

Nest-mediated seed dispersal

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Abstract Many plant seeds travel on the wind and through animal ingestion or adhesion; however, an overlooked dispersal mode may lurk within those dispersal modes. Viable seeds may remain attached or embedded within materials birds gather for nest building. Our objective was to determine if birds inadvertently transport seeds when they forage for plant materials to build, insulate, and line nests. We also hypothesized that nest-mediated dispersal might be particularly useful for plants that use mating systems with self-fertilized seeds embedded in their stems. We gathered bird nests in temperate forests and fields in eastern North America and germinated the plant

material. We also employed experimental nest boxes and performed nest dissections to rule out airborne and fecal contamination. We found that birds collect plant stem material and mud for nest construction and inadvertently transport the seeds contained within. Experimental nest boxes indicated that bird nests were not passive recipients of seeds (e.g., carried on wind), but arrived in the materials used to construct nests. We germinated 144 plant species from the nests of 23 bird species. A large proportion of the nest germinants were graminoids containing self-fertilized seeds inside stems—suggesting that nest dispersal may be an adaptive benefit of closed mating systems. Avian nest building appears as a dispersal pathway for hundreds of plant species, including many non-native species, at distances of at least 100–200 m. We propose a new plant dispersal guild to describe this phenomenon, caliochory (calio = Greek for nest).

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Data Accessibility The data generated and analyzed for the current study are available in the SUNY Buffalo State Digital Commons [http://digitalcommons.buffalostate.edu/biology_data/2/].

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Introduction

Dispersal shapes the distribution and structure of ecological communities (Hubbell 2001; Levine and Murrell 2003; Nathan and Muller-Landau 2000; Pulliam 2000), yet many mysteries remain in plant seed dispersal (Bullock et al. 2002; Clobert et al. 2001; Traveset et al. 2014). For example, some non-native plant invaders are widespread, yet experimental investigations suggest that they are poor seed dispersers (Cain et al. 1998; Christen and Matlack 2009; Traveset et al. 2014). Even species with seemingly apparent adaptations for dispersal, such as downy appendages for wind loft, may be inaccurately assigned a dispersal mode based on seed morphology, or they may receive additional, seemingly unintended, dispersal services (Bullock et al. 2002; Higgins et al. 2003; Levine and Murrell 2003). Given these discrepancies, still unknown or underappreciated dispersal modes likely contribute to seed movement.

Animals disperse most plant species (60–80%), and most of those are dispersed by mammals and birds (Traveset et al. 2014). Bird seed dispersal mechanisms via seeds adhered to feathers (epizoochory) and from fruits passed through the digestive system (endozoochory) are well known (e.g., Sorensen 1986; Stiles 1980), but seed dispersal via bird nest foraging remains cryptic (Dean et al. 1990; Milton et al. 1998). Given that there are ~1300 published papers on endozoochory and ~1200 on wind- and water-dispersed (anemochory and hydrochory) seeds (Soons et al. 2016), comparatively little information exists on nests as a pathway for avian seed dispersal (2 published papers; Dean et al. 1990; Milton et al. 1998).

Many plants employ mixed mating systems that produce both outcrossed (genetically mixed, “chasmogamous”) and selfed (self-pollinated, “cleistogamous”) seeds. Cleistogamous flowers remain permanently closed (Culley and Klooster 2007; Goodwillie et al. 2005) and, in many cleistogamous plants, particularly grass species, the selfed seeds remain within the plant stem. Plant stems often persist through winter months and into spring, retaining viable seeds (Cheplick 2010). Because birds gather recalcitrant plant material in spring to construct and line nests (Dean et al. 1990; Longland and Clements 1995; Milton et al. 1998), plants employing a cleistogamous mating system may be well suited for nest-mediated seed dispersal. Moreover, some traits

associated with wind dispersal, such as downy seeds, may increase their desirability to birds seeking downy nest lining material (Dean et al. 1990; Milton et al. 1998). However, it is also possible that open bird nests simply capture and accumulate wind-dispersed seeds and/or avian fecal deposition (Dean et al. 1990; Milton et al. 1998).

Our objective was to use observational and experimental approaches to investigate bird nest foraging as a viable plant dispersal mechanism. We hypothesized that bird nest building acts as a direct disperser of seeds rather than nests simply acting as passive recipients of wind- and fecal-dispersed seeds. We also hypothesized that bird-mediated dispersal via nest foraging would most benefit cleistogamous plants, which generally are open habitat graminoids with seeds embedded in stems. Moreover, a common pattern in plant species invasion is an association with roads and forest edges (Gelbard and Belnap 2003; Mortensen et al. 2009; Parendes and Jones 2000; Warren II et al. 2013). Roads and forest edges are considered conduits for species invasion with human activities along these corridors proffered as the most likely mechanism of invasion. A high number of bird species also choose these ecotones for nesting, particularly along forest edges and waterways (Collias and Collias 1984; Gates and Gysel 1978; Keyel et al. 2013). We examined non-native plant species in bird nests, and we specifically targeted *Microstegium vimineum* (Japanese stiltgrass) because it is a widespread non-native plant in the study area, but its dispersal ability appears inadequate for that distribution (Miller and Matlack 2010; Warren II et al. 2013). We hypothesized that avian nest dispersal might be a cryptic dispersal mode for *M. vimineum* and other non-native species, and we expected to find greater non-native species richness in avian nests near edge habitats.

Materials and methods

We collected 87 bird nests from forested, edge, and open habitats in the Piedmont and southern Appalachian Mountains of Georgia ($n = 24$) and North Carolina ($n = 63$) from January 2012 to November 2013 (23 of those nests were from established nest boxes). Searches occurred after the breeding season and only unoccupied nests were collected, including

nests from nest boxes that we encountered during our searches. The nests were placed in plastic bags and stored at -18°C . We recorded the habitat type where each nest was recorded, and we measured the distances to the nearest forest edge and to the nearest road as some species of birds and many non-native plants are associated with these habitat types. In addition, to estimate the potential dispersal distance for non-native plants via bird nest foraging, we measured the distance to the nearest *M. vimineum* population.

All collected nests were kept at -18°C for 60 days to treat any seeds that require stratification. We then spread the nest material on 25×50 cm seed trays with potting soil and irrigated them to promote seed germination in the greenhouse facilities at the Coweeta Hydrologic Laboratory. Plants were grown long enough for identification, which was 9 months in some cases and pulled before producing their own seeds. We also used 10 control trays with potting soil but no nests added to confirm that seedlings came from nests and not soil or other sources.

Because seeds occurring in nests may be passively dispersed (i.e., the nest acted as a depository for wind-dispersed seeds or deposited through fecal material), we constructed 27 experimental bird nest boxes to conduct seed counts from any bird nests constructed within the boxes. The nest boxes were $18 \times 13 \times 27$ cm with a 4-cm-diameter entrance and a removable side panel. The bird nest boxes were suspended 1.2 m high on a wooden pole. In late winter 2012, we placed 9 nest boxes at each of three sites: Tessentee, the Coweeta Hydrologic Laboratory (Otto, NC, U.S.), and Athens, GA (U.S.). At each site, there were three transects with nests being placed in *M. vimineum* populations qualitatively observed to be heavily invaded, moderately invaded, and absent patches. We collected nests from 9 boxes that were used by birds in fall 2013 and stored them at -18°C to prevent decay of plant and seed material. We subsampled vegetation from the 9 nests within the nest boxes to generate seed count data. We used seeds from nest boxes because the boxes retained any senesced seeds and there was low likelihood of seed contamination. Seeds were separated from nest plant and fecal material and counted. Loose, unattached seeds also were counted.

We identified reported dispersal modes for the nest germinants using the Royal Botanic Gardens Kew Seed Information Database Version 7.1 (SID 2008).

We classified plants according to cotyledon (monocot, dicot), life history (annual, perennial), and type (forb, graminoid, woody) using The PLANTS Database (USDA 2016). We delineated cleistogamous species in the germinated nests using Culley and Klooster (2007), Lord (1981), Oakley et al. (2007), and Watson and Dallwitz (1992). Plant nomenclature follows Weakley (2015). We determined the bird species that built each nest using Harrison (1998).

We tested whether non-native plants were found closer to roads and forest edges than native plants using Student's *t* tests in the R statistical software program (R Development Core Team 2017). We tested for differences in seed location in nests (attached to stem, in fecal matter or unattached seeds that may have separated from plant material after nest building or passively landed in constructed nests) using analysis of deviance (ANODEV) with a generalized linear model assuming Poisson error distribution and Chi square to evaluate entire terms in the R statistical software program (R Development Core Team 2017).

We collected abandoned bird nests in North Carolina and Georgia (U.S.) under the following permits and acceptable use policies: USFWS Federal Migratory Bird Scientific Collecting Permit MB67572A-0, Georgia DNR Scientific Collecting Permit 29-WJH-13-24 (2013/2014), Georgia DNR Scientific Collecting Permit 29-WBH-12-77 (2012/2013), University of Georgia AUP #: A2012 03-018-Y1-A0 (under John Maerz for collecting bird nests), and University of Georgia AUP #: A2013 01-003-R2 (under Jeff Hepinstall-Cymerman for collecting rodent nests).

Results

Nests were collected from shrubs ($n = 43$), closed nest boxes ($n = 23$), trees ($n = 9$), under human structures, such as the house eaves ($n = 8$), on the ground ($n = 3$), and in the grass ($n = 1$). A total of 2,180 plants of 144 plant species and 37 families germinated from the bird nests (Supplement 1) with a mean ($\pm$ SE) of 5.2 ± 0.7 plant species per nest. The plants were mostly dicot (66%), annual (53%), and forbs (59%), though monocot graminoids also were prevalent (34%). Chasmogamy was the more common mating system by species (57%), but closed mating

(cleistogamy) was more common by overall seedling abundance (53%). Most of the plants were from the Asteraceae and Poaceae families, and 34% of the plant species (44% overall abundance) were non-native species. The most common nest-dispersed plants by frequency of nests in which they germinated were *Cardamine hirsuta* (occurred in 26% of all nests; occurred in 69% of the bird species' nests), *Cerastium glomeratum* (13%; 28%), *Conyza canadensis* (17%; 50%), *Digitaria ciliaris* (22%; 50%), *Digitaria ischaemum* (17%; 44%), *Poa annua* (10%; 38%), and *Veronica arvensis* (25%; 63%) [Supplement 1]. These 7 species accounted for 46% of the total plants and 86% were annual, 71% cleistogamous, and 71% non-native. No plants germinated from control trays (no nests) placed with the germination trays, indicating no outside contamination in the experiments.

There were 23 bird species that built nests of four types: mud [e.g., *Turdus migratorius* (American robin)], grass [e.g., *Sialia sialis* (Eastern bluebird)], moss [e.g., *Baeolophus bicolor* (tufted titmouse)], and humus [e.g., *Troglodytes aedon* (house wren)]. Most plant species were found in the nests of *T. migratorius* and *S. sialis*, which accounted for 46% of the germinated plants [Supplement 2]. Overall, grass nest-building species were the most common (42%) followed by those that used humus (38%). Mud nest-building species were the least common (13%) but their nests contained 37% of the germinated plants. Grass nests contained 41% of the plants and humus contained 19%.

Most nests were collected in shrubs (49%), and those nests contained 46% of the plants (S2). Nest boxes were the next most common substrate (26%), and those nests contained 36% of the plants. More than half (52%) of the nests were collected in developed areas (e.g., residential neighborhoods), including the two bird species that built nests containing the highest percentage of plant species (*T. migratorius* and *S. sialis*), and developed habitat nests contained 63% of the germinated plants. Field habitat was the next most common nest collection habitat (39%), and it contained 25% of the plant species (the sum of percentages for bird habitat use is >100 as several birds used multiple habitats). Forest habitat contained 26% of the bird nests collected, but these nests contained very few viable seeds (7%).

The previously reported dispersal syndrome for most (40%) of the plants that we germinated from bird

nests was anemochory (wind), followed by epizoochory (attached to animal) and endozoochory (ingested by animal) (Fig. 1). Anemochorous plants were about 10% more common in nests from field surveys than nest boxes, but epizoochorous and endozoochorous plants were about 5–10% more common in nest boxes than survey nests. Hydrochorous plants were rarely found in nest boxes but made up about 5% of the plants in survey nests. The nest boxes contained 43% of the plant species, but were only used by 25% of the bird species (with only *T. aedon* and *Poecile carolinensis* using both). The mud nest-building bird species never used the nest boxes.

The mean ($\pm$ SE) distance for bird nests from the nearest road was 54 ± 8 m and from the nearest forest edge was 161 ± 9 m. Non-native plant species occurred in nests significantly closer to roads than native species (t -value = 4.06, $df = 225.86$, p value <0.001; native = 73 ± 12 m; non-native = 20 ± 4 m) (Fig. 2a), and non-native plants occurred in nests significantly closer to forest edges (t -value = 5.19, $df = 273.74$, p value <0.001; native = 194 ± 13 m; non-native = 101 ± 11 m) (Fig. 2b). Nests that germinated *M. vimineum* ($n = 4$) were found 1–100 m (37 ± 22 m) from the nearest *M. vimineum* populations.

For the experimental nest boxes, we collected 9 nests from our 27 constructed bird nest boxes. We found 211 ± 9 seeds per nest. There were significantly more seeds that remained attached to plant material (60.6%) than unattached (27.6%) or found in fecal material (11.8%) ($df = 2$, $dev. = 178.54$, $resid. dev. = 899.18$; Fig. 3).

Discussion

The process of nest building appears as a potential dispersal pathway for many plant species. We showed that seeds in bird nests did not just arrive on the wind, or come from fecal matter or feathers, but rather were attached to the plant material (and mud) used to construct, insulate, and line nests. Dean et al. (1990) suggested that plants germinating from bird nests might be termed “nest-dispersed.” Caliology is the study of nest composition and function (Dixon 1902), as ‘calio’ is the Greek root word for nest. We propose “caliochory” to describe a new plant dispersal guild:

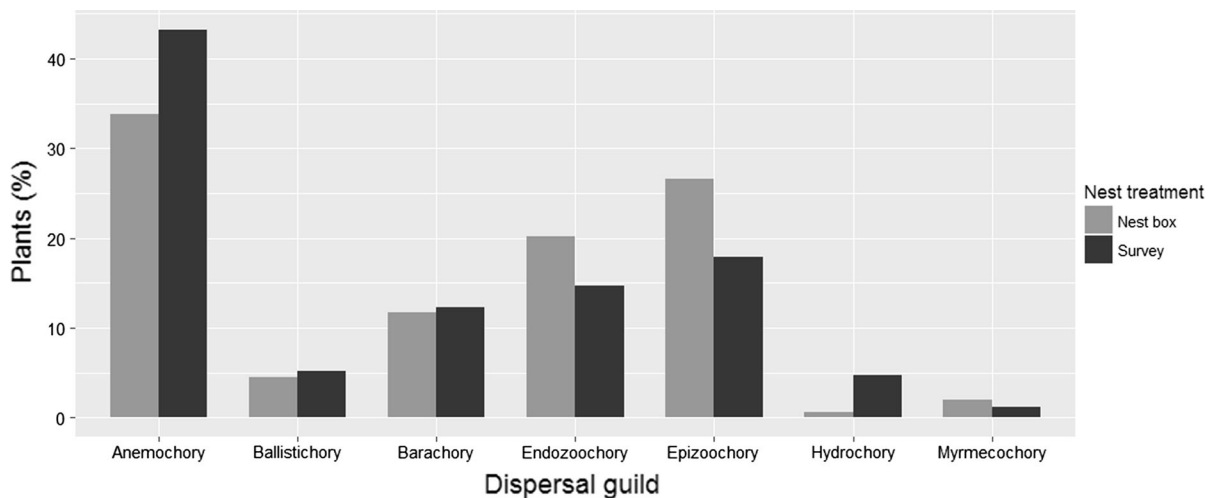


Fig. 1 Barplots showing the percentage of established dispersal guilds in plants germinated from bird nest materials collected from landscape surveys (*Survey*) and nest boxes (*Nest box*). The dispersal guilds are anemochory (wind), ballistichory (explosive), barochory (gravity), endozoochory (animal ingested),

epizoochory (animal attachment), hydrochory (water), and myrmecochory (ants). The bars are shown without error bars because they are percentages of the total (summing to 100% for survey and nest box)

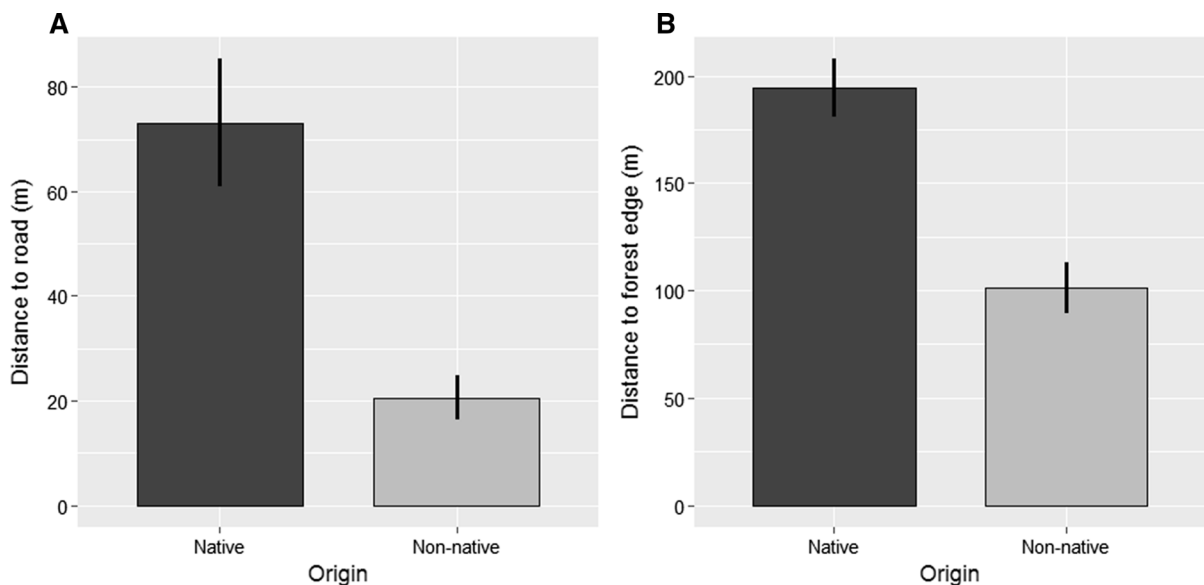


Fig. 2 Barplots showing the mean ($\pm$ SE) distance to the nearest road (**a**) and distance to the nearest forest edge (**b**) for native ($n = 260$) and non-native ($n = 182$) plants germinated from bird nest materials. Non-native plant species in bird nests were found significantly closer to roads (t -value = 4.06,

$df = 225.86$, p value < 0.001; native = 73 ± 12 m; non-native = 20 ± 4 m) and forest edges (t -value = 5.19, $df = 273.74$, p value < 0.001; native = 194 ± 13 m; non-native = 101 ± 11 m) than native species

seed dispersal via bird nests ('chory' is Greek for "to spread").

Previous work suggested that plant seeds may disperse via caliochory, but we found only two serious treatments of the subject, conducted in the southern

Karoo of South Africa (Dean et al. 1990) and the Chihuahuan Desert of the U.S. (Milton et al. 1998). Whereas we non-selectively collected nests of 23 bird species for germination experiments, Dean et al. (1990) targeted 31 common bird species and Milton

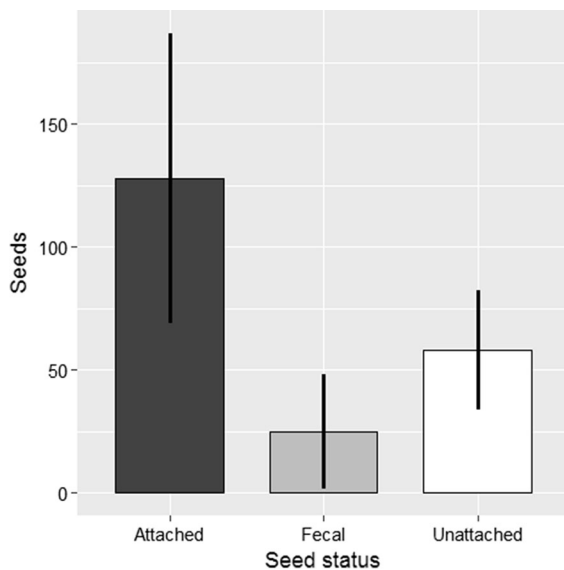


Fig. 3 Boxplot showing mean ($\pm$ SE) number of seeds found in bird nest materials. The seeds were found attached to vegetative material (Attached), loose in the nest (Unattached), or deposited in bird fecal matter (Fecal). Significantly more seeds were found attached to plant material than unattached or in fecal matter ($df = 2$, $dev. = 178.54$, $resid. dev. = 899.18$)

et al. (1998) focused on one bird species. Dean et al. (1990) germinated 55 plant species from bird nest material (22% cleistogamous) and Milton et al. (1998) germinated 34 plant species (38% cleistogamous). By comparison, we germinated 144 plant species (43% cleistogamous). In all cases, these were plants of open habitats with a large component of graminoids.

Many plants fall into multiple dispersal guilds. Similar to our results, Dean et al. (1990) found that the established dispersal guild for most of the nest material plants was anemochory, followed by endozoochory and epizoochory. We employed experimental nest boxes to eliminate the possibility that the nests just act as ‘baskets’ that catch falling seeds and found that anemochorous plants remained prominent. Many birds use soft, cottony, propagules—traits associated with wind dispersal—to line/insulate the inside of their nests (Dean et al. 1990). For instance, in one of our experimental nest boxes, *T. aedon* used anemochorous seed from *Sonchus* spp. (Sow-thistle, $n = 460$ seeds) and *Erechtites hieraciifolius* (Fireweed, $n = 68$ seeds) to line the nest. Hence, seeds with downy pappus, hair-like awns, or feathery plumes may be adapted for anemochory, caliochory, or both. In order to further investigate bird nests as ‘passive’ recipients

of seeds via anemochory, endozoochory, and epizoochory, we examined a subset of nests to determine the status of nest seeds. We found most seeds remained attached to plant material in the nest, with less than half as many unattached and even fewer in fecal matter.

Closed mating systems in which self-fertilized seeds are enclosed in plant stems are evolutionarily counterintuitive as genetic mixing is considered far more adaptive than inbreeding (Culley and Klooster 2007; Darwin 1877; Goodwillie et al. 2005). Some hypotheses suggest that mixed mating might be adaptive because selfed seeds are locally adapted, low cost, and do not require pollinators (Culley and Klooster 2007; Pannell 2009). If dispersal distance is a benefit of cleistogamy, we expected to find viable selfed seeds in recalcitrant plant stems, and cleistogamy common in nest-dispersed plants. Both in the data presented here and in other studies (Dean et al. 1990; Milton et al. 1998), viable seeds remain in overwintered dead plant stem material. Seed stems have been proffered as a means for plants to protect progeny from grazers and, potentially, as a dispersal mode if the stems become attached to grazers or are carried by water flow (Cheplick 2010; Dobrenz and Beetle 1966). Approximately 31–41% of angiosperm species employ mixed mating systems (Goodwillie et al. 2005; Schemske and Lande 1985). We found that 43% of the species germinating from bird nest material were cleistogamous, and 53% of plant abundance was cleistogamous. Notably, cleistogamy was very high in the most common plants we found in bird nests.

A general assumption about cleistogamous seeds is that, because they are retained in the stems or other plant material, they remain near source plants (Culley and Klooster 2007; Schmitt et al. 1985). As such, it is presumed that cleistogamy may preserve local adaptation (and local populations) in the maternal environments where the parent plants successfully reproduced and genetic novelty is unneeded; in turn, chasmogamous seeds are considered better suited to venture into novel, heterogeneous habitats where genetic diversity is beneficial (Culley and Klooster 2007; Holsinger 1986). Our results suggest, however, that distance dispersal may also be a benefit of cleistogamy when seeds retained within plant stems are transported through caliochory. An immediate implication is that cleistogamous seeds may actually travel further in plant stems than chasmogamous seeds

dropped from terminal spikelets. As a result, the assumption that genetic diversity increases with distance from source populations may be inaccurate for species with mixed mating systems, and this assumption could be tested as a means to evaluate the potential importance of caliochory to dispersal.

Dean et al. (1990) noted that the ruderal and non-native species they germinated in bird nests are common along ephemeral rivers in the study area, but they only found 9% of the germinated species were non-native whereas we found 34% non-native species. We found non-native species significantly more common in bird nests closer to roads and forest edges. Bird foraging for nest materials can range up to 65–200 m from the nest (Anderson and Anderson 1957; Surgey et al. 2012). Milton et al. (1998) found that the plant seeds were dispersed at least 20 m via bird nesting materials, whereas we found dispersal of the non-native *M. vimineum* up to 100 m. We note, however, that a more targeted foraging behavior study is needed to estimate robust dispersal distances via caliochory. The association between caliochory and non-native plants may simply be a spurious correlation as roads and forest edges may be good habitat for both non-native species and bird nesting, but bird foraging for nesting materials may explain non-native distance dispersal along edge corridors that heretofore eluded a clear mechanism.

Movement is just one component of dispersal, and determining dispersal effectiveness requires linking seed movement and placement with demographic outcome—information that generally is missing from dispersal research (Traveset et al. 2014). Our data suggest that caliochores are dispersed into habitats similar to those where they were produced, but the next step in this research is to verify that viable nest seeds reach suitable germination strata. The effectiveness of many dispersal modes is species specific (e.g., Warren II and Giladi 2014), and the results shown here suggest the same for caliochory. For nests built in grass substrate, the distance is short and germination success likely. We found most nests in shrubs, however, where seeds may find suitable habitat upon nest disintegration, particularly mud nests. Caliochory also may not be limited to bird nests. We collected three deer mouse (*Peromyscus* spp.) nests and germinated three species (*Carpinus caroliniana* var. *virginiana*, *Conyza canadensis*, and *Phytolacca americana*), suggesting that rodent nests might be

another underappreciated pathway for plant dispersal (*pers. obs.*).

Conclusions

Birds transport viable seeds in their nest materials, a process we term caliochory. Many plant species retain seeds within their stems, a trait that has previously seemed maladaptive but, as we show here, may instead facilitate dispersal during bird foraging for next materials. Moreover, via caliochory, less genetically diverse propagules may travel further from source plants than genetically mixed seeds. Hence, genetic diversity gradients may be reversed, a possibility that requires testing. An unexpected finding was the large number of seeds contained within the mud used by birds to bind and line the nests. Further research is required to verify the veracity of nest materials in seeding successful plant populations, but we provide solid evidence that birds transport viable plant seeds in their nesting materials. With an estimated 10 billion breeding birds in the contiguous U.S. alone (Aldrich et al. 1975; Banks 1979), caliochory may potentially be an overlooked but highly effective dispersal strategy.

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