necessary resource surges that incoming invasive species propagules can take advantage of for establishment (de la Cretaz and Kelty 1999). After the invasive plant establishes a self-sustaining population, continued selective browsing by deer on native species can allow the invader access to a greater proportion of resources. Finally, deer will continue to provide a dispersal vector for the invasive plant's propagules thus increasing the spread rate of the invader through the forest (Kellogg and Bridgham 2004).

This means that some forests, particularly those that are fragmented and near a ready source of non-native species (e.g., urban areas), may simultaneously harbor overly abundant white-tailed deer and a large number of invasive non-native plants. When one of these invasive plants is an ecosystem engineer, two strongly interacting species come to occupy the same food web and together they dramatically change forest structure. To illustrate this 'perfect storm' effect we review the interaction between white-tailed deer and Japanese stilt grass (*Microstegium vimineum*) (Trin.) A. Campus within the deciduous forests of New Jersey, the most densely populated state in the US.

The fate of New Jersey forests

New Jersey is no exception to the trend of deer overabundance in North America. Forest fragmentation, loss of apex predators, and a decrease in hunter participation have lead to very large deer populations in New Jersey (McCullough 1997; Drake et al. 2002). We could find no estimates of what precolonial deer populations were in New Jersey, but as an example of such estimates, McCabe and McCabe (1984) suggest an estimate of 4 deer/km^2 in Wisconsin before European colonists. In 1999, the average minimum deer density in New Jersey was just over 14 deer/km^2 (Drake et al. 2002), and in one extreme case, 82 deer were counted in one square kilometer in Hunterdon County, NJ in 2000 (Drake et al. 2002). Overbrowsing has been shown to occur at deer densities of >4/km^2 (Alverson et al. 1988) thus it is likely that nearly all of New Jersey's forests are in an overbrowsed state and for many areas the degree of overbrowsing is severe.

If there was a perfect engineering plant invader to take advantage of the overbrowsed status of New Jersey's deciduous forests it is Japanese stilt grass (*Microstegium vimineum*), a shade-tolerant annual C-4 grass introduced to the US from Japan and China (Fairbrothers and Gray 1972; Horton and Neufeld 1998; Kourtev et al. 1998). Stilt grass was first detected in 1919 in Knoxville, TN (Barden 1987). In less than 100 years since this initial detection, stilt grass invaded the entire US east coast from Florida to Massachusetts (Barden 1987; Mehrhoff et al. 2003). This species first arrived in New Jersey in 1959 (Fairbrothers and Gray 1972), but has only become invasive in New Jersey's forests in the past 20 years (Kourtev et al. 1998; Aronson 2007).

Stilt grass possesses several life-history traits that make it a common and detrimental invader to deciduous forests. First, it thrives in disturbed habitats such as forest edges and along roads, each of which are a common feature of the fractured forests of New Jersey and other heavily populated areas. Second, its ability to tolerate low light levels allows it to invade understory habitat deep within closed canopy forests (Redman 1995; Horton and Neufeld 1998). The presence of a robust midcanopy and overstory canopy will prevent the establishment of stilt grass, however if the midcanopy is sparse it will establish (Cole and Weltzin 2005). Third, once stilt grass establishes a beachhead in a forest, it forms dense monospecific stands that crowd out native vegetation (Aronson 2007). Stilt grass ranges in height from 30 to 100 cm, far taller than most tree and shrub seedlings (Aronson 2007) and has a high

competitive ability (Leicht et al. 2005; Morrison et al. 2007). Fourth, stilt grass produces copious seeds which remain in the soil seed bank for at least 3 years (Barden 1987). And finally, Japanese stilt grass alters soil-based ecosystem processes (Ehrenfeld et al. 2001). These changes in abiotic conditions adversely affect native plant communities thereby further increasing the invasibility of these forests (Ehrenfeld et al. 2001; Kourtev et al. 2002).

Stilt grass and white-tailed deer interact in such a way that the invader readily establishes and reaches dominance in the native forests of New Jersey. White-tailed deer move over relatively large areas (with home ranges averaging up to 233 ha and 221 ha for males and females, respectively; Tierson et al. 1985). Consequently, deer regularly move between fragmented habitats that harbor large populations of stilt grass and more intact forests, and thus they may serve as one of several primary dispersal agents for stilt grass propagules into the forest interior. Overabundant deer will reduce, if not eliminate, the midcanopy of most interior forests thus creating light conditions where stilt grass propagules can establish (Cole and Weltzin 2005). Finally, since white-tailed deer do not eat stilt grass, they serve to maintain stilt grass dominance through selective herbivory, which has been documented for other invasive species (Kellogg and Bridgham 2004).

Thus, when these two engineers co-occur, the species composition and vegetative structure of New Jersey's deciduous forests is completely transformed (Aronson 2007). A once healthy understory comprised of native shrubs and saplings (Fig. 1a) is greatly reduced via overbrowsing. The resulting forest structure includes almost no midcanopy with two possible understories. The first is composed of a dense monoculture of stilt grass with patches of garlic mustard (*Alliaria petiolata*), another invasive exotic (Fig. 1b), and the second is a barren understory of leaf litter absent of any vertical structure (Fig. 1c).

This newly created structure and composition appears to be persistent thus forming what Royo and Carson (2006) term a recalcitrant understory. These authors suggest that a recalcitrant understory has at least one of following attributes: (1) the understory exists as a denser and more extensive ground cover, and has lower diversity, as compared to the historical understory, (2) it can alter the path and rate of succession by outcompeting tree seedlings for light, and (3) once established, the understory layer can repel potential invaders and can persist for several decades. In mid-Atlantic deciduous forests, normal successional pathways are stalled by the recalcitrant understory composed of stilt grass and maintained by deer overbrowsing (Pedersen and Wallis 2004). Stilt grass crowds out competitors,
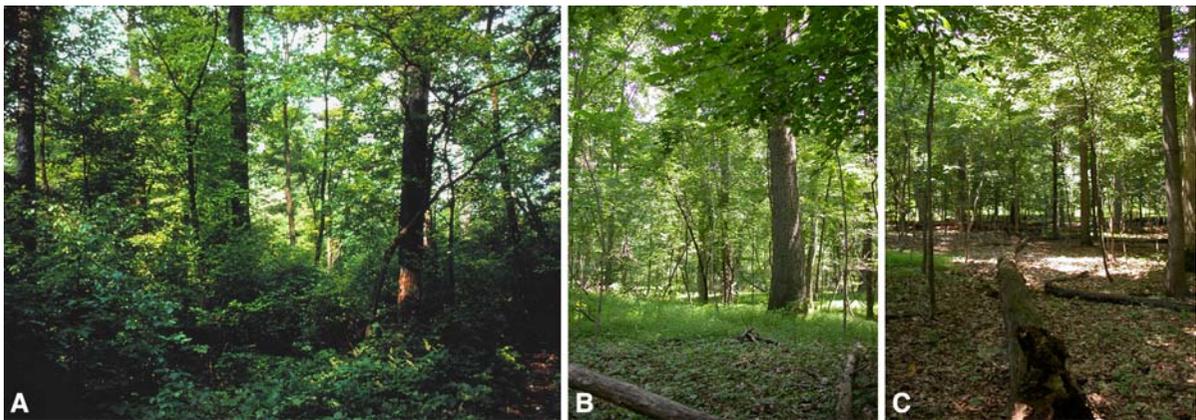
Fig. 1 Time series of photos from Hutcheson Memorial Forest (HMF) in Somerset County, New Jersey. HMF is mixed oak-hickory forest with 26 ha of old growth surrounded by secondary forest, old fields, and farm fields. (**a**) Shows the forest in 1976 with an intact shrub layer. Overbrowsing by deer and non-native plant invasion have changed the forest understory and midcanopy from native saplings, shrubs and herbs such as *Viburnum acerifolium*, *Circaea lutetiana*, and *Podophyllum peltatum* (Davison 1981) to, (**b**) a dense understory composed mostly of *Microstegium vimineum* and another exotic invasive, *Alliaria petiolata* (foreground) (2005) and (**c**) leaf litter with small patches of *Microstegium vimineum* (2005). Photograph (**a**) is courtesy of Jim Quinn and (**b**) and (**c**) are courtesy of Myla Aronson

reducing access to light and altering nutrient availability in the soil (Redman 1995; Leicht et al. 2005). The result is the regeneration failure of the dominant native trees of these forests such as *Quercus alba* and *Quercus rubra* (Vidra et al. 2006; Aronson 2007). Seedlings of species that can grow in these conditions may penetrate the stilt grass layer but are then subject to deer browsing (Aronson 2007), which often reduces their ability to compete for the resources that are available (Vidra et al. 2006).

This situation is a recipe for a long-term wholesale change in ecological communities within the fragmented forests of New Jersey and places like it. While existing native canopy trees are still alive, there are few midcanopy trees of the same species waiting to take their place once they perish (Aronson 2007). Instead, the midcanopy species that can survive the dual ecological filters (George and Bazzaz 1999) of stilt grass and deer browse are non-native trees such as *Acer platanoides* and *Ailanthus altissima*, and formerly less dominant native trees such as *Fraxinus americana* and *Prunus serotina* (Aronson 2007). We do not yet know which species will ultimately comprise the dominant canopy layer of these new forests because we do not know what the new long-term successional pathway looks like for forests that are subject to the combined effects of stilt grass invasion and white-tailed deer overbrowsing. However, like many US deciduous forests, we may be witnessing gradual deforestation of the remaining forest fragments of New Jersey from the bottom up (Pedersen and Wallis 2004).

Cascading effects

Each engineer involved in this scenario will have its own effect on animal community structure (Fig. 2a), and the co-existence of the two engineers is more likely when forest fragmentation is high (Fig. 2b). However, because the two engineers can have synergistic interactions, mostly flowing from the deer to the invader, their combined effect on forest-dependent animals may be much worse than expected from each species alone (Fig. 2). To illustrate this, we review evidence that white-tailed deer and stilt grass have combined to cause relatively rapid declines in forest understory birds in New Jersey.

The decline of forest birds over parts of their breeding ranges in North America has been well
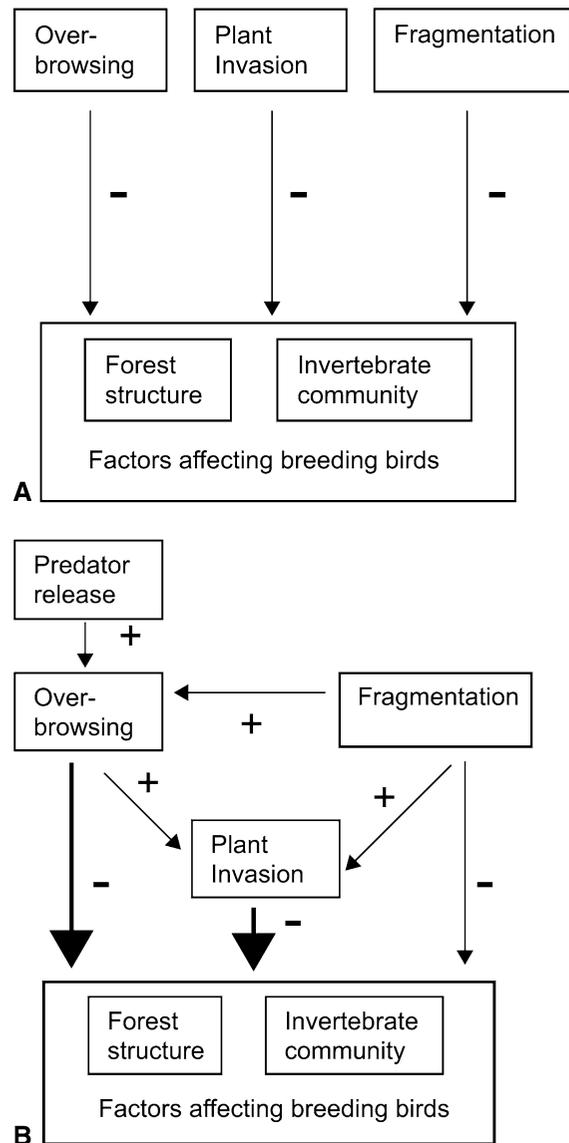

Fig. 2 The effects of fragmentation, overbrowse, and invasive plants individually on the avian community (**a**), and where they facilitate each other, thereby having a greater effect in concert than they do individually (**b**). Signs represent the direction of the effect and the thickness of the arrow represents effect size

documented over the past 30 years (Robbins et al. 1989; Peterjohn et al. 1995; Ballard et al. 2003). Several hypotheses have been put forth to explain these observed declines, most of which point to habitat loss and fragmentation of the breeding grounds as the drivers of decreasing densities (Bohning-Gaese et al. 1993; Petit et al. 1995); for example, forest fragmentation allows brown-headed cowbirds (*Molothrus ater*) to infiltrate forest patches

and lay their eggs in the nests of a wide variety of songbird hosts (Robinson et al. 1995; Robbins et al. 1989; Donovan et al. 1995, 1997). Also, increased nest predation rates are a common feature of forest fragments (Wilcove 1985; Porneluzi et al. 1993; Robinson et al. 1995; Donovan et al. 1995). Together these factors have combined to create a source-sink dynamic for breeding birds across the fragmented deciduous forests of the US (Pulliam 1988; Porneluzi et al. 1993; Donovan et al. 1995).

Forest fragmentation also facilitates the overabundance of white-tailed deer and the invasion of forests by stilt grass or other engineering invasive plants. The forest structure created by these two engineers individually or in concert is devoid of the necessary vegetation structure that many birds require for breeding. Microhabitat preference among breeding birds is adaptive and under selection (Martin 1998), which implies that cues used to select these habitats are indicators of essential fitness components such as nest building materials, nest sites, enemy free space, and food (Jeffries and Lawton 1984). Birds are thought to select territories based on James' (1971) concept of niche gestalt; the bird's overall perception of vegetation structure. The guilds of ground and midcanopy nesting and foraging birds are extremely susceptible to structural changes within forest habitat (McShea et al. 1995; McShea and Rappole 2000; Allombert et al. 2005b). Thus, forests influenced by white-tailed deer overbrowsing and plant invasion may not fit a bird's niche gestalt since these forests will have experienced a profound change in vegetation structure within these subcanopy layers.

This observation raises the possibility that the disappearance of birds that nest in the understory and midcanopy of North American forests is driven in part by habitat losses stemming from a far more subtle process than the loss of forest due to expanding agriculture or urban development. Essentially, the patches of forests that remain in the wake of land use change may still be lost to these bird guilds due to the removal of key vegetative structures by deer and invasive plants. It also raises the possibility that forest patches that are large enough to be considered population sources for understory and midcanopy breeding birds under normal circumstances (i.e., are large enough to escape brood parasites and nest predators) may be converted into unsuitable habitat via overbrowsing and plant invasion.

If forest understories are being dramatically altered by deer and invasive plants, the birds that nest in the understory and midcanopy of forest fragments may show dramatically different population trends than birds that utilize the intact canopies of these same forests. To evaluate this possibility, we used the US Geological Survey breeding bird survey (BBS) analysis website to calculate abundance trend estimates for all forest species in the state of New Jersey from 1980 to 2005. Information was restricted only to routes conducted by persons deemed "consistent" by USGS analysts, and to species with no less than 14 samples for the period of analysis. This resulted in a trend analysis for 22 species (Table 1), one of which we dropped (Wild Turkey, *Meleagris gallopavo*) due to its prevalence in multiple habitat types other than forest. Regional abundance trends for New Jersey were calculated as weighted averages of individual route trends for the State, using the equation estimators of Link and Sauer (1994). Variance in the abundance trend estimator is calculated through bootstrapping. More information on conducting analyses on BBS data can be found at the website, http://www.mbr-pwrc.usgs.gov/bbs/bbs2004.html.

Once abundance trend estimates were obtained for forest breeding birds, we collected data on nesting behavior for each species, such as typical nest location and height, from the Birds of North America Online (Poole 2005). Using these data we classified all 21 forest birds based on their primary nesting strata within the forest as either canopy, midcanopy, or shrub/ground breeders. We also used data on primary migratory strategy to further classify each species as either a resident or neotropical migrant. We hypothesized that migratory species that nest primarily between the ground and the midcanopy forest layers would be the most affected by deer overbrowsing, stilt grass invasion, or both.

Between 1980 and 2005, all ground and midcanopy nesting forest birds have experienced greater declines in abundance than birds that breed in the canopy of these same forests (Fig. 3). The ground and midcanopy guilds include the only species that evidenced statistically significant abundance declines within the state of New Jersey between 1980 and 2005 (Table 1). The only birds to show statistically significant positive increases in abundance within New Jersey forests are those that nest in the canopy (Table 1). The same trends hold for both resident and

Table 1 Forest bird species included in our Breeding Bird Survey (BBS) analysis for New Jersey

Species	Nest strata	Migration strategy	Adjusted trend	*n*	*P*
Black-Billed Cuckoo (*Coccyzus erythropthalmus*)	Shrub/ground	Neotropical	−7.7219	19	**0.0114**
Rose-Breasted Grosbeak (*Pheucticus ludovicianus*)	Midstory	Neotropical	−5.5342	14	**0**
Yellow-Billed Cuckoo (*Coccyzus americanus*)	Midstory	Neotropical	−4.5324	31	**0.0725**
Veery (*Catharus fuscescens*)	Shrub/ground	Neotropical	−3.4201	15	**0.0036**
Wood Thrush (*Hylocichla mustelina*)	Shrub/ground	Neotropical	−2.2257	32	**0.0146**
Ovenbird (*Seiurus aurocapilla*)	Shrub/ground	Neotropical	−1.9196	32	**0.0517**
Black-and-White Warbler (*Mniotilta varia*)	Midstory	Neotropical	−4.724	26	0.1186
Hairy Woodpecker (*Picoides villosus*)	Midstory	Resident	−2.945	20	0.2498
Carolina Chickadee (*Poecile carolinensis*)	Canopy	Resident	−2.3554	23	0.2154
Scarlet Tanager (*Piranga olivacea*)	Midstory	Neotropical	−1.5734	30	0.1166
Red-Eyed Vireo (*Vireo olivaceus*)	Midstory	Neotropical	−1.4215	31	0.2919
Downy Woodpecker (*Picoides pubescens*)	Midstory	Resident	−1.0293	31	0.2704
Eastern Wood-Pewee (*Contopus virens*)	Midstory	Neotropical	−0.8329	32	0.5477
Pine Warbler (*Dendroica pinus*)	Canopy	Resident	−0.8246	21	0.6868
Tufted Titmouse (*Baeolophus bicolor*)	Canopy	Resident	1.1053	32	**0.0485**
Red-Bellied Woodpecker (*Melanerpes carolinus*)	Canopy	Resident	5.7565	30	**0**
Blue-Gray Gnatcatcher (*Polioptila caerulea*)	Canopy	Neotropical	0.5882	24	0.7214
Warbling Vireo (*Vireo gilvus*)	Canopy	Neotropical	1.4173	16	0.5222
Great Crested Flycatcher (*Myiarchus crinitus*)	Midstory	Neotropical	1.631	30	0.2074
White-Breasted Nuthatch (*Sitta carolinensis*)	Canopy	Resident	1.6647	26	0.3277
American Redstart (*Setophaga ruticilla*)	Midstory	Neotropical	3.4367	15	0.1539

Only species occurring on more than 14 survey routes and with reliable observers during the period of record are included in the analysis. Species are classified by the location within the vertical structure of the forest where they tend to nest (shrub/ground, midcanopy, and canopy) and by migration tendency (resident versus neotropical migrant). The adjusted trend in Table 1 represents the estimated percentage change in abundance per year across the region from 1980 to 2005. Significant *P*-values are presented in bold face and data are sorted in descending order from the most statistically significant negative trend toward the most statistically positive trend

neotropical migrants, however we note that all of the statistically significant declines we show are neotropical migrants (Table 1).

While we cannot pin these declines directly on a particular ecological mechanism, we can propose two scenarios by which these two ecosystem engineers may interact to affect understory bird populations in New Jersey. In the first scenario deer overbrowsing eliminates understory and midcanopy habitat independent of plant invasion thus directly decreasing densities of birds that rely on these forest elements (Fig. 2a). This mechanism has been shown previously in deciduous forests outside of New Jersey (McShea et al. 1995; McShea and Rappole 2000), and given the high abundance of deer in the State, this effect by itself could well account for much of the decline we show in Fig. 3. In the second scenario, stilt grass invasion serves to prevent the shrub layer

from returning (Leicht et al. 2005; Vidra et al. 2006; Aronson 2007), thus maintaining overbrowsed forests in a state unsuitable for understory and midcanopy birds for long periods regardless of short-term fluctuations in deer abundance (Fig. 2b). In addition, the presence of stilt grass may transform the forest floor into a state that is unsuitable for ground-nesting birds beyond the influence of deer overbrowsing alone. The invasive understory may not provide basic resources such as nest sites or food thus deterring birds from selecting invaded habitat. Birds that do attempt to nest within the stilt grass understory may suffer the consequences of suboptimal habitat selection. For example, it has been shown that birds nesting in invasive exotic plant species experienced higher predation than those nesting in natives (Schmidt and Whelan 1999). Since these scenarios are not mutually exclusive, experimental
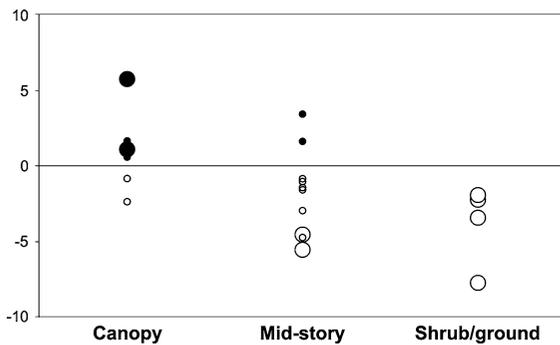
Fig. 3 Plotted abundance trend estimates from 1980 to 2005 for 21 forest breeding bird species in New Jersey. Estimates are classified based on dominant vertical nesting location (canopy, midcanopy, or shrub/ground). Solid circles indicate species that show a positive trend in annual abundance change, whereas open circles represent species experiencing a negative trend. The zero line represents no change in abundance through time. Large circles indicate that the trend is statistically significant, whereas small circles indicate nonsignificance. On the y-axis labels can be translated as a percentage. For example, a species sitting at the −5.0 level can be said to declining in abundance by an estimated 5% per year

manipulation is necessary to determine which is driving the understory bird decline we show in Fig. 3.

Conclusions

Jones et al. (1997) point out that there should be complex relationships between the members of a community and ecosystem engineers and certainly this complexity must grow when two (or more) engineers themselves strongly interact. We have detailed one such case for US northern deciduous forests, and evidence suggests that the impact of this interaction is a drastic alteration of forest structure and composition. While overbrowsing by white-tailed deer has led to large changes across the northern US (Rooney and Waller 2003; Rooney et al. 2004), most of these forests are not also subject to invasion by engineering invasive plants. This situation may reflect a lack of opportunity for invasion instead of an inherent resistance to invasion (Lockwood et al. 2007). Certainly stilt grass is spreading rapidly across the northeastern US (Merhoff et al. 2003) and there is no reason to suspect that it would fail to establish within most overbrowsed US deciduous forests. Any engineering invader may have the same effect, however, and

indeed some engineering native understory species may fit the description we provide here for stilt grass (e.g., hay-scented fern, *Dennstaeditia punctilobula*; de la Cretaz and Kelty 1999).

The failure of forests to show signs of regenerating in the face of this dynamic suggests that we may be witnessing the early stages of a much larger impact (e.g., Pedersen and Wallis 2004; Aronson 2007). The ecological filters imposed by these engineering species are severe and seem to reinforce one another to either slow or prevent native plant successional dynamics. As the dominant native canopy trees begin to die out either through natural senescence or via non-native insect and pathogen attacks (Lockwood et al. 2007), the successional pathway these forests take will be influenced by what trees can survive these filters. In New Jersey, at least some of these trees are non-natives (Aronson 2007). In addition, the change in forest structure is apparently having a profound effect on the animal species that rely on native forest structure for nesting or foraging, including driving entire guilds of birds to very low numbers. Since these are the species that serve as seed dispersers and pollinators in these forests and thus drive succession to some extent, there is likely yet another suite of unexpected successional dynamics imbedded in this situation.

The scenario that we describe shares some similarities with the invasional meltdown of Simberloff and Von Holle (1999). However, here one of our interacting species, white-tailed deer, is an overabundant native species and not a classic non-native species that was purposefully introduced to North America from another continent (see, e.g., the definition in Lockwood et al. 2007). Our observations of degradation in the forests of New Jersey suggest that there is merit to extending the invasional meltdown scenario to include positive interactions between invasive species and overabundant native species. We do note that our example is another in the string of supposedly supportive evidence of invasional meltdowns that is a short-term observation of facilitative interactions between two species, with lack of evidence documenting accelerated invasive species establishment (Simberloff 2006). This may however be a matter of time, and taking a proactive approach to invasive species management may be the most effective way to eradicate them (Simberloff 2003).

The bright side to this situation is that we know the two engineering species that are driving the changes. Thus if we wish to restore these ecosystems back to a state that includes more native species (e.g., dominated by native trees), the engineering species should be the target of management (Byers et al. 2006). Royo and Carson (2006) provide a shortlist of possible restoration options when faced with a recalcitrant understory, which are likely of some use for the impacted forests we describe here. These options are geared toward shifting the abiotic balance such that some seedlings of the dominant native trees can establish within the existing understory and thus begin regenerating the forest canopy. A key to this approach is reducing the abundance of white-tailed deer. The obvious way to achieve this is to increase hunting and perhaps set regulations so that they achieve maximum deer population reduction. There is much room for exploration in terms of reducing deer herds in North America and elsewhere since many ungulate management plans do not take into account ecological restoration of forests (Holsman 2000; Riley et al. 2003).

We have merely put several pieces of an ecological puzzle together in this review, drawing heavily on our observation of the status of deciduous forests in New Jersey. There is a great deal that we do not know about the fate of New Jersey and other northern deciduous forests; for example, we do not fully understand the mechanistic links between deer overbrowsing and plant invasions, especially in terms of the plant invaders' impact on the deer (i.e., positive or negative). Similarly, we do not understand the full landscape context for these mechanisms, making it difficult for us to predict how broadly the scenario we describe will extend. We provided one example of cascading effects but our evidence is through correlation only. Such effects are certainly amenable to field experimentation, especially in the context of forest restoration and efforts to increase hunter participation. The results from such experiments are certain to modify our conclusions here. Finally, there is a clear need to understand how successional dynamics have changed in these impacted forests and to explore management options that can push these forests back toward a state that includes more native species.

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