

Rola konsumentów nasion i patogenów glebowych
w rekrutacji siewek inwazyjnych gatunków drzew
na przykładzie dębu czerwonego i klonu jesionolistnego

The role of granivores and soil pathogens in seedling
recruitment of invasive tree species:
the case of northern red oak and ash-leaved maple

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PhD Thesis

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1. List of original publications:

My doctoral dissertation consists of four publications listed below:

Wróbel A. 2014. Wpływ gryzoni na regenerację lasu z uwzględnieniem zaburzeń naturalnych i antropogenicznych (Influence of the rodents on forest regeneration considering natural and anthropogenic disturbances). *Sylvan* 158(9):714-720. [IF = 0.691]

Wróbel A., Zwolak R. 2017. Deciphering the effects of disperser assemblages and seed mass on patterns of seed dispersal in a rodent community. *Integrative Zoology* 12(6):457-467. doi: 10.1111/1749-4877.12265. [IF = 2.140]

Wróbel A., Zwolak, R. 2019. Habitat-dependent seed dispersal of an introduced tree species by native rodents. *Forest Ecology and Management* 433:563-568. doi: 10.1016/j.foreco.2018.11.036. [IF = 3.126]

Wróbel A., Crone E. E., Zwolak R. 2019. Differential impacts of soil microbes on native and co-occurring invasive tree species. *Ecosphere* 10(7), e02802. doi: 10.1002/ecs2.2802. [IF = 2.746]

2. Abstract

Biotic interactions are often essential in tree regeneration. In particular, introduced tree species can establish new biotic interactions with native species what, in turn, may affect invasion dynamics. In my dissertation, I examined this notion using tree-rodent and tree-soil microbiota interactions as examples. In particular:

- 1) I reviewed current knowledge about the role of rodents in forest regeneration after disturbance, particularly in temperate managed forest stands. I discussed a dual effect of the rodents on forest regeneration, which includes both mutualistic and antagonistic interactions with tree seeds;
- 2) I examined whether various members of a granivorous rodent community differ in their effectiveness as seed removal agents in northern red oak (*Quercus rubra*) in its native range. I found that granivorous rodents of different body sizes strongly vary in their interactions with acorns (smaller-sized rodent species provided lower quality seed dispersal services when compared with larger ones);
- 3) I described how habitat-related differences in seed dispersal affect susceptibility of distinct habitat types to plant invasions. I examined the fate of invasive northern red oak and native pedunculate oak (*Quercus robur*) acorns dispersed by native rodents in different European forest types. My findings suggest that habitat-dependent patterns in seed dispersal may promote recruitment of northern red oak at the edges of invaded range;
- 4) I tested whether introduced and native tree species are differentially influenced by the Janzen-Connell effect caused by soil-borne organisms. I used congeneric pairs of invasive and native *Quercus* and *Acer* species as a study system. The results indicated that weakened Janzen-Connell effect might contribute to successful invasions of certain non-native trees.

My findings improve general understanding of factors involved in seed dispersal, seedling establishment, and the differential roles that biotic interactions play in the recruitment of native vs. invasive tree species.

3. Streszczenie

Interakcje biotyczne są często kluczowymi czynnikami w rekrutacji nowych pokoleń drzew. Co więcej, interakcje między obcymi gatunkami drzew a rodzimą biocenozą mogą wpływać na dynamikę inwazji. W mojej pracy zbadalam powyższe zagadnienia, wykorzystując za przykłady interakcje między drzewami a gryzoniami i mikroorganizmami glebowymi. W szczególności:

- 1) Dokonałam przeglądu obecnej wiedzy na temat roli gryzoni w odnowieniu lasu po zaburzeniach, w szczególności w lasach gospodarczych klimatu umiarkowanego. Rozpatrzyłam dwojaki wpływ gryzoni, co obejmuje zarówno mutualistyczne, jak i antagonistyczne interakcje z nasionami drzew;
- 2) Przetestowałam, czy poszczególne gatunki gryzoni współwystępujące na danym terenie różnią się w swojej efektywności jako roznosiciele nasion dębu czerwonego (*Quercus rubra*) na jego rodzimym obszarze. Wyniki wykazały, że nasionożerne gryzonie różniące się wielkością ciała mają odmienny wpływ na los żołądzi (mniejsze gatunki gryzoni mniej efektywnie roznosiły nasiona w porównaniu do większych gatunków);
- 3) Przedstawiłam, jak różnice w roznoszeniu nasion wpływają na podatność odmiennych siedlisk na inwazję roślin. Zbadalam los nasion inwazyjnego dębu czerwonego i rodzimego dębu szypułkowego (*Quercus robur*) wynoszonych przez rodzime gatunki gryzoni w różnych typach lasów. Moje wyniki wskazują, że wzorce roznoszenia nasion zależne od rodzaju siedliska mogą sprzyjać odnowieniu dębu czerwonego na granicy jego występowania poza jego naturalnym zasięgiem;
- 4) Sprawdziłam, czy efekt Janzena-Connella spowodowany działalnością mikroorganizmów glebowych odmiennie wpływa na introdukowane i rodzime gatunki drzew. W tym celu wykorzystałam dwie pary gatunków drzew składających się z gatunku inwazyjnego i rodzimego należących do tego samego rodzaju: *Quercus* i *Acer*. Wyniki wykazały, że

osłabiony efekt Janzena-Connella może przyczynić się do postępującej inwazji niektórych introdukowanych gatunków drzew.

Moje wyniki pomogą lepiej zrozumieć czynniki zaangażowane w dyspersję nasion, rozwój siewek i odmienną rolę wybranych interakcji biotycznych w odnowieniu się zarówno rodzimych, jak i introdukowanych gatunków drzew.

4. Introduction

Trees dominate terrestrial ecosystems of Earth and deliver a vast array of ecological goods and services (Pan *et al.* 2013). Therefore, tree recruitment is of major ecological importance. While patterns in tree recruitment have typically been explained by direct effects of the physical environment on plant performance and competition (Koricheva *et al.* 1998; Poorter and Rose 2005; Kiær *et al.* 2013), it is crucial not to overlook the important influence of interspecific interactions. Indeed, the evidence that performance of many tree species is highly dependent on the actions of other organisms is quickly growing (Hawkes and Sullivan 2001; Lekberg and Koide 2005; Barton and Koricheva 2010; Albert *et al.* 2015). Among such organisms, those that can act both as mutualists and antagonists are particularly interesting, as their effects on plant recruitment can drastically change with ecological context (Bronstein 1994, Kiers *et al.* 2010). In my dissertation, I focused on two very different groups of organisms, whose role in plant recruitment can vary along the mutualism-antagonism continuum: granivorous rodents and soil microorganisms.

Granivorous rodents are crucial seed removal agents in many large-seeded plants, including ecologically and economically important taxa, such as Fagaceae species (oaks and beeches) (Perea *et al.* 2011; Bieberich 2016; Zwolak *et al.* 2016; Bogdziewicz 2018) and pines (Vander Wall 2003, 2019; Summers 2011). Rodents have been demonstrated to shape tree species composition by selective seed predation (Ostfeld *et al.* 1997; Ivan and Swihart 2000; García *et al.* 2005). However, removing and burying single seeds into shallow burrows (so called ‘scatter-hoarding’) by rodents is also described as an essential factor in seed germination and seedling establishment (Vander Wall 1990; Wenny 2001; Zwolak *et al.* 2016). This dual effect of rodents on tree regeneration requires conducting research on both the negative and the positive aspects of rodent activity in relation to ecological conditions (i.e. in a context-dependent manner).

Interactions of trees and soil microorganisms (i.e. bacteria and fungi found in soil) are also of intense interest in the context of tree recruitment (Bever 2003; Kulmatiski *et al.* 2008; Schnitzer *et al.* 2011; Comita *et al.* 2014; Bennett *et al.* 2017). Some soil microorganisms have been described as tree mutualists, e.g. enhancing tree fitness through improved assimilation of nutrients (Gyaneshwar *et al.* 2002; Larimer *et al.* 2010; Rashid *et al.* 2016). On the other hand, soil pathogens can affect tree distribution in a manner proposed by the Janzen-Connell hypothesis. This hypothesis states that diversity of plant communities in natural ecosystems is promoted by host-specific enemies that reduce survival of seeds or seedlings in a density- or distance-dependent manner (Janzen 1970; Connell 1971). Thus, seeds or seedlings close to or in areas with high density of conspecific adults suffer higher mortality due to increased activity of soil pathogens (Mills and Bever 1998; Packer and Clay 2000; Yamazaki *et al.* 2008; Reinhart 2012). Although this phenomenon is well described in many tropical tree species, the Janzen-Connell effect driven by soil microorganisms is still understudied in most temperate tree species, especially in Europe (Comita *et al.* 2014).

Determining the mechanisms and effects of both mutualistic and antagonistic relationships is particularly relevant in studies of invasive species. In the introduced range, alien tree species often lose their mutualists and natural enemies, yet find new species to interact with. For example, an introduced tree species may face a new guild of seed dispersers with food-hoarding tactics different than those in native range (Myczko *et al.* 2014; Bogdziewicz *et al.* 2018). Moreover, seed removal, seed predation or caching intensity may differ between co-occurring alien and congeneric native tree species (Blaney and Kotanen 2001; Myczko *et al.* 2014; Bogdziewicz *et al.* 2018). However, such comparisons in nut-bearing trees are rare, especially across habitats. Moreover, although the Janzen-Connell hypothesis constitutes one of the most widely accepted mechanisms of maintaining forest diversity and determining plant distribution, it does not make clear predictions concerning alien species. One of the generalities

that emerge from current research on invasive plants is that plants in their non-native ranges tend to be facilitated by soil biota, while native plant species tend to be negatively affected by the accumulation of host-specific soil pathogens (e.g., Reinhart and Callaway 2004; Agrawal *et al.* 2005; Gundale *et al.* 2014; Bardgett and van der Putten 2014). This leads to a conclusion that lack of specialized pathogens may help alien species to invade new areas more effectively. Such phenomenon is well described especially in black cherry (*Prunus serotina*) invading Europe (Reinhart *et al.* 2003, 2010, 2011), but comprehensive studies on other invasive tree species are lacking (see Reinhart and Callaway 2004 for a rare exception).

I addressed these gaps in current knowledge by designing a research project on tree-rodent and tree-microbe interactions in congeneric, native and non-native tree species: pedunculate oak (*Quercus robur*) and northern red oak (*Q. rubra*) as well as Norway maple (*Acer platanoides*) and ash-leaved maple (= boxelder, *A. negundo*). The specific aim of my project was to determine how tree regeneration may be affected by (1) rodents, in relation to habitat disturbance (a literature review), (2) granivorous rodents in native or non-native oaks, and (3) soil microbes in northern red oak and ash-leaved maple in their non-native range. My dissertation consists of four published articles (called below ‘chapters’): one review and three research papers.

In chapter 5.1. (“Influence of the rodents on forest regeneration considering natural and anthropogenic disturbances”), I reviewed the current knowledge on the role of rodents in forest regeneration after disturbance, particularly in temperate managed stands (Wróbel 2014). I discussed a dual effect of the rodents on forest regeneration which includes both negative (seed and seedlings consumption) and positive (seed dispersal) aspects. I also demonstrated that the positive impact of rodents can be enhanced while negative minimized through proper management, such as providing appropriate microhabitats for seed caching, or maintaining continuity of forest stands.

In chapter 5.2 (“Deciphering the effects of disperser assemblages and seed mass on patterns of seed dispersal in a rodent community”), I examined whether members of a granivorous rodent community consisting of species of different body size vary in their effectiveness as seed removal agents in northern red oak, and how this relationship may be altered by seed size (Wróbel and Zwolak 2017). The study was conducted in Harvard Forest in Massachusetts, USA, where northern red oak constitutes a native species. Contrasting proportions of either predated or cached seeds revealed that granivorous rodents of different body sizes may strongly differ in their interactions with northern red oak acorns in its native range and vary in their potential influence on recruitment of this tree species.

In chapter 5.3 (“Habitat-dependent seed dispersal of an introduced tree species by native rodents”), I described how habitat-related differences in seed dispersal could affect susceptibility of distinct habitat types to plant invasions (Wróbel and Zwolak 2019). This study was conducted in Poland. I examined the fate of acorns of invasive northern red oak and native pedunculate oak dispersed by yellow-necked mice (*Apodemus flavicollis*) in three different forest types that are widespread in Central Europe. I found that fate of experimental seeds differed between species as well as forest types. My findings also suggest that differences in rodent-mediated seed dispersal may promote recruitment of northern red oak at the edges of invaded range.

In the chapter 5.4 (“Differential impacts of soil microbes on native and co-occurring invasive tree species”), I tested whether native and invasive tree species may be influenced by the Janzen-Connell effect caused by soil-borne organisms (Wróbel *et al.* 2019). I used congeneric pairs of invasive and native tree species in Europe: ash-leaved maple vs. Norway maple (*Acer platanoides*), and northern red oak vs. pedunculate oak. My findings indicated that weakened Janzen-Connell effect generated by soil microorganisms might contribute to successful invasions of certain non-native plant species.

In summary, I investigated various aspects of both mutualistic and antagonistic tree-rodent and tree-microorganism interactions. I used a comprehensive, experimental approach to demonstrate that granivorous rodents and soil microbes play an essential role in seed dispersal, seedling distribution, and recruitment success of the studied tree species. My results also suggest that biological invasions may be intensified by establishing new mutualistic interactions between alien trees and native seed dispersers on the one hand, and escaping natural enemies such as soil pathogens on the other. These findings will improve general understanding of tree recruitment, in particular in the context of interactions between invaders and indigenous communities. I hope that better understanding of mechanisms of tree invasions will help to protect native ecosystems from alien species, improve forest management and contribute towards preserving forest ecosystems for future generations.

The part of my research on the role of granivorous rodents in northern red oak dispersal in the US (Wróbel and Zwolak 2017; Chapter 5.2 of this dissertation) was financially supported by the (Polish) National Science Centre grant Harmonia 2014/15/B/NZ8/00213 awarded to Rafał Zwolak. The research on habitat-dependent red oak acorn dispersal (Wróbel and Zwolak 2019; Chapter 5.3) and on the Janzen-Connell effect in native and invasive *Quercus* and *Acer* species (Wróbel *et al.* 2019; Chapter 5.4) was financially supported by the grant Preludium 2015/17/N/NZ9/00946 from the National Science Centre, Poland, awarded to Aleksandra Wróbel.

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5. Doctoral dissertation

Below are given the full texts of publications included in my dissertation.

5.1. Wpływ gryzoni na regenerację lasu z uwzględnieniem zaburzeń naturalnych i antropogenicznych

(Influence of the rodents on forest regeneration considering natural and anthropogenic disturbances)

Aleksandra Wróbel

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Wpływ gryzoni na regenerację lasu z uwzględnieniem zaburzeń naturalnych i antropogenicznych

Influence of the rodents on forest regeneration considering natural and anthropogenic disturbances

ABSTRACT

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The role of the rodents in forest regeneration includes both negative (seed and seedlings consumption) and positive (seed dispersal) aspects. The objective of this paper is to review the knowledge of this dual effect of the rodents on forest regeneration after disturbance, particularly in temperate managed forest stands. Many studies have demonstrated that consumption of seeds and seedlings by rodents can substantially inhibit regeneration of forest stands after disturbance. Small mammal predation on oak, pine and European beech seeds and seedlings contributes to reduced forest regeneration after tree harvest and natural disturbances such as fires. On the other hand, some rodent species may promote seed dispersal towards deforested areas. Moreover, they frequently prefer nesting and caching of acorns near structures providing shelter. Such structures are abundant in disturbed areas and appear to promote higher survival of cached seeds. Furthermore, there are certain techniques of seed and seedling protection against small mammals, e.g., planting seeds in the soil, using polyethylene tubes to raise seedlings, or providing alternative food for rodents. The positive impact of the rodents can be enhanced and negative minimized through proper management, such as providing appropriate microhabitats for seed caching, or maintaining continuity of canopy cover/forest stands.

KEY WORDS

anthropogenic disturbances, forest management, forest regeneration, natural disturbances, rodents

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Wstęp

Zaburzenia w ekosystemach leśnych są powszechnie występującym zjawiskiem [Dobrowolska 2010]. Definiuje się je jako proces usuwający lub niszczący biomasę [Grime 1979]. Z kolei Szwagrzyk [2000] określił zaburzenia jako „zwykle jednorazowe działanie czynnika zewnętrznego prowadzące do zniszczenia struktury ekosystemu, zbiorowiska lub populacji, a także do znacznej zmiany w dostępności zasobów bądź do znacznej zmiany parametrów fizycznych środowiska”. Ze względu na sposób powstawania dzielimy zaburzenia na naturalne i antropogeniczne [Dobrowolska 2010]. Do zaburzeń naturalnych w ekosystemach leśnych możemy zaliczyć m.in. wiatrolomy, pożary i gradacje owadów, zaś do antropogenicznych przede wszystkim rębnie [Dobrowolska 2010]. W większości lasów strefy umiarkowanej zaburzenia antropogeniczne mają obecnie większe znaczenie niż naturalne [Bogdziewicz, Zwolak 2014]. W nowoczesnym leśnictwie coraz bardziej popularne staje się pozostawianie danej powierzchni po zaburzeniu działaniu spontanicz-

nych procesów regeneracyjnych [Dobrowolska 2007, 2010]. Powstawanie nowych pokoleń wielu gatunków drzew, szczególnie tych z dużymi nasionami, zależy często od aktywności zwierząt. Dobrze poznana jest rola nasionożernych ptaków, w tym sójki zwyczajnej (*Garrulus glandarius*) i innych krukowatych, w dyspersji nasion oraz ich pozytywny wpływ na rozwój lasu [Darley-Hill, Johnson 1981; Mosandl, Kleinert 1998]. Małe ssaki były do niedawna rozpatrywane przede wszystkim jako konsumenci nasion i siewek, ostatecznie ograniczający rozwój roślin. Obecnie bada się także ich pozytywną rolę w dyspersji i lokowaniu nasion w odpowiednich do wykiełkowania siedliskach [Jensen 1985; Vander Wall 1990, 2001]. Niejasny jest jeszcze wpływ gryzoni na regenerację lasu na powierzchniach po zaburzeniach naturalnych i antropogenicznych w strefie klimatu umiarkowanego, a badania stosowane publikowane w czasopiśmie leśnych skupiają się niemal wyłącznie na negatywnej roli gryzoni jako konsumentów nasion i siewek [Kerr 2000; Birkedal i in. 2009; Huggard, Arsenault 2009].

Celem niniejszej pracy jest usystematyzowanie wiedzy na temat pozytywnego i negatywnego wpływu tej grupy zwierząt na odnowienie lasu po zaburzeniach, ze szczególnym uwzględnieniem użytkowanych gospodarczo lasów strefy umiarkowanej.

Rola gryzoni w regeneracji ekosystemu leśnego

Wpływ zespołów gryzoni na powstawanie nowych pokoleń drzew jest niezaprzeczalny [Vander Wall 1990, 2001]. Gryzonie uważane są za najważniejszych konsumentów nasion w lasach strefy umiarkowanej. Poprzez selektywne żerowanie mogą one decydować o składzie gatunkowym drzewostanu [Ostfeld i in. 1997; Ivan, Swihart 2000; García i in. 2005]. Z drugiej strony małe ssaki znane są z tworzenia spiżarni i zakopywania nasion w ściółce [Vander Wall 1990, 2001]. W ten sposób odgrywają często kluczową rolę w lokowaniu diaspor w mikrosiedliskach odpowiednich do ich wykiełkowania [Jensen 1985; Vander Wall 1990; Wenny 2001]. Niemniej ostateczny wynik interakcji drzewa-gryzonie zależy od wielu czynników środowiskowych, m.in. występowania lat nasiennych (u wielu gatunków drzew) [Jensen 1985; Bogdziewicz, Wróbel 2012], obecności gatunków konkurujących z nimi o pokarm, np. ssaków kopytnych [Muñoz, Bonal 2007], czy występowania efektu krawędzi [Takahashi i in. 2006, 2007]. Ponadto gryzonie w niejednakowy sposób preferują nasiona i siewki poszczególnych gatunków drzew i krzewów [Jensen 1985; Borowski 2007]. Zwykle wybierają gatunki bardziej obfitujące w składniki odżywcze – w naszym klimacie będą to dęby (*Quercus* sp.), klony (*Acer* sp.), leszczyna pospolita (*Corylus avellana*) i buk zwyczajny (*Fagus sylvatica*), a w dużo mniejszym stopniu sosna zwyczajna (*Pinus sylvestris*) i świerk pospolity (*Picea abies*) [Jensen 1985; Borowski 2007]. Wszystkie te czynniki mogą wpływać na decyzje gryzoni względem nasion (selekcja gatunkowa, konsumpcja, zakopywanie), co ostatecznie może oddziaływać na regenerację lasu.

Wpływ gryzoni na regenerację lasu po zaburzeniach

Powierzchnie po zaburzeniach dostarczają dodatkowych mikrosiedlisk, chętnie wykorzystywanych przez gryzonie do żerowania i gniazdowania: mogą to być powalone drzewa, kupy chrustu, szybko rozwijające się kępy traw itp. [Takahashi i in. 2006, 2007]. Niektóre gatunki, np. mysz leśna (*Apodemus flavicollis*) i norniki (*Microtus* sp.), często nawet zwiększają swoją liczebność po zaburzeniach, właśnie ze względu na powstanie korzystnych siedlisk, które stanowią dla nich ważne refugia przed presją drapieżniczą [Bogdziewicz, Zwolak 2014].

Na terenach po zaburzeniu odnawiający się drzewostan zwykle cechuje się składem gatunkowym sprzed wystąpienia zaburzenia [Dobrowolska 2007]. Niekoniecznie więc muszą pojawiać się jako pierwsze gatunki powszechnie uważane za pionierskie, tj. brzozy (*Betula* sp.) bądź sosny

(*Pinus* sp.) [Dobrowolska 2007]. Wcześniej mogą się odnowić np. dęby i buk zwyczajny [Dobrowolska 2007], u których dyspersja i przeżywalność nasion są w dużym stopniu zależne od gryzoni [Jensen 1985].

Fragmentacja lasu, która jest częstym efektem zarówno zaburzeń naturalnych, jak i antropogenicznych, może negatywnie wpływać na przeżywalność nasion wykorzystywanych przez gryzonia [Santos, Tellería 1997]. Badania prowadzone na dębie ostrolistnym w centralnej Hiszpanii (*Quercus ilex*) wskazują, że im mniejsza powierzchnia drzewostanu, tym konsumpcja żołądździ jest intensywniejsza (nawet ponad trzydziestokrotnie) [Tellería i in. 1991; Santos, Tellería 1997]. Jest to głównie spowodowane dużo wyższą liczebnością gryzoni w mniejszych fragmentach lasu. Niemniej gryzonia mogą ograniczać rozmnażanie płciowe dębu, nie wpływając na rozwój ramet [Santos, Tellería 1997]. Efekt ten może być szczególnie negatywny dla gatunków rozmnażających się przede wszystkim lub wyłącznie za pomocą nasion.

Dla regeneracji lasu nie bez znaczenia może być rodzaj drzewostanu, jaki otacza płat po zaburzeniu. Nasiona mogą osiągać wyższą przeżywalność, znajdując się na terenie przylegającym do lasu mieszanego aniżeli liściastego [Birkedal i in. 2009]. Może to być spowodowane preferencjami siedliskowymi gryzoni względem lasu liściastego, co przyczynia się do ich zwiększonej liczebności, a tym samym zwiększonej konsumpcji diaspor [Birkedal i in. 2009]. W ten sposób również cykliczne, gwałtowne wzrosty liczebności gryzoni mogą negatywnie oddziaływać na przeżywalność nasion [Pucek i in. 1993].

Działalność gryzoni jest postrzegana jako problem zwłaszcza przy wysiewaniu nasion drzew na terenach zrębów. Badania w Danii i Szwecji wykazały, że mysz leśna, normica ruda (*Myodes glareolus*) i mysz zaroślowa (*Apodemus sylvaticus*) mają silnie negatywny wpływ na sztucznie zasiane żołądździe i bukiew [Birkedal i in. 2009]. Niemalże wszystkie nasiona zostały odnalezione i wykorzystane przez gryzonia, w wyniku czego wykiełkowało tylko niewielka liczba siewek [Birkedal i in. 2009].

Myszaki leśne (*Peromyscus maniculatus*) mogły przyczynić się do ograniczonej regeneracji lasu iglastego po pożarze w stanie Montana w Stanach Zjednoczonych [Zwolak i in. 2010]. W miejscach wystąpienia naturalnego pożaru zwykle tworzą się warunki odpowiednie do rozwoju nowych pokoleń sosny żółtej (*Pinus ponderosa*) i diaglezji zielonej (*Pseudotsuga menziesii*) [Agee 1993; Zwolak i in. 2010], jednak na obszarach spalonych przeżywalność nasion wykorzystywanych przez gryzonia jest drastycznie niższa niż na nietkniętych żywiołem [Zwolak i in. 2010]. Myszaki mogą odgrywać tutaj przede wszystkim rolę konsumentów nasion, a nie przyczyniać się do ich dyspersji. Z kolei sosna alepska (*Pinus halepensis*) w Hiszpanii jest mniej narażona na konsumpcję przez myszy (*Apodemus* spp.) na obszarach popożarowych, a ich wykluczenie przyczyniło się jedynie do niewielkiego wzrostu przeżywalności siewek [Broncano i in. 2008]. W stanie Kalifornia w Stanach Zjednoczonych działalność szczuroskoczka (*Dipodomys agilis*), szczuroskoczka kalifornijskiego (*Chaetodipus californicus*) i myszaka leśnego pozytywnie wpływają na dyspersję nasion sosny Coultera (*Pinus coulteri*), choć niekoniecznie na ich dalszy rozwój [Borchert i in. 2003]. Co najmniej 23% ukrytych przez małe ssaki nasion ma szansę na wykiełkowanie [Borchert i in. 2003], jednak prawdopodobnie nie rekompensuje to strat poniesionych przez roślinę w ramach konsumpcji nasion [Zwolak, Crone 2012]. Nasiona sosny Coultera są w niewielkim stopniu przenoszone przez wiatr, więc gryzonia odgrywają tu istotną rolę. Zatem charakter wpływu gryzoni na regenerację lasu po pożarze w dużym stopniu zależy od położenia geograficznego terenu.

Poszczególne gatunki gryzoni występujące na tym samym terenie mogą mieć odmienne oddziaływanie na rośliny. Norniki pensylwańskie (*Microtus pennsylvanicus*) mogą mieć silnie

ograniczający wpływ na rozwój siewek drzew pojawiających się na granicy las-łąka poprzez ich zgryzanie [Ostfeld i in. 1997]. Z drugiej strony pośrednio wywierają pozytywny wpływ na rośliny w fazie nasion, wygrywając konkurencję z myszakami białostopymi (*Peromyscus leucopus*) i zmniejszając liczebność ich populacji [Grant 1972]. W ten sposób bowiem minimalizują działalność myszaków znanych z intensywnej konsumpcji nasion [Ostfeld i in. 1997]. Oba gatunki mogą znacząco spowalniać zalesianie się terenów otwartych, szczególnie jeśli występują w dużych liczebnościach.

Szacuje się, że tylko w 3% polskich nadleśnictw gryzonie, przede wszystkim nornik bury (*Microtus agrestis*), wyrządzają poważniejsze szkody ekonomiczne [Borowski 2007]. Większość z tych nadleśnictw znajduje się w Sudetach, gdzie w latach 70. XX wieku miała miejsce katastrofa ekologiczna spowodowana opadem kwaśnych deszczy [Borowski 2007], stąd straty spowodowane działalnością gryzoni mogą być bardziej wyraźne niż w przeciętnych warunkach. Dodatkowo straty ekonomiczne w leśnictwie spowodowane działalnością gryzoni są w dużym stopniu związane z porami roku. Szacuje się, że w Europie około 70% szkód jest wyrządzanych zimą, zaś latem i jesienią – po około 15%. Wiosną gryzonie zwykle nie powodują strat [Borowski 2007].

Małe ssaki mogą także odgrywać pozytywną rolę w regeneracji lasu po zaburzeniach. Przykładowo żołędzie dębu kasztanolistnego (*Quercus serrata*) znajdujące się na granicy między zrębem zupełnym a lasem liściastym z dębem jako dominującym gatunkiem były intensywniej wynoszone przez myszy (*Apodemus speciosus* i *A. argenteus*) w kierunku otwartej przestrzeni aniżeli lasu [Takahashi i in. 2006]. W latach nasiennych przeżywalność żołędzi była dużo wyższa niż w nienasiennych. Podobne rezultaty uzyskano w wyniku badań trzech innych gatunków drzew i krzewów: kasztana japońskiego (*Castanea crenata*), dębu mongolskiego (*Quercus mongolica*) i orzecha mandżurskiego (*Juglans mandshurica*) [Takahashi i in. 2007]. Zatem gryzonie, kosztem dużej konsumpcji nasion, mogą przyczyniać się do dyspersji nasion w kierunku terenów wylesionych. Siewki wielu gatunków drzew lepiej się rozwijają w płatach powstałych po zaburzeniu aniżeli pod koroną drzew [Gray, Spies 1996]. Co więcej, myszy preferują ukrywanie żołędzi i gniazdowanie w pobliżu chrustu, pni, kłód i powalonych drzew, które występują obficie na powierzchniach po zaburzeniach i gdzie nasiona wykazują większą przeżywalność [Takahashi i in. 2006, 2007]. Biorąc pod uwagę kierunek dyspersji nasion, można więc dojść do wniosku, że gryzonie mogą pozytywnie wpływać na naturalną regenerację lasu na rębniach, szczególnie w roku o dużej podaży nasion. Jednak intensywna dyspersja niekoniecznie rekompensuje straty poniesione przez konsumpcję nasion [Zwolak, Crone 2012].

Sposoby ochrony nasion i siewek przed działalnością gryzoni

Regeneracja drzewostanu ma związek z losem nowych pokoleń drzew w pierwszym roku od zasiewu [Madsen, Löf 2005]. Na jej powodzenie wywiera też duży wpływ pora roku. Drzewa sztucznie zasiane wiosną mają większą szansę na dalszy rozwój aniżeli zasiane jesienią [Madsen, Löf 2005]. Wynika to prawdopodobnie z dostępności dla gryzoni innego rodzaju pokarmu. Dodatkowo coraz częściej odchodzi się od tworzenia monokultur na rzecz lasów mieszanych [Stanturf, Madsen 2002; Madsen, Löf 2005], co, biorąc pod uwagę selektywność pokarmową gryzoni [Jensen 1985; Borowski 2007], może zmniejszać ich presję na dany gatunek drzewa. Rozwijane są też metody ochrony nasion i siewek przed działalnością małych ssaków [Madsen, Löf 2005]. Możemy do nich zaliczyć m.in. wkopywanie nasion w ściółkę na głębokość kilku centymetrów czy stosowanie specjalnych biodegradowalnych polietylenowych rurek ochraniających nasiona [Nilsson i in. 1996; Madsen, Löf 2005]. Metody te nie gwarantują pełnej ochrony, choć na pewno zwiększają szansę rozwoju zasianych drzew. Innym sposobem na zmniejszenie

presji gryzoni na drzewa w początkowych stadiach (nasiona – kiełkowanie – siewka) jest dostarczanie zwierzętom alternatywnego pokarmu [Sullivan, Sullivan 2004]. W ten sposób można zwiększyć przeżywalność siewek aż o 20-25% w przypadku gryzoni o szerokim spektrum pokarmowym, np. norników i nornic [Sullivan, Sullivan 2004] i niektórych gatunków typowo nasionożernych, np. wiewiórek *Tamiasciurus hudsonicus* i *Spermophilus columbianus* [Sullivan, Klenner 1993]. Metoda ta bywa jednak nieskuteczna w przypadku zespołów gryzoni posiadających różne preferencje pokarmowe, np. żyjących na jednym terenie myszaków, norników i myszy *Reithrodontomys megalotis* [Sullivan, Sullivan 2004]. W walce z gryzoniami nieskuteczne okazało się ich usuwanie z danego obszaru [Sullivan 1979]. Małe ssaki są bowiem zdolne do szybkiej rekolonizacji z sąsiadujących terenów, więc wyeliminowane osobniki są szybko zastępowane nowymi [Halle 1993].

Podsumowanie

Wpływ gryzoni na regenerację lasu jest wciąż niejasny i trudny do przewidzenia ze względu na złożoność ekosystemów i aktualnego kontekstu ekologicznego. W naturalnych warunkach rola małych ssaków jako roznosicieli nasion może być kluczowa dla rozwoju wielu gatunków roślin [Vander Wall 1990, 2001]. Wydaje się jednak, że z ekonomicznego punktu widzenia gryzonie jako konsumenci nasion i siewek mogą zasadniczo spowalniać regenerację drzewostanu po zaburzeniu [Takahashi i in. 2006, 2007; Birkedal i in. 2009; Zwolak i in. 2010]. Pozytywne oddziaływanie małych ssaków może zostać wzmocnione, m.in. poprzez zapewnienie odpowiednich mikrosiedlisk do lokowania nasion (kupy chrustu, powalone drzewa, kłody, pnie itp.). Z kolei przy sztucznym wspomaganiu regeneracji negatywne oddziaływanie gryzoni może zostać zminimalizowane, m.in. poprzez (1) zachowanie spójności drzewostanów, (2) tworzenie nasadzeń i zasiewów wówczas, gdy przewidywana liczebność gryzoni jest niewielka (np. wiosną, a nie jesienią), (3) uwzględnianie rodzaju drzewostanu otaczającego płat przyszłej rębni, (4) unikanie tworzenia monokultur na wylesionych powierzchniach, z uwzględnieniem preferencji pokarmowych danych gatunków gryzoni oraz (5) stosowanie technik chroniących nasiona i siewki przed gryzoniami.

W pracach leśnych coraz częściej zwraca się uwagę na odnowienie naturalne drzewostanu, w którym gryzonie odgrywają niewątpliwie ważną rolę [Dobrowolska 2010]. Dotychczas zanotowane obserwacje spontanicznych odnowień w Polsce, m.in. w lesie ochronnym „Szast” w Puszczy Piskiej, wskazują na możliwość uzyskania zadowalających efektów naturalnej regeneracji różnych gatunków drzew na powierzchniach pozbawionych lasu w wyniku zaburzenia [Dobrowolska 2007, 2010]. Do wyciągnięcia dokładniejszych wniosków niezbędna jest większa liczba badań w tym zakresie, głównie ze względu na złożoność układów ekologicznych. Należy pamiętać, że presja ze strony gryzoni jest tylko jednym z całego szeregu czynników wpływających na rozwój drzewostanu, do których należą m.in. typ gleby i nawodnienie oraz presja na rośliny ze strony ssaków kopytnych.

Podziękowania

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SUMMARY

Influence of the rodents on forest regeneration considering natural and anthropogenic disturbances

Disturbances, both natural (e.g., windthrow or fires) and anthropogenic (e.g., timber harvest), are a commonly occurring phenomenon in forest ecosystems. Research on the role of rodents in forest regeneration after disturbances used to be focused primarily on seed and seedling consumption, and their influence was recognized as clearly negative. Recently, there is an increase in studies on the positive role of caching and dispersal of tree seeds by small mammals. The objective of this paper is to review the knowledge about the positive and negative impacts of rodents on forest regeneration after disturbance, particularly in temperate managed forest stands.

Many studies demonstrated that consumption of seeds and seedlings by rodents can substantially inhibit regeneration of forest stands after disturbance. In Europe, the yellow-necked mouse (*Apodemus flavicollis*), the bank vole (*Myodes glareolus*), and the wood mouse (*A. sylvaticus*) are able to consume almost all planted acorns and beech seeds. In North America, seed predation by the deer mouse (*Peromyscus maniculatus*) may contribute to reduced regeneration of coniferous forest after fire. The Pennsylvania voles (*Microtus pennsylvanicus*) limit succession by grazing seedlings that emerge on the border of forest and old fields. The old field succession is also hindered by intensive consumption of tree seeds by the white-footed mouse (*P. leucopus*).

On the other hand, some rodent species may contribute to seed dispersal towards deforested areas. For example, on the border of a clear-cut and a deciduous forest, the Konara oak (*Quercus serrata*), the Mongolian oak (*Q. mongolica*), the Japanese chestnut (*Castanea crenata*), and the Manchurian walnut (*Juglans mandshurica*) are intensively dispersed by mice (*A. speciosus* and *A. argenteus*) towards open spaces rather than into the forest. Moreover, rodents frequently prefer nesting and caching of acorns near structures providing shelter. Such structures are abundant in disturbed areas and appear to promote higher survival of cached seeds. Furthermore, there are certain methods of seed and seedling protection against small mammals, e.g., planting seeds in the soil to a depth of a few centimeters, the use of biodegradable polyethylene tubes, or providing alternative food for rodents.

The positive impact of small mammals can be enhanced through actions such as providing proper microhabitats for seed caching. In turn, the negative impact of rodents can be minimized by: (1) maintaining continuity of forest stands/canopy cover, (2) planting seedlings and sowing seeds when rodent abundances are low, (3) taking into consideration types of stands that surround proposed harvest units, (4) avoiding planting monocultures on deforested areas and (5) using of techniques of the seed and seedling protection against small mammals. However, it is important to note that rodents constitute only one of many factors that influence forest regeneration.

5.2. Deciphering the effects of disperser assemblages and seed mass on patterns of seed dispersal in a rodent community

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ORIGINAL ARTICLE

Deciphering the effects of disperser assemblages and seed mass on patterns of seed dispersal in a rodent community

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Abstract

The sizes of both seed dispersers and seeds are traits that are likely to interact to influence seed fate in many synzoochoric plant species. Here, we examined whether members of a granivorous rodent community consisting of species of different body size vary in their effectiveness as seed dispersers, and how this relationship may be altered by seed size. We marked northern red oak (*Quercus rubra*) acorns with plastic tags and placed them in size-selective rodent exclosures. The exclosures allowed differential access of rodent groups based on different body size: (i) small (e.g. *Peromyscus* spp.); (ii) small and medium (e.g. *Tamias striatus*); and (iii) small, medium and large (e.g. *Sciurus carolinensis*) species of rodents. Acorn removal did not differ among exclosure types, but more seeds were missing when removed by small rodents, probably because of larderhoarding. The treatments did not influence the relative frequency of acorn consumption. However, small rodents cached considerably fewer and partially ate more acorns than the other 2 groups. The mean dispersal distance was the longest for cages with medium openings, intermediate for cages with large openings and the shortest for cages with small openings. Acorn mass positively affected the probability of caching and this relationship was unaffected by exclosure type. In conclusion, granivorous rodents of different body sizes strongly differed in their interactions with acorns, with small rodents acting primarily as acorn predators and medium and large species contributing significantly more to dispersal of red oaks.

Key words: acorn dispersal, initial seed fate, plant–animal interactions, rodent community, scatterhoarding

INTRODUCTION

Most zoochoric plants rely on multiple species of seed dispersers (Vander Wall 1990; Schupp & Fuentes 1995; Cheng *et al.* 2005; Forget *et al.* 2005; Beck & Vander Wall 2010). However, animal species often use seeds differently with respect to quantity (i.e. number of seeds dispersed) and quality (e.g. relative proportion of seeds cached) (Schupp 1993; Hollander & Vander Wall

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2004; Bellocq *et al.* 2005; Cheng *et al.* 2005; Muñoz & Bonal 2008; Beck & Vander Wall 2010; Galetti *et al.* 2013; Pesendorfer & Koeing 2016; Pesendorfer *et al.* 2016). Both of these factors affect seed dispersal effectiveness (*sensu* Schupp *et al.* 2010). Such interspecific differences between seed dispersers in response to various seed characteristics often result in dramatically different patterns of seed dispersal. For example, frugivores often have species-specific seed deposition sites, which might promote or hinder seed survival and reproduction (Wenny 2001; Jordano *et al.* 2007), and individuals of some granivore species scatterhoard single seeds in shallow caches, while other dispersers larderhoard seeds too deep for successful germination (Lu & Zhang 2008; Beck & Vander Wall 2010; Pesendorfer & Koeing 2016). In addition, different species of granivores vary in the proportion of seeds cached versus consumed (Hollander & Vander Wall 2004; Cheng *et al.* 2005). In the case of scatterhoarders, these variable responses often determine whether their interaction with plants is mutualistic or antagonistic (Theimer 2005; Jorge & Howe 2009; Zwolak & Crone 2012).

Among granivorous rodents, body size is a key functional trait that affects seed dispersal (e.g. Díaz 1994; Muñoz & Bonal 2008; Yi & Wang 2015). As a general rule, larger species are able to remove larger seeds and use a wider spectrum of seed sizes than smaller species (Díaz 1994; Westcott & Graham 2000; Jordano *et al.* 2007; Galetti *et al.* 2008; Muñoz & Bonal 2008). Moreover, larger species usually have greater home ranges and transport seeds greater distances than smaller species (Fragoso 1997; Sun *et al.* 1997; Jansen *et al.* 2004, 2012; Spiegel & Nathan 2007; Muñoz & Bonal 2008; Galetti *et al.* 2008, 2013). Thus, body size of seed dispersers is often correlated with dispersal effectiveness (Spiegel & Nathan 2007; Galetti *et al.* 2013).

In addition, seed size often determines seed fate in rodent-dispersed plant species. In both intraspecific and interspecific comparisons, larger seeds are often cached more frequently (Jansen *et al.* 2002, 2004; Vander Wall 2003; Xiao *et al.* 2004; Zhang *et al.* 2008; Wang *et al.* 2014), and dispersed farther than smaller seeds (Jansen *et al.* 2002; Xiao *et al.* 2004; Steele *et al.* 2015; Yi & Wang 2015). However, the opposite has also been observed (Brewer 2001; Moles *et al.* 2003). The probability that seeds will be removed may decrease when the ratio of seed size to rodent size is too high and transporting seeds becomes too costly for the disperser (Muñoz & Bonal 2008; Galetti *et al.* 2013). Moreover, the impact of seed size on effectiveness of dispersal might

change with dispersal stage. For example, larger acorns of Liaodong oaks (*Quercus liaotungensis*) were harvested more frequently and dispersed farther by rodents, but had lower survival after caching in comparison to smaller acorns (e.g. Zhang *et al.* 2008). Thus, although researchers agree that disperser decisions often constitute a selective force in shaping seed size (Gómez 2004; Xiao *et al.* 2004; Galetti *et al.* 2013; Wang *et al.* 2013; Yi & Wang 2015), the relationship between seed mass and dispersal efficiency of granivores remains unclear.

The link between seed mass and dispersal efficiency becomes even more complex when a plant is dispersed by a guild of seed consumers. Thus, it can be argued that understanding these interactions requires a community-level perspective rather than focusing on the effectiveness of a single dispersal agent (Strauss & Irwin 2004).

We examined how rodents of various body size influence seed dispersal of the northern red oak (*Quercus rubra*) by presenting acorns to rodents inside size-selective rodent enclosures. We hypothesized that dispersal quantity (the number of removed acorns) will be highest when all members of the granivore rodent community have access to acorns, but larger species will provide higher quality of dispersal (measured here as the proportion of cached acorns). Small and medium-sized dispersers of the northern red oak (mice [*Peromyscus* spp.] and eastern chipmunks [*Tamias striatus* Linnaeus, 1758]) are thought to consume or larderhoard acorns, whereas larger rodents, such as eastern grey squirrels (*Sciurus carolinensis* Gmelin, 1788), are known as avid scatterhoarders (Hadj-Chikh *et al.* 1996; Steele *et al.* 1996). Furthermore, we expected that larger species would disperse seeds at greater distances than smaller species. This prediction is based on the general relationship between body mass, home range and distances traveled in mammals (Lindstedt *et al.* 1986). Finally, we expected that all species will preferentially choose larger acorns for caching and smaller acorns for consumption based on the evidence from numerous studies on seed dispersal by rodents (Jansen *et al.* 2004; Moore *et al.* 2007; Steele *et al.* 2014) as well as the optimality prediction that caching requires effort that should be reserved for the most profitable food items (Gerber *et al.* 2004; Wang *et al.* 2014).

MATERIALS AND METHODS

Study site and rodent species

The study was conducted in Harvard Forest, located in the town of Petersham in north-central Massachusetts, USA (42.5°N, 72°W). This region is characterized by a cool, moist temperate climate. The average air temperature is 20 °C in July and −7 °C in January. The annual precipitation averages 1100 mm, and is distributed fairly evenly throughout the year.

Four experimental sites, 1–9 km apart, were established in transition hardwood forests dominated by northern red oak and red maple (*Acer rubrum*). The ground flora and the understory layer were poorly developed at our stands. In 2014, the acorn crop at Harvard Forest was characterized by a moderate crop of northern red oak acorns, with 3.4 ± 1.2 (mean \pm SE) acorns per m² (unpublished data).

At our study sites, there are at least 5 rodent species that consume acorns: mice from genus *Peromyscus* (white-footed mice [*P. leucopus* Rafinesque, 1818], deer mice [*P. maniculatus* Wagner, 1845], or both: these species were not distinguished in this study), red-backed voles (*Myodes gapperi* Vigors, 1830), eastern chipmunks (*Tamias striatus* Linnaeus, 1758), southern flying squirrels (*Glaucomys volans* Linnaeus, 1758) and eastern grey squirrels (*Sciurus carolinensis* Gmelin, 1788). These rodents differ widely in body size and mass: deer mouse weighs from 10 to 24 g, white-footed mouse from 20 to 30 g, red-backed vole from 14 to 42 g, southern flying squirrel from 45 to 82 g, eastern chipmunk from 66 to 150 g, and eastern grey squirrel from 400 to 600 g.

Seed preparation

We collected mature, fresh red oak acorns near the study sites and made one composite sample of acorns for the experiment. This was done to minimize the effect of seed characteristics that may be associated with a single tree source. All acorns were floated in water to exclude those that were non-viable (i.e. moldy, broken or infested by *Curculio* sp. larvae). We randomly chose 600 sound acorns for the seed tracking experiment. The average mass of experimental acorns was 4.620 ± 1.440 g (mean \pm SD; minimum = 1.08 g, maximum = 8.17 g). 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 (100-mm length, 0.2-mm diameter) to the acorn and attached a red plastic tag (20 \times 40 mm) to the opposite end of the wire (Xiao *et al.* 2006; Yi *et al.* 2008). The set comprised of wire and tag weighed approximately 0.14 g. Each acorn was weighed (\pm 0.01 g) and

its tag individually numbered. Seed tagging (and most other methods of seed marking) could influence rodent behavior (Wróbel & Zwolak 2013), but in this study we evaluated relative differences in dispersal of identically-marked seeds.

Selective rodent exclusions

Rodent exclosures were constructed of wooden frames (1 \times 1 \times 0.5 m) covered with 1.25-cm mesh hardware cloth for the sides, roof and floor (Moore *et al.* 2007). To test the proposed hypotheses we cut holes on sides of exclosures that either allowed access by: (i) small rodents (mice and red-backed voles only); (ii) small and medium-sized rodents (mice, red-backed voles, eastern chipmunks and southern flying squirrels); or (iii) all rodents, including eastern gray squirrels. All 3 of these treatments excluded large consumers such as white-tailed deer (*Odocoileus virginianus* Zimmermann, 1780) or wild turkey (*Meleagris gallopavo* Linnaeus, 1758). The access holes in the exclosure were the following sizes: 2.5 \times 2.5 cm for the “small” treatment (1); 5 \times 5 cm for the “medium” treatment (2); and 10 \times 10 cm for the “large” treatment (3). At each study site, we placed 3 exclosures (1 per treatment). Cages within each site were located \geq 70 m from one another, and filled with 50 randomly chosen experimental acorns (50 acorns \times 3 exclosures \times 4 study sites). We deployed the experiments in October 2014, and monitored acorn removal and fate each morning during the first 10 days, and then conducted checks 14, 28, 227 and 360 days after placement of the acorns. If marked acorns were removed, the area around the cage (20-m radius) was searched. For all recovered acorns or tags, we measured the distance from the cage of origin and divided their post-dispersal fates into 5 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 soil); (iv) “left on surface” (i.e. deposited intact on the surface); and (v) “missing” (i.e. not recovered within the search area).

Seed disperser identification

To verify whether the exclusion treatments effectively separated small, medium and large rodents, we used camera traps (Reconyx HyperFire PC800 Professional; Reconyx, Inc., Holmen, Wisconsin, USA). The cameras were set up during the first 13 days of this study at 20–30-cm distance in front of cages. Because there were more cages than cameras, we monitored all study cages

sequentially. Pictures were taken in sets of 5 with 1-min pauses between series. Each set of pictures was treated as an independent arrival of a seed disperser. Pictures of animals outside the cages were not counted as visits.

Statistical analysis

We analyzed whether exclosure treatment and acorn mass influenced: (i) the proportion of seeds removed; (ii) the proportion of seeds removed and found; (iii) the proportion of removed seeds that were found and consumed; (iv) the proportion of removed seeds that were not consumed and cached; (v) the proportion of removed seeds that were not consumed entirely but partially eaten; and (vi) removal distance. In analyses (i)–(v), we used binomial error distribution (logit link), and in analysis (vi) Gaussian error distribution (identity link) with removal distances log-transformed. The analysis was conducted in R using lme4 package (Bates *et al.* 2011; R Development Core Team 2013), with mixed models fitted by maximum likelihood using a Laplace approximation. In each model, we entered cage treatment, acorn mass, and their interaction (only if significant) as fixed effects, whereas site and exclosure (nested within site) were included as random effects. Testing for statistical significance was conducted with Wald χ^2 -tests (package “car” [Fox & Weisberg 2011]).

RESULTS

Seed disperser identification

We obtained 431 recordings of rodents from all cages. The most frequently occurring removal agents were individuals of *Peromyscus* spp. which accounted for 91% of all rodent visits in cages with small openings, 73% in cages with medium openings and 76% in cages with large openings (Table 1). Red-backed voles were not recorded in cages with small openings and only

rarely in cages with medium and large holes (2% and 5% of rodent visits, respectively). Eastern chipmunks visited mostly cages with medium openings, where they accounted for 21% of recorded visits (versus only 6% in cages with small openings and 1% in cages with large openings). Southern flying squirrels mostly entered cages with large openings (13% of all visits in this treatment), with rare appearance also in cages with medium (4% of visits) and even small openings (1% of all rodent visits in this type of cage). Eastern grey squirrels were the rarest seed removal agents: they were not recorded in cages with small openings, and accounted for 1% of rodent visits in cages with medium openings and 4% in cages with large openings.

Seed removal and retrieval

Rodents removed 94% (48% within first 10 days) of acorns from cages with small openings, 96% (54% within first 10 days) from cages with medium openings, and 99% (57% within first 10 days) from cages with large openings ($\chi^2 = 5.746$, $df = 2$, $P = 0.06$; Fig. 1; Table 2). Moreover, the probability of removal tended to increase with acorn mass ($\chi^2 = 3.498$, $df = 1$, $P = 0.06$ for combined data). This tendency was pronounced over the first 2 weeks after the experiments were deployed (after 10 days: $\chi^2 = 16.737$, $df = 1$, $P < 0.001$; after 14 days: $\chi^2 = 10.283$, $df = 1$, $P = 0.001$), but not over longer timeframes (results non-significant after 28, 227 and 360 days). Adding quadratic effects of acorn mass did not improve the fit of the models.

In total, we retrieved 71% of acorns removed from cages. The treatments significantly differed in the proportion of acorns found after removal ($\chi^2 = 14.687$, $df = 2$, $P < 0.001$). This proportion was the lowest for cages with small openings (56%), intermediate for cages with large openings (72%), and the highest for medium openings (85% of acorns found after removal: Fig. 1). In ad-

Table 1 Numbers of rodent visits at different exclusion treatments (small, medium and large openings in exclusion cages)

Rodent species	Size group	Exclosure treatment			
		Small	Medium	Large	Total
Mice <i>Peromyscus</i> sp.	Small	64 (91%)	144 (73%)	125 (76%)	333
Red-backed vole	Small	0 (0%)	4 (2%)	9 (5%)	13
Eastern chipmunk	Medium	4 (6%)	41 (21%)	2 (1%)	47
Southern flying squirrel	Medium	2 (3%)	7 (4%)	21 (13%)	30
Eastern grey squirrel	Large	0 (0%)	1 (1%)	7 (4%)	8
Total	All	70 (100%)	197 (100%)	164 (100%)	431

Percentages in parentheses are calculated from the number of total records in particular exclosure treatments.

dition to this effect, heavier seeds were significantly less likely to be found, regardless of cage type ($\chi^2 = 17.413$, $df=1$, $P < 0.001$).

Seed fate

The enclosure treatments did not differ in the propor-

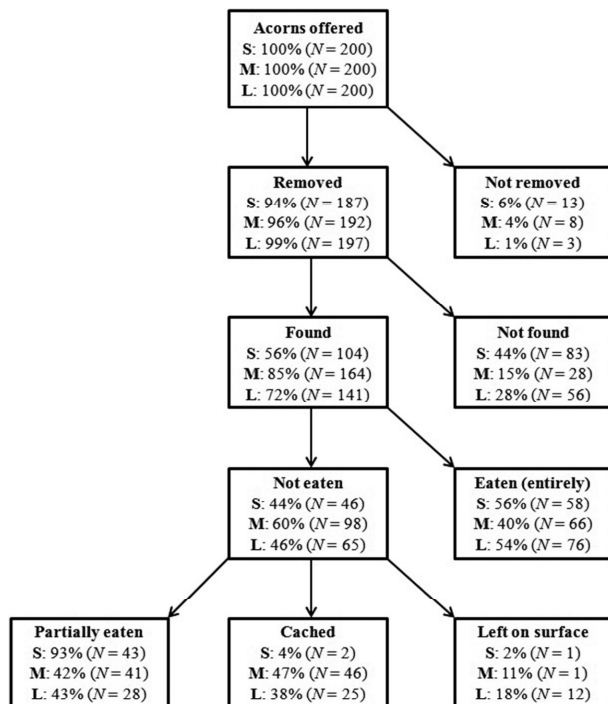


Figure 1 Diagram of initial acorn fate, showing the percentages and numbers of acorns for each fate category. At each step, percentages are calculated from the number of acorns at the previous level. S, “small” treatment; M, “medium” treatment; L, “large” treatment; N, number of acorns.

tion of acorns that were consumed after removal ($\chi^2 = 2.583$, $df = 2$, $P = 0.28$; Fig. 1). In comparison to other treatments, uneaten acorns from cages with small openings were rarely found cached (4% vs 47% for acorns from cages with medium openings and 38% for acorns from cages with large openings; $\chi^2 = 6.800$, $df = 2$, $P = 0.03$; Fig. 1), but were often partially eaten (93% vs 42% for medium-sized and 43% for large-sized cages; $\chi^2 = 18.007$, $df = 2$, $P < 0.001$; Fig. 1). Regardless of rodent exclusion treatment, heavier seeds had significantly higher probability to be cached ($\chi^2 = 8.213$, $df = 1$, $P = 0.004$). In addition, heavier seeds had lower probability of being partially eaten ($\chi^2 = 23.924$, $df = 1$, $P < 0.001$). However, the negative effect of seed mass on the probability of partial consumption was significantly stronger in cages with large opening than in cages with medium and small openings (interaction treatment \times weight: $\chi^2 = 53.967$, $df = 2$, $P < 0.001$).

When considering the total numbers of seeds offered ($N = 200$ for each treatment), rodents cached 1% and completely consumed 29% of acorns from cages with small openings. In the treatment with medium-sized openings, rodents cached 23% and completely consumed 33% of acorns. For acorns from cages with large openings, these proportions equaled 13% for caching and 38% for complete consumption.

Removal distance

The mean acorn dispersal distance was significantly greater at enclosures with medium openings (253.1 ± 11.9 cm, mean \pm SE, $N = 76$) than for cages with large openings (184.5 ± 13.7 cm, mean \pm SE, $N = 28$), and for cages with small openings (179.0 ± 14.3 cm, mean \pm SE, $N = 28$) ($\chi^2 = 18.647$, $df = 2$, $P < 0.001$; Fig. 2a). Seeds eaten *in situ* were excluded from the analysis of removal distance, but most seed consumption took place

Table 2 Summary of main generalized linear mixed models testing effects of enclosure treatments on seed fate

Seed fate	Enclosure treatments			Enclosure treatments \times Weight		
	df	χ^2	P-value	df	χ^2	P-value
Removal	2	5.746	0.06	2	0.809	0.67
Retrieval	2	14.687	<0.001 [†]	2	0.325	0.85
Consumption	2	2.583	0.28	2	1.668	0.43
Caching	2	6.800	0.03 [†]	2	1.567	0.46
Partial consumption	2	18.007	<0.001 [†]	2	53.967	<0.001 [†]
Removal distance	2	18.647	<0.001 [†]	2	0.608	0.74

[†]Significant effects. $N = 600$ acorns. df, degrees of freedom.

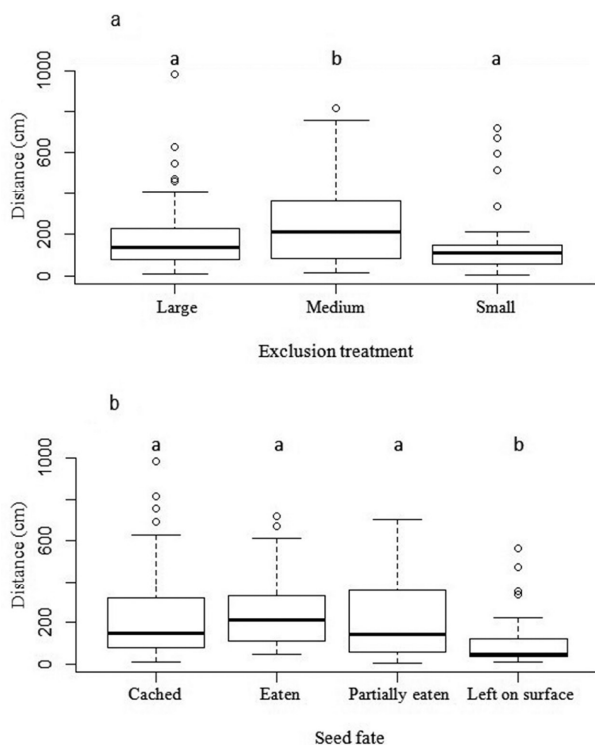


Figure 2 Distance of acorn dispersal in relation to (a) exclusion treatments (cages with openings of different size) and (b) overall fate of removed seeds. Boxes denote 25th, 50th and 75th percentiles; whiskers denote the farthest data points within 1.5 interquartile range; and the open circles denote data points beyond the 1.5 interquartile range. Different letters indicate difference at $P < 0.05$.

inside experimental cages for all treatments (66%, 82% and 75% of all eaten seeds were eaten *in situ* from cages with small, medium and large openings, respectively; $\chi^2 = 0.002$, $df = 2$, $P = 0.97$). Seeds consumed (excluding those that were eaten inside the cages) were moved farthest on average (238.8 ± 10.9 cm, mean \pm SE), while seeds left uneaten on the surface were moved the shortest distance (123.67 ± 13.4 cm, mean \pm SE; Fig. 2b). The mean removal distances of acorns across fates (regardless of treatment) were significantly different ($\chi^2 = 30.312$, $df = 3$, $P < 0.001$; Fig. 2b). Acorn mass had no influence on removal distance ($\chi^2 = 0.502$, $df = 1$, $P = 0.48$).

DISCUSSION

The separation of species by size was not perfect in

our experiment. Cages with small openings were visited mostly by mice, cages with medium openings by mice and chipmunks, and cages with large openings by mice and squirrels: the southern flying squirrel (medium-sized species) and the eastern grey squirrel (large-sized species). Therefore, to highlight species-specific differences, we will refer to cages with small openings as “mice” treatment, to cages with medium openings as “mice–chipmunks” treatment, and to cages with large openings as “mice–squirrels” treatment.

This study allowed us to draw conclusions about the efficiency of seed dispersal by nested granivore communities. Acorn dispersal by the entire rodent community was characterized by a high proportion of acorns cached that were also moved the greatest distances. However, contrary to one of our hypotheses, exclusion of large species (eastern grey squirrels) had little influence on acorn dispersal. This may be due to the fact that the relative abundance of eastern grey squirrels at our study sites was low and, hence, their role as acorn dispersers was constrained by low densities. In turn, medium-sized rodents (represented mostly by the eastern chipmunk) significantly enhanced seed dispersal effectiveness in terms of caching rates, which went from 1% in “mice” treatment to 23% in “mice–chipmunks” treatment. Acorns offered in cages with small openings (“mice” treatment) were dispersed with markedly lower efficiency: consumption was frequent, caching was rare and dispersal distances were short. Thus, relatively modest experimental changes in the assemblage of seed dispersers strongly affected acorn dispersal. These results support the notion that understanding of plant recruitment patterns requires integrating seed dispersal services provided by the community of dispersers rather than focusing on single species (see e.g. Schupp *et al.* 2010; González-Castro *et al.* 2015).

Almost all acorns were removed from the cages. As we predicted, the proportion of removed acorns increased with the size of cage openings, but the magnitude of this increase was surprisingly small. This result, along with results from camera traps, suggests that mice were responsible for the majority of acorn removal at our study sites. These findings contrast with results of a similar study conducted in Ontario, Canada (Bellocq *et al.* 2005), where the entire rodent community (including mice) removed 2.5 times more northern red oak acorns than did only mice. This discrepancy might be caused by differences in the small mammal community composition (higher abundance of eastern grey squirrels and lack of chipmunks and flying squirrels in Bellocq *et al.*

2005). Alternatively, higher acorn production during experiments described in Bellocq *et al.* (2005) could satiate mice.

Similar proportions of seeds were found eaten in all treatments, suggesting that red oak acorn consumption is either independent of composition of rodent community or that this pattern was driven by high activity of mice at all exclosures. However, scatterhoarding was extremely rare in the “mice” treatment. This type of caching usually improves chances of seed germination by reducing the probability of consumption by strict seed predators and protects seeds from desiccation and other abiotic factors (Vander Wall 1990, 2001; Haas & Heske 2005). The rarity of scatterhoarding in the “mice” treatment is in agreement with results of previous studies, which indicate that *Peromyscus* spp. often larderhoard seeds (Sullivan 1978; Vander Wall 1990; Vander Wall *et al.* 2001), and only rarely cache them in topsoil (see Vander Wall *et al.* [2001] and Beck & Vander Wall [2010] for documented examples of scatterhoarding by *Peromyscus* mice). In line with this reasoning, we retrieved considerably fewer acorns removed from cages of “mice” treatment than from the 2 other exclosure treatments. The missing acorns were probably larderhoarded by mice. It is unlikely that acorns were dispersed beyond our search area because dispersal distances were the lowest for acorns at “mice” exclosures. Thus, if our interpretation of the fate of missing seeds is correct, the missing acorns represent mostly losses for the northern red oak because larderhoarded seeds are placed too deep for successful germination (Vander Wall 1990). In the “mice” treatment, missing acorns were almost 3 times as frequent as when eastern chipmunks were included (44% vs 15%).

The highest proportion of seeds scatterhoarded occurred in the “mice–chipmunks” treatment (cages with medium openings). These results were surprising because adult eastern chipmunks are thought to usually larderhoard (Vander Wall & Jenkins 2011), with less common cases of caching at shallow depths performed mostly by juveniles and females with litters (Clarke & Kramer 1994). However, it is also possible that some of the cached seeds represented initial scatterhoarding by chipmunks and mice, performed as a means of rapid sequestration of acorns, which are later larderhoarded. In contrast to mice and chipmunks, eastern grey squirrels are known as typical scatterhoarders (Hadj-Chikh *et al.* 1996; Steele *et al.* 1996), yet acorns were cached as often in the “mice–chipmunks” treatment as in the “mice–squirrels” treatment (cages with large openings). The

lack of difference between treatments probably reflects relatively low visitation rates of grey squirrels (and high by flying squirrels) in the “mice–squirrels” treatment.

Rodents often partially consume large seeds such as acorns (Steele *et al.* 1993; Perea *et al.* 2010). Partial consumption often leads to desiccation and exposes the seed to predators and pathogens (Perea *et al.* 2010). However, as a defense mechanism, many seeds respond to partial consumption through accelerated germination and production of longer roots. Thus, partial consumption is not always equivalent to seed predation (Steele *et al.* 1993; Pérez *et al.* 2008; Perea *et al.* 2010). In this study, partial consumption of acorns was particularly frequent in “mice” treatment. Smaller (e.g. mouse-sized) granivores are more likely to eat only a part of large seeds and abandon the remainder (e.g. Perea *et al.* 2010; Yang & Yi 2012). Thus, despite relatively low caching rates by *Peromyscus* spp., mice might contribute to oak dispersal and recruitment to a larger degree than was recognized previously. Future studies evaluating the impact of partial seed consumption on post-dispersal seed survival will improve the understanding of the role of *Peromyscus* spp. mice in acorn dispersal.

Seeds placed in “mice–chipmunks” treatment were characterized by the longest dispersal distances. This result is counterintuitive because eastern grey squirrels are thought to have the highest dispersal capabilities among the tested species, and generally larger rodents are expected to move seeds further. This pattern may be explained by the fact that grey squirrels visited the cages at rather low numbers. Indeed, all dispersal distances were relatively short compared to those reported elsewhere for grey squirrels (Steele *et al.* 2001, 2014; Moore *et al.* 2007). If a higher proportion of seeds had been dispersed by grey squirrels (and lower by mice), the mean seed dispersal distance would probably have been greater.

In all exclosure treatments, rodents preferentially removed heavier acorns, but this pattern disappeared after the first 2 weeks, probably because the largest acorns were already gone. This finding is in agreement with results of most studies on scatterhoarding rodents (reviewed in Lichti *et al.* 2016): when conspecific seeds are considered, rodents usually prefer larger seeds because they provide more energy. However, acorn mass did not affect acorn consumption at our sites. In general, the influence of acorn mass on predation probability varies considerably among studies (Lichti *et al.* 2015), with positive (e.g. Janzen 1971; Brewer 2001; Gómez 2004), negative (e.g. Jansen *et al.* 2002, 2004; Gómez

et al. 2008) and no associations reported (Zhang *et al.* 2008).

There was no association between dispersal distance and the mass of acorns. This pattern contrasts with results of several other studies on scatterhoarding rodents, which showed greater distances for heavier seeds (Jansen *et al.* 2004; Xiao *et al.* 2005; Steele *et al.* 2014, but see Brewer 2001). In our study, most acorns were dispersed by mice: perhaps the higher food value of large acorns was counterbalanced by higher travel costs (small-sized rodents have restrictions for acorn handling: Muñoz & Bonal 2008); thus, there was no effect of acorn mass on dispersal distance. Nevertheless, our results have to be treated with caution because heavier acorns were less likely to be found than small acorns (see below). Moreover, the relationship between acorn mass and dispersal could be altered by the presence of wires and tags. We note, however, that the mass of the tags represented only a small fraction of the acorn weight (see “Methods”).

In addition, heavier seeds were less likely to be found after removal, regardless of the enclosure type. Because we did not find an effect of acorn mass on removal distance, we suppose that heavier seeds were preferentially larderhoarded rather than dispersed beyond our search area. This pattern may be explained by the high contribution of mice to seed removal in all enclosure treatments (see Bellocq *et al.* [2005] for a situation where grey squirrels were responsible for the majority of removal events), and it might reduce fitness of large acorns relative to smaller acorns.

As a final caveat, seed removal (including both dispersal and predation) is extremely dynamic both spatially and temporally. Seed removal by rodents varies both among species and within a species (and even temporally within an individual: e.g. Clarke & Kramer 1994), depending upon many environmental conditions, such as food availability (Vander Wall 2002b; Zhang *et al.* 2008; Zwolak *et al.* 2016), shrub density (Gómez *et al.* 2008) and presence of other herbivores (e.g. ungulates [Muñoz & Bonal 2007]), which makes understanding of seed removal systems more complicated. Our study focused on a small part of this phenomenon because we evaluated only initial seed fate. We did not take into account potential species-specific differences in seed deposition sites and their post-deposition fate: rodents often remove seeds from their own caches and either consume them or recache elsewhere (Vander Wall & Joyner 1998; Vander Wall 2002a). Moreover, cached seeds may be pilfered by conspecifics or heterospecifics (Vander Wall 2002a; Muñoz & Bonal 2011; Jansen *et al.*

2012). The propensity for recaching and pilferage might differ among species. Thus, future studies should aim to evaluate final seed fate and quantify the probability that seeds harvested by different species survive and establish.

CONCLUSIONS

We observed at least 5 rodent species harvesting, consuming and dispersing northern red oak acorns. We demonstrated that the rodents studied here, which vary significantly in body size, also differ in their impact on seed fate. In partial support of our hypothesis, especially medium-sized species (represented by eastern chipmunks and southern flying squirrels) and, to a lesser extent, large (represented by eastern grey squirrels) species provided more effective acorn dispersal than smaller species represented by *Peromyscus* mice. These conclusions are probably conservative because our experimental methods did not allow us to separate the effect of each rodent species. Instead, our experiments simulated a situation in which various rodent species were sequentially removed from the community to evaluate the impact of different assemblages of rodents on dispersal success. Even when *Peromyscus* spp. were the most abundant cage visitors in all treatments, a decrease in their visitation rates significantly improved dispersal services. When other species were allowed to remove seeds, seed caching rates and removal distances were dramatically enhanced. This suggests that slight differences in rodent communities can lead to drastic differences in seed dispersal effectiveness.

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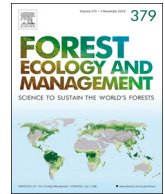
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5.3. Habitat-dependent seed dispersal of an introduced tree species by native rodents

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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; Biebrich, 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 (Biebrich, 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

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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 Zwołak, 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-m² 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 Zwołak, 2013; Wróbel and Zwołak, 2017). The set comprised of wire and tag weighed ~ 0.16 g. Behavior of scatterhoarders might be affected by seed tagging (Wróbel and Zwołak, 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 ($df = 1$, $\chi^2 = 1704.058$, $P < 0.001$; Fig. 1). In both years of the study, red oaks produced more seeds than pedunculate oaks ($df = 1$, $\chi^2 = 462.071$, $P < 0.001$; Fig. 1) and acorn availability was higher at invaded than uninvaded oak sites ($df = 1$, $\chi^2 = 4.913$, $P = 0.028$; Fig. 1).

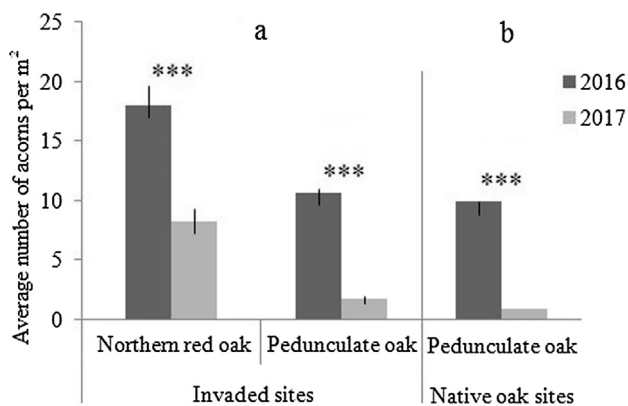


Fig. 1. Average acorn crop of northern red oak and pedunculate oak (\pm SE) during two study years in relation to type of stand. Different letters (a, b) indicate a significant difference between types of stand ($P < 0.05$) while stars (***) indicate significant differences between years ($P < 0.001$). Seeds were counted on the forest floor in 1-m² quadrats located under 20 individuals of northern red oak and 40 (20 \times 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 \times 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 \times 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%; $df = 1$, $\chi^2 = 12.000$, $P = 0.001$; 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 \times 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).

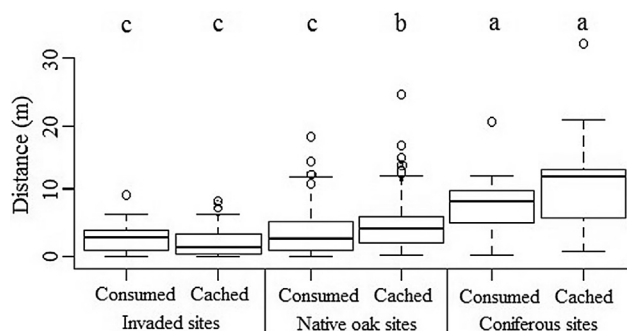


Fig. 2. The distances of acorn removal (\pm SE) in relation to fate and type of stand of removed seeds.

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 \pm 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* \times *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 larderhoarding 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).

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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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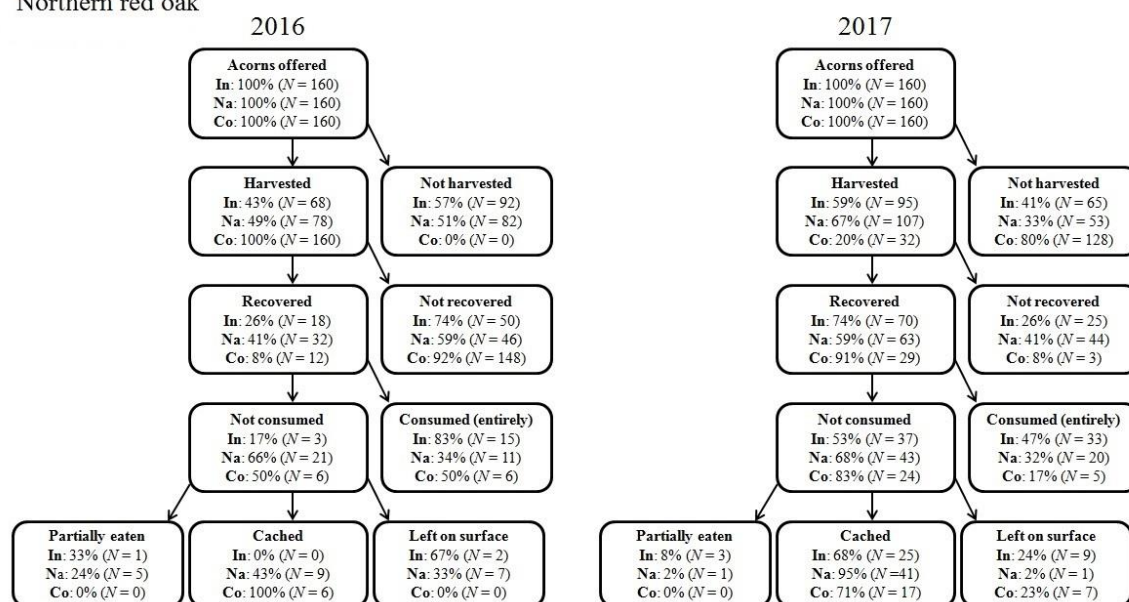
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Supplementary material

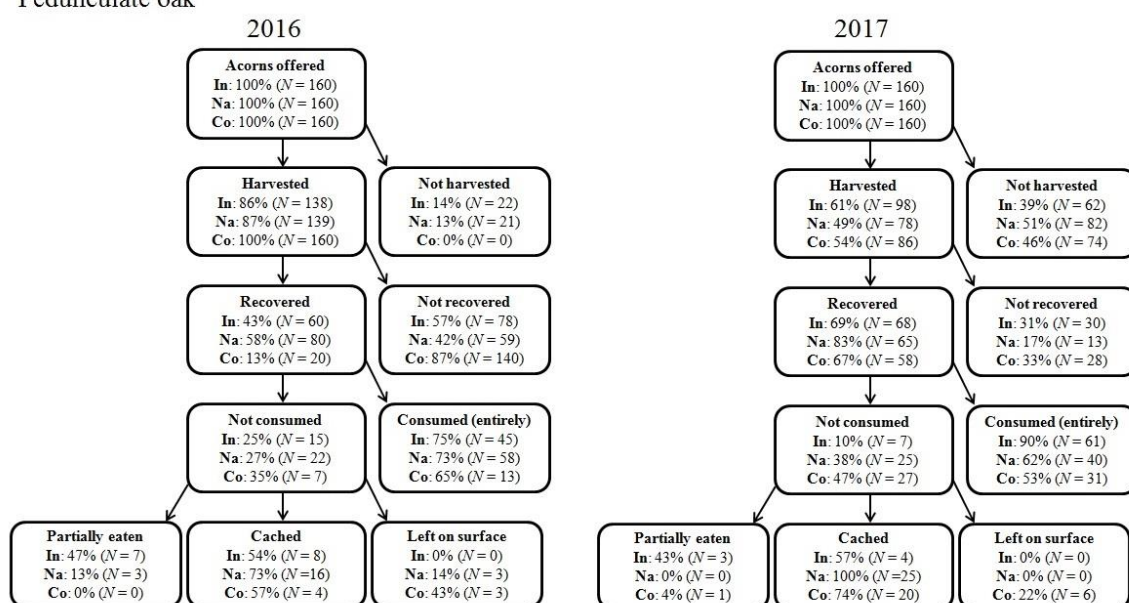
Appendix S1. Diagrams of the seed fates of northern red oak and pedunculate oak

experimental acorns in three types of stand during two years of study (2016 and 2017). The percentages and numbers of acorns are shown for each fate category. At each step, percentages are calculated from the number of acorns at the previous level. In, invaded sites; Na, native oak sites; Co, coniferous sites; *N*, number of acorns

Northern red oak



Pedunculate oak



Appendix S2. Results of generalized linear mixed models for (a) probability of seed harvest, (b) recovery of harvested seeds, (c) probability that seeds will be found consumed (d), probability that harvested but not consumed seeds will be found cached, and (e) distance of seed removal. *Type of stand* denotes native oak sites or coniferous sites relative to invaded sites; *Species* denotes pedunculate oak relative to red oak, and *Year* denotes 2017 relative to 2016. Effects significant at the $P < 0.05$ level are given in bold.

Dispersal stage		Estimate	SE	z or t	P
a) Seed harvest					
	Intercept	1.290	1.572	0.82	0.412
Type of stand	Native oak sites	0.884	1.961	0.45	0.652
	Coniferous sites	2.147	1.956	1.10	0.272
Species	Pedunculate oak	5.510	1.482	3.72	>0.001
Year	2017	-2.042	1.373	-1.49	1.369
Species × Year	Pedunculate oak × 2017	-4.601	1.955	-2.25	0.019
	Intercept	1.395	1.580	0.88	0.377
	Pedunculate oak × 2016	4.601	1.955	2.25	0.019
b) Recovery					
	Intercept	-0.889	0.397	-2.42	0.015
Type of stand	Native oak sites	0.632	0.453	1.40	0.163
	Coniferous sites	-1.807	0.459	-3.94	>0.001
Species	Pedunculate oak	0.460	0.276	1.67	0.095
Year	2017	1.804	0.462	3.90	>0.001
Type of stand × Year	Native oak sites × 2017	-0.789	0.641	-1.23	0.219
	Coniferous sites × 2017	1.905	0.685	2.78	0.005
	Intercept	0.915	0.352	2.60	0.009
	Native oak sites × 2016	0.789	0.641	1.23	0.219
	Coniferous sites × 2016	-1.905	0.686	-2.77	0.005
c) Consumption					

	Intercept	0.288	0.717	0.40	0.688
Type of stand	Native oak sites	-0.588	0.710	-0.83	0.408
	Coniferous sites	-1.447	0.776	-1.86	0.062
Species	Pedunculate oak	2.017	0.627	3.22	0.001
Year	2017	-0.463	0.609	-0.76	0.448
d) Caching					
	Intercept	-1.405	0.905	-1.55	0.121
Type of stand	Native oak sites	2.415	0.923	2.62	0.009
	Coniferous sites	1.169	0.928	1.26	0.208
Species	Pedunculate oak	0.995	0.770	1.29	0.196
Year	2017	1.665	0.779	2.14	0.033
e) Removal distance					
	Intercept	5.155	0.339	15.21	>0.001
Type of stand	Native oak sites	0.314	0.390	0.80	0.207
	Coniferous sites	1.357	0.411	3.30	0.003
Species	Pedunculate oak	0.272	0.185	1.47	0.084
Year	2017	-0.229	0.191	-1.20	0.402
Fate	Consumed	0.296	0.265	1.12	0.198
Type of stand × Fate	Native oak sites × Consumed	-0.969	0.323	-3.00	0.003
	Coniferous sites × Consumed	-0.336	0.377	-0.85	0.402
	Intercept	5.192	0.364	14.28	>0.001
	Native oak sites × Cached	0.969	0.323	3.00	0.003
	Coniferous sites × Cached	0.336	0.379	0.89	0.376

5.4. Differential impacts of soil microbes on native and co-occurring invasive tree species

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Differential impacts of soil microbes on native and co-occurring invasive tree species

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Abstract. The Janzen-Connell effect is often generated by interactions between trees and soil microbes while the enemy release hypothesis states that invasive species are released from regulation by natural enemies. Thus, the strength of the Janzen-Connell effect could differ between native vs. nonnative plants. We tested this hypothesis with congeneric pairs of invasive and native tree species in Europe: boxelder (*Acer negundo*) vs. Norway maple (*A. platanooides*), and Northern red oak (*Quercus rubra*) vs. pedunculate oak (*Q. robur*). We conducted greenhouse experiments using soil sterilization treatments, field experiments on distance-dependent germination, and field surveys of early life stages of the focal species. Greenhouse and field experiments demonstrated patterns consistent with Janzen-Connell effect that is most likely caused by negative distance dependence in seed germination and stem growth which was found in both genera of the native, but not the invasive trees. Soil sterilization experiments suggested that these effects are driven by interactions with soil biota. Field surveys revealed the Janzen-Connell pattern in the distribution of seedlings and saplings of the native, but not the invasive *Acer* species. Our findings indicate that weakened Janzen-Connell effect might contribute to successful invasions of certain nonnative plant species.

Key words: congeneric comparison; distance dependence; enemy release hypothesis; invasion; Janzen-Connell hypothesis; plant–soil biota interactions.

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INTRODUCTION

Species invasions are a source of agricultural and economic losses worldwide and represent a major threat for biodiversity (Vitousek et al. 1997, Mack et al. 2000). However, despite considerable research effort, our understanding of the factors that allow certain species to dominate novel communities has not led to high predictive certainty. Although certain factors have been shown to be important in particular instances, these appear to be idiosyncratic among systems (Hawkes 2007, Moles 2012). It may be that we need to reframe this question as, “How often is a particular mechanism important?” rather than “Is a particular mechanism important?”

(cf. Moles 2012). In this paper, we evaluate the role of plant–soil feedbacks in determining differences in distribution and performance of native and invasive tree seedlings. We use these data to examine three hypotheses: (1) native plants experience more negative soil feedback than invasive congeners (Reinhart and Callaway 2004, Vilá and Weiner 2004, Meiners 2005), (2) negative soil feedback is stronger near adult conspecific plants (Packer and Clay 2000, Bever 2003, Comita 2014), and (3) these feedbacks lead to different patterns of seedling distribution in native and invasive plants in the field.

In general, one hypothesis for the success of invasive species is that they are released from regulation by natural enemies (the enemy release

hypothesis; Blossey and Nötzold 1995, Keane and Crawley 2002, Heger and Jeschke 2014), particularly soil microbes (Packer and Clay 2000, Agrawal et al. 2005, Reinhart and Callaway 2006, Gundale et al. 2014). Negative soil community feedbacks mediate the outcome of competitive plant–plant interactions (Van der Heijden 1998, Bever 2003, Bever et al. 2015, Albornoz et al. 2017, Bachelot et al. 2017), shape local distribution of plant species (Packer and Clay 2000, Klironomos 2002, Reinhart and Callaway 2006, Bachelot et al. 2017), provide distance-dependent regulation of expanding populations (Bever 1994, Reinhart et al. 2003, Mordecai 2011, Comita 2014), and help to maintain plant species diversity (Augspurger and Kelly 1984, Van der Putten et al. 1993, Mills and Bever 1998, Klironomos 2002, Bever 2003, Gundale et al. 2014, Bever et al. 2015). In some cases, invasive plants have been shown to avoid the regulation by soil organisms since interactions of alien species with other organisms are often thought to be weakened in nonnative range (Packer and Clay 2000, Callaway et al. 2001, 2004, Agrawal et al. 2005, Reinhart and Callaway 2006, Gundale et al. 2014).

The enemy release hypothesis is in many ways the inverse of the longer-standing Janzen-Connell hypothesis, one of the most widely accepted mechanisms of maintaining forest diversity and determining plant distribution (Comita 2014). The Janzen-Connell hypothesis proposes that diversity of plant communities in natural ecosystems is promoted by host-specific enemies that reduce survival of seeds or seedlings in a density- and/or distance-dependent manner (Janzen 1970, Connell 1971). Seeds or seedlings close to or in areas with high density of conspecific adults suffer higher mortality due to increased activity of seed predators, herbivores, and pathogens. In this case, individuals have a greater negative impact on conspecifics than on heterospecifics. By preventing conspecific trees from creating clumped distributions, this mechanism contributes to the formation of mixed communities. Recent studies have demonstrated that the Janzen-Connell effect is often generated by interactions with soil organisms (Van der Heijden 1998, Mordecai 2011, Gundale et al. 2014, Bachelot et al. 2017, Deniau et al. 2018), which is consistent with the notion that release from natural

enemies for invasive species may disrupt coexistence mechanisms and allow one species (the invasive one) to dominate a community.

Thus, the invasiveness of tree species may be driven by differential impact of natural enemies responsible for the Janzen-Connell effect on native and invasive trees. Invaders probably encounter non-adapted and therefore less damaging enemies that differ in density, species composition, and diversity relative to their native ranges. If the Janzen-Connell effect is an important mechanism of coexistence in natural communities (Bever 2003, Comita 2014), and if it is caused by interactions with soil pathogens that act as natural enemies, the absence of this effect in alien species may partially explain their advantage over native species. However, soil organisms that interact with plants include not only pathogens, but also important mutualists (Van der Heijden 1998, Paudel et al. 2014, Bachelot et al. 2017). One of the generalities that emerge from current research on invasive plants is that plants in their nonnative ranges tend to be facilitated by soil biota, while native plant species tend to be negatively affected by the accumulation of host-specific portions of the soil biota (Reinhart and Callaway 2004, Agrawal et al. 2005, Gundale et al. 2014, Bardgett and van der Putten 2014). A tree species whose abundance is limited by soil pathogens in its native range may become locally more abundant in its nonnative range where control by the soil community is absent or facilitation is stronger (Packer and Clay 2000, Reinhart et al. 2003, Gundale et al. 2014, Bever et al. 2015). This may lead to high potential for invasiveness of plants in new regions, where such feedback does not occur.

In this study, we tested whether native and invasive tree species are influenced by the Janzen-Connell effect caused by soil-borne organisms. As model species, we used congeneric pairs consisting of species nonnative vs. native to Europe, that is, the boxelder (*Acer negundo*) vs. the Norway maple (*A. platanoides*), and the Northern red oak (*Quercus rubra*) vs. the pedunculate oak (*Q. robur*). Past work with the two *Acer* species (Reinhart and Callaway 2004, Saccone et al. 2010, Porté et al. 2011) has shown that soil feedbacks are an important contributor to invasiveness in their respective native ranges.

For this species pair, the questions in this study are whether these effects take the distance-dependent form hypothesized by the Janzen-Connell hypothesis and, to a lesser extent, whether the same patterns hold in different regions of Europe and North America than the original studies. For the *Quercus* species, we did not yet know at the outset of this study whether soil communities were an important component of invasiveness or coexistence in their native ranges (but see Reinhart et al. 2012). Both boxelder and the Northern red oak have been introduced to Europe from North America at the turn of XVIII and XIX centuries for planting in gardens and to enrich impoverished forest stands. However, multiple contemporary studies have demonstrated a negative impact of these trees on diversity and abundance of native vascular plant species (Maeglin and Ohmann 1973, Wozniwoda 2002, Saccone et al. 2010, Wozniwoda et al. 2014). Thus, the boxelder and the Northern red oak are considered highly invasive in Europe.

We conducted field surveys of early life stages of the focal species, greenhouse experiments using soil inoculation treatments, and field experiments on distance-dependent germination probabilities to test the hypothesis that negative plant–soil feedbacks are stronger in the native than in the invasive trees. Based on the enemy release hypothesis, we expected that in greenhouse conditions, seed germination and seedling development (measured by biomass, stem height, and root length) would be negatively affected by soil collected under adult conspecifics in native, but not in invasive species (Prediction 1). Based on the Janzen-Connell hypothesis, we expected that germination probability of seeds sown in the field would increase with distance to conspecifics in the native, but not in the invasive tree species (Prediction 2). Based on the net effects of both processes, we predicted that the average distance of seedlings and saplings from adult conspecifics would be lower in the invasive than in the native species (Prediction 3).

METHODS

Study sites

Fieldwork was conducted in Puszcza Zielonka (52°30'N, 17°82'E; 78 m a.s.l.) and Wielkopolski National Park (52°16'N 16°48'E; 65 m a.s.l.), both

located in Greater Poland Voivodeship, Poland. This region is characterized by mild temperate climate and mostly flat topography. The average air temperature ranges from −2.5°C in January to 18.2°C in July, and the annual precipitation averages 520 mm. We established study sites in managed 50- to 70-yr-old stands. Forest at our plots was transformed by former forest management, replacing mixed and broadleaved forests with monocultures of Scots pine (*Pinus sylvestris*) before the 50s of XX century (Nowak et al. 2000). After that time, Wielkopolski National Park (a national park since 1957) and some parts of Puszcza Zielonka (a landscape park since 1993) have become protected areas with enhanced natural regeneration. The two areas are characterized by the abundant occurrence of numerous species of alien woody plants (Gazda and Szwa-grzyk 2016). For both *Acer* species, study sites included mixed forests dominated by *Populus* spp. and Scots pine, while for both *Quercus* species, mixed mesic forests dominated by common hornbeam (*Carpinus betulus*) and Scots pine. Understorey and the ground flora were poorly developed at our stands and included mostly the common wood sorrel (*Oxalis acetosella* L.), *Carex* spp., and the male fern (*Dryopteris filix-mas* L.).

Observations and experiments

To test Prediction 1 (germination and seedling development are negatively affected by soil collected close to adult conspecifics in native, but not in invasive species), we conducted a greenhouse experiment in spring and summer 2016 and 2017 at the Faculty of Biology of Adam Mickiewicz University in Poznań. We collected soil samples near the tree trunk (1 m; hereafter “under conspecifics”) and at greater distance (13 m; hereafter “away from conspecifics”) from 10 randomly chosen adult trees of each study species that grew at our field sites. The samples were placed in plastic bags separately and kept in a refrigerator no longer than two weeks (Reinhart and Callaway 2004). The substrate used for sowing seeds was obtained by mixing 25 mL of either non-sterilized or sterilized soil (collected either close to or far from the tree trunk) + ~2.5 L sterilized garden soil. This method helps to avoid differences in the bioavailability of minerals due to sterilization, which otherwise could confound the results (Troelstra et al. 2001). Thus, the

experiment had a 2×2 factorial design: 2 distances (under and away from conspecifics) \times 2 soil types (non-sterilized or sterilized). The sterilization was conducted by autoclaving the soil for three hours in 121°C . We did not mix soil collected under different trees of the same species because such a procedure leads to falsely precise effect estimates (Reinhart and Rinella 2016). For the greenhouse experiment, we purchased all seeds from a local nursery. Before performing the experiment, the seeds were cleaned up of potential pathogens by placing them in 5% bleach solution for 10 min, and then rinsing with deionized water. We used 16 seeds per each soil sample (eight for non-sterilized and eight for sterilized soil type), and thus, we planted 80 seeds per each type of substrate in each tree species ($10 \text{ trees} \times 2 \text{ distances} \times 2 \text{ soil treatments} \times 8 \text{ seeds} = 320 \text{ seeds per species per year}$). All seeds were put out in both soil types in individual plastic pots ($5 \times 5 \times 5 \text{ cm}$) in 32 greenhouses ($100 \times 40 \times 50 \text{ cm}$) randomly, and regularly watered. Each greenhouse contained pots with soil collected either close to or far from conspecifics, but from both sterilization treatments, with sterilized and non-sterilized soil pots located at least 20 cm apart. The data were collected during four months after planting seeds in the experimental substrate. We counted germinated seeds weekly. Stem height, root length, and total fresh biomass were measured at the end of the experiment.

To test Prediction 2 (on distance-dependent germination in native, but not in invasive species), we conducted an experimental field study in autumn 2015 and 2016. We randomly chose several adult ($\geq 50 \text{ cm}$ in diameter at breast height) individuals of each species (14 for *A. negundo*, 14 for *A. platanoides*, 13 for *Q. rubra*, and 12 for *Q. robur*). We created three transects, each with sampling points at four distances from a tree: 1, 5, 9, and 13 m (see Packer and Clay 2000, Reinhart and Callaway 2004, Yamazaki et al. 2008 for similar approach). The neighborhood of all experimental points was also chosen randomly because the distance between heterogeneous trees was shorter than the length of our transects. At each point, we set up stations marked with wooden stakes where we planted seeds of the focal species. Seeds for planting were collected at study plots outside the observational

transects. In 2015, there were insufficient numbers of *Q. robur* acorns on study sites, and thus, we purchased seeds from a local forest nursery. We sowed five seeds at each experimental station ($5 \text{ seeds} \times 4 \text{ distances} \times 3 \text{ transects} = 60 \text{ seeds per each tree}$). The number of seedlings that emerged at each point was determined next spring.

To test Prediction 3 (shorter distances from adult conspecifics in invasive than native species), we conducted an observational field study in spring and early summer in 2016 and 2017. We used the same adult trees as in the experimental field study described above. However, during the study, we excluded one *Q. robur* tree because its surroundings were disturbed by logging. We counted conspecific seedlings ($\leq 0.5 \text{ m}$ height) and saplings ($0.5\text{--}3 \text{ m}$ height) at three transects (length 13 m; width 1 m) originating from each adult individual.

Data analyses

Statistical analyses were conducted in R with glmmADMB and lme4 packages (Fournier et al. 2012, R Development Core Team 2017, Bates et al. 2015, Skaug et al. 2016), using generalized linear mixed models and linear mixed models fitted by maximum likelihood using a Laplace approximation. Testing for statistical significance was conducted with Wald chi-square tests (package car, Fox and Weisberg 2011, 1 degree of freedom in each test). In the greenhouse experiments (Prediction 1), we analyzed whether the distance from the nearest conspecific adult and soil sterilization affect (1) the probability of germination, (2) biomass, (3) stem height, and (4) root length in all tested species. In analysis (1), we used binomial error distribution (logit link); in analyses (2–4), we used Gaussian error distribution (identity link). Explanatory variables consisted of the location (soil collected close or far from adult tree), sterilization type (soil sterilized or non-sterilized), and their interaction, while source tree and greenhouse were included as random effects. In the field experimental study (Prediction 2), we analyzed whether (5) the distance from the nearest conspecific adult affects the probability of germination in all species (binomial error distribution, logit link). In the field observational study (Prediction 3), we analyzed whether (6) native vs. nonnative congeners differ in the average distance of recruits (both

seedlings and saplings) to the nearest conspecific adult (Gaussian error distribution, identity link). In both the field observational and experimental studies, distance to the nearest conspecific was entered as fixed effect (continuous in the field studies and binary in the greenhouse study), while site, tree, and transect were included as nested random effects. When needed, we log-transformed response variables to improve the distribution of residuals.

RESULTS

Seed germination and properties of seedling emerged in greenhouse experiments

In support of Prediction 1, germination of the native, but not of the invasive species, was higher in sterilized than unsterilized soil from under adult conspecifics (marginally significant Sterilization \times Distance effect in Table 1, Figs. 1, 2). In addition, the probability of germination was higher in unsterilized soil samples collected away from adult conspecifics than in samples collected under adults in *A. platanoides* and *Q. robur* (distance effect in Table 1, Fig. 1).

We found a positive effect of soil sterilization on the biomass of *A. negundo* and *Q. robur* (although in the latter the effect was slightly above the nominal significance threshold: sterilization effect in Table 1, Fig. 2), and a negative effect of soil from further distance on biomass of

Q. rubra (distance effect in Table 1, Fig. 2). Yet, in contrast to our predictions, the effects of sterilization on biomass did not depend on soil origin (non-significant Sterilization \times Distance effects in Table 1, Figs. 1, 2).

The average stem height increased with sterilization in both *Acer* species and *Q. robur* (Table 1, Figs. 1, 2). Moreover, the effect of sterilization was affected by distance from the conspecific trees in both native (Fig. 1) and invasive (Fig. 2) trees (Table 1), supporting Prediction 1.

We did not find any significant effects of sterilization, distance, or interaction between them on root length of focal species (Table 1).

Seed germination in field experiments

Seed germination did not depend on the distance from the adult conspecifics in invasive species (*A. negundo*: $\chi^2 = 0.036$, $P = 0.85$; *Q. rubra*: $\chi^2 = 0.473$, $P = 0.49$; Fig. 3). However, the probability of seed germination increased with the distance in native species (from 25% at 1 m to 38% at 13 m in *A. platanoides*: $\chi^2 = 4.809$, $P = 0.03$, and from 29% at 1 m to 40% at 13 m in *Q. robur*: $\chi^2 = 6.195$, $P = 0.05$; Fig. 3). Thus, Prediction 2 was supported for both *Acer* and *Quercus*.

Field surveys of early life stages

Seedlings and saplings occurred significantly further from adult conspecifics in *A. platanoides* than in *A. negundo* (mean \pm SE: *A. platanoides*:

Table 1. Effect of treatments on germination and seedling establishment in the greenhouse experiment.

Dependent variables	Fixed effects	Invasive species				Native species			
		<i>A. negundo</i>		<i>Q. rubra</i>		<i>A. platanoides</i>		<i>Q. robur</i>	
		χ^2	P	χ^2	P	χ^2	P	χ^2	P
Germination	Sterilization	0.171	0.679	0.034	0.853	4.075	0.936	0.014	0.906
	Distance	0.119	0.730	0.000	0.998	0.065	0.044	1.300	0.254
	Sterilization \times Distance	0.954	0.329	0.022	0.881	3.786	0.052	3.402	0.065
Biomass	Sterilization	5.632	0.018	0.397	0.529	1.688	0.194	3.459	0.063
	Distance	1.054	0.305	5.156	0.023	2.054	0.152	0.913	0.339
	Sterilization \times Distance	0.281	0.596	0.154	0.695	2.172	0.141	0.606	0.436
Stem height	Sterilization	15.455	<0.001	0.020	0.887	13.555	<0.001	5.170	0.023
	Distance	0.046	0.829	0.046	0.831	0.030	0.862	0.283	0.594
	Sterilization \times Distance	0.682	0.409	2.240	0.134	8.848	0.003	7.449	0.006
Root length	Sterilization	0.370	0.543	1.178	0.278	0.490	0.484	1.435	0.231
	Distance	2.829	0.093	2.521	0.112	0.008	0.930	0.782	0.376
	Sterilization \times Distance	0.082	0.775	1.154	0.283	1.108	0.292	0.064	0.800

Notes: Data were fitted with a general linear mixed model and tested with the likelihood ratio statistic. Root length of *Acer negundo*, *Quercu robur*, and *Quercu rubra* was log-transformed. Each statistical test was conducted on 1 degree of freedom. Significant results are shown in boldface type.

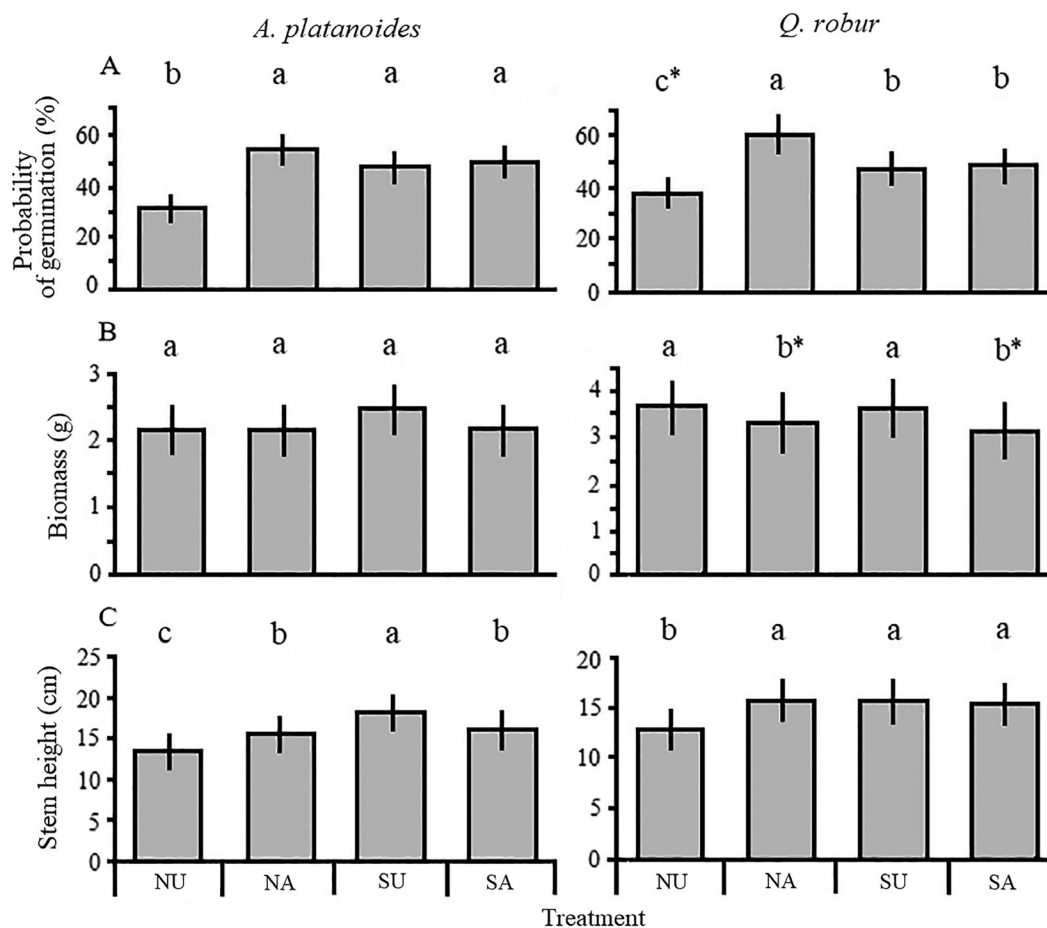


Fig. 1. Estimated (A) probability of germination, (B) biomass, and (C) stem height of native tree species with regard to treatment in the greenhouse experiment (NU, non-sterilized soil collected under conspecifics; NA, non-sterilized soil collected away from conspecifics; SU, sterilized soil collected under conspecifics; SA, sterilized soil collected away from conspecifics). Different letters indicate differences significant at $P < 0.05$, and letters with asterisk differences are marginally significant ($P < 0.10$).

7.92 ± 0.12 m, $N = 973$; *A. negundo*: 5.22 ± 0.19 m, $N = 440$; $\chi^2 = 13.395$, $P < 0.001$; Fig. 4), supporting Prediction 3. However, we did not find any difference in this regard between the two oaks (*Q. robur*: 5.61 ± 0.50 m, $N = 40$; *Q. rubra*: 6.77 ± 0.62 m, $N = 68$; $\chi^2 = 0.336$, $P = 0.56$; Fig 3).

DISCUSSION

Our results support the notion that invasive species are affected less by negative interactions with soil biota (consistent with the enemy release hypothesis) and that these effects decline with

distance from the parent plant (consistent with the Janzen-Connell hypothesis). However, these effects led to the expected patterns of seedling distributions in *Acer* but not in *Quercus* (see Table 2 for a summary of our predictions vs. findings). Our findings are consistent with previous studies in similar systems consisting of *Acer* species (Reinhart and Callaway 2004, Saccone et al. 2010, Porté et al. 2011, Lamarque et al. 2012). Responses of *Quercus* sp. seem to be less generalizable (Vansteenkiste et al. 2005, Reinhart et al. 2012, Sheffer et al. 2013, Bogdziewicz et al. 2018b, c). Our results for *Quercus* also echo Deniau et al. (2017), who detected

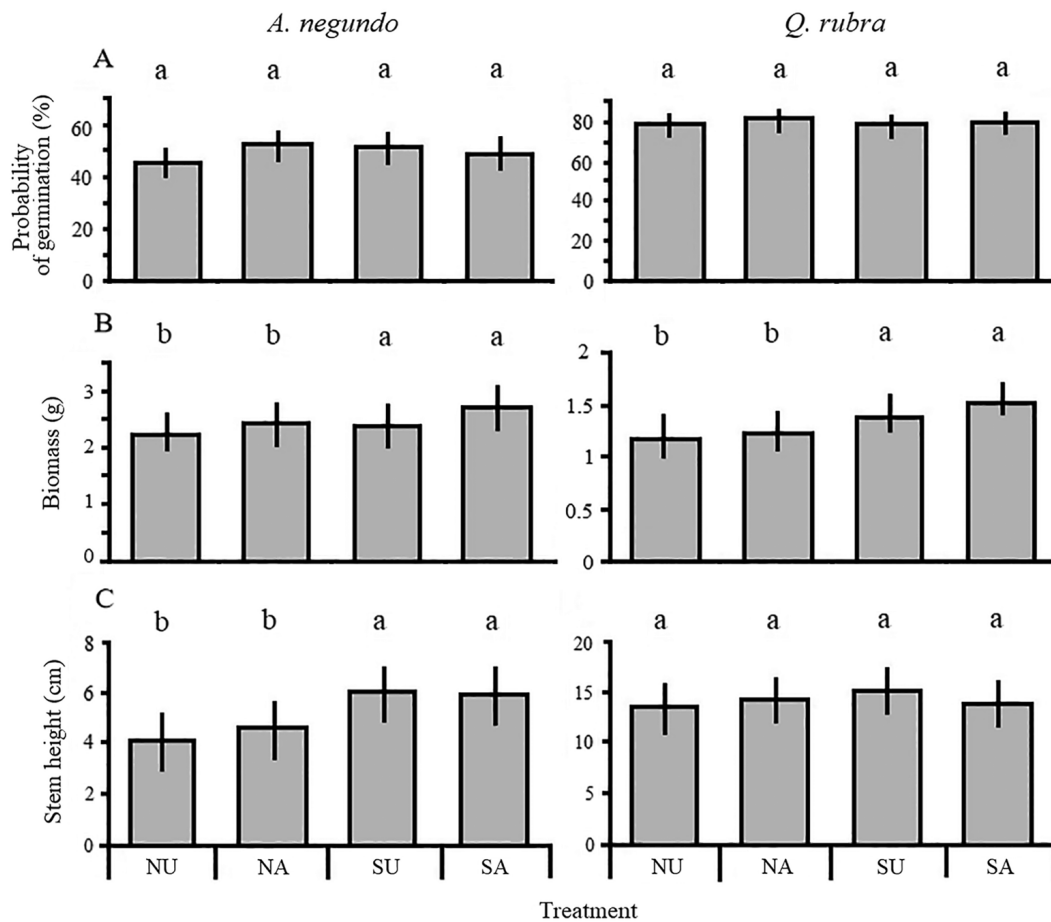


Fig. 2. Estimated (A) probability of germination, (B) biomass, and (C) stem height of invasive tree species with regard to treatment in the greenhouse experiment (NU, non-sterilized soil collected under conspecifics; NA, non-sterilized soil collected away from conspecifics; SU, sterilized soil collected under conspecifics; SA, sterilized soil collected away from conspecifics). Different letters indicate differences significant at $P < 0.05$, and letters with asterisk differences are marginally significant ($P < 0.10$).

Janzen-Connell-like patterns of tree seedling performance in native European oaks, but attribute these to a wider variety of positive and negative feedbacks between heterospecific and conspecific individuals. In *Acers*, distribution patterns in the field are broadly consistent with the Janzen-Connell hypothesis driven by distance dependence in natives but not in invasives. In some ways, this result reinforces a past study, in which both boxelder (invasive in Europe) and Norway maple (invasive in North America) grew better on soils from invaded than from native range (Reinhart and Callaway 2004). However, our results differed from theirs in that their distance-

dependent effects reflected stronger positive feedback in the nonnative range, whereas we detected only negative feedback. In fact, contrary to several previous studies (Klironomos 2002, Reinhart and Callaway 2004, Saccone et al. 2010, Paudel et al. 2014, Gundale et al. 2014, Badalamenti et al. 2015, but see Beckstead and Parker 2003), we found only negative effects of soil biota across all four tested species. In previous experiments conducted on *Acers*, transplanted juveniles were used (Reinhart and Callaway 2004, Saccone et al. 2010, Porté et al. 2011, but see Meiners 2005) while our study was focused on germination and development directly after germination.

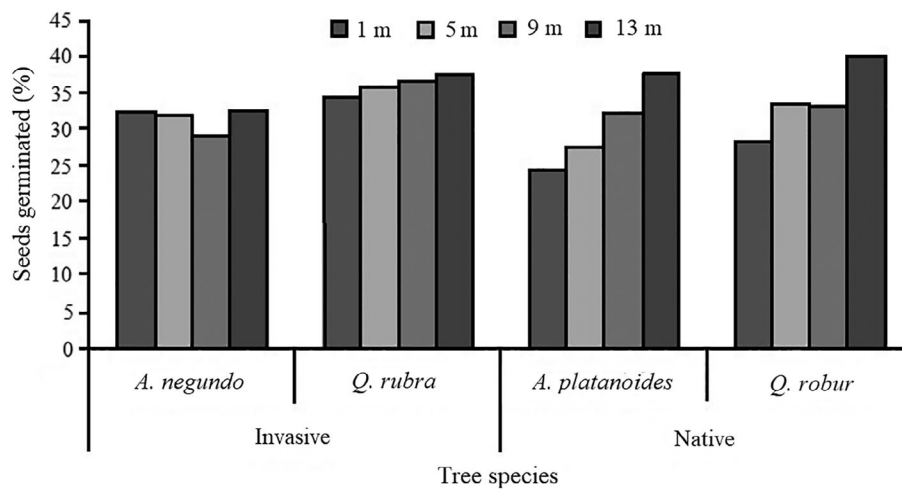


Fig. 3. Germination of seeds sown in the field at different distances to adult conspecifics.

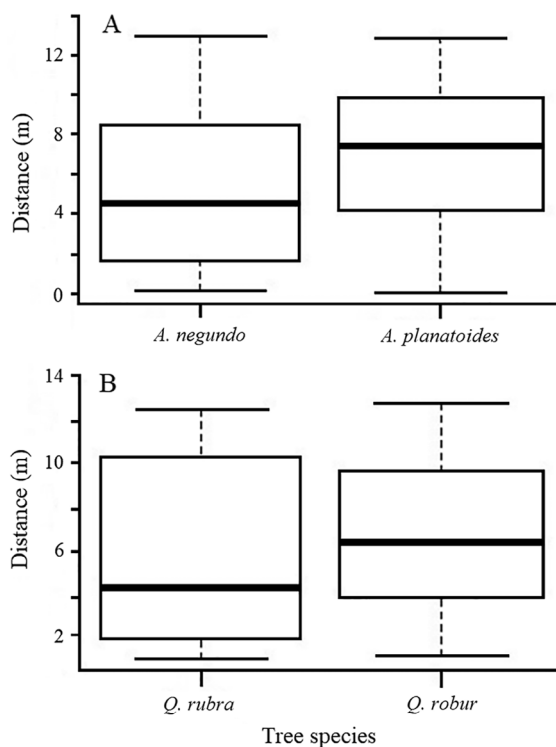


Fig. 4. Distance of recruits from adult conspecifics in (A) *Acer* and (B) *Quercus* species. Boxes denote 25th, 50th, and 75th percentiles; whiskers denote the farthest data points within 1.5 interquartile range; and the open circles denote data points beyond the 1.5 interquartile range.

Thus, this difference could reflect differential effects on different life stages as well as possible geographic variation between the specific regions of other studies.

In contrast, *Quercus* seedlings did not show patterns consistent with release from Janzen-Connell effects (even though invasive seedlings were less inhibited by soil biota than native ones in mechanistic experiments). In their native range, red oaks are often unable to establish under their own canopy (Vansteenkiste et al. 2005, Sheffer et al. 2013, but see Reinhart et al. 2012). This inhibitory effect seems to be absent in the invaded range (this study, Bogdziewicz et al. 2018b). However, lack of Janzen-Connell pattern in natural regeneration of both oak species might indicate that soil microbes have the potential to limit native oak recruitment as predicted by the Janzen-Connell hypothesis (and demonstrated in our greenhouse and field experiments), but other factors suppress this pattern in the field. As an example, probability of rodent seed predation on *Q. rubra* and *Q. petraea* was lower rather than higher close to adult trees (thus distance had negative rather than positive effect on seed survival) (Bogdziewicz et al. 2018b), potentially counteracting the pathogen effect. Moreover, *Q. rubra* in the nonnative range is rarely attacked by pre-dispersal seed predators when compared with both the co-occurring *Q. petraea* and with conspecifics in the native range (Bogdziewicz et al. 2018a, c). Furthermore, it is less often

Table 2. Summary of tested predictions and research findings.

Predictions	Response variables	Results
(1) Seed germination and seedling development (measured by biomass, stem height, and root length) will be negatively affected by soil collected under adult conspecifics in native, but not in invasive species	Germination	Confirmed in both <i>Acer</i> and <i>Quercus</i> (results marginally significant)
	Biomass	Not confirmed
	Stem height	Confirmed in both <i>Acer</i> and <i>Quercus</i>
	Root length	Not confirmed
(2) Germination probability will increase with distance to conspecifics in the native, but not in the invasive tree species	Germination	Confirmed in both <i>Acer</i> and <i>Quercus</i>
(3) The average distance of seedlings and saplings from adult conspecifics will be lower in invasive than in native species	Distance	Confirmed in <i>Acer</i>

consumed by rodents than the native oak, but also less readily dispersed by mice (*Apodemus flavicollis*) and jays (*Garrulus glandarius*; Wróbel unpublished manuscript, Myczko et al. 2014, Bogdziewicz et al. 2018b, c). We should also note that seedlings and saplings of both oaks were rather rare on our transects, limiting our power to detect patterns in their distribution.

Our results suggest that at least part of the invasive plant advantage might result from the differential impact of soil biota on native and invasive plants, but that these effects need to be interpreted in a broader context than any single experimental result. Even for *Acer*, not all of our findings unequivocally support our hypothesis of differential impacts of soil microbes on the invasive and the native species. The differences in germination probability and stem growth demonstrated that invasive trees may have an advantage over natives when recruiting close to conspecifics, but seedling biomass and root length were unaffected by soil treatments. In similar studies, seedling establishment was enhanced both under greenhouse conditions (Reinhart et al. 2003) and in the field (Sun et al. 2015). Moreover, stem height and biomass were

increased in seedlings grown in soils from non-native ranges in comparison with native ranges both under greenhouse conditions (Blossey and Nötzold 1995, Reinhart et al. 2003, Reinhart and Callaway 2004) and in field surveys (Jakobs et al. 2004). These contrasts emphasize the importance of considering multiple aspects of individual performance. They also point to the importance of studies such as ours that compare experimental results to field patterns. An even stronger approach would be to incorporate the effects of multiple aspects of species interactions and affected life stages into models that calculate their relative contributions to overall invasiveness (e.g., using matrix population models: Elwood et al. 2018). Although it is beyond the scope of this study, this approach would be a valuable direction for future research.

Past tests of the enemy release hypothesis have taken two approaches (Hawkes 2007): comparing performance of conspecifics in the native and invasive range, and comparing native and invasive congeners in the same location. These approaches test two different ecological hypotheses. The first tests whether invasive plants experience fewer negative interactions than they did in their native ranges, possibly leading to higher abundance in the native than in the invasive range. The second (our approach) tests whether they experience fewer negative interactions than similar native species, which could allow them to reach higher abundance than native species in the invasive range. Few studies have tested for both phenomena (but see Reinhart and Callaway 2004).

While there is a general tendency to consider whether or not a certain mechanism is involved in invasiveness (Reinhart et al. 2003, Colautti et al. 2004, Schultheis et al. 2015, Martínez-García et al. 2016), we find it important to recognize either frequency or strength of such mechanisms. Research on enemy release in invasive species to date has led to inconsistent findings either supporting the hypothesis (Wolfe 2002, Mitchell and Power 2003, Reinhart et al. 2003, Gundale et al. 2014, Correia et al. 2016) or not (Blaney and Kotanen 2001, Beckstead and Parker 2003, Schultheis et al. 2015). Thus, differential impacts of soil biota on native and nonnative plants are likely to provide a mechanism behind some, but not all, successful plant invasions (Reinhart and Callaway 2006). Moreover,

release from pathogens might act synergistically with other forms of enemy release, contributing to the improved performance of invasive plants (Mitchell 2006).

As a caveat, we did not identify soil microorganisms that were responsible for the observed effects. Consequently, we cannot distinguish between direct and indirect effects of soil microbes. For example, in some cases microbes mediate the effects of autotoxicity—they break down root exudates into substances that are toxic to seeds or seedlings (Huang et al. 2013). While our study did not examine the exact mechanism of the harmful effects, it nonetheless supports the notion that soil microbes associated with adult plants harm conspecific seeds and seedlings in native, but not in invasive species. Although mechanisms of coexistence of various species and causes of invasiveness are often considered separately, they may be indeed inevitably linked. The Janzen-Connell effect has been invoked to explain coexistence in plant communities and patterns of tree abundance and rarity (Janzen 1970, Connell 1971, Klironomos 2002, Bever 2003, Freckleton and Lewis 2006, Comita 2014, Kempel et al. 2018) while this phenomenon can also play an important role in plant invasions with recognized differential impacts of enemies. Our results indicate that the strength of Janzen-Connell effect differs between native and invasive tree species, providing mechanism that could contribute to the establishment and spread of alien plants. However, there is probably multitude of factors involved in this process. An important next step would be to identify soil pathogens that cause Janzen-Connell effect in the native species, examine their virulence to *A. negundo* and *Q. rubra*, and evaluate the potential for host-switching to the invasive trees. This could eventually lead to designing effective strategies of invasive plant control and management.

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7. Authorship statements

Authorship statements of PhD candidate

Wróbel A. 2014. Wpływ gryzoni na regenerację lasu z uwzględnieniem zaburzeń naturalnych i antropogenicznych (Influence of the rodents on forest regeneration considering natural and anthropogenic disturbances). *Sylvan* 158(9):714-720. [in Polish]

The role of PhD candidate: the only author

Contribution (100%)

- Collecting and reviewing literature
- Writing of the manuscript
- Revision of the manuscript

Wróbel A., Zwolak R. 2017. Deciphering the effects of disperser assemblages and seed mass on patterns of seed dispersal in a rodent community. *Integrative Zoology* 12(6):457-467. doi: 10.1111/1749-4877.12265.

The role of PhD candidate: first and corresponding author

Contribution (70%)

- Designing of the study
- Collecting field data (including study site establishment, seed tracking experiments and setting camera traps)
- Data preparation and analysis
- Interpretation of the results
- Writing of the first draft of the manuscript
- Revision of the manuscript

Wróbel A., Zwolak, R. 2019. Habitat-dependent seed dispersal of an introduced tree species by native rodents. *Forest Ecology and Management* 433:563-568. doi: 10.1016/j.foreco.2018.11.036

The role of PhD candidate: first and corresponding author

Contribution (80%)

- Designing of the study
- Collecting field data (including study site establishment, seed tracking experiments and setting camera traps)
- Data preparation and analysis
- Interpretation of the results
- Writing of the first draft of the manuscript
- Revision of the manuscript

Wróbel A., Crone E. E., Zwolak R. 2019. Differential impacts of soil microbes on native and co-occurring invasive tree species. *Ecosphere* 10(7), e02802. doi: 10.1002/ecs2.2802

The role of PhD candidate: first and corresponding author

Contribution (70%)

- Designing of the study
- Collecting field data (including study site establishment, field censuses and experiments)
- Conducting greenhouse experiments (including collecting soil samples, maintaining seedling cultivation)
- Data preparation and analysis
- Interpretation of the results
- Writing of the first draft of the manuscript
- Revision of the manuscript

Poznań, 10.08.2019



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Authorship statement of co-author of the 'Deciphering the effects of disperser assemblages and seed mass on patterns of seed dispersal in a rodent community' article

Authorship statement

I confirm that I am the co-author of the paper: Wróbel A., Zwolak R. 2017. Deciphering the effects of disperser assemblages and seed mass on patterns of seed dispersal in a rodent community. Integrative Zoology 12(6):457-467. doi: 10.1111/1749-4877.12265.

I declare that my contribution to this paper included

- designing of the study
- interpretation of the results
- writing and revision of the manuscript.

As the supervisor, I confirm that Aleksandra Wróbel had a major contribution (70%) to this study and was a leading author.

Poznań, 25.08.2019



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Authorship statement of co-author of the 'Habitat-dependent seed dispersal of an introduced tree species by native rodents' article

Authorship statement

I confirm that I am the co-author of the paper: Wróbel A., Zwolak, R. 2019. Habitat-dependent seed dispersal of an introduced tree species by native rodents. Forest Ecology and Management 433:563-568. doi: 10.1016/j.foreco.2018.11.036.

I declare that my contribution to this paper included

- designing of the study
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Poznań, 25.08.2019



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Authorship statement of co-author of the 'Differential impacts of soil microbes on native and co-occurring invasive tree species' article

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I declare that my contribution to this paper included

- creating the idea of the study
- revision of the first draft of the manuscript.

Medford MA, September 7th, 2019



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