Instytut Dendrologii Polskiej Akademii Nauk

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Środowiskowe uwarunkowania sukcesu ekologicznego gatunków inwazyjnych: *Prunus serotina*, *Quercus rubra* i *Robinia pseudoacacia*

Environmental determinants of the ecological success of invasive species:
Prunus serotina, *Quercus rubra* **and** *Robinia pseudoacacia*

Praca doktorska
wykonana w Pracowni Ekologii
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Pracę dedykuję Rodzicom
w podzięce za wychowanie
i wspieranie pasji

Podziękowania

Pragnę złożyć serdeczne podziękowania wszystkim osobom, bez których niniejsza praca nie doszłaby do skutku.

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Spis treści

Lista publikacji stanowiących rozprawę doktorską

Wyniki badań zostały opublikowane w następujących artykułach naukowych:

1. **Dyderski M.K.**, Jagodziński A.M. 2018. Drivers of invasive tree and shrub natural regeneration in temperate forests. Biological Invasions, 20, 9, 2363-2379. doi: 10.1007/s10530-018-1706-3.

2. **Dyderski M.K.**, Jagodziński A.M. 2018. Low impact of disturbance on ecological success of invasive tree and shrub species in temperate forests. Plant Ecology, 219, 1369-1380. doi: 10.1007/s11258-018-0885-4.

3. **Dyderski M.K.**, Jagodziński A.M. 2019. Functional traits of acquisitive invasive woody species differ from conservative invasive and native species. NeoBiota, 41, 91-113. doi: 10.3897/neobiota.41.31908.

Abstract

Invasive species of trees and shrubs are one of the major threats to biological diversity worldwide. Despite numerous studies on their chorology, ecology and impacts, still there is a little known about determinants of its spread. For that reason, I aimed to assess the determinants of invasive trees and shrubs natural regeneration ecological success. As a model species I chose *Prunus serotina* Ehrh., *Quercus rubra* L. and *Robinia pseudoacacia* L. – the most frequent alien tree species in European forest ecosystems. I hypothesized that: (1) propagule pressure will be the most important predictor of natural regeneration of studied species ecological success, (2) higher frequency and size of disturbance will facilitate natural regeneration of studied species, and (3) biomass allocation and specific leaf area of studied species will be responsive to environmental factors – soil fertility and light availability. The study was conducted in Wielkopolski National Park (W Poland), in the set of 378 permanent plots, observed for three years.

The biomass of seedlings and saplings of the studied species was the mostly affected by factors describing propagule pressure – proximity and quantity of parental trees. Disturbance indices revealed the low correlation with biomass and density of studied species natural regeneration. Functional traits of the studied species weakly responded to environmental gradients – the differences among the species studied were higher than intraspecific variability.

The study revealed that propagule pressure is a crucial factor determining spread of invasive trees and shrubs. Moreover, studied invasive species benefit from functional difference from their native competitors. Due to acquisitive strategy *P. serotina* and *R. pseudoacacia* have higher biomass allocation into foliage and higher specific leaf area than *Q. rubra*. In contrast, conservative *Q. rubra* invests more in roots and has higher overall biomass. These two strategies, connected with different ecological optima of species studied, allow for ecological success in different types of forest ecosystems. For that reason, efficient management of invasive woody species needs targeting both on propagule pressure and invaded ecosystems properties.

Streszczenie

Inwazyjne gatunki drzew i krzewów stanowią zagrożenie dla różnorodności biologicznej w skali globalnej. Pomimo licznych badań dotyczących ich chorologii, ekologii oraz oddziaływania na ekosystemy, nadal niewiele wiemy na temat czynników warunkujących ich rozprzestrzenianie się. Z tego powodu celem pracy było określenie środowiskowych uwarunkowań sukcesu ekologicznego odnowienia naturalnego inwazyjnych gatunków drzew i krzewów. Jako przykładowe gatunki wybrałem *Prunus serotina* Ehrh., *Quercus rubra* L. oraz *Robinia pseudoacacia* L. – najczęściej występujące obce taksony drzew w ekosystemach leśnych Europy. Postawiłem trzy hipotezy badawcze: (1) czynniki związane z dostępnością propagul będą kluczowymi predyktorami sukcesu ekologicznego badanych taksonów, (2) większa częstość i natężenie zaburzeń sprzyjać będzie sukcesowi ekologicznemu badanych gatunków oraz (3) alokacja biomasy i specyficzna powierzchnia liści odnowienia naturalnego badanych gatunków wykaże odpowiedź na cechy środowiskowe – żyzność oraz dostępność światła. Badania przeprowadziłem na terenie Wielkopolskiego Parku Narodowego (zachodnia Polska), w układzie 378 stałych poletek badawczych, obserwowanych przez trzy lata.

Biomasa siewek i starszych nalotów badanych gatunków była w największym stopniu determinowana przez zmienne opisujące dostępność propagul – bliskość oraz liczbę drzew rodzicielskich. Wskaźniki zaburzeń były słabo skorelowane z biomasą i zagęszczeniem odnowienia naturalnego badanych neofitów. Ich cechy funkcjonalne wykazały słabą odpowiedź na gradienty środowiskowe.

Uzyskane wyniki wskazują na kluczowe znaczenie dostępności propagul dla rozprzestrzeniania się inwazyjnych gatunków drzew i krzewów. Gatunki te zyskują również przewagę z uwagi na różnice w strategii życiowej w stosunku do rodzimych konkurentów. Reprezentujące strategię akwizycyjną *P. serotina* i *R. pseudoacacia* alokują więcej biomasy do liści i mają większą specyficzną powierzchnię liści. *Q. rubra* zaś alokuje więcej biomasy do korzeni i ma większą biomasę całkowitą. Te strategie oraz zróżnicowane wymagania ekologiczne pozwalają badanym gatunkom na kolonizację zróżnicowanych siedlisk. Z tego względu efektywne zarządzanie inwazyjnymi gatunkami drzew i krzewów wymaga skupienia zarówno na źródłach propagul, jak i właściwościach kolonizowanych ekosystemów.

1. Wstęp

Wieloletni wpływ człowieka na środowisko przyrodnicze doprowadził do znacznych przekształceń biosfery, które w ostatnich latach przybrały na sile w takim stopniu, że obecne czasy nazwano epoką antropocenu (Capinha i in. 2015; Ceballos i in. 2015; Steffen i in. 2015). Współcześnie jednym z głównych zagrożeń dla różnorodności biologicznej, oprócz zmian klimatycznych (Wang i in. 2016; Dyderski i in. 2018; Steinbauer i in. 2018) i utraty siedlisk naturalnych (Wilson 2002; Kaplan i in. 2009; Dullinger i in. 2015), są inwazje biologiczne (Elton 1958; Richardson i in. 2000; Vilà i in. 2011; Tokarska-Guzik i in. 2012). Z uwagi na duże zdolności przekształcania środowiska oraz swoją długowieczność, inwazyjne gatunki drzew i krzewów stanowią szczególnie duże zagrożenie dla środowiska przyrodniczego (Elton 1958; Faliński 1968; Richardson 1998; Richardson i Rejmánek 2011).

Drzewa i krzewy modyfikują dostępność zasobów: światła (np. Emborg 1998; Knight i in. 2008; Niinemets 2010; Jagodziński i in. 2018c), wody (np. Cienciala i in. 1992; Kučerová i in. 2008; Fay i Lavoie 2009), czy substancji odżywczych w glebie (np. Vitousek 1990; Ehrenfeld 2003; Reich i in. 2005; Mueller i in. 2012; Aerts i in. 2017). Mają również istotny wpływ na tempo obiegu materii w ekosystemie (np. Allison i Vitousek 2004; Hobbie i in. 2006; Jo i in. 2016; Horodecki i Jagodziński 2017). Siedliskotwórcza rola roślin drzewiastych determinuje skład gatunkowy biocenoz innych grup organizmów, np. roślinność runa (np. Barbier i in. 2008; Knight i in. 2008; Rawlik i in. 2018), florę mszaków (np. Barkman 1958; Mežaka i in. 2012; Jagodziński i in. 2018d; Wierzcholska i in. 2018), biotę grzybów mykoryzowych (np. Dickie i in. 2006; Trocha i in. 2012; Kałucka i Jagodziński 2016), czy faunę glebową (np. Hendrychová i in. 2012; Mueller i in. 2016; Kamczyc i in. 2018). Skład gatunkowy drzewostanu modyfikuje także wzrost i przeżywalność odnowienia naturalnego drzew i krzewów (np. Kolb i in. 1990; Canham i in. 1994; Holeksa i in. 2007; Dech i in. 2008; Szwagrzyk i Szewczyk 2008). Z uwagi na tak szerokie oddziaływania, większość inwazyjnych gatunków drzew i krzewów określanych jest mianem „inżynierów środowiska"(ang. *ecosystem engineers*; np. Crooks 2002; Allison i Vitousek 2004; Corenblit i in. 2014), czyli gatunków typu *transformers* wg klasyfikacji Richardsona i in. (2000).

Najnowsze ujęcia koncepcyjne z zakresu ekologii inwazji dzielą czynniki odpowiedzialne za sukces ekologiczny obcych gatunków na trzy grupy (Lonsdale 1999; Lockwood i in.

2005; Richardson i in. 2011). Pierwsza z nich dotyczy cech biologicznych danego taksonu. Pewne cechy funkcjonalne roślin (Wright i in. 2004; Chave i in. 2009; Tecco i in. 2010; Díaz i in. 2016) są powiązane z większą zdolnością do ekspansji w warunkach wtórnego zasięgu geograficznego. Cechy te dotyczą inwestycji w struktury umożliwiające skuteczną konkurencję – np. gęstość drewna (Tecco i in. 2010) lub specyficzną powierzchnię liści (Grotkopp i in. 2010; te Beest i in. 2015), a także cechy umożliwiające szybką i skuteczną propagację (Baker 1974; Thompson i Davis 2011; Pyšek i in. 2015). Druga grupa określa właściwości ekosystemu, który może być potencjalnie skolonizowany przez dany gatunek obcy (Lonsdale 1999; Alpert i in. 2000; Herben i in. 2004). Cechy te dotyczą głównie dostępności zasobów – substancji odżywczych w glebie, wody czy światła (Knight i in. 2008; Matzek 2011; Jo i in. 2015; Jagodziński i in. 2018c), obecności konkurentów (Robakowski i Bielinis 2011; Sanderson i Antunes 2013; Dyderski i in. 2017), patogenów lub roślinożerców (Blossey i Notzold 1995; Reinhardt i in. 2003; Mitchell i Power 2003) czy reżimu zaburzeń (Chmura i Sierka 2007; Chabrerie i in. 2008; Corenblit i in. 2014). Trzecia grupa czynników określa dostępność propagul danego gatunku. Dostępność ta wyrażana jest przez różne zmienne pośrednie, np. odległość od źródła nasion (Pairon i in. 2006; Jagodziński i in. 2015; Straigytė i in. 2015; Woziwoda i in. 2018), udział gatunku w polu powierzchni przekroju pierśnicowego drzewostanu (Vanhellemont i in. 2009), intensywność uprawy (Křivánek i in. 2006; Pyšek i in. 2009) czy obecność w pobliżu źródeł propagul gatunków obcych (Pairon i in. 2006; Dyderski i in. 2015).

Przegląd dotychczas opublikowanych prac wskazuje, że większość publikacji z zakresu ekologii inwazji dotyczy zwykle analiz chorologicznych (np. Tokarska-Guzik 2005; Richardson i Pyšek 2012; Donaldson i in. 2014; Vieira i in. 2014; Dyderski i Jagodziński 2016) albo badań nad wpływem poszczególnych gatunków na ekosystemy (Allison i Vitousek 2004; Chmura 2013; Hulme i in. 2013; Aerts i in. 2017; Essl i in. 2017). Niewiele prac dotyka tematu rozprzestrzeniania się inwazyjnych gatunków roślin drzewiastych (np. Danielewicz i Maliński 2003; Aslan i in. 2012; Straigytė i in. 2015; Woziwoda i in. 2018). Prace te zwykle dotyczą dyspersji nasion, a niewiele z nich pochyla się nad sukcesem ekologicznym odnowienia naturalnego, które kształtuje przyszły skład gatunkowy drzewostanu (Baraloto i in. 2005). Często badania te wykonywane są w trakcie jednego sezonu wegetacyjnego, co biorąc pod uwagę sezonowość owocowania niektórych gatunków (Burns i Honkala 1990) może ograniczać wnioskowanie na podstawie uzyskiwanych wyników. Co więcej, większość badań wykonywanych

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w ostatnich latach kwantyfikuje sukces ekologiczny gatunku za pomocą zagęszczenia lub estymowanego pokrycia w zdjęciu fitosocjologicznym (Knight i in. 2008; Halarewicz 2012; Major i in. 2013; Jagodziński i in. 2015; Vítková i in. 2017). Niewiele prac dostarcza informacji o biomasie (np. Annighöfer i in. 2012; Jagodziński i in. 2018c), która może być później porównywana do wyników eksperymentów prowadzonych w warunkach kontrolowanych (np. Gorchov i Trisel 2003; Grotkopp i in. 2010; González-Muñoz i in. 2014; Kawaletz i in. 2014).

2. Cele i hipotezy

Celem rozprawy doktorskiej jest określenie czynników środowiskowych odpowiedzialnych za sukces ekologiczny trzech inwazyjnych gatunków roślin drzewiastych: *Prunus serotina*, *Quercus rubra* oraz *Robinia pseudoacacia*. W badaniach przyjęto następujące hipotezy:

(1) czynniki związane z dostępnością propagul będą kluczowymi predyktorami sukcesu ekologicznego badanych taksonów. Hipoteza ta nawiązuje do *propagule pressure hypothesis* zaproponowanej przez Lonsdale (1999) i wielokrotnie testowanej w różnych warunkach (np. Davies i in. 2005; Lockwood i in. 2005; Vanhellemont i in. 2009; Woziwoda i in. 2018). Dotychczas w większości prac próbowano oceniać wpływ dostępności propagul na sukces ekologiczny gatunków inwazyjnych w oderwaniu od cech ekosystemu czy gatunku, a zastosowane metody nie pozwalały dokładnie określić hierarchii ważności poszczególnych zmiennych (Pyšek i in. 2009; Vanhellemont i in. 2009; Terwei i in. 2013). Nasze wcześniejsze prace wskazują również na interakcje pomiędzy zmiennymi określającymi dostępność propagul i cechy środowiska (Jagodziński i in. 2015; Dyderski i in. 2017; Jagodziński i in. 2018c; Woziwoda i in. 2018; Dyderski i Jagodziński 2019a);

(2) większa częstość i natężenie zaburzeń w ekosystemie leśnym sprzyjać będzie sukcesowi ekologicznemu badanych gatunków, zgodnie z przewidywaniami hipotezy umiarkowanych zaburzeń, które chwilowo zwiększają możliwości kolonizacji przez gatunki inwazyjne (Davis i in. 2000; Closset-Kopp i in. 2007; Chabrerie i in. 2008);

(3) alokacja biomasy oraz specyficzna powierzchnia liści odnowienia naturalnego badanych gatunków wykaże odpowiedź na cechy środowiskowe – żyzność oraz dostępność światła (Grotkopp i in. 2010; Karolewski i in. 2013; Giertych i in. 2015; Hale i in. 2016).
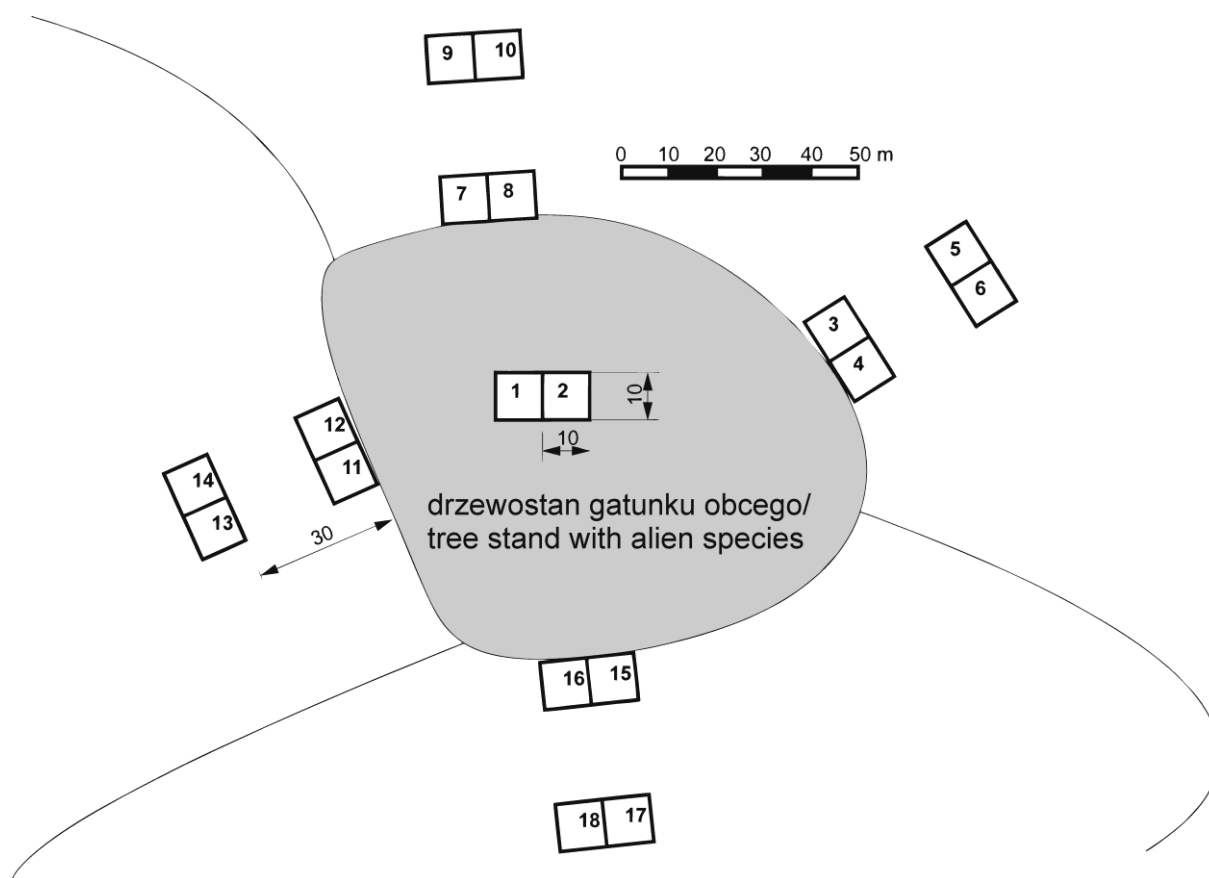
3. Materiał i metody

3.1. Badane gatunki

W celu przeanalizowania wzorców inwazji biologicznych drzew i krzewów wybrano trzy gatunki modelowe, o różnych cechach biologicznych: czeremchę amerykańską *Prunus serotina* Ehrh., dąb czerwony *Quercus rubra* L. oraz robinię akacjową *Robinia pseudoacacia* L. Gatunki te były wprowadzane do lasów jako domieszki biocenotyczne oraz produkcyjne. Są one rozpowszechnione zarówno w lasach Polski (Gazda i Augustynowicz 2012; Tokarska-Guzik i in. 2012), jak i Europy (Lambdon i in. 2008; Wagner i in. 2017). Stanowią zagrożenie dla wielu typów ekosystemów, między innymi dla siedlisk przyrodniczych Natura 2000 (Tokarska-Guzik i in. 2012; Carboneras i in. 2018). Gatunki te łączy pochodzenie – wszystkie występują naturalnie we wschodniej części Ameryki Północnej (Burns i Honkala 1990).

3.2. Układ powierzchni badawczych

Na miejsce badań w ramach pracy doktorskiej wybrałem Wielkopolski Park Narodowy (WPN) z uwagi na ograniczony zakres realizowanych tu działań gospodarczych oraz obfitość obcych gatunków drzew i krzewów w nim odnotowanych. W WPN stwierdzono najwięcej obcych taksonów roślin drzewiastych spośród wszystkich parków narodowych w Polsce (Purcel 2009; Gazda i Szwagrzyk 2016). Na terenie WPN założono 21 bloków powierzchni badawczych po 18 poletek o wielkości 100 m² każde, z centrum bloku w drzewostanie macierzystym (monokulturze *Q. rubra* lub *R. pseudoacacia* lub drzewostanie sosnowym z owocującym podszytem *P. serotina*). Poletka zostały rozmieszczone parami: jedna para w centrum drzewostanu macierzystego, cztery pary poletek tuż za granicą drzewostanu macierzystego (każda z czterech par założona w osi głównych kierunków świata) i kolejne cztery pary poletek badawczych w odległości 30 m od nich (Ryc. 1). Poletka reprezentowały pełen zakres zmienności leśnych zbiorowisk roślinnych występujących na glebach mineralnych – od borów sosnowych *Leucobryo-Pinetum* po łęgi zboczowe *Querco-Ulmetum minoris violetosum odoratae*. Większość poletek reprezentowała leśne zbiorowiska zastępcze z sosną zwyczajną na siedliskach grądów oraz pomiędzy acydofilnymi dąbrowami *Calamagrostio arundinaceae-Quercetum* a grądami *Galio sylvatici-Carpinetum*. Z uwagi na silne zróżnicowanie terenowe, zarówno związane z geomorfologią, jak i roślinnością, powierzchnie zostały usytuowane po dwie obok siebie, aby zapewnić minimalną liczbę powtórzeń.

Ryc. 1. Schemat bloku z poletkami badawczymi

3.3. Zbiór danych

Na każdej z 378 powierzchni badawczych co roku wykonywano spis florystyczny z określeniem pokrycia roślin w dziewięciostopniowej skali ilościowości Braun-Blanqueta. Zmierzono również wysokość oraz średnicę w szyi korzeniowej drzewek wszystkich badanych gatunków występujących w warstwie nalotu (do 50 cm wysokości) na powierzchniach badawczych. W lipcu 2017 roku pozyskano drzewa modelowe w celu opracowania równań allometrycznych pozwalających na estymację biomasy odnowienia naturalnego badanych neofitów oraz określenie ich cech funkcjonalnych. Łącznie zebrano 647 roślin: 356 osobników *P. serotina* (195 siewek i 161 starszych nalotów), 133 osobniki *Q. rubra* (72 siewki i 61 starszych nalotów) i 158 osobników *R. pseudoacacia* (94 siewki i 64 starszych nalotów). Dla porównania zebrano również odnowienie naturalne czterech najczęściej współwystępujących gatunków rodzimych: 75 starszych nalotów i 48 siewek *Acer platanoides*, 91 i 341 *A. pseudoplatanus*, 23 i 59 *Fagus sylvatica* oraz 29 i 78 *Q. petraea*.

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Rośliny wybierano w sposób losowy, a liczba zebranych osobników zależała od ich zagęszczenia na poletkach. Rośliny były wybierane z obszaru o szerokości 5 m wokół poletek badawczych, aby nie zakłócić wyników dalszych obserwacji.

Drzewka rozdzielono na komponenty biomasy – korzenie, liście oraz łodygę. Rozdzielony materiał roślinny suszono w temperaturze 65°C oraz ważono z dokładnością do 0,001 g. Liście z drzew modelowych zeskanowano w celu określenia ich powierzchni. Następnie obliczono biomasę całkowitą, udział biomasy liści, łodygi i korzeni w biomasie całkowitej, powierzchnię rzutu liści, stosunek powierzchni liści do biomasy całkowitej oraz specyficzną powierzchnię liści (SLA, stosunek powierzchni liści do masy liści). W celu estymacji biomasy na poletkach badawczych opracowano równania allometryczne – funkcje nieliniowe pozwalające na określenie biomasy osobniczej na podstawie wymiarów drzew modelowych. Przetestowano 10 postaci funkcji stosowanych w innych badaniach dotyczących biomasy drzew i krzewów (Jagodziński i in. 2018a,b,c).

Dla każdej pary poletek określono strukturę drzewostanu, dostępność światła (indeks ażurowości koron drzew, *diffusive non-interceptance;* DIFN) wg metodyki Machado i Reicha (1999). Pomiary DIFN wykonano za pomocą urządzenia LAI-2200 (Li-Cor Inc.), na każdym poletku przeprowadzając cztery serie po 10 pomiarów. Dla każdej pary powierzchni badawczych w marcu 2017 r. zebrano po cztery próby ścioły z ramek o powierzchni 0,2 m². Ściołę wysuszono w temperaturze 65°C oraz rozdzielono na część rozpoznawalną (igły/liście, gałęzie, szyszki/owoce, itp.) i nierozpoznawalną (szczątki roślin w różnych stadiach rozkładu). Próby ścioły poddano także analizie pH oraz zawartości węgla i azotu.

3.4. Analiza danych

Wszystkie analizy wykonano przy użyciu programu R (R Core Team 2018). Do przetwarzania potokowego i wizualizacji danych wykorzystano pakiety z uniwersum *tidyverse*: *dplyr* (Wickham i Francois 2015), *ggplot2* (Wickham 2009) oraz *reshape2* (Wickham 2007). Dla każdego poletka badawczego zestawiono informacje ze spisów florystycznych w celu obliczenia parametrów opisujących roślinność runa. Obliczono średnie ważone ilościowością dla trzech cech funkcjonalnych najlepiej opisujących strategie życiowe roślin – wysokości, SLA oraz masy nasion (Westoby 1998) oraz wskaźników Ellenberga, opisujących wymagania siedliskowe gatunków roślin (Ellenberg

i Leuschner 2010). Dodatkowo obliczono komponenty różnorodności funkcjonalnej – dyspersję, dywergencję, bogactwo i równocenność (Laliberté i Legendre 2010; Laliberté i in. 2014). Określono również bogactwo i różnorodność taksonomiczną, a także wskaźniki zaburzeń opracowane przez Herbena i in. (2016).

W celu weryfikacji hipotezy 1. dla grup odnowienia naturalnego (siewki i starszy nalot) opracowano specyficzne dla gatunku modele *random forest* (Breiman 2001). Algorytm ten składa się z dużej liczby drzew regresyjnych, które wskazują na wartość funkcji odpowiedzi. Zastosowanie wielu drzew, których odpowiedź jest ważona błędem poszczególnych drzew, pozwala na stabilniejszą predykcję estymowanej zmiennej. Modele te pozwalają na określenie ważności poszczególnych predyktorów oraz na określenie przebiegu trajektorii funkcji odpowiedzi przy założeniu stałego poziomu pozostałych predyktorów. Ważność predyktorów została określona za pomocą wartości przyrostu błędu średniokwadratowego (RMSE) przy losowym przetasowaniu danego predyktora w bazie danych. Ponieważ głównym zadaniem badawczym było określenie hierarchii predyktorów, ważność została wyrażona jako procent przyrostu RMSE modelu. Modele wytrenowano za pomocą pakietu *caret* (Kuhn 2008).

W celu weryfikacji hipotezy 2. najpierw określono, w jaki sposób gradient zaburzeń determinuje kompozycję gatunkową roślinności runa na badanych poletkach. W tym celu wykonano nietendencyjną analizę korespondencji (DCA; Hill i Gauch 1980) i za pomocą pasywnej projekcji przedstawiono kierunki zróżnicowania cech opisujących roślinność. Analizy wykonano za pomocą pakietu *vegan* (Oksanen i in. 2018). Do określenia zależności pomiędzy wskaźnikami zaburzeń a zagęszczeniem i biomasą odnowienia naturalnego badanych gatunków zastosowano modele liniowe oraz 95% przedziały ufności wielkości efektu.

W celu weryfikacji hipotezy 3. porównano wartości badanych cech funkcjonalnych gatunków obcych i ich rodzimych konkurentów za pomocą analizy wariancji modelu mieszanego, uwzględniającego poletko badawcze jako efekt losowy. Pozwoliło to na wyłączenie z wnioskowania efektów specyficznych dla poletek badawczych. Modele opracowano za pomocą bibliotek *lmer* i *lmerTest* (Bates i in. 2015; Kuznetsova i in. 2017). W celu określenia różnic w wielości współczynnika zmienności dla par gatunków wykorzystano zmodyfikowany test Krishnamoorthy i Lee (2014) zaimplementowany w bibliotece *cvequality* (Marwick i Krishnamoorthy 2016). Aby określić zmienność cech

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funkcjonalnych w gradientach pH ścioły i dostępności światła dla gatunków zastosowano model *random forest*. W celu określenia ważności cech wykorzystano nieskalowaną wartość przyrostu RMSE przy przetasowaniu zmiennych, obliczoną za pomocą pakietu *DALEX* (Biecek 2018a). Do wizualizacji zmian wyestymowanych wartości badanych cech funkcjonalnych wzdłuż gradientów i różnic pomiędzy gatunkami wykorzystano pakiet *ceterisParibus* (Biecek 2018b).

4. Główne wyniki pracy

4.1. Wpływ dostępności propagul na sukces ekologiczny odnowienia naturalnego badanych neofitów

Publikacja 1. *Drivers of invasive tree and shrub natural regeneration in temperate forests*

Uzyskane wyniki wskazują na większą ważność predyktorów dla zmiennych objaśnianych cech opisujących dostępność propagul niż właściwości ekosystemu (Dyderski i Jagodziński 2018a). W przypadku zarówno siewek, jak i starszych nalotów, zarówno obecność, jak i ilość (wyrażona polem powierzchni przekroju pierśnicowego) drzew matecznych była najważniejszym predyktorem biomasy odnowienia naturalnego badanych gatunków. Cechy związane z właściwościami ekosystemów miały mniejsze znaczenie niż cechy opisujące dostępność propagul. W ten sposób potwierdziłem hipotezę nr 1. Równocześnie w pracy wykazano różnice w krzywych odpowiedzi pomiędzy siewkami i starszym nalotem. Największe wymagania świetlne ma *P. serotina*, podczas gdy *R. pseudoacacia* występowała na poletkach o najmniejszej dostępności światła. Wynik ten jest jednak obciążony wegetatywnym pochodzeniem 30% odnowienia naturalnego tego gatunku, zaopatrywanego przez systemy korzeniowe drzew rodzicielskich. Największe wymagania troficzne ma *R. pseudoacacia*, najmniejsze zaś – *P. serotina*.

4.2. Wpływ zaburzeń na sukces ekologiczny odnowienia naturalnego badanych neofitów

Publikacja 2. *Low impact of disturbance on ecological success of invasive tree and shrub species in temperate forests*

Wyniki analiz wykazały istotny wpływ reżimu zaburzeń na kompozycję gatunkową roślinności runa (Dyderski i Jagodziński 2018b). Pomimo tego, analiza relacji pomiędzy wskaźnikami zaburzeń wg Herbena i in. (2016) a biomasą i zagęszczeniem odnowienia naturalnego badanych gatunków wykazała, że zaburzenia mają niewielki wpływ na ich sukces ekologiczny (Dyderski i Jagodziński 2018b). Niewielka korelacja pomiędzy wskaźnikami zaburzeń a cechami obrazującymi sukces ekologiczny badanych gatunków była istotna statystycznie, lecz nieistotna biologicznie z uwagi na małą wielkość efektu. Największy wpływ zaburzeń na odnowienie naturalne stwierdzono w przypadku wskaźnika częstości zaburzeń w oparciu o całe zbiorowisko roślinne dla biomasy *P. serotina*. Uzyskane w tej pracy wyniki potwierdziły hipotezę nr 2. Świadczą one

o niewielkim wpływie zaburzeń na najmłodsze stadium życiowe inwazyjnych gatunków drzew i krzewów. W świetle wyników wskazujących na największe znaczenie dostępności propagul dla kształtowania się podatności ekosystemów leśnych na inwazje (Dyderski i Jagodziński 2018a) można założyć, że sukces badanych neofitów jest bardziej związany ze stochastycznymi procesami kształtującymi śmiertelność siewek niż z uwolnieniem siewek badanych gatunków przez zaburzenia. Ma to znaczenie dla monitoringu inwazji biologicznych – wskazuje na zwiększoną potrzebę monitorowania tzw. krawędzi inwazji (*invasion edge*), zwłaszcza pod kątem dostępności propagul.

4.3. Czynniki determinujące sukces ekologiczny odnowienia naturalnego badanych neofitów

Publikacja 3. *Functional traits of acquisitive invasive woody species differ from conservative invasive and native species*

Porównanie badanych gatunków inwazyjnych z najczęściej współwystępującymi gatunkami rodzimymi drzew wykazało, że gatunki inwazyjne o strategii akwizycyjnej (*P. serotina* oraz *R. pseudoacacia*) miały większy udział liści w biomasie osobniczej oraz większe SLA niż pozostałe gatunki (Dyderski i Jagodziński 2019b). Gatunek inwazyjny o strategii konserwatywnej (*Q. rubra*) miał najwyższą osobniczą biomasę całkowitą oraz udział korzeni w biomasie. Gatunki inwazyjne zwykle cechował większy współczynnik zmienności badanych cech w porównaniu z gatunkami rodzimymi. Uzyskane wyniki wskazują, że całkowita powierzchnia liści, jako narzędzie konkurencji w warstwie nalotu, może być rozbudowywane na dwa sposoby – przez większą inwestycję w alokację biomasy i morfologię aparatu asymilacyjnego lub przez większe tempo wzrostu (zwiększanie całkowitej biomasy). Obydwie strategie pozwalają badanym gatunkom osiągnąć sukces ekologiczny. Relacje pomiędzy pH ścioły lub dostępnością światła a wartościami cech funkcjonalnych badanych neofitów oraz ich rodzimych konkurentów wykazały, że większe znaczenie w kształtowaniu analizowanych cech ma gatunek niż poziom dostępności zasobów. W ten sposób hipoteza nr 3 została potwierdzona. Nie mniej jednak, zmienność międzygatunkowa badanych cech funkcjonalnych była większa niż zmienność wewnątrzgatunkowa (wzdłuż gradientów środowiskowych), co świadczy o niewielkiej roli plastyczności badanych gatunków w kształtowaniu ich potencjału inwazyjnego.

5. Wnioski

Wyniki uzyskane w toku realizacji niniejszej pracy doktorskiej uzupełniają wiedzę na temat mechanizmów dyspersji inwazyjnych gatunków drzew i krzewów. Dzięki szerokiemu zakresowi analizowanych warunków środowiskowych, rezultaty przeprowadzonych badań można ekstrapolować na inne układy ekologiczne w lasach strefy klimatu umiarkowanego. Pozwolą one na lepsze zrozumienie czynników odpowiedzialnych za sukces ekologiczny młodego pokolenia badanych neofitów.

W wyniku przeprowadzonych badań stwierdzono, że:

- dostępność propagul ma kluczowe znaczenie dla rozprzestrzeniania się inwazyjnych gatunków drzew i krzewów,

- intensywność i częstotliwość zaburzeń w ekosystemie leśnym ma małe znaczenie dla kształtowania się banku nalotów badanych neofitów,

- gatunki te zyskują również przewagę z uwagi na różnice w strategii życiowej w stosunku do rodzimych konkurentów,

- reprezentujące strategię akwizycyjną *P. serotina* i *R. pseudoacacia* alokują więcej biomasy do liści i mają większą specyficzną powierzchnię liści niż *Q. rubra* i gatunki rodzime,

- *Q. rubra* reprezentuje strategię konserwatywną i alokuje więcej biomasy do korzeni i ma większą osobniczą biomasę całkowitą niż pozostałe gatunki,

- obie strategie prowadzą do zamierzonego efektu – wzrostu powierzchni aparatu asymilacyjnego, niezbędnego do wykorzystywania energii słonecznej, która jest deficytowym zasobem na dnie lasu,

- strategie te są również związane z wymaganiami ekologicznymi badanych gatunków, pozwalającymi na kolonizację szerokiego spektrum warunków siedliskowych.

Z tego względu efektywne zarządzanie inwazyjnymi gatunkami drzew i krzewów wymaga skupienia zarówno na źródłach propagul, jak i właściwościach kolonizowanych ekosystemów. Działania ograniczające rozprzestrzenianie się badanych neofitów powinny dotyczyć wczesnego usuwania osobników wytwarzających potomstwo (w tym wegetatywne). Działania związane z modyfikacją właściwości kolonizowanych ekosystemów mogą dotyczyć utrzymania gatunków konkurujących z badanymi neofitami – zarówno w warstwie zielnej, jak i w drzewostanie, np. utrzymywanie wysokiego zwarcia

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koron drzew lub wprowadzanie/promowanie odnowienia naturalnego gatunków o dużym indeksie powierzchni liściowej (np. *Acer platanoides*, *Fagus sylvatica*).

6. Literatura

Aerts R, Ewald M, Nicolas M, Piat J, Skowronek S, Lenoir J, Hattab T, Garzón-López CX, Feilhauer H, Schmidtlein S, Rocchini D, Decocq G, Somers B, Van De Kerchove R, Denef K, Honnay O (2017) Invasion by the Alien Tree *Prunus serotina* Alters Ecosystem Functions in a Temperate Deciduous Forest. Frontiers in Plant Science 8:179.

Allison SD, Vitousek PM (2004) Rapid nutrient cycling in leaf litter from invasive plants in Hawai'i. Oecologia 141:612–619.

Alpert P, Bone E, Holzapfel C (2000) Invasiveness, invasibility and the role of environmental stress in the spread of non-native plants. Perspectives in Plant Ecology, Evolution and Systematics 3:52–66.

Annighöfer P, Mölder I, Zerbe S, Kawaletz H, Terwei A, Ammer C (2012) Biomass functions for the two alien tree species *Prunus serotina* Ehrh. and *Robinia pseudoacacia* L. in floodplain forests of Northern Italy. European Journal of Forest Research 131:1619–1635.

Aslan CE, Rejmánek M, Klinger R (2012) Combining efficient methods to detect spread of woody invaders in urban–rural matrix landscapes: an exploration using two species of Oleaceae. Journal of Applied Ecology 49:331–338.

Baker HG (1974) The Evolution of Weeds. Annual Review of Ecology and Systematics 5:1–24.

Baraloto C, Goldberg DE, Bonal D (2005) Performance trade-offs among tropical tree seedlings in contrasting microhabitats. Ecology 86:2461–2472.

Barbier S, Gosselin F, Balandier P (2008) Influence of tree species on understory vegetation diversity and mechanisms involved – a critical review for temperate and boreal forests. Forest Ecology and Management 254:1–15.

Barkman JJ (1958) Phytosociology and Ecology of Cryptogamic Epiphytes. Van Gorcum and Company, Assen.

Bates D, Mächler M, Bolker B, Walker S (2015) Fitting linear mixed-effects models using lme4. Journal of Statistical Software 67:1–48.

Biecek P (2018a) DALEX: Descriptive mAchine Learning EXplanations. https://cran.r-project.org/web/packages/DALEX/index.html

Biecek P (2018b) ceterisParibus: Ceteris Paribus Plots (What-If Plots) for a Single Observation. https://cran.r-project.org/web/packages/ceterisParibus/index.html

Blossey B, Notzold R (1995) Evolution of increased competitive ability in invasive nonindigenous plants: a hypothesis. Journal of Ecology 83:887–889.

Breiman L (2001) Random forests. Machine Learning 45:5–32.

Burns RM, Honkala BH (1990) Silvics of North America. United States Department of Agriculture, Forest Service; Washington D.C.

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Canham CD, Finzi AC, Pacala SW, Burbank DH (1994) Causes and consequences of resource heterogeneity in forests: interspecific variation in light transmission by canopy trees. Canadian Journal of Forest Research 24:337–349.

Capinha C, Essl F, Seebens H, Moser D, Pereira HM (2015) The dispersal of alien species redefines biogeography in the Anthropocene. Science 348:1248–1251.

Carboneras C, Genovesi P, Vilà M, Blackburn TM, Carrete M, Clavero M, D'hondt B, Orueta JF, Gallardo B, Geraldes P, González-Moreno P, Gregory RD, Nentwig W, Paquet J-Y, Pyšek P, Rabitsch W, Ramírez I, Scalera R, Tella JL, Walton P, Wynde R (2018) A prioritised list of invasive alien species to assist the effective implementation of EU legislation. Journal of Applied Ecology 22:539–547.

Ceballos G, Ehrlich PR, Barnosky AD, García A, Pringle RM, Palmer TM (2015) Accelerated modern human–induced species losses: Entering the sixth mass extinction. Science Advances 1:e1400253.

Chabrerie O, Verheyen K, Saguez R, Decocq G (2008) Disentangling relationships between habitat conditions, disturbance history, plant diversity, and American black cherry (*Prunus serotina* Ehrh.) invasion in a European temperate forest. Diversity and Distributions 14:204–212.

Chave J, Coomes D, Jansen S, Lewis SL, Swenson NG, Zanne AE (2009) Towards a worldwide wood economics spectrum. Ecology Letters 12:351–366.

Chmura D (2013) Impact of alien tree species *Quercus rubra* L. on understorey environment and flora: a study of the Silesian Upland (southern Poland). Polish Journal of Ecology 61:431–442.

Chmura D, Sierka E (2007) The invasibility of deciduous forest communities after disturbance: a case study of *Carex brizoides* and *Impatiens parviflora* invasion. Forest Ecology and Management 242:487–495.

Cienciala E, Lindroth A, Čermák J, Hällgren J-E, Kučera J (1992) Assessment of transpiration estimates for *Picea abies* trees during a growing season. Trees 6:121–127.

Closset-Kopp D, Chabrerie O, Valentin B, Delachapelle H, Decocq G (2007) When Oskar meets Alice: Does a lack of trade-off in r/K-strategies make *Prunus serotina* a successful invader of European forests? Forest Ecology and Management 247:120–130.

Corenblit D, Steiger J, Tabacchi E, González E, Planty-Tabacchi A-M (2014) Ecosystem engineers modulate exotic invasions in riparian plant communities by modifying hydrogeomorphic connectivity: Ecosystem engineers modulate exotic invasions. River Research and Applications 30:45–59.

Crooks JA (2002) Characterizing ecosystem-level consequences of biological invasions: the role of ecosystem engineers. Oikos 97:153–166.

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Danielewicz W, Maliński T (2003) Alien tree and shrub species in Poland regenerating by self-sowing. Rocznik Dendrologiczny 51:205–236.

Davies KF, Chesson P, Harrison S, Inouye BD, Melbourne BA, Rice KJ (2005) Spatial heterogeneity explains the scale dependence of the native-exotic diversity relationship. Ecology 86:1602–1610.

Davis MA, Grime JP, Thompson K (2000) Fluctuating resources in plant communities: a general theory of invasibility. Journal of Ecology 88:528–534.

Dech JP, Robinson LM, Nosko P (2008) Understorey plant community characteristics and natural hardwood regeneration under three partial harvest treatments applied in a northern red oak (*Quercus rubra* L.) stand in the Great Lakes-St. Lawrence forest region of Canada. Forest Ecology and Management 256:760–773.

Díaz S, Kattge J, Cornelissen JHC, Wright IJ, Lavorel S, Dray S, Reu B, Kleyer M, Wirth C, Colin Prentice I, Garnier E, Bönisch G, Westoby M, Poorter H, Reich PB, Moles AT, Dickie J, Gillison AN, Zanne AE, Chave J, Joseph Wright S, Sheremet'ev SN, Jactel H, Baraloto C, Cerabolini B, Pierce S, Shipley B, Kirkup D, Casanoves F, Joswig JS, Günther A, Falczuk V, Rüger N, Mahecha MD, Gorné LD (2016) The global spectrum of plant form and function. Nature 529:167–171.

Dickie IA, Oleksyn J, Reich PB, Karolewski P, Zytkowiak R, Jagodziński AM, Turzanska E (2006) Soil modification by different tree species influences the extent of seedling ectomycorrhizal infection. Mycorrhiza 16:73–79.

Donaldson JE, Hui C, Richardson DM, Robertson MP, Webber BL, Wilson JRU (2014) Invasion trajectory of alien trees: the role of introduction pathway and planting history. Global Change Biology 20:1527–1537.

Dullinger S, Dendoncker N, Gattringer A, Leitner M, Mang T, Moser D, Mücher CA, Plutzar C, Rounsevell M, Willner W, Zimmermann NE, Hülber K (2015) Modelling the effect of habitat fragmentation on climate-driven migration of European forest understorey plants. Diversity and Distributions21:1375–1387.

Dyderski MK, Banaszczak P, Rawlik M, Jagodziński AM (2017) Interaction between invasive and potentially invasive shrub species does not influence relationships between their ecological success and distance from propagule sources. Plant Ecology 218:923–933.

Dyderski MK, Gdula AK, Jagodziński AM (2015) "The rich get richer" concept in riparian woody species – A case study of the Warta River Valley (Poznań, Poland). Urban Forestry & Urban Greening 14:107–114.

Dyderski MK, Jagodziński AM (2016) Patterns of plant invasions at small spatial scale correspond with that at the whole country scale. Urban Ecosystems 19:983–998.

Dyderski MK, Jagodziński AM (2018a) Drivers of invasive tree and shrub natural regeneration in temperate forests. Biological Invasions 20:2363–2379.

Dyderski MK, Jagodziński AM (2018b) Low impact of disturbance on ecological success of invasive tree and shrub species in temperate forests. Plant Ecology 219:2369–1380.

Dyderski MK, Jagodziński AM (2019a) Context-Dependence of Urban Forest Vegetation Invasion Level and Alien Species' Ecological Success. Forests 10:#26.

Dyderski MK, Jagodziński AM (2019b) Functional traits of acquisitive invasive woody species differ from conservative invasive and native species. NeoBiota 41:91–113.

Dyderski MK, Paź S, Frelich LE, Jagodziński AM (2018) How much does climate change threaten European forest tree species distributions? Global Change Biology 24:1150–1163.

Ehrenfeld JG (2003) Effects of exotic plant invasions on soil nutrient cycling processes. Ecosystems 6:503–523.

Ellenberg H, Leuschner C (2010) Vegetation Mitteleuropas mit den Alpen in ökologischer, dynamischer und historischer Sicht. UTB; Stuttgart.

Elton CS (1958) The Ecology of Invasions by Animals and Plants. University of Chicago Press; Chicago.

Emborg J (1998) Understorey light conditions and regeneration with respect to the structural dynamics of a near-natural temperate deciduous forest in Denmark. Forest Ecology and Management 106:83–95.

Essl F, Hulme PE, Jeschke JM, Keller R, Pyšek P, Richardson DM, Saul W-C, Bacher S, Dullinger S, Estévez RA, Kueffer C, Roy HE, Seebens H, Rabitsch W (2017) Scientific and Normative Foundations for the Valuation of Alien-Species Impacts: Thirteen Core Principles. BioScience 67:166–178.

Faliński JB (1968) Stadia neofityzmu i stosunek neofitów do innych komponentów zbiorowiska. Materiały Zakładu Fitosocjologii Stosowanej Uniwersytetu Warszawskiego 25:15–23.

Fay E, Lavoie C (2009) The impact of birch seedlings on evapotranspiration from a mined peatland: an experimental study in southern Quebec, Canada. Mires and Peat 5:1–7.

Gazda A, Augustynowicz P (2012) Obce gatunki drzew w polskich lasach gospodarczych. Co wiemy o puli i o rozmieszczeniu wybranych taksonów? Studia i Materiały Centrum Edukacji Przyrodniczo-Leśnej w Rogowie 14:53–61.

Gazda A, Szwagrzyk J (2016) Introduced species in Polish National Parks: distribution, abundance and management approaches. W: Krumm F, Vítková L (red.) Introduced tree species in European forests: opportunities and challenges. European Forest Institute; Freiburg, ss. 168–175.

Giertych MJ, Karolewski P, Oleksyn J (2015) Carbon allocation in seedlings of deciduous tree species depends on their shade tolerance. Acta Physiologiae Plantarum 37:216.

González-Muñoz N, Castro-Díez P, Godoy O (2014) Lack of superiority of invasive over co-occurring native riparian tree seedling species. Biological Invasions 16:269–281.

Gorchov DL, Trisel DE (2003) Competitive effects of the invasive shrub, *Lonicera maackii* (Rupr.) Herder (Caprifoliaceae), on the growth and survival of native tree seedlings. Plant Ecology 166:13–24.

Grotkopp E, Erskine-Ogden J, Rejmánek M (2010) Assessing potential invasiveness of woody horticultural plant species using seedling growth rate traits. Journal of Applied Ecology 47:1320–1328.

Halarewicz A (2012) Właściwości ekologiczne i skutki rozprzestrzeniania się czeremchy amerykańskiej *Padus serotina* (Ehrh.) Borkh. w wybranych fitocenozach leśnych. Wydawnictwo Uniwersytetu Przyrodniczego; Wrocław.

Hale AN, Lapointe L, Kalisz S (2016) Invader disruption of belowground plant mutualisms reduces carbon acquisition and alters allocation patterns in a native forest herb. New Phytologist 209:542–549.

Hendrychová M, Šálek M, Tajovskỳ K, Řehoř M (2012) Soil properties and species richness of invertebrates on afforested sites after brown coal mining. Restoration Ecology 20:561–567.

Herben T, Chytrý M, Klimešová J (2016) A quest for species-level indicator values for disturbance. Journal of Vegetation Science 27:628–636.

Herben T, Mandák B, Bímová K, Münzbergová Z (2004) Invasibility and species richness of a community: a neutral model and a survey of published data. Ecology 85:3223–3233.

Hill MO, Gauch HG (1980) Detrended correspondence analysis: An improved ordination technique. Vegetatio 42:47–58.

Hobbie SE, Reich PB, Oleksyn J, Ogdahl M, Zytkowiak R, Hale C, Karolewski P (2006) Tree species effects on decomposition and forest floor dynamics in a common garden. Ecology 87:2288–2297.

Holeksa J, Saniga M, Szwagrzyk J, Dziedzic T, Ferenc S, Wodka M (2007) Altitudinal variability of stand structure and regeneration in the subalpine spruce forests of the Pol'ana biosphere reserve, Central Slovakia. European Journal of Forest Research 126:303–313.

Horodecki P, Jagodziński AM (2017) Tree species effects on litter decomposition in pure stands on afforested post-mining sites. Forest Ecology and Management 406:1–11.

Hulme PE, Pyšek P, Jarošík V, Pergl J, Schaffner U, Vilà M (2013) Bias and error in understanding plant invasion impacts. Trends in Ecology & Evolution 28:212–218.

Jagodziński AM, Dyderski MK, Gęsikiewicz K, Horodecki P (2018a) Tree- and Stand-Level Biomass Estimation in a *Larix decidua* Mill. Chronosequence. Forests 9:#587.

Jagodziński AM, Dyderski MK, Gęsikiewicz K, Horodecki P, Cysewska A, Wierczyńska S, Maciejczyk K (2018b) How do tree stand parameters affect young Scots pine biomass? – Allometric equations and biomass conversion and expansion factors. Forest Ecology and Management 409:74–83. 4

Jagodziński AM, Dyderski MK, Horodecki P, Rawlik K (2018c) Limited dispersal prevents *Quercus rubra* invasion in a 14-species common garden experiment. Diversity and Distributions 24:403–414. 4

Jagodziński AM, Dyderski MK, Rawlik M, Banaszczak P (2015) Plantation of coniferous trees modifies risk and size of *Padus serotina* (Ehrh.) Borkh. invasion – Evidence from a Rogów Arboretum case study. Forest Ecology and Management 357:84–94.

Jagodziński AM, Wierzcholska S, Dyderski MK, Horodecki P, Rusińska A, Gdula AK, Kasprowicz M (2018d) Tree species effects on bryophyte guilds on a reclaimed post-mining site. Ecological Engineering 110:117–127.

Jo I, Fridley JD, Frank DA (2016) More of the same? In situ leaf and root decomposition rates do not vary between 80 native and nonnative deciduous forest species. New Phytologist 209:115–122.

Jo I, Fridley JD, Frank DA (2015) Linking above- and belowground resource use strategies for native and invasive species of temperate deciduous forests. Biological Invasions 17:1545–1554.

Kałucka IL, Jagodziński AM (2016) Successional traits of ectomycorrhizal fungi in forest reclamation after surface mining and agricultural disturbances: A review. Dendrobiology 76:91–104.

Kamczyc J, Skorupski M, Dyderski MK, Gazda A, Hachułka M, Horodecki P, Kałucka I, Malicki M, Pielech R, Smoczyk M, Wierzcholska S, Jagodziński AM (2018) Response of soil mites (Acari, Mesostigmata) to long-term Norway spruce plantation along a mountain stream. Experimental and Applied Acarology 76:269-286.

Kaplan JO, Krumhardt KM, Zimmermann N (2009) The prehistoric and preindustrial deforestation of Europe. Quaternary Science Reviews 28:3016–3034.

Karolewski P, Giertych MJ, Żmuda M, Jagodziński AM, Oleksyn J (2013) Season and light affect constitutive defenses of understory shrub species against folivorous insects. Acta Oecologica 53:19–32.

Kawaletz H, Mölder I, Annighöfer P, Terwei A, Zerbe S, Ammer C (2014) Back to the roots: how do seedlings of native tree species react to the competition by exotic species? Annals of Forest Science 71:337–347.

Knight KS, Oleksyn J, Jagodziński AM, Reich PB, Kasprowicz M (2008) Overstorey tree species regulate colonization by native and exotic plants: a source of positive relationships between understorey diversity and invasibility. Diversity and Distributions 14:666–675.

Kolb TE, Steiner KC, McCormick LH, Bowersox TW (1990) Growth response of northern red-oak and yellow-poplar seedlings to light, soil moisture and nutrients in relation to ecological strategy. Forest Ecology and Management 38:65–78.

Krishnamoorthy K, Lee M (2014) Improved tests for the equality of normal coefficients of variation. Computational Statistics 29:215–232.

Křivánek M, Pyšek P, Jarošík V (2006) Planting History and Propagule Pressure as Predictors of Invasion by Woody Species in a Temperate Region. Conservation Biology 20:1487–1498.

Kučerová A, Rektoris L, Štechová T, Bastl M (2008) Disturbances on a Wooded Raised Bog—How Windthrow, Bark Beetle and Fire Affect Vegetation and Soil Water Quality? Folia Geobotanica 43:49–67.

Kuhn M (2008) Building Predictive Models in R Using the caret Package. Journal of Statistical Software 28:1–26.

Kuznetsova A, Brockhoff PB, Christensen RHB (2017) lmerTest: Tests in Linear Mixed Effects Models. Journal of Statistical Software 82: #13.

Laliberté E, Legendre P (2010) A distance-based framework for measuring functional diversity from multiple traits. Ecology 91:299–305.

Laliberté E, Legendre P, Shipley B (2014) FD: Measuring functional diversity (FD) from multiple traits, and other tools for functional ecology. https://cran.r-project.org/package=FD

Lambdon PW, Pyšek P, Basnou C, Hejda M, Arianoutsou M, Essl F, Jarošík V, Pergl J, Winter M, Anastasiu P, Andriopoulos P, Bazos I, Brundu G, Celesti-Grapow L, Chassot P, Delipetrou P, Josefsson M, Kark S, Klotz S, Kokkoris Y, Kühn I, Marchante H, Perglová I, Pino J, Vilá M, Zikos A, Hulme PE (2008) Alien flora of Europe: species diversity, temporal trends, geographical patterns and research needs. Preslia 80:101–149.

Lockwood JL, Cassey P, Blackburn T (2005) The role of propagule pressure in explaining species invasions. Trends in Ecology and Evolution 20:223–228.

Lonsdale WM (1999) Global patterns of plant invasions and the concept of invasibility. Ecology 80:1522–1536.

Machado J-L, Reich PB (1999) Evaluation of several measures of canopy openness as predictors of photosynthetic photon flux density in deeply shaded conifer-dominated forest understory. Canadian Journal of Forest Research 29:1438–1444.

Major KC, Nosko P, Kuehne C, Campbell D, Bauhus J (2013) Regeneration dynamics of non-native northern red oak (*Quercus rubra* L.) populations as influenced by environmental factors:

A case study in managed hardwood forests of southwestern Germany. Forest Ecology and Management 291:144–153.

Marwick B, Krishnamoorthy K (2016) cvequality: Tests for the Equality of Coefficients of Variation from Multiple Groups. R package version 0.1.3. https://cran.r-project.org/package=cvequality

Matzek V (2011) Superior performance and nutrient-use efficiency of invasive plants over non-invasive congeners in a resource-limited environment. Biological Invasions 13:3005–3014.

Mežaka A, Brūmelis G, Piterāns A (2012) Tree and stand-scale factors affecting richness and composition of epiphytic bryophytes and lichens in deciduous woodland key habitats. Biodiversity and Conservation 21:3221–3241.

Mitchell CE, Power AG (2003) Release of invasive plants from fungal and viral pathogens. Nature 421:625–627.

Mueller KE, Eisenhauer N, Reich PB, Hobbie SE, Chadwick OA, Chorover J, Dobies T, Hale CM, Jagodziński AM, Kałucka I, Kasprowicz M, Kieliszewska-Rokicka B, Modrzyński J, Rożen A, Skorupski M, Sobczyk Ł, Stasińska M, Trocha LK, Weiner J, Wierzbicka A, Oleksyn J (2016) Light, earthworms, and soil resources as predictors of diversity of 10 soil invertebrate groups across monocultures of 14 tree species. Soil Biology and Biochemistry 92:184–198.

Mueller KE, Eissenstat DM, Hobbie SE, Oleksyn J, Jagodzinski AM, Reich PB, Chadwick OA, Chorover J (2012) Tree species effects on coupled cycles of carbon, nitrogen, and acidity in mineral soils at a common garden experiment. Biogeochemistry 111:601–614.

Niinemets Ü (2010) A review of light interception in plant stands from leaf to canopy in different plant functional types and in species with varying shade tolerance. Ecological Research 25:693–714.

Oksanen J, Blanchet FG, Kindt R, Legendre P, Michin PR, O'Hara RB, Simpson GL, Solymos P, Henry M, Stevens H, Wagner H (2018) "vegan" 2.3.3. - Community Ecology Package. https://cran.r-project.org/package=vegan

Pairon M, Jonard M, Jacquemart A-L (2006) Modeling seed dispersal of black cherry, an invasive forest tree: how microsatellites may help? Canadian Journal of Forest Research 36:1385–1394.

Purcel A (2009) Obce gatunki drzew i krzewów w Wielkopolskim Parku Narodowym - ich występowanie i rola w biocenozach Parku. Morena 14:35–191.

Pyšek P, Křivánek M, Jarošík V (2009) Planting intensity, residence time, and species traits determine invasion success of alien woody species. Ecology 90:2734–2744.

Pyšek P, Manceur AM, Alba C, McGregor KF, Pergl J, Štajerová K, Chytrý M, Danihelka J, Kartesz J, Klimešová J, Lučanová M, Moravcová L, Nishino M, Sádlo J, Suda J, Tichý L, Kühn I (2015) Naturalization of central European plants in North America: species traits, habitats, propagule pressure, residence time. Ecology 96:762–774.

R Core Team (2018) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.r-project.org/

Rawlik M, Kasprowicz M, Jagodziński AM (2018) Differentiation of herb layer vascular flora in reclaimed areas depends on the species composition of forest stands. Forest Ecology and Management 409:541–551.

Reich PB, Oleksyn J, Modrzynski J, Mrozinski P, Hobbie SE, Eissenstat DM, Chorover J, Chadwick OA, Hale CM, Tjoelker MG (2005) Linking litter calcium, earthworms and soil properties: a common garden test with 14 tree species. Ecology Letters 8:811–818.

Reinhardt F, Herle M, Bastiansen F, Streit B (2003) Economic impact of the spread of alien species in Germany. Umweltbundesamt; Berlin.

Richardson DM (1998) Forestry trees as invasive aliens. Conservation Biology 12:18–26.

Richardson DM, Pyšek P (2012) Naturalization of introduced plants: ecological drivers of biogeographical patterns. New Phytologist 196:383–396.

Richardson DM, Pyšek P, Carlton JT (2011) A compendium of esssential concepts and terminology in invasion ecology. W: Richardson DM (red.) Fifty years of invasion ecology: the legacy of Charles Elton. Blackwell Publishing Ltd; Oxford, ss. 409–420

Richardson DM, Pyšek P, Rejmánek M, Barbour MG, Panetta FD, West CJ (2000) Naturalization and invasion of alien plants: concepts and definitions. Diversity and Distributions 6:93–107.

Richardson DM, Rejmánek M (2011) Trees and shrubs as invasive alien species – a global review. Diversity and Distributions 17:788–809.

Robakowski P, Bielinis E (2011) Competition between sessile oak (*Quercus petraea*) and black cherry (*Padus serotina*): dynamics of seedlings growth. Polish Journal of Ecology 59:297–306.

Sanderson L, Antunes P (2013) The exotic invasive plant *Vincetoxicum rossicum* is a strong competitor even outside its current realized climatic temperature range. NeoBiota 16:1–15.

Steffen W, Broadgate W, Deutsch L, Gaffney O, Ludwig C (2015) The trajectory of the Anthropocene: The Great Acceleration. The Anthropocene Review 2:81–98.

Steinbauer MJ, Grytnes J-A, Jurasinski G, Kulonen A, Lenoir J, Pauli H, Rixen C, Winkler M, Bardy-Durchhalter M, Barni E, Bjorkman AD, Breiner FT, Burg S, Czortek P, Dawes MA, Delimat A, Dullinger S, Erschbamer B, Felde VA, Fernández-Arberas O, Fossheim KF, Gómez-García D, Georges D, Grindrud ET, Haider S, Haugum SV, Henriksen H, Herreros MJ, Jaroszewicz

B, Jaroszynska F, Kanka R, Kapfer J, Klanderud K, Kühn I, Lamprecht A, Matteodo M, Cella UM di, Normand S, Odland A, Olsen SL, Palacio S, Petey M, Piscová V, Sedlakova B, Steinbauer K, Stöckli V, Svenning J-C, Teppa G, Theurillat J-P, Vittoz P, Woodin SJ, Zimmermann NE, Wipf S (2018) Accelerated increase in plant species richness on mountain summits is linked to warming. Nature 556:231–234.

Straigytė L, Cekstere G, Laivins M, Marozas V (2015) The spread, intensity and invasiveness of the *Acer negundo* in Riga and Kaunas. Dendrobiology 74:157–168.

Szwagrzyk J, Szewczyk J (2008) Is Natural Regeneration of Forest Stands a Continuous Process? A Case Study of an Old-Growth Forest of the Western Carpathians. Polish Journal of Ecology 56:623–634.

te Beest M, Esler KJ, Richardson DM (2015) Linking functional traits to impacts of invasive plant species: a case study. Plant Ecology 293–305.

Tecco PA, Díaz S, Cabido M, Urcelay C (2010) Functional traits of alien plants across contrasting climatic and land-use regimes: do aliens join the locals or try harder than them? Journal of Ecology 98:17–27.

Terwei A, Zerbe S, Zeileis A, Annighöfer P, Kawaletz H, Mölder I, Ammer C (2013) Which are the factors controlling tree seedling establishment in North Italian floodplain forests invaded by non-native tree species? Forest Ecology and Management 304:192–203.

Thompson K, Davis MA (2011) Why research on traits of invasive plants tells us very little. Trends in Ecology & Evolution 26:155–156.

Tokarska-Guzik B (2005) The Establishment and Spread of Alien Plant Species (Kenophytes) in the Flora of Poland. Wydawnictwo Uniwersytetu Śląskiego; Katowice.

Tokarska-Guzik B, Dajdok Z, Zając M, Zając A, Urbisz A, Danielewicz W, Hołdyński C (2012) Rośliny obcego pochodzenia w Polsce ze szczególnym uwzględnieniem gatunków inwazyjnych. Generalna Dyrekcja Ochrony Środowiska; Warszawa.

Trocha LK, Kałucka I, Stasińska M, Nowak W, Dabert M, Leski T, Rudawska M, Oleksyn J (2012) Ectomycorrhizal fungal communities of native and non-native *Pinus* and *Quercus* species in a common garden of 35-year-old trees. Mycorrhiza 22:121–134.

Vanhellemont M, Verheyen K, Keersmaeker L, Vandekerkhove K, Hermy M (2009) Does *Prunus serotina* act as an aggressive invader in areas with a low propagule pressure? Biological Invasions 11:1451–1462.

Vieira R, Finn JT, Bradley BA (2014) How does the landscape context of occurrence data influence models of invasion risk? A comparison of independent datasets in Massachusetts, USA. Landscape Ecology 29:1601–1612.

Vilà M, Espinar JL, Hejda M, Hulme PE, Jarošík V, Maron JL, Pergl J, Schaffner U, Sun Y, Pyšek P (2011) Ecological impacts of invasive alien plants: a meta-analysis of their effects on species, communities and ecosystems. Ecology Letters 14:702–708.

Vítková M, Müllerová J, Sádlo J, Pergl J, Pyšek P (2017) Black locust (*Robinia pseudoacacia*) beloved and despised: A story of an invasive tree in Central Europe. Forest Ecology and Management 384:287–302.

Vitousek PM (1990) Biological Invasions and Ecosystem Processes: Towards an Integration of Population Biology and Ecosystem Studies. Oikos 57:7–13.

Wagner V, Chytrý M, Jiménez-Alfaro B, Pergl J, Hennekens S, Biurrun I, Knollová I, Berg C, Vassilev K, Rodwell JS, Škvorc Ž, Jandt U, Ewald J, Jansen F, Tsiripidis I, Botta-Dukát Z, Casella L, Attorre F, Rašomavičius V, Ćušterevska R, Schaminée JHJ, Brunet J, Lenoir J, Svenning J-C, Kącki Z, Petrášová-Šibíková M, Šilc U, García-Mijangos I, Campos JA, Fernández-González F, Wohlgemuth T, Onyshchenko V, Pyšek P (2017) Alien plant invasions in European woodlands. Diversity and Distributions 23:969–981.

Wang C-J, Wan J-Z, Zhang G-M, Zhang Z-X, Zhang J (2016) Protected areas may not effectively support conservation of endangered forest plants under climate change. Environment and Earth Science 75:466.

Westoby M (1998) A leaf-height-seed (LHS) plant ecology strategy scheme. Plant and Soil 199:213–227.

Wickham H (2009) ggplot2: elegant graphics for data analysis. Springer; New York.

Wickham H (2007) Reshaping Data with the {reshape} Package. Journal of Statistical Software 21:1–20.

Wickham H, Francois R (2015) dplyr: A Grammar of Data Manipulation. R package version 0.4.1. Springer; New York

Wierzcholska S, Dyderski MK, Pielech R, Gazda A, Smoczyk M, Malicki M, Horodecki P, Kamczyc J, Skorupski M, Hachułka M, Kałucka I, Jagodziński AM (2018) Natural forest remnants as refugia for bryophyte diversity in a transformed mountain river valley landscape. Science of the Total Environment 640–641:954–964.

Wilson EO (2002) The Future of Life. Knopf; New York

Woziwoda B, Krzyżanowska A, Dyderski MK, Jagodziński AM, Stefańska-Krzaczek E (2018) Propagule pressure, presence of roads, and microsite variability influence dispersal of introduced *Quercus rubra* in temperate *Pinus sylvestris* forest. Forest Ecology and Management 428:35–45.

Wright IJ, Reich PB, Westoby M, Ackerly DD, Baruch Z, Bongers F, Cavender-Bares J, Chapin T, Cornelissen JH, Diemer M, Flexas J, Garnier E, Gulias J, Hikosaka K, Lamont BB, Lee T, Lee W, Lusk C, Midgley JJ, Navas ML, Niinemets Ü, Oleksyn J, Osada N, Poorter H, Poot P, Prior

L, Pyankov VI, Roumet C, Thomas SC, Tjoelker MG, Veneklaas EJ, Villar R (2004) The worldwide leaf economics spectrum. Nature 428:821–827.

Oświadczenia

Oświadczenie kierującego pracą

Oświadczam, że niniejsza praca została przygotowana pod moim kierunkiem i stwierdzam, że spełnia ona warunki do przedstawienia jej w postępowaniu o nadanie stopnia doktora nauk biologicznych.
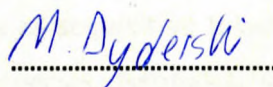
Kórnik, 8 kwietnia 2019 r.

Oświadczenie autora pracy

Świadom odpowiedzialności prawnej oświadczam, że niniejsza rozprawa doktorska została napisana przeze mnie samodzielnie i nie zawiera treści uzyskanych w sposób niezgodny z obowiązującymi przepisami.

Oświadczam również, że przedstawiona praca nie była wcześniej przedmiotem procedur związanych z uzyskaniem stopnia doktora w innej jednostce.

Oświadczam ponadto, że niniejsza wersja pracy jest identyczna z załączoną wersją elektroniczną.

Kórnik, 8 kwietnia 2019 r.

mgr inż. Marcin K. Dyderski

Instytut Dendrologii Polskiej Akademii Nauk

Pracownia Ekologii

Kórnik, 8 kwietnia 2019 r.

OŚWIADCZENIE

Oświadczam, że w pracy:

Dyderski M.K., Jagodziński A.M. 2018. Drivers of invasive tree and shrub natural regeneration in temperate forests. Biological Invasions, 20, 9, 2363-2379. doi: 10.1007/s10530-018-1706-3

Mój wkład polegał na udziale w opracowaniu koncepcji i metodyki badań, przeglądzie literatury związanej z analizowanym zagadnieniem, zbiorze danych w terenie, opracowaniu wyników i ich analizie statystycznej oraz na przygotowaniu manuskryptu pracy; pełniłem również rolę autora korespondencyjnego. **Mój udział procentowy szacuję na 90%.**

Dyderski M.K., Jagodziński A.M. 2018. Low impact of disturbance on ecological success of invasive tree and shrub species in temperate forests. Plant Ecology, 219, 1369-1380. doi: 10.1007/s11258-018-0885-4.

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M. Dyderski
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podpis

dr hab. Andrzej M. Jagodziński, prof. ID PAN   Kórnik, 8 kwietnia 2019 r.

Instytut Dendrologii Polskiej Akademii Nauk

Pracownia Ekologii

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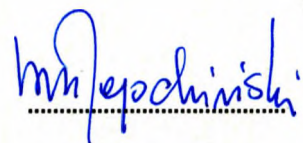
Mój wkład w powstanie tej pracy polegał na udziale w opracowaniu koncepcji i metodyki badań, udziale w interpretacji uzyskanych wyników, udziale w przygotowaniu manuskryptu artykułu i odpowiedzi na recenzje. **Mój udział procentowy szacuję na 10%.**

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podpis

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ORIGINAL PAPER

Drivers of invasive tree and shrub natural regeneration in temperate forests

Marcin K. Dyderski · Andrzej M. Jagodziński

Abstract We assessed drivers of ecological success along resource availability gradients for three invasive woody species: *Prunus serotina* Ehrh., *Quercus rubra* L. and *Robinia pseudoacacia* L. We aimed to check how much of invasion success, measured by invader biomass, is explained by propagule pressure and plant community invasibility. Using 3 years of observations from 372 study plots (100 m² each) in temperate forests of Wielkopolski National Park (Poland) we investigated the hierarchy of predictors and partial dependencies using the random forest method. Our study indicated that propagule pressure explained more variance in success of invaders than invasibility—describing availability of resources and competitors in understory vegetation. We also found different responses of seedlings and saplings, connected with dependence on stored carbohydrates, which decreased seedling responses to resource availability gradients.

However, resource availability (light and leaf litter predictors) had greater influence than predictors describing understory vegetation. Based on importance and response strength the species studied may be arranged by decreasing requirements for soil fertility and acidity: *P. serotina* < *Q. rubra* < *R. pseudoacacia*, whereas for light requirements and competition vulnerability the order is: *P. serotina* > *Q. rubra* > *R. pseudoacacia*. However, low light requirements of *R. pseudoacacia* may be biased by high proportion of sprouts supplied by parental trees. Results provide guidelines for effective management of invasive woody species in forest ecosystems and describe complex interactions between factors studied on ecological success of invaders.

Keywords Propagule pressure · Invasibility · *Prunus serotina* · *Quercus rubra* · *Robinia pseudoacacia* · Seedlings and saplings biomass

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Introduction

Among functional groups of invasive plant species, woody plants are distinguished by their long lifespan (Richardson 1998; Richardson et al. 2000; Richardson and Rejmánek 2011). For that reason their establishment and first year of life is crucial for further development and dispersal (Baraloto et al. 2005). Thus, as dispersal is the key factor that allows

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naturalized species to become invasive (Richardson et al. 2000; Chytrý et al. 2008; Dyderski and Jagodziński 2016), ecological success of young regeneration determines the ultimate success of woody invaders. In comparison with short-lived (herbaceous) taxa, assessment of woody species requires more complex studies, also accounting for more predictors and potential interactions (e.g. Richardson 1998; Pyšek et al. 2014; Brundu and Richardson 2016).

Natural regeneration of both native and invasive species faces numerous limiting factors. The abiotic conditions most limiting to growth of young trees are usually water, light and nutrient availability (Niinemets and Valladares 2006; Ellenberg and Leuschner 2010). However, levels of these factors are also influenced by other species co-occurring within the plant community (Tilman 1986). Competitive potential of a plant species is a derivate of its life strategy (Westoby 1998; Grime 2006), which results from its functional traits and their level of fitness to environmental conditions, particularly expression of resource acquisition strategies, e.g. specific leaf area, leaf photosynthetic capacity or specific root length (Cornelissen et al. 2003; Pierce et al. 2013; Díaz et al. 2016; Kunstler et al. 2016). Natural regeneration of woody species competes with different species and may "win" and reach the next level of development only in particular conditions. Thus, ecological success of invasive species depends on characteristics of the recipient plant community—habitat invasibility, which is determined by level of resources (Davis et al. 2000; Godefroid et al. 2005; Funk 2008; Paquette et al. 2012; González-Muñoz et al. 2014), and potential competitors (Chmura 2004; Chmura and Sierka 2005, 2007; Godefroid et al. 2005; Knight et al. 2008).

Biological invasions are driven by three connected factors: habitat invasibility, alien species invasiveness and propagule pressure—quantity and quality of propagules able to establish in new sites (Richardson et al. 2000; Davis et al. 2005; Jeschke 2014). Among them, propagule pressure is the obligatory factor determining invasion success (Lonsdale 1999; Lockwood et al. 2005; Vanhellemont et al. 2009). Numerous studies have confirmed its importance at both large (Křivánek et al. 2006; Pyšek et al. 2009, 2015; Woziwoda et al. 2014) and small spatial scales (Pairon et al. 2006; Deckers et al. 2008; Vanhellemont et al.

2009; Jagodziński et al. 2015; Bonilla and Pringle 2015). Propagule pressure seems to be a crucial driver of relationships between habitat invasibility and ecological success of invasive species. Although most of these interactions were studied within relatively short resource gradients, covering few habitat types (Vanhellemont et al. 2009; Aslan et al. 2012; Terwei et al. 2013; Jagodziński et al. 2015), Davis et al. (2005) conceptualized the relationship between invasibility and propagule pressure as the concept of invasion pressure, which provided a framework to merge both groups of factors. Our previous study (Jagodziński et al. 2018a) also revealed the interactions between propagule pressure and invasibility, but only for one species and in an experimental system.

Despite existing knowledge of factors determining success of biological invasions, it remains unknown whether interactions between, and relative importance of, propagule pressure and invasibility across a wide range of forest types are similar to the limited types reported on by previous studies. Comprehensive review of the community ecology of invasive species (Gallien and Carboni 2017) indicated a lack of clarity on whether processes filtering species colonizing new communities vary along environmental gradients. Moreover, there is an insufficient number of studies on invasive species spread conducted in protected areas, which are especially threatened by biological invasions (Hulme et al. 2014).

We aimed to assess drivers of biomass along resource availability gradients for the three most frequent invasive woody species in temperate Europe (Wagner et al. 2017)—*Prunus serotina* Ehrh., *Quercus rubra* L. and *Robinia pseudoacacia* L.—to assess how much of invasion success (moving along an introduction-naturalization-invasion continuum), measured by invader biomass, is explained by propagule pressure and plant community invasibility. We hypothesized that: (1) propagule pressure explains more variance in ecological success of invaders than invasibility, according to previous studies (e.g. Lonsdale 1999; Jagodziński et al. 2015, 2018a), (2) total biomass of seedlings depends more on propagule pressure than for saplings, as seedlings are more dependent on dispersal than older plants, which require suitable conditions for survival (e.g. Beckage et al. 2005; Knight et al. 2008; Rodríguez et al. 2017), and (3) understory competition, expressed by functional diversity components, have larger effects on ecological success of the

invasive species studied than surrogates of resource availability, as light competition limits occurrence of the species studied (Cierjacks et al. 2013; Jagodziński et al. 2015, 2018a). Because the three species studied differ in biology and ecology, we decided to characterize their invasiveness by comparing their responses to propagule pressure and habitat predictors on the background of their life history traits.

Materials and methods

Studied species

In European woodlands three alien woody species are most frequent: *Prunus serotina* Ehrh., *Quercus rubra* L. and *Robinia pseudoacacia* L. (Wagner et al. 2017). These species have been broadly recorded as invasive in Europe and all of them were widely introduced via forestry, in the eighteenth, nineteenth and seventeenth century, respectively (Muys et al. 1992; Woziwoda et al. 2014; Vítková et al. 2017). These species came from eastern North America and are widely distributed in Western and Central Europe, but their frequency decreases eastwards. *P. serotina* in its native range is a tree with valuable timber, but in Europe its introduction was not successful either in terms of timber production or soil improvement (Muys et al. 1992; Starfinger et al. 2003; Aerts et al. 2017). Its presence strongly influences nutrient cycling (Aerts et al. 2017; Horodecki and Jagodziński 2017). *P. serotina* is dispersed mainly by birds, up to 600 m from the seed source (Pairon et al. 2006; Jagodziński et al. 2015), however ca. 80% of fruits fall beneath the crown of the mother tree (Pairon et al. 2006). *Q. rubra* produces medium-value timber in Europe and due to its long lag-time is considered a weakly invasive species. Its dispersal is limited, as acorns mainly fall close to the parents and are not preferred by birds (Myczko et al. 2014; Bieberich et al. 2016), which are the main long-distance vectors of this species. *R. pseudoacacia* is a wind-dispersed pioneer tree species, important for wood production and providing nectar sources for pollinators, and is also widely used as an ornamental tree (Cierjacks et al. 2013; Vítková et al. 2017). This species transforms soils, due to symbiosis with nitrogen-fixing organisms (Rice et al. 2004). All these species invade forest ecosystems of temperate Europe, ranging from

less fertile coniferous sites to the most fertile riparian sites.

Study area

We conducted our study in Wielkopolski National Park (WNP; W Poland; 52°16'N, 16°48'E). WNP covers 7584 ha and conserves mostly forest ecosystems and very diverse geomorphology connected with the last glaciation. According to the nearest meteorological station in Poznań (c.a. 15 km from WNP) mean annual temperature in 1951–2010 was 8.4 °C and annual precipitation was 521 mm. Forests of WNP were heavily transformed by human activity, especially by former forest management, replacing mixed and broadleaved forests with monocultures of Scots pine. Moreover, before WNP establishment in 1957, the area was a place of numerous introductions of alien trees and shrubs, thus WNP is the national park in Poland with the highest number of alien woody species (Purcel 2009; Gazda and Szwagrzyk 2016). For that reason WNP provides a wide range of soil fertility and tree species composition, as well as variable propagule pressure of alien tree species, which makes WNP a good area for invasion ecology studies. All three species studied are abundant and are present both as an admixture in the tree stands and as monoculture tree stands (Purcel 2009). These advantages, together with known history of forest management and alien species introductions, make WNP a valuable area, especially for studies on biological invasions in forest ecosystems.

Study design

We used a set of 378 plots (squares 100 m² in area) arranged in 21 blocks: nine for *Q. rubra* and six for *P. serotina* and *R. pseudoacacia*. We established more blocks for *Q. rubra* due to lower densities of this species, resulting in lower detection rates. Moreover, within blocks only the central part of each block is located in a parental (monoculture) stand of invasive species (for *P. serotina*, which occurs only as an admixture in tree stands, these are tree stands with high density of fruiting trees), and the remaining plots are also invaded by the other two species. One pair of plots was located within the invasive species monoculture (maternal stand). A second pair of experimental plots was located along each of four sides of the

maternal stand (N, S, E, and W), nearly outside the stand, at the invasion edge (Rodríguez et al. 2017), and a third pair of experimental plots was located 30 m further out from the second set of plot pairs (Fig. 1). This design produced 18 experimental plots with different distances from propagule sources—within the maternal stands, outside maternal stand borders and at a distance of 30 m from maternal stands. Due to the high level of spatial heterogeneity in tree stands, longer distances may result in biases in estimation of the distance effects. Therefore, four classes of distance from propagule source were distinguished: in the propagule source, near the propagule source, 30 m from the propagule source and further than 30 m (plots without a propagule source of the considered species in the nearest neighborhood). Despite concerns, this did not generate pseudoreplications, due to high spatial heterogeneity manifested in high variability of natural regeneration within plots. Due to systematic

distribution of the plots, six of them were located in non-forested vegetation paths and these plots were excluded from analyses, thus the final number of plots was n = 372. This number of plots covered almost whole scale of plant communities typical to Central European forest types—from coniferous forests with *Pinus sylvestris* on podzols and acidophilous *Quercus petraea* forests on brunic soil to *Quercus robur-Carpinus betulus-Acer pseudoplatanus-Tilia cordata*, *Fagus sylvatica* and *Quercus robur-Ulmus minor-Fraxinus excelsior* forests on fertile haplic soils. Study plots covered ten forest types: *Acer platanoides-Tilia cordata-Carpinus betulus*, *Fagus sylvatica*, *Pinus sylvestris-Acer pseudoplatanus*, *Pinus sylvestris-Acer platanoides-Tilia cordata-Carpinus betulus*, *Pinus sylvestris-Prunus serotina*, *Pinus sylvestris-Quercus petraea*, *Quercus petraea*, *Quercus rubra*, and *Robinia pseudoacacia*. Within plots leaf litter pH ranged from 3.83 to 6.44 with an average of 5.20 ± 0.01 and
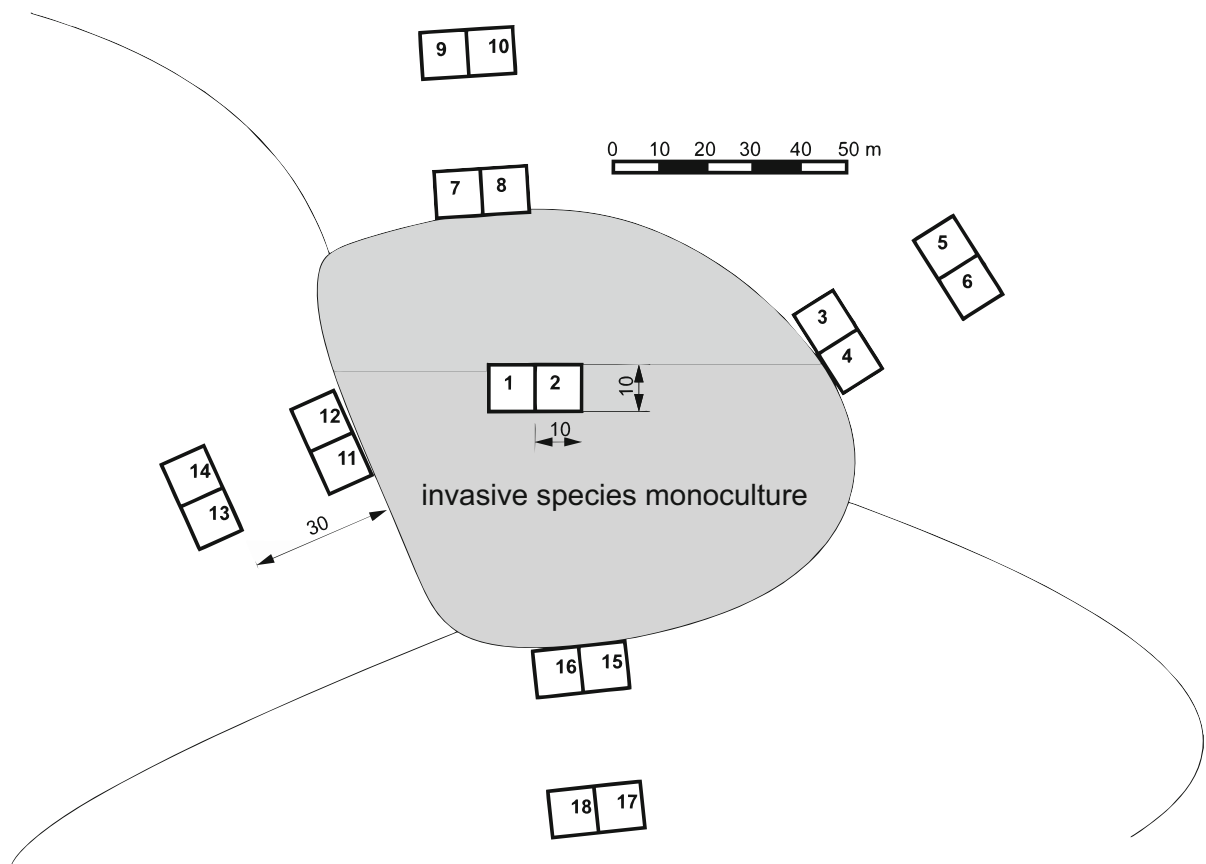

Fig. 1 Scheme for a block of experimental plots in the field. Each block (n = 21) is a set of 18 square plots (100 m²), with a center in the propagule source—an invasive species monoculture or for *P. serotina* a tree stand with a dense fruiting *P. serotina* layer

light availability ranged from 0.007 to 0.251 with an average of 0.044 ± 0.001.

Data collection

In July of 2015, 2016 and 2017 we counted the number of seedlings (defined as individuals germinated in a particular year) and saplings (defined as individuals at least one year old and with height < 0.5 m) within each plot, and in 2015, 2016 and 2017 we also measured root collar diameters (RCD) and heights (H) of the seedlings and saplings. This data was used for biomass calculation for each year. We treated sprouts (i.e. specimens generated through vegetative reproduction from root suckers) as saplings, due to their usually larger dimensions and connectivity with their parental organism. After measuring 28,703 seedlings, we found that height measurements of up to 30 seedlings is enough to cover the range of variance in seedling heights, and thus in 2017 for that age class we measured up to 30 heights, due to high seedling densities in some study plots (in cases of 50 plots with *P. serotina* and 23 with *R. pseudoacacia*). For these plots we used mean dimensions of seedlings to calculate individual biomass and multiplied by seedling density to produce biomass of seedlings. This did not affect calculated biomass, due to low SE of the mean for seedling total biomass (TB). In total we measured 39,664 plants. During these inventories we also investigated vegetation species composition and abundance using the Braun-Blanquet method: for each plant species in the understory (forest layer up to 50 cm) we assigned one of nine cover degrees in an alphanumeric scale. Moreover, in 2015 we assessed tree stand structures for study plots within larger (0.02–0.20 ha) plots, where diameter at breast height was measured for all trees and basal area (BA) was computed for each tree species.

In August 2016 we measured canopy openness index (diffuse non-interceptance; DIFN) in each plot, using an LAI-2200 plant canopy analyzer (Li-Cor Inc., Lincoln, NE, USA). For each plot we recorded four series of ten samples, using the methodology of Machado and Reich (1999). We chose August for the measurement time, as our previous studies showed that canopy openness was lowest during this month due to maximal canopy foliage development (Knight et al. 2008); thus, we accounted for the minimal light availability within our model. Light was an important

predictor in previous invasion ecology studies (e.g. Knight et al. 2008; Jagodziński et al. 2018a). To account for rates of nutrient cycling and acidity we used litter mass and pH. We decided to use litter predictors instead of soil, as litter is the main source of nutrients for the uppermost soil horizons. However, these predictors are only proxies for direct measurements of soil predictors. Litter was sampled in March 2017, when its amount was stabilized after winter. For each pair of plots we collected four samples from circular plots (0.16 m^2). Woody debris with diameter > 1 cm was excluded from litter samples. Litter samples were dried in an oven at 65 °C to constant mass and visually divided into two parts: recognizable and decomposed (unrecognizable) parts of litter. Next we weighed both samples using a balance with an accuracy of 1 g and determined proportion of the decomposed part of litter, which is usually higher in tree stands with low rates of organic matter cycling. Litter pH was assessed using a pH-meter in distilled water solution after 24 h.

To assess biomass of natural regeneration we destructively sampled 647 trees in July 2017 (Table S1). We used biomass as a measure of ecological success, because this predictor increases with both increasing density and dimensions, reflecting space filled by the species, and is also claimed to be a good measure of plant fitness (Younginger et al. 2017). For each pair of plots we surveyed an area with radius of 5 m around the plot borders and randomly selected up to five specimens for each species, according to available number of specimens and species densities within plots. We excluded heavily damaged and browsed plants, unless there were no alternative specimens in the area examined. This accounted for the joint effects of lower growth and resistance to herbivory in suboptimal sites. This approach also resulted in unequal numbers of sample trees per species: 356 sample trees of *P. serotina* (195 seedlings and 161 saplings), 133 of *Q. rubra* (72 seedlings and 61 saplings) and 158 of *R. pseudoacacia* (94 seedlings and 64 saplings). These unequal numbers resulted from unequal distributions of natural regeneration of the species studied within the study plots. Each sample tree was dug up, cleaned and divided into roots, stems with branches and leaves. We excluded acorns which were still attached to *Q. rubra* and *Q. petraea* seedlings from the total biomass (TB). For each sample tree we also measured RCD and H.

Within the sampled tree dataset we found that 14 of 161 (8.7%) *P. serotina* and 23 of 64 (35.9%) *R. pseudoacacia* saplings had root suckers, and for these sample trees we did not include belowground biomass, because their root system was part of the parental plant. However, despite this belowground biomass exclusion, we included them in the dataset because their aboveground biomass also contributed to the understory. We did not assess whether each of the plants that were not destructively sampled were vegetative or generative reproduction, to not influence their survival probability, which would undermine future usage of permanent plots.

Data analysis

All analyses were conducted using R software (R Core Team 2017). Prior to modelling datasets were centered, scaled and processed using Yeo-Johnson power transformations (Yeo and Johnson 2000) to stabilize variance, increase normality of distributions and overcome problems with different magnitudes of variables. This preprocessing was carried out using the *caret::preProcess()* function (Kuhn 2008). As our data has hierarchical structure, which may influence model outcomes (Roberts et al. 2017), we decided to assess potential blocking effects of the plot layout in the field. We checked whether the most important predictors describing resource availability—DIFN, litter mass and pH—showed clustering related to the blocks. We performed k-means clustering using six clusters (the optimal cluster number was estimated by the elbow method) using the *stats::kmeans()* function. Then we compared clusters with principal components analysis of centered and scaled values of the analyzed predictors and we visually inspected how the blocks were arranged within the ordination space (Figure S1). This analysis showed that potential blocking effects were related to the availability of resources rather than spatial proximity, and therefore for further analyses we decided to use modelling methods that did not account for the arrangement of blocks.

To predict TB of the species studied we used allometric equations, following Jagodziński et al. (2018a, b). Because our sample trees were collected within plots and blocks, they differed in dimensions and plot design expressed different resource availabilities rather than spatial structures (Figure S1). We quantified

how much variance in TB was explained by dimensions and by resource availability predictors (litter mass, pH and DIFN) using boosted regression tree models (Elith et al. 2008). Influence of the latter predictor explained 10.2, 9.0 and 0.0% for *Q. rubra*, *P. serotina* and *R. pseudoacacia*, respectively, thus we decided to use the simplest approach—linear and non-linear allometric models. From ten formulas of allometric relationships used by Jagodziński et al. (2018a, b) we chose the model with the lowest AIC (Table S2). For *P. serotina* TB = $0.03917 \times DRC^{2.13334} \times H^{0.49044}$ (with mean error of 0.059 and $R^2 = 0.880$), for *Q. rubra* TB = $0.004935 \times DRC^{1.672448} \times H^{1.371159}$ (with mean error of 0.067 and $R^2 = 0.852$) and for *R. pseudoacacia* TB = $0.004002 \times DRC^{1.078374} \times H^{1.203052}$ (with mean error of 0.013 and $R^2 = 0.955$).

We analyzed vegetation patterns using functional traits provided by BiolFlor (Klotz et al. 2002), BryoAtt (Hill et al. 2007) and LEDA (Kleyer et al. 2008) databases, as well as ecological indicator values (EIV; Ellenberg and Leuschner 2010). For each plant species we extracted EIV for light, fertility, soil reaction, moisture, continentality and temperature, as well as canopy height, leaf mass, size, dry matter content, specific leaf area (SLA), growth form, seed mass and number per shoot, reproduction mode and Grime's (Grime 2006) life strategy (Table S3). These traits were used for calculation of functional diversity components: functional dispersion (FDis), functional divergence (FDiv), functional evenness (FEve) and functional richness (FRic). These components describe distribution of species' functional traits for each sampled plant community within a hypervolume of traits (Mason et al. 2005; Laliberté and Legendre 2010; Pla et al. 2011), indicating prevalence of processes shaping species composition of the community. High values of FDiv indicate numerous functional ways of resource acquisition, which is associated with higher competition, similar to high FEve, indicating lack of one dominant type of resource acquisition. High values of FRic and FDis indicate numerous functional plant types and low level of habitat filtering in the plant community (Kotowski et al. 2010; Hedberg et al. 2014; Dyderski et al. 2016; but see Kraft et al. 2015). Moreover, to characterize dominant plant strategies, we used three community-weighted mean (CWM) values of functional traits: SLA, height and seed mass, according to the LHS

concept (Westoby 1998) and global spectrum of plant functions (Díaz et al. 2016). All functional diversity components and CWMs used for analyses of particular invasive species studied were calculated excluding that species, to avoid circular reasoning and biased variable importance, connected with different functional traits (Thomsen et al. 2016), for example, overestimated importance of seed mass CWM for *Q. rubra*, with its high value of this trait. Usage of functional diversity components allows conclusions about impact of plant community on the species of interest (Kurokawa et al. 2010; D'Astous et al. 2013; Jagodziński et al. 2017; Czortek et al. 2018).

In our dataset some predictors were correlated, because they reflect different aspects of phenomena studied. For example, propagule source presence/absence and basal area correlation coefficient r was 0.56 for *P. serotina*, but the former predictor reflected mere presence of seed source and the latter predictor reflected its quantity. For that reason and for better ecological interpretation we decided not to exclude them from analyses. Only three pairs of predictors had correlation coefficients (r) > 0.6—species richness and Shannon's index (0.73), FRich and species richness (0.65) and litter mass and proportion of decomposed part of litter (0.6). To ensure that our results were not biased by year-to-year dynamics, in modelling we used averaged vegetation predictors and biomasses for each plot. This averaging was also necessary as some predictors, e.g. tree stand and litter predictors as well as DIFN, were measured only once and combining them with more variable predictors would bias their importance. To assess influence of factors describing resource availability, propagule pressure and competitors we used the random forest method (RF; Breiman 2001), trained using the *caret::train()* function (Kuhn 2008). We chose RF due to its good performance in cases of collinear variables, non-normal distributions of predictors and high predictive power. As an alternative, we also tested boosted regression trees (Elith et al. 2008), which showed lower fitness—lower coefficients of determination and higher RMSE (Fig. S2). Due to differences in survival, we assessed biomass of seedlings, saplings and total natural regeneration of each species separately. For each RF model we produced two results/outputs –importance of variables and partial dependence plots. Variable importance is expressed by mean decrease in accuracy (%IncMSE),

which is a percentage increase of mean squared error of the result when the considered variable was permuted. Partial dependence plots express impact of a single variable on a response when all remaining predictors within a given model are constant.

Results

Biomass of natural regeneration

Natural regeneration of *R. pseudoacacia*, *Q. rubra* and *P. serotina*, was found in 165, 194 and 239 plots, respectively. Biomass of natural regeneration for these three species within study plots ranged from 0.00 to 257.19 kg ha^{-1}, with an average of 1.52 ± 0.36 kg ha^{-1} (Fig. 2). However, medians for each species seedlings and saplings did not exceed 1 kg ha^{-1}. For *P. serotina* total biomass ranged from 0 to 9.61 kg ha^{-1}, with an average of 0.81 ± 0.09 kg ha^{-1}; for *Q. rubra* from 0.00 to 257.19 kg ha^{-1}, with an average of 1.04 ± 0.69 kg ha^{-1} and for *R. pseudoacacia* from 0.00 to 1.81 kg ha^{-1}, with an average of 0.07 ± 0.01 kg ha^{-1}. Mean proportions of total seedling biomass within plots were 30.7 ± 2.3, 29.8 ± 2.7 and $48.7 \pm 3.2\%$ for *P. serotina*, *Q. rubra* and *R. pseudoacacia*, respectively.

Hierarchy of predictors

RF models explained from 56.5% (*R. pseudoacacia* seedlings) to 78.3% of variance (*P. serotina* total) in the biomass of the species studied and included from 3 to 10 predictors (Table 1). Two of the most important predictors for each species and biomass type were presence of parental trees in the plot or in the nearest neighborhood and basal area of parental trees in the tree stand (Table 1). Exceptions were saplings and total biomass of *Q. rubra*, for which the second most important predictor was litter mass. Nevertheless, %IncMSE connected with nearest presence of propagule source ranged from 30.2 to 50.2%. Basal area of parental trees had the highest importance for *P. serotina* and the lowest for *Q. rubra*. This predictor also was more important for seedlings than saplings. The second group of predictors was connected with leaf litter predictors. The most important of them was litter mass, however its importance for *R.*
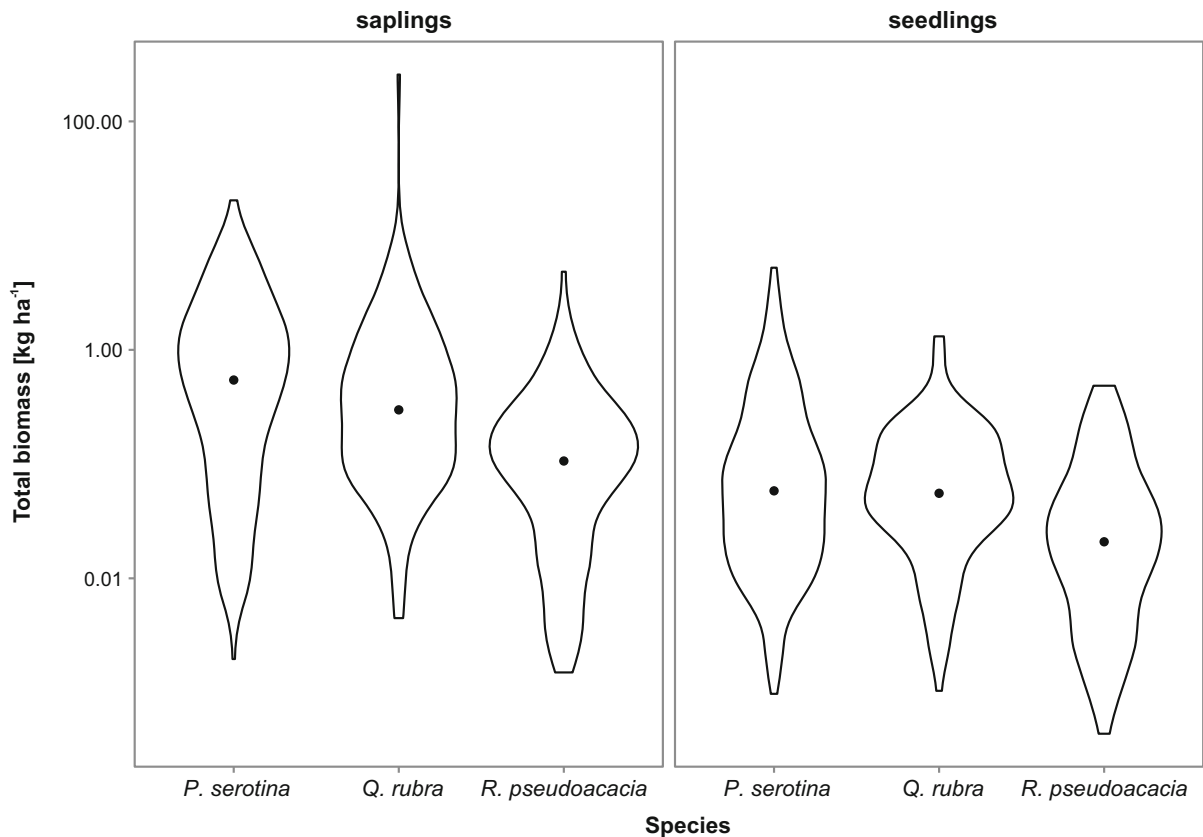
Fig. 2 Distributions of sapling and seedling biomass for each species within study plots (n = 372). Distributions are shown by violin plots—the wider the shape is, the more frequent the particular value of the variable is. Dots inside the violins indicate medians. Note log-transformation of y-axis

pseudoacacia was lower than for the other species. Leaf litter predictors were the most important for *P. serotina*, especially for seedlings. Litter pH usually had lower importance than litter mass, with the exception of total *R. pseudoacacia* biomass. Fraction of decomposed material in litter was included only in the model of total *P. serotina* biomass. Light availability, expressed by DIFN, had the highest importance for *R. pseudoacacia* and the lowest for *Q. rubra*. Among predictors expressing tree stand features, number of tree species had higher importance than tree stand BA. Tree stand species richness was most important for *R. pseudoacacia*, and least for *Q. rubra*. Tree stand BA had the highest importance for *R. pseudoacacia*. Among understory predictors the highest importance was species richness, which had the highest importance for *P. serotina* and *Q. rubra*. Its importance was higher for saplings and total biomass than for seedlings. Understory species diversity,

expressed by Shannon's index had the highest importance for *R. pseudoacacia*. CWMs describing functional traits of understory had the lowest importance for *Q. rubra* and the highest for *P. serotina*. For an average, the most important CWM was plant height. For *Q. rubra* the most important was CWM of SLA. Functional diversity indices was the group of predictors with the lowest importance. However, among species FRic, FDis and FEve were most important for *P. serotina* and FDiv for *Q. rubra*. In most cases values of importance of functional diversity components were higher for saplings than seedlings.
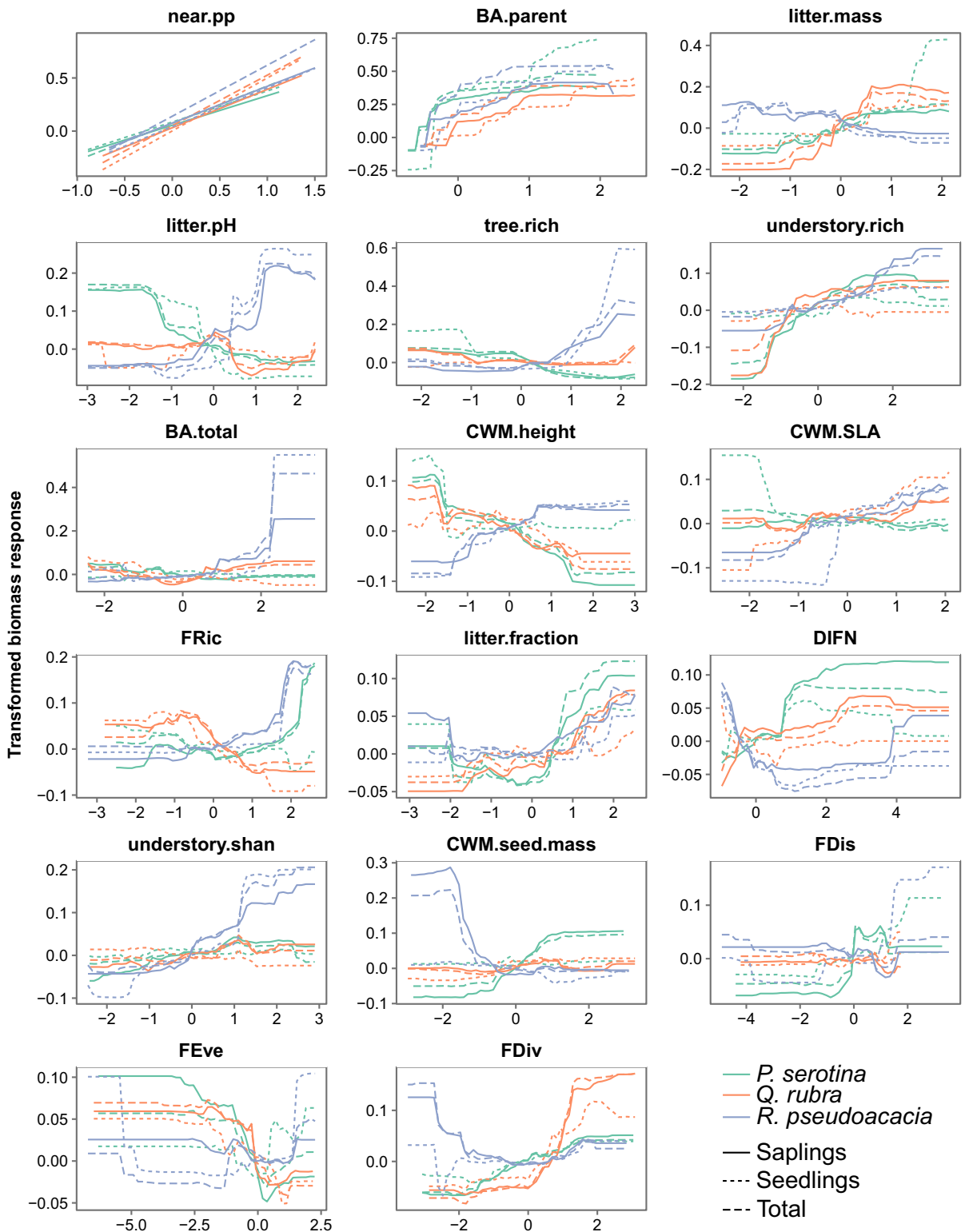
Impact of predictors on studied species biomass

Partial dependence plots (Fig. 3) revealed that response of saplings to presence of propagule source in the vicinity was lower than response of seedlings. All species biomasses increased with proportion of

Table 1 Importance (mean decrease of accuracy; %IncMSE) of 17 predictors within random forest models for seedlings, saplings and total natural regeneration biomass of the three species studied

Predictor	Abbreviation	P. serotina seedlings	P. serotina saplings	P. serotina total	Q. rubra seedlings	Q. rubra saplings	Q. rubra total	R. pseudoacacia seedlings	R. pseudoacacia saplings	R. pseudoacacia total
Near presence of the propagule source (boolean)	near.pp	**33.7**	**31.8**	**36.5**	**54.7**	**43.3**	**50.2**	**47.5**	**30.2**	**48.8**
Basal area of parental trees (m² ha⁻¹)	BA.parent	**40.0**	**24.3**	**25.9**	**22.0**	**19.9**	**22.2**	**26.1**	**21.1**	**25.0**
Litter mass (kg ha⁻¹)	litter.mass	**24.8**	**19.0**	**20.2**	**14.0**	**27.8**	**24.1**	16.1	**14.3**	**15.5**
Litter pH	litter.pH	**20.1**	**16.0**	**17.3**	12.5	14.0	**14.2**	20.5	**13.3**	**19.7**
Tree stand species richness	tree.rich	15.9	13.7	**15.3**	5.6	11.1	11.0	**24.1**	**14.3**	**19.8**
Understory species richness	understory.rich	10.5	**21.9**	**19.1**	6.8	**19.1**	**14.9**	7.2	10.7	7.9
Total basal area (m² ha⁻¹)	BA.total	11.9	11.3	11.4	7.1	9.3	8.3	21.1	10.7	**16.4**
CWM of plants height (m)	CWM.height	11.6	**15.9**	**12.7**	9.2	11.2	14.0	11.3	8.7	**10.5**
CWM of specific leaf area (SL0041) (cm² g⁻¹)	CWM.SLA	14.0	7.9	7.5	12.5	10.8	11.8	19.4	7.7	10.2
Functional richness	FRic	7.6	10.3	**12.9**	**12.9**	13.1	14.1	10.0	9.4	**10.8**
Fraction of decomposed material in litter	litter.fraction	13.6	13.0	**15.8**	4.8	10.9	11.2	8.2	7.5	6.1
Light availability—fraction of the open sky	DIFN	11.3	11.3	9.3	5.8	8.2	8.3	11.2	10.4	**13.9**
Understory species diversity (Shannon index)	understory.shan	8.5	10.2	6.2	5.1	8.5	8.9	14.5	11.6	**11.3**
CWM of seed mass	CWM.seed.mass	8.3	**14.1**	**13.9**	5.6	4.7	4.7	6.8	**12.2**	10.0
Functional dispersion	FDis	8.0	13.8	12.2	3.9	5.6	5.2	6.5	7.1	6.4
Functional evenness	FEve	8.4	12.0	10.9	7.2	4.9	5.9	4.6	4.8	4.3
Functional divergence	FDiv	5.9	5.3	6.8	3.4	9.8	13.1	− 0.8	3.1	2.5
Model R²		0.695	0.740	0.783	0.589	0.671	0.594	0.565	0.713	0.752

Variables with bolded importance were included in the final model. Variables are shown in order of decreasing mean %IncMSE

◄ **Fig. 3** Partial dependence plots showing impacts of particular variables (abbreviations and predictors importance in Table 1) on response functions of biomass for biomass types and species studied, when all remaining predictors were constant. Response and variables were centered, scaled and processed by Yeo-Johnson power transformation

parent trees in basal area, up to thresholds at which response curves reached plateaus. This threshold was reached first by *Q. rubra*, then by *R. pseudoacacia* and finally by *P. serotina*. However, the response curve was steepest for *R. pseudoacacia* total biomass. Increasing litter mass was associated with increasing biomass of *P. serotina* and *Q. rubra* and decreasing biomass of *R. pseudoacacia*. Only seedlings of *P. serotina* showed a steeper response curve at the higher range of litter mass than saplings and total biomass. Responses to DIFN differed among species studied: biomasses of *P. serotina* and *Q. rubra* increased with increasing DIFN, however biomass of *P. serotina* seedlings in the highest fraction of DIFN range decreased. Biomass of *Q. rubra* decreased with increasing tree stand species richness and biomasses of *P. serotina* and *R. pseudoacacia* increased. The positive response of *R. pseudoacacia* was steeper in the highest range of tree stand species richness, especially for seedlings. This species showed a similar response to tree stand BA. The biomasses of all species studied increased with increasing understory species richness, however in the case of seedlings the size effect was minimal.

Discussion

Model limitations

Despite the high number of predictors studied, some of them are only proxies for direct measurements. For example, litter traits are surrogates for soil chemistry, which is crucial for plant growth (e.g. Mueller et al. 2012; Aerts et al. 2017). We also did not divide regeneration into generative and vegetative specimens. Another potential drawback may result from low variability of climatic conditions, which drive the distributions of species studied at large spatial scales (Dyderski et al. 2018). Resource availability gradients do not account for water availability, as we did not sample dry and wet habitat types, due to their

relatively low abundance, thus soil moisture effects were not studied. Nevertheless, the large number of study plots and temporal variation increased robustness of the conclusions.

Impact of propagule pressure on species invasion success

Almost all models showed that propagule pressure was the most important influence on invasion success, expressed by biomass of natural regeneration. Propagule source presence and propagule quantity both contribute to increasing propagule pressure, however, they each account for a different aspect of propagule availability. Different species reacted in a different way to presence and quantity: *Q. rubra* depended more on propagule vicinity than *R. pseudoacacia* and *P. serotina* was the least dependent among species studied. However, *P. serotina* had the highest importance of propagule quantity, similar to other studies (e.g. Chabrerie et al. 2008; Vanhellemont et al. 2009; Terwei et al. 2013). The important role of propagule pressure has been confirmed for numerous woody species (e.g. Pyšek et al. 2009; Sinclair and Arnott 2015; Rodríguez et al. 2017), and also for the species studied (e.g. Vanhellemont et al. 2009; Woziwoda et al. 2014; Jagodziński et al. 2015). Ecological success of *P. serotina* and *Q. rubra*, expressed either as seedling density (Pairon et al. 2006; Riepšas and Straigytė 2008; Jagodziński et al. 2015) or biomass (Jagodziński et al. 2018a) decreased with distance from propagule source. Although *Q. rubra* acorns are not preferred by birds (Myczko et al. 2014; Bieberich et al. 2016), its maximum dispersal distance referred to in the literature is higher than that of *P. serotina* (1500 vs. 600 m), which is eaten by numerous bird species (Bartkowiak 1970; Deckers et al. 2008). The high importance of fruiting tree BA may also reflect the fact that ca. 80% of fruits fall beneath the crowns of *P. serotina* and birds may disperse only 20% of them (Pairon et al. 2006). Lower importance of propagule source BA for *Q. rubra* may suggest better dispersal of this species, e.g. by rodents (Bieberich et al. 2016). Another explanation may result from with high seed mass and stored carbohydrates allowing growth in unsuitable conditions (Ziegenhagen and Kausch 1995). Under this assumption, even a single tree in the stand may produce an effective number of seedlings, and due to their low densities, may result

in biomass similar to the other species despite the low contribution of *Q. rubra* to tree stand BA.

Propagule pressure increases the probability of alien species establishment in the plant community (Lonsdale 1999; Lockwood et al. 2005; Vanhellemont et al. 2009). For that reason plots with lower availability of seeds or sprouts are less invasible than those with higher availability. Due to probability of vegetative reproduction, effects of these variables may be biased, as the species studied are able to sprout (Closset-Kopp et al. 2007; Vítková et al. 2017). Although 10–50% of *P. serotina* natural regeneration may result from vegetative reproduction (Closset-Kopp et al. 2007), our study reports a fraction (8.7%) similar to our previous study in Rogów Arboretum (Jagodziński et al. 2015). For *R. pseudoacacia* it was 35.9%, but due to young age of fruiting (Burns and Honkala 1990), there were no differences between presence of fruiting and sprouting trees in the vicinity of the plots. The high advantage of *R. pseudoacacia* in plots with presence of propagule source may also result from its capacity for nitrogen fixation, which fertilizes the soil (Rice et al. 2004; Cierjacks et al. 2013).

Impact of resource availability on studied species biomass

The most important factors related to availability of resources were those connected with leaf litter. These predictors were most important for *P. serotina*. However, the highest %IncMSE in this study was for litter mass as a predictor of *Q. rubra* saplings, and the highest effect size was for seedlings. The presence of *Q. rubra* in the overstory usually maintains a thick layer of leaf litter, due to its low decomposition rate (Horodecki and Jagodziński 2017). Thus, in this particular case its effect cannot be clearly separated. Nevertheless, both species showed similar tendencies for litter pH—their biomass decreased with increasing litter pH, which is an indicator of higher fertility. Both *P. serotina* and *Q. rubra* have been reported from fertile deciduous forests (Chmura 2004, 2013; Woziwoda et al. 2014; Dyderski et al. 2015; Jagodziński et al. 2015). *P. serotina* was claimed to prefer the poor and medium fertility sites of coniferous forests, and the species was planted there as a soil improver (Muys et al. 1992; Starfinger et al. 2003), but also reached high densities on habitats of fertile deciduous forests

(Jagodziński et al. 2015). Our study confirmed earlier observations that *P. serotina* reaches higher ecological success in less fertile and more acidic plots (Zerbe and Wirth 2006; Chabrerie et al. 2008; Knight et al. 2008; Halarewicz 2012; Terwei et al. 2016). In contrast, *R. pseudoacacia* reached the highest biomass in plots with low litter mass, low proportion of decomposed material and high pH. This indicated that although *R. pseudoacacia* may occur in less fertile sites, it has the highest growth potential in the most fertile habitats. For that reason this species effectively invades riparian forests (e.g. Terwei et al. 2013; Dyderski et al. 2015; Marozas et al. 2015).

One of the most surprising results was low importance of light availability for the majority of species studied, in contrast with other studies indicating higher importance of light availability on invasion success (e.g. Knight et al. 2008; Paquette et al. 2012; Rodríguez et al. 2017). The relatively low light requirements shown by *R. pseudoacacia* were opposite to other studies (Groninger et al. 1997; Cierjacks et al. 2013). However, due to relatively high proportion of seedlings in the biomass, which was highest in the stands with lowest light availability, it may be an effect of low competition within the understory. Nevertheless, seedling survival is low (Dyderski *unpubl.*). Another important factor is high proportion of sprouts, which may be supplied with nutrients by parental trees, and partially independent of light availability. Groninger et al. (1997) used only trees obtained from generative reproduction, thus our results are not comparable. However, in plots with high light availability *R. pseudoacacia* also reached high biomass. Dominance of propagule pressure over invasibility may be connected with their interaction, conceptualized by Davis et al. (2005), who elaborated a model showing how propagule pressure may modify invasibility, with the two variables working together to produce 'invasion pressure'.

Impact of interactions with overstory and understory on biomass

Interactions with other members of plant communities have been claimed to be drivers of invasibility from the beginning of invasion ecology, when Elton (1958) formulated the hypothesis of biotic resistance. This concept assumed that higher species richness in plant communities may decrease invasibility. This concept

was recently confirmed for small plots (Brown and Peet 2003; Parker et al. 2010; Iannone et al. 2016), however at larger spatial scales recent studies confirmed that relationships between species richness of native and alien species or invader ecological success (expressed as abundance or density) are positive (Lonsdale 1999; Stohlgren et al. 1999, 2006; Knight et al. 2008; Dyderski et al. 2015, but see Parker et al. 2010). Increasing ecological success of the invasive species studied here in plots with higher species richness confirms this theory. Understory species richness was most important for *P. serotina* and *Q. rubra* saplings and total biomass, but not for seedlings. This may result from the effects of seed storage, allowing supplies of carbohydrates to seedlings which are independent of competition. The species with the lowest seed mass—*R. pseudoacacia*—did not show a similar response.

CWM of seed mass had the highest significance for *P. serotina* and *R. pseudoacacia* saplings. The biomass of *P. serotina* increased with increasing seed mass CWM. This may be driven by frequently co-occurring *Quercus petraea* and *Q. rubra* with high seed mass at a similar ecological scale, but also may reflect bird-mediated dispersal (Pairon et al. 2006; Deckers et al. 2008; Kurek et al. 2015; Dylewski et al. 2017). Terwei et al. (2016) interpreted a similar relationship obtained in floodplain forest as evidence for *P. serotina* shade tolerance, which has not been confirmed in our study. Biomass of *R. pseudoacacia* decreased with increasing CWM of seed mass, which may reflect its ruderal character and preference for disturbed sites (Cierjacks et al. 2013; Vítková et al. 2017), as low seed mass is connected with disturbance tolerance (Westoby 1998). *P. serotina* responded negatively to height CWM, which shows its negative response to understory competition. Similarly Terwei et al. (2013) found a negative relationship between density of *P. serotina* and herb layer cover.

Differences between studied species and management implications

According to our results, management of species studied should primarily focus on removing propagule sources. If these species are planted according to their commercial value (Woziwoda et al. 2014) or ecosystem services (Vítková et al. 2017), invasion management should be focused on plant communities in the neighborhoods of plantations by shaping conditions not supporting the spread of invaders, e.g. by limiting light availability, planting competing native species or removing emerging saplings or juvenile specimens. Introduction of these best management practices for invasive woody species into forestry is crucial for limiting further invasion of these species (Brundu and Richardson 2016).

References

Aerts R, Ewald M, Nicolas M et al (2017) Invasion by the alien tree *Prunus serotina* alters ecosystem functions in a temperate deciduous forest. Front Plant Sci 8:179. https://doi.org/10.3389/fpls.2017.00179

Aslan CE, Rejmánek M, Klinger R (2012) Combining efficient methods to detect spread of woody invaders in urban–rural matrix landscapes: an exploration using two species of Oleaceae. J Appl Ecol 49:331–338. https://doi.org/10.1111/j.1365-2664.2011.02097.x

Baraloto C, Goldberg DE, Bonal D (2005) Performance trade-offs among tropical tree seedlings in contrasting micro-habitats. Ecology 86:2461–2472. https://doi.org/10.1890/04-1956

Bartkowiak S (1970) Ornitochoria rodzimych i obcych gatunków drzew i krzewów. Arbor Kórn 15:237–261

Beckage B, Lavine M, Clark JS (2005) Survival of tree seedlings across space and time: estimates from long-term count data. J Ecol 93:1177–1184. https://doi.org/10.1111/j.1365-2745.2005.01053.x

Bieberich J, Lauerer M, Aas G (2016) Acorns of introduced *Quercus rubra* are neglected by European Jay but spread by mice. Ann For Res 59:249–258. https://doi.org/10.15287/afr.2016.522

Bonilla NO, Pringle EG (2015) Contagious seed dispersal and the spread of avian-dispersed exotic plants. Biol Invasions

⁂ Springer

17:3409–3418. https://doi.org/10.1007/s10530-015-0966-4

Breiman L (2001) Random forests. Mach Learn 45:5–32. https://doi.org/10.1023/A:1010933404324

Brown RL, Peet RK (2003) Diversity and invasibility of southern Appalachian plant communities. Ecology 84:32–39. https://doi.org/10.1890/0012-9658(2003)084

Brundu G, Richardson DM (2016) Planted forests and invasive alien trees in Europe: a Code for managing existing and future plantings to mitigate the risk of negative impacts from invasions. NeoBiota 30:5–47. https://doi.org/10.3897/neobiota.30.7015

Burns RM, Honkala BH (1990) Silvics of north America. U.S. Dept. of Agriculture Forest Service, Washington, DC

Chabrerie O, Verheyen K, Saguez R, Decocq G (2008) Disentangling relationships between habitat conditions, disturbance history, plant diversity, and American black cherry (*Prunus serotina* Ehrh.) invasion in a European temperate forest. Divers Distrib 14:204–212. https://doi.org/10.1111/j.1472-4642.2007.00453.x

Chmura D (2004) Penetration and naturalisation of invasive alien plant species (neophytes) in woodlands of the Silesian Upland (southern Poland). Nat Conserv 60:3–11

Chmura D (2013) Impact of alien tree species *Quercus rubra* L. on understorey environment and flora: a study of the Silesian Upland (southern Poland). Pol J Ecol 61:431–442

Chmura D, Sierka E (2005) The occurrence of invasive alien plant species in selected forest nature reserves in southern Poland as a conservation problem. Nat Conserv 62:3–11

Chmura D, Sierka E (2007) The invasibility of deciduous forest communities after disturbance: a case study of *Carex brizoides* and *Impatiens parviflora* invasion. For Ecol Manag 242:487–495. https://doi.org/10.1016/j.foreco.2007.01.083

Chytrý M, Maskell LC, Pino J et al (2008) Habitat invasions by alien plants: a quantitative comparison among Mediterranean, subcontinental and oceanic regions of Europe. J Appl Ecol 45:448–458. https://doi.org/10.1111/j.1365-2664.2007.01398.x

Cierjacks A, Kowarik I, Joshi J et al (2013) Biological flora of the British Isles: *Robinia pseudoacacia*. J Ecol 101:1623–1640. https://doi.org/10.1111/1365-2745.12162

Closset-Kopp D, Chabrerie O, Valentin B et al (2007) When Oskar meets Alice: does a lack of trade-off in r/K-strategies make *Prunus serotina* a successful invader of European forests? For Ecol Manag 247:120–130. https://doi.org/10.1016/j.foreco.2007.04.023

Core Team R (2017) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna

Cornelissen JHC, Lavorel S, Garnier E et al (2003) A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. Aust J Bot 51:335–380. https://doi.org/10.1071/BT02124

Czortek P, Delimat A, Dyderski MK et al (2018) Climate change, tourism and historical grazing influence the distribution of *Carex lachenalii* Schkuhr—A rare arctic-alpine species in the Tatra Mts. Sci Total Environ 618:1628–1637. https://doi.org/10.1016/j.scitotenv.2017.10.001

D'Astous A, Poulin M, Aubin I, Rochefort L (2013) Using functional diversity as an indicator of restoration success of a cut-over bog. Ecol Eng 61(Part B):519–526. https://doi.org/10.1016/j.ecoleng.2012.09.002

Davis MA, Grime JP, Thompson K (2000) Fluctuating resources in plant communities: a general theory of invasibility. J Ecol 88:528–534. https://doi.org/10.1046/j.1365-2745.2000.00473.x

Davis MA, Thompson K, Philip Grime J (2005) Invasibility: the local mechanism driving community assembly and species diversity. Ecography 28:696–704. https://doi.org/10.1111/j.2005.0906-7590.04205.x

Deckers B, Verheyen K, Vanhellemont M et al (2008) Impact of avian frugivores on dispersal and recruitment of the invasive *Prunus serotina* in an agricultural landscape. Biol Invasions 10:717–727. https://doi.org/10.1007/s10530-007-9164-3

Díaz S, Kattge J, Cornelissen JHC et al (2016) The global spectrum of plant form and function. Nature 529:167–171. https://doi.org/10.1038/nature16489

Dyderski MK, Jagodziński AM (2016) Patterns of plant invasions at small spatial scale correspond with that at the whole country scale. Urban Ecosyst. https://doi.org/10.1007/s11252-015-0524-y

Dyderski MK, Gdula AK, Jagodziński AM (2015) "The rich get richer" concept in riparian woody species—a case study of the Warta River Valley (Poznań, Poland). Urban For Urban Green 14:107–114. https://doi.org/10.1016/j.ufug.2014.12.003

Dyderski MK, Czapiewska N, Zajdler M et al (2016) Functional diversity, succession, and human-mediated disturbances in raised bog vegetation. Sci Total Environ 562:648–657. https://doi.org/10.1016/j.scitotenv.2016.04.102

Dyderski MK, Paź S, Frelich LE, Jagodziński AM (2018) How much does climate change threaten European forest tree species distributions? Glob Change Biol 24:1150–1163. https://doi.org/10.1111/gcb.13925

Dylewski Ł, Kurek P, Wiatrowska B et al (2017) Man-made perching sites—electricity pylons accelerate fleshy-fruited plants succession in farmlands. Flora 231:51–56. https://doi.org/10.1016/j.flora.2017.04.004

Elith J, Leathwick JR, Hastie T (2008) A working guide to boosted regression trees. J Anim Ecol 77:802–813. https://doi.org/10.1111/j.1365-2656.2008.01390.x

Ellenberg H, Leuschner C (2010) Vegetation Mitteleuropas mit den Alpen in ökologischer, dynamischer und historischer Sicht. UTB, Stuttgart

Elton CS (1958) The ecology of invasions by animals and plants. University of Chicago Press, Chicago

Funk JL (2008) Differences in plasticity between invasive and native plants from a low resource environment. J Ecol 96:1162–1173

Gallien L, Carboni M (2017) The community ecology of invasive species: where are we and what's next? Ecography 40:335–352. https://doi.org/10.1111/ecog.02446

Gazda A, Szwagrzyk J (2016) Introduced species in Polish National Parks: distribution, abundance and management approaches. In: Krumm F, Vítková L (eds) Introduced tree species in European forests: opportunities and challenges. European Forest Institute, Freiburg, pp 168–175

Godefroid S, Phartyal SS, Weyembergh G, Koedam N (2005) Ecological factors controlling the abundance of non-native invasive black cherry (*Prunus serotina*) in deciduous forest understory in Belgium. For Ecol Manag 210:91–105. https://doi.org/10.1016/j.foreco.2005.02.024

González-Muñoz N, Castro-Díez P, Godoy O (2014) Lack of superiority of invasive over co-occurring native riparian tree seedling species. Biol Invasions 16:269–281. https://doi.org/10.1007/s10530-013-0516-x

Grime JP (2006) Plant strategies, vegetation processes, and ecosystem properties. Wiley, Hoboken

Groninger JW, Zedaker SM, Fredericksen TS (1997) Stand characteristics of inter-cropped loblolly pine and black locust. For Ecol Manag 91:221–227. https://doi.org/10.1016/S0378-1127(96)03863-7

Halarewicz A (2012) Właściwości ekologiczne i skutki rozprzestrzeniania się czeremchy amerykańskiej *Padus serotina* (Ehrh.) Borkh. w wybranych fitocenozach leśnych. Wydawnictwo Uniwersytetu Przyrodniczego, Wrocław

Hedberg P, Kozub Ł, Kotowski W (2014) Functional diversity analysis helps to identify filters affecting community assembly after fen restoration by top-soil removal and hay transfer. J Nat Conserv 22:50–58. https://doi.org/10.1016/j.jnc.2013.08.004

Hill MO, Preston CD, Bosanquet SDS, Roy DB (2007) BRYOATT: attributes of British and Irish mosses, liverworts and hornworts. Centre for Ecology and Hydrology, Huntingdon

Horodecki P, Jagodziński AM (2017) Tree species effects on litter decomposition in pure stands on afforested post-mining sites. For Ecol Manag 406:1–11. https://doi.org/10.1016/j.foreco.2017.09.059

Hulme PE, Pyšek P, Pergl J et al (2014) Greater focus needed on alien plant impacts in protected areas: plant invasion impacts in protected areas. Conserv Lett 7:459–466

Iannone BV, Potter KM, Hamil K-AD et al (2016) Evidence of biotic resistance to invasions in forests of the Eastern USA. Landsc Ecol 31:85–99. https://doi.org/10.1007/s10980-015-0280-7

Jagodziński AM, Dyderski MK, Rawlik M, Banaszczak P (2015) Plantation of coniferous trees modifies risk and size of *Padus serotina* (Ehrh.) Borkh. invasion—Evidence from a Rogów Arboretum case study. For Ecol Manag 357:84–94. https://doi.org/10.1016/j.foreco.2015.08.011

Jagodziński AM, Horodecki P, Rawlik K, Dyderski MK (2017) Do understorey or overstorey traits drive tree encroachment on a drained raised bog? Plant Biol 19:571–583. https://doi.org/10.1111/plb.12569

Jagodziński AM, Dyderski MK, Horodecki P, Rawlik K (2018a) Limited dispersal prevents *Quercus rubra* invasion in a 14-species common garden experiment. Divers Distrib 24:403–414. https://doi.org/10.1111/ddi.12691

Jagodziński AM, Dyderski MK, Gęsikiewicz K et al (2018b) How do tree stand parameters affect young Scots pine biomass?—Allometric equations and biomass conversion and expansion factors. For Ecol Manag 409:74–83. https://doi.org/10.1016/j.foreco.2017.11.001

Jeschke JM (2014) General hypotheses in invasion ecology. Divers Distrib 20:1129–1134. https://doi.org/10.1111/ddi.12258

Kleyer M, Bekker RM, Knevel IC et al (2008) The LEDA Traitbase: a database of life-history traits of the Northwest European flora. J Ecol 96:1266–1274. https://doi.org/10.1111/j.1365-2745.2008.01430.x

Klotz S, Kühn I, Durka W (2002) BIOLFLOR—Eine Datenbank zu biologisch-ökologischen Merkmalen der Gefäßpflanzen in Deutschland. Schriftenreihe für Vegetationskunde, Bundesamt für Naturschutz, Bonn

Knight KS, Oleksyn J, Jagodzinski AM et al (2008) Overstorey tree species regulate colonization by native and exotic plants: a source of positive relationships between understorey diversity and invasibility. Divers Distrib 14:666–675. https://doi.org/10.1111/j.1472-4642.2008.00468.x

Kotowski W, Beauchard O, Opdekamp W et al (2010) Waterlogging and canopy interact to control species recruitment in floodplains. Funct Ecol 24:918–926. https://doi.org/10.1111/j.1365-2435.2009.01682.x

Kraft NJB, Adler PB, Godoy O et al (2015) Community assembly, coexistence and the environmental filtering metaphor. Funct Ecol 29:592–599. https://doi.org/10.1111/1365-2435.12345

Křivánek M, Pyšek P, Jarošík V (2006) Planting history and propagule pressure as predictors of invasion by woody species in a temperate region. Conserv Biol 20:1487–1498. https://doi.org/10.1111/j.1523-1739.2006.00477.x

Kuhn M (2008) Building predictive models in R using the caret package. J Stat Softw 28:1–26. https://doi.org/10.18637/jss.v028.i05

Kunstler G, Falster D, Coomes DA et al (2016) Plant functional traits have globally consistent effects on competition. Nature 529:204–207. https://doi.org/10.1038/nature16476

Kurek P, Sparks TH, Tryjanowski P (2015) Electricity pylons may be potential foci for the invasion of black cherry *Prunus serotina* in intensive farmland. Acta Oecol 62:40–44

Kurokawa H, Peltzer DA, Wardle DA (2010) Plant traits, leaf palatability and litter decomposability for co-occurring woody species differing in invasion status and nitrogen fixation ability. Funct Ecol 24:513–523. https://doi.org/10.1111/j.1365-2435.2009.01676.x

Laliberté E, Legendre P (2010) A distance-based framework for measuring functional diversity from multiple traits. Ecology 91:299–305. https://doi.org/10.1890/08-2244.1

Lockwood JL, Cassey P, Blackburn T (2005) The role of propagule pressure in explaining species invasions. Trends Ecol Evol 20:223–228. https://doi.org/10.1016/j.tree.2005.02.004

Lonsdale WM (1999) Global patterns of plant invasions and the concept of invasibility. Ecology 80:1522–1536. https://doi.org/10.1890/0012-9658(1999)080

Machado J-L, Reich PB (1999) Evaluation of several measures of canopy openness as predictors of photosynthetic photon flux density in deeply shaded conifer-dominated forest understory. Can J For Res 29:1438–1444. https://doi.org/10.1139/x99-102

Marozas V, Cekstere G, Laivins M, Straigyte L (2015) Comparison of neophyte communities of *Robinia pseudoacacia* L. and *Acer negundo* L. in the eastern Baltic Sea region cities of Riga and Kaunas. Urban For Urban Green 14:826–834. https://doi.org/10.1016/j.ufug.2015.08.003

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Mason NWH, Mouillot D, Lee WG, Wilson JB (2005) Functional richness, functional evenness and functional divergence: the primary components of functional diversity. Oikos 111:112–118. https://doi.org/10.1111/j.0030-1299.2005.13886.x

Mueller KE, Eissenstat DM, Hobbie SE et al (2012) Tree species effects on coupled cycles of carbon, nitrogen, and acidity in mineral soils at a common garden experiment. Biogeochemistry 111:601–614. https://doi.org/10.1007/s10533-011-9695-7

Muys B, Maddelein D, Lust N (1992) Ecology, practice and policy of black cherry (*Prunus serotina* Ehrh.) management in Belgium. Silva Gandav 57:28–45

Myczko Ł, Dylewski Ł, Zduniak P et al (2014) Predation and dispersal of acorns by European Jay (*Garrulus glandarius*) differs between a native (Pedunculate Oak *Quercus robur*) and an introduced oak species (Northern Red Oak *Quercus rubra*) in Europe. For Ecol Manag 331:35–39. https://doi.org/10.1016/j.foreco.2014.07.027

Niinemets Ü, Valladares F (2006) Tolerance to shade, drought, and waterlogging of temperate Northern Hemisphere trees and shrubs. Ecol Monogr 76:521–547. https://doi.org/10.1890/0012-9615(2006)076

Pairon M, Jonard M, Jacquemart A-L (2006) Modeling seed dispersal of black cherry, an invasive forest tree: how microsatellites may help? Can J For Res 36:1385–1394. https://doi.org/10.1139/x06-018

Paquette A, Fontaine B, Berninger F et al (2012) Norway maple displays greater seasonal growth and phenotypic plasticity to light than native sugar maple. Tree Physiol 32:1339–1347. https://doi.org/10.1093/treephys/tps092

Parker JD, Richie LJ, Lind EM, Maloney KO (2010) Land use history alters the relationship between native and exotic plants: the rich don't always get richer. Biol Invasions 12:1557–1571. https://doi.org/10.1007/s10530-009-9568-3

Pierce S, Brusa G, Vagge I, Cerabolini BEL (2013) Allocating CSR plant functional types: the use of leaf economics and size traits to classify woody and herbaceous vascular plants. Funct Ecol 27:1002–1010. https://doi.org/10.1111/1365-2435.12095

Pla L, Casanoves F, Di Rienzo J (2011) Quantifying functional biodiversity. Springer, Dordrecht

Purcel A (2009) Obce gatunki drzew i krzewów w Wielkopolskim Parku Narodowym—ich występowanie i rola w biocenozach Parku. Morena 14:35–191

Pyšek P, Křivánek M, Jarošík V (2009) Planting intensity, residence time, and species traits determine invasion success of alien woody species. Ecology 90:2734–2744. https://doi.org/10.1890/08-0857.1

Pyšek P, Jarošík V, Pergl J et al (2014) Temperate trees and shrubs as global invaders: the relationship between invasiveness and native distribution depends on biological traits. Biol Invasions 16:577–589. https://doi.org/10.1007/s10530-013-0600-2

Pyšek P, Manceur AM, Alba C et al (2015) Naturalization of central European plants in North America: species traits, habitats, propagule pressure, residence time. Ecology 96:762–774. https://doi.org/10.1890/14-1005.1

Rice SK, Westerman B, Federici R (2004) Impacts of the exotic, nitrogen-fixing black locust (*Robinia pseudoacacia*) on nitrogen-cycling in a pine–oak ecosystem. Plant Ecol 174:97–107. https://doi.org/10.1023/B:VEGE.0000046049.21900.5a

Richardson DM (1998) Forestry trees as invasive aliens. Conserv Biol 12:18–26. https://doi.org/10.1111/j.1523-1739.1998.96392.x

Richardson DM, Rejmánek M (2011) Trees and shrubs as invasive alien species—a global review. Divers Distrib 17:788–809. https://doi.org/10.1111/j.1472-4642.2011.00782.x

Richardson DM, Pyšek P, Rejmánek M et al (2000) Naturalization and invasion of alien plants: concepts and definitions. Divers Distrib 6:93–107. https://doi.org/10.1046/j.1472-4642.2000.00083.x

Riepšas E, Straigyté L (2008) Invasiveness and ecological effects of red oak (*Quercus rubra* L.) in Lithuanian forests. Balt For 14:122–130

Roberts DR, Bahn V, Ciuti S et al (2017) Cross-validation strategies for data with temporal, spatial, hierarchical, or phylogenetic structure. Ecography 40:913–929. https://doi.org/10.1111/ecog.02881

Rodríguez J, Lorenzo P, González L (2017) Different growth strategies to invade undisturbed plant communities by *Acacia dealbata* Link. For Ecol Manag 399:47–53. https://doi.org/10.1016/j.foreco.2017.05.007

Sinclair JS, Arnott SE (2015) Strength in size not numbers: propagule size more important than number in sexually reproducing populations. Biol Invasions 18:497–505. https://doi.org/10.1007/s10530-015-1022-0

Starfinger U, Kowarik I, Rode M, Schepker H (2003) From desirable ornamental plant to pest to accepted addition to the flora?—the perception of an alien tree species through the centuries. Biol Invasions 5:323–335. https://doi.org/10.1023/B:BINV.0000005573.14800.07

Stohlgren TJ, Binkley D, Chong GW et al (1999) Exotic plant species invade hot spots of native plant diversity. Ecol Monogr 69:25–46. https://doi.org/10.1890/0012-9615(1999)069

Stohlgren TJ, Jarnevich C, Chong GW et al (2006) Scale and plant invasions: a theory of biotic acceptance. Preslia 78:405–426

Terwei A, Zerbe S, Zeileis A et al (2013) Which are the factors controlling tree seedling establishment in North Italian floodplain forests invaded by non-native tree species? For Ecol Manag 304:192–203. https://doi.org/10.1016/j.foreco.2013.05.003

Terwei A, Zerbe S, Mölder I et al (2016) Response of floodplain understorey species to environmental gradients and tree invasion: a functional trait perspective. Biol Invasions 18:2951–2973. https://doi.org/10.1007/s10530-016-1188-0

Thomsen MS, Wernberg T, South PM, Schiel DR (2016) To include or not to include (the invader in community analyses)? That is the question. Biol Invasions 18:1515–1521. https://doi.org/10.1007/s10530-016-1102-9

Tilman D (1986) Resources, competition and the dynamics of plant communities. In: Crawley M (ed) Plant ecology. Blackwell Scientific Publications, Oxford, pp 51–75

Vanhellemont M, Verheyen K, Keersmaeker L et al (2009) Does *Prunus serotina* act as an aggressive invader in areas with a

low propagule pressure? Biol Invasions 11:1451–1462. https://doi.org/10.1007/s10530-008-9353-8

Vítková M, Müllerová J, Sádlo J et al (2017) Black locust (*Robinia pseudoacacia*) beloved and despised: a story of an invasive tree in Central Europe. For Ecol Manag 384:287–302. https://doi.org/10.1016/j.foreco.2016.10.057

Wagner V, Chytrý M, Jiménez-Alfaro B et al (2017) Alien plant invasions in European woodlands. Divers Distrib 23:969–981. https://doi.org/10.1111/ddi.12592

Westoby M (1998) A leaf-height-seed (LHS) plant ecology strategy scheme. Plant Soil 199:213–227. https://doi.org/10.1023/A:1004327224729

Woziwoda B, Potocki M, Sagan J et al (2014) Commercial forestry as a vector of alien tree species-the case of *Quercus rubra* L. introduction in Poland. Balt For 20:131–141

Yeo I-K, Johnson RA (2000) A new family of power transformations to improve normality or symmetry. Biometrika 87:954–959. https://doi.org/10.1093/biomet/87.4.954

Younginger BS, Sirová D, Cruzan MB, Ballhorn DJ (2017) Is biomass a reliable estimate of plant fitness? Appl Plant Sci 5:1600094. https://doi.org/10.3732/apps.1600094

Zerbe S, Wirth P (2006) Non-indigenous plant species and their ecological range in Central European pine (*Pinus sylvestris* L.) forests. Ann For Sci 63:189–203. https://doi.org/10.1051/forest:2005111

Ziegenhagen B, Kausch W (1995) Productivity of young shaded oaks (*Quercus robur* L.) as corresponding to shoot morphology and leaf anatomy. For Ecol Manag 72:97–108. https://doi.org/10.1016/0378-1127(94)03482-C

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Low impact of disturbance on ecological success of invasive tree and shrub species in temperate forests

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Low impact of disturbance on ecological success of invasive tree and shrub species in temperate forests

Marcin K. Dyderski (ID) · **Andrzej M. Jagodziński** (ID)

Abstract Disturbance is claimed to be one of the most important triggers of biological invasions. There is a lack of data about disturbance impacts on the youngest life stage of invasive trees and shrubs. Thus, we aimed to assess the role of disturbances in shaping responses of natural regeneration of three model invasive species—*Prunus serotina* Ehrh., *Quercus rubra* L., and *Robinia pseudoacacia* L.—to disturbances in forest plant communities. Our study was conducted over 3 years on 372 study plots (100 m^2), across nine types of temperate forests in Wielkopolski National Park (Poland). Disturbance was assessed using ecological indicator values for disturbance severity and frequency. Our study revealed the high importance of disturbance on species composition of understory vegetation. We also found relationships between ecological success (density and biomass of natural regeneration) of invaders and disturbance indices. These models were statistically significant but their effect sizes were low. Due to the low effect sizes, we can state only limited conclusions about impact of disturbance on ecological success of invasive species natural regeneration. The results suggest that for seedlings (up to 50 cm height—threshold between understory and shrub layer) disturbance, a leading factor in biological invasions of numerous taxa, has a small role in this case. Thus, we may assume that their ecological success is connected with stochastic processes in populations of the invader's seedlings, rather than with stochastic release from competition caused by disturbances.

Keywords Black cherry · Northern red oak · Black locust · Intermediate-disturbance hypothesis · Saplings

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Introduction

Biological invasions are one of the major threats to biodiversity (Mack et al. 2000; Davis 2003; Essl et al. 2017). Ecological success of invasive species is a derivate of three groups of factors: species invasiveness, habitat invasibility, and propagule pressure. Species invasiveness compromises life history traits

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providing advantages over native species, which allow alien species to establish in their secondary range (e.g., Tecco et al. 2010; Pyšek et al. 2014; Gallien et al. 2016). Habitat invasibility describes its vulnerability to colonization by alien species (e.g., Lonsdale 1999; Alpert et al. 2000; Richardson and Pyšek 2006). Propagule pressure reflects quantity, quality, and availability of alien species' dispersal units (e.g., Lockwood et al. 2005; Křivánek et al. 2006; Vanhellemont et al. 2009). However, invasion success depends not merely on these factors treated separately, but rather on their interactions (e.g., Alpert et al. 2000; Davis et al. 2005; Jagodziński et al. 2015).

Disturbance is a catastrophic event removing part of the ecosystem biomass, caused by biotic or abiotic factors. Examples include biotic insect outbreaks (Jonášová and Prach 2004; Kučerová et al. 2008; Zeppenfeld et al. 2015) and abiotic wildfires (Clarke et al. 2015; Benscoter et al. 2015; Frelich et al. 2017). Human activity may also create disturbance events (e.g., Prach et al. 2001, 2014; Dyderski et al. 2016). Disturbance regimes differ in both frequency and severity, i.e., length of interval between consecutive disturbance events and in proportion of biomass destroyed during single disturbance events (Herben et al. 2016, 2018). Thus, some plant species are adapted to disturbed habitats, which is manifested in their life strategies (Grime 2001; Pierce et al. 2013; Herben et al. 2018), reflecting their functional traits (Baker 1974; Westoby 1998; Prach et al. 2001). For that reason, disturbance is one of the major factors shaping species composition of vegetation in some biomes (Turetsky and Louis 2006; Johnstone et al. 2016; Frelich et al. 2017).

Disturbance dependency is an example of invasion ecology concepts merging these aspects (Hobbs and Huenneke 1992; Chabrerie et al. 2008; Jeschke 2014; Rodríguez et al. 2017). This concept assumes that invasive species reach higher ecological success in disturbed sites (habitat parameter). As intermediate disturbances lead to increase of species richness (Fox 1979), according to the biotic acceptance theory (Stohlgren et al. 2006), this leads to the increase of alien species richness. Moreover, changes in disturbance frequency and intensity (both increase and decrease), as well as change of disturbance type may alter the species composition and create the opportunities for invasive species (Hobbs and Huenneke 1992). For that reason, species with functional traits

favoring disturbance have higher spread availability in the secondary range (invasiveness). Moreover, disturbed sites may attract species that are vectors of propagules, e.g., frugivorous birds, increasing propagule availability (propagule pressure). Disturbance is also claimed to be a reason for invasions in agroecosystems (Baker 1974; Groves 2006), riparian landscapes (Pyšek and Prach 1993; Richardson et al. 2007; Dyderski and Jagodziński 2016), or urban ecosystems (Knapp et al. 2010; Jarošík et al. 2011; Obidziński et al. 2016), as well as in natural forests (Chmura and Sierka 2007). Nevertheless, our literature review did not find studies about disturbance impacts on the youngest life stage of invasive trees and shrubs.

The aim of this study was to assess the role of disturbances in shaping forest understory vegetation and responses of invasive tree and shrub species to disturbances in forest plant communities. Based on earlier studies on invasion ecology we hypothesized that (1) disturbances are more important factor shaping species composition of vegetation than fertility gradient, (2) invasive species perform better (i.e., reaching higher biomass and density of natural regeneration) in plant communities with more frequent and more severe disturbances, and (3) invasive species will respond differently to disturbance indices—competitive species responses will be negative and ruderal species responses positive.

Materials and methods

Species studied

As model species, we used the three most frequent woody alien species invading forest ecosystems in Europe (Wagner et al. 2017): *Prunus serotina* Ehrh., *Quercus rubra* L., and *Robinia pseudoacacia* L. All these species come from the eastern part of North America and were introduced for forest management purposes (Starfinger et al. 2003; Cierjacks et al. 2013; Woziwoda et al. 2014). *P. serotina* in its native range is a tree but in Europe it is most frequently a tall shrub. Due to high rate of leaf litter decomposition, *P. serotina* was widely used as a soil improver (Muys et al. 1992; Aerts et al. 2017; Horodecki and Jagodziński 2017). *P. serotina* is able to wait out unfavorable environmental conditions (insufficient light availability) by slow growth rates of seedlings

(Closset-Kopp et al. 2007) and benefit from opportunity windows in resource availability (Chabrerie et al. 2008). This species is mainly dispersed by birds (Pairon et al. 2006). *Q. rubra*, due to large seed mass, is a species strongly dependent on propagule pressure (Riepšas and Straigytė 2008; Myczko et al. 2014; Jagodziński et al. 2018), but also able to use carbohydrate reserves stored in the acorn (Ziegenhagen and Kausch 1995). *R. pseudoacacia* is a wind-dispersed, pioneer tree species, that usually colonizes disturbed areas (Cierjacks et al. 2013; Vítková et al. 2017; Sádlo et al. 2017), especially due to its ability to fix nitrogen (Boring and Swank 1984; Rice et al. 2004). Thus, the species studied have differing responses to disturbance. In Poland, *P. serotina* prefers less-fertile sites and *R. pseudoacacia*—those more fertile, while *Q. rubra*—both less-fertile and more fertile sites (Chmura 2004; Halarewicz 2012; Gazda and Szwagrzyk 2016).

Study area

The study was conducted in the forests of Western Poland, within Wielkopolski National Park (52°16′N, 16°48′E). This national park covers an area of 7584 ha and its aim is to preserve a valuable post-glacial landscape, including valleys, moraine hills, and lakes. Climate of the study area is temperate, transitional between oceanic and continental. In the years 1951–2010, mean annual temperature was 8.4 °C and mean annual precipitation was 521 mm (Poznań meteorological station, c.a. 15 km from the study area). Main soil types are luvisols (47%) and brunic and haplic soils (30%), podzols constitute 7% (Nowak et al. 2000). Forests cover 61% of Wielkopolski National Park, and the most frequent plant associations are *Galio sylvatici-Carpinetum*, *Calamagrostio arundinaceae-Quercetum*, and *Querco roboris-Pinetum*. However, some patches are covered by fertile riparian forests (*Fraxino-Alnetum*, *Querco-Ulmetum minoris*) or poor coniferous forests (*Leucobryo-Pinetum*). Nevertheless, large areas of deciduous forests were planted with *Pinus sylvestris* before the national park was established in 1957 (Nowak et al. 2000). This replacement caused transformation of both vegetation and soil chemistry by nutrient leaching and acidification (Binkley and Giardina 1998; Zerbe and Wirth 2006). Another negative aspect of human impacts was introductions of alien woody species (Purcel 2009;

Gazda and Szwagrzyk 2016). This resulted in the presence of pure stands of alien species surrounded by large areas of forest ecosystems with different levels of disturbances and human impacts. Therefore, Wielkopolski National Park seems to be an excellent place to test hypotheses about impacts of disturbances on ecological success of invasive species.

Study design

In the study area, we established 21 block sites (nine for *Q. rubra*, six for *P. serotina*, and six for *R. pseudoacacia*), each with a central monoculture stand of invasive species housing a total of 378 plots (squares 100 m² in area). For study design details, see Dyderski and Jagodziński (2018). In the case of *P. serotina*, occurring only as an admixture in tree stands, these are tree stands with high densities of fruiting trees. In the central part of each monoculture, we established a pair of study plots. Along each of the four sides (N, S, E, and W) of the central pair, we established two pairs of plots: one nearly outside the stand—at the invasion edge, and the second pair 30 m from the invasion edge. The invasion edge was defined as the border between crowns of the invasive species monoculture and the surrounding trees. Thus, each study block compromised 18 study plots. The study design did not generate pseudoreplications, which may be expected due to short distances between plots in blocks, because of the high spatial heterogeneity. This was manifested in high variability of natural regeneration within plots, light availability, and microsite occurrences. Because plots were distributed systematically, six of them were located within forest vegetation paths and were therefore excluded from analyses, so that the final number of plots was $n = 372$. The plots were divided into nine categories according to dominant tree species: *Acer platanoides-Tilia cordata-Carpinus betulus*, *Fagus sylvatica*, *Pinus sylvestris-Acer pseudoplatanus*, *Pinus sylvestris-Acer platanoides-Tilia cordata-Carpinus betulus*, *Pinus sylvestris-Prunus serotina*, *Pinus sylvestris-Quercus petraea*, *Quercus petraea*, *Quercus rubra*, and *Robinia pseudoacacia* (Online Resource 1). The variability of light availability, different tree stand types, and microsite presence, allowed us to assume that the experimental design did not produce spatial clusters connected with block arrangement, which would have needed to be accounted for in the statistical design,

e.g., by application of mixed models (Roberts et al. 2017).

During July of 2015-2017, we measured root collar diameters and heights of all trees of the study species on each plot shorter than 0.5 m (in total 39664 plants). Using allometric equations developed on sample trees (356 of *P. serotina*, 133 of *Q. rubra* and 158 of *R. pseudoacacia*) harvested in a 5-m buffer zone around the study plots (Online Resource 2; Dyderski and Jagodziński 2018), we estimated their total above- and belowground biomass. In addition to natural regeneration of the study species, we assessed species composition of understory vegetation, recording species identities and abundances using the Braun-Blanquet method. We also measured canopy openness index (diffuse non-interceptance; DIFN) using an LAI-2200 plant canopy analyzer (Li-Cor Inc., Lincoln, NE, USA). For each plot, we recorded four series of ten samples. The measurements were conducted in August 2016, as our previous studies indicated that this month has maximal canopy foliage development (Knight et al. 2008). In March 2017, we collected four samples of leaf litter from circular plots (0.16 m^2). The samples were dried in the oven at 65 °C to constant mass and weighed using a balance with an accuracy of 1 g. Litter pH was assessed using an electronic pH-meter in distilled water solution after 24 h. We used these variables as approximations of nutrient cycling rates and soil acidity in forest ecosystems.

Data analysis

Using data about vegetation species composition for each study plot, we calculated community-weighted means (CWM) of disturbance indices proposed by Herben et al. (2016). These indices reflect disturbance severity, expressed as fraction of community biomass being destroyed, and disturbance frequency, expressed as logarithm of mean time between disturbance events. These indices were developed based on expert assessment of vegetation typological units (phytosociological classes) and calibrated using a dataset of vegetation samples. The indices are correlated with functional traits reflecting disturbance responses—height, seed mass, and clonality (Herben et al. 2016). Because disturbances in forest ecosystems may affect only the understory or the whole community, we decided to analyze both types of disturbance measures.

To assess the factors shaping vegetation species composition, we performed Detrended Correspondence Analysis (DCA) using the *vegan::decorana()* function (Oksanen et al. 2016). This type of multivariate analysis was chosen due to long environmental gradients (> 3 SD units). As an unconstrained analysis, DCA reveals dispersion of points in ordination space, reflecting particular species abundances within study plots. To determine factors correlated with the gradients revealed, we used the *vegan::envfit()* function (Oksanen et al. 2016) for passive projection of environmental factors: DIFN, litter mass, disturbance indices, and CWMs of specific leaf area (SLA), canopy height, and seed mass—functional traits describing plant life strategies, according to LHS concept (leaf-height-seed; Westoby 1998). LHS traits were obtained from the LEDA database (Kleyer et al. 2008). We also used proportion of species representing phytosociological classes (Ratyńska et al. 2010) and life strategies (Klotz et al. 2002). CWM computation was done using the *FD::functcomp()* function (Laliberté et al. 2014).

We used ordinary least squares regression to check the strength of relationships between the measures of invasive species ecological success (density and biomass of natural regeneration) and disturbance indices. Prior to analyses, we log-transformed densities and biomasses, due to log-normal distributions. Because high numbers of observations increase statistical significance of low differences between treatments as expressed by *p* values, for our case of $n = 1116$ (372 plots × 3 years), we resigned from interpretation of *p* values, which could be biased by reporting statistically significant results with little or no biological meaning (the so-called '*p* value hacking'), according to the American Statistical Association (Wasserstein and Lazar 2016). Instead, we focused on correlation coefficients and effect sizes. To evaluate the latter, we compared 95% confidence intervals (CI) of predicted measures of invasive species ecological success. This was done by inputting the 0.025, 0.5, and 0.975 quantiles of disturbance indices into the regression equation and visualizing the range of the values obtained. The wider the CI of predicted values, the higher the effect of the considered factor on the dependent variable. Although only *R. pseudoacacia* has assigned disturbance indices values, in regressions, we used disturbance indices calculated excluding the study species, to avoid

circular reasoning (Thomsen et al. 2016). All analyses were conducted using R software (R Core Team 2017).

Results

Impact of disturbance on understory vegetation

DCA (Fig. 1, Table 1) revealed two main gradients in differentiation of vegetation species composition. The first gradient (across DCA1 axis) was identified as availability of light and soil nutrients: from poor *P. sylvestris* sites with high light availability at the left to fertile oak-hornbeam and *R. pseudoacacia* forests at the right. This gradient also reflected functional traits connected with competition—life strategy 'c' (competitors) and high SLA CWM. The differentiation along DCA1 axis was reflected both at the tree stand and understory species composition levels, which was reflected by opposite proportions of *Vaccinio-Piceetea* and *Querco-Fagetea* species cover. The second distinct gradient (along DCA2 axis) described disturbance intensity. Low values of DCA2 indicated the presence of stress-tolerant species and ancient forest indicator species, whereas high values—presence of 'r' strategy species—were an indicator of frequent and severe disturbances. This was also correlated with proportion of meadow species (*Molinio-Arrhenatheretea*). The range of whole community disturbance frequency index ranged from − 1.986 to − 1.107, with an average of − 1.761 ± 0.004, which indicated a mean turnover interval of c.a. 58 years. The analogous index for the herb layer ranged from − 1.252 to − 0.526, with an average of − 0.781 ± 0.002, which indicated a mean turnover interval of c.a. 16 years. Whole community disturbance severity index ranged from 0.224 to 0.447, with an average of 0.296 ± 0.001 and herb layer severity index ranged from 0.042 to 0.381, with an average of 0.172 ± 0.002.
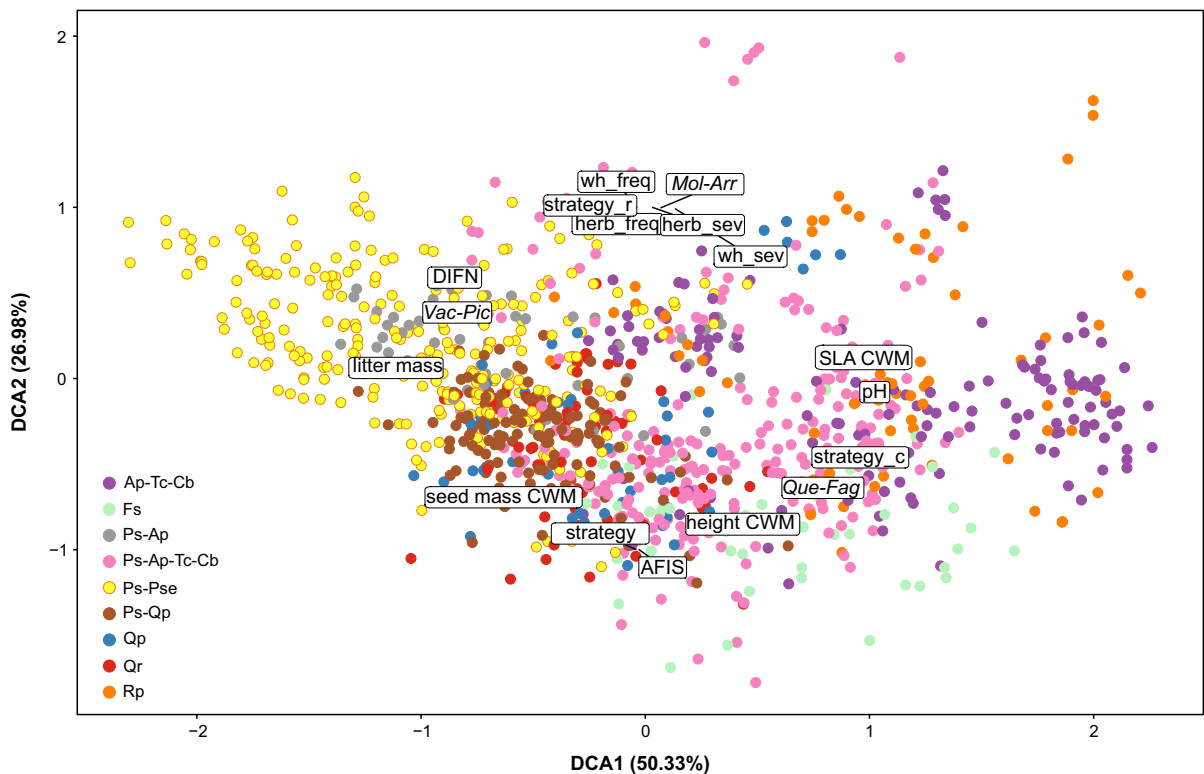

Fig. 1 DCA results conducted on understory vegetation of sample plots in three growing seasons (*n* = 1116). Labels represent passively projected environmental variables (Table 1), colors represent tree stand types: Ap-Tc-Cb, *Acer platanoides-Tilia cordata-Carpinus betulus*; Fs, *Fagus sylvatica*; Ps-Ap, *Pinus sylvestris-Acer pseudoplatanus*; Ps-Ap-Tc-Cb, *Pinus sylvestris-Acer platanoides-Tilia cordata-Carpinus betulus*; Ps-Pse, *Pinus sylvestris-Prunus serotina*; Ps-Qp, *Pinus sylvestris-Quercus petraea*; Qp, *Quercus petraea*, Qr, *Quercus rubra*; Rp, *Robinia pseudoacacia* (Table S1)

Table 1 Parameters of environmental variables fitted to the DCA analysis results

Parameter	Abbreviation	DCA1	DCA2	R^2	p
Light availability (diffuse non-interceptance)	DIFN	− 0.7295	0.6840	0.431	0.001
Litter mass	Litter mass	− 0.9877	0.1561	0.478	0.001
Litter pH	pH	0.9999	0.0156	0.593	0.001
Cover of species from class *Molinio-Arrhenatheretea*	*Mol-Arr*	0.0699	0.9976	0.281	0.001
Querco-Fagetea	*Que-Fag*	0.8269	− 0.5623	0.572	0.001
Vaccinio-Piceetea	*Vac-Pic*	− 0.9567	0.2910	0.553	0.001
Cover of ancient forest indicator species	AFIS	− 0.0276	− 0.9996	0.134	0.001
Whole community disturbance frequency index	Wh_freq	− 0.0378	0.9993	0.518	0.001
Whole community disturbance severity index	Wh_sev	0.1345	0.9909	0.226	0.001
Herb layer disturbance frequency index	Herb_freq	− 0.0487	0.9988	0.167	0.001
Herb layer disturbance severity index	Herb_sev	0.0327	0.9995	0.361	0.001
CWM of canopy height	Height CWM	0.3097	− 0.9508	0.152	0.001
CWM of specific leaf area	SLA CWM	0.9998	0.0208	0.209	0.001
CWM of seed mass	Seed mass CWM	− 0.6126	− 0.7904	0.131	0.001
Proportion of 'c' strategy species (competitors)	Strategy_c	0.8313	− 0.5559	0.066	0.001
Proportion of 'r' strategy species (ruderals)	Strategy_r	− 0.1115	0.9938	0.023	0.002
Proportion of 's' strategy species (stress-tolerant)	Strategy_s	− 0.0415	− 0.9991	0.071	0.001

Determination coefficient R^2 and p value were obtained based on permutation test with 999 iterations

CWM community-weighted mean

Impact of disturbance on invasive species ecological success

Analysis of correlations between disturbance indices and measures of success of invasive species natural regeneration (density and biomass) revealed low values of correlation coefficients. However, strength of correlations and size effects varied among species, disturbance indices, and life stages (Fig. 2, Table 2, Online Resource 3). The highest correlation coefficients were found for *P. serotina* seedling density and total *P. serotina* density and biomass, and effect of herb layer disturbance frequency index on *R. pseudoacacia* density and biomass (both seedlings and total). *P. serotina* density and biomass had the highest correlation coefficients in relationships with whole community frequency index and herb layer severity index, and the lowest—with herb layer frequency index. *R. pseudoacacia* biomass and density were most closely correlated with herb layer frequency index. *Q. rubra* did not show any relationships with the disturbance indices studied. Regarding direction of correlation (positive or negative), we found that most of the correlations with $r > 0.2$ were positive. An

exception was response of *R. pseudoacacia* density to herb layer frequency index. However, response of *R. pseudoacacia* biomass to the same index was positive. The best fit predictor for *P. serotina* total density—whole community frequency index—predicted CI of 9.6–670.2 ind. ha^{-1}, with median of 33.5 ind. ha^{-1}, whereas real CI was 0.0–19812.5 ind. ha^{-1} and a median of 100 ind. ha^{-1}. The best predictor for *R. pseudoacacia* seedling density—herb layer frequency index—predicted CI of 0.9–26.3 ind. ha^{-1}, with median of 6.2 ind. ha^{-1}, whereas real CI was 0.0–13550.0 ind. ha^{-1}, with median of 0 ind. ha^{-1}.

Discussion

Impact of disturbance on vegetation species composition

Our study revealed that disturbance was the second factor characterizing vegetation species composition. Due to the extent of the fertility gradient, determining dominant tree species, this group of factors shaped the first gradient. Different tree species have different soil
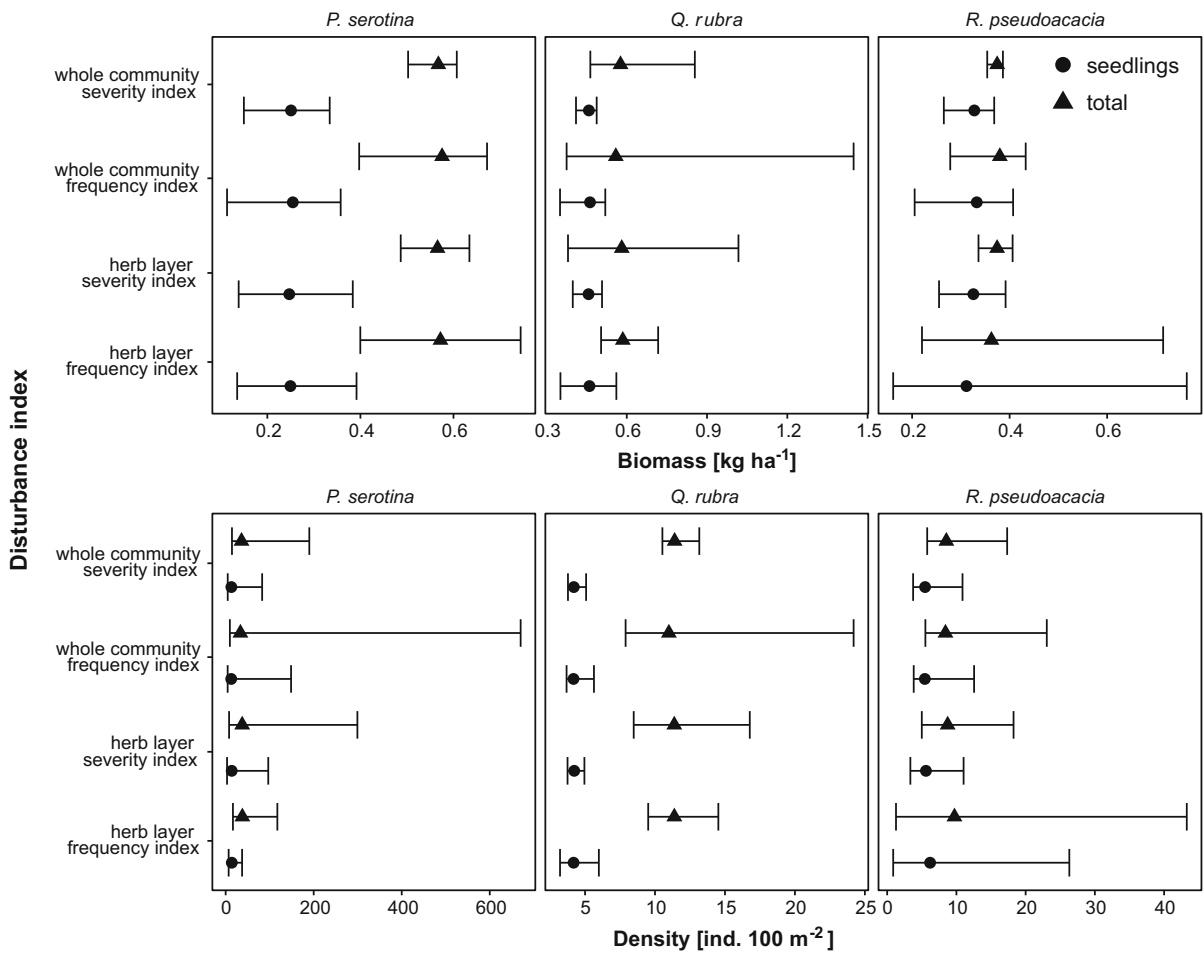
Fig. 2 Effect sizes for invasive species biomass and density prediction based on disturbance indices, modeled using simple regression (Online Resource 3). Points represent biomass or density predicted for median value of each disturbance indices, whiskers—range of 95% CI (i.e., values of 0.025 and 0.975 quantiles). Length of CI reflects relative size effect of each disturbance index within a panel

requirements (Ellenberg 1988; Kozlowski and Pallardy 1997), but their presence also shapes soil properties by altering biogeochemical cycles (e.g., Reich et al. 2005; Hobbie et al. 2006; Mueller et al. 2012). For that reason, the fertility gradient was superior over the disturbance gradient. Our previous study conducted in the same set of study plots (Dyderski and Jagodziński 2018) revealed that soil fertility proxies influenced biomass of natural regeneration of the species studied. Patterns of invasive species abundance along fertility gradient would be related to the biotic acceptance theory, which states that plant communities richer in native species are richer in alien species (Stohlgren et al. 2006). This pattern was also confirmed in relationship between

native species richness and invasive species abundance (Knight et al. 2008). Species richness is related with soil fertility (Tilman 1986), which also may limit some alien species (e.g., Pyšek and Prach 1993; Chmura 2004; Halarewicz 2012). However, the importance of soil fertility proxies in our previous study (Dyderski and Jagodziński 2018) was lower than importance of propagule pressure.

The disturbance gradient was connected with the presence of ruderals and species typical to meadows and pastures (*Molinio-Arrhenatheretea*) and negatively correlated with cover of ancient forest species indicators. The latter is a group of forest specialists, connected with undisturbed, long-lasting forests (Peterken 1974; Hermy et al. 1999; Dyderski et al.

Table 2 Pearson's correlation coefficients (*r*) between quantity of invasive species studied (rows, biomasses, and densities of seedlings) and all plants in regeneration layers up to 0.5 m height (total) and disturbance indices (columns; Herben et al. 2016). For regression parameters see Online Resource 3

Dependent variable	Whole community index		Herb layer index	
	frequency	severity	frequency	severity
Biomass				
P. serotina seedlings	0.083	0.107	− 0.017	0.110
P. serotina total	0.361	0.186	0.105	0.300
Q. rubra seedlings	− 0.109	− 0.040	− 0.068	− 0.075
Q. rubra total	0.361	0.186	0.105	0.300
R. pseudoacacia seedlings	0.031	0.121	− 0.204	0.117
R. pseudoacacia total	0.048	0.103	− 0.066	0.097
Density				
P. serotina seedlings	0.249	0.226	0.065	0.265
P. serotina total	0.329	0.222	0.128	0.297
Q. rubra seedlings	0.013	0.028	0.027	0.015
Q. rubra total	0.048	0.011	0.004	0.036
R. pseudoacacia seedlings	0.079	0.089	− 0.238	0.096
R. pseudoacacia total	0.099	0.102	− 0.235	0.111

2017). These correlations provide convincing evidence that disturbance indicators elaborated by Herben et al. (2016) allow for good assessment of vegetation response to disturbances.

Impact of disturbance on studied species responses

Our study revealed that although disturbances (represented here by indices) are important factors shaping understory vegetation species composition, they have low importance in shaping ecological success of the invasive species studied. This result may seem to contradict previous studies (e.g., Chmura and Sierka 2007; Chabrerie et al. 2008; Rodríguez et al. 2017). However, the difference is connected with the life stage that we studied—natural regeneration. Seedlings of the invasive woody species reflect only one of the stages of the invasion process (Sebert-Cuvillier et al. 2007). Although this stage is crucial for further growth of invaders and their reproduction, our results show that seedling performance is shaped to only a low degree by disturbance. For that reason, our results do not contradict the previous findings, but show the exception to the general rule. Nevertheless, another study we conducted revealed that the most important predictors of biomasses of the species studied were factors describing propagule pressure (Dyderski and Jagodziński 2018). Invasion success is usually controlled by interaction of propagule pressure and

invasibility (Davis et al. 2005). Thus, disturbance regime, as only one aspect of invasibility, cannot be the crucial predictor for ecological success of the species studied.

One of the possible reasons influencing the low impact of disturbance could be the relatively short gradient of disturbances within our dataset. We assumed this to be a limitation of our approach. However, Hobbs and Huenneke (1992) claim that any change of disturbance regime may create opportunity for invasive species. Herben et al. (2016) elaborated their indices for the whole range of vegetation types, from pleuston communities to the most stable forests. The highest disturbance turnover, typical to pleuston vegetation or crops, cannot possibly occur in forest ecosystems, given the high proportion of biomass destroyed annually. Values of the disturbance frequency indicators for the whole community were higher than proposed for forest plant communities (Herben et al. 2016), whereas values of herb layer disturbance frequency indicators were lower. According to the bimodal distribution of indicator values presented by Herben et al. (2016), the range of values obtained by us cover the range of the first distribution peak around − 2. Similarly, values of severity index from our study covered the peak between 0.1 and 0.4. For that reason, we can assume that our study covered the sustainable proportion of disturbance gradients that occur in forest plant communities. This is also

supported by the important role in shaping the species composition of vegetation shown by DCA (Fig. 1).

Different responses of disturbance of particular species studied

Despite the low importance and effect sizes of the patterns studied, we expected differences in responses of the invasive species studied to disturbance indices, connected with species biology. However, these conclusions are limited, due to low effect sizes of the relationships studied. The species most expected to be prone to disturbance, *Q. rubra* did not exhibit any relationship to the parameters studied, likely as a result of seedling dependence on carbohydrates stored in acorns (Sork 1984; Ziegenhagen and Kausch 1995). However, this effect should be lower for the case of the total regeneration layer. One possible explanation may be the ability of persistence in unsuitable conditions for one or two growing seasons, similar to the Oskar strategy of *P. serotina* (Closset-Kopp et al. 2007). Nevertheless, *P. serotina* showed positive responses to disturbances, supporting results of earlier studies (Closset-Kopp et al. 2007; Chabrerie et al. 2008; Jagodziński et al. in prep.).

For *R. pseudoacacia*, the highest correlation coefficient was found in a negative relationship between its ecological success and understory disturbance frequency index. This species is known for acting as ruderal—occupation of disturbed areas, wind dispersal, and production of large number of seeds (Cierjacks et al. 2013; Vítková et al. 2017). For that reason, we assume that this pattern may be an effect of presence of numerous *R. pseudoacacia* in plots with low light availability, thus favoring forest specialists (Dzwonko 1993; Hermy et al. 1999). In contrast, plots with abundant open habitat species did not host abundant natural regeneration of *R. pseudoacacia*.

Our study revealed that although disturbance indices are important factors shaping understory vegetation species composition, it has low importance in shaping ecological success of the invasive species studied. Due to the low effect sizes, we can state only limited conclusions about impacts of disturbance on ecological success of natural regeneration of the invasive species studied. The results suggest that for seedlings (up to 50 cm height) disturbance, a leading factor in biological invasions for numerous taxa, has a small role in this case. Our previous study (Dyderski

and Jagodziński 2018) revealed the crucial role of propagule pressure in shaping ecological success of natural regeneration for these species. Thus, we may assume that their ecological success is more connected with stochastic processes in the invader's seedling populations than with stochastic release from competition caused by disturbances. This possibility would lead to two management implications. Firstly, risk assessments should account not for disturbed sites, but rather for propagule sources. Secondly, the regeneration layer needs monitoring as random processes, not predictable using data about disturbances, may lead to quick release of invaders (Hobbs and Huenneke 1992).

References

Aerts R, Ewald M, Nicolas M et al (2017) Invasion by the alien tree *Prunus serotina* alters ecosystem functions in a temperate deciduous forest. Front Plant Sci 8:179. https://doi.org/10.3389/fpls.2017.00179

Alpert P, Bone E, Holzapfel C (2000) Invasiveness, invasibility and the role of environmental stress in the spread of nonnative plants. Perspect Plant Ecol Evol Syst 3:52–66. https://doi.org/10.1078/1433-8319-00004

Baker HG (1974) The evolution of weeds. Annu Rev Ecol Syst 5:1–24. https://doi.org/10.1146/annurev.es.05.110174.000245

Benscoter BW, Greenacre D, Turetsky MR (2015) Wildfire as a key determinant of peatland microtopography. Can J For Res 45:1132–1136. https://doi.org/10.1139/cjfr-2015-0028

Binkley D, Giardina C (1998) Why do tree species affect soils? The warp and woof of tree-soil interactions. Biogeochemistry 42:89–106. https://doi.org/10.1023/A:1005948126251

Boring LR, Swank WT (1984) Symbiotic nitrogen fixation in regenerating black locust (*Robinia pseudoacacia* L.) stands [North Carolina]. For Sci 30:528–537

Chabrerie O, Verheyen K, Saguez R, Decocq G (2008) Disentangling relationships between habitat conditions, disturbance history, plant diversity, and American black cherry (*Prunus serotina* Ehrh.) invasion in a European temperate forest. Divers Distrib 14:204–212. https://doi.org/10.1111/j.1472-4642.2007.00453.x

Chmura D (2004) Penetration and naturalisation of invasive alien plant species (neophytes) in woodlands of the Silesian Upland (southern Poland). Nat Conserv 60:3–11

Chmura D, Sierka E (2007) The invasibility of deciduous forest communities after disturbance: a case study of *Carex brizoides* and *Impatiens parviflora* invasion. For Ecol Manag 242:487–495. https://doi.org/10.1016/j.foreco.2007.01.083

Cierjacks A, Kowarik I, Joshi J et al (2013) Biological Flora of the British Isles: *Robinia pseudoacacia*. J Ecol 101:1623–1640. https://doi.org/10.1111/1365-2745.12162

Clarke PJ, Keith DA, Vincent BE, Letten AD (2015) Post-grazing and post-fire vegetation dynamics: long-term changes in mountain bogs reveal community resilience. J Veg Sci 26:278–290. https://doi.org/10.1111/jvs.12239

Closset-Kopp D, Chabrerie O, Valentin B et al (2007) When Oskar meets Alice: does a lack of trade-off in r/K-strategies make *Prunus serotina* a successful invader of European forests? For Ecol Manage 247:120–130. https://doi.org/10.1016/j.foreco.2007.04.023

Core Team R (2017) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna

Davis MA (2003) Biotic globalization: does competition from introduced species threaten biodiversity? Bioscience 53:481–489. https://doi.org/10.1641/0006-3568(2003)053%5b0481:BGDCFI%5d2.0.CO;2

Davis MA, Thompson K, Grime PJ (2005) Invasibility: the local mechanism driving community assembly and species diversity. Ecography 28:696–704. https://doi.org/10.1111/j.2005.0906-7590.04205.x

Dyderski MK, Jagodziński AM (2016) Patterns of plant invasions at small spatial scale correspond with that at the whole country scale. Urban Ecosyst. https://doi.org/10.1007/s11252-015-0524-y

Dyderski MK, Jagodziński AM (2018) Drivers of invasive tree and shrub natural regeneration in temperate forests. Biol Invasions 20(9):2363–2379. https://doi.org/10.1007/s10530-018-1706-3

Dyderski MK, Czapiewska N, Zajdler M et al (2016) Functional diversity, succession, and human-mediated disturbances in raised bog vegetation. Sci Total Environ 562:648–657. https://doi.org/10.1016/j.scitotenv.2016.04.102

Dyderski MK, Tyborski J, Jagodziński AM (2017) The utility of ancient forest indicator species in urban environments: a case study from Poznań, Poland. Urban For Urban Green 27:76–83. https://doi.org/10.1016/j.ufug.2017.06.016

Dzwonko Z (1993) Relations between the floristic composition of isolated young woods and their proximity to ancient woodland. J Veg Sci 4:693–698. https://doi.org/10.2307/3236135

Ellenberg H (1988) Vegetation ecology of central Europe. Cambridge University Press, Cambridge

Essl F, Hulme PE, Jeschke JM et al (2017) Scientific and normative foundations for the valuation of alien-species impacts: thirteen core principles. Bioscience 67:166–178. https://doi.org/10.1093/biosci/biw160

Fox JF (1979) Intermediate-disturbance hypothesis. Science 204:1344–1345. https://doi.org/10.1126/science.204.4399.1344

Frelich LE, Reich PB, Peterson DW (2017) The Changing Role of Fire in Mediating the Relationships among Oaks, Grasslands, Mesic Temperate Forests and Boreal Forests in the Lake States. J Sustain For 36:421–432. https://doi.org/10.1080/10549811.2017.1296777

Gallien L, Saladin B, Boucher FC et al (2016) Does the legacy of historical biogeography shape current invasiveness in pines? New Phytol 209:1096–1105. https://doi.org/10.1111/nph.13700

Gazda A, Szwagrzyk J (2016) Introduced species in Polish National Parks: distribution, abundance and management approaches. In: Krumm F, Vítková L (eds) Introduced tree species in European forests: opportunities and challenges. European Forest Institute, Freiburg, pp 168–175

Grime PJ (2001) Plant strategies, vegetation processes, and ecosystem properties, 2nd edn. Wiley, Chichester

Groves RH (2006) Are some weeds sleeping? Some concepts and reasons. Euphytica 148:111–120. https://doi.org/10.1007/s10681-006-5945-5

Halarewicz A (2012) Właściwości ekologiczne i skutki rozprzestrzeniania się czeremchy amerykańskiej *Padus serotina* (Ehrh.) Borkh. w wybranych fitocenozach leśnych. Wydawnictwo Uniwersytetu Przyrodniczego, Wrocław

Herben T, Chytrý M, Klimešová J (2016) A quest for species-level indicator values for disturbance. J Veg Sci 27:628–636. https://doi.org/10.1111/jvs.12384

Herben T, Klimešová J, Chytrý M (2018) Philip Grime's fourth corner: are there plant species adapted to high disturbance and low productivity? Oikos. https://doi.org/10.1111/oik.05090

Hermy M, Honnay O, Firbank L et al (1999) An ecological comparison between ancient and other forest plant species of Europe, and the implications for forest conservation. Biol Conserv 91:9–22. https://doi.org/10.1016/S0006-3207(99)00045-2

Hobbie SE, Reich PB, Oleksyn J et al (2006) Tree species effects on decomposition and forest floor dynamics in a common garden. Ecology 87:2288–2297. https://doi.org/10.1890/0012-9658(2006)87%5b2288:TSEODA%5d2.0.CO;2

Hobbs RJ, Huenneke LF (1992) Disturbance, diversity, and invasion: implications for conservation. Conserv Biol 6:324–337. https://doi.org/10.1046/j.1523-1739.1992.06030324.x

Horodecki P, Jagodziński AM (2017) Tree species effects on litter decomposition in pure stands on afforested post-mining sites. For Ecol Manag 406:1–11. https://doi.org/10.1016/j.foreco.2017.09.059

Jagodziński AM, Dyderski MK, Rawlik M, Banaszczak P (2015) Plantation of coniferous trees modifies risk and size of *Padus serotina* (Ehrh.) Borkh. invasion—Evidence from

a Rogów Arboretum case study. For Ecol Manage 357:84–94. https://doi.org/10.1016/j.foreco.2015.08.011

Jagodziński AM, Dyderski MK, Horodecki P, Rawlik K (2018) Limited dispersal prevents *Quercus rubra* invasion in a 14-species common garden experiment. Divers Distrib 24:403–414. https://doi.org/10.1111/ddi.12691

Jarošík V, Pyšek P, Kadlec T (2011) Alien plants in urban nature reserves: from red-list species to future invaders? NeoBiota 10:27–46. https://doi.org/10.3897/neobiota.10.1262

Jeschke JM (2014) General hypotheses in invasion ecology. Divers Distrib 20:1129–1134. https://doi.org/10.1111/ddi.12258

Johnstone JF, Allen CD, Franklin JF et al (2016) Changing disturbance regimes, ecological memory, and forest resilience. Front Ecol Environ 14:369–378. https://doi.org/10.1002/fee.1311

Jonášová M, Prach K (2004) Central-European mountain spruce (*Picea abies* (L.) Karst.) forests: regeneration of tree species after a bark beetle outbreak. Ecol Eng 23:15–27. https://doi.org/10.1016/j.ecoleng.2004.06.010

Kleyer M, Bekker RM, Knevel IC et al (2008) The LEDA Traitbase: a database of life-history traits of the Northwest European flora. J Ecol 96:1266–1274. https://doi.org/10.1111/j.1365-2745.2008.01430.x

Klotz S, Kühn I, Durka W (2002) BIOLFLOR—Eine Datenbank zu biologisch-ökologischen Merkmalen der Gefäßpflanzen in Deutschland. Schriftenreihe für Vegetationskunde, Bundesamt für Naturschutz

Knapp S, Kühn I, Stolle J, Klotz S (2010) Changes in the functional composition of a Central European urban flora over three centuries. Perspect Plant Ecol Evol Syst 12:235–244. https://doi.org/10.1016/j.ppees.2009.11.001

Knight KS, Oleksyn J, Jagodzinski AM et al (2008) Overstorey tree species regulate colonization by native and exotic plants: a source of positive relationships between understorey diversity and invasibility. Divers Distrib 14:666–675. https://doi.org/10.1111/j.1472-4642.2008.00468.x

Kozlowski TT, Pallardy SG (1997) Physiology of woody plants, 2nd edn. Academic Press, San Diego

Křivánek M, Pyšek P, Jarošík V (2006) Planting history and propagule pressure as predictors of invasion by woody species in a temperate region. Conserv Biol 20:1487–1498. https://doi.org/10.1111/j.1523-1739.2006.00477.x

Kučerová A, Rektoris L, Štechová T, Bastl M (2008) Disturbances on a wooded raised bog—how windthrow, bark beetle and fire affect vegetation and soil water quality? Folia Geobot 43:49–67

Laliberté E, Legendre P, Shipley B (2014) FD: Measuring functional diversity (FD) from multiple traits, and other tools for functional ecology. URL: https://cran.r-project.org/web/packages/FD/

Lockwood JL, Cassey P, Blackburn T (2005) The role of propagule pressure in explaining species invasions. Trends Ecol Evol 20:223–228. https://doi.org/10.1016/j.tree.2005.02.004

Lonsdale WM (1999) Global patterns of plant invasions and the concept of invasibility. Ecology 80:1522–1536. https://doi.org/10.1890/0012-9658(1999)080%5b1522:GPOPIA%5d2.0.CO;2

Mack RN, Simberloff D, Mark Lonsdale W et al (2000) Biotic invasions: causes, epidemiology, global consequences, and control. Ecol Appl 10:689–710. https://doi.org/10.1890/1051-0761(2000)010%5b0689:BICEGC%5d2.0.CO;2

Mueller KE, Eissenstat DM, Hobbie SE et al (2012) Tree species effects on coupled cycles of carbon, nitrogen, and acidity in mineral soils at a common garden experiment. Biogeochemistry 111:601–614. https://doi.org/10.1007/s10533-011-9695-7

Muys B, Maddelein D, Lust N (1992) Ecology, practice and policy of black cherry (*Prunus serotina* Ehrh.) management in Belgium. Silva Gandav 57:28–45

Myczko Ł, Dylewski Ł, Zduniak P et al (2014) Predation and dispersal of acorns by European Jay (*Garrulus glandarius*) differs between a native (Pedunculate Oak *Quercus robur*) and an introduced oak species (Northern Red Oak *Quercus rubra*) in Europe. For Ecol Manag 331:35–39. https://doi.org/10.1016/j.foreco.2014.07.027

Nowak G, Kara M, Bernat Z, Cykowiak Z (2000) Wybrane zagadnienia z planu ochrony ekosystemów leśnych Wielkopolskiego Parku Narodowego. Morena 7:85–129

Obidziński A, Mędrzycki P, Kołaczkowska E et al (2016) Do David and Goliath Play the Same Game? Explanation of the Abundance of Rare and Frequent Invasive Alien Plants in Urban Woodlands in Warsaw, Poland. PLOS ONE 11:e0168365. https://doi.org/10.1371/journal.pone.0168365

Oksanen J, Blanchet FG, Kindt R, et al (2016) "vegan" 2.3.3.—Community Ecology Package. URL http://CRAN.R-project.org/package=vegan

Pairon M, Jonard M, Jacquemart A-L (2006) Modeling seed dispersal of black cherry, an invasive forest tree: how microsatellites may help? Can J For Res 36:1385–1394. https://doi.org/10.1139/x06-018

Peterken GF (1974) A method for assessing woodland flora for conservation using indicator species. Biol Conserv 6:239–245. https://doi.org/10.1016/0006-3207(74)90001-9

Pierce S, Brusa G, Vagge I, Cerabolini BEL (2013) Allocating CSR plant functional types: the use of leaf economics and size traits to classify woody and herbaceous vascular plants. Funct Ecol 27:1002–1010. https://doi.org/10.1111/1365-2435.12095

Prach K, Pyšek P, Bastl M (2001) Spontaneous vegetation succession in human-disturbed habitats: a pattern across seres. Appl Veg Sci 4:83–88. https://doi.org/10.1111/j.1654-109X.2001.tb00237.x

Prach K, Řehounková K, Lencová K et al (2014) Vegetation succession in restoration of disturbed sites in Central Europe: the direction of succession and species richness across 19 seres. Appl Veg Sci 17:193–200. https://doi.org/10.1111/avsc.12064

Purcel A (2009) Obce gatunki drzew i krzewów w Wielkopolskim Parku Narodowym—ich występowanie i rola w biocenozach Parku. Morena 14:35–191

Pyšek P, Prach K (1993) Plant invasions and the role of riparian habitats: a comparison of four species alien to Central Europe. J Biogeogr 20:413–420. https://doi.org/10.2307/2845589

Pyšek P, Jarošík V, Pergl J et al (2014) Temperate trees and shrubs as global invaders: the relationship between

invasiveness and native distribution depends on biological traits. Biol Invasions 16:577–589. https://doi.org/10.1007/s10530-013-0600-2

Ratyńska H, Wojterska M, Brzeg A, Kołacz M (2010) Multi-medialna encyklopedia zbiorowisk roślinnych Polski. NFOSiGW, UKW, IETI

Reich PB, Oleksyn J, Modrzynski J et al (2005) Linking litter calcium, earthworms and soil properties: a common garden test with 14 tree species. Ecol Lett 8:811–818. https://doi.org/10.1111/j.1461-0248.2005.00779.x

Rice SK, Westerman B, Federici R (2004) Impacts of the exotic, nitrogen-fixing black locust (*Robinia pseudoacacia*) on nitrogen-cycling in a pine–oak ecosystem. Plant Ecol 174:97–107. https://doi.org/10.1023/B:VEGE.0000046049.21900.5a

Richardson DM, Pyšek P (2006) Plant invasions: merging the concepts of species invasiveness and community invasibility. Prog Phys Geogr 30:409–431. https://doi.org/10.1191/0309133306pp490pr

Richardson DM, Holmes PM, Esler KJ et al (2007) Riparian vegetation: degradation, alien plant invasions, and restoration prospects. Divers Distrib 13:126–139. https://doi.org/10.1111/j.1366-9516.2006.00314.x

Riepšas E, Straigyté L (2008) Invasiveness and Ecological Effects of Red Oak (*Quercus rubra* L.) in Lithuanian Forests. Balt For 14:122–130

Roberts DR, Bahn V, Ciuti S et al (2017) Cross-validation strategies for data with temporal, spatial, hierarchical, or phylogenetic structure. Ecography 40:913–929. https://doi.org/10.1111/ecog.02881

Rodríguez J, Lorenzo P, González L (2017) Different growth strategies to invade undisturbed plant communities by *Acacia dealbata* Link. For Ecol Manag 399:47–53. https://doi.org/10.1016/j.foreco.2017.05.007

Sádlo J, Vítková M, Pergl J, Pyšek P (2017) Towards site-specific management of invasive alien trees based on the assessment of their impacts: the case of *Robinia pseudoacacia*. NeoBiota 35:1–34. https://doi.org/10.3897/neobiota.35.11909

Sebert-Cuvillier E, Paccaut F, Chabrerie O et al (2007) Local population dynamics of an invasive tree species with a complex life-history cycle: a stochastic matrix model. Ecol Model 201:127–143. https://doi.org/10.1016/j.ecolmodel.2006.09.005

Sork VL (1984) Examination of seed dispersal and survival in red oak, *Quercus rubra* (Fagaceae), using metal-tagged acorns. Ecology 65:1020–1022. https://doi.org/10.2307/1938075

Starfinger U, Kowarik I, Rode M, Schepker H (2003) From desirable ornamental plant to pest to accepted addition to the flora?—the perception of an alien tree species through the centuries. Biol Invasions 5:323–335. https://doi.org/10.1023/B:BINV.0000005573.14800.07

Stohlgren TJ, Jarnevich C, Chong GW et al (2006) Scale and plant invasions: a theory of biotic acceptance. Preslia 78:405–426

Tecco PA, Díaz S, Cabido M, Urcelay C (2010) Functional traits of alien plants across contrasting climatic and land-use regimes: do aliens join the locals or try harder than them? J Ecol 98:17–27. https://doi.org/10.1111/j.1365-2745.2009.01592.x

Thomsen MS, Wernberg T, South PM, Schiel DR (2016) To include or not to include (the invader in community analyses)? That is the question. Biol Invasions 18:1515–1521. https://doi.org/10.1007/s10530-016-1102-9

Tilman D (1986) Resources, competition and the dynamics of plant communities. In: Crawley M (ed) Plant Ecology. Blackwell Scientific Publications, Oxford, pp 51–75

Turetsky MR, Louis VLS (2006) Disturbance in Boreal Peatlands. In: Wieder RK, Vitt DH (eds) Boreal peatland ecosystems. Springer, Berlin Heidelberg, pp 359–379

Vanhellemont M, Verheyen K, Keersmaeker L et al (2009) Does *Prunus serotina* act as an aggressive invader in areas with a low propagule pressure? Biol Invasions 11:1451–1462. https://doi.org/10.1007/s10530-008-9353-8

Vítková M, Müllerová J, Sádlo J et al (2017) Black locust (*Robinia pseudoacacia*) beloved and despised: a story of an invasive tree in Central Europe. For Ecol Manag 384:287–302. https://doi.org/10.1016/j.foreco.2016.10.057

Wagner V, Chytrý M, Jiménez-Alfaro B et al (2017) Alien plant invasions in European woodlands. Divers Distrib 23:969–981. https://doi.org/10.1111/ddi.12592

Wasserstein RL, Lazar NA (2016) The ASA's statement on p-values: context, process, and purpose. Am Stat 70:129–133. https://doi.org/10.1080/00031305.2016.1154108

Westoby M (1998) A leaf-height-seed (LHS) plant ecology strategy scheme. Plant Soil 199:213–227. https://doi.org/10.1023/A:1004327224729

Woziwoda B, Potocki M, Sagan J et al (2014) Commercial forestry as a vector of alien tree species-the case of *Quercus rubra* L. introduction in Poland. Balt For 20:131–141

Zeppenfeld T, Svoboda M, DeRose RJ et al (2015) Response of mountain *Picea abies* forests to stand-replacing bark beetle outbreaks: neighbourhood effects lead to self-replacement. J Appl Ecol 52:1402–1411. https://doi.org/10.1111/1365-2664.12504

Zerbe S, Wirth P (2006) Non-indigenous plant species and their ecological range in Central European pine (*Pinus sylvestris* L.) forests. Ann For Sci 63:189–203. https://doi.org/10.1051/forest:2005111

Ziegenhagen B, Kausch W (1995) Productivity of young shaded oaks (*Quercus robur* L.) as corresponding to shoot morphology and leaf anatomy. For Ecol Manag 72:97–108. https://doi.org/10.1016/0378-1127(94)03482-C

Publikacja 3.

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Functional traits of acquisitive invasive woody species differ from conservative invasive and native species

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RESEARCH ARTICLE

Functional traits of acquisitive invasive woody species differ from conservative invasive and native species

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Abstract

One of the most important sources of invasiveness is species' functional traits and their variability. However, there are still few studies on invasive tree species traits conducted along resource gradients that allow for a comparison of acquisitive and conservative strategies. We aimed to assess the differences in trait variation among native, alien conservative and alien acquisitive tree species along resource availability gradients (soil fertility and light availability) and to assess the traits variability of the species studied along resources availability gradients. Our study compared invasive tree species in Europe (*Prunus serotina* Ehrh., *Quercus rubra* L. and *Robinia pseudoacacia* L.) with their native competitors (*Acer pseudoplatanus* L., *A. platanoides* L., *Quercus petraea* (Matt.) Liebl. and *Fagus sylvatica* L.). The study was conducted on 1329 seedlings and saplings collected in a system of 372 study plots in W Poland. For each individual we assessed leaf, stem and root mass ratios, total biomass, leaf area ratio, specific leaf area and projected leaf area. Two invasive species (*P. serotina* and *R. pseudoacacia*) represented a more acquisitive strategy than native species – along litter pH and light availability gradients these species had higher leaf mass fraction, specific leaf area and leaf area ratio. In contrast, *Q. rubra* had the highest total biomass and root mass fraction. Alien species usually had higher coefficients of variation of studied traits. This suggests that relatively high projected leaf area, as a way of filling space and outcompeting native species, may be reached in two ways – biomass allocation to leaves and control of leaf morphology or by overall growth rate. High variability of invasive species traits also suggests randomness in seedling survival, which similarly to the neutral theory of invasion, highlights the necessity of including randomness in modelling biological invasions.

Introduction

The success of invasive plant species is connected to three main groups of factors: propagule pressure, habitat invasibility and species invasiveness. Interactions among them determine the successful spread of alien species in their exotic ranges (Davis et al. 2005; Jeschke 2014; Ricciardi et al. 2017). Propagule pressure shapes the arrival of new specimens and depends on distance to the propagule source (e.g. Jagodziński et al. 2015), propagule quantity and quality (Sinclair and Arnott 2015). Habitat invasibility expresses ecosystem vulnerability to invasion (Alpert et al. 2000; Davis et al. 2005). Species invasiveness is defined by life history traits determining ability to colonize new areas (Alpert et al. 2000; Grotkopp et al. 2010; Pyšek et al. 2014).

Most studies highlight several traits responsible for effective reproduction and spread (Pyšek et al. 2015; Capinha et al. 2015; Bonilla and Pringle 2015), as well as growth rate or traits connected with resource acquisition (Grotkopp et al. 2010; Tecco et al. 2010; te Beest et al. 2015). One of the most important features of invasive species concerns adaptation to new habitat conditions – enemies or levels of resources (Funk 2008; Jeschke 2014).

Species fitness is the ability to reach ecological success (survive, grow and reproduce) in a particular type of environment (Davidson et al. 2011). One measure of adaptation is phenotypic plasticity. This index reflects the difference in particular species traits within two levels of resources, related to the maximum trait value (Valladares et al. 2000). Studies of invasive species usually reported higher phenotypic plasticity of alien species in comparison with their native relatives (e.g. Davidson et al. 2011; Godoy et al. 2011; Paquette et al. 2012), which is claimed to be responsible for the effective spread of invasive species (Richards et al. 2006). Experimental design allows for a reduction of the number of factors studied and unbiased estimation of their influence, but does not reflect interactions of real factors in the field. However, field trials in natural conditions do not allow for determination of phenotypic plasticity, but only level of trait variability, which depends on both phenotype and genotype. Although few studies have assessed functional traits in the field (e.g. Kuehne et al. 2014; Lieurance and Landsbergen 2016; Heberling and Mason 2018) most of them covered few habitat types and treated resource levels discretely. For that reason there is a lack of gradient studies examining trait responses in multiple comparable sites along major environmental gradients (Hulme and Bernard-Verdier 2018). Moreover, studies based on phylogenetically-related pairs of species do not reflect real relationships between species in ecosystems (Hulme 2008).

Invasive species usually represent higher values of traits connected with size, growth rate, leaf-area allocation and shoot allocation (van Kleunen et al. 2010). Tecco et al. (2010) found two general trends of variation in trait syndromes: acquisitive (high SLA) and conservative (low SLA). In the case of woody species, alien species had a more acquisitive growth strategy in comparison with native species. This strategy was called 'try harder' – alien plants exhibited higher values of traits responsible for resource acquisition than their native competitors. For example, higher SLA than those of native savannah species is responsible for the success of invasive *Chromolaena odorata* (te Beest et al. 2015).

In contrast, Grotkopp et al. (2010) found lack of differences in acquisitive traits between invasive and non-invasive species, but instead found differences in growth and assimilation rates. However, there are still few studies on invasive tree species conducted along resource gradients that allow for a comparison of acquisitive and conservative strategies.

We aimed to assess the differences in trait variation among native alien tree species and traits variability along resource availability gradients (i.e. soil fertility, approximated by litter pH, and light availability). We hypothesized that: (1) similarly to the observations of Tecco et al. (2010), invasive species will express a more acquisitive set of functional traits than their native competitors; (2) according to previous studies (e.g. Richards et al. 2006; Davidson et al. 2011; Godoy et al. 2011) invasive species will exhibit higher variation of the traits studied and (3) according to 'try hard' strategy typical of alien species (Tecco et al. 2010), alien species will be more responsive to environmental gradients of resources availability.

Methods

Species studied

We studied the three alien tree species that are most frequent in European woodlands: *Prunus serotina* Ehrh., *Quercus rubra* L. and *Robinia pseudoacacia* L. (Wagner et al. 2017). These species came from eastern North America and have been introduced via forestry, in the 18th, 19th and 17th centuries, respectively (Muys et al. 1992; Cierjacks et al. 2013; Woziwoda et al. 2014). All the species strongly modify invaded habitats by influencing leaf litter decomposition (Dobrylovská 2001; Horodecki and Jagodziński 2017), nutrient cycling (Rice et al. 2004; Aerts et al. 2017) and light availability (Knight et al. 2008; Chmura 2013; Jagodziński et al. 2018). *R. pseudoacacia* is dispersed by wind (Cierjacks et al. 2013; Vítková et al. 2017), *P. serotina* by birds (Pairon et al. 2006; Jagodziński et al. 2015; Dylewski et al. 2017) and *Q. rubra* by birds and rodents (Myczko et al. 2014; Bieberich et al. 2016). *P. serotina* and *R. pseudoacacia* are mid-successional species while *Q. rubra* – late-successional, which is manifested in their abundance and disturbance responses (Dyderski et al. 2018). For comparison we chose the four native species most frequent within study plots: *Acer pseudoplatanus* L., *A. platanoides* L., *Quercus petraea* (Matt.) Liebl. and *Fagus sylvatica* L. In a preliminary inventory of natural regeneration in 2015 these species were found in 80.1%, 46.5%, 68.5% and 34.9% of 372 study plots, respectively, in comparison with *P. serotina* (59.9%), *Q. rubra* (44.6%) and *R. pseudoacacia* (23.6%). The native species chosen were not phylogenetically related to the invasive species, but are their most frequent competitors in the regeneration layer. *A. platanoides* and *A. pseudoplatanus* are mid-successional species dispersed by wind while *F. sylvatica* and *Q. petraea* are late-successional species dispersed by birds and rodents. Despite the affiliation of the species being studied in successional stages, the pattern of species co-occurrence did not follow the division into early-, mid- and late-successional species (Suppl. material 1: Fig. S1).

Study area

We conducted our study in the Wielkopolski National Park (WNP; W Poland; 52°16'N, 16°48'E; 7584 ha). The main aim of conservation in WNP is to preserve a valuable post-glacial landscape, including valleys, moraine hills and lakes. The climate in WPN is temperate, transitional between oceanic and continental. Mean annual temperature in Poznań (c.a. 15 km from WNP) was 8.4 °C and mean annual precipitation was 521 mm for the years 1951–2010. Dominant soil types in the study area are luvisols (47%) and brunic and haplic soils (30%), while podzols constitute only 7% (Nowak et al. 2000). The most frequent plant associations are *Galio sylvatici-Carpinetum* (fertile broadleaved forest dominated by *Quercus*, *Carpinus* and *Tilia*), *Calamagrostio arundinaceae-Quercetum* (acidophilous forest with *Q. petraea*) and *Querco roboris-Pinetum* (mixed *Quercus-Pinus* forest). However, there are small vegetation patches of both fertile riparian forests (*Fraxino-Alnetum*, *Querco-Ulmetum minoris*) and poor coniferous forests (*Leucobryo-Pinetum*). Most of the fertile sites were planted with *Pinus sylvestris* before the national park establishment in 1957 (Nowak et al. 2000). Moreover, WNP is the national park with the highest richness of alien woody taxa in Poland (158; Purcel 2009; Gazda and Szwagrzyk 2016). There are pure stands of alien species surrounded by large areas of forest ecosystems with different levels of disturbances and human impacts. This makes WNP an excellent place to test hypotheses about the impact of disturbances on the ecological success of invasive species.

Study design

The study design covers a set of 378 plots (100 m²) arranged in 21 blocks: nine for *Q. rubra* and six for *P. serotina* and *R. pseudoacacia* with the central part of each block located in a monoculture stand of invasive species (Dyderski and Jagodziński 2018a, b). Because *P. serotina* occurs only as an admixture in tree stands, as central parts we used tree stands with high densities of fruiting *P. serotina* trees in the shrub layer. In the center of each block we established a pair of study plots. Then, we established additional pairs of study plots along each of the four sides (N, S, E, and W) nearly outside the stand, at the invasion edge (the border between crowns of the invasive species monoculture and the surrounding trees; Rodríguez et al. 2017). The next four pairs were located 30 m from the invasion edge. This design generated 18 study plots within each block. Six study plots were excluded, as due to their systematic distribution, these plots were located outside the forest vegetation. Thus, the final number of plots was n=372. Study plots represented most of the vegetation types occurring in Wielkopolski National Park and wide gradients of resource availability: litter pH ranging from 3.83 to 6.44 and light availability ranging from 0.7 to 25.1% of the open sky (see details of measurements below). The variability of microsites conditions within the plot system (Dyderski and Jagodziński 2018a, b), was accounted for in the study design by including the 'plot' term as a random effect in mixed models (Roberts et al. 2017).

Data collection

In July 2017 we destructively harvested sample trees: seedlings (defined as individuals germinated in a particular year) and saplings (defined as individuals at least one year old and with height < 0.5 m). We divided natural regeneration into seedlings and saplings due to low seedlings survival (Beckage and Clark 2003; Knight et al. 2008; Canham and Murphy 2016), supply of carbohydrates stored in seed (Curt et al. 2005; Ziegenhagen and Kausch 1995) and differences in morphology affecting the functional traits studied (Cierjacks et al. 2013; Annighöfer et al. 2016). We surveyed an area within a 5 m wide buffer around each plot pair and we randomly selected up to five specimens for each species. The number of harvested plants was proportional to the available number of specimens and species densities within plots. We did not collect heavily damaged and browsed plants, unless there were no alternative specimens in the area examined. This accounted for the joint effects of lower growth and resistance to herbivory in suboptimal sites (Dyderski and Jagodziński 2018b). Field study within uncontrolled growth conditions resulted in unequal numbers of sample trees per species: 75 saplings and 48 seedlings of *A. platanoides*, 91 and 341 of *A. pseudoplatanus*, 23 and 59 of *F. sylvatica*, 141 and 191 of *P. serotina*, 29 and 78 of *Q. petraea*, 56 and 71 of *Q. rubra* and 37 and 89 of *R. pseudoacacia*. This inequality was an effect of unequal distributions of natural regeneration of the species within the study plots (Dyderski and Jagodziński 2018a, b). We dug each sample tree, and then carefully cleaned and divided it into roots, stems with branches and leaves. We did not include acorns which were still attached to *Q. rubra* and *Q. petraea* seedlings in the total biomass. We excluded from the dataset 14 *P. serotina* and 23 *R. pseudoacacia* saplings which had root suckers.

After separation, all sample tree biomass components were packed into envelopes, unfolded and transported into the laboratory. Leaves which were suitable for scanning, according to Cornelissen et al. (2003), were dried separately in a special press. All material was dried in an oven with forced air circulation at 65 °C (UN 750 and ULE 600, Memmert GmbH+Co.KG, Germany), to a constant mass. All biomass components were weighed using a BP 210 S (Sartorius, Göttingen, Germany) with an accuracy of 0.001 g. Leaves were scanned using WinFOLIA 2013 PRO software (Regent Instruments Inc., Quebec, Canada) to measure their leaf area. From the area and leaf dry biomass of scanned leaves, specific leaf area (SLA) was calculated, as leaf area divided by leaf mass. We also calculated leaf area ratio (LAR) as a ratio of projected leaf area (PLA; SLA multiplied by total leaf biomass) and TB (total biomass), as well as leaf mass fraction (lmf), stem mass fraction (smf) and root mass fraction (rmf). We analyzed traits of biomass allocation (lmf, smf, rmf) expressed as plant investment in particular organs – acquisition of limiting resources (Jagodziński and Oleksyn 2009; Poorter et al. 2015; Lieurance and Landsbergen 2016). TB was used as an overall plant fitness measure reflecting space filled by the species, and is also claimed to be a good measure of plant fitness (Younginger et al. 2017). We chose three leaf traits: SLA reflecting resource use efficiency within foliage (Wright et al. 2004; Díaz et al. 2016), PLA reflecting filling of space by foliage (Jagodziński et al. 2016) and LAR as a measure of whole plant investment in foliage efficiency. These factors are known to vary across soil fertility and light availability gradients.
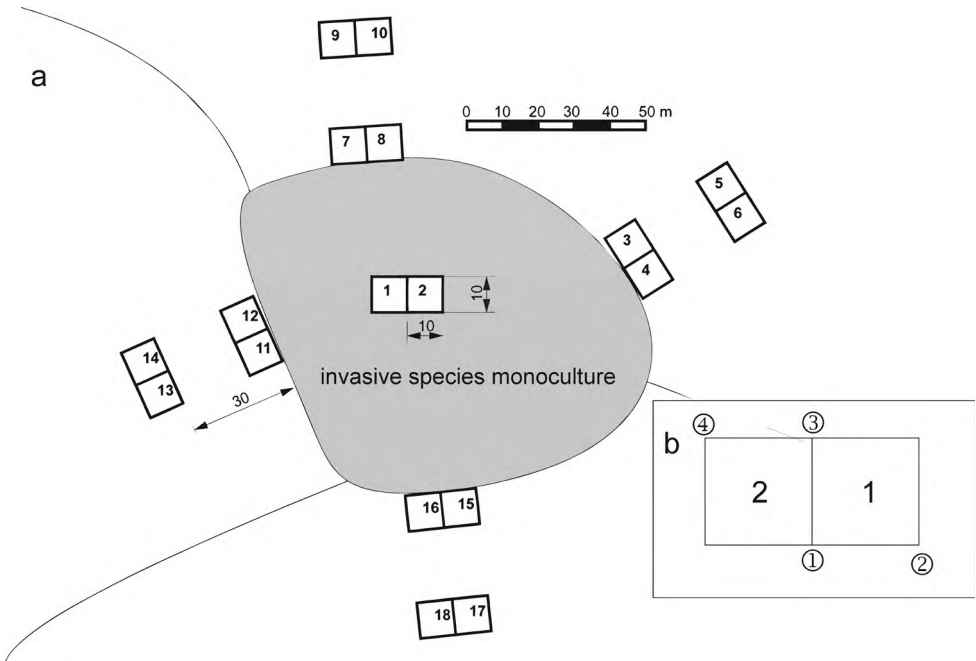
Figure 1. Study design: **a** scheme for a block of experimental plots in the field (each of 21 blocks is a set of 18 100 m² square plots; Dyderski and Jagodziński 2018a, b) **b** scheme for litter collection (circles with numbers 1–4 are 0.16 m² litter samples, collected in March 2017).

To characterize environmental gradients we used light availability and litter pH. We measured light availability as canopy openness index (diffuse non-interceptance; DIFN) using an LAI-2200 plant canopy analyzer (Li-Cor Inc., Lincoln, NE, USA). For each plot pair we recorded eight series of ten samples (four for each single plot) in August 2016. Although light availability was not measured in the year of harvest, we found low differences in light availability expressed by Ellenberg's ecological indicator community-weighted mean values between 2016 and 2017. The differences ranged from 0.00 to 1.37, with an average of 0.23±0.02, in nine-degree scale, which is within the range of interannual species turnover, as the highest changes we found in plots with low number of species. Thus, we assumed that light availability did not change between 2016 and 2017 significantly. In March 2017 we collected four samples of leaf litter from circular plots (0.16 m²; Fig 1b). Litter pH was assessed using an electronic pH-meter in distilled water solution after 24 hours. We used litter pH as a proxy for nutrient cycling rates and soil acidity in forest ecosystems (Bigelow and Canham 2002). However, as this variable explains only part of the variability in soil fertility, we encourage caution in interpretation, as one component of soil fertility may be masked by another, not related to litter pH, e.g. nitrogen:phosphorus ratio.

Data analysis

Our study design covered three invasive species with different biologies and we did not choose native species as phylogenetically-related pairs, but rather the most frequent competitors. For that reason we did not test specific alien-native species pairs but we compared each alien species to each native. For comparison of mean trait values of species we used one-way mixed-effects ANOVA followed by a Tukey *post hoc* test, implemented in the *multcomp::glht()* function. In this model we treated species as a fixed effect and plot as a random effect, to account for plot-specific effects, such as microsite variability and other unknown effects. Mixed models were developed using the *lmerTest::lmer()* function (Bates et al. 2015; Kuznetsova et al. 2017). To assess differences between saplings and seedlings within each species-trait combinations we used t-tests implemented in *stats::t.test()* function. Due to multi-species comparisons we decided not to apply any restrictions on p-values following Moran (2003).

To compare variability of the traits studied we assessed differences in trait coefficients of variation (CV) between two species using Krishnamoorthy and Lee's (2014) modified signed-likelihood ratio test (M-SLR test) implemented in the *cvequality::mslr_test()* function (Marwick and Krishnamoorthy 2016). This test has lower rates of type I error and more power across a range of conditions than the widely used (e.g. Funk 2008; Paquette et al. 2012) asymptotic test of Feltz and Miller (1996). Moreover, the M-SLR test allows for uneven sample numbers, which is necessary for our study design.

To assess the differences among species across resources availability gradients we used random forest algorithm (Breiman 2001). This method has a good performance in case of non-normal distributions of studied parameters, accounts for interaction between correlated predictors and has also a high predictive power. Its potential drawback might be an overfitting, which limits potential model transferability. To stabilize variance and avoid the influence of different units of predictors, prior to analyses we centered and scaled predictors, i.e. we subtracted mean values and divided by SD. To decrease overfitting we used repeated cross-validation by randomly splitting a dataset into training and validation sets within each iteration of model building (10 repeats 10 times) in the *caret::train()* function (Kuhn 2008). Within each iteration 75% of the dataset was used as training set and 25% – as validation set. To conclude about models output we provided information about variable importance, expressed as drop-out loss, i.e. loss in model RMSE when a particular variable is perturbed within the data table. Drop-out loss, similarly to RMSE, is expressed in the units of dependent variable. To show differences between species studied and interactions between species and resource availability we used partial dependence plots. These plots show output predicted for each observation, assuming constant value of other variables. As a constant value algorithm inputs mean values of parameters. These analyses were conducted using DALEX and ceterisParibus packages (Biecek 2018a, b). All analyses were conducted using R software (R Core Team 2018).

Results

Differences in trait values among species

Analysis of mean values of traits revealed statistically significant differences among the species studied (p<0.001; Fig. 2, Suppl. material 1: Table S1). Two species (*Q. rubra* and *Q. petraea*) had the highest TB and *Q. rubra* had the highest PLA. Two invasive species (*P. serotina* and *R. pseudoacacia*) had the highest SLA, LAR and leaf mass fraction and the lowest root mass fraction. Comparing seedlings and saplings we found statistically significant (p<0.05) differences in 38 of 47 species-trait pairs studied (Fig. 2, Suppl. material 1: Table S2). We did not find statistically significant differences (p>0.05) in the case of *Q. petraea* and *R. pseudoacacia* leaf mass fraction, *F. sylvatica* and *Q. rubra* PLA, *Q. petraea* and *Q. rubra* root mass fraction, *A. platanoides* and *F. sylvatica* seedlings SLA and *R. pseudoacacia* TB.

Coefficients of variation of traits

Analysis of trait CVs within species pairs in most cases revealed statistically significant differences in CVs between species (Fig. 3). Within native species *F. sylvatica* usually had higher CVs of functional traits than other native species and did not, statistically, differ significantly in any CV with *A. platanoides*. *P. serotina* and *R. pseudoacacia* had significantly higher CVs statistically of most traits studied than native species. The exceptions were higher CV of smf in *A. pseudoplatanus* saplings and LAR in *A. pseudoplatanus* seedlings than *P. serotina*, and higher TB CVs for *Acer* spp. than *R. pseudoacacia*. Moreover, all native species saplings had higher CVs of PLA than *R. pseudoacacia* saplings.

Trait variability among species and along resource availability gradients

Random forest models revealed that in all traits except SLA in case of seedlings species identity was the most important factor shaping trait values (Table 1). In general, SLA, LAR and lmf decreased with increasing DIFN, however differences among species studied were higher than differences along resource availability gradients (Figs 4, 5). We noted similar traits reaction to soil pH, while in the highest range of pH (over 6.0), SLA, LAR and lmf decrease was higher than in pH up to 6.0. Root mass fraction increased with increasing DIFN but decreased with increasing pH. TB increased with both increasing DIFN and pH. In terms of leaf investment (SLA, LAR, lmf) *R. pseudoacacia* presented the highest values across both DIFN and pH gradients, *P. serotina* had intermediate SLA and LAR, in comparison with native species. *Q. rubra* had the lowest values, while it had the highest total biomass and PLA, as well as similar rmf as native *Q. petraea*.
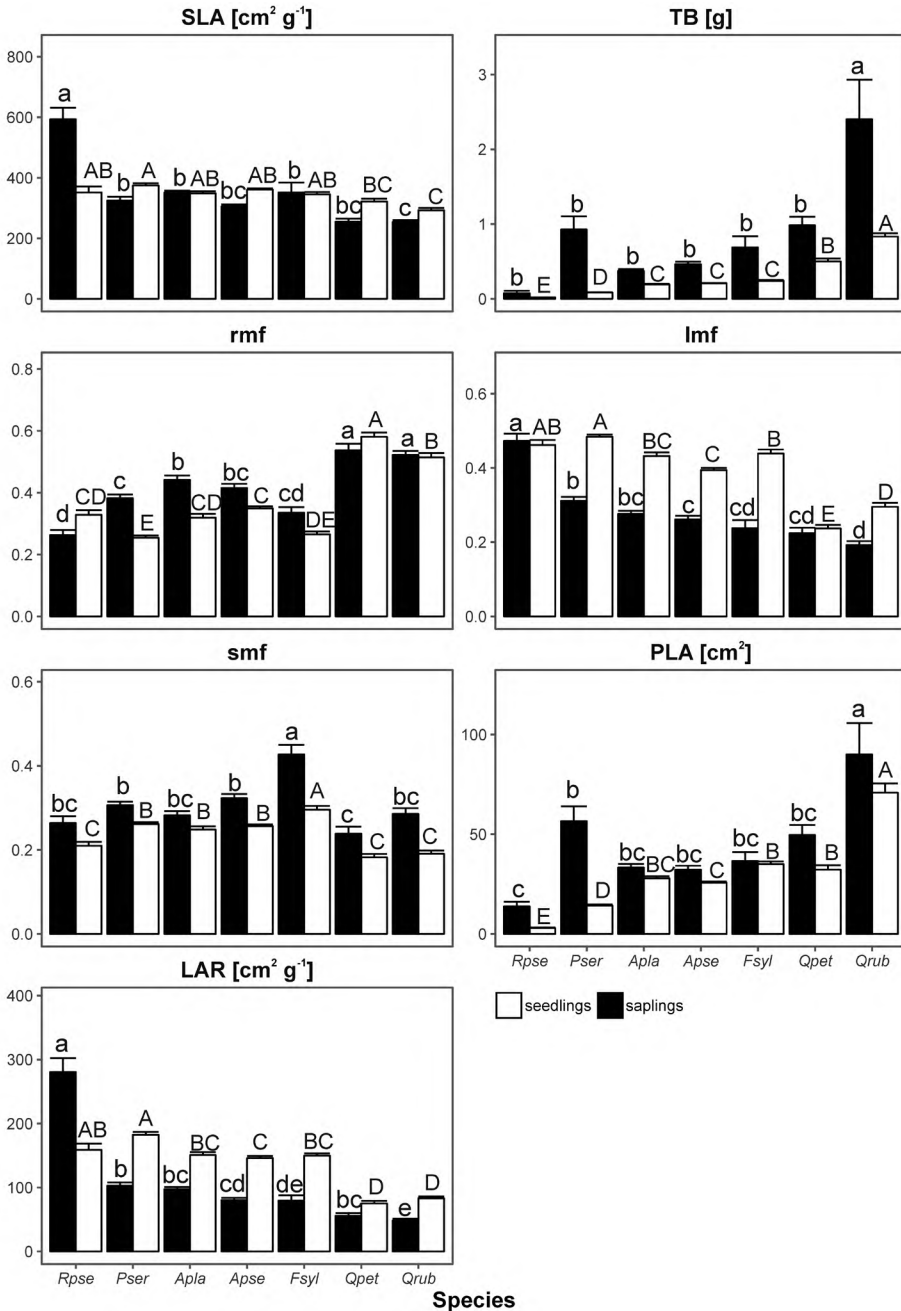
Figure 2. Mean (+SE) values of species traits of natural regeneration: SLA – specific leaf area (cm² g⁻¹), TB – total biomass [g], rmf – root mass fraction, lmf – leaf mass fraction, smf – stem mass fraction, PLA – projected leaf area [cm²], LAR – leaf area ratio [cm² g⁻¹]. Differences were assessed using one-way mixed effects ANOVA and Tukey *post hoc* tests – species marked by the same letter (lower-case letters for saplings and upper-case letters for seedlings) did not differ significantly statistically (p<0.05). ANOVA details are provided in Suppl. material 1: Table S1. Species are ordered according to successional stages.

Figure 3. Coefficients of variation for age stages and parameters: SLA – specific leaf area (cm² g⁻¹), TB – total biomass [g], rmf – root mass fraction, lmf – leaf mass fraction, smf – stem mass fraction, PLA – projected leaf area [cm²], LAR – leaf area ratio [cm² g⁻¹]. The same letters species which did not differ statistically significantly (p>0.05) in pairwise comparisons by modified signed-likelihood ratio (M-SLR) tests of differences. Tests revealed the same division into species groups for both saplings and seedlings.
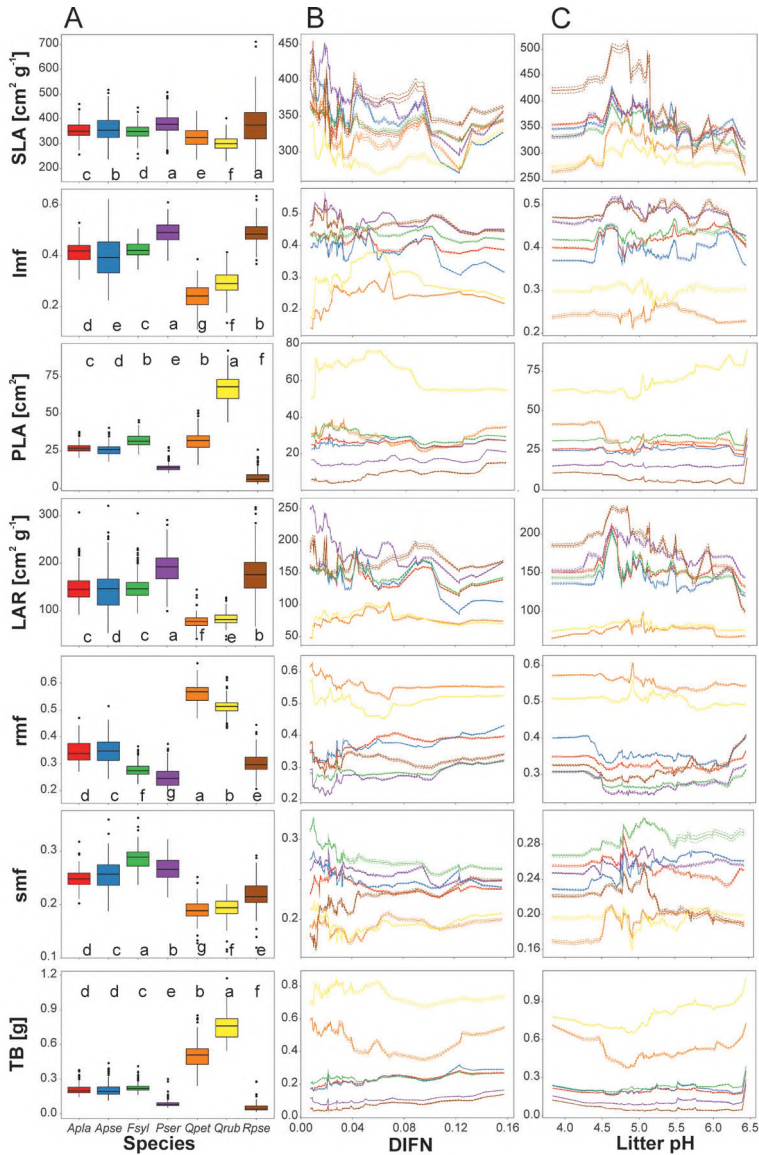
Figure 4. Saplings traits variability of the species studied across predictors explained by a random forest model. Partial dependence plots (ceteris paribus plots) show changes of predicted values when a particular predictor is changed while all remaining predictors are constant (i.e. mean value) – in the middle (**B**) and right (**C**) column we showed interactions between species and DIFN and litter pH. In the left column (**A**) we showed partial group predictions – predicted trait values assuming constant levels of other predictors, boxes represent interquartile range and median, whiskers represent minimum-maximum range, abbreviations of species: *Apla – Acer platanoides*, *Apse – A. pseudoplatanus*, *Fsyl – Fagus sylvatica*, *Pser – Prunus serotina*, *Qpet – Quercus petraea*, *Qrub – Q. rubra*, *Rpse – Robinia pseudoacacia*; traits: SLA – specific leaf area, lmf – leaf mass fraction, PLA – projected leaf area, LAR – leaf area ratio, rmf – root mass fraction, smf – stem mass fraction, TB – total biomass. For further details see Table 1. Species marked by the same letter did not exhibit significant statistical difference in predicted trait values, according to the Tukey posteriori test at p=0.05.
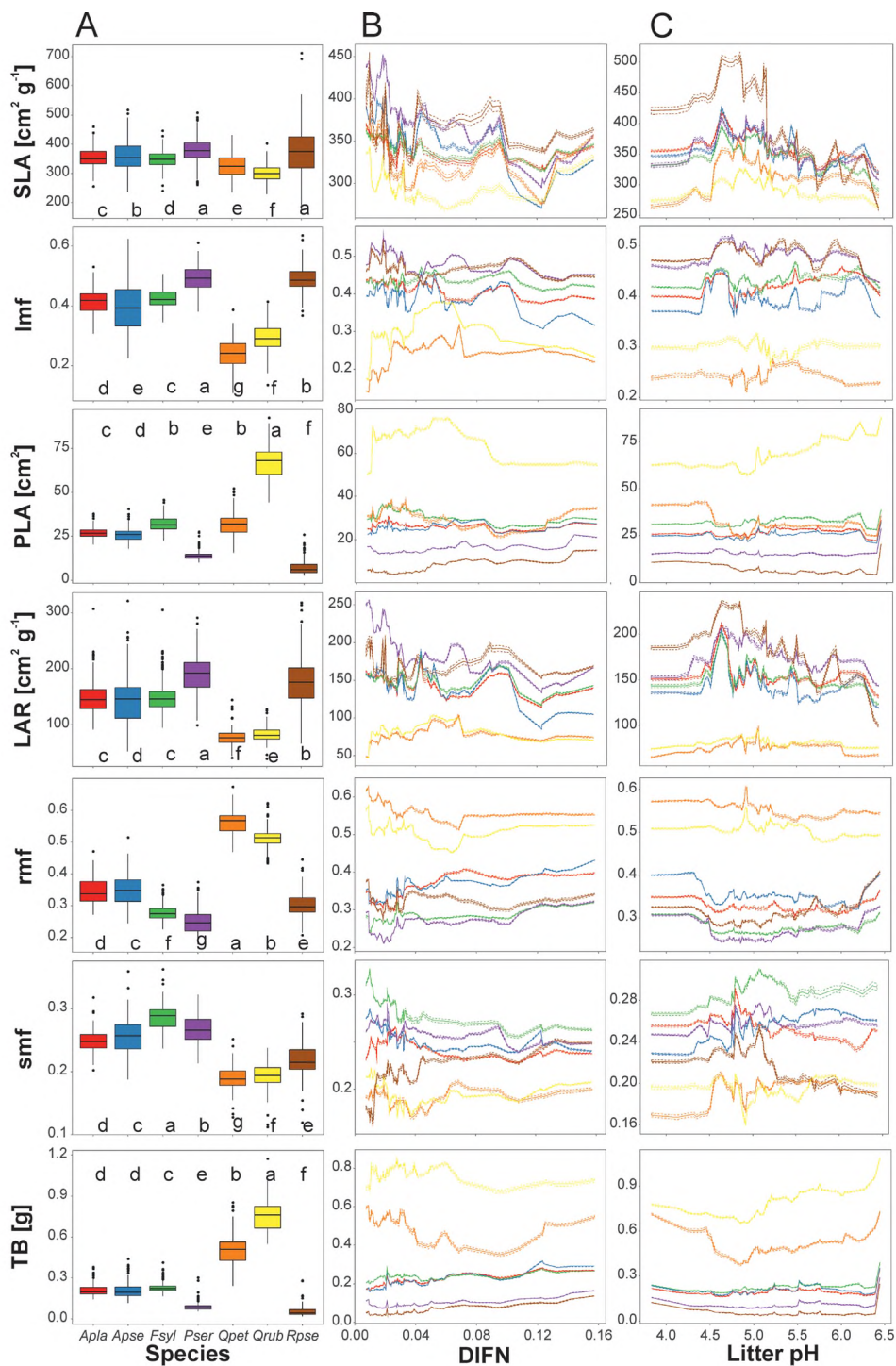
Figure 5. Seedlings traits variability of the species studied across predictors explained by a random forest model. For explanations see Fig. 4.

Table 1. Parameters of random forest models for traits and age classes and predictors importance expressed by drop-out loss of RMSE. Abbreviations: SLA – specific leaf area, lmf – leaf mass fraction, PLA – projected leaf area, LAR – leaf area ratio, rmf – root mass fraction, smf – stem mass fraction, TB – total biomass. Bold value indicate predictor with the highest importance.

Age	Trait	Unit	R^2	RMSE	Drop-out loss of RMSE – pH	Drop-out loss of RMSE – DIFN	Drop-out loss of RMSE – species
saplings	SLA	cm^2 g^{-1}	0.585	95.040	106.517	94.999	**181.012**
	Lmf	–	0.431	0.095	0.104	0.094	**0.121**
	PLA	cm^2	0.212	60.257	60.768	61.505	**66.031**
	LAR	cm^2 g^{-1}	0.696	46.944	50.947	53.637	**85.165**
	Rmf	–	0.405	0.113	0.108	0.126	**0.131**
	Smf	–	0.147	0.095	0.088	0.094	**0.096**
	TB	g	0.279	1.603	1.618	1.893	**1.912**
seedlings	SLA	cm^2 g^{-1}	0.129	99.242	**92.906**	89.672	90.265
	Lmf	–	0.436	0.094	0.091	0.102	**0.146**
	PLA	cm^2	0.552	14.887	15.474	15.687	**27.284**
	LAR	cm^2 g^{-1}	0.408	53.011	55.492	55.876	**71.275**
	Rmf	–	0.468	0.109	0.105	0.111	**0.172**
	Smf	–	0.178	0.072	0.073	0.074	**0.084**
	TB	g	0.662	0.161	0.160	0.163	**0.329**

Discussion

Trait values

Our study revealed that alien and native species differed the most in SLA, rmf, lmf and LAR; however the variability was usually not related to the resource gradients. This is connected with high inter-specific variability of functional traits, which results from different morphology and phylogeny of species studied (e.g. Poorter et al. 2015). For example, analysis of seasonal variability of 12 herbaceous species SLA, biomass and TLA(i.e. along DIFN temporal gradient) growing in the same locality also revealed a higher range of interspecific differences than during ontogeny within species (Jagodziński et al. 2016). For that reason previous studies focused on phylogenetically-related pairs of species (e.g. Grotkopp et al. 2010), to reduce phylogenetic structures from analyses (Roberts et al. 2017). However, in natural conditions species are co-occurring regardless of phylogenetic relativity. Thus, the success of some invasive species is claimed to be connected to being different from native species in terms of functional traits, e.g. by colonizing empty niches or by ability to break habitat filtering (Melbourne et al. 2007; Hierro et al. 2005).

   The differences among species reflect higher investment in leaves and a more acquisitive strategy of alien species, especially in the cases of *P. serotina* and *R. pseudoacacia*. These species used higher investment in foliage and higher SLA as ways of increasing PLA. SLA is a strongly acquisitive trait, correlated with photosynthetic capacity (Wright et al. 2004), as well as with ruderal and competitive life strategies (Westoby 1998). *Q. rubra* did not differ in these traits from native species but revealed higher biomass allocation to root systems. This is in line with previous observations indicating higher root:shoot ratio of *Q. rubra* (Kuehne et al. 2014). The investment in leaves and

roots is a predictor of total biomass (Enquist and Niklas 2002; Poorter et al. 2015) – the higher these parameters are, the lower the total biomass. However, this assessment covered the whole spectrum of plants. At the stage of saplings higher investment in leaves resulted in higher total leaf area and competitive advantage over native species in limited light availability (te Beest et al. 2015). Nevertheless, previous studies are equivocal in assessing differences in lmf and rmf between alien and native species. Some of these studies indicated a lack of differences in rmf (Grotkopp et al. 2010; Matzek 2011) while some showed higher rmf (Kuehne et al. 2014) and some lower rmf (Paquette et al. 2012; González-Muñoz et al. 2014) of alien species. Biomass allocation to the root systems also depends on root competition (Kawaletz et al. 2014). Investment in acquisitive traits causes a competitive advantage over native species (Blossey and Notzold 1995; te Beest et al. 2015).

Our study revealed differences between seedlings and saplings in case of most traits and species. These differences are mostly connected with different leaves morphology (Cierjacks et al., 2013; Annighöfer et al., 2016). The youngest leaves are usually thinner than older ones, which results in higher SLA and PLA. This may influence low survival of seedlings (Beckage and Clark 2003; Canham and Murphy 2016; Knight et al. 2008). For TB and PLA, seedlings of alien species had lower values than native species, while saplings had higher values. This may show that alien species do not have a biomass advantage in the first year of life. This comparison of alien and native species is biased by the outstandingly high biomass of *Q. rubra*. However, this species also differs from the other alien species studied in leaf-root allocation. This may indicate that the alien species studied had two ways to achieve the same goal – high leaf area. In the case of smaller plants the goal was realized by changes in biomass allocation and in the case of *Q. rubra* – by high biomass. Similar differentiation of alien species into acquisitive and conservative was found by Tecco et al. (2013). Higher biomass production and PLA was also mentioned as a factor connected with invasiveness (Grotkopp et al. 2010; Kuehne et al. 2014; Jo et al. 2015).

Trait variability

Our results revealed that *P. serotina* and *R. pseudoacacia* mostly had higher CV than native species. However, this was not always connected with higher variability of alien species traits along resources availability gradients, which may indicate high variability of trait values within young generations of invasive species. Most previous studies revealed differences in phenotypic plasticity between alien and native species (Paquette et al. 2012; Lamarque et al. 2013; Hou et al. 2014). Kuehne et al. (2014) did not find differences in phenotypic plasticity of *Q. rubra* and three co-occurring native species. Our study indicated that for acquisitive traits, variability of *Q. rubra* traits, expressed by interaction with environmental gradients, also did not differ from native species.

Assuming high propagule pressure, observed high variation in trait values may be the reason for their ecological success. However, most of the previous studies found that this variability was connected to phenotypic plasticity (e.g. Davidson et al. 2011;

Paquette et al. 2012; Lamarque et al. 2013). Nevertheless, in our study we cannot distinguish which part of variability is driven by phenotypic plasticity, due to lack of data about each individual provenance. Neutral theory assumes similar probability of mortality, speciation and reproduction within the same functional guild (Hubbell 2001). Application of this theory to invasion ecology highlights the need of accounting for the randomness in modeling community structure and functioning (Daleo et al. 2009). This randomness may be reflected in high variation of traits and high density of alien species seedlings and saplings, which allow for survival of the best fit individuals. This interpretation is strongly in line with previous studies highlighting the role of propagule pressure in ecological success of invasive species (Lockwood et al. 2005; Vanhellemont et al. 2009; Pyšek et al. 2015; Dyderski and Jagodziński 2018a). This speculation may be solved by testing whether survival of alien species seedlings depends on resource availability per plot, or shows a random pattern.

Trait responses to resource gradients

Our study revealed that alien species had a more acquisitive strategy of light acquisition, expressed by higher LAR than native species. The effects of resource availability on the leaf traits studied – lmf, LAR and SLA – were lower than differences between alien and native species. Also Robakowski et al. (2018) found high importance of light availability on lmf, rmf and photosynthesis efficiency in *P. serotina* and *Q. petraea*. Previous studies usually considered the effects of resource availability on particular species (Funk 2008; Lamarque et al. 2013; Kuehne et al. 2014) or phylogenetically related pairs of alien and native species (Allison and Vitousek 2004; Grotkopp et al. 2010; Matzek 2011). Only a few studies accounted for ecologically related alien and native species – i.e. co-occurring in one ecosystem type (González-Muñoz et al. 2014; Kuehne et al. 2014; te Beest et al. 2015). This lack of real relationship was raised as an important concern by Hulme (2008). Moreover in our study alien species occur and regenerate spontaneously in the study plot system.

Comparing litter pH and light availability gradients, differences between alien and native species traits were usually clearer along the DIFN gradient. The exception was PLA and (for saplings only), SLA and TB. We would expect that SLA will differ mostly due to light availability, as this factor drives SLA variability (Jagodziński et al. 2016). However, as SLA is nitrogen-dependent (Wright et al. 2004; Díaz et al. 2016), this trait also differed with litter pH, which is a proxy for general soil fertility and nitrogen content. For that reason SLA increases with litter pH and decreases with DIFN (Table 1). In the cases of lmf and LAR effect sizes of pH were lower. This indicates that general investment in foliage – both based on higher allocation and on leaf morphology (SLA) – is a reaction to light availability. Thus, as invasive species studied strongly modify environment, especially light availability and litter chemistry (e.g. Allison and Vitousek 2004; Knight et al. 2008; Horodecki and Jagodziński 2017), traits of natural regeneration might be influenced by invasive species presence in overstory. This feedback may be more important in case of alien species studied, as their abundance is strongly

related to the presence of parental trees (Dyderski and Jagodziński 2018a). However, native species are also able to strongly decrease light availability (e.g. *Acer* spp., *Fagus sylvatica*) or rate of nutrients cycling by low decomposition rate of leaf litter (Dobrylovská 2001; Horodecki and Jagodziński 2017). Thus, in our study we investigated effect of resources availability rather than alien-native species-specific effects of overstory.

Consequences for ecological success of invasive species

Invasive species studied revealed three different patterns of biomass investment differentiating them from the native species. *R. pseudoacacia* realized strategy 'try hard' in terms of investment in foliage, supporting the suggestion of Tecco et al. (2010) that invasive species invest more in acquisitive traits. In contrast, *Q. rubra* represents rather conservative strategy (Tecco et al. 2013) – invests in traits connected with persistence – low SLA, and in belowground resources competition. However, this strategy seems to be effective, as this species reaches higher individual biomass and high projected leaf area. Although *P. serotina* has higher lmf, its SLA and LAR places this species among native ones. This would suggest that *P. serotina* rather 'joins the locals' – represents similar life strategy to its most frequent competitors. All of these strategies lead to high total leaf area, which allows for out-shading native vegetation and reducing competitors (te Beest et al. 2015). The three species studied are the most frequent alien woody species in European forests (Wagner et al. 2017). Therefore, we conclude that both strategies are effective ways to reach ecological success, in contrast to Tecco et al. (2010; 2013), who claimed that an acquisitive strategy is more efficient. However, we found very limited support for variability of traits across interactions of species and resource gradients. Despite high variability and differences among species, this suggest that invasive species success is not related to the species traits variability. Thus, all three species are rather limited by propagule pressure, which is the main factor driving their biomass in the plant communities studied (Dyderski and Jagodziński 2018a). High variability of invasive species traits also suggests randomness in seedling survival, which similarly to neutral theory of invasion, highlights the necessity of including randomness in modelling biological invasions.

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References

Aerts R, Ewald M, Nicolas M, Piat J, Skowronek S, Lenoir J, Hattab T, Garzón-López CX, Feilhauer H, Schmidtlein S, Rocchini D, Decocq G, Somers B, Van De Kerchove R, Denef K, Honnay O (2017) Invasion by the Alien Tree *Prunus serotina* Alters Ecosystem Functions in a Temperate Deciduous Forest. Frontiers in Plant Science 8: 179. https://doi.org/10.3389/fpls.2017.00179

Allison SD, Vitousek PM (2004) Rapid nutrient cycling in leaf litter from invasive plants in Hawai'i. Oecologia 141: 612–619. https://doi.org/10.1007/s00442-004-1679-z

Alpert P, Bone E, Holzapfel C (2000) Invasiveness, invasibility and the role of environmental stress in the spread of non-native plants. Perspectives in Plant Ecology, Evolution and Systematics 3: 52–66. https://doi.org/10.1078/1433-8319-00004

Annighöfer P, Ameztegui A, Ammer C, Balandier P, Bartsch N, Bolte A, Coll L, Collet C, Ewald J, Frischbier N, Gebereyesus T, Haase J, Hamm T, Hirschfelder B, Huth F, Kändler G, Kahl A, Kawaletz H, Kuehne C, Lacointe A, Lin N, Löf M, Malagoli P, Marquier A, Müller S, Promberger S, Provendier D, Röhle H, Sathornkich J, Schall P, Scherer-Lorenzen M, Schröder J, Seele C, Weidig J, Wirth C, Wolf H, Wollmerstädt J, Mund M (2016) Species-specific and generic biomass equations for seedlings and saplings of European tree species. European Journal of Forest Research 135: 313–329. https://doi.org/10.1007/s10342-016-0937-z

Bates D, Mächler M, Bolker B, Walker S (2015) Fitting linear mixed-effects models using lme4. Journal of Statistical Software 67: 1–48. https://doi.org/10.18637/jss.v067.i01

Beckage B, Clark JS (2003) Seedling Survival and Growth of Three Forest Tree Species: The Role of Spatial Heterogeneity. Ecology 84: 1849–1861. https://doi.org/10.1890/0012-9658(2003)084[1849:SSAGOT]2.0.CO;2

Bieberich J, Lauerer M, Aas G (2016) Acorns of introduced Quercus rubra are neglected by European Jay but spread by mice. Annales of Forest Research 59: 249–258. https://doi.org/10.15287/afr.2016.522

Bigelow SW, Canham CD (2002) Community organization of tree species along soil gradients in a north-eastern USA forest. Journal of Ecology 90: 188–200. https://doi.org/10.1046/j.0022-0477.2001.00655.x

Blossey B, Notzold R (1995) Evolution of increased competitive ability in invasive nonindigenous plants: a hypothesis. Journal of Ecology 83: 887–889. https://doi.org/10.2307/2261425

Bonilla NO, Pringle EG (2015) Contagious seed dispersal and the spread of avian-dispersed exotic plants. Biological Invasions 17: 3409–3418. https://doi.org/10.1007/s10530-015-0966-4

Canham CD, Murphy L (2016) The demography of tree species response to climate: seedling recruitment and survival. Ecosphere 7: e01424. https://doi.org/10.1002/ecs2.1424

Capinha C, Essl F, Seebens H, Moser D, Pereira HM (2015) The dispersal of alien species redefines biogeography in the Anthropocene. Science 348: 1248–1251. https://doi.org/10.1126/science.aaa8913

Chmura D (2013) Impact of alien tree species *Quercus rubra* L. on understorey environment and flora: a study of the Silesian Upland (southern Poland). Polish Journal of Ecology 61: 431–442.

Cierjacks A, Kowarik I, Joshi J, Hempel S, Ristow M, von der Lippe M, Weber E (2013) Biological Flora of the British Isles: *Robinia pseudoacacia*. Journal of Ecology 101: 1623–1640. https://doi.org/10.1111/1365-2745.12162

Cornelissen JHC, Lavorel S, Garnier E, Diaz S, Buchmann N, Gurvich DE, Reich PB, Ter Steege H, Morgan HD, Van Der Heijden MGA, Pausas JG, Poorter H (2003) A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. Australian Journal of Botany 51: 335–380. https://doi.org/10.1071/BT02124

Curt T, Coll L, Prévosto B, Balandier P, Kunstler G (2005) Plasticity in growth, biomass allocation and root morphology in beech seedlings as induced by irradiance and herbaceous competition. Annals of Forest Science 62: 51–60. https://doi.org/10.1051/forest:2004092

Daleo P, Alberti J, Iribarne O (2009) Biological invasions and the neutral theory. Diversity and Distributions 15: 547–553. https://doi.org/10.1111/j.1472-4642.2009.00576.x

Davidson AM, Jennions M, Nicotra AB (2011) Do invasive species show higher phenotypic plasticity than native species and, if so, is it adaptive? A meta-analysis. Ecology Letters 14: 419–431. https://doi.org/10.1111/j.1461-0248.2011.01596.x

Davis MA, Thompson K, Philip Grime J (2005) Invasibility: the local mechanism driving community assembly and species diversity. Ecography 28: 696–704. https://doi.org/10.1111/j.2005.0906-7590.04205.x

Díaz S, Kattge J, Cornelissen JHC, Wright IJ, Lavorel S, Dray S, Reu B, Kleyer M, Wirth C, Colin Prentice I, Garnier E, Bönisch G, Westoby M, Poorter H, Reich PB, Moles AT, Dickie J, Gillison AN, Zanne AE, Chave J, Joseph Wright S, Sheremet'ev SN, Jactel H, Baraloto C, Cerabolini B, Pierce S, Shipley B, Kirkup D, Casanoves F, Joswig JS, Günther A, Falczuk V, Rüger N, Mahecha MD, Gorné LD (2016) The global spectrum of plant form and function. Nature 529: 167–171. https://doi.org/10.1038/nature16489

Dobrylovská D (2001) Litter decomposition of red oak, larch and lime tree and its effect on selected soil characteristics. Journal of Forest Science 47: 477–485.

Dyderski MK, Jagodziński AM (2018a) Drivers of invasive tree and shrub natural regeneration in temperate forests. Biological Invasions 20: 2363–2379. https://doi.org/10.1007/s10530-018-1706-3

Dyderski MK, Jagodziński AM (2018b) Low impact of disturbance on ecological success of invasive tree and shrub species in temperate forests. Plant Ecology 219: 1369–1380. doi:10.1007/s11258-018-0885-4

Dylewski Ł, Kurek P, Wiatrowska B, Jerzak L, Tryjanowski P (2017) Man-made perching sites – electricity pylons accelerate fleshy-fruited plants succession in farmlands. Flora 231: 51–56. https://doi.org/10.1016/j.flora.2017.04.004

Enquist BJ, Niklas KJ (2002) Global allocation rules for patterns of biomass partitioning in seed plants. Science 295: 1517–1520. https://doi.org/10.1126/science.1066360

Feltz CJ, Miller GE (1996) An asymptotic test for the equality of coefficients of variation from k populations. Statistics in Medicine 15: 647–658. https://doi.org/10.1002/(SICI)1097-0258(19960330)15:6<647::AID-SIM184>3.0.CO;2-P

Funk JL (2008) Differences in plasticity between invasive and native plants from a low resource environment. Journal of Ecology 96: 1162–1173. https://doi.org/10.1111/j.1365-2745.2008.01435.x

Gazda A, Szwagrzyk J (2016) Introduced species in Polish National Parks: distribution, abundance and management approaches. In: Krumm F, Vítková L (Eds) Introduced tree species in European forests: opportunities and challenges. European Forest Institute, Freiburg, 168–175.

Godoy O, Valladares F, Castro-Díez P (2011) Multispecies comparison reveals that invasive and native plants differ in their traits but not in their plasticity. Functional Ecology 25: 1248–1259. https://doi.org/10.1111/j.1365-2435.2011.01886.x

González-Muñoz N, Castro-Díez P, Godoy O (2014) Lack of superiority of invasive over co-occurring native riparian tree seedling species. Biological Invasions 16: 269–281. https://doi.org/10.1007/s10530-013-0516-x

Grotkopp E, Erskine-Ogden J, Rejmánek M (2010) Assessing potential invasiveness of woody horticultural plant species using seedling growth rate traits. Journal of Applied Ecology 47: 1320–1328. https://doi.org/10.1111/j.1365-2664.2010.01878.x

Heberling JM, Mason NWH (2018) Are endemics functionally distinct? Leaf traits of native and exotic woody species in a New Zealand forest. PLOS ONE 13: e0196746. https://doi.org/10.1371/journal.pone.0196746

Hierro JL, Maron JL, Callaway RM (2005) A biogeographical approach to plant invasions: the importance of studying exotics in their introduced and native range. Journal of Ecology 93: 5–15. https://doi.org/10.1111/j.0022-0477.2004.00953.x

Horodecki P, Jagodziński AM (2017) Tree species effects on litter decomposition in pure stands on afforested post-mining sites. Forest Ecology and Management 406: 1–11. https://doi.org/10.1016/j.foreco.2017.09.059

Hou Y-P, Peng S-L, Lin Z-G, Huang Q-Q, Ni G-Y, Zhao N (2014) Fast-growing and poorly shade-tolerant invasive species may exhibit higher physiological but not morphological plasticity compared with non-invasive species. Biological Invasions 17: 1555–1567. https://doi.org/10.1007/s10530-014-0815-x

Hubbell SP (2001) The unified neutral theory of biodiversity and biogeography. Princeton University Press, Priceton, 390 pp.

Hulme PE (2008) Phenotypic plasticity and plant invasions: is it all Jack? Functional Ecology 22: 3–7. https://doi.org/10.1111/j.1365-2435.2007.01369.x

Hulme PE, Bernard-Verdier M (2018) Comparing traits of native and alien plants: Can we do better? Functional Ecology 32: 117–125. https://doi.org/10.1111/1365-2435.12982

Jagodziński AM, Dyderski MK, Rawlik K, Kątna B (2016) Seasonal variability of biomass, total leaf area and specific leaf area of forest understory herbs reflects their life strategies. Forest Ecology and Management 374: 71–81. https://doi.org/10.1016/j.foreco.2016.04.050

Jagodziński AM, Dyderski MK, Rawlik M, Banaszczak P (2015) Plantation of coniferous trees modifies risk and size of *Padus serotina* (Ehrh.) Borkh. invasion – Evidence from a Rogów Arboretum case study. Forest Ecology and Management 357: 84–94. https://doi.org/10.1016/j.foreco.2015.08.011

Jagodziński AM, Oleksyn J (2009) Ecological consequences of silviculture at variable stand densities. II. Biomass production and allocation, nutrient retention. Sylwan 3: 147–157.

Jagodziński AM, Wierzcholska S, Dyderski MK, Horodecki P, Rusińska A, Gdula AK, Kasprowicz M (2018) Tree species effects on bryophyte guilds on a reclaimed post-mining site. Ecological Engineering 110: 117–127. https://doi.org/10.1016/j.ecoleng.2017.10.015

Jeschke JM (2014) General hypotheses in invasion ecology. Diversity and Distributions 20: 1129–1134. https://doi.org/10.1111/ddi.12258

Jo I, Fridley JD, Frank DA (2015) Linking above- and belowground resource use strategies for native and invasive species of temperate deciduous forests. Biological Invasions 17: 1545–1554. https://doi.org/10.1007/s10530-014-0814-y

Kawaletz H, Mölder I, Annighöfer P, Terwei A, Zerbe S, Ammer C (2014) Back to the roots: how do seedlings of native tree species react to the competition by exotic species? Annales of Forest Science 71: 337–347. https://doi.org/10.1007/s13595-013-0347-z

Knight KS, Oleksyn J, Jagodzinski AM, Reich PB, Kasprowicz M (2008) Overstorey tree species regulate colonization by native and exotic plants: a source of positive relationships between understorey diversity and invasibility. Diversity and Distributions 14: 666–675. https://doi.org/10.1111/j.1472-4642.2008.00468.x

Krishnamoorthy K, Lee M (2014) Improved tests for the equality of normal coefficients of variation. Computational Statistics 29: 215–232. https://doi.org/10.1007/s00180-013-0445-2

Kuehne C, Nosko P, Horwath T, Bauhus J (2014) A comparative study of physiological and morphological seedling traits associated with shade tolerance in introduced red oak (*Quercus rubra*) and native hardwood tree species in southwestern Germany. Tree Physiology 34: 184–193. https://doi.org/10.1093/treephys/tpt124

Kuhn M (2008) Building Predictive Models in R Using the caret Package. Journal of Statistical Software 28, 1–26. https://doi.org/10.18637/jss.v028.i05

Kuznetsova A, Brockhoff PB, Christensen RHB (2017) lmerTest: Tests in Linear Mixed Effects Models 82. http://dx.doi.org/10.18637/jss.v082.i13

Lamarque LJ, Porté AJ, Eymeric C, Lasnier J-B, Lortie CJ, Delzon S (2013) A Test for Pre-Adapted Phenotypic Plasticity in the Invasive Tree *Acer negundo* L. PLOS ONE 8: e74239. https://doi.org/10.1371/journal.pone.0074239

Lieurance D, Landsbergen K (2016) The influence of light habitat on the physiology, biomass allocation, and fecundity of the invasive shrub Amur honeysuckle (*Lonicera maackii*, Caprifoliaceae). The Journal of the Torrey Botanical Society 143: 415–426. https://doi.org/10.3159/TORREY-D-15-00056.1

Lockwood JL, Cassey P, Blackburn T (2005) The role of propagule pressure in explaining species invasions. Trends in Ecology and Evolution 20: 223–228. https://doi.org/10.1016/j.tree.2005.02.004

Marwick B, Krishnamoorthy K (2016) cvequality: Tests for the Equality of Coefficients of Variation from Multiple Groups. R package version 0.1.3. https://cran.r-project.org/web/packages/cvequality/

Matzek V (2011) Superior performance and nutrient-use efficiency of invasive plants over non-invasive congeners in a resource-limited environment. Biological Invasions 13: 3005–3014. https://doi.org/10.1007/s10530-011-9985-y

Melbourne BA, Cornell HV, Davies KF, Dugaw CJ, Elmendorf S, Freestone AL, Hall RJ, Harrison S, Hastings A, Holland M, Holyoak M, Lambrinos J, Moore K, Yokomizo H (2007) Invasion in a heterogeneous world: resistance, coexistence or hostile takeover? Ecology Letters 10: 77–94. https://doi.org/10.1111/j.1461-0248.2006.00987.x

Moran MD (2003) Arguments for rejecting the sequential Bonferroni in ecological studies. Oikos 100: 403–405. https://doi.org/10.1034/j.1600-0706.2003.12010.x

Muys B, Maddelein D, Lust N (1992) Ecology, practice and policy of black cherry (*Prunus serotina* Ehrh.) management in Belgium. Silva Gandavensis 57: 28–45. https://doi.org/10.21825/sg.v57i0.885

Myczko Ł, Dylewski Ł, Zduniak P, Sparks TH, Tryjanowski P (2014) Predation and dispersal of acorns by European Jay (*Garrulus glandarius*) differs between a native (Pedunculate Oak *Quercus robur*) and an introduced oak species (Northern Red Oak *Quercus rubra*) in Europe. Forest Ecology and Management 331: 35–39. https://doi.org/10.1016/j.foreco.2014.07.027

Nowak G, Kara M, Bernat Z, Cykowiak Z (2000) Wybrane zagadnienia z planu ochrony ekosystemów leśnych Wielkopolskiego Parku Narodowego. Morena 7: 85–129.

Pairon M, Jonard M, Jacquemart A-L (2006) Modeling seed dispersal of black cherry, an invasive forest tree: how microsatellites may help? Canadian Journal of Forest Research 36: 1385–1394. https://doi.org/10.1139/x06-018

Paquette A, Fontaine B, Berninger F, Dubois K, Lechowicz MJ, Messier C, Posada JM, Valladares F, Brisson J (2012) Norway maple displays greater seasonal growth and phenotypic plasticity to light than native sugar maple. Tree Physiology 32: 1339–1347. https://doi.org/10.1093/treephys/tps092

Poorter H, Jagodzinski AM, Ruiz-Peinado R, Kuyah S, Luo Y, Oleksyn J, Usoltsev VA, Buckley TN, Reich PB, Sack L (2015) How does biomass distribution change with size and differ among species? An analysis for 1200 plant species from five continents. New Phytologist 208: 736–749. https://doi.org/10.1111/nph.13571

Purcel A (2009) Obce gatunki drzew i krzewów w Wielkopolskim Parku Narodowym – ich występowanie i rola w biocenozach Parku. Morena 14: 35–191.

Pyšek P, Jarošík V, Pergl J, Moravcová L, Chytrý M, Kühn I (2014) Temperate trees and shrubs as global invaders: the relationship between invasiveness and native distribution depends on biological traits. Biological Invasions 16: 577–589. https://doi.org/10.1007/s10530-013-0600-2

Pyšek P, Manceur AM, Alba C, McGregor KF, Pergl J, Štajerová K, Chytrý M, Danihelka J, Kartesz J, Klimešová J, Lučanová M, Moravcová L, Nishino M, Sádlo J, Suda J, Tichý L, Kühn I (2015) Naturalization of central European plants in North America: species traits, habitats, propagule pressure, residence time. Ecology 96: 762–774. https://doi.org/10.1890/14-1005.1

R Core Team (2018) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria

Ricciardi A, Blackburn TM, Carlton JT, Dick JTA, Hulme PE, Iacarella JC, Jeschke JM, Liebhold AM, Lockwood JL, MacIsaac HJ, Pyšek P, Richardson DM, Ruiz GM, Simberloff D, Sutherland WJ, Wardle DA, Aldridge DC (2017) Invasion Science: A Horizon Scan of Emerging Challenges and Opportunities. Trends in Ecology and Evolution 32: 464–474. https://doi.org/10.1016/j.tree.2017.03.007

Rice SK, Westerman B, Federici R (2004) Impacts of the exotic, nitrogen-fixing black locust (*Robinia pseudoacacia*) on nitrogen-cycling in a pine-oak ecosystem. Plant Ecology 174: 97–107. https://doi.org/10.1023/B:VEGE.0000046049.21900.5a

Richards CL, Bossdorf O, Muth NZ, Gurevitch J, Pigliucci M (2006) Jack of all trades, master of some? On the role of phenotypic plasticity in plant invasions. Ecology Letters 9: 981–993. https://doi.org/10.1111/j.1461-0248.2006.00950.x

Robakowski P, Bielinis E, Sendall K (2018) Light energy partitioning, photosynthetic efficiency and biomass allocation in invasive *Prunus serotina* and native *Quercus petraea* in relation to light environment, competition and allelopathy. Journal of Plant Research 131: 505–523. https://doi.org/10.1007/s10265-018-1009-x

Roberts DR, Bahn V, Ciuti S, Boyce MS, Elith J, Guillera-Arroita G, Hauenstein S, Lahoz-Monfort JJ, Schröder B, Thuiller W, Warton DI, Wintle BA, Hartig F, Dormann CF (2017) Cross-validation strategies for data with temporal, spatial, hierarchical, or phylogenetic structure. Ecography 40: 913–929. https://doi.org/10.1111/ecog.02881

Rodríguez J, Lorenzo P, González L (2017) Different growth strategies to invade undisturbed plant communities by *Acacia dealbata* Link. Forest Ecology and Management 399: 47–53. https://doi.org/10.1016/j.foreco.2017.05.007

Sinclair JS, Arnott SE (2015) Strength in size not numbers: propagule size more important than number in sexually reproducing populations. Biological Invasions 18: 497–505. https://doi.org/10.1007/s10530-015-1022-0

te Beest M, Esler KJ, Richardson DM (2015) Linking functional traits to impacts of invasive plant species: a case study. Plant Ecology 216: 293–305. https://doi.org/10.1007/s11258-014-0437-5

Tecco PA, Díaz S, Cabido M, Urcelay C (2010) Functional traits of alien plants across contrasting climatic and land-use regimes: do aliens join the locals or try harder than them? Journal of Ecology 98: 17–27. https://doi.org/10.1111/j.1365-2745.2009.01592.x

Tecco PA, Urcelay C, Díaz S, Cabido M, Pérez-Harguindeguy N (2013) Contrasting functional trait syndromes underlay woody alien success in the same ecosystem. Austral Ecology 38: 443–451. https://doi.org/10.1111/j.1442-9993.2012.02428.x

Valladares F, Wright SJ, Lasso E, Kitajima K, Pearcy RW (2000) Plastic Phenotypic Response to Light of 16 Congeneric Shrubs from a Panamanian Rainforest. Ecology 81: 1925–1936. https://doi.org/10.1890/0012-9658(2000)081[1925:PPRTLO]2.0.CO;2

van Kleunen M, Ewald W, Markus F (2010) A meta-analysis of trait differences between invasive and non-invasive plant species. Ecology Letters 13: 235–245. https://doi.org/10.1111/j.1461-0248.2009.01418.x

Vanhellemont M, Verheyen K, Keersmaeker L, Vandekerkhove K, Hermy M (2009) Does *Prunus serotina* act as an aggressive invader in areas with a low propagule pressure? Biological Invasions 11: 1451–1462. https://doi.org/10.1007/s10530-008-9353-8

Vítková M, Müllerová J, Sádlo J, Pergl J, Pyšek P (2017) Black locust (*Robinia pseudoacacia*) beloved and despised: A story of an invasive tree in Central Europe. Forest Ecology and Management 384: 287–302. https://doi.org/10.1016/j.foreco.2016.10.057

Wagner V, Chytrý M, Jiménez-Alfaro B, Pergl J, Hennekens S, Biurrun I, Knollová I, Berg C, Vassilev K, Rodwell JS, Škvorc Ž, Jandt U, Ewald J, Jansen F, Tsiripidis I, Botta-Dukát Z, Casella L, Attorre F, Rašomavičius V, Ćušterevska R, Schaminée JHJ, Brunet J, Lenoir J, Svenning J-C, Kącki Z, Petrášová-Šibíková M, Šilc U, García-Mijangos I, Campos JA, Fernández-González F, Wohlgemuth T, Onyshchenko V, Pyšek P (2017) Alien plant invasions in European woodlands. Diversity and Distributions 23: 969–981. https://doi.org/10.1111/ddi.12592

Westoby M (1998) A leaf-height-seed (LHS) plant ecology strategy scheme. Plant and Soil 199: 213–227. https://doi.org/10.1023/A:1004327224729

Woziwoda B, Potocki M, Sagan J, Michal Z, Tomusiak R, Wilczynski S (2014) Commercial forestry as a vector of alien tree species-the case of *Quercus rubra* L. introduction in Poland. Baltic Forestry 20: 131–141.

Wright IJ, Reich PB, Westoby M, Ackerly DD, Baruch Z, Bongers F, Cavender-Bares J, Chapin T, Cornelissen JH, Diemer M, Flexas J, Garnier E, Gulias J, Hikosaka K, Lamont BB, Lee T, Lee W, Lusk C, Midgley JJ, Navas ML, Niinemets Ü, Oleksyn J, Osada N, Poorter H, Poot P, Prior L, Pyankov VI, Roumet C, Thomas SC, Tjoelker MG, Veneklaas EJ, Villar R (2004) The world-wide leaf economics spectrum. Nature 428: 821–827. https://doi.org/10.1038/nature02403

Younginger BS, Sirová D, Cruzan MB, Ballhorn DJ (2017) Is Biomass a Reliable Estimate of Plant Fitness? Applied Plant Science 5: 1600094. https://doi.org/10.3732/apps.1600094

Ziegenhagen B, Kausch W (1995) Productivity of young shaded oaks (*Quercus robur* L.) as corresponding to shoot morphology and leaf anatomy. Forest Ecology and Management 72: 97–108. https://doi.org/10.1016/0378-1127(94)03482-C

Supplementary material 1

Supplementary materials
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Data type: statistical data
Explanation note: **Table S1.** Mixed-effects ANOVA models of traits studied (LAR – leaf area ratio [cm^2 g^{-1}], lmf – leaf mass fraction, PLA – projected leaf area [cm^2], rmf – root mass fraction, SLA – specific leaf area (cm^2 g^{-1}), smf – stem mass fraction, TB – total biomass [g]) and across species studied. R^{2}m is the amount of variance explained by fixed effects only and R^{2}c – by both fixed and random effects.; **Table S2.** Differences between seedlings and saplings in traits studied (LAR – leaf area ratio [cm^2 g^{-1}], lmf – leaf mass fraction, PLA – projected leaf area [cm^2], rmf – root mass fraction, SLA – specific leaf area (cm^2 g^{-1}), smf – stem mass fraction, TB – total biomass [g]) within species studied assessed using t-tests.; **Figure S1.** Species Co-occurrence matrix for seedlings and saplings of the species studied. Co-occurrence was calculated using co-occur R package (https://cran.r-project.org/web/packages/cooccur/index.html), based on presence-absence of species studied with 372 study plots in 2015. The type of co-occurrence (positive, negative and random) between species pairs was assessed basing on observed and expected occurrence probabilities.

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