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Birds that Eat Nonnative Buckthorn Fruit (*Rhamnus cathartica* and *Frangula alnus*, Rhamnaceae) in Eastern North America

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ABSTRACT: The buckthorns *Rhamnus cathartica* and *Frangula alnus* are nonnative invasive species in North America whose seeds are primarily dispersed by birds. This paper presents the first major compilation of the bird species that eat *R. cathartica* and *F. alnus* in eastern North America, where these buckthorns are most invasive and have few common congeners. Using fecal samples, observations, and an extensive literature search, I document 46 bird species that consume *R. cathartica* and *F. alnus*, and discuss which are the most competent dispersers of the seeds. I also correct a frequently repeated belief that “blackbirds” are efficient dispersers of *R. cathartica* and *F. alnus*.

Index terms: *Frangula alnus*, glossy buckthorn, *Rhamnus cathartica*, common buckthorn, birds

INTRODUCTION

Birds are common dispersers of fleshy-fruited plants and play a key role in the spread of nonnative species (Gosper et al. 2005). The success of fleshy-fruited plant invaders is, in part, dependent on the presence of appropriate dispersers, which may vary by geographic region (Buckley et al. 2006).

Common or European Buckthorn (*Rhamnus cathartica* L.) and Glossy Buckthorn (*Frangula alnus* Mill., syn. *Rhamnus frangula*) are well-established nonnative invasive shrubs in North America, originating in Europe and western Asia. *Rhamnus cathartica* was likely introduced in the northeastern United States prior to 1800, was in the Midwest by 1839, and in eastern Canada by 1864 (Kurylo and Endress 2012). It is now found over much of North America north of mid-continent, but most commonly in the upper Midwest, the Northeast, and southern Quebec and Ontario (Knight et al. 2007; Qaderi et al. 2009; Zouhar 2011; USDA 2013). *Frangula alnus* was introduced to North America around 1800, in Ohio prior to 1932, and is now established in much of central and northeastern North America (Howell and Blackwell 1977; Dukes et al. 2009; USDA 2013).

Both species have small, inconspicuous flowers that form drupes, which ripen from green to purple-black, typically containing two to four seeds (Godwin 1936; Kurylo et al. 2007; Zouhar 2011). Birds are the primary dispersers of both *R. cathartica* and *F. alnus* (Godwin 1936; Hampe and Bairlein 2000; Knight et al. 2007; McCay and McCay 2009; Zouhar 2011). However, relatively little has been published identifying specific bird species that consume fruits

of these buckthorns in the wild, and some frequently cited sources provide incorrect information on which birds disperse the seeds. The spread, distribution, and population dynamics of nonnative plant species can only be fully understood by confirming the identity of their dispersers (Schupp et al. 2010; Westcott and Fletcher 2011).

This paper provides a list of *R. cathartica* and *F. alnus* consumers based on the author's fecal sample studies and compiled observations, as well as a literature search, and discusses which bird species are efficient dispersers of the seeds. Further, it corrects a frequently repeated error in the literature regarding a family of birds that is reported to disperse *R. cathartica* and *F. alnus* in North America.

METHODS

There are at least 12 species of native *Rhamnus* and *Frangula* west of the Mississippi, three of which (*R. lanceolata* Pursh, *R. alnifolia* L'Hér., and *F. caroliniana* (Walter) A. Gray) are also found in eastern North America (Kartesz 2013; USDA 2013). To reduce false hits on those species, my literature and online searches focused on the Great Lakes states (Wisconsin, Illinois, Michigan, Indiana, Ohio, Pennsylvania, New York), New England (Maine, New Hampshire, Vermont, Massachusetts, Connecticut, Rhode Island), and eastern Canada (Ontario, Quebec, New Brunswick, Nova Scotia, Prince Edward Island; neither *R. cathartica* nor *F. alnus* is present in Newfoundland). *Rhamnus cathartica* and *F. alnus* are generally widespread and common in these locations, whereas the other native species and two additional introduced species (*R. utilis* Decne. and *R. davurica* Pall.) are not present, uncommon, and/or restricted to specific habitats (Qaderi et al.

2009; Reznicek et al. 2011; Chadde 2012; Weeks and Weeks 2012; USDA 2013). The bird fauna in other eastern states where the target buckthorns occur, however, is comparable to the searched area.

Fecal Sampling

Fecal samples were collected during fall banding operations of the Rouge River Bird Observatory (RRBO) on the campus of the University of Michigan-Dearborn, Dearborn, Wayne County, Michigan. The campus is located just outside the city of Detroit, and includes a 120-ha natural area that is primarily secondary forest and old fields. This site is fairly typical of many urban or suburban parks and natural areas in eastern North America, with a high percentage of nonnative vegetation (for a complete site description, see Craves 2007, 2009). Birds representing over 90% of the genera of the principal frugivorous passerines of eastern North America (Willson 1986) have been banded at this site, providing a good opportunity to examine fruit in their diets.

Samples were collected from *Catharus* thrushes from 2007 to 2012 and from all birds that defecated seeds from 2009 to 2012 for an ongoing study of the diet of fall migratory birds. Samples were obtained from birds as they were being released from mist nets, from the clean cloth bags that each individual bird was transported and held in prior to being banded, and/or from droppings obtained while the bird was being processed. Seeds found in fecal samples were identified under a microscope using a reference collection compiled from fruits collected on site, as well as photographs of seeds from various print and online sources. All identifications were verified by at least two people.

From 2007 to 2012, a total of 1208 fecal samples comprising 7880 individual seeds were collected from 18 bird species. Only seven seeds were not identified to at least genus.

Feeding Observations

Bird surveys were conducted for RRBO

primarily by the author, but also students and volunteers. These were performed mostly on campus, but also at several nearby urban parks and residential sites in southeast Michigan. From 2006 to 2012, experienced observers were asked to record observations of birds eating fruit. Seventy-seven observations from the months of July through February were recorded over the period, representing 21 bird species foraging on 19 fruit species. These observations were largely peripheral to other tasks, so they do not represent a random sample, but do add to the data set.

Literature Searches

I searched multiple online databases and websites, including Google Scholar, six major peer-reviewed journal publishers (BioOne, Elsevier, ProQuest, ScienceDirect, Springer, Wiley), the Searchable Ornithological Research Archive (15 ornithological journals), Birds of North America Online (life histories of over 700 bird species), and nine regional or state bird or natural history journals. I did not specify a start date, and searched through mid-2013. I searched using the term “bird” in combination with terms including “*Rhamnus*”, “*cathartica*”, and “*Frangula*”, “fruit”, “diet”, “disperse”, and “consume”, which returned hundreds of hits with many redundancies.

Listservs

I performed similar searches in the online archives of 32 birding listservs (email lists or forums that cater to birders discussing sightings, identification, etc.) serving the states and provinces in the relevant region; not all states have these listservs or archives, and some states have more than one. Archives spanned the years 1998–2013. I only included seasonally appropriate messages that included sufficient overall detail indicating observer credibility.

If authors did not mention a specific buckthorn species and I doubted that the buckthorn species noted was either *R. cathartica* or *F. alnus* (due to location, habitat description, context, etc.), I did not include that account in my results.

RESULTS

Considering all sources, I was able to document 46 species of birds from 16 families and 31 genera as consumers of *R. cathartica* or *F. alnus* (Table 1).

Buckthorn seeds, among other taxa, were found in fecal samples from eight bird species. *Rhamnus cathartica* seeds were found in 43% of all samples ($n = 1208$), and in 44% of the samples from the eight species ($n = 1167$). *Frangula alnus* seeds were found in 6% of all samples, and 7% of the samples from the six species in which they were found ($n = 1163$). All the species that defecated *F. alnus* seeds also defecated *R. cathartica* seeds (although not necessarily in the same samples). Two bird species, White-breasted Nuthatch and Northern Cardinal, defecated *R. cathartica* seeds but not *F. alnus* seeds (see Table 1 for scientific names).

Twelve bird species were observed foraging on buckthorn fruit. All were observed using *R. cathartica*, while four species (American Robin, Gray Catbird, European Starling, and Cedar Waxwing) were also seen eating *F. alnus* fruit.

My literature search located reports of birds eating buckthorn, judged to be either *R. cathartica* or *F. alnus*, for 26 species from six states and one province. There were 128 reports of 33 species of birds eating *R. cathartica* or *F. alnus* from 10 states and one province found on the internet archives of birding listservs or forums.

DISCUSSION

In evaluating Internet and regional journal reports of birds eating *R. cathartica* or *F. alnus*, I found some bias towards uncommon or rare bird species. These birds attract attention, and their behavior is often noted in detail. This explains the reports of six species that are vagrants to eastern North America: Fork-tailed Flycatcher, Mountain Bluebird, Townsend's Solitaire, Varied Thrush, Phainopepla, and Western Tanager. As rarities, these species were well documented and their food sources were noted. Common or secretive species may not merit this kind of scrutiny, documenta-

Table 1. North American bird species reported to eat the fruit of *Rhamnus cathartica* or *Frangula alnus* in nature in eastern North America. Taxonomy follows the American Ornithologists' Union's Checklist of North American Birds, 7th ed., and all of its supplements (<checklist.aou.org>).

	Data Sources ^a	Locations, if noted
ORDER ANSERIFORMES		
<u>Family Anatidae: Swans, Geese, and Ducks</u>		
Wood Duck, <i>Aix sponsa</i>	Lit (Ridley [1930], who cited the work of Mabbott [1920], but erroneously as "Marrott")	
ORDER PICIFORMES		
<u>Family Picidae: Woodpeckers and allies</u>		
Northern Flicker, <i>Colaptes auratus</i>	Int	NY
ORDER PASSERIFORMES		
<u>Family Tyrannidae: Tyrant Flycatchers</u>		
Fork-tailed Flycatcher, <i>Tyrannus savana</i>	Lit (Iliff and Lovitch 2007)	NH
<u>Family Vireonidae: Vireos</u>		
Philadelphia Vireo, <i>Vireo philadelphicus</i>	Lit (Barrientos 2010)	WI
Red-eyed Vireo, <i>Vireo olivaceus</i>	Int	NY
<u>Family Sittidae: Nuthatches</u>		
White-breasted Nuthatch <i>Sitta carolinensis</i>	Fec	MI
<u>Family Turdidae: Solitaires, Thrushes, and allies</u>		
Eastern Bluebird, <i>Sialia sialis</i>	Lit (Huggins 1993, Lange 1998, Peterson 2008), Int, Obs	ME, MI, NY, WI
Mountain Bluebird, <i>Sialia currucoides</i>	Lit (Guthrie and Davis 1975)	NY
Townsend's Solitaire, <i>Myadestes townsendi</i>	Lit (Tessen 1981; Lange 1985, 1987, 1988; Manson 1990, Bowen 1997, Wood 1998), Int	MI, NY, ON, WI
Gray-cheeked Thrush, <i>Catharus minimus</i>	Fec	MI
Swainson's Thrush, <i>Catharus ustulatus</i>	Lit (Barrientos 2010), Int, Fec	IL, MI, WI
Hermit Thrush, <i>Catharus guttatus</i>	Int, Obs, Fec	MI, ON
Wood Thrush, <i>Hylocichla mustelina</i>	Lit (Granlund 1997)	WI
American Robin, <i>Turdus migratorius</i>	Lit (Comey 1902, Hoyt 1956, Lange 1984, Wheelwright 1986, Catling and Porebski 1994, Witmer 1996, Peterson 2001, Purcell 2003, Peterson 2008, Barrientos 2010), Int, Obs, Fec	IL, MA, MI, NY, ON, VT, WI
Varied Thrush, <i>Ixoreus naevius</i>	Lit (Weir 1983)	ON
<u>Family Mimidae: Mockingbirds, Thrashers, and allies</u>		
Gray Catbird, <i>Dumetella carolinensis</i>	Lit (Judd 1895, Moulton 1921, Barrientos 2010, Labbe 2011, Smith et al. 2011), Int, Obs, Fec	MA, MI, ON, PA, WI
Northern Mockingbird, <i>Mimus polyglottos</i>	Lit (Jacobs et al. 1981; Graves 1995; Lange 1997, 2005), Int	IL, NY, ON, WI
Brown Thrasher, <i>Toxostoma rufum</i>	Lit (Judd 1895)	
<u>Family Sturnidae: Starlings</u>		
European Starling, <i>Sturnus vulgaris</i>	Lit (Lindsey 1939, Catling and Porebski 1994, Purcell 2003), Int, Obs	IL, MI, NY, ON

Continued

Table 1. (Cont'd).

	Data Sources ^a	Locations, if noted
<u>Family Bombycillidae: Waxwings</u>		
Bohemian Waxwing, <i>Bombycilla garrulus</i>	Lit (Bent 1950, Lound and Lound 1958, Bauers 1962, Mack 1978, Clark 1979, Diers 1986, Catling and Porebski 1994, Peterson 1996, Crowell 1996), Int	NY, ON, VT, WI
Cedar Waxwing <i>Bombycilla cedrorum</i>	Lit (Scheider 1977, Lehman 1989, Catling and Porebski 1994, Crowell 1996, Witmer 1996, Gregoire and Gregoire 1999, Purcell 2003), Int, Obs, Fec	IL, MI, VT, NY, ON
<u>Family Ptiliogonatidae: Silky-flycatchers</u>		
Phainopepla, <i>Phainopepla nitens</i>	Lit (Boldt 1994), Int	ON, WI
<u>Family Parulidae: Wood Warblers</u>		
Tennessee Warbler, <i>Oreothlypis peregrina</i>	Int	IL
Orange-crowned Warbler, <i>Oreothlypis celata</i>	Int	IL, IN
Cape May Warbler, <i>Setophaga tigrina</i>	Int	IL
Magnolia Warbler, <i>Setophaga magnolia</i>	Int	NY
Blackpoll Warbler, <i>Setophaga striata</i>	Int, Obs	MI, OH
Black-throated Blue Warbler, <i>Setophaga caerulescens</i>	Int	NY, ON, PA
Yellow-rumped Warbler, <i>Setophaga coronata</i>	Lit (Barrientos 2010), Int, Obs	MI, NY, WI
Black-throated Green Warbler, <i>Setophaga virens</i>	Int	NY
<u>Family Emberizidae: Sparrows</u>		
Eastern Towhee, <i>Pipilo erythrophthalmus</i>	Lit (Barrientos 2010)	WI
American Tree Sparrow, <i>Spizella arborea</i>	Int	IL
Fox Sparrow, <i>Passerella iliaca</i>	Int	NY, ON
White-throated Sparrow, <i>Zonotrichia albicollis</i>	Lit (Barrientos 2010), Int	NY, WI
White-crowned Sparrow, <i>Zonotrichia leucophrys</i>	Lit (Barrientos 2010), Obs	MI, WI
<u>Family Cardinalidae: Tanagers, Cardinals, New World Grosbeaks, and Buntings</u>		
Summer Tanager, <i>Piranga rubra</i>	Int	NY
Scarlet Tanager, <i>Piranga olivacea</i>	Int	IL, ON
Western Tanager, <i>Piranga ludoviciana</i>	Int	ON
Northern Cardinal, <i>Cardinalis cardinalis</i>	Lit (Barrientos 2010), Int, Fec	MI, NY, WI
Rose-breasted Grosbeak, <i>Pheucticus ludovicianus</i>	Lit (Catling and Porebski 1994), Int, Obs	MI, ON, WI
<u>Family Icteridae: Blackbirds, Meadowlarks, and Orioles</u>		
Baltimore Oriole, <i>Icterus galbula</i>	Int	ON, WI

Continued

Table 1. (Cont'd).

	Data Sources ^a	Locations, if noted
<u>Family Fringillidae: Finches and allies</u>		
Pine Grosbeak, <i>Pinicola enucleator</i>	Lit (Brooks 1979, Peterson 1986), Int	NH, NY, ON
House Finch, <i>Haemorhous mexicanus</i>	Int, Obs	MI, NY
Purple Finch, <i>Haemorhous purpureus</i>	Lit (Pitzrick 1981, Pratt 2001), Int	IL, NY, VT, WI
Evening Grosbeak, <i>Coccothraustes vespertinus</i>	Lit (Brooks 1979)	NY
<u>Family Passeridae: Old World Sparrows</u>		
House Sparrow, <i>Passer domesticus</i>	Obs	MI

^aData sources: Lit = Literature search; Int = Internet archives of birding listservs and forums; Obs = observations made in southeast Michigan; Fec = seeds found in fecal samples of birds banded by the author at the University of Michigan-Dearborn.

tion, or even show up in published reports, although many records were from field trip leaders, seasonal bird survey compilers, and avid birders who provided detail on foraging sites and habits of many bird species in their reports.

The literature and online searches, and my own research, focused on the northeastern part of the continent. All the bird species reported with the exception of the vagrants mentioned above and three northerly breeding species (Bohemian Waxwing, Pine Grosbeak, and Evening Grosbeak), occur in the remainder of the range of *R. cathartica* and *F. alnus* in eastern North America at some point during the year. My compilation shares eight of the nine most highly ranked genera (in degree of frugivory) in Willson's (1986) list of the principal frugivorous birds in eastern North America.

Despite a slight bias toward rare birds, a filtered geographic focus, and the fact that some accounts may not have been uncovered, I regard this sample as representative of the bird species most apt to eat *R. cathartica* or *F. alnus* in eastern North America.

One group of birds that is notably absent is "blackbirds." Numerous resources, particularly invasive species management materials, fact sheets, and other publications, state that the fruit of both *R. cathartica* and *F. alnus* is "...efficiently dispersed by starlings, blackbirds, ..." (e.g., Butterfield

et al. 1996; NBII/ISSG 2005a, b; Jull 2007; Stork 2007; Anon. 2013; Sturtevant et al. 2013). In North America, "blackbirds" are commonly assumed to be the New World blackbirds in the family Icteridae.

The inclusion of blackbirds as buckthorn dispersers apparently originated in one of the earliest reviews of buckthorn ecology (Converse 1984), which cites Ridley (1930). Ridley's work was a collection of previously published data on the dispersal of plants. Ridley lists the dispersal of *R. cathartica* under "*Merula vulgaris*, the Blackbird." He is referring to the Common Blackbird, *Turdus merula*, a species in the Turdidae, or thrush, family (Gill and Donkster 2013), which is entirely unrelated to the New World blackbirds. Further, Ridley cites Woodruffe-Peacock (1918) as his source. Woodruffe-Peacock described "blackbirds" eating *R. cathartica* in North Lincolnshire, England, but states, "When I say blackbird...I mean that species [no scientific name given] and the rest of the common British Turdi [sic]." Ridley does list a few North American Icteridae as fruit consumers, but does not list either *R. cathartica* or *F. alnus* in their reported diets.

There is little evidence from my research—which included Beal's reports on the stomach contents of thousands of New World blackbirds (Beal 1896, 1900) and similar results reported by Goddard (1969) and Williams and Jackson (1981)—that New World blackbirds are frequent consumers

of any fruit, much less *R. cathartica* or *F. alnus*. The inclusion of "blackbirds" without clarification regarding the proper taxonomic designation as dispersers of buckthorn in North America appears to be a misinterpretation of the primary literature, which has been repeated numerous times. (Likewise, "elk" is listed as a disperser of *R. cathartica*, citing Ridley, but tracing that back to the source indicates that this actually refers to moose, *Alces alces*).

Not all bird species that forage on *R. cathartica* or *F. alnus* are competent dispersers of the seeds. While the dynamics of seed dispersal by animals is complex, important measures of the effectiveness of dispersers include the type and degree of their frugivory, and relative abundance (Jordano and Schupp 2000; Godínez-Alvarez and Jordano 2007; Schupp et al. 2010). Frugivorous species might be considered poor dispersers if they eat the pulp or juices of a fruit then drop or digest the seeds, or leave the seed attached to the plant (Johnson et al. 1985; Willson 1986; Snow and Snow 1988; Jordano and Schupp 2000; Buckley et al. 2006; Schupp et al. 2010). Examples of inefficient dispersers noted by those authors include birds in the genera *Icterus* (orioles), *Piranga* (tanagers), *Pheucticus* (grosbeaks), and *Zonotrichia* (sparrows); small birds such as warblers (Parulidae); finches (Fringillidae); and the Northern Cardinal. My observations of six species (Blackpoll Warbler, Yellow-rumped Warbler, White-crowned Sparrow, Rose-breasted Grosbeak, House Finch, and

House Sparrow) foraging on *R. cathartica* are in agreement. No individuals of these species were seen swallowing the seeds; all dropped them under the parent plant.

In contrast, thrushes, mimids, starlings, and waxwings usually swallow small fruits similar in size to *R. cathartica* and *F. alnus* and later defecate the seeds (Johnson et al. 1985; Meyer and Witmer 1998; Craves, pers. obs.). Birds in these families (Turdidae, Mimidae, Sturnidae, and Bombycillidae) are among the most highly frugivorous in eastern North America (Thompson and Willson 1979; Willson 1986; Malmberg and Willson 1988; Parrish 1997; LaFleur and Rubega 2009). Herrera and Jordano (1981) consider medium-sized birds, such as most members of these families, which have high visitation rates to fruiting plants, as likely to disperse the most seeds.

With the exception of reports of single rare birds, the majority of reports in the literature or in internet archives did not provide a specific number of individuals of a species feeding on buckthorn, so no attempt was made to quantify the frequency of buckthorn consumption among species. However, several species were often noted as feeding on buckthorn in flocks, sometimes reported as being in the hundreds of birds: American Robin, Cedar Waxwing, and Bohemian Waxwing. Robins are the most abundant and widespread Turdidae in North America, and are gregarious in the nonbreeding season when feeding flocks can exceed 250 individuals (Sallabanks and James 1999). Both species of waxwings are highly social throughout the year, with the largest flocks occurring in winter (Witmer et al. 1997; Witmer 2002).

European Starlings are considered one of the most numerous bird species on the continent and are very gregarious all year (Cabe 1993). I did not find reports of starlings feeding in large numbers on buckthorn, but this may be due to a general disdain of this introduced species by many people, resulting in a lack of detailed reporting. Further, starlings prefer to forage in large open areas and in North America tend to avoid wooded or forested sites (Cabe 1993), perhaps reducing the numbers encountered by researchers or

birders who typically make observations in more natural habitats.

The other families and species of birds that are efficient seed dispersers (other members of the Turdidae and the Mimidae) are not as social or quite as abundant as robins, waxwings, and starlings. Further, most migrant species in these families, such as Swainson's Thrush, Wood Thrush, and Gray Catbird, for example, are only present in eastern North America during the breeding season. European Starlings are resident year-round (Cabe 1993). American Robins and Cedar Waxwings do make seasonal movements, but are present over much of the continent most or all of the year (Witmer et al. 1997; Sallabanks and James 1999). Bohemian Waxwings have a much more northerly breeding distribution, but make periodic large southerly movements in winter, when they can occur in large numbers in the Northeast and Upper Great Lakes (Witmer 2002). These species, then, have a longer overlap with the fruiting period of *R. cathartica* and *F. alnus* in northeastern North America than most of the other dispersers in Table 1.

Westcott and Fletcher (2011) note that likely dispersers of invasive species can be predicted by knowledge of the invasive species' dispersers in their native range. In the Old World, *R. cathartica* and *F. alnus* are dispersed by (among others) many thrushes in the genus *Turdus*, (the sole New World member being American Robin), European Starling, and Bohemian Waxwing (Ridley 1930; Godwin 1936; Snow and Snow 1988).

Birds in the families Turdidae, Mimidae, Sturnidae, and Bombycillidae appear to be the most efficient dispersers of *R. cathartica* and *F. alnus* in eastern North America. Key species in those families are American Robin, both species of waxwings, and European Starling due to: (1) their high degree of frugivory; (2) medium body size, allowing them to swallow buckthorn fruit whole; (3) abundance; and (4) long seasonal residency in the region.

Bohemian Waxwings are irregular winter visitors to the northern portions of eastern

North America and, thus, may be responsible only for sporadic and geographically limited dispersal of buckthorns. The reluctance of starlings to penetrate wooded sites, especially in fall and winter (Fischl and Caccamise 1985; Cabe 1993; Clergeau et al. 1998), indicates that they are probably best at dispersing buckthorns throughout more urban sites or in agricultural areas.

Given all the evidence, it is reasonable to conclude that American Robins and Cedar Waxwings, with their broad habitat preferences, which include forested areas, along with the other favorable life history traits noted above, are the most important dispersers of *R. cathartica* or *F. alnus* in eastern North America, as well as in other regions where the ranges of these birds and plants overlap.

Finally, contrary to some published sources, "blackbirds" (Icteridae) in North America rarely consume buckthorn and are not frequent or competent dispersers of *R. cathartica* or *F. alnus*.

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systems, and the interactions of native and invasive species.

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