Avian dispersal of an invasive oak is modulated by acorn traits and the presence of a native oak

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ABSTRACT

Successful invasions of non-native plants often depend on establishing mutualistic interactions with native organisms. Animal seed dispersers can greatly enhance the spread of invasive plants. Emerging seed dispersal mutualisms might also result in indirect interactions between non-native and native plants, mediated by shared dispersal agents. We investigated tripartite interactions between Eurasian jays (*Garrulus glandarius*), non-native northern red oaks (*Quercus rubra*), and native pedunculate oaks (*Q. robur*) in a lowland forest of Central Europe. We estimated the probability of acorn removal for both oak species in single vs. mixed treatment, and the effects of acorn length, width, and weight. We also radio-tracked removed acorns to determine their fate. While jays preferred to harvest the native acorns, they also removed almost all offered acorns of the invader. The removal rate of non-native acorns increased when the two oak species co-occurred, and was modulated by acorn traits: jays selected red oak acorns that were long and narrow. In comparison to pedunculate oak acorns, those of red oak were transported shorter distances and were more likely to be consumed rather than cached. Altogether, dispersal of red oaks by jays was less intense and brought smaller benefits relatively to the dispersal of pedunculate oak. Yet, these differences were moderate, and jays provided effective dispersal of both oaks. Our results highlight the role of keystone native seed dispersers in the expansion of non-native plants. Furthermore, they illustrate how dispersal quantity of non-native plants can be facilitated by the presence of native plants that attract shared seed dispersers.

1. Introduction

Developing new interactions with native species, either positive or negative, affects the pace and pattern of invader encroachment into new areas (Mitchell et al., 2006). In particular, transport by animals can greatly enhance the ability of non-native plants to disperse and invade natural habitats (Richardson et al., 2000; Lenda et al., 2012). Conversely, failing to establish dispersal mutualism with new partners in the invaded range can impede the spread of non-native animal-dispersed plants. Thus, the replacement of lost seed dispersers from plant's native range with new ones in its introduced range can determine invader's colonizing success (Richardson et al., 2000). While theory often focuses on success vs. failure in establishing new mutualisms, the quality of such newly established interactions can be equally important for naturalization and invasions of non-native plants. Yet, factors that shape this quality have rarely been assessed.

Numerous nut-bearing woody plants are dispersed by scatterhoarders, which store seeds in a large number of small caches (Vander Wall, 1990). Mutualisms between plants and scatterhoarders are conditional because they act as seed predators or dispersers depending on whether the harvested seed is consumed or not (Zwolak and Crone, 2012; Gómez et al., 2019; Zwolak et al., 2020). Thus, their interactions with non-native plants can either accelerate or slow down the invasions. However, attempting to gauge this outcome in isolated, pairwise interactions might be misleading. Most seed dispersal mutualisms are diffuse (Gómez et al., 2019). As a consequence, the new disperser of the non-native plant typically also interacts with the competing native plants. If the quality of dispersal services differs between the non-native and the native plants, it

might tilt the competitive advantage towards or away from the invader (Bogdziewicz et al., 2019). Thus, the final outcome will likely depend on relative quality of seed dispersal in the non-native vs. the native species. This is further complicated by the possibility of indirect interactions between plants mediated through the shared seed disperser (e.g. Carlo, 2005). Granivores adjust their decision depending on the relative abundance of co-occurring seed species and their perceived value (Lichti et al., 2014; Bogdziewicz et al., 2019; Yang et al., 2020). Thus, the presence of native seeds can modify the dispersal of non-native species, and vice-versa. In extreme cases, invasive alien plants can disrupt seed dispersal of native plants (Traveset and Richardson, 2006).

Finally, interactions with new mutualists in the invaded range subject the non-native plants to new selective pressures. These pressures can result in rapid evolutionary changes in invaders (Moran and Alexander, 2014; Colautti and Lau, 2015). This phenomenon has been investigated mostly in invasive organisms with short generation time, but several prominent examples come also from invasive trees (reviewed in Zenni et al., 2016). Seed dispersing animals have specific preferences for seed size, shape, and chemical composition (Pons and Pausas, 2007a; Siepielski and Benkman, 2007; Lichti et al., 2017). Thus, they can promote establishment of plants with particular seed traits, create trade-offs between different seed characteristics, and shape seed traits through selective pressure.

In this paper, we investigated direct and indirect interactions between Eurasian jays (*Garrulus glandarius*), invasive northern red oaks (*Quercus rubra*; hereafter 'red oak') and native pedunculate oaks (*Q. robur*) in a lowland forest of Central Europe. Jays might represent a crucial disperser of the red oak in the invasive range. While rodents harvest the red oak acorns at roughly similar rates relatively to the native acorns (Bieberich, 2016; Merceron et al., 2017; Wróbel and Zwolak, 2019; Bogdziewicz et al., 2020), they provide relatively low-quality dispersal. Both in the native and the invasive oak, the risk of acorn consumption by mice is high and the benefits of acorn caching are unlikely to compensate it (Bogdziewicz et al., 2020; see also Gómez et al., 2008 for similar findings in *Q. ilex*). Therefore, red oak dispersal success and propagule pressure might heavily depend on the dispersal by Eurasian jays. Jays have been reported to prefer removing native relative to the red oak acorns (Bossema, 1979; Myczko et al., 2014; Bieberich, 2016). However, seed dispersal success often depends on the post-removal seed fate rather than just seed removal rate (Schupp et al., 2010; Zwolak and Crone, 2012). Yet, the fate of red oak acorns removed by jays has not been investigated so far.

We build on previous studies of jay-red oak interactions that focused on the acorn removal stage (Myczko et al., 2014; Bieberich, 2016) by investigating also post-removal acorn fate. Specifically, we (1) evaluated the quality of red oak acorn dispersal by jays, relative to the dispersal of native pedunculate oak, (2) examined whether indirect interactions with the native oak influence dispersal of the invasive oak, and (3) evaluated whether acorn selection by jays can exert selective pressures on the invasive oak. We predicted that jays would remove red oak seeds at lower rates than pedunculate oak acorns, but would provide high quality seed dispersal of the red oak in terms of caching rates. This is because long dormancy and relatively high tannin levels make red oak acorns a prime caching resource (Smallwood et al., 2001). We also expected that invasive acorns would be harvested at higher rates in the presence of native acorns, and vice versa: the native acorns will be harvested at lower rates when presented with the red oak acorns. If red oak acorns are less preferred for harvest (Bossema, 1979; Myczko et al., 2014; Bieberich, 2016), the quality of a foraging patch will be highest when it contains only native acorns, intermediate for mixed species, and lowest when it consists solely of invasive acorns. Finally, we predicted that jays would prefer to harvest red oak acorns that resemble native acorns most, i.e. narrow and long, and are thus easier to handle in a beak (see Bossema, 1979; Bieberich, 2016). If our predictions are correct, Eurasian jays and indirect interactions with native oaks may accelerate red oak invasion.

2. Materials and methods

2.1. Natural history

In Europe, oaks (*Quercus* spp.) are dispersed mostly by Eurasian jays (Vander Wall, 1990; Gómez, 2003; Myczko et al., 2014; Kurek et al., 2019). Jays place single acorns in shallow caches in the ground or leaf litter, where they are protected from desiccation and consumption by strict predators (Bossema, 1979). An individual jay caches thousands of acorns each fall, well in excess of bird's energetic needs (Clayton et al., 1996). Acorns that remain unrecovered ensure oak regeneration (Vander Wall, 1990; Kollmann and Schill, 1996). Acorn dispersal by jays is a highly valuable ecosystem service (Hougner et al., 2006), and the interaction between oaks and jays has become a textbook example of mutualism (Steele, 2021).

The red oak, native to North America, was introduced to Europe in the XVII century (Gazda and Augustynowicz, 2012; Dyderski et al., 2020). Currently, it covers over 350 000 ha in the invaded range (Nicolescu et al., 2020) and is considered the most common alien broadleaved tree in Europe (Gazda and Augustynowicz, 2012; Bieberich, 2016). Its environmental impacts include reducing the cover and richness of understory vegetation, and altering chemistry, nutrient availability, and microbial communities of the soil (Gazda and Augustynowicz, 2012; Bonifacio et al., 2015; Dyderski et al., 2020; Stanek et al., 2020, 2021). In the native range, red oak acorns are dispersed by squirrels and mice (Wróbel and Zwolak, 2017; Steele, 2021), and by the blue jay (*Cyanocitta cristata*) (Moore and Swihart, 2006). However, when introduced to Europe, the red oak lost its natural seed dispersers and faced a new guild of seed removal agents.

2.2. Study sites

The study was conducted from October to November in 2020 in Zielonka Forest, located in Greater Poland Voivodeship, Poland (52°30′ N, 17°82′ E). This region is characterized by a mild temperate climate. The average air temperature ranges from −2.5 °C in January to 18.2 °C in July, and the annual precipitation averages 520 mm. Pedunculate oak is widespread in Zielonka Forest, however, the red oak is also abundant in certain stands. We established our experiments in managed old-growth forest stands with age up to 80 years. The study area was covered mostly by mixed forests *Querco-Pinetum* dominated by Scots pine (*Pinus sylvestris*), *Galio odorati-Fagetum* and *Luzulo pilosae-Fagetum* with European beech (*Fagus sylvatica*) and broadleaved oak forests. Other forest types, dominated by *Pinus sylvestris*, *Picea abies*, *Populus* spp. *Alnus glutinosa* and *Robinia pseudoacacia*, and small clear-cuts (approx. 1 ha) were patchily distributed among above described background. Tree species such as hornbeam (*Carpinus betulus*) and elm (*Ulmus minor*) occurred occasionally.

We conducted two separate experiments. In Experiment 1, we monitored acorn removal by jays. In Experiment 2, we radio-tracked acorns to reveal the fate of seeds removed by jays. In both experiments, we used acorns of both red oak and pedunculate oak. Due to poor seed crop in 2020, all acorns were purchased from forest nursery located in Greater Poland Voivodeship. The acorns were freshly collected. We excluded acorns that were moldy, broken, or infested by *Curculio* spp. larvae.

2.3. Experiment 1: Seed removal

We randomly chose 450 sound acorns of each oak species. We measured length (±0.1 mm), width (±0.1 mm), and mass (±0.01 g) of each acorn, and individually numbered them with a black marker. The acorns were offered at 30 feeders, i.e., wooden platforms fixed on 1.5-m high poles. The feeders were placed at least 400 m from each other. We assigned all feeders to one of three treatments (10 feeders per treatment): (1) only red oak acorns (30 per feeder), (2) only pedunculate oak

acorns (30 per feeder), or (3) a mix of acorns of both oak species (15 acorns per species at each feeder). Seed removal was monitored for seven days in the late-October. We conducted checks in days 1–5 and 7 after seed placement. Three feeders (one per treatment) were not visited by birds at all, so we excluded them from the analysis. We used six camera traps (Reconyx HyperFire PC800 Professional and Reconyx HyperFire PC900 Professional, Reconyx, Inc., Holmen, Wisconsin, USA) rotated among feeders to verify that jays were the only animals responsible for acorn removal.

2.4. Experiment 2: Seed radio-tracking

The seed tracking experiment was conducted for 22 days in November. We used radiotransmitters TXA-001G, produced by Telenax™. Each transmitter weighed 0.5 g and was equipped with a flexible, 13-cm long antenna (diameter: 0.25 mm). The transmitters were inserted into acorns (Pons and Pausas, 2007b; Kurek et al., 2019). Each experimental acorn weighed > 5 g to accommodate the transmitter inside. We cut the basal end of the acorn, drilled cotyledons as little as possible, and placed the transmitter inside longitudinally. The acorns were then closed and sealed with CA glue, leaving the antenna protruding from the acorn (Kurek et al., 2019). Transmitters emitted the signal in the USB band in 11 different frequencies ranging from 150 to 151 MHz. The acorns were offered during daytime (09:00–15:00) at seven feeders previously used in the Experiment 1. The feeders were chosen due to their relative proximity to stands with various tree species composition and were located 1.20–4.45 km from each other. At each feeder, we offered one experimental acorn and a mix of several (3–6) non-tagged acorns of both oak species to encourage jays to visit. We verified that only jays removed the acorns via direct observation. We started radio-tracking after observing removal of an experimental acorn. For all recovered acorns or transmitters, we marked a GPS point to estimate the distance from the feeder of origin and categorized the post-dispersal fate as either: 'cached' (i.e., sound acorn hidden in the litter, soil or trees) or 'consumed' (i.e., only a transmitter found). Dispersal distances were analyzed for cached seeds only. We additionally noted whether the acorn was transported into a forest patch with or without oak individuals within a 50-m radius (i.e., forest type). Here, our goal was to evaluate potential differences between the oaks in the ability to colonize new sites (Woziwoda et al., 2019). Within a 10-m radius, we also visually estimated understory [%], i.e., bushes and young trees above 150 cm but below the main canopy layer, and ground vegetation cover [%], i.e., the herbaceous layer that grows over an area of the forest floor below 100 cm. Both invasive and native oaks prefer light or moderately shaded environment for seedling establishment (Bossema, 1979; Annighöfer et al., 2015; Dyderski et al., 2020), thus dense understory and vegetation cover can hinder oak recruitment. If the experimental acorn was found undamaged after removal, it was re-used in the following days. In total, we used 11 red oak acorns and 18 pedunculate oak acorns with radiotransmitters.

2.5. Statistical analysis

The analyses were conducted in R (version 4.0.2). We used Welch *t*-test to compare length, width, and mass or red and pedunculate acorns used in Experiment 1. Seed removal was analyzed with mixed effects Cox models fitted with package 'coxme' (Therneau, 2020). All pedunculate oak acorn were removed in the first day of the experiment regardless of their traits or experimental treatments. In the case of red oak, we analyzed whether acorn removal was influenced by (a) treatment (acorns in mixed or monospecific treatments), (b) acorn length, (c) acorn width, and (d) acorn mass. Feeder ID was entered as a random effect. We focused on removal rates rather than the final proportion of removed acorns because the removal rate is a more sensitive measure of granivore preferences, and is ecologically meaningful because it determines how long acorns are exposed to mortality factors such as strict

seed predators (e.g. ungulates: Van Ginkel et al., 2013).

The results of Experiment 2 (seed radio-tracking) were analyzed with generalized linear mixed models fitted with package 'glmmTMB' (Brooks et al., 2017). We analyzed whether northern red oak and pedunculate oak acorns that were removed by jays differed in: (i) the probability of consumption, (ii) the probability of caching, (iii) seed removal distance, and the following features of habitat where dispersed seed were placed: (iv) forest type, i.e., absence (coded as 0) or presence (coded as 1) of oak individuals in 50-m radius, (v) proportion of understory cover, and (vi) proportion of floor vegetation cover. Thus, we fitted 6 models, each with a different response variable. In models (i), (ii) and (iv), we used binomial error distribution (logit link). In models (iii), (v) and (vi), we used Gaussian error distribution (identity link) with seed removal distances log-transformed, and understory and floor vegetation cover logit-transformed. In all models, explanatory variables included oak species and day of the experiment (linear and quadratic effect, to account for potential changes in jay behavior over time). Feeder ID was entered as a random effect. Raincloud plots were prepared with package 'raincloudplots' (Allen et al., 2021).

3. Results

3.1. Experiment 1: Acorn removal

3.1.1. Acorn traits

Acorns of pedunculate oak were longer (df = 774.5, t = 21.6, $P < 0.001$) and narrower (df = 807.4, t = -26.9, $P < 0.001$) than acorns of red oak (Fig. 1). However, we found no significant differences in acorn mass between the species (df = 790.4, t = 0.86, $P = 0.39$; Fig. 1).

3.1.2. Acorn removal rates

The cameras recorded 26 visits to feeders, all by jays. Ninety-four percent of red oak acorns and 100% of pedunculate oak acorns were removed, and all pedunculate oak acorns were taken during the first day of the experiment. The difference in acorn removal rate was significant (df = 1, z = 5.55, $P < 0.001$; Fig. 2). Presence of pedunculate oak acorns enhanced removal of red oak acorns, although the effect was only marginally significant ("treatment" effect, Fig. 2; Table 1). We also found a positive effect of acorn length and a negative effect of acorn width on the removal rate (Table 1). Acorn mass did not affect the rate of removal (Table 1).

3.2. Experiment 2: Acorn radio-tracking

3.2.1. Acorn caching and consumption

Each feeder was visited simultaneously by 1–6 jays. Jays removed 116 acorns with radiotransmitters (N = 44 for red oak and N = 72 for pedunculate oak). One removed acorn (red oak) was not found. One hundred and one acorns were cached. Of all cached acorns, 85% were hidden in leaf litter or moss, 10% were cached in mineral soil, and 5% were stored in tree cavities. Red oak had lower estimated probability of caching than pedunculate oak (77% vs. 96%, $P = 0.03$; Table 2). In addition, the probability of caching changed over time (Fig. 3; Table 2).

Fourteen acorns were consumed. Red oak acorns had far higher estimated probability of consumption than pedunculate oak acorns (24% vs. 3%, Table 2). The probability of acorn consumption also varied with time (Table 2).

3.2.2. Seed removal distance and caching sites

Red oak acorns were dispersed by jays at shorter distances than pedunculate oak acorns (mean 80.5 m, range 6–256 m for red oak, and mean 101.1.0 m, range 5–310 m for pedunculate oak acorns, Fig. 4; Table 2).

Almost all acorns were dispersed into woodlands. Only one acorn was cached in *Brassica oleracea* crop field. Estimated probabilities of seed placement in forest patches with presence of any oak individuals
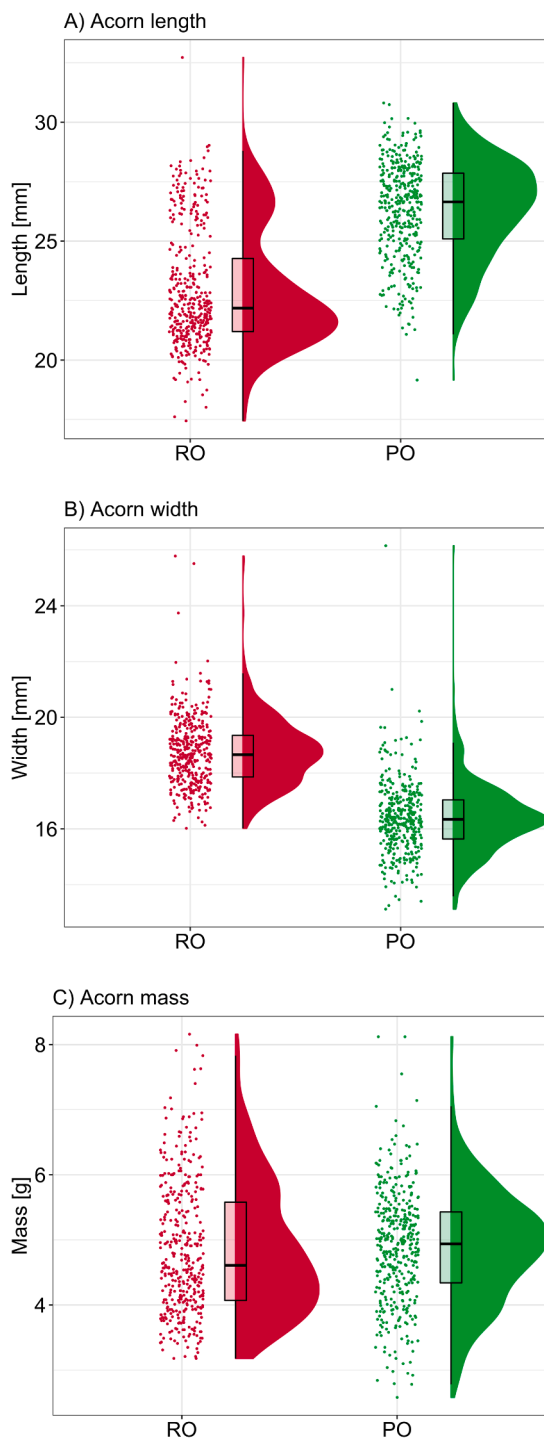
Fig. 1. Red oak (RO) acorns are (A) shorter and (B) wider than pedunculate oaks (PO), but (C) acorn mass is similar for the two species. Raincloud plot shows the individual observations (points), boxplots (the lower and upper hinges of boxplots correspond to the first and third quartiles), and their probability distribution. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

were similar for both oak species (30% for red oak vs. 34% for pedunculate oak, Table 2). Caching sites of the two species did not differ in understory cover, nor floor vegetation cover (Table 2).

4. Discussion

Seed dispersal by scatterhoarders is a sequential process that involves seed removal, transportation, caching, and often consumption (Vander Wall, 1990; Schupp et al., 2010; Pesendorfer et al., 2016; Lichti et al., 2017). When dispersed by Eurasian jays, acorns of the pedunculate oak had an advantage over the red oak at most, but not all of these stages. However, we also found that the most pronounced advantage of the pedunculate oak (in acorn removal rates) is mitigated when pedunculate and red oak acorns co-occur. Thus, indirect interactions between the oaks mediated by their mutualistic partner appear to improve quantity of dispersal (sensu Schupp et al., 2010) in the invasive species.

In accordance with our expectations, jays removed pedunculate oak acorns at higher rates than red oak acorns. Such a difference could be expected because Eurasian jays have a strong preference for pedunculate oak acorns over other seeds, even of other large-seeded native trees, e.g., European beech (*Fagus sylvatica*) or hazel (*Corylus* spp.) (Bossema, 1979). There can be several causes of the observed disparity in acorn harvest rates. Pedunculate oak acorns differ from red oak acorns in nutritional content, e.g., red oak acorns have considerably higher lipid concentration (Bogdziewicz et al., 2018). Acorns of the North American *Q. rubra* have also high tannin content. However, this aspect is unlikely to matter in Central Europe because in the invaded range the tannin concentration is reduced relatively to the native range and similar to that found in pedunculate oak acorns (Bogdziewicz et al., 2018). Shape is another potentially important factor. Acorns wider than 17–19 mm cannot be swallowed by Eurasian jays and have to be carried in the beak, which limits the number of acorns carried per flight (Pons and Pausas, 2007a). The native acorns are usually under this limit, and the red oak acorns above (Fig. 1). This makes the native acorns easier to handle, and less energetically costly to carry. Finally, red oak acorns have thicker shells than the pedunculate oak acorns (Bossema, 1979; Bogdziewicz et al., 2018). Jays dehusk acorns before eating them, thus thick shells increase time and energy expenditure during handling, and probably reduce the relative value of acorns. In fact, blue jays (a North American species) were found to avoid oak species with hard seed coat (Moore and Swihart, 2006). Considering the strong preference for the pedunculate oak, the presence of red oak is unlikely to disrupt the mutualistic interactions between jays and the native oak (Traveset and Richardson, 2006).

Even though pedunculate oak acorns were preferred by the Eurasian jays, the red oak acorns were still commonly removed and carried away (see also Myczko et al., 2014). Moreover, consistently with our predictions, the removal of red oak acorns increased when they co-occurred with the pedunculate oak acorns (but contrary to predictions, we found no effect of the presence of red oak acorns on the removal of native acorns). This happened even though the pedunculate acorns quickly disappeared from the mixed trays, leaving the red oak acorns alone. Most likely, individuals anticipating a repeat of their recent successful foraging formed a habit of visits to the feeder. Regardless of the specific mechanism, this pattern can reflect a greater propensity of jays to visit and forage at patches where both species co-occur, relative to pure red oak patches. In such manner, the red oak can benefit from the presence of the pedunculate oak. The phenomenon where indirect effects of co-occurring plants with shared dispersers increase the quantity or quality of seed dispersal (sensu Schupp et al., 2010) is known as "seed dispersal facilitation" (Carlo, 2005). Finding facilitation between the two oak species contrasts with parallel studies on rodents. The presence of pedunculate oak acorns did not affect red oak removal rates, but reduced the likelihood of caching by mice (Bogdziewicz et al., 2019), therefore reducing dispersal quality (Schupp et al., 2010).

Our results differ from Bieberich (2016), who reported similar rates of acorn removal by jays in single- and mixed-species treatments. However, the statistical analysis in Bieberich (2016) was not controlled for time (day of month), which was found to modulate acorn removal rates in this study and in Myczko et al. (2014). This variable was particularly likely to obscure differences in acorn removal because the single- and mixed-species treatments were conducted at separate times
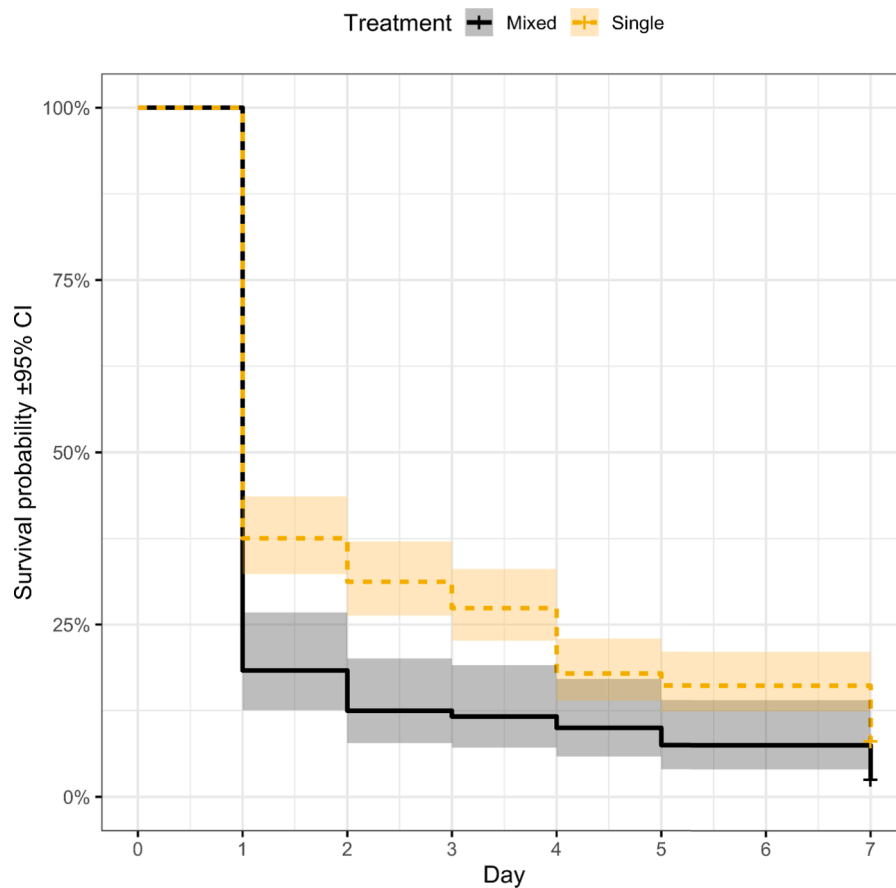
Fig. 2. Red oak acorns tended to be removed faster when they were mixed with pedunculate oak acorns than when they were offered alone. Survival probability of red oak acorns in the mixed treatment (red oak acorns offered together with pedunculate oak acorns) and in the single treatment (red oak acorns offered alone). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 1

Factors influencing the removal rate of red oak acorns: treatment (red oak acorns mixed with pedunculate oak acorns, relatively to offered separately), acorn length, acorn width, and acorn mass. Removal was estimated using mixed effects Cox models.

Variable	Estimate (SE)	z-value	P-value
Treatment	0.60 (0.31)	1.87	0.06
Length	0.13 (0.04)	3.28	0.001
Width	−0.29 (0.08)	−3.60	<0.001
Mass	0.02 (0.14)	0.17	0.86

(first the single-species, then the mixed-species treatment: Table 1 in Bieberich, 2016). The discrepancy emphasizes the importance of controlling for potential confounders in regression techniques (Gelman and Hill, 2006).

As a caveat, most studies on indirect seed-seed effects (including ours and Bieberich, 2016) investigate this phenomenon with feeding station experiments. In the future, such tests should be supplemented by stand or landscape-level data to verify that effects observed in small-scale experiments are still apparent at larger scales.

We also documented phenotypic selection of red oak acorns that occurred at the stage of acorn removal by Eurasian jays. The jays are remarkably selective when harvesting acorns. They rely mostly on visual cues to assess multiple aspects of acorn conditions, e.g., infestation, damage, ripeness, and size (Bossema, 1979; Pesendorfer et al., 2016). Generally, when size is concerned, most scatterhoarding species display a preference towards larger seeds, up to a limit set by handling constraints (Muñoz and Bonal, 2008; Bartlow et al., 2011). Eurasian jays

also prefer large pedunculate oak acorns (Bossema, 1979; Pons and Pausas, 2007a). In contrast, blue jays prefer smaller red oak acorns in its native range in North America (Moore and Swihart, 2006; Bartlow et al., 2011). Yet, we did not detect selection for size (measured here with acorn mass) of the red oak acorns in the invaded range. Instead, Eurasian jays selected long and slim acorns, probably because of throat limitation that makes it impossible to store wide acorns in the esophagus (Bossema, 1979; Pons and Pausas, 2007a). In addition, round acorns might be more difficult to carry in the beak. Regardless of the precise mechanism underlying the preference, this finding indicates that the selective pressure exerted on red oak acorns by their avian dispersers can be different in the native and the invaded range. However, comprehensive evaluation of potential evolutionary changes in the acorn traits is beyond the scope of our work because it would require data on oak recruitment.

Once removed, red oak tended to be dispersed over shorter distances than pedunculate oak acorns. Yet, the average dispersal distance about 100 m in both species. While jays are capable of transporting acorns up to several kilometers away from the seed source (Vander Wall, 1990; Pesendorfer et al., 2016), the transportation distance is habitat-specific. In closed woodlands, jays usually disperse seeds no more than several hundred meters away, and typically less than that (Bossema, 1979; Gómez, 2003; Pons and Pausas, 2007b; Kurek et al., 2019; this study). The transportation distance is also affected by the number of transported acorns: the fewer acorns carried by jays, the shorter their removal distance (Bossema, 1979). Furthermore, less valuable acorns tend to be carried over shorter distances than more valuable ones (Moore et al., 2007). Thus, the difference in the transportation distance between the native and the invasive acorns in this study could result from the fact that red oak acorns are less convenient to carry and fewer could be taken

Table 2
Factors influencing the probability of acorn caching, consumption, transportation distance, and placement in sites with different habitat characteristics (forest type, understory cover, and ground vegetation cover). Effects were estimated with six different GLMMs, see Methods for details.

Variable	Estimate (SE)	z-value	P-value
Seed caching			
Intercept	1.21 (0.55)	2.18	0.03
Pedunculate oak	1.88 (0.87)	2.16	0.03
Day	9.25 (4.68)	1.98	0.05
Day^2	−7.24 (3.81)	−1.90	0.06
Seed consumption			
Intercept	1.23 (0.55)	−2.05	0.04
Pedunculate oak	−2.37 (0.97)	−2.43	0.02
Day	−10.33 (4.83)	−2.14	0.03
Day^2	9.44 (4.09)	2.31	0.02
Transportation distance			
Intercept	3.90 (0.19)	20.42	<0.001
Pedunculate oak	0.45 (0.22)	2.08	0.04
Day	−0.93 (1.32)	−0.70	0.48
Day^2	−1.54 (1.07)	− 1.43	0.15
Forest type			
Intercept	−0.89 (0.75)	−1.19	0.23
Pedunculate oak	0.26 (0.58)	0.45	0.65
Day	4.63 (5.09)	0.91	0.36
Day^2	1.43 (3.25)	0.44	0.66
Understory cover			
Intercept	−2.54 (0.85)	−2.99	0.003
Pedunculate oak	−0.62 (0.99)	−0.63	0.53
Day	−5.24 (6.10)	−0.86	0.39
Day^2	6.61 (5.26)	1.26	0.21
Floor vegetation cover			
Intercept	−2.97 (0.84)	−3.52	<0.001
Pedunculate oak	1.07 (0.98)	1.09	0.28
Day	18.78 (5.77)	3.25	0.001
Day^2	0.27 (5.17)	0.05	0.96

per trip, that red oak acorns as less valuable than pedunculate oak acorns, or a combination of these factors.

Finally, red oak acorns were more likely to be eaten and less likely to be cached in comparison to pedunculate acorns. From the plant perspective, acorn consumption represents an obvious cost of the dispersal by jays and caching is one of its main benefits. Buried acorns benefit from reduced exposure to strict seed predators and adverse abiotic factors such as desiccation (Zwolak and Crone, 2012). Consequently, cached acorns germinate and produce seedlings with higher probability relatively to acorns on that remain on the forest floor (Bogdziewicz et al., 2020). While the reduced caching and increased consumption probability indicate that the quality of acorn dispersal is lower for the red than for the native oak, the uneaten acorns of both species were cached in similar habitats in terms of forest type or density of vegetation cover. Thus, once acorns were dispersed, they received
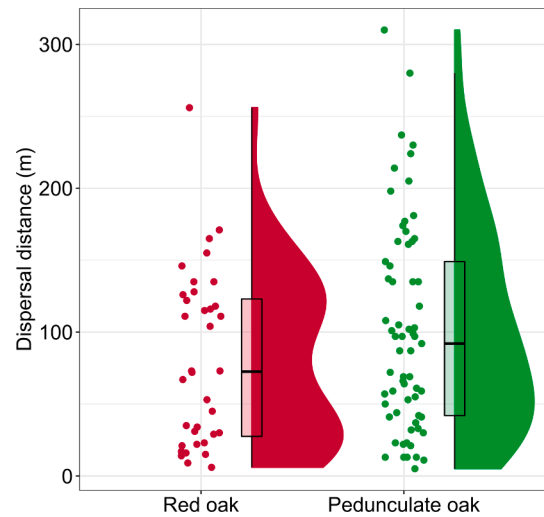

Fig. 4. Red oak acorns were dispersed over shorter distances than pedunculate oak acorns. Raincloud plot shows the individual observations (points), boxplots (the lower and upper hinges of boxplots correspond to the first and third quartiles), and their probability distribution. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)
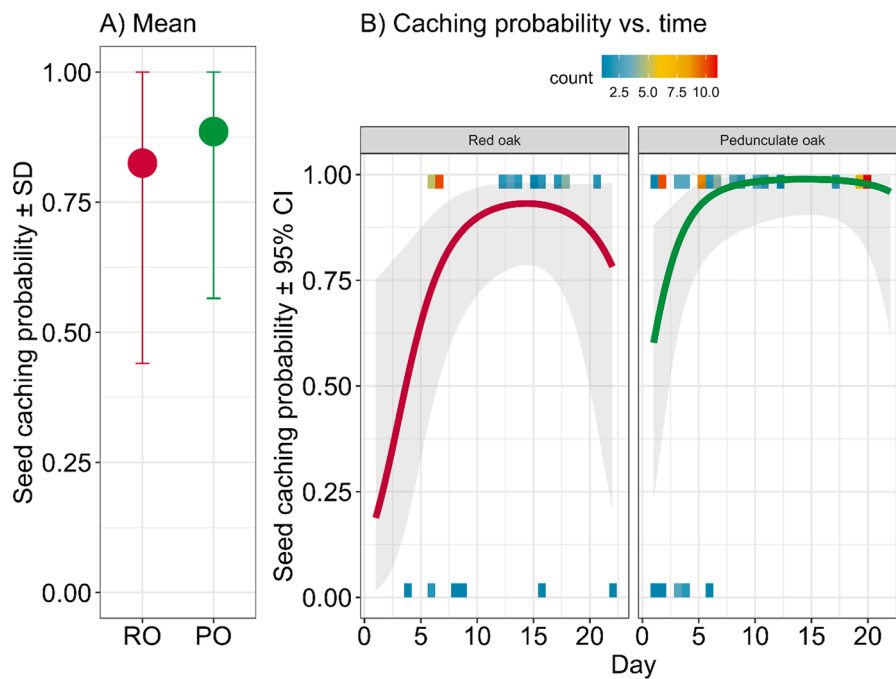

Fig. 3. Red oak (RO) acorns had reduced probability of caching relatively to pedunculate oak (PO) acorns (A), and the probability of caching varied with time (B). (A) Mean caching probability of red and pedunculate oaks. (B) Probability of acorn caching vs. time. Prediction lines are derived from binomial GLMM. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

similar advantages.

Propagule pressure has been identified as the main determinant of red oak invasion (Dyderski and Jagodziński, 2018; Jagodziński et al., 2018; Woziwoda et al., 2018). It has been suggested that dispersal of the red oak is ineffective (Major et al., 2013) and that this limits its invasion potential (Nicolescu et al., 2020). However, while red oak typically occurs at relatively low adult abundance in its invasive range, it has become widespread in many European countries (Gazda and Augustynowicz, 2012; Dyderski et al., 2020; Nicolescu et al., 2020). Moreover, red oak saplings often dominate forest understory even when its adult trees are severely outnumbered by the pedunculate oak in the canopy (Myczko et al., 2014; Woziwoda et al., 2019). These patterns indicate that numerous red oak acorns travel efficiently and successfully produce seedlings. Our results suggest a mechanism responsible for the efficient dispersal: acorn transportation and caching by the Eurasian jay. Jays are important dispersers of even less preferred seed species (Moore and Swihart, 2006). Given that rodents provide relatively low-quality acorn dispersal (Bogdziewicz et al., 2019, 2020), Eurasian jays are the main dispersal agents of the red oak in its invasive range. Our results indicate that differences between the dispersal of the alien and the invasive oak species by jays (i.e., relatively slower removal rates, moderately shorter transportation distance, and lower caching probability in the red oak) were rather subtle (see Figs. 3 & 4). Thus, the Eurasian jay plays an important role in red oak expansion. Furthermore, the dispersal of red oak is increased by the presence of native acorns and modulated by red oak acorn traits. High acorn production of red relatively to pedunculate oaks (Bogdziewicz et al., 2018; Woziwoda et al., 2019; Wróbel and Zwolak, 2019) can compensate for higher consumption costs of dispersal by jays, and, along with other factors (e.g., Woziwoda et al., 2019; Wróbel and Zwolak, 2019), explain the recruitment advantage of red over the pedunculate oak.

We note that our study was conducted in a year when natural acorn availability was low. This factor probably influenced acorn removal rates, which were relatively high in our study, and selectiveness of dispersers, because they tend to be less discriminating when seeds are scarce (Schupp et al., 2019). It is possible that during years with high acorn availability, differences in jay-mediated dispersal of the native vs. the invasive acorns are more pronounced, and jay selection of acorns with particular traits is even stronger.

In conclusion, we found an intricate interplay among factors that determine seed dispersal, including plant species, seed traits, and indirect plant-(disperser)-plant interactions. These factors influence seed choice and fate, and ultimately the probability of recruitment. In the investigated pair of species, dispersal of non-native seeds was less intense and less advantageous than dispersal of native seeds provided by the same, shared dispersal agent. Yet, even seed dispersal that appears inferior in comparison to the dispersal of native species can be good enough to provide an effective mechanism for rapid spread of a non-native plant.

Even more generally, our results highlight the vital role of native seed dispersers in the expansion of non-native plants. Animals that disperse seeds provide a keystone ecological service in many ecosystems, but since these mutualisms tend to have low specificity, they can easily incorporate invasive plants, which then receive dispersal benefits similar to native plants. This dual role of animals, as seed dispersers of native and non-native plants, contributes to the challenges associated with the control of invasive species.

CRediT authorship contribution statement

Aleksandra Wróbel: Conceptualization, Methodology, Investigation, Formal analysis. **Przemysław Kurek:** Conceptualization, Methodology, Investigation, Writing – review & editing. **Michał Bogdziewicz:** Conceptualization, Formal analysis, Writing – review & editing. **Dorota Dobrowolska:** Resources, Writing – review & editing. **Rafał Zwolak:** Conceptualization, Methodology, Resources, Formal

analysis, Writing – original draft, Funding acquisition.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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