



Insect responses to invasive shrubs: Implications to managing thicket habitats in the northeastern United States



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ABSTRACT

In the northeastern United States, many species are affiliated with early-successional forests and shrublands, collectively referred to as thickets. The abundance of these habitats has declined substantially in recent decades and, of those that remain, many have been colonized by exotic shrubs. We investigated how invasive shrubs may affect these habitats by focusing on possible changes to local insect communities because insects represent a diverse assemblage that is known to respond to changes in plant composition. Additionally, modifications of insect communities may affect the suitability of habitats to other organisms that prey on them. We compared insect abundance, richness, and phenology among four sites with different levels of exotic shrub cover using flight-intercept traps and beat sampling of individual shrubs. Captive lepidopteran larvae also were used to investigate preferences for foliage from native and exotic shrubs and short-term survival when larvae were exclusively fed foliage from either native or exotic shrubs. Habitats with a large proportion of cover by invasive shrubs had an abundance of generalist and pest insects, whereas sites dominated by native shrubs supported more lepidopterans, more herbivorous insects, and more rare species. Captive lepidopteran larvae avoided foliage from invasive shrubs and a majority of those provided with such a diet died. We conclude that invasive shrubs may alter local insect communities and that those modifications can reduce the suitability of thicket habitats to other organisms (e.g., nesting songbirds). The enhancement and expansion of thicket habitats has become a management priority in the region, yet activities that are applied to maintain these habitats (e.g., controlled burns, mowing, and cuts) can increase the likelihood of exotic plant invasions. We summarize guidelines that may help avoid a management dilemma when dealing with this issue.

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1. Introduction

In the northeastern United States, many species utilize the resources found in early-successional forests and shrublands (Litvaitis et al., 1999; DeGraaf and Yamasaki, 2000). Such habitats (collectively referred to as *thickets*) were historically abundant in this region as a consequence of wide-spread clearing of forests for agriculture (Litvaitis, 1993; Foster et al., 2002). Although the abundance of young forests has returned to levels more consistent with natural-disturbance regimes (Trani et al., 2001; Lorimer and White, 2003), development of coastal areas and pine barrens (Noss et al., 1995), loss of wetlands (Dahl, 1990), construction of dams that subsequently reduced riparian habitats (Hall et al., 2011), and local extirpation of beavers (*Castor canadensis*; Gotie and Jenks,

1982) have decreased the abundance of naturally occurring shrublands (Litvaitis et al., 1999). Consequently, remaining thickets are often small and disjunct (Litvaitis, 1993), and their coverage continues to decline (Brooks, 2003). In response to these changes in habitat availability, natural resource agencies in the region have made the expansion of early-successional forests and shrublands a conservation priority (Litvaitis, 2003; Oehler, 2003; Litvaitis et al., 2013).

The attraction to thicket habitats by a diverse group of obligate and facultative consumers is likely a consequence of the richness of vascular plants (Howard and Lee, 2003) that create unique structural characteristics (especially dense cover near ground level) and diverse foraging opportunities (Matlack and Litvaitis, 1999). Physical properties of shrublands and early-successional forests also result in distinct microclimates that are rare or absent in closed-canopy forests, including intense light, high temperatures, and low soil moisture (Matlack and Litvaitis, 1999). These features are important to some invertebrates. Male katydids (*Atlantiscus testaceus*) call from low vegetation, usually 20–30 cm above the

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ground. Male *Scudderia* (another katydid) also call from emergent shrubs or small trees in otherwise open habitats (D.L. Wagner, University of Connecticut, personal communication). Although vertebrates principally respond to structural characteristics of their habitats, many insects are dependent upon the abundance and distribution of particular plants, including those associated with thicket habitats. For example, New Jersey tea (*Ceanothus americana*), a shrub of open, sandy areas, is the only plant host in the New England region for five species of Lepidoptera, including the mottled skipper (*Erynnis martialis*) that is now believed to be extirpated from the region (Litvaitis et al., 1999). Other shrubs in thickets that are rich in specialist insect herbivores include sweetfern (*Comptonia peregrina*), sumacs (*Rhus spp.*), and blueberries (*Vaccinium spp.*). Lupine (*Lupinus perennis*) is the sole host of the federally-endangered Karner blue butterfly (*Lycaeides melissa samuelis*), two other butterflies of regional conservation concern (frosted elfin [*Incisalia irus*] and persius dusky wing [*Erynnis persius*]), and a number of microlepidopterans (Forbes, 1923; Haack, 1993).

Managing thicket habitats usually requires regular application of some form of disturbance (e.g., prescribed burning, mowing, or cutting) that removes or limits tree growth (Oehler et al., 2006). Such disturbances are known to facilitate the colonization and spread of exotic, invasive plants (e.g., Hobbs and Huenneke, 1992; Johnson et al., 2006). Additionally, some species of invasive shrubs, including autumn olive (*Elaeagnus umbellata*) and multiflora rose (*Rosa multiflora*) were intentionally planted in thicket habitats to increase food and cover for game species (Gill and Healy, 1974). As a result, many sites currently managed as thickets support extensive populations of invasive shrubs.

The replacement of native plants by exotic species may have consequences beyond changing local plant communities; they may also affect other trophic levels. For example, phytophagous insects may be deterred by unpalatable exotic plants (Tallamy, 2004; Burghardt et al., 2010; Tallamy et al., 2010). Although the effects of insects on exotic plant fitness have been well-researched (see review of Keane and Crawley, 2002), studies on the effects of invasive plants on insect communities have been less frequent and patterns are inconsistent among studies (McEvoy, 2002; Tallamy, 2004). Insect diversity and abundance can be reduced in habitats invaded by exotic plants (Colautti et al., 2004; Harris et al., 2004; Tallamy and Shropshire, 2009; Burghardt et al., 2010). Exotic plants have also been shown to support different guilds of insects than native plants (Harris et al., 2004; Proches et al., 2008; Ballard et al., 2013). On the other hand, some investigators have reported minimal effects of exotic plants on native insects (Williamson, 1996; Davis, 2003). Preference and cafeteria-style experiments also have provided conflicting results. In some studies, insects preferred exotic plants (e.g., Gross et al., 2001; Agrawal and Kotanen, 2003; Lankau et al., 2004), whereas others have reported preferences for native plants (e.g., White et al., 2008; Tallamy et al., 2010).

Phytophagous insects are an important component in food webs and are included in the diet of many species of birds, mammals, reptiles, and amphibians (Wilson, 1987; Weis and Berenbaum, 1988). Lepidopteran larvae, an important food source for many wildlife species, have reduced abundance and species richness in areas of nonnative plants (Burghardt et al., 2010). Colonization of a site by invasive plants could, therefore, reduce the suitability of thicket habitat to organisms of higher trophic levels. Supporting such a response, Williams and Karl (2002) found that the abundance of native birds was less and exotic birds were more common in habitats supporting exotic shrubs. Ortega et al. (2006) also reported a decline in songbird reproductive success as an apparent response to reductions in insect abundance in habitats invaded by an exotic forb. In New Hampshire (northeastern U.S.), pilot studies found that exotic shrubs in thicket habitats tended to support fewer insects and such reductions seemed to affect obligate

consumers, especially songbirds that rely on insects to feed nestlings (B. Clifford and J. Panaccione; University of New Hampshire; unpublished reports).

Given the importance of thicket habitats and their vulnerability to invasion, we initiated an investigation of the effects of exotic shrubs on overall insect communities. In addition to comparing insect abundance on native and exotic shrubs, we speculated that invasive shrubs could alter local insect phenology, as some invasive shrubs are known to leaf out earlier and go through senescence later than native shrubs (Woods, 1993; Trisel, 1997). The effects of shrub phenology, however, may depend on the palatability of invasive shrubs to local insects and to other wildlife species. Invasive shrubs may also alter the physical structure of habitats used by non-herbivorous insects and other taxa. Therefore, our specific objectives were to (i) determine if insect abundance, family richness, and phenology are affected by exotic shrub invasions at the site level, (ii) compare insect abundance and family richness on individual native versus invasive shrubs, and (iii) investigate insect consumption patterns on foliage from native and exotic shrubs.

2. Methods

2.1. Study sites

Our study occurred in southeastern New Hampshire, a region dominated by hemlock-beech-oak-pine forests (*Tsuga canadensis*–*Fagus grandifolia*–*Quercus rubra*–*Pinus strobus*; Sperduto and Nichols, 2004). The climate is humid continental, with warm and humid summers and cold and wet winters (Climate Change Research Center, 1998). There is relatively uniform precipitation throughout the year.

Satellite images and aerial photographs were used to identify four study sites in Rockingham and Strafford counties. Sites ranged from 1 to 2.5 ha and all were abandoned agricultural fields that were managed by infrequent mowing for at least 30 years. A description of vegetation for all sites was based on line-intercept inventories (Bonham, 1989). Transects were systematically placed 50 m apart. At alternate 10-m intervals, vegetation type (graminoid/forb/fern/woody) was recorded and woody plants were identified to species (Johnson et al., 2006). Common native shrubs and young trees included arrowwood (*Viburnum dentatum*), gray dogwood (*Cornus racemosa*), silky dogwood (*C. amomum*), black cherry (*Prunus serotina*), and quaking aspen (*Populus tremuloides*). Common invasive shrubs included autumn olive (*E. umbellata*), glossy buckthorn (*Frangula alnus*), common buckthorn (*Rhamnus cathartica*), exotic honeysuckles (*Lonicera spp.*), multiflora rose (*R. multiflora*), and Japanese barberry (*Berberis thunbergii*). Sites were designated as *Native* or *Invasive* based on the extent of cover by invasive shrubs (Table 1). Surrounding land use among all sites was a mix of second-growth forests and pastures.

2.2. Data collection and analysis

2.2.1. Insect abundance, richness, and phenology

We examined how insect abundance, richness, and phenology varied with the amount of volumetric shrub coverage. To characterize the overall insect community (abundance and richness) within a study site, 10 flight-intercept traps (British Museum of Natural History, 1974) were positioned at each site. This method samples a broad range of insects, by capturing insects when they collide with the intercept mesh or as they descend from nearby vegetation. Traps were distributed systematically 35 m apart, and insects were retrieved every seven days from 18 June to 6 September 2007 and from 5 May to 6 September 2008. The second

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