Habitat-dependent seed dispersal of an introduced tree species by native rodents

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ABSTRACT

Invasions of many plant species strongly depend on propagule pressure. Thus, habitat-related differences in seed dispersal could affect susceptibility of distinct habitat types to plant invasions. We examined the fate of northern red oak (*Quercus rubra*, invasive in Europe) and pedunculate oak (*Quercus robur*, native in Europe) acorns dispersed by yellow-necked mice (*Apodemus flavicollis*) in (i) hardwood stands invaded by northern red oak, (ii) uninvaded hardwood stands dominated by native oaks, and (iii) uninvaded coniferous stands dominated by Scots pine (*Pinus sylvestris*). Regardless of forest type, mice preferred to harvest and consume pedunculate rather than red oak acorns. Similarly, acorn harvest rates were unaffected by forest type. However, the fate of acorns, and thus effectiveness of seed dispersal, varied considerably among forest types. Acorns had the highest probability of being cached in uninvaded hardwood stands, while coniferous stands were characterized by the longest seed dispersal distances and a high proportion of missing seeds (probably indicating larderhoarding). Relative to the other forest types, stands with northern red oak were characterized by a combination of low acorn caching rates and short dispersal distances. These findings suggest that differences in rodent-mediated seed dispersal might increase recruitment rates of northern red oak at the edges of invaded range.

1. Introduction

Human activities such as horticulture and forestry constitute major reasons of introduction of alien plant species into new ecosystems (Richardson, 1998). Some of these intruders become invasive, causing economic losses and threatening local biodiversity (Pimentel et al., 2005). Yet, even though invasive species represent an urgent and growing conservation problem, the mechanisms of biotic invasions and factors that determine susceptibility of particular ecosystems to alien plant encroachment are still not fully understood.

Different susceptibility to invasion (a.k.a. "invasibility") of ecosystems (Emery and Gross, 2006; Chytrý et al., 2008a, 2008b; Dyderski and Jagodziński, 2018) plays a crucial role in the initial phase of colonization by alien species (Chytrý et al., 2008a, 2008b) and might be influenced by the identity of dominant plant species (Emery and Gross, 2006; MacDougall and Turkington, 2005). However, existing studies on ecosystem and habitat-specific invasibility have focused mostly on exploring interspecific competition among plants and on the effects of abiotic factors such as soil type and light availability (Emery and Gross, 2006; Theoharides and Dukes, 2007; Dyderski and Jagodziński, 2018). Yet, one generality that emerged from past studies on mechanisms of

plant invasions is that the invasion process heavily depends on propagule pressure (Lonsdale, 1999; Cordeiro, et al. 2004; Lockwood et al., 2005; Theoharides and Dukes, 2007; Chytrý, 2008b; Simberloff, 2009; St Clair et al., 2016; Dyderski and Jagodziński, 2018). This suggests that invasibility might be strongly influenced by other, less intensely studied biotic interactions, such as those with seed-dispersing animals (Cordeiro, et al. 2004; Pearson et al., 2011, 2014; Maron et al., 2012; Connolly et al., 2014; Traveset and Richardson, 2014; Bieberich, 2016; St Clair et al., 2016).

Many plants, including nut-producing trees, are dispersed by scatterhoarders: animals that feed on seeds, but also cache some of them in shallow soil for future consumption (Jansen et al., 2002; Vander Wall, 2010; Lichti et al., 2014, Lichti et al., 2014). Thus, scatterhoarders play a dual role of seed predators and seed dispersers (Zwolak and Crone, 2012). Seed predation by scatterhoarders might mediate biotic resistance against plant invaders (Allington et al., 2013; Connolly et al., 2014; St Clair et al., 2016, Bogdziewicz et al., 2018c). On the other hand, preferential dispersal of exotic plant species by scatterhoarders might facilitate biotic invasions (Bieberich, 2016; Lenda et al., 2018; Bogdziewicz et al., 2018c). Thus, if foraging behavior of scatterhoarders is habitat-specific, then different habitats might vary in their

susceptibility to invasion.

Our research directly addressed this issue. We examined whether differences in seed consumption and dispersal by rodent scatterhoarders could contribute to differential susceptibility of different forest types to invasion of northern red oak (*Quercus rubra*). This oak species is native to North America and recognized as invasive in its introduced range in Europe (Gazda and Augustynowicz, 2012; Major et al., 2013; Woziwoda et al., 2014a,2014b). Ecological effects of the invasion include reduced establishment of native plant species due to the thick layer of northern red oak leaf litter and diminished light availability (Woziwoda et al., 2014a), and concomitant decrease in fungi and animal species associated with native plant communities (Gazda and Augustynowicz, 2012; Woziwoda et al., 2014a). In its natural range, northern red oak strongly depends on interactions with seed dispersers, especially granivorous rodents (Smallwood et al., 2001; Steele, 2008; Wróbel and Zwolak, 2017). When introduced to Europe, northern red oak lost both its natural mutualists (including seed dispersers) and antagonists (including seed consumers), but faced a new guild of granivores and entirely new ecosystems to invade. Colonization success of northern red oak differs markedly among habitats (Major et al., 2013; Jagodziński et al., 2018; Woziwoda et al., 2018), but mechanisms behind these differences remain unknown. However, a number of studies reported that red oak invasion is strongly limited by seed dispersal (Major et al., 2013; Bieberich, 2016; Merceron, et al. 2017; Myczko et al., 2017; Bogdziewicz et al. 2018c; Jagodziński et al., 2018; Woziwoda et al., 2018).

We examined the fate of northern red oak acorns and native pedunculate oak (*Quercus robur*) acorns harvested by rodents in three types of forest stands in Central Europe: (i) invaded hardwood stands comprised of northern red oak, pedunculate oak, and European beech (*Fagus sylvatica*), (ii) uninvaded hardwood stands dominated by pedunculate oak, and (iii) uninvaded coniferous Scots pine (*Pinus sylvestris*) stands. Revealing habitat-specific patterns of acorn consumption and dispersal can contribute to more mechanistic understanding of red oak colonization success: if acorns are more readily consumed in some forest types, such forests will be more resistant to invasion. In contrast, if acorns are more readily cached or transported further, such forests will be more susceptible to invasion. Additionally, habitat-mediated differences in consumption and dispersal of red vs. pedunculate oak might affect competitive interactions between these two species (Dangremond et al., 2010, Bogdziewicz et al., 2018c).

2. Methods

2.1. Study site and rodent species

The study was conducted over two years (2016 and 2017), in Puszcza Zielonka, 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 Puszcza Zielonka, however, northern red oak is also abundant in certain stands.

We established study sites in twelve managed 89–110 year-old stands, divided evenly into three groups: (1) sites in hardwood stands comprised of northern red oak, pedunculate oak, and European beech (hereafter 'invaded sites'), (2) sites in hardwood stands, dominated by the pedunculate oak and without northern red oak (hereafter 'native oak sites'), and (3) sites in coniferous stands comprised almost exclusively of Scots pine and without any oak individuals (hereafter 'coniferous sites'). The understory layer was poorly developed and comprised mostly of the common wood sorrel (*Oxalis acetosella*) in invaded sites, grasses (*Carex* spp.) in native oak sites, and mosses (mainly *Dicranum polysetum*) in coniferous stands.

Behavior of animals that disperse seeds is often influenced by seed abundance (Theimer, 2005; Vander Wall and Beck, 2012). Therefore, in both years of the study, we measured the seed crop of northern red oak in invaded sites and pedunculate oak in both invaded and native oak sites. We counted acorns on the ground (Touzot et al., 2018), in early October. We randomly selected five adult oaks of each species per site (when the two species co-occurred) and counted seeds in two 1-m^2 quadrats per tree. The quadrats were located 1 m and 5 m from the trunk of the focal tree. Across all sites, we sampled acorns under 20 individuals of northern red oak and 40 individuals of pedunculate oak per year.

2.2. Seed preparation and experimental design

Acorns of both oak species were collected near our study sites. We floated all acorns in water and excluded those that were moldy, broken, or infested by *Curculio* sp. larvae. Then, we randomly chose 480 sound acorns of each oak species per year (480 acorns × 2 species × 2 years = 1920 in total) for the seed tracking experiment. The average mass (± SD) of experimental acorns was 4.71 ± 0.60 g (min. = 2.1 g, max. = 9.75 g) in northern red oak and 4.05 ± 0.90 g (min. = 1.9 g, max. = 7.2 g) in pedunculate oak. We pierced a 1-mm diameter hole through the husk at the basal end of each acorn without damaging the cotyledon and the embryo, and then inserted and tied a steel wire (150-mm length, 0.22-mm diameter) to the acorn and attached an individually numbered red plastic tag (20 × 40 mm) to the opposite end of the wire (Xiao and Zhang, 2006; Wróbel and Zwolak, 2013; Wróbel and Zwolak, 2017). The set comprised of wire and tag weighed ∼ 0.16 g. Behavior of scatterhoarders might be affected by seed tagging (Wróbel and Zwolak, 2013, Kempter et al., 2018), but we limited the potential for bias by evaluating relative differences in dispersal of identically marked seeds.

The seed tracking experiments were conducted in October 2016 and October 2017, when most sound acorns of both oak species can be found on the forest floor. At each study site, we placed four seed stations, two per each oak species. Stations within each site were located ≥ 40 m from one another, and supplied with 20 randomly chosen experimental acorns of either northern red oak or pedunculate oak (20 acorns × 2 oak species × 2 stations × 3 stand types × 4 study sites = 960 acorns per year). We monitored acorn removal and fate each morning during the first 10 days, and then conducted checks 14, 28, 45, and 60 days after placement of the acorns. If marked acorns were removed, the area around the seed station was searched in 25-m radius (although a few seeds were accidentally found at longer distances). For all recovered acorns or tags, we measured the distance from the station of origin and divided their post-dispersal fates into five categories: (i) 'eaten' (i.e. only a tag and seed fragments remained), (ii) 'partially eaten', i.e. only basal area of the acorn was consumed, but the apical part that contains embryo was left undamaged, (iii) 'cached', i.e. buried in the topsoil, (iv) 'left on surface', i.e. deposited intact on the surface, and (v) 'missing', i.e. not recovered within the search area. Seed fate diagrams are presented in the Appendix S1.

2.3. Seed disperser identification

We used camera traps Reconyx HyperFire PC800 Professional™ to identify taxa responsible for acorn removal. The cameras were set up during the first 7 days of this study at ∼ 0.4 m distance in front of the seed stations. Since there were more stations than cameras, we monitored all stations sequentially. Pictures were taken in sets of five with one-minute pauses between series. Each set of pictures was treated as an independent arrival of a seed disperser. We recorded 195 visits of seed foragers from most of the stations: we did not obtain recordings from one invaded site because the camera trap was lost. The only recorded seed removal agents were individuals of *Apodemus* spp., and trapping conducted for another research project indicated that the only *Apodemus* mice at our sites are yellow-necked mice (*A. flavicollis*) (M. Zduniak, *unpublished data*).

2.4. Statistical analysis

Data analysis was conducted in R using glmmADMB and lme4 packages (Fournier et al., 2012; R Core Team, 2017; Bates et al., 2015; Skaug et al, 2016), with generalized mixed models fitted by maximum likelihood using a Laplace approximation. When analyzing acorn crop, we entered type of stand, oak species and year as fixed effects, whereas site and tree were included as random effects.

In the seed tracking experiments, analyses were conducted on final acorn fate. We analyzed whether the stand types differed in (i) the overall proportion of seeds harvested, (ii) the proportion of seeds harvested and found, (iii) the proportion of harvested seeds that were found consumed, (iv) the proportion of harvested, unconsumed seeds that were found cached, and (v) removal distance. In analyses (i)–(iv), we used binomial error distribution (logit-link), and in analysis (v) Gaussian error distribution (identity link) with removal distances log-transformed. In each model, we entered type of stand, oak species, and year as fixed effects, whereas site and station (nested within site) were included as random effects. When analyzing acorn crop, we entered type of stand and year as fixed effects, whereas site and tree were included as random effects. The response variable was the number of acorns found under a given tree (average from the two quadrants) and we used Gaussian error distribution. Testing for statistical significance was conducted with Wald chi-square tests (package 'car': Fox and Weisberg, 2011), with Wald z-tests (command 'summary' in 'lme4' package) used as post-hoc tests to evaluate differences among stand types. Our initial model included all two- and three-way interactions among the fixed-effect variables. We arrived at the final model through backward elimination of non-significant interaction terms.

3. Results

3.1. Acorn crop

In both oak species, acorn production was markedly higher in 2016 than in 2017 (df = 1, χ^2 = 1704.058, P < 0.001; Fig. 1). In both years of the study, red oaks produced more seeds than pedunculate oaks (df = 1, χ^2 = 462.071, P < 0.001; Fig. 1) and acorn availability was higher at invaded than uninvaded oak sites (df = 1, χ^2 = 4.913, P = 0.028; Fig. 1).
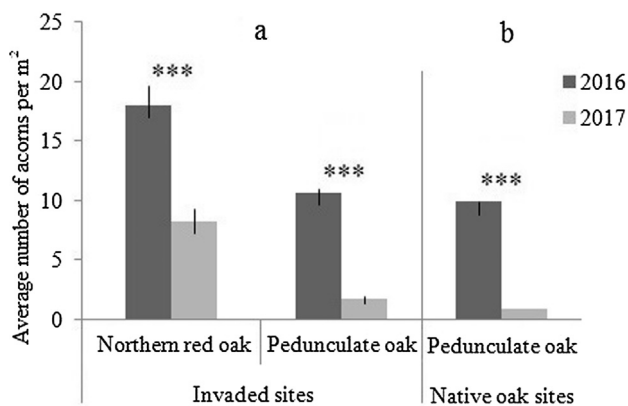

Fig. 1. Average acorn crop of northern red oak and pedunculate oak (± SE) during two study years in relation to type of stand. Different letters (a, b) indicate a significant difference between types of stand (P < 0.05) while stars (***) indicate significant differences between years (P < 0.001). Seeds were counted on the forest floor in 1-m² quadrats located under 20 individuals of northern red oak and 40 (20 × 2 types of stand) individuals of pedunculate oak per year.

Table 1
Fixed effects of final generalized linear mixed models describing the fate of experimental acorns. †Significant effects. N = 1920 acorns. df, degrees of freedom. See Appendix S2 for more details about effect sizes

Fixed effects			
(a) Seed harvest	**df**	χ^2	**P**
Type of stand	2	1.443	0.486
Species	1	12.000	0.001†
Year	1	1.669	0.196
Species Year	1	5.540	0.018†
(b) Recovery			
Type of stand	2	13.075	0.001†
Species	1	2.785	0.095
Year	1	14.430	> 0.001†
Type of stand × Year	2	9.173	0.010 †
(c) Consumption			
Type of stand	2	3.862	0.145
Species	1	10.364	0.001†
Year	1	0.576	0.448
(d) Caching			
Type of stand	2	8.259	0.016†
Species	1	1.672	0.196
Year	1	4.567	0.033†
(e) Removal distance			
Type of stand	2	14.536	> 0.001†
Species	1	2.162	0.141
Fate	1	4.750	0.029†
Year	1	1.441	0.230
Type of stand × Fate	2	9.874	0.007†

3.2. Seed harvest and recovery

Overall, rodents harvested 65% of all experimental seeds, with no difference between years or stands (non-significant *Year* and *Type of stand* effects in Table 1a; see Appendix S1 for more details). While northern red oak acorns were harvested at lower rates than pedunculate oak, this effect was found only in 2016, when the acorn crop was high (64% vs. 91%; df = 1, χ^2 = 12.000, P = 0.001; Table 1a).

Seed recovery was lower at coniferous sites (only 27% of harvested acorns found) than at the two other stand types (54% at invaded sites and 59% at native oak sites: *Type of stand* effect in Table 1b) and this difference was stronger in 2016 than in 2017 (*Type of stand* × *Year* interaction in Table 1b) (details in Appendix S1). We recovered similar proportions of harvested acorns of both oak species (42% for northern red oak and 51% for pedunculate oak; non-significant *Species* effect in Table 1b). In general, acorn recovery was lower in 2016 (year of high acorn crop) than in 2017 (low acorn crop) (31% vs. 74%; *Year* effect in Table 1b).

3.3. Seed consumption and caching

Proportions of acorns consumed (both *in situ* and removed) did not differ among sites or between years (non-significant *Type of stand* and *Year* effects in Table 1c). However, rodents consumed a lower proportion of red than pedunculate oak acorns (38% vs. 69%; *Species* effect in Table 1c; see Appendix S1 for more details).

Proportions of harvested and uneaten acorns that were cached (rather than left on surface after removal) differed among stand types (83% in native stands, 74% in coniferous stands, and 57% in invaded ones: *Type of stand* effect in Table 1d; see Appendix S1 for more details). Similar proportions of acorns of both oak species were cached after removal (72% for northern red oak and 70% for pedunculate oak; non-significant *Species* effect in Table 1d). Finally, acorns were cached less frequently in 2016 (year of higher acorn production) than in 2017 (year of lower acorn production) (54% vs. 76%; *Year* effect in Table 1d).
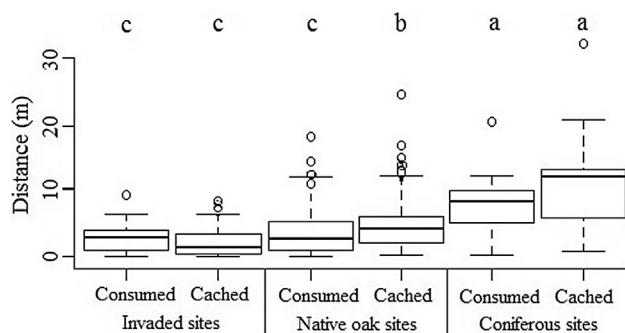
Fig. 2. The distances of acorn removal (± SE) in relation to fate and type of stand of removed seeds.

3.4. Removal distance

Estimated removal distances were significantly longer in the coniferous sites than in two other stand types (*Type of stand* effect in Table 1e; Fig. 2). However, we found no difference between acorns of the two oaks (northern red oak, mean ± SE: 4.46 ± 0.42 m, *N* = 165; pedunculate oak: 5.47 ± 0.38 cm, *N* = 206) or between years (non-significant *Species* and *Year* effects in Table 1e). In addition, acorns found cached appeared to be moved further than acorn found eaten, but this effect was found only at the native oak sites (significant *Type of stand* × *Fate* interaction in Table 1e; Fig. 2).

4. Discussion

Some, but not all aspects of rodent foraging on acorns were habitat-specific. While the probabilities of acorn harvest ('quantity of dispersal' *sensu* Schupp et al., 2010) and acorn consumption were similar across forest types, the forests differed in the recovery of harvested acorns, probability of caching after removal, and dispersal distance (affecting 'quality of dispersal', Schupp et al., 2010). All these differences might influence habitat invasibility.

Fewer acorns were recovered in the coniferous forest than in the native oak and the invaded forest. Even though differences in the probability of acorn recovery do not inform directly about acorn fate, they can hint to unobserved ecological processes. There are several phenomena that can lead to significant differences among habitats in acorn recovery rate. First, such differences can result from differential probability of long-distance acorn dispersal. While acorns in coniferous forest were dispersed further than in the two other forest types, long-distance acorn dispersal is unlikely to be the sole cause of the non-recovery because *Apodemus* mice rarely move seeds further than our 25-m search radius (e.g. Li and Zhang, 2003; Muñoz and Bonal, 2011).

Another process that could contribute to the loss of tracked acorns is larderhoarding, i.e. storing seeds in large caches located in deep burrows (Vander Wall, 1990). *Apodemus* mice are known to use a mixed caching strategy that involves both scatter- and larderhoarding (Jensen, 1985; Lu and Zhang, 2008). Thus, the lower proportion of recovered seeds might suggest more frequent larder-hoarding in coniferous sites in comparison to two other site types, and thus lowered quality of seed dispersal (larderhoarded seeds are usually placed too deep underground to survive: Vander Wall, 1990). However, this negative effect might be counterbalanced by relatively frequent caching in topsoil and the long acorn dispersal distances in coniferous stands.

In contrast to larderhoarding, caching seeds in topsoil usually improves their germination and chances of seedling establishment (Vander Wall, 1990; Zwolak and Crone, 2012; ; Lichti et al., 2017; Bogdziewicz et al., 2018b). Probability that dispersed acorns will be cached rather than left on surface was higher at stands that have not been invaded by red oak, i.e. in the coniferous forest and the native oak forest. This difference might translate into more successful regeneration

of northern red oak in uninvaded relatively to invaded forest: once its acorns reach uninvaded stands, they have a high probability of being cached by mice. We also note that our experimental results agree with observational data indicating that northern red oak seedlings in coniferous forest grow predominantly from rodent caches (Woziwoda et al., 2018).

Finally, acorns were transported furthest in the coniferous forest, intermediate distances at the native oak sites, and the shortest distances at the invaded sites. These differences could potentially influence the rate of invasion: although distances of acorn movement by mice are short when compared to transportation by jays (Pons and Pausas, 2007; Pesendorfer et al., 2016) propagule pressure quickly declines with distance from adult northern red oaks (Major et al., 2013; Jagodziński et al., 2018; Woziwoda et al., 2018). This pattern indicates that most acorn dispersal occurs at a relatively small scale and hints to an important role of rodents in the northern red oak invasion.

Why did seed fate vary among forest types? The most likely reason for these differences are changes in acorn availability, and therefore in their relative value. When food items are valuable, foragers are expected to devote more time and energy in their acquisition and protection; accordingly, scatterhoarders have been found to invest more in seed harvest, transport, and caching when seeds were rare than when seeds were abundant (Shimada, 2001; Schnurr et al, 2002; Lichti et al., 2014). Acorns are rare in uninvaded coniferous forest. They can be found at edges of such stands (Woziwoda et al., 2018) or inside, when they are transported there by Eurasian jays (*Garrulus glandarius*) (even though Eurasian jays prefer to harvest the native over the invasive oak acorns, they transport seeds frequently enough that natural regeneration of *Q. rubra* can occur in forest stands that do not include its adult individuals: Myczko et al., 2014; Bieberich, 2016; Kurek and Dobrowolska, 2016; Jagodziński et al., 2018; Woziwoda et al., 2018). The high relative value of acorns could explain their higher dispersal distances by mice in coniferous forest (seed transportation distance by rodents typically declines with seed availability: Jansen et al., 2004; Moore et al., 2007; Zwolak et al., 2016; but see: Vander Wall, 2002) and increased larderhoarding rates. When seeds are rare, scatterhoarders can afford carrying them into a larder, but when seeds are abundant it is more cost-effective to bury them at the spot (Tsurim and Abramsky, 2004). Similarly, changes in acorn abundance explain differences in the proportion of removed acorns that were cached rather than left on the forest floor. Caching was more frequent when acorn availability was relatively low: in uninvaded compared to invaded sites and in 2017 compared to 2016, probably because rodents had higher motivation to hide acorns when competition for them was more intense (Shimada, 2001; Schnurr et al, 2002; Murray et al., 2006; Lichti et al., 2014, 2017).

Mice preferred to harvest and consume native rather than invasive acorns, probably due to higher tannin concentrations and considerably thicker shells of the northern red oak acorns (Bogdziewicz et al., 2018a), but other decisions (e.g. whether to cache acorns or how far to transport them) were unaffected by acorn species. Moreover, the preference at the harvest and consumption stage (and the lack of preferences at other stages) did not change with forest type. This is in apparent contrast with a recent study that demonstrated indirect effects between pedunculate oaks and northern red oaks: when acorns of both oak species were offered in mixed patches, rodents increased caching of pedunculate oak acorns and reduced caching of the northern red oak acorns (Bogdziewicz et al., 2018c). Thus, we could expect differences in caching between stands where the two oak species co-occur (the invaded sites) and where they do not (the native oak sites). We did not detect such effects, perhaps due to differences in scale: while in Bogdziewicz et al. (2018c) acorns were offered in mixed groups, in our study the seed stations always consisted of one species and we did not control for the abundance and presence of acorns in the nearest vicinity. Thus, even in the invaded forest many of the seed stations could be in areas with conspecific acorns only, concealing potential indirect effects.

As a caveat, many aspects of seed fate demonstrated marked temporal variation, associated probably with changes in acorn production (differences between the high and the low acorn crop years). This finding emphasizes the need for long-term seed dispersal studies, conducted across a range of seed availabilities. However, temporal changes in the quantity and quality of seed dispersal also indicate that invasive species might experience opportunity windows for successful recruitment, associated with periods of increased efficiency of animal-mediated seed dispersal.

5. Conclusions

Relatively to stands with northern red oak, uninvaded stands were characterized by high acorn caching rates (at the native oak sites) and increased dispersal distances (at the coniferous stands). The combination of low acorn caching rates and short dispersal distances at the invaded sites translates into lower quality dispersal, relatively to uninvaded sites. Given that propagule pressure appears to be the main determinant of northern red oak invasion (Major et al., 2013; Jagodziński et al., 2018; Woziwoda et al., 2018), differences in rodent-mediated seed dispersal might contribute to high recruitment rates of the northern red oak at the edges of invaded range. They might also explain observed high susceptibility of Scots pine forest to invasion by red oak observed in former studies (Jagodziński et al., 2018; Woziwoda et al., 2018). This is an important conservation problem in Central Europe, where Scots pine forests cover over 28 million hectares (Lust et al., 2001).

Acknowledgements

Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2018.11.036.

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