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Invasion process of alien plants due to environmental changes and internet trade

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Abstract

The dispersal of invasive alien species is currently one of the most important scientific problems in ecology and is among the practical issues of conservation biology. Usually, studies on invasive species focus on the negative impact of exotic species on native flora and fauna, whereas research on mechanisms of alien plant dispersal during the early stages of the invasion process is still rare. The dynamic of the invasion process is usually shaped by the duration of the lag phase, i.e. the period of time between the first introduction of an alien species into a new region and the beginning of its invasive spread. The presented dissertation is a large-scale study of three of the most important aspects of invasion, namely, the release of alien species from the lag phase, the progress and cascading effects of the invasive species in the environment, and human-related long-distance transportation of alien propagules.

Chapter I shows that changes in agricultural land use after political transformation, combined with the behaviour of rooks *(Corvus frugilegus)* as native seed-dispersing birds, led to the release of the alien walnut *Juglans regia* from a lag phase. The invasion of the walnut in Central Europe was preceded by the longest lag phase ever known among any invasive plant species in the world. This species had been introduced to Central Europe by monks in the 13th century as a medical plant; however, it became invasive at the end of the 20th century, as a result of the coincidence of two profound changes in native disperser ecology and politically related changes in land use.

Populations of rooks increased because the species was protected by law in the second half of the 20th century and hunting of this bird ceased. Rooks are major dispersers of walnut seeds; moreover, they are known for caching behaviour. Rooks preferentially hide walnut seeds in arable fields, managed pastures and meadows and avoid abandoned fields. However, over 90% of wild walnuts occurred in abandoned fields. Thus, the habitat invaded by the walnut did not match the habitat where walnut seeds were cached. This indicates that

cessation of field management enabled the growth of cached walnut seeds and the subsequent invasion. In managed fields, saplings were damaged or cut during the process of ploughing and cutting each year. The invasion of the walnut was noted almost throughout Poland, which suggests that only large-scale land abandonment could disrupt the time lag and cause the rapid spread of this alien species. Vast changes occurred in Poland after 1989 when socialism collapsed and millions of hectares of farmland were abandoned. The oldest wild growing walnuts were about 20 years old, which matches exactly the time since the political transformation in Poland. The mean age of wild walnuts growing in abandoned fields correlated with the age of these fields, suggesting that most specimens started to grow shortly after land abandonment.

Chapter II shows that alien walnuts, after invading the semi-natural habitat of abandoned farmland, spread into forests due to the involvement of another native bird seed disperser, namely, jays *(Garrulus glandarius)*, and passive transportation by gravity in variable weather conditions. Jays cached walnut seeds in forests. It was also noted that the red squirrel *(Scirus vulgaris)* carried walnut seeds into forests, albeit much more rarely compared to jays. Forests located in depressions below the level of the surrounding landscape had higher probabilities of walnut occupancy. The density of walnuts in forests was positively correlated with density of jays, which often harvested seeds from fruiting walnuts in abandoned fields, irrespective of their distance from a forest. Jays also frequently visited walnuts planted in human settlements, but only in the proximity of forests. Walnut seeds hidden by rooks in arable fields passively reach forest edges, especially in sloping fields and after rainy days. This finding adds to our understanding of seed dispersal into forests and underlines the importance of local landscape structure and shape of local terrain for the invasion process.

The invasion of the walnut demonstrates the complexity of mechanisms involved in the dispersal of alien species occurring at the edge of human settlements and semi-natural habitats. **Chapter III** shows the importance of human behaviour and the development of new technologies in introducing alien species to new areas. Nowadays, many alien species can be bought in online garden shops. This internet trade has caused invasive alien plant species to be transported over longer distances than in traditional sales. The curve of distance distribution was flattened and only slightly skewed for internet trade compared with traditional sales, for which distributions included peaks and were skewed to the right. Therefore internet commerce created novel modes of long-distance dispersal, while traditional sales resembled more natural dispersal modes. As well, analysis of sales through the biggest Polish internet auction portal showed that the number of alien specimens sold via the internet has increased markedly over recent years. The complexity of direct and indirect interactions between people and invasive alien species shows that human-related factors must be better recognised and incorporated into dispersal models as a key variable.

Keywords:

Dispersal, internet commerce, invasive alien species, lag phase, land use change.

Streszczenie

Inwazje biologiczne są jednym z najważniejszych i najaktualniejszych problemów we współczesnej ekologii i ochronie przyrody. Mają także ogromne znaczenie dla rolnictwa, poprzez negatywne oddziaływanie na glebę, zapylacze, płazy i ptaki. Gatunki obce, najczęściej zostają sprowadzone na nowe terytoria na wiele lat wcześniej zanim zaadoptują się do nowego środowiska na tyle, żeby nastąpiła ich eksplozja demograficzna i stały się inwazyjne. Jest to tak zwana faza uśpienia (*ang.* lag phase), czyli czas jaki upływa między wprowadzeniem obcego gatunku a momentem kiedy zaczyna się jego eksplozja demograficzna i negatywny wpływ na rodzimą bioróżnorodność. Faza uśpienia jest słabo poznanym zjawiskiem w procesie biologicznych inwazji. Generalnie, inwazje roślin zależą od trzech czynników: źródła nasion, odpowiedniego siedliska i odpowiednich rozsiewaczy. Obcy gatunek drzewa – orzech włoski (*Juglans regia*) był uprawiany od wieków w Europie Środkowej i do niedawna nie notowano go nigdzie poza obszarem upraw. Tymczasem orzech włoski został zaobserwowany w dużej liczbie na opuszczonych gruntach rolnych. Wyniki badań prezentowanych w **Rozdziale I** pokazały, że głównym wektorem nasion orzecha włoskiego na grunty orne jest rodzimy gawron (*Corvus frugilegus*). W ciągu ostatnich 50 lat liczebność populacji gawronów wyraźnie się zwiększyła, ptaki te zmieniły miejsca noclegowisk i żerowisk w sezonie jesiennym, na okolice miast i wsi. Tam też przeważnie uprawia się orzechy w przydomowych ogródkach, oraz zlokalizowane są plantacje orzecha włoskiego. Gawrony preferencyjnie żerują na gruntach ornych, gdzie także chowają nasiona orzecha włoskiego, jako zapasy pokarmu. Po zaprzestaniu upraw na gruntach ornych, siewki tej rośliny przestają być niszczone przez sezonowe prace polowe, co umożliwia im wzrost. W Polsce na skutek transformacji politycznej i upadku socjalizmu w 1989 roku, zmienił się sposób użytkowania gruntów, a powierzchnia opuszczonych gruntów ornych sięgała nawet 12 milionów hektarów. Stworzyło to odpowiednie siedlisko dla orzecha i umożliwiło jego

inwazję. Wyniki przedstawionych badań pozwalają twierdzić, że zmiana użytkowania ziemi przez rolników na ogromną skalę i koincydencja rozwoju populacji odpowiednich rozsiewaczy, transportujących nasiona tej obcej rośliny na dalekie dystanse (nawet powyżej 1 km), stworzyły szansę inwazji gatunku, który nigdy nie występował poza obszarem upraw i nigdy nie był brany pod uwagę jako potencjalnie inwazyjny. Pośród osobników rosnących na opuszczonych gruntach rolnych aż 10% produkowało nasiona, które mogą być źródłem nasion dla zwierząt mniej chętnie, niż gawrony, odwiedzających siedliska synantropijne. Z drugiej strony, zwiększa się liczebność leśnych zwierząt znanych z zoochorii, które ulegają synantropizacji, czego przykładem może być sójka *Garrulus glandarius*. To sprawia, iż ptaki te coraz częściej mogą wchodzić w interakcje z orzechami włoskimi rosnącymi w ogrodach czy sadach.

Rozdział II pokazuje, że orzech włoski zaczyna być licznym gatunkiem/coraz częściej spotykanym również w lasach, a głównym wektorem jego nasion w tym przypadku jest wspomniana sójka, która, podobnie jak gawron, robi zapasy nasion na zimę. Orzech włoski był liczny w lasach położonych blisko siedzib ludzkich, gdzie uprawiano orzechy włoskie, a także na przyległych opuszczonych polach, na których notowano orzechy włoskie. Dodatkowym, choć równie ważnym czynnikiem zwiększającym prawdopodobieństwo i sukces inwazji była struktura i rzeźba krajobrazu. Przeprowadzony eksperyment pozwala sugerować, że część nasion schowanych przez gawrony na gruntach ornych spływa wraz z opadami do lasów położonych poniżej pól uprawnych, dlatego liczebność siewek orzecha włoskiego w lasach położonych poniżej linii pól uprawnych, była wyższa niż w lasach, które były położone w płaskim otoczeniu lub na szczytach pagórków. Przykład inwazji orzecha w Centralnej Europie pokazuje, że inwazje biologiczne są procesem bardzo dynamicznym, wywierającym silne efekty kaskadowe w ekosystemach.

Inwazja orzecha włoskiego jest dobrą ilustracją dyspersji obcych gatunków z siedzib ludzkich do pół-naturalnych i naturalnych siedlisk na lokalną skalę. Jednakże zanim obce gatunki roślin będą mogły rozprzestrzeniać się w nowych rejonach, muszą zostać w dużej liczbie sprowadzone i uprawiane przez ludzi. Jest to niezbędne do wytworzenia żywotnych nasion. Dlatego też transport gatunków inwazyjnych na dalekie dystanse determinuje to jakie obce gatunki, i kiedy staną się inwazyjne w danym regionie.

Nowym zjawiskiem socjologicznym, który może mieć duże znaczenie w rozprzestrzenianiu obcych gatunków jest internet. Wynika to z tego, że handel internetowy w znacznie mniejszym stopniu, niż handel tradycyjny, ogranicza rodzaj towaru i odległość na jaką jest transportowany. Celem badań opisanych w **Rozdziale III** było scharakteryzowanie roli sprzedaży internetowej w rozprzestrzenianiu się obcych inwazyjnych gatunków roślin. Sprawdzano jakie dystanse pokonują one w procesie sprzedaży w porównaniu do tradycyjnej sprzedaży w sklepach ogrodniczych. Badania pokazały, że gatunki inwazyjne sprzedawane przez internet były transportowane na większe dystanse, niż te sprzedawane w tradycyjny sposób w sklepach. Sprzedaż internetowa powodowała, że rozkład dystansów na jakie transportowane były inwazyjne gatunki był bardziej spłaszczony (platykurtyczny) niż w przypadku sprzedaży tradycyjnej, gdzie rozkłady dystansów przypominały naturalną dyspersję roślin.

Niniejsze badania pokazują, jak ważną rolę w kształtowaniu inwazji biologicznych i ich efektów odgrywają czynniki bezpośrednio związane z działalnością człowieka. Czynniki historyczne, mające miejsce wiele lat wcześniej mogą nieoczekiwanie determinować to, że nowe gatunki staną się inwazyjne w późniejszym okresie. Prezentowana rozprawa doktorska sugeruje także, że dalsze badania w tym temacie są niezbędne. W szczególności, uwzględnienie interakcji obcych gatunków z rolnictwem, zmianami w użytkowaniu ziemi, demografią oraz współczesnymi upodobaniami (względem roślin ogrodowych) i stylem życia ludzi może znacznie uzupełnić modele dynamiki inwazji oraz polepszyć zrozumienie tego zjawiska.

Słowa kluczowe:

Czas uśpienia inwazji, dyspersja, gatunki inwazyjne, sprzedaż internetowa, zmiany w rolnictwie

Introduction

The problem of invasive species was widely described for the first time in a book by Charles Elton (*The Ecology of Invasions by Animals and Plants*, 1958). Thereafter, the ecology of invasive alien species developed, becoming one of the most up-to-date and growing topics of ecology in the late 1990s (see the review by Richardson and Pysek 2008). Establishing a single coherent and accurate definition of invasive alien species along with the linked terminology (Table 1, page16) for the study of this new and complex phenomenon took many years. Even after 50 years of research on invasions, the definition of invasive species provided by scientists and the most important organisations engaged in conservation biology, such as the World Conservation Union (IUCN), Convention on Biological Diversity and Global Invasive Species Program (GISP), was inconsistent. Notwithstanding, the expanded definition created over the past ten years by the IUCN and GISP states that an invasive species is "a species that becomes established in natural or semi-natural ecosystems or habitats, is an agent of change, and threatens native biological diversity" (IUCN 2000).

In plants, typical invasive alien species are those which produce large numbers of small seeds which are dispersed by wind, easily germinate on a wide range of soils and are fast-growing (Gurevitch and Padilla 2004, Latzel *et al*. 2011). Such plants are not only very able competitors for resources such as space, water, light and pollinators, but they can also actively outcompete native species through allelopathy and pollen pollution (Funk and Vitousek 2007). Alien invasive plants strongly affect biodiversity, ecosystem services and are among the most important reasons for species extinction (Richardson and Pysek 2008, Latzel *et al*. 2011, Pysek *et al*. 2012). Therefore, studying the biology of invasive species is one of the main goals of conservation biology.

Lag phase and invasion debt

Most researchers of invasive species focus almost exclusively on suddenly expanding alien species. However, the number of alien species not currently spreading, but potentially invasive, is huge. European flora consists of 5,789 naturalized alien species (Lambdon *et al.* 2008); at least 3,427 naturalized alien species occur in North America (Qian and Ricklefs 2006); there are 2,741 such species in Australia and 2,136 in New Zealand (Diez *et al.* 2009) but an impact on the environment has been quantified for fewer than 200 alien plants, not all of them considered invasive (Hulme *et al*. 2013). Therefore, the major challenge is predicting which species will threaten native ecosystems, biodiversity and human economy. This is not a straightforward task, since many newly introduced species do not become established immediately but rather go through a period during which they occur in rare and small populations and therefore may be considered as having a low level of impact and a very slight chance of becoming invasive. This period is called a time lag or lag phase (Table 1) and can last as long as hundreds of years, after which the species may become entirely extinct in a given area or may start to expand its numbers, spatial range and impact. Baker (1965) first recognized the basic mechanisms of release from the lag phase, including hybridization and overcoming constraints based on landscape structure and biological and environmental barriers to population expansion (Baker 1965, Kowarik 1995, Crooks 2005). Currently, climate change, genetic adaptation, human activity such as transportation, frequent long distance dispersal and changes in land use (Ellstrand and Schrierenbeck 2000, Hobbs and Humphries 1995, Sakai *et al*. 2001, Walther *et al.* 2009) are the main drivers of the transition from lag phase into invasive spread. Nevertheless, empirical evidence is still rare and the mechanisms leading to the disruption of the lag phase are not entirely understood (Crooks 2005).

Among the above-mentioned factors, changes in land management and human activity such as common new methods of transportation of seeds are of primary importance in the invasion progression. They result in an increasing number of seeds or seedlings of alien species introduced in a given area (a phenomenon called propagule pressure, Table 1), leading to an increased chance of new invasions in new ecosystems (Crooks 2005, Lockwood *et al.* 2005).

Farmland is a kind of ecosystem highly susceptible to invasions, because soil and plant coverage is frequently removed by field work, leading to strong and frequent local disturbances (Fox 1979, Byers 2002, Chytry *et al*. 2008). Moreover, arable land frequently comprises areas where people plant new alien species as crops or decorative plants, and thus the risk of introducing a potentially invasive alien is high (Pandi *et al*. 2014). Farmland is also a very dynamic ecosystem where both intensification of land use and abandonment play dominant roles in shaping population processes. This dynamism was especially apparent in Central Europe, where large state collective farms (PGRs) were the main system of agricultural land management until the late 1980s. PGRs were large farms, financed by national governments for many years. After the political transformation in 1989, these governments stopped giving supplementary financial support for agriculture; consequently, large farms were abandoned or taken over by private owners, causing the abandonment of approximately 12 million hectares in Poland (Orłowski 2004). The amount of abandoned land decreased after the accession of the countries in this region to the European Union; nevertheless, this period of cessation of farming was long enough to cause substantial changes in biodiversity and functioning of ecosystems (Stoate 2009). These changes also affected invasions of alien species that consequently created interactions with crops, native plants and dispersers that are complex, exceedingly unpredictable and appear many years after their initial introduction. These future consequences of invasion are called invasion debt, which has only recently been recognized as one of the most important phenomena linked to invasion (Seabloom *et al*. 2006, Essl *et al.* 2011, Bennett *et al.* 2012). Essl *et al.* (2011), defined this term (Table 1) in the context of a phenomenon whereby certain historical factors are more responsible than present-day factors for current patterns of the richness of exotic species. For example, the socioeconomical situation in the early 20th century was a factor which better explained the number of currently established alien species in the wild than factors such as gross domestic products (GDP) starting from the year 2000 (Essl *et al*. 2011). Essl *et al.* (2011) explained invasion debt as parallel to extinction debt, being the consequence of certain forcing events in the past that were the reason for a number of species being doomed to eventual extinction at present or in the future. Invasion debt is closely linked with the number of species destined for eventual immigration (immigration credit) following forcing events such as political or sociological changes (Jackson and Sax 2010).

The importance of long-distance dispersal in invasions

As stated above, lag phase and associated invasion debt are the least understood phenomena in invasion ecology. However, most research suggests that their length may depend on long-distance dispersal (Nathan 2006). Species can become successful invaders only if they can be dispersed to suitable habitats. Extreme movement by an invasive species is often attributable to various forms of human transportation which enable alien species to penetrate geographical barriers and to colonize new localities as well as escape from the lag phase of colonization (Chittka and Schürkens 2001, Margolis *et al*. 2005, Tatem 2009).

In recent years there has been a great deal of trade through internet sales with an associated transportation network (Bauer and Colgan 2002, Freund and Weinhold 2004). However, the ways in which the relatively new global phenomenon of internet commerce may be affecting the dispersal modes of invasive alien plants on landscape or regional scales is poorly understood.

Currently, many alien plant species, some of them invasive, are available for sale in garden shops (Rixon *et al.* 2005, Dehnen-Schmutz 2007). These plants are sold both traditionally and via internet. Internet trade is much less constrained by considerations such as type of transportation and distances which alien invasive species may travel from shop to customer. Hence, it is probable that internet commerce increases the distances over which alien species are dispersed and facilitates the purchase of invasive species, and thus increases propagule pressure from invasive species (Kikillus *et al.* 2012). However, this has not been tested empirically.

Table 1. Definition of terms used in this dissertation

Term	Definition
Alien invasive species	an alien species (non-native, or outside its natural range and dispersal potential) which becomes established in natural or semi-natural ecosystems or habitats, is an agent of change, and threatens native biological diversity and human economy (IUCN 2000)
Alien species	used interchangeably with **introduced species, non-native species, non-indigenous species, exotic species**. Species that are introduced in a given region directly or indirectly due to human activities (Richardson *et al*. 2000).
Forcing event	an important event following which some alien species are enabled to spread in the future; an event which induces invasion and invasion debt.
Immigration credit	the number of species committed to eventual immigration following a forcing event such as socioeconomical changes, changes in land use, etc. (Jackson and Sax 2010).
Invasion debt	Latent expansion of range and impact of exotic species in the absence of new anthropogenic introductions, after a high-impact sociological or environmental change (Essl *et al.* 2011).
Propagule pressure	used interchangeably with **introduction effort**. A measure of the number of individuals and number of introduction events of an alien species into a non-native region (Groom 2006)
Time lag	used interchangeably with **lag phase**. The time between initial introduction and subsequent population explosion, or simply a delay in transition between phases of invasion, e.g., appearance, population growth, range expansion and impact (Crooks 2005)

The aim of this study

This study has three aims: firstly, to show how changes in agricultural land use, combined with the behavior of native dispersing animals, affect the disruption of the lag phase and the subsequent invasion of alien tree species that have never been considered potentially invasive (Chapter 1*); secondly, to analyze invasion as a multi-step process occurring in different habitats and at different spatio-temporal scales (Chapter 2**); thirdly, to demonstrate the role of internet commerce, which may affect the dispersal potential of invasive alien species and alter the modes of long-distance dispersal by which plants usually travel in nature (Chapter 3***).

* Chapter 1 occurs in references such as Lenda M., Skorka P., Knops J.M.H.., Moroń D., Tworek S., Woyciechowski M. (2012). Plant establishment and invasions: an increase in a seed disperser combined with land abandonment cause an invasion of the non-native walnut in Europe. *Proceeding of the Royal Society B – Biological Sciences,* 279, 1491-7.

** Chapter 2 occurs in references as Lenda M, Skorka P, Woyciechowski M. Cascading effects of changes in land use on the invasion of the walnut *Juglans regia* in forest ecosystems, unpublished

*** Chapter 3 occurs in references as Lenda M., Skórka P., Knops J.M.H., Moroń D., Sutherland W.J., Kuszewska K., Woyciechowski M. (2014). Effect of the Internet Commerce on Dispersal Modes of Invasive Alien Species. *PLoS ONE*, 9, e99786. doi:10.1371/journal.pone.0099786

General discussion

Socioeconomic changes and their effects on the environment seem to be underestimated by ecologists; nevertheless, undoubtedly, sociological factors, human demographical explosion and pursuit of comfort strongly affect biodiversity (Seabloom *et al.* 2006, Essl *et al.* 2011, Simberloff 2013, Pe'er *et al.* 2014). Invasions of alien species are among the main signs of human-mediated impact on ecosystems. Surprisingly, the current number of established and naturalized alien species in Europe is related to occurrences from the past, including socioeconomic indicators from the early twentieth century, but not from the current one (Essl *et al.* 2011). Therefore, the present socioeconomic situation may result in considerable additional accumulation of alien species in the future and creation of a large invasion debt.

One of the best examples illustrating the phenomenon of invasion debt is the invasion of the walnut in Central Europe following the political transformation there (Chapter 1). To be successful, plant invasions always require the simultaneous concurrence of a permanent seed source, a suitable habitat, and dispersers which transport seeds for long distances. The lack of any one of these factors usually causes the alien species to persist in a lag phase which can last as long 800 years, as was noted for the walnut in Poland. There were three main factors in the past which determined the walnuts' invasion following centuries of lag phase. First, the walnut was introduced into gardens by monks in the Middle Ages and, as a valuable plant, became very popular in human settlements. The main disperser of the walnut seeds in farmland was the rook, *Corvus frugilegus* (Chapter 1). The population of corvids, after enjoying the protection of the law over the past 50 years, increased in numbers. Rooks, feeding on cultivated walnuts, started to inhabit human settlements. Additionally, the political transformation 25 years ago resulted in large-scale land abandonment, creating a perfect settlement, not colonized and extremely vulnerable due to disturbances, for invasive species.

Before becoming protected, rooks foraging in an agricultural landscape were treated as pests (Tomiałojć 1990). They collected walnut seeds from backyards and plantations, carried them to ploughed fields and buried them in soil as a supply; however, they avoided caching seeds in abandoned land. It follows that only vast land abandonment could have triggered a great chance for seeds deposited in soil as a seedbank to germinate and freely grow, which was impossible when fields were plowed (Chapter 1). Wild walnuts were found on abandoned land tracts as large as 1000 ha, with 10% already mature and producing seeds. Therefore, land-use change combined with changes in dispersal can cause the rapid increase of a non-native species, enabling it to become invasive. This has cascading effects on entire farmland and forest ecosystems (Chapter 1 and 2). Thus, species that are non-native and non-invasive may become invasive, as habitats and dispersers change after a forcing event such as socioeconomical transformation.

The invasion of the walnut is also interesting in view of the fact that as a species it produces relatively big, heavy seeds, which should be a physical barrier to the dispersal process, since not many seed dispersers can carry them. For this reason the walnut was never considered potentially invasive. Nevertheless, the value of fatty and highly nutritional seeds, easily available within a semi-natural post-farmland habitat, may increase the frequency of zoochory (Snow and Snow 1988). This may cause far wilder, not synantropized species which previously had no opportunity to interact with walnuts to become new seed dispersers (Chapter 2). According to Kowarik (1995), successful invasions are usually linked to lag phases longer than those of failed invasions. This can be explained by a number of new relationships between alien species and native seed dispersers, microorganisms and adaptations to climate. On one hand, the risk of cascading effects of alien species on the ecosystem is higher if the lag phase is extended; on the other, there is a simultaneous risk that such delayed invasions will be more successful.

A good example of how links with native animals are shaped by the occurrence of invasive species in farmland is the early stage of the walnut invasion as described in forests (Lenda *et al*. 2014, Chapter 2). The involvement of new native seed dispersers such as jays (*Garrulus glandarius*) and squirrels (*Sciurus vulgaris*) carrying seeds into forests shows how complex and dynamic the invasion process is. The new seed dispersers create opportunities for walnuts to colonize different habitats which are much more natural and diverse than farmland. This also enhances the general invasiveness potential of this species. Therefore, the harmful effects of wild-growing walnuts might be much more serious than previously estimated (Guzik 2009). Moreover, the unexpected impact of walnut seed banks created by rooks in arable fields on the progression of the invasion into forests was enhanced by passive dispersal linked with interactions between gravity, the shape of the terrain and weather conditions. Walnut seeds hidden in arable fields by rooks passively reached forest edges, especially in sloping fields bordered by forests, adding to propagule pressure in forest ecosystems and underlining the importance of local terrain configuration on the processes of invasion.

The influx of walnuts into forest ecosystems was indeed multipath. Forest occupancy by, and abundance of, walnuts were positively correlated with cover of abandoned fields and human settlements inhabited by seed-bearing walnuts. The density of walnuts in forests was positively correlated with that of jays, which often harvested walnut seeds in abandoned fields independently of their distance from the forest. These birds also frequently visited walnuts planted in human settlements, but only those in the proximity of forests. This indicates that the invasion of alien walnuts into agricultural landscapes has vast spatio-temporal cascading effects that have led to their further colonization of forest ecosystems. The complexity of the direct and indirect interactions between walnut seeds and all native dispersers, combined with politically related changes in land use, indicates that the invasion debt, while impossible to predict, is certainly substantial.

The spread of the walnut shows that human settlements may act as pools of invasion, determining the number, occupancy, and spatial pattern of alien invasive species dispersal into natural ecosystems and habitats (Chapter 1, Chapter 2). It illustrates in detail what may happen if many people plant the same species in one region and do not monitor the eventual fate of the seeds of that species. However, this is the final scenario of an invasion mechanism already functioning on the edge of human settlements and (semi-) natural habitats. Nevertheless, uncontrolled commerce in exotic species is the starting point of all known invasions, causing initial propagule pressure in the regions where buyers come from. This precisely determines the spatial distribution of invaded areas (Kikillus *et al.* 2012). New alien species may easily adapt and spread if there is a higher number of individuals in one region that can cross genes and mutate. Commerce in alien species is also one of the ways alien invasive species may cross geographical barriers and become dispersed over long distances into new habitats (Kikillus *et al.* 2012). Therefore, the distances over which such species are transported after being sold are crucial for the success of invasions, given that distance dispersal is one of the most important factors for colonizing new habitat patches (Lockwood *et al*. 2005, Nathan *et al*. 2008, Chapter 3). The distances over which alien invasive species travel when sold in internet shops can exceed one hundred kilometers; thus e-commerce very frequently causes dispersal over exceptionally long distances, whereas traditional sales are followed by local transportation limited to distances of 50 km or less. Moreover, a study by Lenda *et al*. 2014 (Chapter 3) clearly shows that e-commerce is characterized by greater dispersal distances in comparison with traditional sales, with the latter resembling natural long-distance dispersal. This can be seen in the example of rooks, which caused the long-distance dispersal of walnut seeds. Birds are generally regarded as very good vectors in long-distance dispersal. Walnuts were transported mostly less than 200 meters from the tree, but there were exceptional cases in which birds carried seeds for distances over 1 km. However, these distances are small compared with those over which plants are transported in internet commerce. Thus, e-commerce has created novel modes of long-distance dispersal, while traditional sales resemble more natural dispersal modes. Moreover, analysis of sales on the biggest Polish internet auction portal showed that the number of alien specimens sold via the internet has increased remarkably over recent years. Therefore, internet commerce is likely to increase the rate at which ecological communities become homogenized and increase the spread of invasive species through increasing the rate of long-distance dispersal; moreover, similarly to changes in land use, it can generate invasion debt.

The previous political system in Central and Eastern Europe affected not only agricultural land management, but also, above all, the movement of people, e.g., immigration, emigration and trade between distant places, even within a single country (McGlade 2001). This former restriction caused the number of new introduced species and successful invasions was low during cold war and socialism (Chiron *et al*. 2010). Earlier, international trade was restricted, as described by McGlade (2001). The volume of merchandise exported from Western to Eastern European countries during the communist era never exceeded 5% of the total volume traded from Western Europe to other regions of the world (McGlade 2001). The embargo caused Eastern Europe to experience a lesser number of new invasive species than the West until the transformation (Chiron *et al*. 2010). The political transformation enabled people to travel and to sell goods virtually beyond any control; moreover, this happened almost at the same time that the internet, a revolutionary system of communication between people, became more popular. The internet enabled people not only to communicate, but also to sell things very conveniently irrespective of transportation distances. In Poland, in 1996, the first and most popular portal featuring internet auctions was set up, marking the beginning of e-commerce in this country. In the same way that previous restrictions on commerce in goods held down the number of alien or invasive species that were sold and transported over long distances, uncontrolled and convenient internet commerce acted in the opposite way.

The research presented in this dissertation indicates that the invasion of alien species is a very complex process which involves natural mechanisms of dispersal, interaction with humans and the general socioeconomic situation in a given region. Invasions are augmented by the growth of modern technologies, such as the internet, underlining the strong connection between alien species and the development of human civilization.

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Chapter I

Lenda M., Skórka P., Knops J.M.H., Moroń D., Tworek S., Woyciechowski M. (2012). Plant establishment and invasions: an increase in a seed disperser combined with land abandonment cause an invasion of the non-native walnut in Europe. Proceedings of the Royal Society B – Biological Sciences, 279, 1491-1497.

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Plant establishment and invasions: an increase in a seed disperser combined with land abandonment causes an invasion of the non-native walnut in Europe

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Successful invasive species often are established for a long time period before increasing exponentially in abundance. This lag phase is one of the least understood phenomena of biological invasions. Plant invasions depend on three factors: a seed source, suitable habitat and a seed disperser. The non-native walnut, *Juglans regia*, has been planted for centuries in Central Europe but, until recently, has not spread beyond planted areas. However, in the past 20 years, we have observed a rapid increase in walnut abundance, specifically in abandoned agricultural fields. The dominant walnut disperser is the rook, *Corvus frugilegus*. During the past 50 years, rooks have increased in abundance and now commonly inhabit human settlements, where walnut trees are planted. Central Europe has, in the past few decades, experienced large-scale land abandonment. Walnut seeds dispersed into ploughed fields do not survive, but when cached into ploughed and then abandoned fields, they successfully establish. Rooks preferentially cache seeds in ploughed fields. Thus, land-use change combined with disperser changes can cause rapid increase of a non-native species, allowing it to become invasive. This may have cascading effects on the entire ecosystem. Thus, species that are non-native and not invasive can become invasive as habitats and dispersers change.

Keywords: agriculture; behaviour; caching; lag-phase; land management; policy

1. INTRODUCTION

Invasive alien species can change the entire ecosystem and can cause declines in biodiversity [1,2]; therefore, biological invasions are a major research topic in ecology and conservation biology [3–5]. Factors such as fast growth, allelopathy and shading can provide competitive advantages for non-native species that allow them to successfully colonize new habitats [6–9]. However, for many invasions, a lag-phase is observed [4,10], in which alien species are present at a low population size before a demographic explosion in abundance occurs [4,10,11]. This lag phase can be explained by changes in biotic (e.g. availability of pollinators or dispersers), abiotic (e.g. climate, habitat fragmentation) and/or human-related factors (e.g. land-use changes), but documented examples are rare [10,11].

One such alien, long-established, but non-invasive plant species in Europe is the Persian walnut (*Juglans regia*, hereafter walnut; see electronic supplementary material, S1). Walnut trees produce heavy, fat seeds and are valued for their wood. Extensively cultivated in residential areas, walnut trees were first introduced to monasteries in Europe in the Middle Ages [12]. However, recently, we have observed a rapid increase in their abundance in semi-natural habitats, which raises the question of what has changed in the ecology of this species that has caused this increase.

Invasive alien species often have small, wind-dispersed seeds, but for many species an effective animal disperser is crucial for successful spread [13]. Alien plant dispersal by animals can be either by a generalized disperser, such as canids and bears [14,15] or by a more specialized, mutualistic disperser, such as ants [16] or some birds consuming fleshy fruits [13,17]. Plants that produce large seeds are rarely invasive [13,18]. However, large seeds can be an attractive food source, and dispersers that transport and cache seeds may strongly facilitate an invasion [19–21]. Large tree seeds like walnuts are frequently eaten and cached by corvids [20,22], such as the rook *Corvus frugilegus* [21,23,24]. Rooks traditionally avoided humans and restricted their foraging to open areas. However, in recent decades, because of restricted hunting, rooks have changed their behaviour, do not avoid humans, and commonly occur in residential areas [25,26]. This change in behaviour has led rooks to frequently harvest and cache walnut seeds.

Agricultural land abandonment induces huge ecosystem changes in soils, biodiversity and ecosystem services [27,28], but detailed records of these changes are

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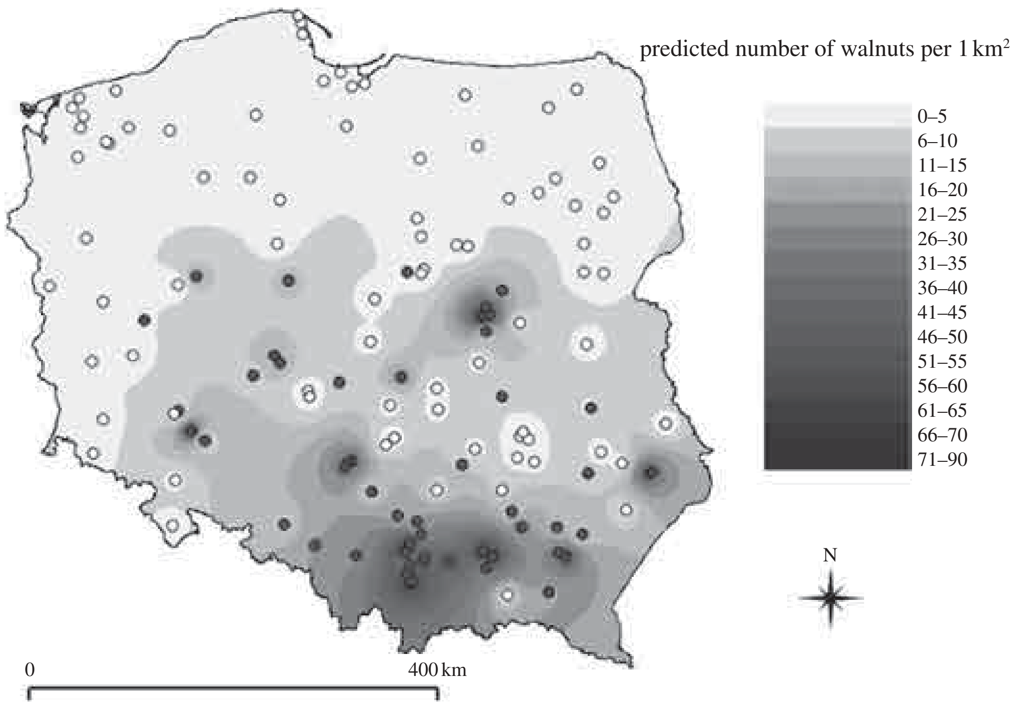

Figure 1. The absence/presence in 1 × 1 km plots and interpolated density of wild walnut trees and seedlings in agricultural landscapes of Poland. Dark circles indicate plots where at least one wild walnut was found, white circles are plots where walnuts were absent. The interpolation was performed with an inverse distance method in Quantum GIS software.

rare. Recent studies show that land abandonment can induce both positive and negative changes in native fauna and flora [29,30]. However, land-use change, and especially land abandonment, can also lead to drastic disturbance changes [28] and thereby provide new opportunities for alien species to become invasive. In many countries, land abandonment is often related to major political changes. For example, in Central Europe, the collapse of socialism in the 1990s led to dramatic changes in agricultural landscapes [31–33]. However, not much is known about the biodiversity or ecosystem consequences of this change [34,35]. In Poland, abandoned agricultural fields currently amount to 2 million ha (12% of all agricultural land) [32].

In this study, we examined the different aspects of the walnut invasion in Poland. Specifically, we examined: (i) where the walnut seed sources are located, (ii) who disperses the seeds, (iii) into which habitats seeds are dispersed, (iv) which habitats are invaded; (v) then we examined how land-use change and disperser changes have induced the recent rapid invasion of walnut in Central Europe.

2. MATERIAL AND METHODS

(a) *Walnut distribution at the landscape and regional scales*

We randomly selected ten 1.5 × 1.5 km landscape plots in Southern Poland located in agricultural landscapes. Within these plots, we mapped the areas of abandoned fields (former ploughed fields, $n = 479$ in total), ploughed fields, grasslands, woodlands and human settlements. The mean (±s.e.) area covered by abandoned fields in the 10 landscape plots was 12.5 ± 2.2%; ploughed fields covered 60.2 ± 4.3%, grasslands 10.5 ± 2.7%, woodlands 7.2 ± 1.5% and human settlements 9.2 ± 1.4%. We counted all walnut trees growing within these landscape plots in the summer and autumn of 2007 (three plots) or 2008 (seven plots). We noted the habitat where wild walnuts grew, the diameter and height of the trees, and the number of seed-bearing trees.

The age of wild walnut trees was calculated on the basis of their diameters measured at 30 cm above ground level, or at ground level in the case of saplings less than 3 years old [36] (for details see electronic supplementary material, S1). Because determining the exact time of field abandonment was very difficult, we have abandonment times for only 215 out of 479 fields.

To estimate the factors affecting the presence and abundance of walnut trees at the regional scale, we randomly selected 130 plots (1 × 1 km each) spread throughout agricultural landscapes in Poland (figure 1). We counted walnut trees and corvids in these plots between June and September annually from 2007 to 2010 (electronic supplementary material, S1).

(b) *Corvid–walnut interactions*

We examined corvid abundance and behaviour in three plots randomly selected from the 10 used for the walnut tree surveys. Counts were made from the middle of August to the end of December 2008 at roughly 7-day intervals. Each visit lasted 2 h. We noted the number of birds and their foraging habitat as well as all cases of caching walnut seeds and the habitat where the seeds were cached. We also determined how many walnut seeds were available for dispersers during the season, distances covered by corvids carrying walnuts and the number of cached seeds (see electronic supplementary material, S1). Moreover, we estimated the exact rate of seed caching, excavating and crushing in selected ploughed fields in the three landscape plots (electronic supplementary material, S1). Because rooks are the dominant disperser of walnut seeds, we only describe the rook behaviour.

(c) *Analysis*

We checked for spatial autocorrelation in the data by means of Moran's I statistics [37]. If significant autocorrelation was found (the presence and abundance of walnut trees at a regional scale—see below), we used spatial statistics: autologistic or simultaneous autoregressive models [38]. Otherwise, traditional general linear mixed models were used. In regression models, data were standardized before calculations to allow direct comparison of beta values. For more details on statistical methods, see electronic supplementary material, S1.

Estimates of statistical parameters are quoted with standard errors (s.e.) throughout the text. All analyses were performed in SAM v. 4.0 [39] and SAS v. 9.1.

3. RESULTS

(a) *Walnut seed source*

We found a total of 725 mature (older than 30 years) walnut trees in farmyards and gardens within human settlements in each of the 10 study landscape plots. We did not find any mature walnut trees in other habitats within the landscape plots. Thus, planted trees are the current seed source.

(b) *Rook foraging behaviour*

Among all corvids observed during weekly surveys ($n =$ 3927 individuals), 88% were rooks, 10% jackdaws (*Corvus monedula*) and 2% carrion crows (*Corvus corone cornix*). We observed 325 caching events by rooks and 23 by carrion crows, but none by jackdaws. The first two species carried walnut seeds collected on or below trees from villages to agricultural habitats.

At the regional scale, we found a positive correlation (corrected for spatial autocorrelation) between the number of foraging rooks and the number of walnut trees in plots ($r = 0.604$, $p < 0.001$, $n = 130$ plots; figure S1 in electronic supplementary material, 2). This relationship was also significant ($r = 0.567$, $p < 0.001$, $n = 130$) after excluding the effects of the proximity of towns.

The abundance changes of rooks in three selected landscape plots significantly correlated with the availability of walnut seeds (figure S2 in electronic supplementary material, 2). The number of birds crushing seeds followed the dynamics of birds caching seeds with about a two-week lag (correlation coefficient between number of birds caching and number crushing seeds two weeks later: $r^2 =$ 0.650, $p = 0.005$, $n = 17$; correlation coefficient between the number of birds caching and the number crushing seeds at the same time: $r^2 = 0.352$, $p = 0.193$, $n = 19$; figure S2 in electronic supplementary material, 2). Over the entire season, we counted 325 rooks caching seeds and 129 rooks crushing seeds in fields, which indicated that 2.5 times more seeds were being hidden than eaten during the study period.

In total, from the beginning of September until the end of November 2008, we observed 968 incidences of rooks caching walnut seeds and 348 incidences of these birds excavating and crushing nuts (ratio of seeds dug up and crushed to cache was 0.359) in selected ploughed fields. Rooks cached 3.78 ± 0.37 walnut seeds h^{-1} ha^{-1} ($n =$ 378 1 h observation samples), and during the same observation periods crushed 1.25 ± 0.14 seeds h^{-1} ha^{-1} ($n =$ 378). The rate of seed excavating and crushing was highest at the end of October and beginning of November and was not influenced by the time of day (figure S3 in electronic supplementary material, 2).

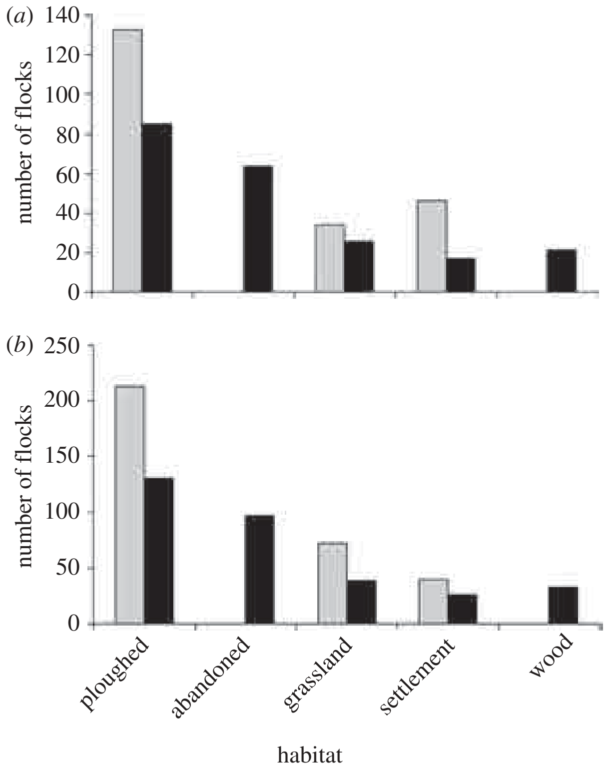

Figure 2. Rook preferences for (*a*) foraging habitats ($\chi^2_4 = 164.02$, $p < 0.001$, $n = 213$ flocks) and (*b*) habitats for seed caching ($\chi^2_4 = 218.45$, $p < 0.001$, $n = 325$ rooks). Grey bars indicate observed values; black bars indicate expected values calculated on the assumption that there were no preferences (number of flocks and birds should be proportional to the share of the habitats in the landscape). Observed values are pooled numbers of flocks/birds noted in three 1.5×1.5 km landscape plots where detailed behavioural observations were made (ploughed, managed ploughed fields; abandoned, abandoned fields (former ploughed fields); grassland, grasslands (meadows, pastures); settlement, human settlements; wood, glades in woods).

(c) *Rook walnut seed dispersal*

Rooks preferred ploughed fields and grasslands when foraging on invertebrates and weeds (figure 2; electronic supplementary material, 3). Rooks hid walnut seeds in ploughed fields but never cached seeds in abandoned fields (figure 2). We also observed jays (*Garrulus glandarius*) and red squirrels (*Sciurus vulgaris*) carrying seeds but these species always cached them in forests; because we observed only few seedlings in forest habitats we do not consider them further here. Rooks carried walnuts from villages to ploughed fields for distances that were usually below 500 m, although sometimes up to or over 1 km (figure S4 in electronic supplementary material, 2).

In 2008, six ploughed fields were abandoned in the study area. Seventy-nine foraging rooks, including those caching walnuts ($n = 13$), were observed in these fields in 2007 but not in 2008, 2009 or 2010. In the autumn of 2008, we found 42, 15, 20, 5, 11 and 20 walnut seedlings, respectively, in those fields. One field was ploughed again in 2009 (the one with 20 walnut seedlings). The numbers of seedlings on the remaining fields 2 years after abandonment were 50, 13, 29, 19, 14, respectively, while in 2010 there were 51, 10, 31, 24, 13 (table S1 in electronic supplementary material, 2).

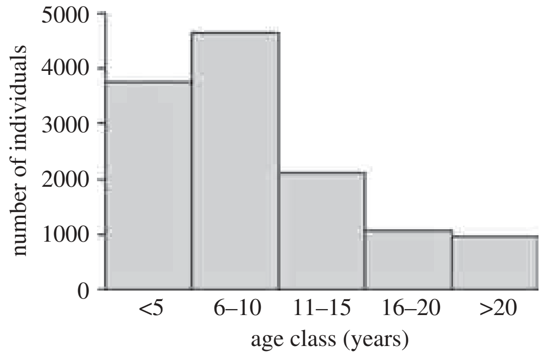

Figure 3. Age distribution of wild walnuts growing in abandoned fields in Poland. Data comes from 10 1.5 × 1.5 km landscape plots in Southern Poland.

We found in 2008 that 21 of the 30 examined ploughed fields contained walnut first-year seedlings, with a mean density of 19.6 ± 2.8 seedlings ha^{-1} (electronic supplementary material, S3). In 2009, in another set of 30 ploughed fields, walnut seedlings were found in 14 fields, with a mean density of 15.4 ± 3.8 seedlings ha^{-1}. All these seedlings were short enough not to be cut by the combine grain harvester. In both years, all seedlings were later destroyed during ploughing.

(d) *Walnut-invaded habitat*

In the 10 surveyed 1.5 × 1.5 km landscape plots, we found a total of 12 529 walnut seedlings, of which 96 per cent grew in abandoned fields and 4 per cent in ploughed field margins (e.g. roadsides, drainage ditches; electronic supplementary material, S3). Among all walnut seedlings, 10 per cent were producing seeds (electronic supplementary material, S3). We did not find any walnut seedlings in grasslands. Walnut occupied 48.4 ± 5.1% of the abandoned fields in the 10 landscape plots. Where walnuts occurred, the average density within abandoned fields was 125.2 ± 9.0 seedlings ha^{-1}, or with abandoned fields comprising 12.5 per cent the mosaic of habitats within this agricultural landscape, 557 individuals per 1 km^2.

The age distribution of the walnut seedlings was right-skewed, with the oldest individuals slightly over 20 years old (figure 3 and electronic supplementary material, 3). We found a positive relationship between years since management cessation and the mean age of walnuts (GLMM: $F_{1,5.9} = 107.21$, $p < 0.001$, $r^2 = 0.724$; figure 4).

The occurrence and density of walnut seedlings in the abandoned fields in 10 landscape plots were positively correlated with distance to the nearest human settlement (tables S2, S3 and figures S5, S6 in electronic supplementary material, 2) and significantly increased with years since cessation of field management (electronic supplementary material, S2).

We found walnut seedlings in 50 out of 130 examined 1 × 1 km plots. At the regional scale, the probability of walnut seedling occurrence increased with the cover of abandoned fields within the plot and the proximity of towns (table S4 and figure S7 in electronic supplementary material, 2). The probability of walnut seedling occurrence was negatively related to geographical latitude ($\beta = -1.001 \pm 0.241$, $r^2 = 0.25$, $p < 0.001$); i.e. in Southern Poland, walnuts occurred more frequently (figure 1). We did not find a significant effect of altitude on walnut seedling occurrence ($\beta = 0.133 \pm 0.116$, $p = 0.254$). We also found a statistically significant positive spatial autocorrelation at distances of up to 100 and between 200 and 300 km and a negative spatial autocorrelation at distances above 300 km (figure S8 in electronic supplementary material, 2).

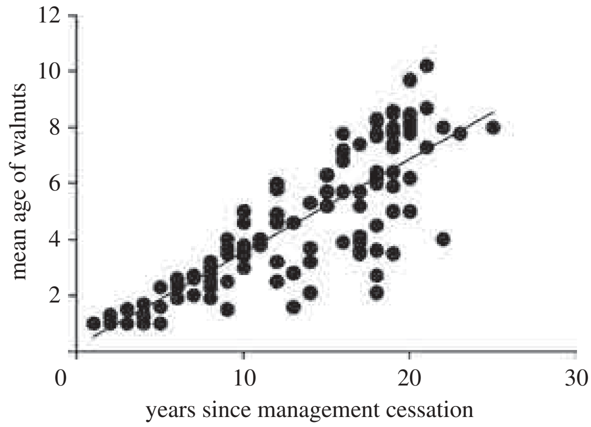

Figure 4. Relationship between years since field abandonment and mean age of walnuts. Dots represent mean age of walnuts calculated per abandoned field.

The number of walnut seedlings in the plots where this species was found varied from 1 to 86 individuals (mean 23.8 ± 3.8) and was positively dependent on the cover of abandoned fields in the plots and distance to the nearest town (table S5 and figure S9 in electronic supplementary material, 2). A statistically significant negative spatial autocorrelation was also found for the number of individuals at a distance of 200 km (figure S8 in electronic supplementary material, 2).

4. DISCUSSION

Many more species are introduced than actually spread and become successful invaders. This is especially the case for plant species where, because of agricultural or ornamental values, numerous species have been introduced that have not spread beyond planted individuals. However, ultimately some species do spread, often following an extended period after first planting. This observed lag-phase in abundance leads to the question of why and what changes after introduction induce a species to become invasive. To answer this question, we need to consider that invasion is a multi-step process that depends on three key factors: seed availability, availability of suitable habitat and dispersal from seed source to the suitable habitat.

The walnut tree in Central Europe provides an example of a lag-phase in a plant invasion. Monks in the middle Ages introduced walnut trees to this area because of the trees' edible seeds, wood, and medical properties [12]. Walnut trees are widely planted in Poland in gardens within villages and towns, providing a widespread seed source, but walnuts have not spread and become invasive until the past two decades. This recent spread can be linked to changes in land use that provide a suitable habitat and changes in the behaviour of the dominant disperser. We found that mature walnut trees occurred only within human settlements. However, we found walnut seedlings in many regions of Poland, indicating that the dispersal of this species from gardens to semi-natural habitats has occurred across the entire country. This recent increase in growth of walnut trees can be linked with the abundance and behaviour of the rook, the dominant disperser. Since the cessation of hunting 50 years ago, rooks have increased in abundance and changed their behaviour by increasingly using human settlements [25,26]. In human settlements, rooks are now collecting and caching walnut seeds, and thereby have become an efficient seed-disperser for walnuts. Rooks cached seeds only in ploughed fields, and all walnut saplings that we found are in recently abandoned ploughed fields. Widespread agricultural land abandonment started in Poland after the political changes of 1989, and the walnut age distribution in abandoned fields correlates with the time of agricultural abandonment. Thus, all three key factors—seed source, disperser and habitat—fit together to allow the walnut to become a successful invasive species.

The current main disperser of walnut seeds is the rook and, to a lesser extent, the carrion crow—both native birds in Europe [25]. According to historical ornithological data, rooks were much less numerous in Europe at the beginning of the twentieth century and, more importantly, rookeries and roosts occurred mostly in small forests in agricultural areas [26]. Thus, chances for rooks to interact with planted walnut trees were very rare. A substantial change in the rook population started about 50 years ago when the species acquired legal protection in many countries [26,40]. The population of rooks grew rapidly and birds started to use human settlements where easily available human-related food resources could be found [25]. There also was a well-documented shift from breeding colonies located in small forests in agricultural areas to colonies in parks within towns and villages [26,40]. Our study also demonstrates that the phenology of walnut seed maturation and the abundance of rooks coincide with each other. Most rooks remain in the urban environment after the breeding season, often roost in large flocks and forage in surrounding farmlands, with an increase in abundance during September and October caused by the appearance of migrating birds in this period [26]. This explains the positive correlation between human settlements and the occurrence and abundance of walnut trees at the landscape and regional scales in our study. The synanthropization and following synurbanization of the rook inevitably has led to the increased number of interactions with planted walnut trees. The other corvid caching walnut seed, the carrion crow, has also been colonizing cities and villages, but its population size is still much smaller than the rook [25].

During foraging and caching of walnut seeds, rooks preferentially choose ploughed fields and avoid older abandoned fields. In comparison with ploughed fields, abandoned fields are usually covered by tall grasses, dense herbaceous plants and shrubs (electronic supplementary material, S3; [28]). Insects, spiders and snails are unable to hide on bare ground. Birds can find large amounts of easy-to-catch and injured invertebrates on freshly ploughed fields [41]. Short or absent vegetation also guarantee good visibility and early detection of predators or competitors [42]. Rooks are not an exception; many birds, including shrikes (*Lanidae*), birds of prey and gulls (*Laridae*) prefer to forage among short vegetation on ploughed fields and grasslands [43,44]. The habitat where rooks cached walnut seeds in our study area corresponds to results of earlier studies indicating that corvids preferred ploughed fields in agricultural landscapes [20,22]. Caching food is common among different groups of animals, especially rodents and corvids [23,45,46]. Their brains are developed well enough to provide good cognitive skills and spatial memory [21,47,48]. Their memory is not perfect, however, and they forget many stockpiles [21,45].

Rooks flew long distances, often more than 500 m, with walnut seeds providing a long-distance dispersal vector for the walnut that facilitates a rapid spread in agricultural landscapes. Rooks' stockpiling habits may help explain these longer flights. These birds usually keep an eye on other individuals known to covet and rob others' stockpiles [49]. Therefore, with seeds predestined to be hidden, it may be profitable for a bird to fly alone and further, to hide the seeds in a safer, secluded place where there are no other corvids present (but see [20]). We observed many walnut seeds being buried in ploughed fields over short time periods. This indicates that the seed bank of this plant in ploughed fields is probably large. Seeds hidden by corvids in soil are buried; birds act in the same way as walnut growers who bury them in a few centimetres of soil. Seed burial is also a critical step in the growth process because it reduces the chances of seed predation by other animals [50], and enhances seed stratification.

There are several other studies that have also found that native dispersers and land abandonment can facilitate plant invasions. For instance, buckthorn *Rhamnus cathartica* is rapidly dispersed by frugivorous birds following agricultural abandonment in the USA [51]. The importance of dispersers and seed sources was also pointed out by Gosper *et al.* [13], who showed that native birds caused the invasion of many fleshy fruited plants in Australia. These studies show that land-use changes may lead to the creation of suitable habitat for invasive species and that co-occurrence of appropriate native dispersers can enable a spread.

We found that 10 per cent of all wild walnut seedlings in the abandoned fields already bear seeds. This seed source's location, far from human settlements, may lead to further expansion as these seeds are now available to other dispersers like red squirrels and jays that do not forage in human settlements. In addition, as these dispersers do not preferentially cache seeds in ploughed fields, they may move seeds to other landscape elements, leading to the spread of walnuts beyond the recently abandoned ploughed fields.

Walnut trees' dominance may also lead to cascading, large ecosystem and diversity changes, because walnut trees release juglone, an allelopathic chemical, which can have strong impacts on the growth of other plants ([4,5], M. Lenda, P. Skórka, D. Moroń & M. Woyciechowski 2007–2011, unpublished data). This allelopathic chemical can have a widespread impact; the North American-native black walnut *Juglans nigra*, for instance, has a toxic zone that extends up to 25 m from the trunk [52].

The walnut invasion that we observed is not restricted to Poland. Casual observations in the Czech Republic, Slovakia, Hungary and Ukraine also revealed that wild walnuts grow in many agricultural areas (M. Lenda, P. Skórka, D. Moroń & M. Woyciechowski 2007–2011, unpublished data), suggesting a spread in other Central and Eastern European countries. Interestingly, floristic monographs on walnut either do not mention that it may spread in large numbers to natural or semi-natural habitats or that it was believed that wild walnuts were rarely found [53,54].

5. CONCLUSION

Plant invasions are a multistep process requiring a seed source, seed dispersal and availability of suitable habitat that can be colonized. Here, we show that changes in the native rook's population size and caching behaviour combined with vast land abandonment led to the rapid invasions of the long-established, but not invasive, walnut. If habitats and dispersers change owing to changes in climate or human socioeconomics, other previously non-invasive alien species may become invasive. Poland has a native flora of 2500 species and 460 introduced alien plant species [55,56], and even more exotic species are established in other countries [57]. We cannot predict which species will become invasive in the future. However, the large number of established non-native species makes it certain that other previously non-invasive species will become invasive. Thus, as habitat destruction can lead to an extinction debt [58], introduced alien species can provide an invasion debt—a future ecological cost when habitats or dispersers change.

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SUPPLEMENT 1

METHODS IN DETAILS

1. Study species

The natural habitat of the walnut *Juglans regia* (Juglandaceae; syn. common walnut, Persian walnut) lies between the Black Sea basin, Turkey, Central Asia, and the Himalayas where it grows in mixed and deciduous forests [1,2]. This well-known tree has attractive, tasty, fat seeds and thus it has been cultivated for centuries outside its natural range, for example in Central Europe and North America. In Poland, walnut was introduced to monasteries in the Middle Ages and is adapted to the climatic and edaphic conditions [3]. It is known that walnut injects allelopathic substances into the soil, namely juglone, which may cause losses in biodiversity due to the growth inhibition of other plants [4,5, Lenda et al. unpublished]. All parts of this plant, including leaves and flowers, contain this secondary metabolite [4,6]. The walnut has pinnate foliage and its flowers are catkins. The flowers are wind pollinated. The pollen may also be dangerous to humans because of frequent and serious allergic effects [7].

Walnut is sensitive to low temperatures and can be damaged by frost late in spring (e.g. in May) when the leaves and flowers emerge. The tree starts bearing seeds when its 8-10 years old and the seeds, popularly called nuts, ripen during September and October [1-3].

2. Calculation of the age of wild walnuts

The age of wild walnuts was calculated on the basis of their diameters measured 30 cm above ground level or at ground level in the case of saplings under 3 years old [8]. We cut 50 wild walnuts and counted the growth rings as described in Loacker *et al.* [8]. These trees were collected from 30 different fields located throughout Poland in 2010. We then measured the diameter and we calculated a simple regression ($F_{1,48} = 291.25$, $P < 0.001$, $r^2 = 0.858$, $n=50$) between the age of trees and their diameters as follows:

Age of walnut(years) = 0.089(0.005)*Diameter(mm) – .148(0.511)
Standard errors are given in brackets.

3. How many walnut seeds were available for dispersers during the season?

To determine how many walnut seeds were available for dispersers during the season we followed method described by Tamura and co-workers [9]. We selected nine adult walnut trees (three in each landscape plot where the behaviour of corvids was studied in detail) growing in old orchards and gardens (where seeds were not collected by people) within human settlements. Furthermore, four owners of trees agreed not to collect seeds during our sampling. Three quadrats (2 m × 2 m) were established on the ground below each walnut. The seeds found in the quadrats were counted at weekly intervals from 15 August to 30 December 2008. To prevent double counting, seeds were collected during each count. This method gives rough rather than precise estimates of number of seeds available.

4. Rate of seed caching and crushing in selected fields

To estimate the exact rate and number of walnut seeds cached in arable fields we randomly selected nine fields (three fields within each landscape plot; mean field size: 0.81 ha ± 0.06, range: 0.49 – 1.1 ha, n = 9) where we observed the number of rooks caching, and excavating and crushing walnut seeds. Each field was observed 14 times from the beginning of September to the beginning of December 2007 at roughly weekly intervals. During the survey the selected fields were visited three times per day to find possible within-day differences in rate of food caching and crushing. During every visit each field was observed for one hour (thus one field was observed for three hours per survey day and 42 hours in total). The three one-hour observations started between 0700-0900, 1000-1200, and 1300-1500 hours. Observers sat in a hide about 50-100 m from the field and used 10×50 binoculars.

5. Distances covered by corvids carrying walnuts

To establish distances covered by corvids carrying walnuts we observed corvids taking seeds from trees or from under trees growing in gardens. We chose 21 trees (seven trees in each of three plots where the behaviour of corvids was studied in detail) growing in gardens at the edge of villages and observed by binoculars (10×50) where seeds were carried.

Subsequently, observers walked to the cache site and determined the distance covered by birds using a GPS (Garmin GPSmap 60CSx). The observation sites guaranteed good visibility and generally it was quite easy to observe where birds took seeds. We conducted these observations in 2007, 2008 and 2010.

6. Regional factors determining the occurrence of walnuts in Polish farmland

To estimate factors affecting the presence and abundance of walnuts at the regional scale we selected 130 plots (1×1 km each) spread throughout agricultural landscapes in Poland. Originally we randomly selected 160 plots but we did not receive responses from several observers. We, and trained volunteers, visited these plots once between June and September in 2007-2010. As we were interested in walnuts occurring in farmland, agricultural land had to cover ca. 70 % of the plot [10]. During this visit the observer walked for one hour through the plot and noted all wild walnuts and their habitats and counted all foraging corvids. For each plot we also noted the distance to the nearest town, because the corvids in this study were vectors of walnut and are known to roost in towns and forage in adjacent farmland.

Thus, we expected a positive effect of the town's proximity on the presence and abundance of wild walnuts.

7. Statistical analysis

To analyze which factors affected the presence and number of walnuts in abandoned fields we used generalized linear mixed models (GLMM) with logit and identity link-functions, respectively. In both models the following explanatory variables were included: size of the abandoned field, distance to the nearest human settlement, distance to the nearest abandoned field. Landscape plot ID was assigned as a random effect. Distance to the nearest human settlement was an index of the distance to the source of seeds. 71 % of houses in villages had fruiting walnut trees in backyards, gardens and small adjacent orchards (n = 1020 farmyards in 45 villages, authors' unpublished data). Time since cessation of field management was very difficult to collect and we gathered such data for only 215 out of 479 abandoned fields. Therefore, we analyzed the effect of time since cessation of field management of this factor separately in the GLMM.

To estimate which habitat corvids select for foraging and seed caching we compared the number of birds as well as the number of flocks noted within a given habitat type with the availability (percentage share within the plot) of these habitat types (see above). The number of flocks was used because corvids often forage in flocks, thus an analysis of the number of individuals may be biased due to a supposed lack of data independence. This, however, is not a problem in food caching since this behaviour was always displayed by individual birds. Chi-square tests were used in these analyses. Lack of preferences denoted the situation when the number of individuals and the number of flocks foraging or caching seeds in a given habitat type was proportional to the share of this habitat in the plot area. The data were summed across the three plots in which bird observations were carried out.

To analyze factors affecting the presence and abundance of walnuts within 1×1 km plots spread throughout Poland we used autologistic regression and simultaneous autoregression (SAR) as implemented in SAM software which takes autocorrelation into account [11,12]. To check if there is any geographical pattern (West-East and South-North) in plot occupancy and abundance of walnuts we included latitudinal and longitudinal coordinates as independent variables. The effects of these explanatory variables were examined by fitting ordinary logistic regression and linear regression.

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SUPPLEMENT 2

Figure 1. Correlation between number of rooks and number of wild walnuts in 1×1 km plots in Poland (n = 130 plots).

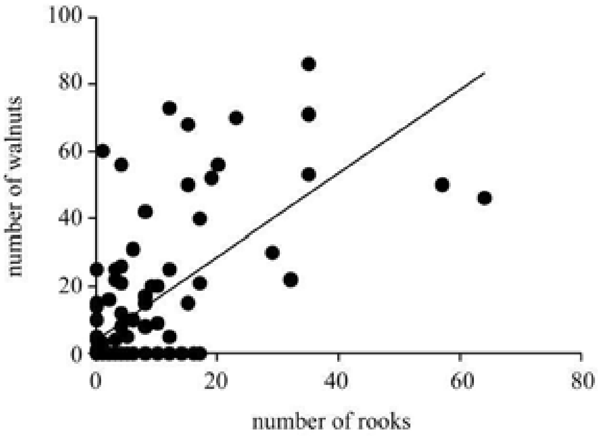


Figure 2. Dynamics of (a) availability of walnut seeds, (b) number of rooks, (c) number of rooks caching seeds and (d) number of rooks crushing seeds.

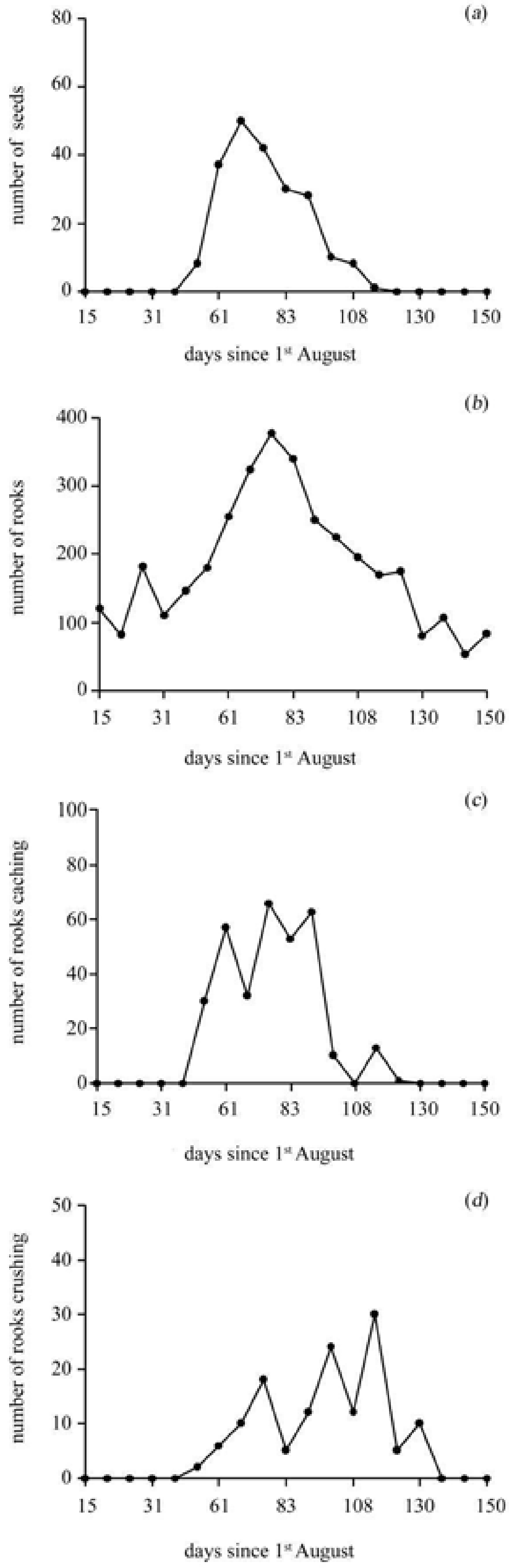


Figure 3. Dynamics of (a) number of walnut seeds cached by rooks and (b) number of walnut seeds crushed by rooks in selected fields. We did not find any within-day differences in rate of seed caching (GLMM $F_{1,\ 371.4} = 0.14$, beta = 0.028 ± 0.073, P = 0.705, n = 378). We found that the rate of seed caching was highest in October and lower in September and November (nonlinear effect in GLMM $F_{1,\ 371.0} = 106.71$, beta = -2.278 ± 0.221, P < 0.001, n = 378. The GLMM explained 21 % of the variance in the dataset. The rate of seed excavating and crushing was highest at the end of October and beginning of November (nonlinear effect in GLMM $F_{1,\ 371} = 55.99$, beta = -0.023 ± 0.003, P < 0.001, n = 378) but time of day did not influence the rate of this behaviour (GLMM $F_{1,\ 373} = 0.20$, beta = 0.015 ± 0.035, P = 0.659, n = 378). This model explained only 10 % of the variance. Assuming that the rate of seed caching is constant within a day, that the period of walnut seeding lasts from the middle of September to the middle of October (30 days), that the duration of a day is 8 hours, and that 36 % of seeds are retrieved then we can roughly estimate that during one season 581 walnut seeds are cached and remain in the soil per ha of arable field in the studied agricultural landscapes.

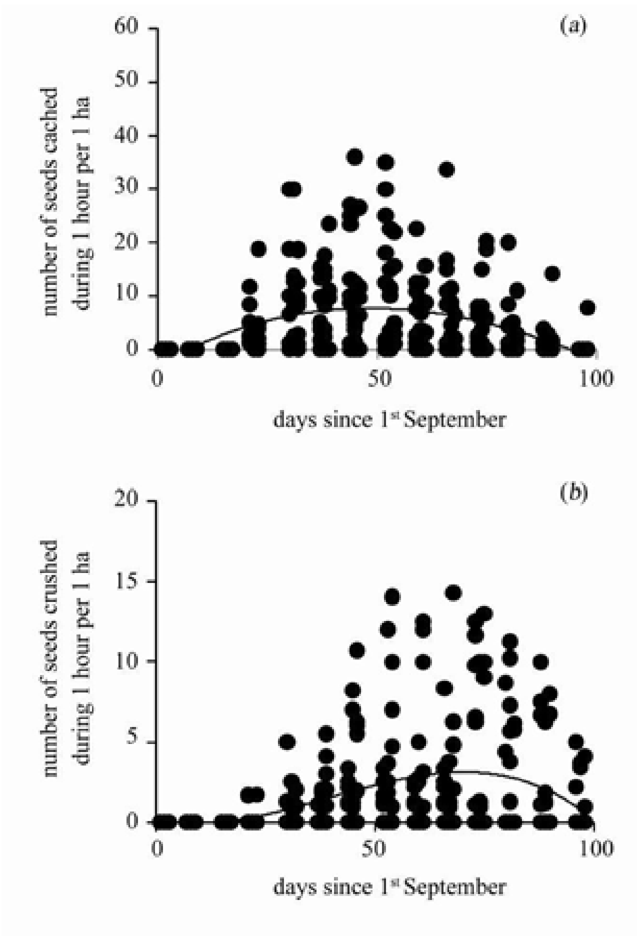


Figure 4. The distribution of flight distances of rooks carrying walnut seeds (distance from the source tree to the caching site; n = 164 birds).

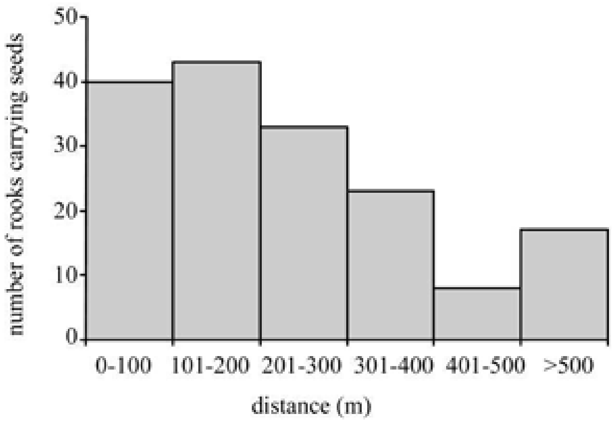


Table 1. Direct evidence that walnuts in abandoned fields originate from the soil seed bank created by corvids before management cessation. In 2008 six previously managed fields were set-aside in the study area. In 2007 these fields were under cereals (three fields), potatoes (two) and beet (one). In 2009 one field was cultivated again. 79 foraging rooks including those caching walnuts (n = 13) were observed in these fields in 2007 but not in 2008, 2009 or 2010. In the table below number of walnut seedlings found is given.

field	area (m^2)	2007	walnut seedlings 2008	walnut seedlings 2009	walnut seedlings 2010
1	4000	cultivated (cereals)	42	50	51
2	3400	cultivated (cereals)	15	13	10
3	3750	cultivated (cereals)	20	29	31
4	1200	cultivated (potatoes)	5	19	24
5	2250	cultivated (beet)	11	14	13
6	7200	cultivated (potatoes)	20	cultivated (potatoes)	cultivated (vegetables)

Table 2. Generalized linear mixed model of factors affecting the presence of wild walnut trees in abandoned fields at the landscape scale. $R^2_{McFadden} = 0.33$ (n = 479 abandoned fields).

Variable	Beta	SE	F	df	P
Field area	-0.235	0.202	1.353	1, 474.2	0.245
Distance to human settlements	-0.302	0.041	54.255	1, 465.9	<0.001
Distance to nearest abandoned field	0.023	0.02	1.322	1, 408.2	0.251

Figure 5. Comparison of (a) area, (b) distance to human settlements, (c) distance to nearest abandoned field and (d) years since management cessation of abandoned fields in which walnuts were present (n = 236) and absent (n = 243). In the case of years since management cessation, sample sizes were 148 abandoned fields with walnut trees and 67 without. Means with 95% confidences are presented. Key: *** - P < 0.001.

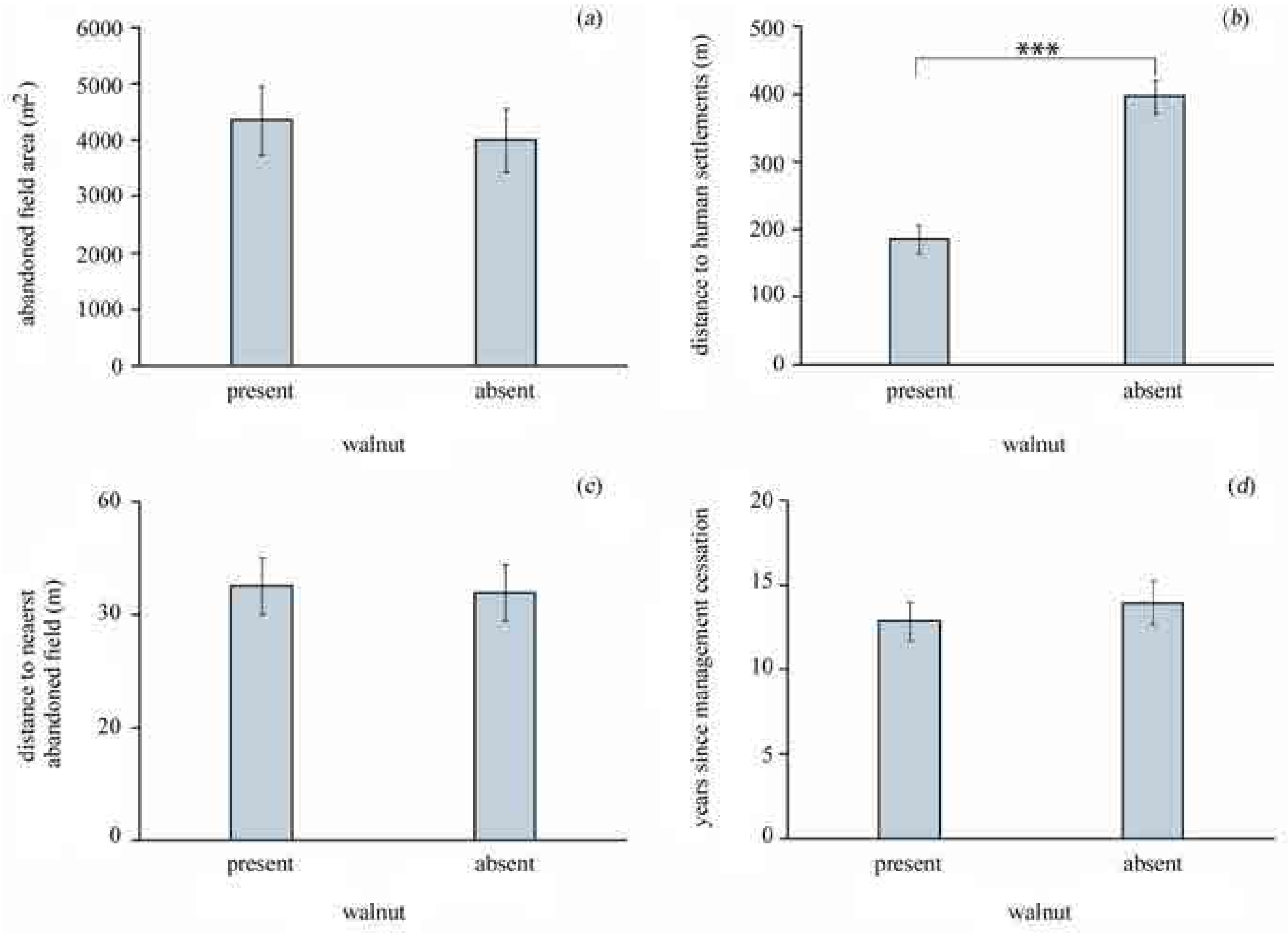


Table 3. General linear mixed model of factors affecting the density of walnut trees in abandoned fields at the landscape scale. $R^2 = 0.28$ (n = 236 abandoned fields with walnuts).

Variable	Beta	SE	F	df	P
Field area	-0.038	0.023	2.730	1, 123.4	0.101
Distance to human settlements	-0.301	0.031	94.278	1, 188.0	<0.001
Distance to nearest abandoned field	-0.033	0.025	1.742	1, 219.8	0.188

Figure 6. Effects of (a) area, (b) distance to human settlements, (c) distance to nearest abandoned field and (d) years since management cessation on density of walnuts growing in abandoned fields (n = 236 abandoned fields). In the case of years since management cessation sample sizes were 148 abandoned fields with walnuts.

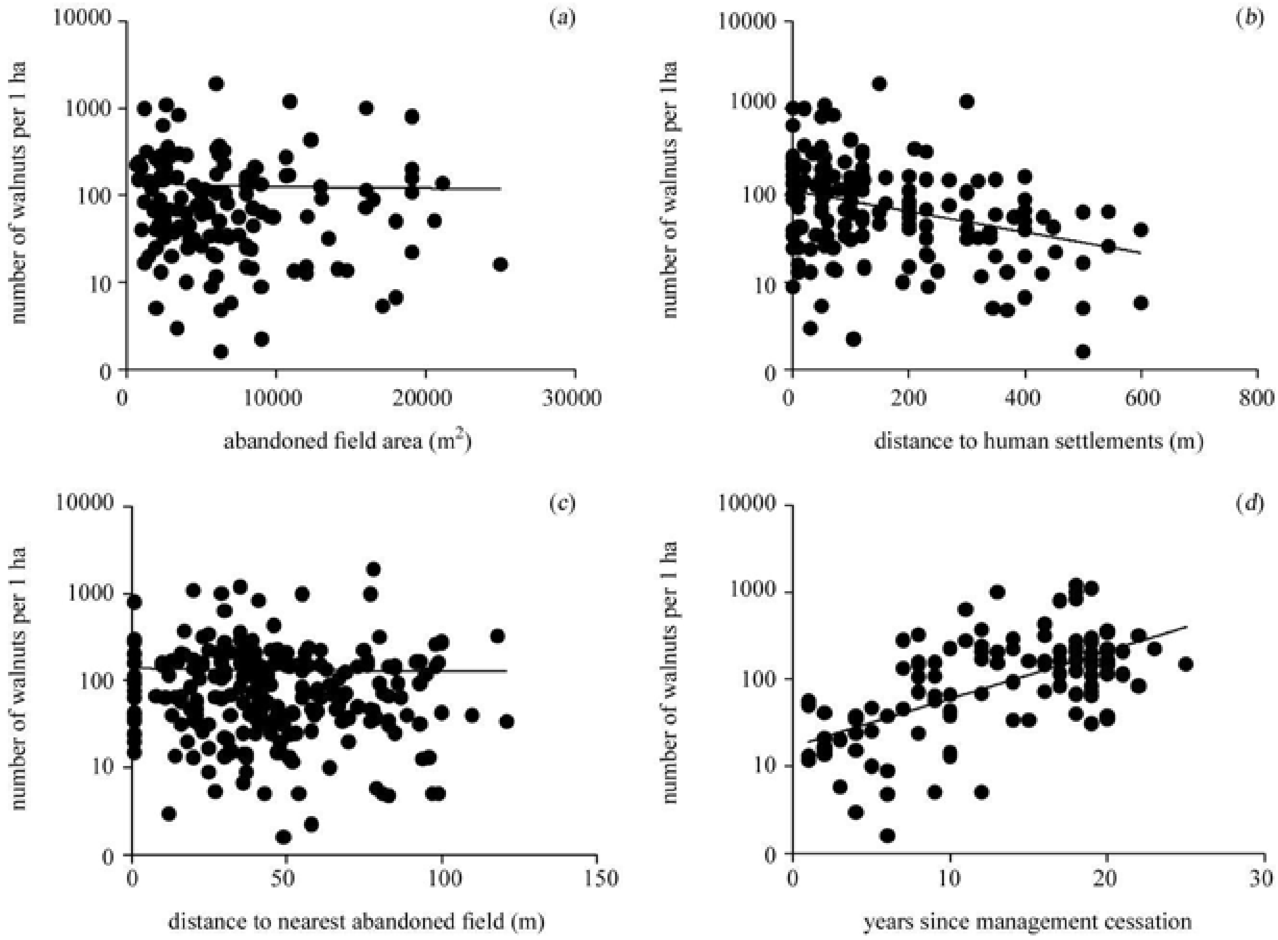


Table 4. Autologistic model of factors affecting the presence of walnuts in agricultural areas at the regional scale (1×1 km plots) . $R^2_{McFadden} = 0.62$ (n = 130 plots).

Variable	Beta	SE	t	P
Cover of abandoned land	1.248	0.428	2.915	0.004
Cover of forest	-0.062	0.377	-0.165	0.869
Cover of human settlements	0.415	0.328	1.267	0.205
Distance to nearest town	-1.162	0.390	-2.976	0.003

Figure 7. Comparison of (a) cover of abandoned fields, (b) cover of forests, (c) cover of human settlements and (d) distance to nearest town in 1×1 km plots on which walnuts were present (n = 50) and absent (n = 80). Means with 95% confidence intervals are presented. Key: ***- P = 0.001.

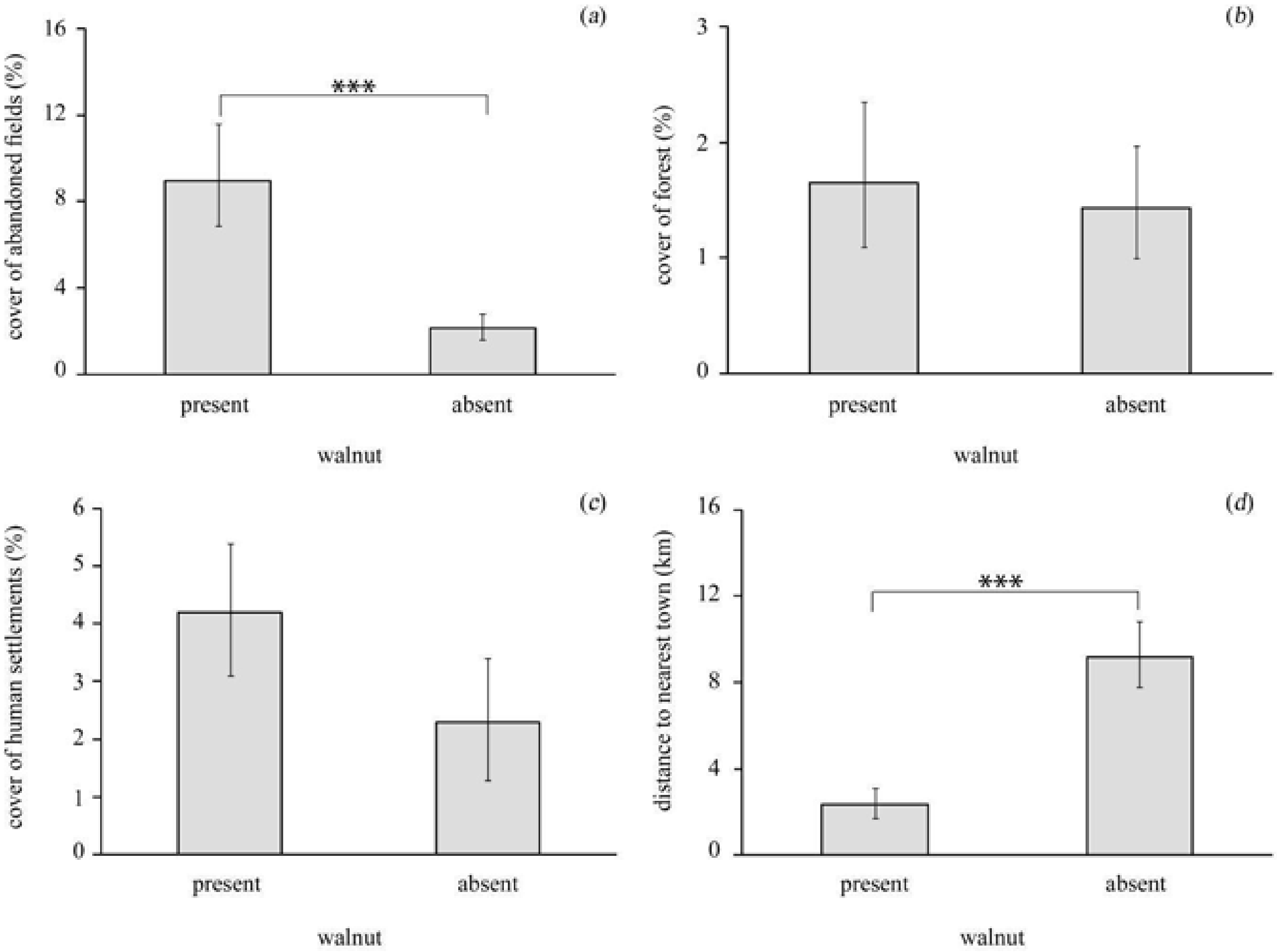


Figure 8. Spatial autocorrelogram for (a) plot occupancy and (b) number of wild walnuts in 1×1 km plots in Poland. White circles indicate spatial autocorrelations significant at the $\alpha < 0.05$ level.

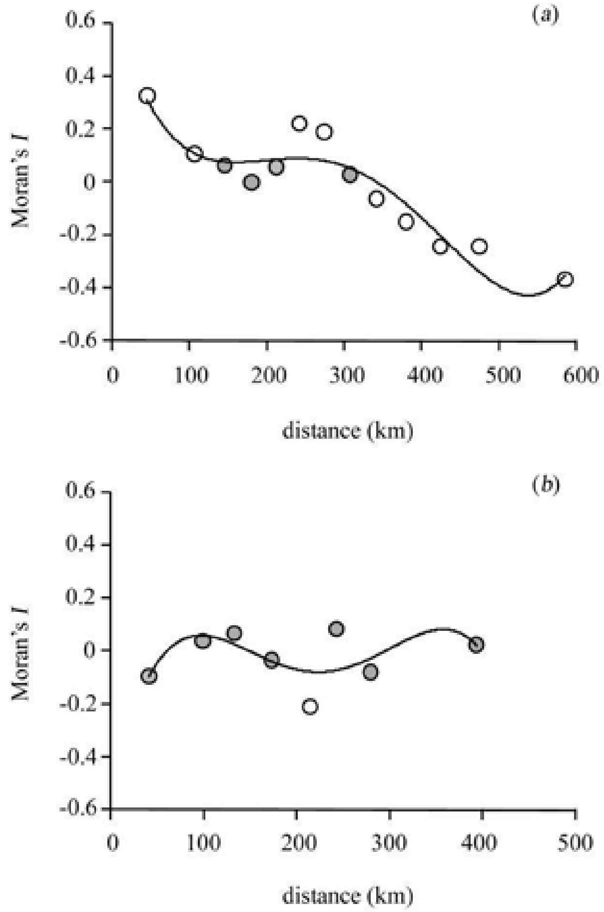
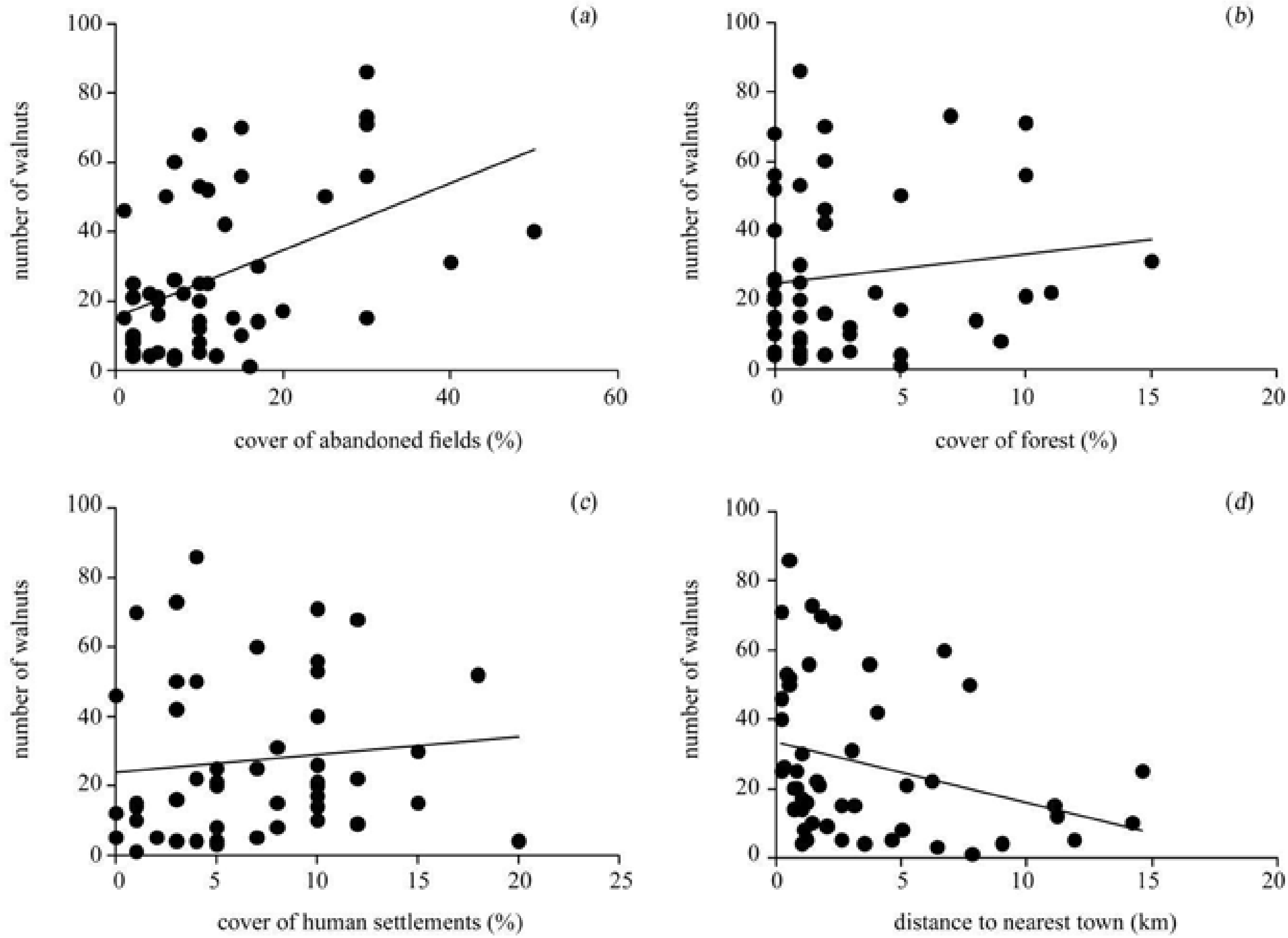


Table 5. Autoregressive model of factors affecting the number of walnuts in agricultural areas at the regional scale (1×1 km plots). $R^2 = 0.61$ (n = 50 plots with walnuts).

Variable	Beta	SE	t	P
Cover of abandoned land	0.755	0.266	2.836	0.007
Cover of forest	-0.396	0.686	-0.578	0.566
Cover of human settlements	-0.656	0.595	-1.101	0.277
Distance to nearest town	-1.652	0.777	-2.125	0.039

Figure 9. Effects of (a) cover of abandoned fields, (b) cover of forests, (c) cover of human settlements and (d) distance to nearest town on number of wild walnuts in 1×1 km plots (n = 50).



SUPPLEMENT 3

Walnuts occur in abandoned fields in the agricultural landscapes of Poland.

Over 10 % of wild walnuts already produce seeds.

Most wild walnuts are young trees.

Rook *Corvus frugilegus* – the major disperser of walnut seeds in agricultural landscapes.

Rooks preferentially forage on managed arable fields. They also cache walnut seeds in plowed fields.

Walnut saplings grow in managed fields (e.g. cereal crops). Most are cut during harvesting and the rest are destroyed during plowing. Walnuts can grow only if fields are abandoned or set-aside. This means that the invasion of this species in agricultural landscapes of Poland was possible only after the political transformation in 1989 and associated vast agricultural land abandonment.

At the regional scale, wild walnuts occur frequently near towns. During autumn, most rooks roost in towns and forage in surrounding agricultural areas and villages where they can find walnut seeds.

A higher proportion of abandoned fields in the landscape increases the presence and number of wild walnuts at the regional scale.

Chapter II

Lenda M., Skórka P.,Woyciechowski M. Cascading effects of changes in land use on the invasion of the walnut Juglans regia in forest ecosystems. In preparation to Ecology

Cascading effects of changes in land use on the invasion of the walnut *Juglans regia* in forest ecosystems

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Abstract

In recent decades, the alien walnut (*Juglans regia*) has become invasive in agricultural landscapes of Central Europe due to abandonment of land and an increase in the populations of native dispersers, namely rooks (*Corvus frugilegus*). In this study, we tested whether the presence of abandoned fields with seed-bearing alien walnuts, landscape structure and management may facilitate further invasion of this tree into forest habitats through the involvement of other native seed dispersers, like jays (*Garrulus glandarius*) and passive dispersal by gravity during variable weather conditions. We selected 102 forests in southern Poland where we estimated the presence and density of the walnut along with the density of jays as the dominant walnut seed dispersers in this ecosystem. We also estimated the rate of seed harvesting by jays on walnuts growing in abandoned fields and in human settlements. Forest occupancy by walnuts and their densities were positively correlated with cover of abandoned fields and human settlements by seed-bearing walnuts. We have found that the main walnut seed dispersers into forests are jays but also marginally squirrels. Forests located in depressions lower than the surrounding landscape had higher probabilities of walnut occupancy. The density of walnuts in forests was positively correlated with that of jays, which often harvested walnut seeds in abandoned fields independently of their distance from a forest. This bird also frequently visited walnuts planted in human settlements, but only in the proximity of forests. We also demonstrated that walnut seeds hidden in arable fields by rooks may passively reach forest edges, especially in sloping fields, which adds to propagule pressure in forest ecosystems and underlines the importance of local terrain configuration on the processes of invasion. Our study indicates that the invasion of alien walnuts into agricultural landscapes has vast spatio-temporal cascading effects that have led to their further colonisation of forest ecosystems. The complexity of direct and indirect interactions between walnut seeds and novel native dispersers, combined with politically related changes in land use, indicates that the invasion debt, while impossible to predict, is certainly substantial.

Keywords: alien trees, corvids, farmland, invasion debt, lag phase, seed dispersal, woodland

1. Introduction

The dynamic of the invasion process is usually shaped by the extended lag phase, i.e. the period of time between the first introduction of an alien species into a new region and the beginning of invasive spread (Richardson *et al.* 2000, Pysek *et al.* 2010, Lenda *et al.* 2012). The length of the lag phase usually depends on the climate of origin, number of introduced individuals (propagule pressure) and landscape structure (Kowarik 1995, Walther *et al.* 2009, Caplat *et al.* 2012, Lenda *et al.* 2012). Landscape structure affects dispersal, and thus may trigger the advance of a population of an alien species from lag into invasive spread, or, if dispersal is low, keep an established alien species in lag (Caplat *et al.* 2012, Lenda *et al.* 2012). However, landscape structure is not exclusively static, as in the case of topography, but can also be dynamic, which is linked with land use changes. These factors may interact, leading to facilitation of the invasion process; although, documented examples of this are rare (Caplat *et al.* 2012).

For long-lived plant species like trees or shrubs, the lag phase may be substantial, lasting decades or even centuries, as in the case of the walnut (*Juglans regia*) in abandoned agricultural landscapes of Central Europe. The invasion of this tree was preceded by the longest lag phase (over 700 years) ever known among invasive plant species (Lenda *et al.* 2012). Walnut invasion was a multistep process, encompassing the increase of the seed source; the growth of the rook population (*Corvus frugilegus*), the main dispersers of walnut seeds into arable fields; and the cessation of large-scale cultivation which created a suitable habitat for this species to grow in following the political transformation of 1989 (Lenda *et al.* 2012). The invasion of walnut indicates that the long presence of an alien species in an environment combined with land use change may generate a large invasion debt, which is usually underestimated because we are unable to predict further consequences of the invasion

(Essl *et al.* 2012, Bennett *et al.* 2013, Rejmanek 2014). For example, invasions may have spatio-temporal cascading effects, in cases where alien species invading one habitat may then move forward into other habitats through the involvement of different dispersal mechanisms. Walnuts that have invaded farmland may induce numerous spatial cascading effects that may influence different natural habitats, such as forests and the native species therein.

Forests in temperate regions have been always regarded as relatively resistant to alien species invasions; however, recent studies show a growing number of alien invasive species found in this ecosystem (Essl *et al.* 2012, Rejmanek 2014), including alien walnuts, which are beginning to colonise forests in Central Europe (Loacker *et al.* 2007, Tokarska-Guzik *et al.* 2012). Invasive woody species such as the walnut may cause drastic changes in forest ecosystems through alterations of its species composition and structure, including decreased leaf-litter processing rates, disturbance of carbon cycles, quality of litter inputs, growth rates of native plants and forest invertebrates, and changes in the dispersal of native fruit-bearing trees (Jäger *et al.* 2009, Fang and Wang 2011, Tye and Drake 2012, Dzikiti *et al.* 2013, Saure *et al.* 2013). Therefore, recognising early stages of invasions in forests is crucial for effective nature conservation and forestry.

Basically, three mechanisms may explain walnut dispersal into forests. These mechanisms include dynamic factors such as land-use changes and subsequent alterations in landscape structure, interactions with native dispersers, and static factors such as topography. The first of these mechanisms suggests that new native seed-caching dispersers typical for forests, such as jays and squirrels, are involved in the dispersal of walnut seeds, and that they are utilising a new source of walnut seeds, namely, walnuts growing in abandoned fields and producing fruit. Therefore, the occurrence of walnuts and their densities in forests should be positively correlated with the cover of abandoned fields by walnuts producing seeds in the surrounding landscape. One might also expect that abandoned fields with wild walnuts close to forests are visited by dispersers more often than abandoned fields located further from forest patches.

The second mechanism relies on interactions between seeds of alien walnuts planted in human settlements and the process of synanthropisation of native seed dispersers formerly typical for forest habitats. As jays and squirrels become more common in residential areas (Tomiałojć and Stawarczyk 2003, Babińska-Werka and Żółw 2008, Hordowski 2009, Żmihorski *et al.* 2010) they may have the opportunity to interact with planted walnuts, to carry their seeds to forests and cache them there as a food supply. Thus, walnut occupancy and density in forests should be positively correlated with the cover of human settlements in the surrounding landscape, while dispersers should visit human settlements close to forests more frequently than more distant ones.

Finally, topography and passive transportation, by gravity and intense weather phenomena (e.g. rain), of seeds previously hidden by rooks in the soil of arable fields may add to the invasion process. Walnut seeds hidden in fields on slopes should be passively transported during periods of rainy weather for greater distances, so as to occasionally reach forest edges, than seeds hidden in flat and level fields. If this mechanism indeed plays a role in the spread of walnuts, then edge amount that is at a level below the surrounding arable fields should positively affect the occupancy and density of walnuts in forests.

All of the above-mentioned mechanisms suggest that the walnut invasion is a very complex process leading to cascading effects in ecosystems, and that the interaction of both static and dynamic heterogeneities may determine the progress of the invasion. In this study we examined these multi-step mechanisms and the ecological consequences of the early stage of the walnut invasion in forest ecosystems. We tested the following hypotheses:

1. The occupancy and density of alien walnuts in forests positively depend on the covers of abandoned fields and human settlements by seed-bearing walnuts in the surrounding landscape.

2. Mature walnuts growing in abandoned fields and within human settlements are seed sources for native dispersers which carry the seeds to forests.

3. The main vector of the transport of walnut seeds to forests is jays.

4. The harvesting rate of walnut seeds taken by dispersers from gardens and abandoned fields with mature walnuts depends on the proximity of forests.

5. The occupancy and density of alien walnuts in forests depend on the shape of the terrain, namely the area of forest edge lying at a level below the fields bordering on these forests.

6. Passive transportation by gravity may carry walnut seeds hidden in arable fields by rooks to forests.

2. Methods

2.1. Study plant species and dispersers

The study species is the walnut, *Juglans regia* (Juglandaceae). The natural geographical range of this species, alien to Central Europe, lies between the Black Sea basin, Turkey, Central Asia, and the Himalayas, where it grows in mixed and deciduous forests (Huntley and Birks 1983, Zohary and Hopf 1988). This well-known tree has attractive, tasty, fatty seeds and thus has been cultivated for centuries outside its natural range, for example in Central Europe and North America. In Poland, the walnut was introduced to monasteries in Middle ages (Gomez 1992) but has become invasive since the political transformation of 1989 and the subsequent abandonment of agricultural land (Lenda *et al.* 2012). An increasing number of rooks, noted for their caching behaviour, have created a large bank of walnut seeds in the soil of arable fields every year. Cultivation damages these seeds and seedlings, making the growth of seeds cached in arable fields impossible. However, in 1989, the collapse of socialism and the ensuing large-scale cessation of the management of arable fields created an opportunity for the seed bank of the walnut to grow and invade agricultural landscapes. The walnut injects allelopathic substances, namely juglone, into the soil, which may cause losses in biodiversity by inhibiting the growth of other plants (Vander Wall 2001, Ercisli *et al.* 2005, Lenda *et al.* unpublished). All parts of this plant, including leaves and flowers, contain this secondary metabolite (Ercisli *et al.* 2005). The walnut is a large tree (up to 35 m tall) and can grow in almost any well-drained soil (Huntley and Birks 1983, Zohary and Hopf 1988, Carrion and Sanchez-Gomez 1992). The walnut is characterised by pinnate foliage and its flowers are wind-pollinated catkins.

The Eurasian jay, *Garrulus glandarius*, is a medium-sized corvid native to all of Europe and Central Asia, typically inhabiting forests. Its population has been growing in Poland for about 50 years after being taken under legal protection in 1952 (Tomiałojć 1989). The growing population of this species is also linked with its colonisation of urbanised landscapes, associated both with an increasing number of individuals there and with the utilisation of food available close to human settlements (Kuczyński and Chylarecki 2012). The population of jays in urbanised landscapes is still less than that of rooks; however, jays usually accumulate food supplies and carry seeds of native, woody trees and shrubs, for example *Corylus avellana*, *Quercus petraea*, *Quercus robur* and *Fagus sylvatica*, into forests and therefore are among the most important seed dispersers there. Jays migrate short distances during autumn; thus there are certain periods of time during which they often enter, and are more abundant in, agricultural landscapes.

2.2. Habitat, presence and density of walnuts and their dispersers in forests

We selected 102 forest patches located in agricultural landscapes of southern Poland (Fig. 1, Supporting Information 1). To estimate occupancy, we counted all of the walnuts within these forest patches. Two surveys were conducted between June and September 2011 in all forest patches. During these surveys, observers took arbitrary paths and noted all walnut saplings and trees. Each individual tree was marked with a plastic label bearing a unique number and its position was marked on maps and in a GPS system (Garmin 60CSx). Each survey was conducted by a different individual. The time spent searching for walnuts varied between 30 minutes in the smallest forest patches to 20 hours in the largest. In the largest forests, a single survey had to be conducted over two consecutive days. Surveys were conducted between 8:00 a.m. and 6:00 p.m.

To estimate density, we established one transect in each forest patch. This transect varied in length between 160 and 4885 m (mean ± SE = 910 ± 94 m). Each transect was conducted along the longest side of the patch (in some forest patches, this was not a perfect straight line due to complicated patch geometry) and began and ended at one of the patch's edges. All saplings and trees were counted in a 2-metre belt along the transect. The density of walnuts in a given forest was calculated two ways. First, we divided the number of walnuts found in two surveys by the area of the patch. Second, we divided the number of walnuts recorded along transects and divided by the transect area. Both estimates were strongly positively correlated ($r = 0.907$, $P < 0.001$); thus, in further analyses, we used only estimates from transects, as they were probably more accurate.

Dispersers of walnut seed were counted in forest patches along the same transects where walnuts were sampled. Three counts were done between the beginning of September and middle of October 2011. All jays and squirrels heard or observed in the 100-m-wide belt were counted.

2.3. Landscape composition around forest patches and characteristics within patches

For each forest patch we estimated the cover by mature wild walnuts of abandoned fields, human settlements and other forests within a 500 m radius of the forest boundary. This calculation was based on aerial photographs and direct mapping of abandoned land in fields with the use of GPS (Garmin 60SX). Calculations were performed in the Quantum GIS 1.8 system. The proportion of forest edge located at a level below the surrounding agricultural landscape was measured directly in the field by GPS, using its path tracking mode.

We also measured three confounding variables that could also potentially affect the presence and density of walnuts. These were: the shape index of the patch, the proportion of deciduous trees and canopy openness. Shape index is an adjusted index proposed by Bogaert and his co-workers (Bogaert *et al.* 2000). The proportion of deciduous trees was estimated along the transects where walnuts were counted. Canopy openness was measured at random points in forests. Up to 35 photos of the canopy in each forest patch were taken with a digital camera (Nikon Coolpix). All photos were taken in the same manner, with the camera aimed straight up at the canopy layer using the camera's default settings. Digital photos were then converted into black and white mode using ImageJ software and the proportion of white area used as an estimate of canopy openness. The mean derived from all photos within the patch was used in analyses.

We also checked the diameter, height and number of seed-bearing walnut trees, provided they were mature. In 2010 and 2011 we also counted all planted walnuts (sources of seeds) in gardens in human settlements within a radius of 500 m from forests.

2.4. Dispersers: walnut interactions

In order to determine which animals carry seeds to forests, we choose 10 different forests with walnut saplings and, for each forest, the four nearest walnut trees growing in human settlements and the four nearest in abandoned fields, and checked which disperser species collected seeds there and carried them into the forest. Observations started in the mornings between 9 and 11 a.m. or in the afternoons between 2 and 4 p.m. and lasted 2 hours. We made seven such surveys between the beginning of September and middle of October in 2009. As we found that jays were the major disperser of walnut seeds to forests, the description of methods below is devoted to the behaviour of this bird.

To estimate the dispersal potential of walnut seeds from human settlements and abandoned fields into forests, we choose adult walnut trees located at various distances from forests and observed the rate of visitation and seed removal by jays and squirrels. We chose 30 walnuts growing in human settlements and 30 in abandoned fields. Distances from the forest edge to each walnut tree varied between 10 m and 500 m. Each walnut tree was in a separate household or in a separate abandoned field. Each tree was observed three times between the beginning of September and the end of October 2011. Each observation lasted three hours and started between 9 a.m. and 3 p.m. The sum of the observations at each given tree encompassed the time between 9 a.m. and 6 p.m. We calculated the mean number of visits by dispersers and the number of seeds removed per tree in one hour.

To find out how often and where walnut seeds are cached, we observed the caching behaviour of a number of jays in 10 forest patches. The observation of caching behaviour in jays was not as straightforward as in the case of rooks (Lenda *et al.* 2012). Jays are more secretive than rooks, and not as conspicuous. Thus, we selected forests that were less than 5 ha in area. We decided on this because it enabled satisfactory visibility of the area both within the patch and at its edges. Jays also cache walnut seeds in larger forests, as indicated by our occasional observations (unpublished data). Each forest was observed 14 times from the beginning of September to the beginning of November 2011 at roughly weekly intervals. During the survey the selected forests were visited three times per day to find possible differences within a single day in the rate of caching and crushing of food. For each visit, the forest was observed for one hour (thus one forest patch was observed for three hours per survey day and for 42 hours total). The three one-hour observations began between 7 and 9 a.m., 10 a.m. and 12 noon, and 1 and 3 p.m. Observers hid themselves in a location from which the entire area within and at the edge of the forest was visible. We used 8×50 binoculars.

2.5. The role of gravity in the passive transportation of seeds from arable land into forests

To establish whether seeds hidden by rooks in arable lands undergo secondary passive dispersal to forests due to gravity and weather conditions, we chose six arable fields that bordered on forests. Half of them were flat and level, while the remainder were graded towards forests (slope 10–15%). Our study area is a naturally hilly area (Supporting Information). We used wooden balls, 4 cm in diameter, that were additionally painted with a bitter nail enamel to provide a taste unpleasant to animals, so as to prevent them from collecting them (animal-based transportation). The balls were orange and individually numbered and thus were very easy to find in arable fields. We placed 100 balls in each arable field in the middle of October 2010 and mapped their location every second day for three weeks. Balls were placed at a distance of 100 m from the forest border. We noted weather conditions each day prior to each count. Thus, 600 balls were placed in total. Agricultural work had ended at the time of the experiment. Rooks usually hide seeds under the ground; however, during agricultural work these seeds often are uncovered and exposed to environmental conditions. Therefore, in this experiment we aimed to learn whether passive dispersal and the shape of the terrain may add to the colonisation of forests by walnuts, as suggested by occupancy analysis (see Results).

3. Statistical analysis

3 1. Occupancy and density

Analysis was done in two steps: (i) a check for spatial autocorrelation and multicollinearity and (ii) an estimate of the impact of environmental variables on walnut occupancy and density in forest patches. We used Moran's I correlograms to see if there was spatial aggregation in terms of occupancy and density (Legendre 1993). However, since we found no significant spatial autocorrelation, we used standard statistical tests. We found that the variables were either not correlated or only moderately correlated (Supporting Information 1) and that this level of correlation does not cause a multicollinearity problem, as it is often believed that regression models are robust in terms of multicollinearity if the correlation between variables is lower than $r = |0.6|$ (Mertler and Vannatta 2002). All these analyses were run using SAM 4.0 statistical software (Rangel *et al.* 2010).

The relationship between environmental variables and walnut presence and density was analysed using generalised linear models (GLM) with binomial and Gaussian error variance and logit and identity link-functions, respectively. In all generalised linear models, we built all possible model combinations, including a null model with intercept only. We ranked models according to their ΔAICc values. We considered models with ΔAICc values lower than 2 as equally good (Burnham and Anderson 2002). We used model averaging to estimate function slopes of parameters of interest (Burnham and Anderson 2002) and applied a 99% confidence set. Thus, when averaging, we also used models that had ΔAICc values higher than 2. Finally, model weights (the probability that a given model is the best) were used to define the relative importance of each explanatory variable across the full set of models evaluated by summing the weight values of all possible models that included the explanatory variable of interest (Burnham and Anderson 2002).

When necessary, we used square-root transformation to reduce the effects of outliers and normalise distribution (Quinn and Keough 2002). Moreover, in all regression models, variables were standardised to allow a direct comparison of slope (beta) estimates (larger beta values indicate stronger relationships between explanatory and dependent variables).

3.2. Estimating seed harvesting rates in different habitats and at different distances from forests

Using a general linear model, we analysed how visitation rate (mean number of birds per hour) and harvesting rate (mean number of walnut seeds removed from a tree by jays and carried to a forest) depend on habitat type (abandoned field vs human settlements) and distance from forest edge (continuous variable). We also introduced the interaction term between habitat type and the distance from a forest to see if the harvesting rate changed with distance from a forest in the same manner between two different habitats. SPSS v21 software was used.

3.3. Estimating the effect of gravity on seed passive dispersal

We used generalised liner mixed models (GLMM) to describe the effect of gravity on seed dispersal. We analysed three dependent variables separately: (i) mean distance travelled by seeds between consecutive days, (ii) net displacement (distance between starting point and location at the end of experiment) of seeds and (iii) proportion of seeds that reached the forest border. In each model we used field type (level vs inclined) as a fixed factor. When analysing the mean distance travelled between consecutive counts, we included the effect of weather conditions (presence or absence of rain) during the preceding day.

In our analysis of mean travelling distance and net displacement we used GLMM with Gaussian error and identity link function. When determining whether a seed reached a forest border (or not), we used a model with binomial error variance and logit link function. Field ID was assigned as a random factor in all models. In GLMM, for mean distance, we also used dummy seed identity as an additional random effect. When analysing the net displacement and proportion of seeds that reached the forest edge, we used only dummy seeds with a complete history (62 balls disappeared during the experiment).

All estimates of statistical parameters (means, betas) throughout the text are quoted with standard errors (SE) and 95% confidence intervals (CI).

4. Results

4.1. Habitat, forest occupancy and density of walnuts

Walnuts were found in 64 out of 102 (63%) studied forest patches. We noted a total of 2,272 walnuts, including 403 on transects. The mean density of wild growing walnuts was 2.8 ± .25 individuals per hectare (range: 0.4–10). Only 24 (1%) walnuts produced seeds and all but two grew at forest edges (see Supporting Information 1). The age of most walnuts was less than 3 years (see Supporting Information 1).

Model selection indicated the best five models explaining forest occupancy by alien walnuts (Table 2). The most important variables that positively affected the presence of walnuts were covers of human settlements (slope = 0.206 ± 0.04, 95% CI: 0.128 - 0.284, importance = 1.000) and abandoned fields with mature wild walnuts (slope = 0.1277 ± 0.039, 95% CI: 0.050 - 0.204, importance = 0.980, Table 2). Forests that were elevated over surrounding areas had lower walnut occupancies (slope = - 0.142 ± 0.038, 95% CI: -0.216 to - 0.067, importance = 0.997, Table 2). Other variables that positively affected forest occupancy by forests were shape index (slope = 0.034 ± 0.015, 95% CI: 0.011 - 0.069, importance = 0.340), density of jays (slope = 0.031 ± 0.012, 95 % CI: 0.007- 0.055, importance = 0.303) and forest area (slope = 0.026 ± 0.013, 95% CI: 0.001- 0.051, importance = 0.289, Table 2). Also, forest cover within a 500 m radius was in the best models; however, estimates of the function slope overlapped with zeroes, indicating that this relationship was not significant (slope = - 0.003 ± 0.002, 95 % CI: - 0.007 to 0.001, importance = 0.256, Tab. 2).

Model selection showed that the four best models explained, on average, 52% of the variation in density of walnuts in forest patches (Table 2). Density was positively correlated with forest shape index (slope = 0.124 ± 0.027, 95% CI: 0.012 - 0.177, importance = 0.999), density of jays (slope = 0.055 ± 0.020, 95 % CI: 0.016 - 0.093, importance = 0.824), share of deciduous trees (slope = 0.051 ± 0.018, 95 % CI: 0.015 - 0.086, importance = 0.752), cover of abandoned fields by mature wild walnuts (slope = 0.035 ± 0.011, 95% CI: 0.012 - 0.057, importance = 0.518) and cover of human settlements (slope = 0.029 ± 0.009, 95% CI: 0.011 - 0.047, importance = 0.427, Table 2). Densities were lower in forest elevated above the surrounding area (slope = - 0.061 ± 0.022, 95 % CI: - 0.0105 to - 0.018, importance = 0.879, Tab. 2).

4.2. Walnut dispersers and dispersal potential to forest habitat

We found that two forest species visited walnuts and harvested seeds (Fig. 2). These were jays and rarely red squirrels. The most abundant dispersers of walnut seeds were rooks; however, this species never carried seeds to forests, but always to agricultural land or to gardens. Two other corvids, the magpie (*Pica pica*) and hooded crow (*Corvus cornix*) cached walnut seeds only in the area of human settlements or in agricultural land. The jackdaw, *Corvus monedula*, seems to visits walnuts only occasionally. Woodpeckers were also seen in this area; however, they did not harvest walnut seeds.

Overall, jays visited walnuts planted in abandoned fields (mean = 4.0 ± 0.1 jays per hour) more often than those planted in human settlements (mean = 2.8 ± 0.3 jays per hour, GLM $F_{1.56}$ = 11.825, P < 0.001); the visitation rate decreased with distance from a forest ($F_{1.56}$ = 65.541, P < 0.001, Fig. 3a). However, there was a statistically significant relationship between the distance from a forest and the habitat where walnuts grew (GLM $F_{1.56}$ = 30.024, P < 0.001). The visitation rate for jays was much higher in human settlements than in abandoned fields where there was a forest within 200 m (Fig. 3a). In contrast, the rate of seed harvesting by jays on walnuts growing in abandoned fields decreased only slightly with distance from a forest (Fig. 3a).

Similarly, jays removed more seeds from walnuts occurring in abandoned fields (mean = 3.5 ± 0.1 seeds removed per hour) than in human settlements (mean = 1.8 ± 0.2 seeds removed per hour, GLM $F_{1.56} = 11.980$, $P = 0.001$). However, there was a statistically significant relationship between the distance from a forest and the habitat where walnuts grew (GLM $F_{1.56} = 45.409$, $P < 0.001$). Seed removal rate was higher in human settlements than in abandoned fields if there was a forest within 200 m, but rapidly decreased with greater distances (Fig. 3b). As in the case of visitation rate, seed harvesting by jays on walnuts growing in abandoned fields decreased only slightly with distance from a forest (Fig. 3b).

We observed only 23 visits of red squirrels to walnuts (Fig. 2).

We observed 42 cases of jays hiding various seeds in all 10 forests. Sixteen of these were jays hiding walnut seeds, 14 oak acorns and 3 unidentified seeds.

Only two observations of red squirrels hiding seeds were noted: one walnut seed and one common hazel.

4.3. Passive dispersal due to gravity and weather conditions

We found that the mean distance travelled by dummy seeds per two days was greater in sloping fields than in level ones (GLMM $F_{1.3544} = 27.236$, $P < 0.001$, n = 8,562 distances, Fig. 4a). The distances were greater when, on the day before counting, there had been rain (GLMM F1.442 = 5.116, $P = 0.024$, n = 8,562 distances, Fig. 4d).

Similarly, the net displacement of seeds was higher in sloping fields than in level ones (GLMM $F_{1.4} = 53.635$, $P = 0.002$, n = 538 seeds, Fig. 4b). Consequently, the probability of dummy seeds reaching the forest edge after three weeks was three times higher than in level fields (GLMM $F_{1.16} = 12.549$, $P = 0.003$, n = 538 seeds, Fig. 4c).

5. Discussion

In Europe, over 300 alien plant species, each of which may significantly affect the environment (Vilà *et al.* 2010, Pysek and Hulme 2011), are recognised as invasive. Probably most of these species remain in extended lag phases, which make new invasions unpredictable and very difficult to detect. Substantial socioeconomical and political changes may determine which of these alien species will become invasive. Therefore, one of the key issues to study is early stages of invasions (Puth and Post 2005). In this research we studied the early invasion of the walnut in Polish forests scattered over an agricultural landscape. We demonstrated that if an invasive species invades one habitat type, for example abandoned fields, it may later unexpectedly elicit novel interactions with native dispersers and the landscape structure that have vast cascading effects on other, very distinct, forest ecosystems.

We have found that the walnut is widespread in forest patches in southern Poland; however, its densities are still low in comparison with those found in forests in the Alps and on abandoned agricultural land (Loacker *et al.* 2007, Lenda *et al.* 2012). Although the number of alien woody species that can be found in deciduous forests in Europe is much higher than had ever been predicted, it usually takes many years before the density of such alien tree species becomes significant and the species is considered invasive (Essl *et al.* 2012, Kowarik 2013, Pysek 2013, Rejmanek 2014). Moreover, even if the number of these species is substantial in forests, detecting all individuals and assessing their impact on forest ecosystems may be much more difficult than for herbal or shrublike plants which are often easy to detect, as they grow in clusters (Pysek 2013). Even such rare alien species present in forests may create a considerable invasion debt which can be assessed only after a longer period of time because of seed dispersal, the changing behaviour of some animals typical for forests, and effects on soil properties and microfauna (Essl *et al.* 2012, Rejmanek 2014). It has been suggested that the longer the time it takes to establish a woody species, the more successful it is as an invader (Kowarik 1995). This is probably because new linkage with native elements of ecosystems, such as soil organisms and dispersers belonging to different species, requires time to evolve. Therefore, the multiple, beneficial and frequent interactions between native and alien species on one hand and freedom from enemies in new habitats or regions on the other may facilitate the establishment and enormous spread of alien populations (Colautti *et al.* 2004, Essl *et al.* 2012, Rejmanek 2014).

In our study, forests invaded by walnuts were surrounded to a greater extent by abandoned fields with wild walnuts than by fields where walnuts have not been found. Previously published data about the invasion of walnuts in post-agricultural landscapes showed that over 10% of wild walnuts found in abandoned fields were already producing seeds (Lenda *et al.* 2012). Thus, they may be an important food resource for the native forest animals, which in turn may change over from collecting seeds of native trees to collecting walnut seeds. Some species may collect and transport walnut seeds over great distances to be eaten in safe places or cached as long-term food supplies (Bednekoff and Balda 1996, Emery and Clayton 2001, Cristol 2005, Clayton *et al.* 2007). The species best known for this latter behaviour in forests are jays (*Garrulus glandarius*) and red squirrels (*Sciurus vulgaris*) (Rice-Oxley 1993, Kort and Clayton 2006, Clayton *et al.* 2007). We confirmed this. Although jays prefer forests, they are very mobile, entering agricultural landscapes in autumn (Gomez 2003), and thus may visit abandoned fields with wild walnuts bearing seeds at this time, carry the seeds, and cache them in forests. Despite our finding that the mean number of individual fruits growing on wild walnuts in abandoned fields was smaller than that found in gardens (Lenda *et al.* 2012), abandoned fields can be safer foraging habitats for forest species collecting seeds, as they are not disturbed by humans and the noise typical for urbanised areas. This suggests that abandoned fields may be a new and unrecognised walnut invasion pool. The cover of human settlements has also positively affected the presence of walnuts in forest patches. This factor has equally affected the occurrence and density of wild-growing walnuts in abandoned arable fields, meadows and pastures (Lenda *et al.* 2012), however, the presence of this species in forests has not been tested (Loacker *et al.* 2007). Walnuts are planted mainly within human settlements, mostly villages, but also in towns and their suburbs. Over 70% of gardens in villages include walnuts, and, as we have shown, the closer a garden walnut is to the forest, the higher the probability that it is visited by dispersers. Thus, the larger and closer to the forest a village is, the higher the availability of walnut seeds will be for the dispersers. Many other invasive alien species, for example, goldenrods (Guzikowa and Maycock 1986) and impatiens (*Impatiens sp.*), also originate from gardens; thus gardens may act as invasion hotspots where alien species are frequently and repeatedly introduced (Chittka and Schürkens 2001, Drake and Lodge 2004, Pandi *et al.* 2014).

We also found that other patch characteristics played a role in the occurrence and density of walnuts in forests. Larger forests with more complicated shapes had higher occurrences and densities of walnuts. Patch size is generally one of the most important predictors of the occurrence of species (Prugh *et al.* 2008), including invasive ones (Lenda *et al.* 2010). Its importance arises from the metapopulation concept (Levins 1969) stating that larger patches are characterised by a higher probability of colonisation and local populations therein incur a lower risk of extinction.

The shape of the patch indirectly indicates the length of its perimeter. The more diverse the shape was, the greater was the observed impact of the surrounding habitat (Nams 2011). Thus, the irregularity of a habitat patch may be related to a greater influx of seeds into forests from the surrounding fields (see below) and the higher mobility of potential seed dispersers at patch edges (Nams 2014). Also, edges may be preferred by walnut seed dispersers. Pons and Pausas (2008) found that the population density of jays was positively related to the length of the perimeter and the density of the edge as well as the patch shape index.

5.1. Disperser behaviour

The main disperser of walnut seeds into forests from abandoned farmland and gardens were jays and, marginally, squirrels. These are typical forest species, which collect many types of seeds as supplies; however, some seeds are usually lost during flight or forgotten in caching sites. The growing synanthropisation of these forest species leads to chances for interaction with novel food sources characteristic for human settlements. Similarly to rooks, which colonised human settlements in the middle of the twentieth century (Dyrcz 1966), jays also became protected in 1952, subsequently increased in number, and started to forage, as well as inhabit, human settlements (Kuczyński and Chylarecki 2012). A similar effect of synanthropisation and synurbanisation has also been observed in the case of squirrels (Babińska-Werka and Żółw 2008). Jays are known as very important seed dispersers for native trees such as *Querqus sp.*, *Corylus avellana* and *Fagus sylvatica*, but this may be changing, as we have found that jays are the main dispersers of walnut seeds into forests. This suggests that jays may be switching from the smaller and less fatty seeds of native species to the highly nutritious seeds of invasive species. Myczko *et al.* (2014) have already shown that jays living in forests eat seeds of overabundant alien and invasive oaks, namely the northern red oak (*Quercus rubra* L.). In our study, red squirrels also carried walnut seeds to forests; however, the rate of visitation by this species was rather low, and currently jays are superior dispersers of the invasive walnut in this habitat.

We found that the dispersal of walnut seeds by jays occurred starting from two habitats. Jays visited walnuts occurring in abandoned fields more often than those planted in human settlements. However, the visitation rate was higher in human settlements when they were close to forests, decreasing quickly with their distance from the forest edge. This result for jays may confirm that even though in abandoned fields there may be higher numbers of predators such as foxes and birds of prey and a lower number of walnut seeds to harvest, this bird still avoids contact with human settlements. Thus, the presence of abandoned fields with seed-bearing walnuts may promote the invasion of this tree into forests, even if the fields are far from forests.

5.2. Gravity-based dispersal of walnuts in forests

Our results indicate that a large population of rooks hiding seeds in arable fields may interact with the shape of the terrain, weather conditions and management practices, indirectly affecting the invasion of an ecosystem in which rooks are not even present. We have shown for the first time that the location of a seed in soil is not static; actually, seeds, after being hidden by rooks, are very mobile. These birds hide a substantial number (3.8 seeds per hectare per hour on average) of walnut seeds in arable fields (Lenda *et al.* 2012). When these fields are managed (e.g. ploughed), walnut seeds may become exposed (some are buried) on the soil surface to variable weather conditions. These seeds may be flushed into different locations by water during rains, especially when the fields are located on slopes in a hilly landscape. Moreover, cultivation work itself (e.g. harrowing) may transport walnut seeds to forest edges from which they can be further transported by gravity or taken by animals, e.g. into forests. In the process of harrowing, plant remains are often dropped at the field's borders (the authors' unpublished observation). This study confirmed expectations that this mechanism plays an important role in the colonisation of forests; especially those forests located at a level below that of the surrounding arable fields are prone to the influx of walnut seeds in this way. These findings were confirmed by our experiment showing that the passive transport of dummy seeds in sloping fields represents an important factor determining the number of seeds reaching forests. This mechanism of dispersal, including gravity or water flow, is typical for big and heavy fruits and nuts such as coconuts or avocados (Vander Wall 2002). However, cases like this, in which gravity affects dispersal and enables invasion only if the seeds of the invasive species have been earlier buried by native dispersers in arable land, represent a phenomenon previously unknown, though similar effects of gravity, landscape structure and weather phenomena were shown in a study about the invasive black pine (*Pinus nigra*) in New Zealand (Caplat *et al.* 2012). Another example of how landscape structure, topography and rapid weather phenomena can promote invasions in new areas is linked with floods and proximity to rivers (Pysek and Prach 1994). Moreover, climate changes increase the frequency of such extreme weather events as thunderstorms, heavy rains, floods, hurricanes (Forzieri *et al.* 2014); thus the importance of gravity-based and passive transportation of alien propagules may become a much more important driver of successful invasions than it is currently (Walther *et al.* 2011).

5.3. Further prognosis for the dynamics of the walnut invasion

As we have found that wild growing walnuts produce seeds, not only coevolutionary interactions of corvids and squirrels with native woody plant species may be threatened by the walnut invasion. Walnut seeds, much more nutritious than those of native trees, may become available for other animals gathering supplies as well. For example, as important dispersers of native plants in forests, woodpeckers are the equals of jays and squirrels, and some species occurring in Central Europe, e.g. the great spotted woodpecker (*Picoides major*), are well known for foraging on walnut seeds in forests in Asia (Yi *et al.* 2014). Therefore it is urgent to monitor and manage this species in forests.

Summary

The invasion of alien walnuts is a good illustration of complicated cascading effects in ecosystems following the introduction of alien species. We have shown the great variety of

seed dispersal mechanisms which determine the spatial location and success of the invasion. Rooks first hide walnut seeds in arable fields, creating large seed banks. Then, as a result of changes in land use and cessation of management, a habitat is created for walnuts, which then grow there and start to produce seeds, which in turn are a source of propagules carried to forests by new dispersers. The effect of dispersal is habitat-dependent, because seeds are also transported to forests from the primary source of walnut invasions, namely, gardens in human settlements. In addition, gravity and the passive transportation of seeds from arable fields also carry seeds into forests. This is clear evidence that cascading effects following an invasion occur with a substantial time lag. Therefore, it is very important to realise that populations of introduced alien species, along with populations of invasive species, cannot be treated as adhering consistently to dispersal or impact lags. Thus the protection of the environment from alien propagule pressure should be, even at the outset of introduction and efficient management of early invasions, among the main goals of conservation biology and ecology.

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Figures

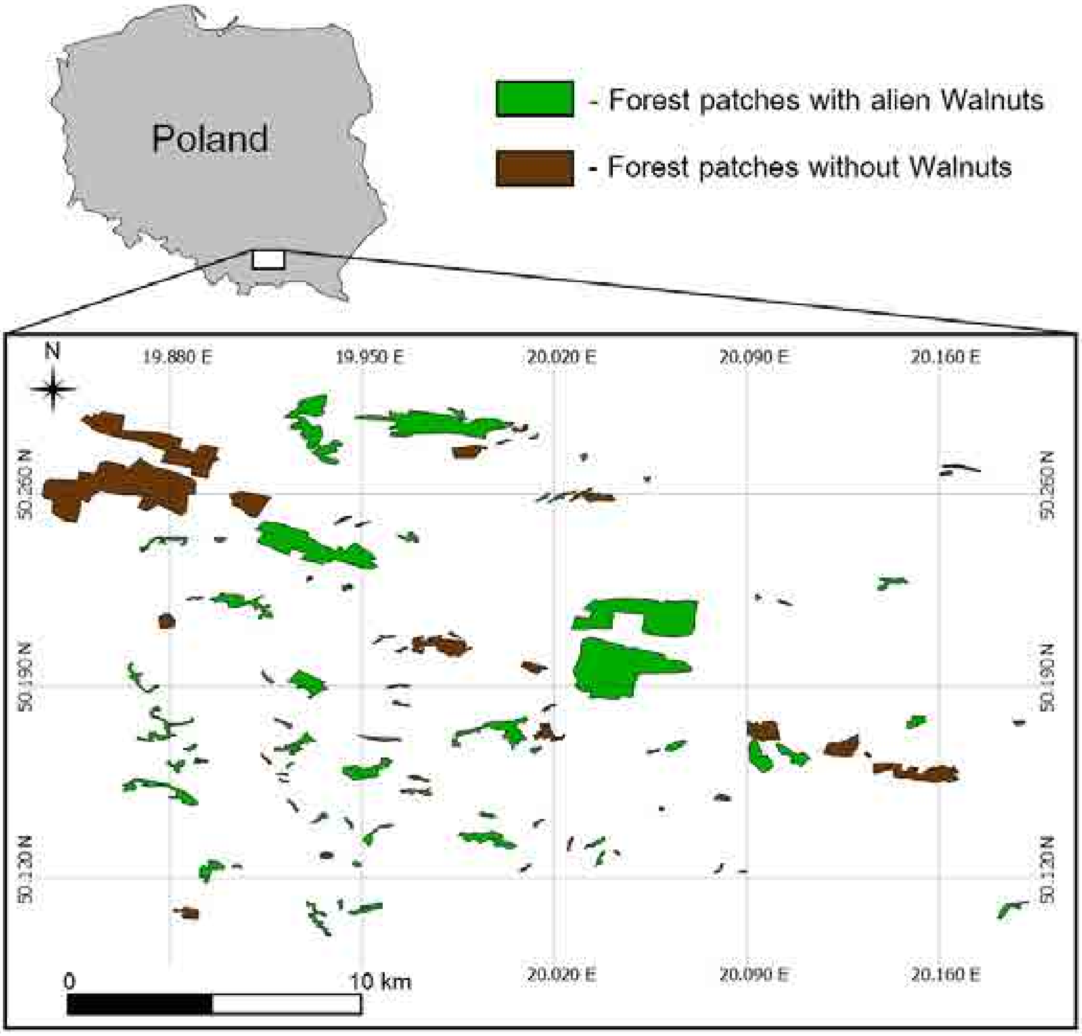


Figure 1. Map of the study area and location of studied forest patches with alien walnut (green patches) and without this species (brown patches).

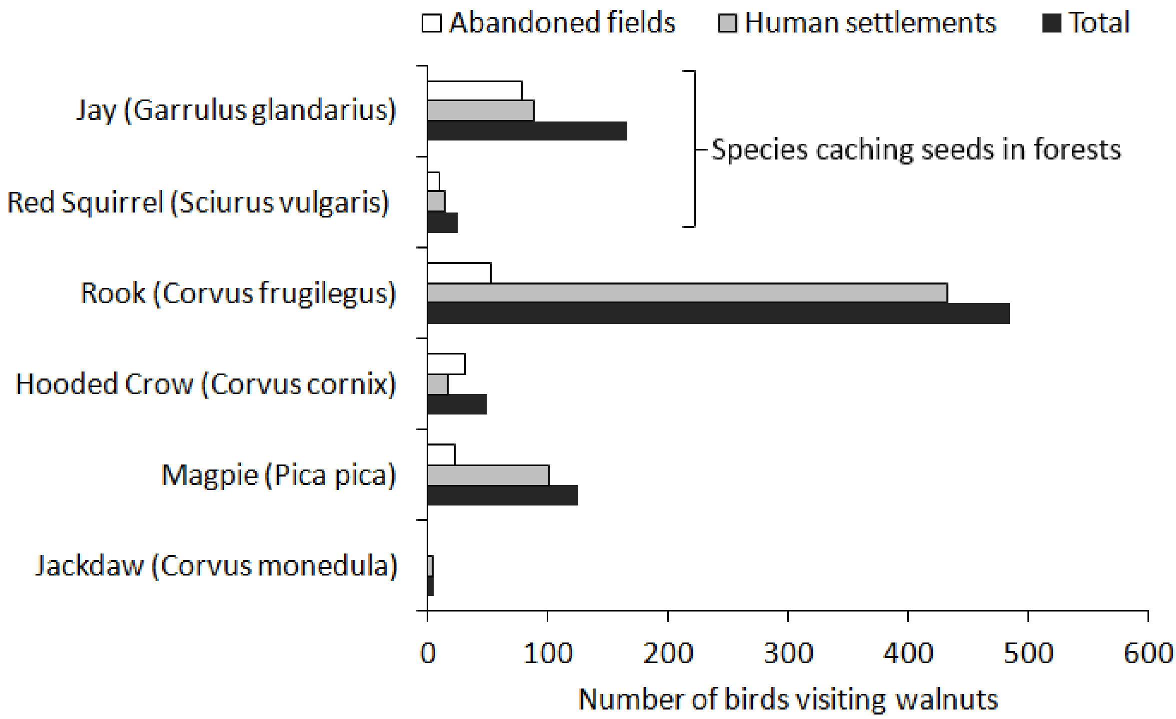
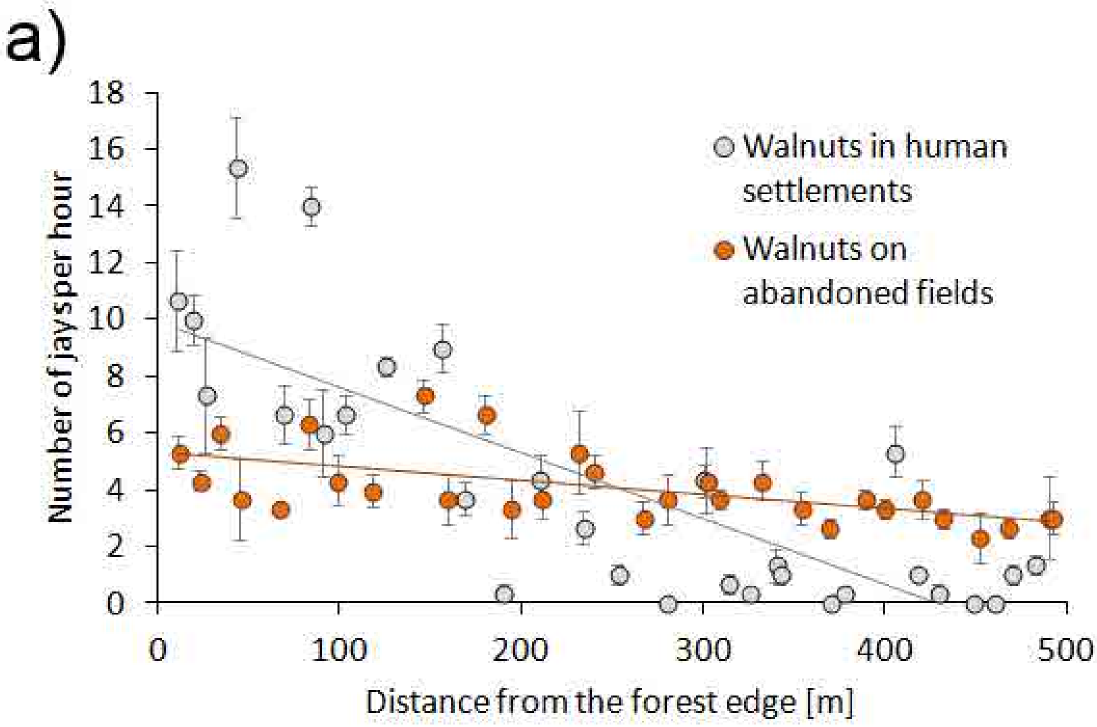


Figure 2. Species visiting seeds bearing walnuts in abandoned fields (white bars) and mature walnuts planted in human settlements (grey bars).



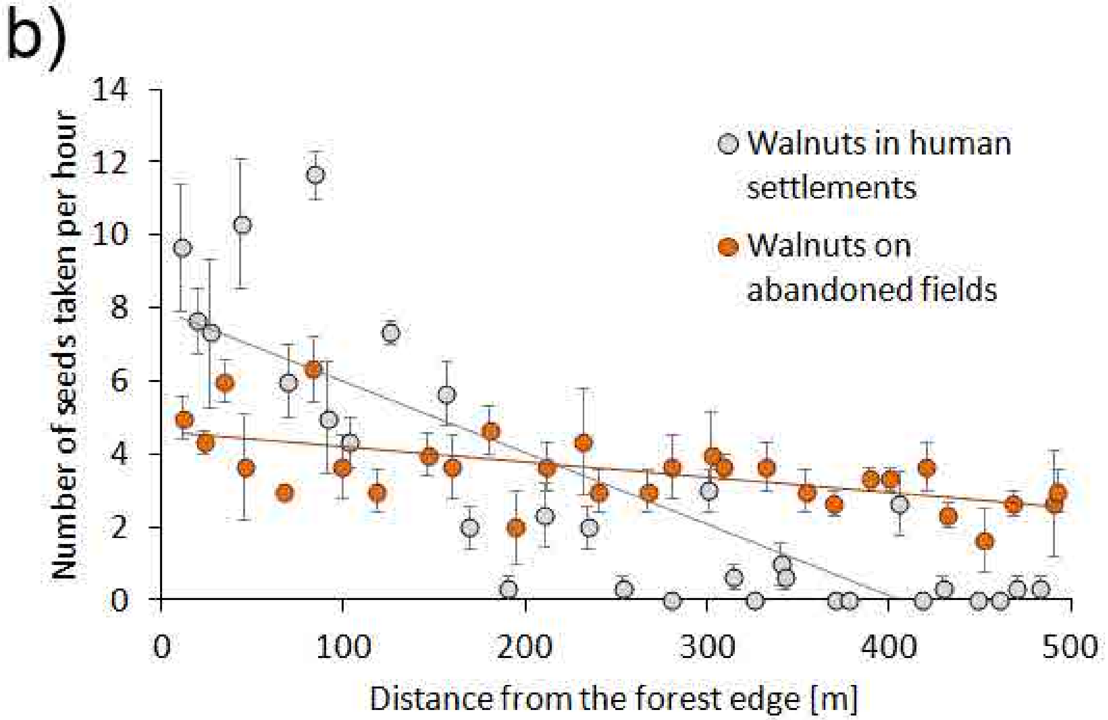


Figure 3. The relationship between (a) jay visitation rate and (b) harvesting rate of seeds on walnuts planted in human settlements (grey dots and lines) and on walnuts growing in abandoned fields (orange dots and lines). Data are means with standard errors (whiskers).

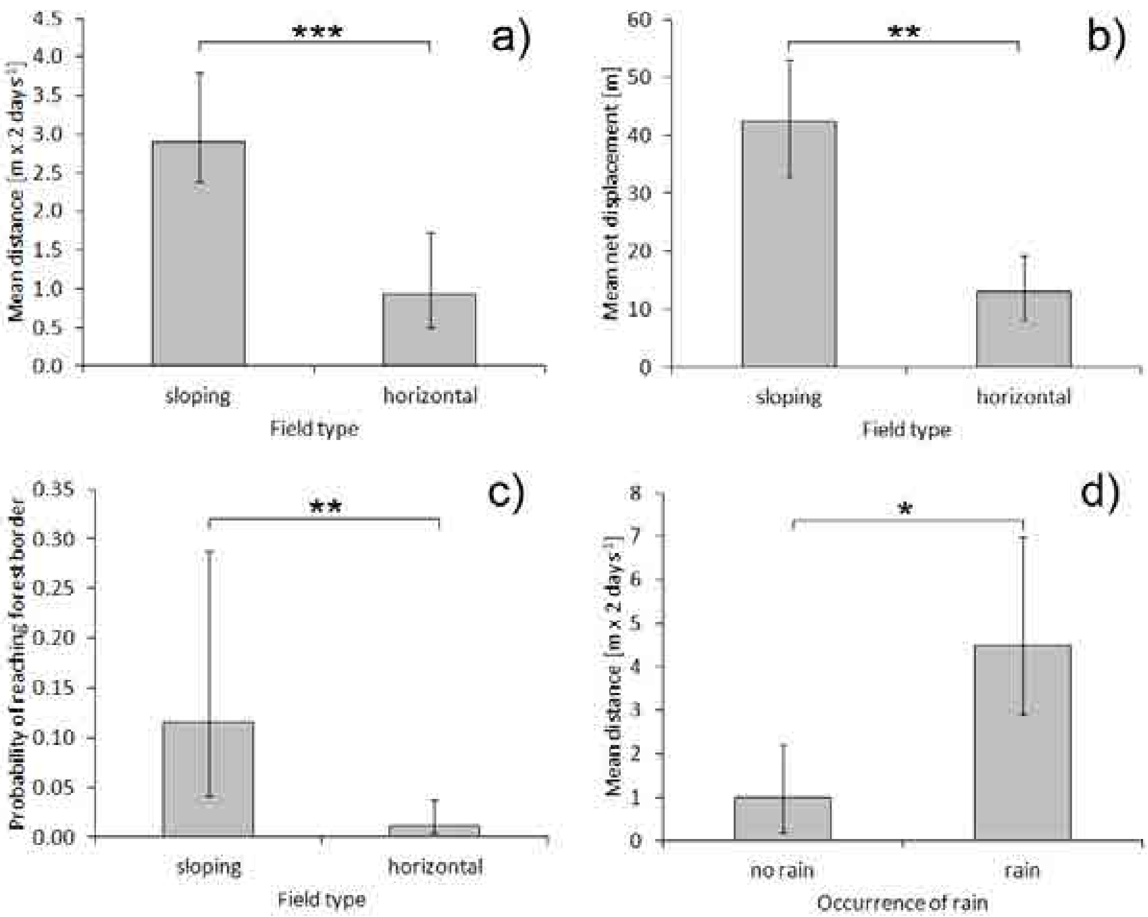


Figure 4. The mean distance (a), net displacement (b) and probability of reaching forest border (c) by dummy walnut seeds in sloping and horizontal fields. The effect of rain (d) on distance covered by dummy seeds is also presented in both field types

Table 1. Basic characteristics of the studied 102 forest patches.

Variabe	Variable code	Mean	SE	Min	Max
Forest patch size (ha)	Area	33.0	8.1	1.2	524.4
Cover (%) of abandoned fields with walnuts bearing seeds in a 500 m radius from a forest patch boundary	Abandoned	11.9	0.9	0	60
Cover (%) of human settlements with walnuts in a 500 m radius from a forest patch boundary	Settlement	15.6	0.9	2	50
Percentage of a forest border that is elevated over the surrounding landscape	Elevation	46.7	2.9	0	100
Cover of other forests in a 500 m radius from a patch boundary	Forest	5.5	0.5	0	25
Percentage share of a deciduous tree species in a forest patch	Deciduous	66.3	3.2	0	100
Forest shape index (the ratio of patch perimeter to the perimeter of a circle of the same size)	Shape	0.025	0.001	0.002	0.064
Canopy openess (%)	Canopy	30.7	1.9	5	64
Transect lenght (m)	-	910	94	160	4885
Density of walnuts per hectare*	-	26.6	1.9	1.8	100
Density of jays per hectare per survey	Jays	1.0	0.1	0	5.8

* - only forests with walnuts included in calculation

Table 2. Best models describing forest occupancy and density of alien walnuts in forest patches. For each model the variance explained by the model (r^2), the Akaike information criterion score (AICc), the difference between the given model and the most parsimonious model (Δ AICc) and Akaike weight (*w*) are listed. For explanations of other variable codes: see Table 1.

Model	r^2	AICc	Δ AICc	*w*
Occurrence of walnuts in forest patches				
Settlements+Abandoned+Elevation	0.43	95.176	0	0.219
Settlements+Abandoned+Elevation+Shape	0.44	95.945	0.769	0.181
Settlements+Abandoned+Elevation+Jays	0.43	96.342	1.167	0.166
Settlements+Abandoned+Elevation+Area	0.43	96.426	1.252	0.163
Settlements+Abandoned+Elevation+Forest	0.43	97.169	1.993	0.144
Density of walnuts in forest patches				
Abandoned+Deciduous+Elevation+Shape+Jays	0.52	-42.522	0	0.183
Deciduous+Elevation+Shape+Jays	0.50	-42.042	0.48	0.165
Settlement+Abandoned+Deciduous+Elevation+ Shape+Jays	0.53	-41.472	1.05	0.149
Settlement+Deciduous+Elevation+Shape+Jays	0.51	-41.317	1.205	0.146

Supporting Information

Photo 1. Examples of young walnuts growing in deciduous forests.

Photos 2. Walnuts often grow at forest edges. Some walnuts also produce seeds there.

Photo 3. Walnuts growing and producing seeds on abandoned fields are often visited by jays.

Photo 4. Walnuts planted in gardens that are in proximity of forests are more willingly visited by jays and squirrels than trees planted in more distant gardens.

Photo 5. Shape of the terrain may affect colonization of forests by walnuts. Forests that are located below the surrounding agricultural land are more prone to passive influx of walnut seeds.

Chapter III

Lenda M., Skórka P., Knops J.M.H., Moroń D., Sutherland W.J., Kuszewska K., Woyciechowski M. (2014). Effect of the Internet Commerce on Dispersal Modes of Invasive Alien Species. PLoS ONE, 9, e99786. doi:10/1371/journal.pone.0099786

PLOS ONE

Effect of the Internet Commerce on Dispersal Modes of Invasive Alien Species

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Abstract

The spread of invasive alien plants has considerable environmental and economic consequences, and is one of the most challenging ecological problems. The spread of invasive alien plant species depends largely on long-distance dispersal, which is typically linked with human activity. The increasing domination of the internet will have impacts upon almost all components of our lives, including potential consequences for the spread of invasive species. To determine whether the rise of Internet commerce has any consequences for the spread of invasive alien plant species, we studied the sale of thirteen of some of the most harmful Europe invasive alien plant species sold as decorative plants from twenty-eight large, well known gardening shops in Poland that sold both via the Internet and through traditional customer sales. We also analyzed temporal changes in the number of invasive plants sold in the largest Polish internet auction portal. When sold through the Internet invasive alien plant species were transported considerably longer distances than for traditional sales. For internet sales, seeds of invasive alien plant species were transported further than were live plants saplings; this was not the case for traditional sales. Also, with e-commerce the shape of distance distribution were flattened with low skewness comparing with traditional sale where the distributions were peaked and right-skewed. Thus, e-commerce created novel modes of long-distance dispersal, while traditional sale resembled more natural dispersal modes. Moreover, analysis of sale in the biggest Polish internet auction portal showed that the number of alien specimens sold via the internet has increased markedly over recent years. Therefore internet commerce is likely to increase the rate at which ecological communities become homogenized and increase spread of invasive species by increasing the rate of long distance dispersal.

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Introduction

Species invasions are both a result and cause of global ecological changes. Numerous studies have shown that invasive alien plant species can often establish and change edaphic conditions in new habitats, change their structure or even create novel invasive-dominated ecosystems [1–8]. However, a key factor is invasive species dispersal; species can only become successful invaders if they can disperse to suitable habitats.

Most plant dispersal is over a short range and it has a right skewed leptokurtic distribution, with a tail of few individuals travelling very long distances [9], [10]. These few long distance dispersers are important in colonization of new areas and in determining the rate of geographical range spread [10], [11]. This tail is the most important factor shaping the invasion mechanisms of alien plant species. The long tail of extreme movements by invasive species is often attributable to various forms of human transportation, which allows alien species to cross geographical barriers and to colonize new localities as well as escape from lag phase of colonization [5], [12–15].

Just as some alien species benefitted from the development of the train network in the UK, such as Oxford Ragwort, whose seeds were carried along the tracks after the trains [16], alien species currently benefit from the worldwide development of vehicle, navy and aerial transportation [12–15]. In recent years much of the trade has been through internet sales, with an associated transportation network [17], [18]. However, we barely understand how the relatively new global phenomenon of internet commerce may affect the dispersal modes of invasive alien plants at landscape or regional scales.

Currently, many alien plant species, including invasive ones, are available for sale in many garden shops [19], [20]. The traditional commercial model in shops or floral markets comprises sales to visiting customers, which limits the type of transportation, and distances on which alien plant species are transported. However, the recent rise in internet sales have included the development of trade in animals and plants to customers who may not even know where the shop is located [21], [22]. Thus, the internet trade is much less constrained in transportation type and distance by which alien invasive species may travel from shop to customer. Consequently, the distribution of distances that are travelled by alien species from a shop to a customer should be less peaked and much less skewed (be more Gaussian-like distribution) than in case of traditional sale, assuming that buyers in the internet are located at random distances from the shop. There are currently few studies that show how internet commerce enhances purchase of invasive species, and so increases propagule pressure of invasive species [22]. There is thus a need to determine how internet commerce affects dispersal modes and the functioning of populations in the environment on landscape or regional scales and how this compares with the traditional shop trade.

The aim of this study was to characterize the role of the internet sale in the long distance dispersal and spread of invasive species. The study was carried out in Poland, where the internet and traditional commerce of garden flowering plants are both relatively well developed. The following hypotheses were tested:

1. Internet trade results in larger movement distances of invasive plant species than does traditional trading, where much of the trade will be to local people.
2. Internet trade is less constrained by the distance and generates distribution of dispersal distances that are less peaked and less skewed than in more limited traditional trading.
3. Seeds are transported on longer distances than seedlings. Seedlings are known to be more fragile and more likely to be collected in person than sent by post.
4. Supply and demand of invasive alien species sold via internet auctions is growing over time indicating increased interest in alien invasive species, what suggests also higher propagule pressure of exotic species.

Materials and Methods

We chose 13 invasive species that are widespread in Poland, some of which are amongst the most harmful invasive plant species in Europe [23], and which were easily available through garden shops and internet auctions. The following species were studied: *Acer negundo*, *Buddleia davidii*, *Echinocystis lobata*, *Elodea canadensis*, *Impatiens glandulifera*, *Prunus serotina*, *Quercus rubra*, *Rhus typhina*, *Robinia pseudoacacia*, *Rosa rugosa*. We also examined the following genera that are rarely distinguishing at the species level so can be sold under the same name (for example whether *Solidago gigantea* or *Solidago canadensis*): *Reynoutria* sp., *Rudbeckia* sp., *Solidago* sp. However, in all cases the species within a genus are similar in biology and habitats they occupy.

Data collection

Comparison of distances that alien invasive plants travelled according to whether sold on-line and by traditional shops

To compare distances on which invasive alien species were transported when sold via internet and in traditional shops, we chose 50 large shops in Poland in different regions of Poland that carried both internet and traditional sale of alien species listed above, and we asked owners to collect data about customers postal codes, sale objects and volume for both internet and traditional commerce. To find suitable shops we searched Google using the phrase: "sklep ogrodniczy"(garden shop) then Yellow Pages portals (www.yellowpages.pl) and Panorama firm (www.panoramafirm.pl, only in polish), the latter is the oldest and best known source for locating all kinds of business including shops. We also selected shops in such a manner that they were dispersed across the entire country. Twenty eight of the owners of these shops agreed to collect the data. We collected data in 2011 for each species on the geographic location of both the shops and customers, number of purchasers, number of plants sold, their life form (whether seedlings or seeds). Shop keepers were aware that data about plant commerce collected by them would be used for further analyses, PhD dissertation, writing scientific papers and publishing. However, they did not know the specific hypotheses that we planned to test. The shop owners were informed about results and ensured that the database will be de-identified, and that they could withdraw the date they had already donated as well as being assured that their personal data (name of the shop and its location etc.) will not be published anywhere. The goal of collected data was to study plant commerce not the human behaviour, and the research possessed no risk to the participants, meaning that the probability and magnitude of harm or discomfort anticipated in the research are not greater in and of themselves than those ordinarily encountered in daily life or during the performance of routine physical or psychological examinations or tests. The data were de-identified. Moreover this research did not involve vulnerable populations and possessed no risk to the participants and, as such, this research did not require Institutional Review Board approval in Poland.

Data provided by the shop owners allowed us to map and visualize the geographical location of the source and destination of each species. Collecting zip codes and location name is a common sales practice as it allows sellers to target subsequent promotions [24]. We also used location name and zip codes to calculate distances between shops and buyers for both internet and traditional sales. We used centroids of the area of a destination location and zip code to calculate the distance transported. We used Quantum 1.7 Wroclaw GIS system.

Temporal changes in the number of invasive species sold on the internet auction portal

In order to check if internet commerce of invasive species has increased during last 6 years, we used data from the public available archive of Allegro (see http://allegro.pl), the largest on-line auction portal in Poland, to collect data on the number of auctions of the selected invasive alien species. We were able to retrieve data from years 2006–2011. We preferred Allegro as a database instead of the previously chosen sample of shops, because we were interested in (i) estimating the number of all cases of the selected alien invasive species for sale in the entire Poland and (ii) number of purchases made by as many as possible customers in the same period. Moreover, the garden shops had no accurate data on the amount of the two types of sale from past 6 years (or had not recorded it) and some of shops had existed for short period of time. The data were public, thus collecting it did not require Institutional Review Board approval.

Data processing and analysis

Distances travelled by alien plants through the different purchasing routes were compared using a general linear mixed model; plant species and shop identity were assigned as random factors. A general linear mixed model is an extension to the general linear model in which the linear predictor contains random effects in addition to the usual fixed effects. They are particularly useful in settings where repeated measurements are made on the same statistical units (for example species in our study), or where measurements are made on clusters of related statistical units (shops in this study). Because of their advantages in dealing with data dependency, mixed effects models are often preferred over more traditional approaches, such as repeated measures ANOVA [25]. Random factors in our analyses account for differences between unspecified traits of species and shops that have not been measured during the study.

We also compared features (skewness and kurtosis) of the distance distribution in both sale types for each plant species. Then, we used paired t-student tests to analyse differences between internet and traditional sales in shops. Skewness is a measure of the degree of asymmetry of a distribution around a mean with zeros indicating symmetrical, positive values for right skewed distributions and negative values for left skewed. Kurtosis measures the degree of peakedness of a distribution. Kurtosis higher and lower than 0 indicate leptokurtic (peaked) distribution and platykurtic (flattened) distribution, respectively.

To compare the distances at which seeds and seedlings were transported in the internet and traditional sale we used general linear mixed model. Sale type (internet vs. traditional), life stage (seeds vs. seedling) and interaction between them were introduced as fixed factors. Species identity and shop identity were random effects. In this model only species with both seeds and seedlings in shops' offer were included.

We used correlation analysis to assess the statistical significance of the temporal trend in the number of internet auctions and number of purchasers in Allegro portal. All statistical analyses were done in SPSS 19.

Results

Comparison of distances that alien invasive plants travelled according to whether sold on-line and from traditional shops

For all species the mean distance from a shop to a purchaser was significantly greater when alien invasive plants were sold through the internet than from traditional trade in shops (GLMM $F_{1,\ 4048} = 42.58$, $P<0.001$, Fig. 1). The effect was consistent among species (Fig. 1). Figure 2 maps, for three species, the distances plants were transported according to whether sold on the internet or in traditional sales; maps for the other species, together with distance distributions, are in Figures S1–S23 in File S1. Also shapes of distributions of distances covered by plants differed between internet and traditional sales. Mean skewness of distance distribution of plants sold via internet was lower than for plants sold in traditional shops (paired *t*-tests: $t_{12} = 5.40$, $P<0.001$, Fig. 3). The kurtosis coefficient for distance distribution of species sold via internet was lower than in plants sold in a traditional manner (paired *t*-tests: $t_{12} = 3.71$, $P = 0.003$, Fig. 3).

The total number of records of purchases from the 28 analyzed shops was 4,050. The number of records involving purchasing seeds was 811 and 3,239 for seedlings. The total number of seeds sold was at least 62,646, and 6,894 for seedlings (in several transactions the number of the plants sold was not specified). For internet commerce the mean transportation distances of seeds were significantly higher (interaction term in GLMM $F_{1,\ 1990} = 13.85$, $P<0.001$ with Tukey post hoc test $P<0.010$) than for seedlings (Fig. 4) but this was not the case for traditional sales (Fig. 4).

Temporal changes in the number of invasive species sold on the internet auction portal

The total sale of 13 selected invasive alien species in the largest Polish internet portal increased over time whether measured as total number of purchasers ($r = 0.98$; $P<0.001$) or auctions ($r = 0.99$; $P<0.001$) (Fig. 5). Both the number of purchasers and the number of auctions increased for most species studied (Figures S24–S36 in File S1).

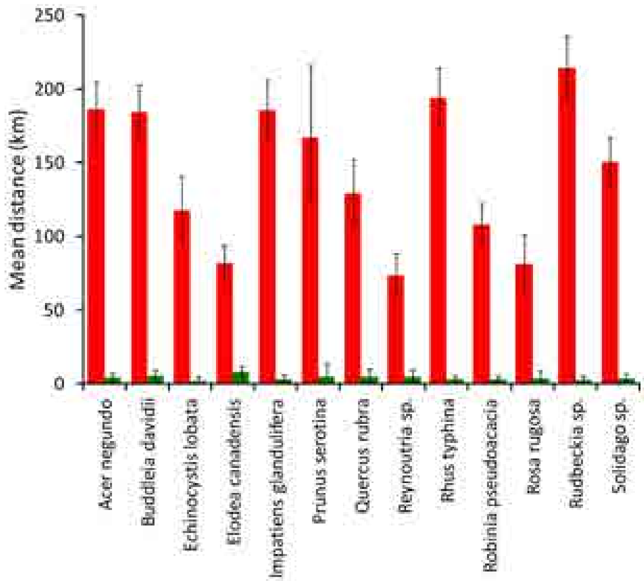

Figure 1. Mean transportation distances for all 13 species traded online (red bars) and in traditional sales (green bars). Whiskers are 95% confidence intervals.
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Discussion

Only 40 years of the internet persistence was necessary for it to become the fastest and the most effective way of communication, but also a very popular means of purchasing goods. Our study shows that socioeconomical changes, especially e-commerce and accessible transport for long distances, modifies dispersal patterns of invasive alien plant species.

Our results clearly show that the distances that invasive species were transported were several times larger if they were ordered by internet than for traditional sales. This result has important ramifications for the understanding invasion processes and indicates that the internet sale generates frequent long-distance dispersal events. Although such long-distance dispersal plays prominent role in invasion ecology and biology of plants [10], [26], natural vectors rarely achieve comparable distances in terrestrial landscapes as the dispersal pattern generated by the internet sale. Therefore such innovative means of species purchasing may play a unique role in alien species invasions. It is believed that the increasing number of the invasions of many groups of organisms is tied to the frequent migration or movements of humans and facilitated long-distance transport [15], [27–30]. Also, frequent long distance dispersal is one of the most important factors triggering alien species from the lag phase into population expansion [31–33]. The role of distant transport in vehicles and plains has been already recognized, however such cases are rare and incidental and usually represents only tail of the longest dispersal distances. The transport and long-distance dispersal events caused by internet sale are regular and become increasingly frequent. Moreover, the shape of distribution of the distances covered by plants sold via internet were flatten and less skewed than in plant sold in a traditional way. The latter was similar to natural dispersal distance distributions, which are highly right skewed and leptokurtic. The distribution of the distances in the internet sale did not resemble any natural (long) distance distribution of dispersing propagules as it was flatten and only little skewed. Thus it is clear that the internet trade generates novel dispersal modes of invasive species.

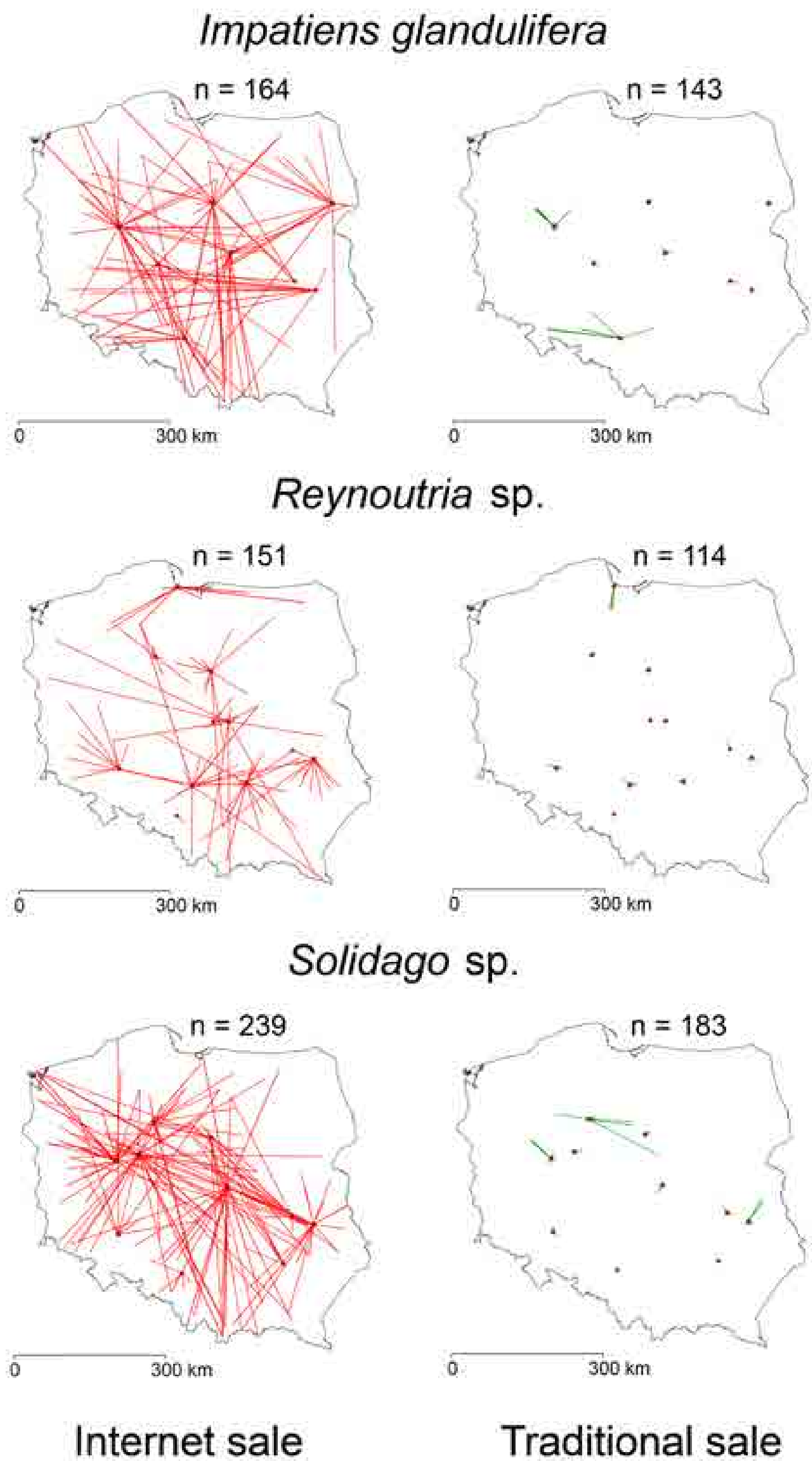

Figure 2. Examples of movement patterns of plants according to the sale type. *Impatiens glandulifera* (a, b), *Reynoutria sp.* (c, d) and *Solidago sp.* (e, f). Red lines indicate distances in the internet trade and green lines in traditional trade. Red dots denote shops locations.
doi:10.1371/journal.pone.0099786.g002

Obviously, natural vectors are, and probably will continue to be, important in the spread of alien species. Wind, native dispersers and floods may enhance dispersal of alien species [34–37], especially in more traditional landscapes and regions or countries where internet sale is still not well developed. However, if the development of internet web progress these regions will be threaten by invasions of alien species. One of the gaps in understanding consequences of plant long distance dispersal, in

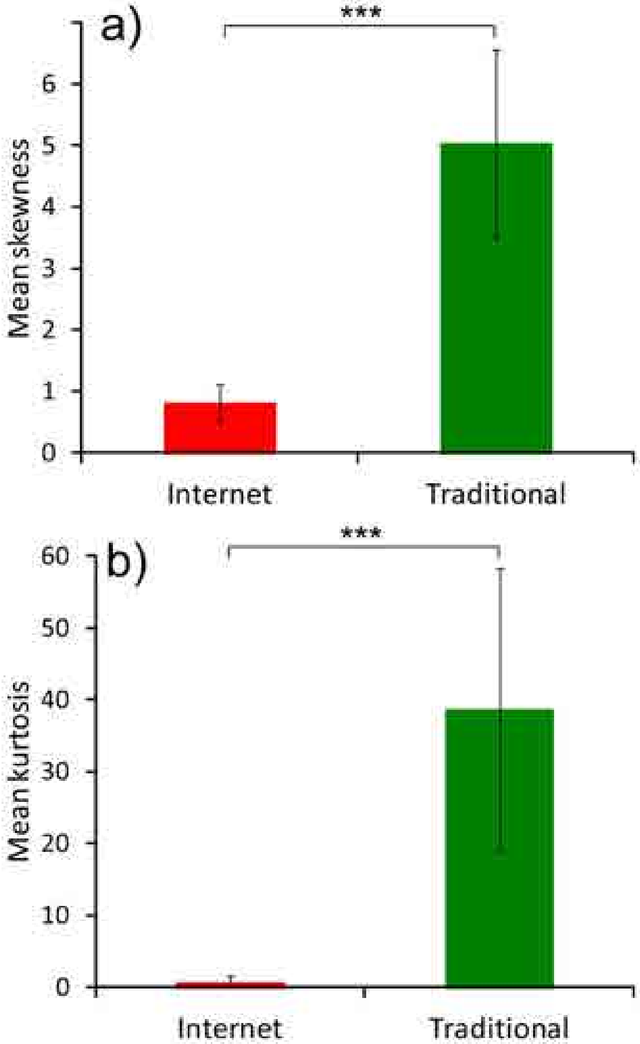

Figure 3. Mean skewness (a) and kurtosis coefficient (b) of distance distribution of invasive plant species traded on-line (red bars) and in a traditional manner (green bars). Explanations: *** - P<0.001. Whiskers are 95% confidence intervals.
doi:10.1371/journal.pone.0099786.g003

general, is that different life stages (seeds, seedlings, adults) may disperse, but documented examples are scarce [10], [38]. This phenomenon was apparent even in the internet sale. In our study seeds were transported on longer distances than seedlings in the internet and this pattern was not shown in traditional sales, probably because purchasers considered seedlings less suitable for long distance postal trade. These differences are likely to have implications for the pattern of use and the probability of establishment. Although seedlings covered slightly shorter distances than seeds the probability of their survival and growth is possibly higher because they are already developed young plants. Usually, only certain proportion of seeds germinate and grow (in a commercial sale it is usually no less than 80%). However, the amount of seeds sold was nine times larger than seedlings indicating that this life form of alien species may be responsible for colonization of new areas and spread. Moreover, seeds may be sometimes lost during transportation adding to occasional spread of alien species outside the gardens (e.g. at road verges) [39].

The frequency with which alien species are transported along a route and delivered to a specific location is strongly associated with

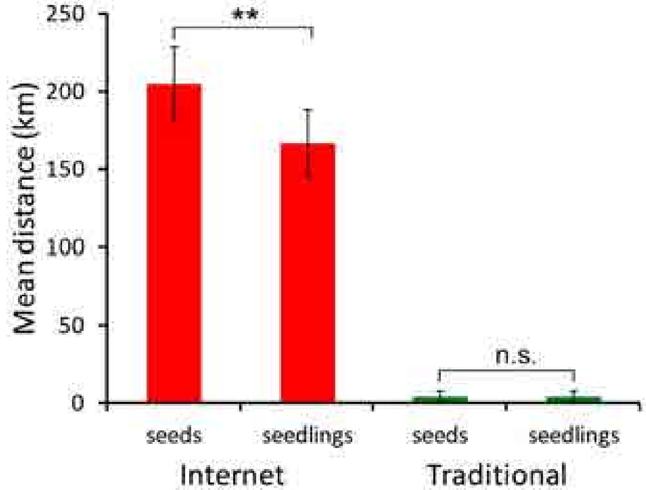

Figure 4. Mean transportation distances of seeds and seedling traded on-line (red bars) and in a traditional manner (green bars). Explanations: ** - P = 0.010; n.s. – statistically non-significant difference. Whiskers are 95% confidence intervals.
doi:10.1371/journal.pone.0099786.g004

the success of dispersion, colonization and subsequent invasion [40–42]. Such human related long distance dispersal and increasing propagule pressure enhance genetic variation in populations and help overcome Allee effects and genetic drift that may otherwise reduce invasion success or keeping the invasion process in a very early stage, in a lag phase [43], [44].

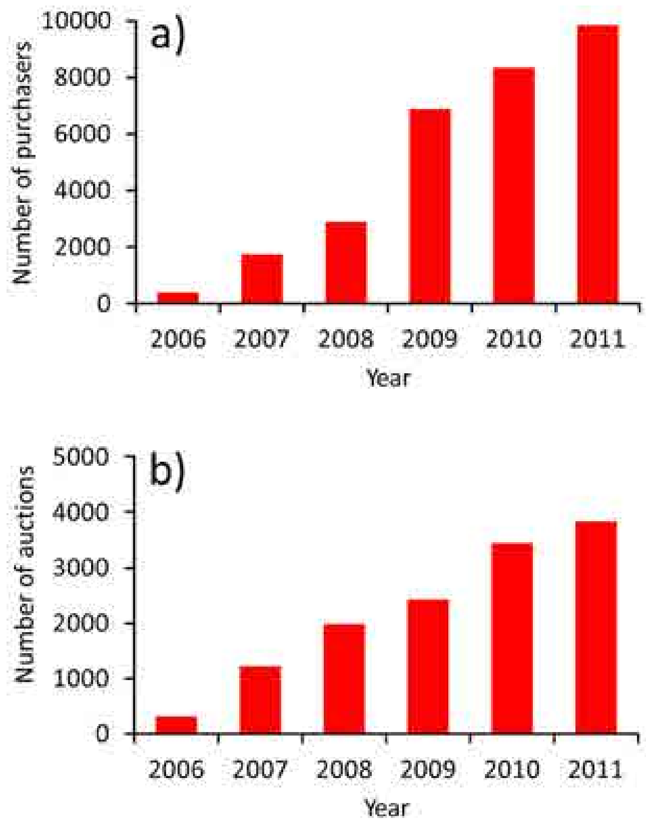

Figure 5. Number of purchasers (a) and number of auctions (b) of 13 invasive alien species in different years in the largest polish internet auctioning portal.
doi:10.1371/journal.pone.0099786.g005

Education of potential human vectors is believed to be main factor that can slow down invasions and prevent new ones. However, the example of 13 chosen invasive species, some of the most harmful ones in Europe, shows that they were commonly sold via internet and the number of purchases on the most popular internet portal increased hugely, over one hundred-fold over last few year's (2006–2011). Thus, the internet commerce clearly enhances not only distance of transport but also potentially increase propagule pressure of invasive alien species because customers buying these species usually plant them in gardens so allowing their escape into natural habitats. This growth in sale of aliens seems to reflect general trend in number of internet users that increased globally by 566% between 2000 and 2012 (see http://www.internetworldstats.com) as a result of convenience and time saving provided by the internet communication and internet transactions. The development of the internet sale included numerous alien plant that are not recognized currently as invasive but may become harmful in future. For example, our survey on the internet portals indicated that there are over 300 decorative alien plant species (with different varieties) that have not been recognized as invasive but have being introducing into Poland (Lenda et al. unpublished). This also indicates that ever increasing number of scientific research on invasive species [45] seems not to be effective in preventing invasions and the reason can be poor reflection of professional reports on society education and effectiveness in preventing invasions.

Alien species sold in the internet may become efficient vectors of alien parasites or pathogens also those harmful for native organisms. Much of the spread to the United Kingdom of ash dieback disease *Hymenoscyphus pseudoalbidus* or the sudden oak death ***Phytophthora ramorum*** in USA was attributed to the movement of saplings for forestry [46], [47]. Therefore, the increased number of alien plants being sold, and large distances they are transported via internet sale, amplifies an environmental hazard and creates invasion debt associated with unrecognized pathogens for which aliens species may be just dispersal vectors [48].

Studies in New Zealand show that alien snails, reptile species and alien established frogs were for sale on the internet [22], [48] and that GMO species, forbidden in that country, were also available and were purchased from internet auctions [22], [48]. Finally, internet sales may be a threat for native fauna and flora not only due to commerce of alien invasive species but also by offering many endangered red listed species [21].

E-commerce contractions and practical recommendation

Countries from European Union, Australia, New Zealand passed legal restrictions (in Poland since 2012) aimed to limit e-commerce of alien and invasive species [22], [48]. However, in all cases sales via the internet still exists, and is even increasing, as sellers may avoid regulations by, for example, changing names of invasive species (like misspelling) or by using very traditional names that are not on police lists (Lenda et al. unpublished).

Solutions to this invasion problem can include increased restrictions, controlling trade, greater enforcement of existing regulations and applying reliable financial fines not only for customers but also for sellers. Further restrictions should limit selling of new alien species or species that are regarded as invasive in other regions of the world. The list of invasive species should be easily accessible for all people and their harmful effects for economy should be estimated in order to caution society about real losses to economy and environment when invasions occur. Sold plants should include information for buyers whether this is an alien or native plant in a given country. More effective reflection of scientific results on invasive species and possible invasion debts on education of society and encouragement for gardeners to grow more benign rather than environmentally damaging plants is desirable.

The growing number of introduced alien species for gardening and agriculture often comes from fashion and follows some recommendations and news in popular media [49]. The society may become much more nature-oriented and aware about environment after watching some nature programs in television or on the internet, or when society follows life-style of some well known, charismatic persons [50–53]. Therefore creating a new fashion of planting native plants might be equally important as legal restrictions.

Conclusions

Our results shed new light on understanding the effects of trade and transportation on spread of alien species by incorporating the increasingly dominating manner of communication between people and societies– the internet. The internet commerce made long distance dispersal very common, which contradicts existing results indicating it is a rare phenomenon. Moreover, internet trade generated shapes of distance distribution that differs from that shown by all other known dispersal vectors. As the number of invasive alien species sold via internet increased over years with the development of e-commerce that may play prominent role for success of alien plants in rapidly changing world.

Thus, a social component of dispersal needs to be included in future dispersal models of alien species. Specifically, further research needs to examine if internet sales affects the spatial pattern of local invasions risks. Buyers' locations may occur in clusters and an examination of socioeconomical factors related to the buyers (such as income, local population size, gross domestic product, education) may provide insights in what drives plant buyers behavior. Ultimately, a better understanding of what drives the buyers of invasive nonnative species may lead to insights in how to manage and limit invasive alien species spread.

Supporting Information

File S1 Detailed data on distances on which invasive alien were transported when sold on-line and in traditional way in studied garden shops (Figures S1–S23), and the rate of ecommerce for these species in popular Polish auctioning internet portal (Figures S24–S36).
(DOCX)

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Author Contributions

Conceived and designed the experiments: ML. Performed the experiments: ML PS KK WJS DM JMHK MW. Analyzed the data: ML PS. Contributed reagents/materials/analysis tools: ML PS KK WJS DM JMHK MW. Wrote the paper: ML PS. Edited and improved the paper: ML PS JMHK WJS MW KK DM.

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Detailed data on distances on which invasive alien were transported when sold on-line and in traditional way in studied garden shops.

1. *Acer negundo*

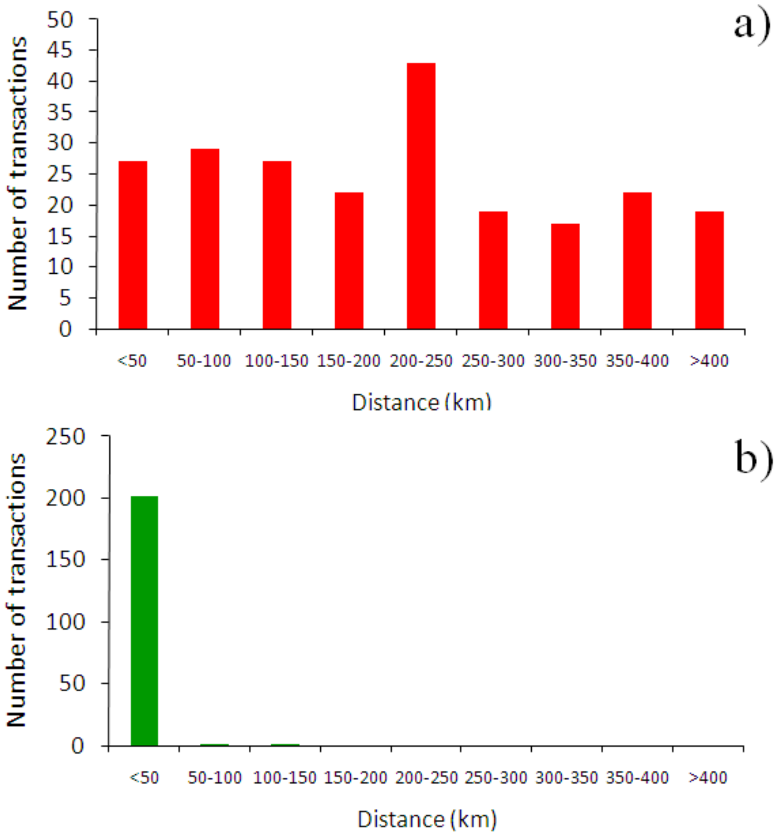

Figure S1. The distribution of the transportation distances of *Acer negundo* in (a) the internet and (b) traditional sale in studied garden shops.

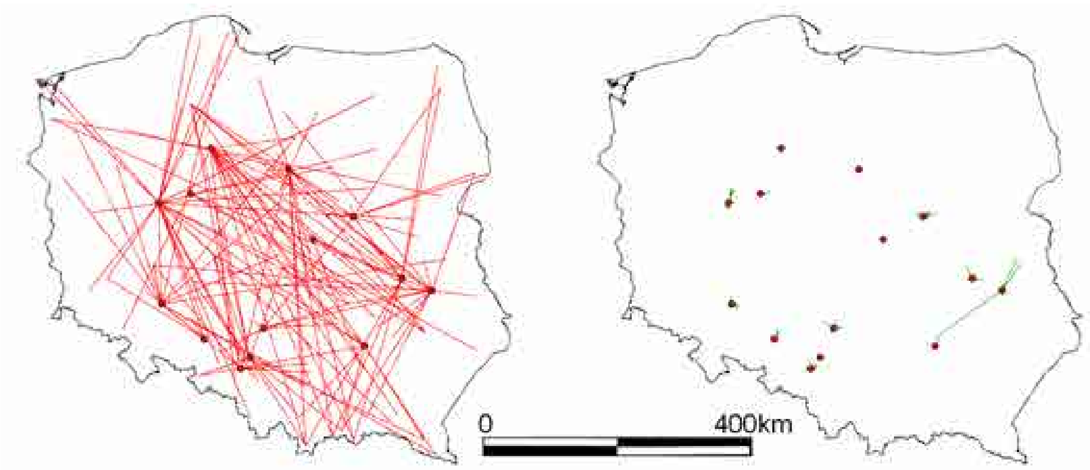

Figure S2. Maps of distances on which plants were transported depending on the sale type in *Acer negundo*. Red lines indicate distances in the internet trade and green lines in a traditional trade. Red dots denote locations of garden shops.

2. *Buddleia davidii*

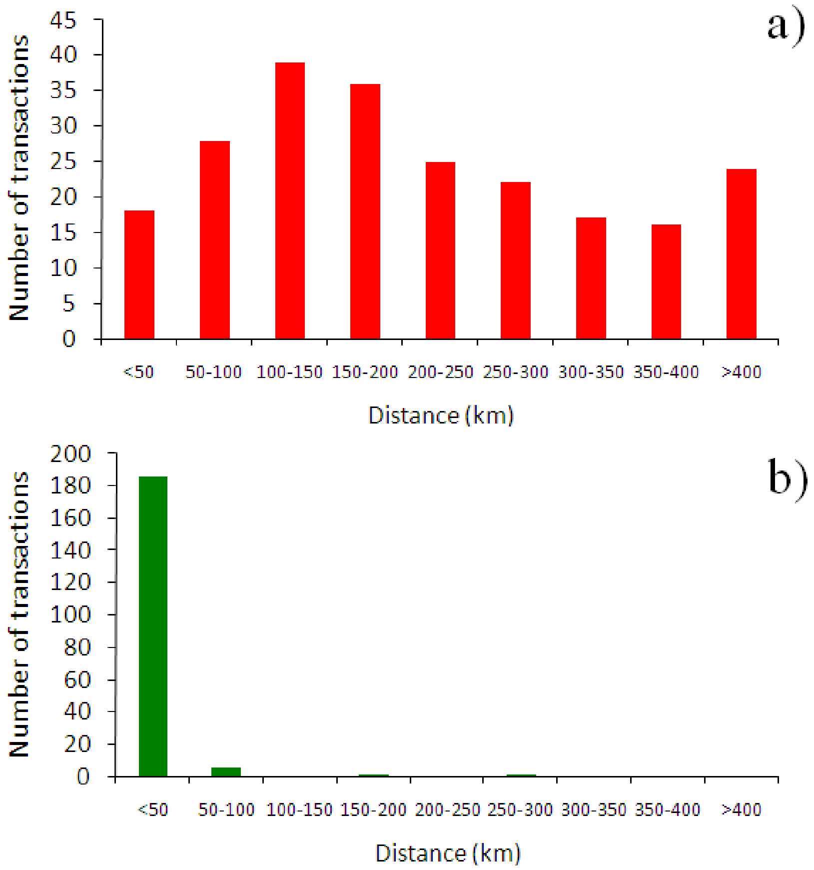

Figure S3. The distribution of the transportation distances of *Buddleia davidii* in (a) the internet and (b) traditional sale in studied garden shops.

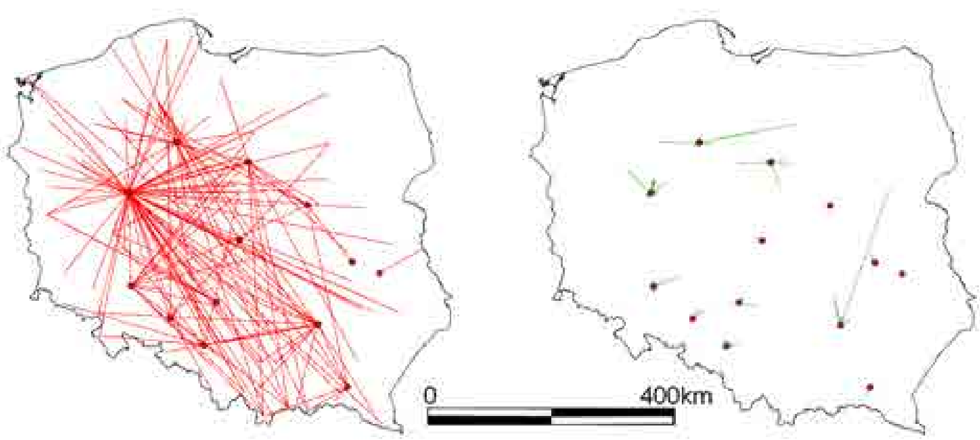

Figure S4. Maps of distances on which plants were transported depending on the sale type in *Buddleia davidii.* Red lines indicate distances in the internet trade and green lines in a traditional trade. Red dots denote locations of garden shops.

3. Echinocystis lobata

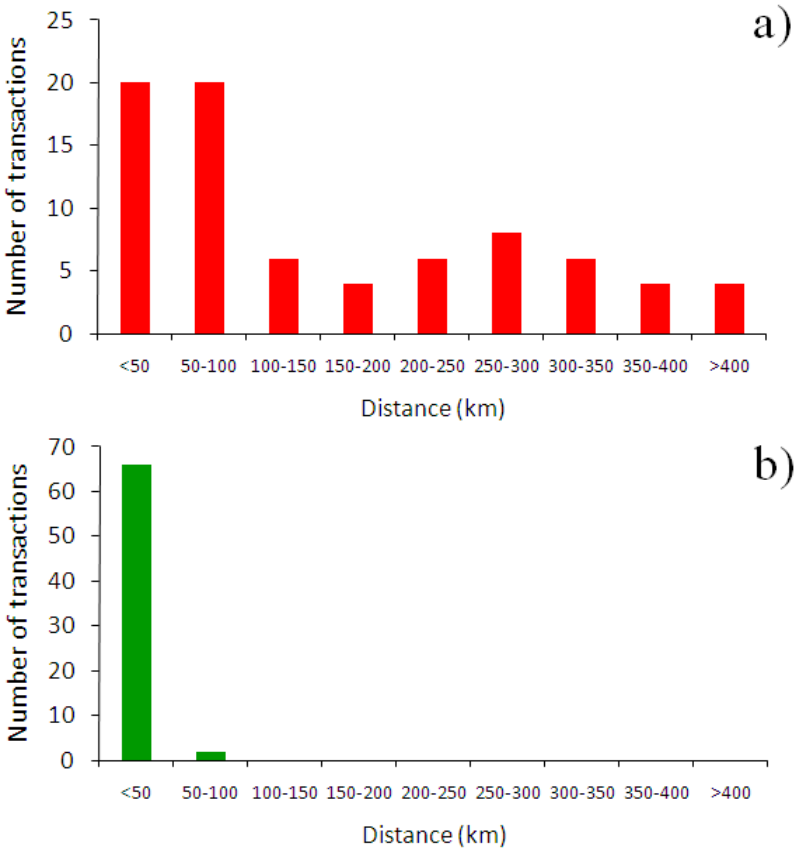

Figure S5. The distribution of the transportation distances of *Echinocystis lobata* in (a) the internet and (b) traditional sale in studied garden shops.

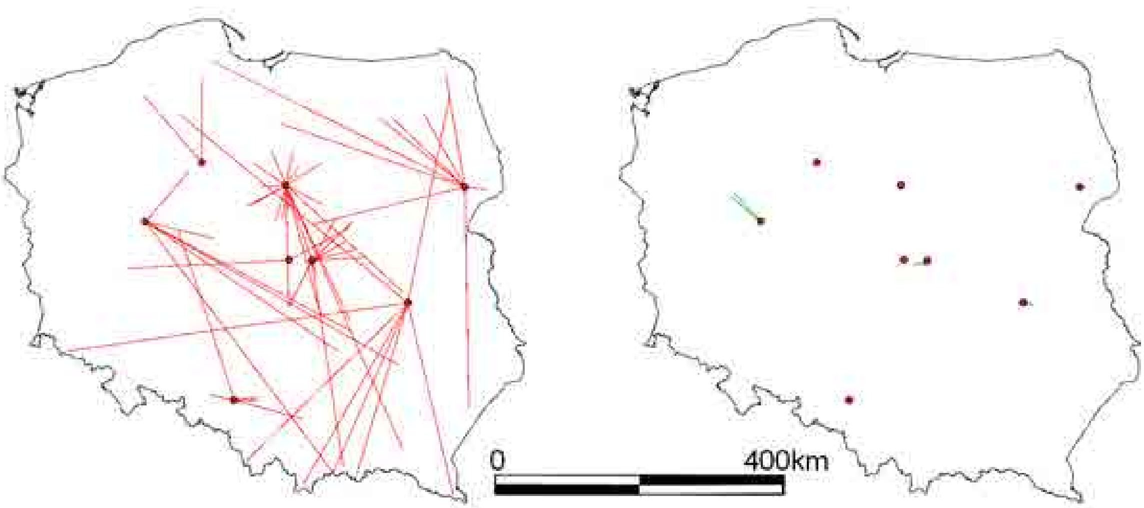

Figure S6. Maps of distances on which plants were transported depending on the sale type in *Echinocystis lobata.* Red lines indicate distances in the internet trade and green lines in a traditional trade. Red dots denote locations of garden shops.

4. *Elodea canadensis*

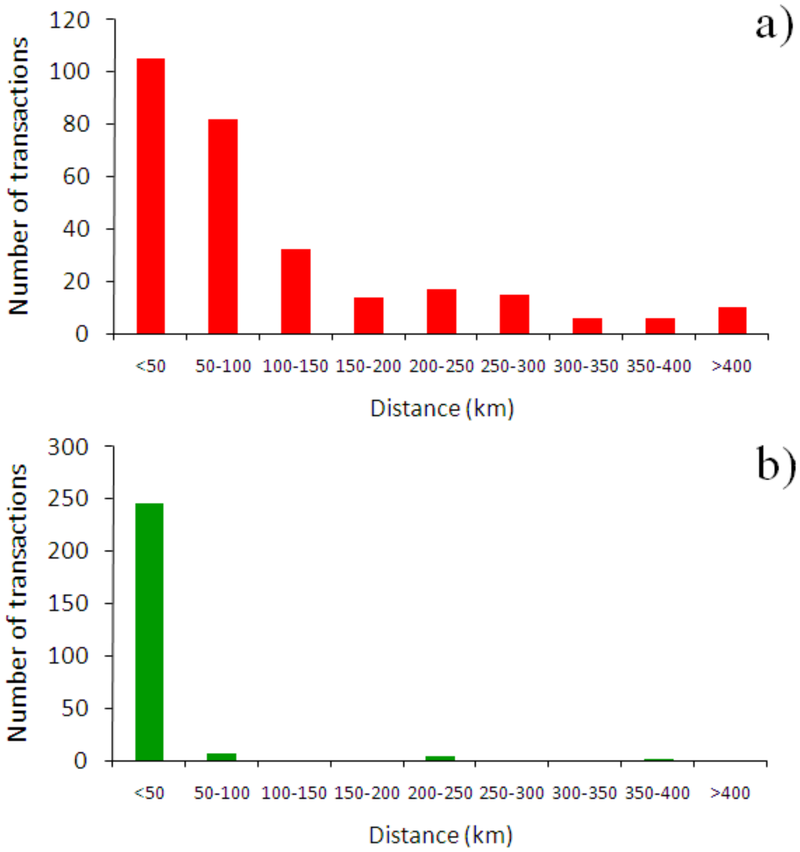

Figure S7. The distribution of the transportation distances of *Elodea canadensis* in (a) the internet and (b) traditional sale in studied garden shops.

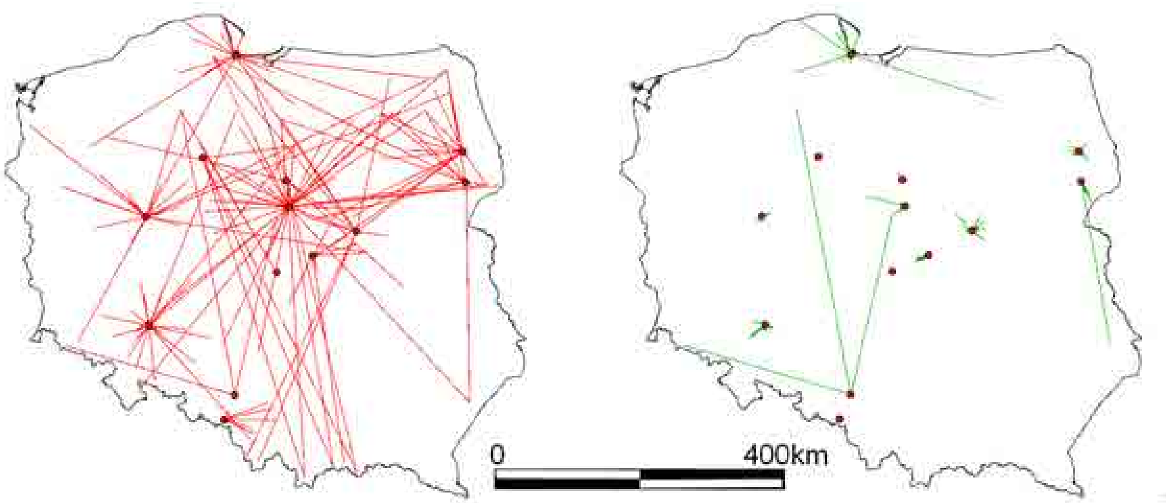

Figure S8. Maps of distances on which plants were transported depending on the sale type in *Elodea canadensis.* Red lines indicate distances in the internet trade and green lines in a traditional trade. Red dots denote locations of garden shops.

5. *Impatiens glandulifera*

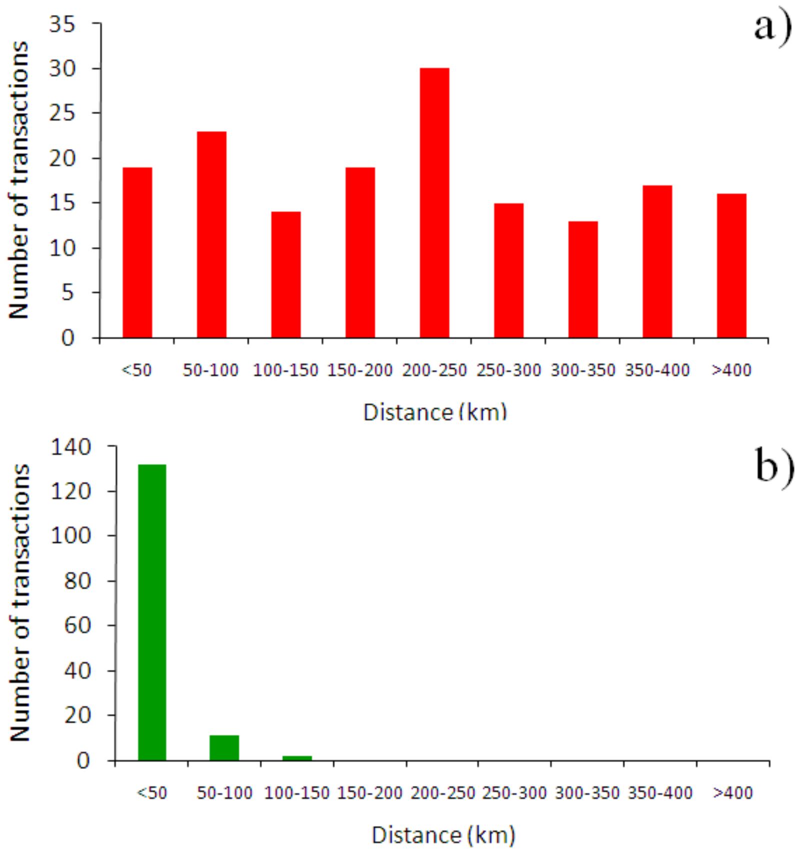

Figure S9. The distribution of the transportation distances of *Impatiens glandulifera* in (a) the internet and (b) traditional sale in studied garden shops.

6. *Prunus serotina*

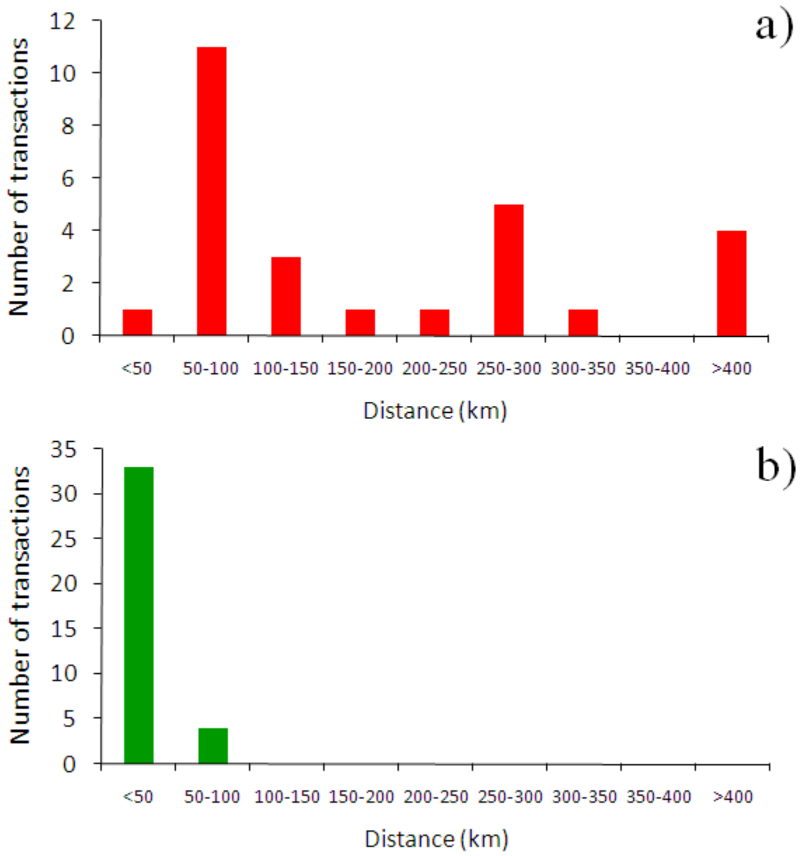

Figure S10. The distribution of the transportation distances of *Prunus serotina* in (a) the internet and (b) traditional sale in studied garden shops.

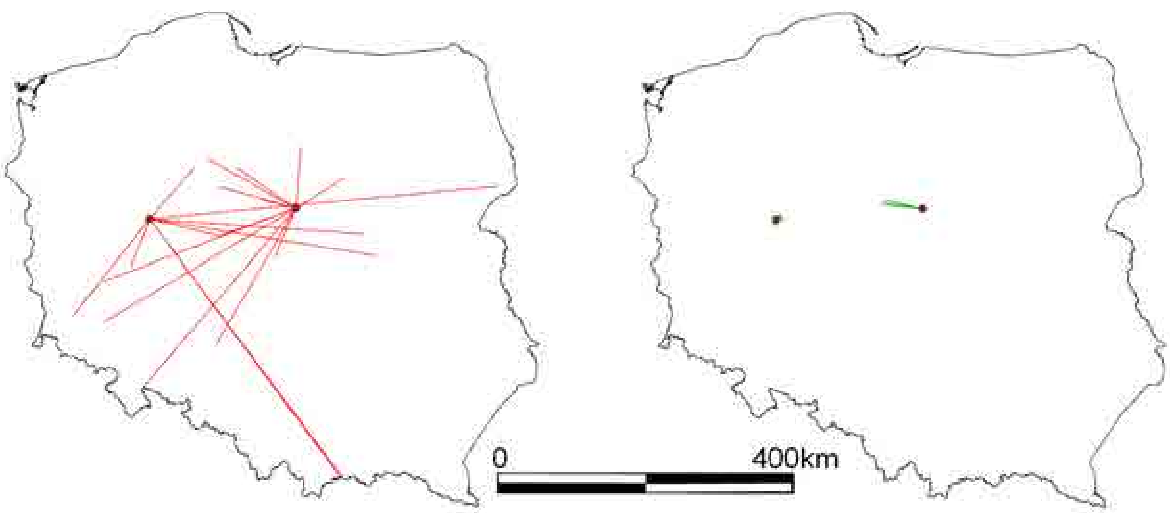

Figure S11. Maps of distances on which plants were transported depending on the sale type in *Prunus serotina.* Red lines indicate distances in the internet trade and green lines in a traditional trade. Red dots denote locations of garden shops.

7. *Quercus rubra*

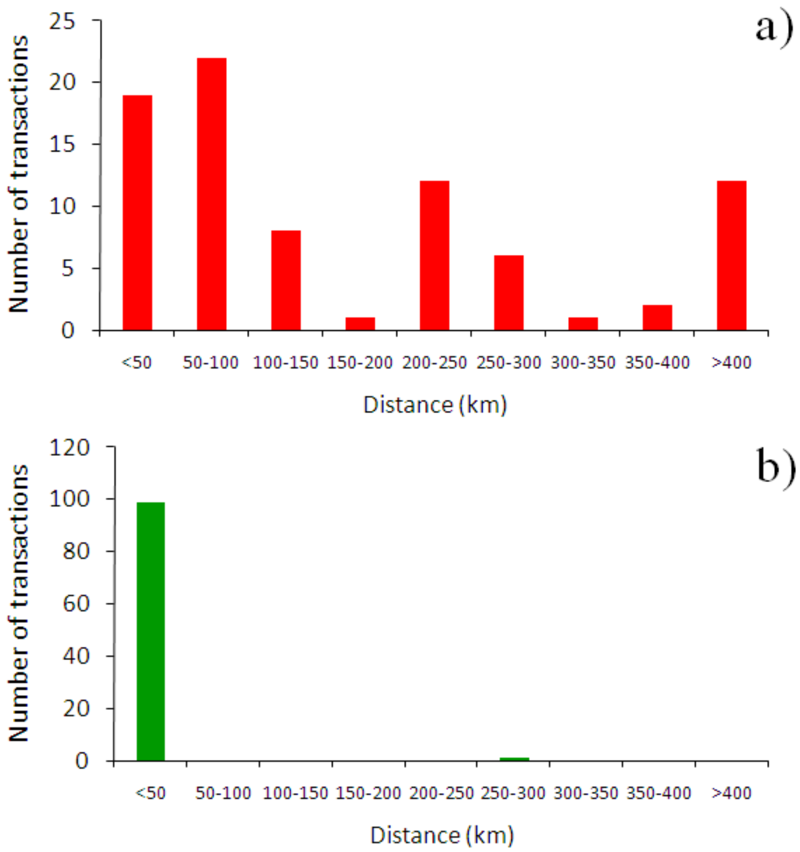

Figure S12. The distribution of the transportation distances of *Quercus rubra* in (a) the internet and (b) traditional sale in studied garden shops.

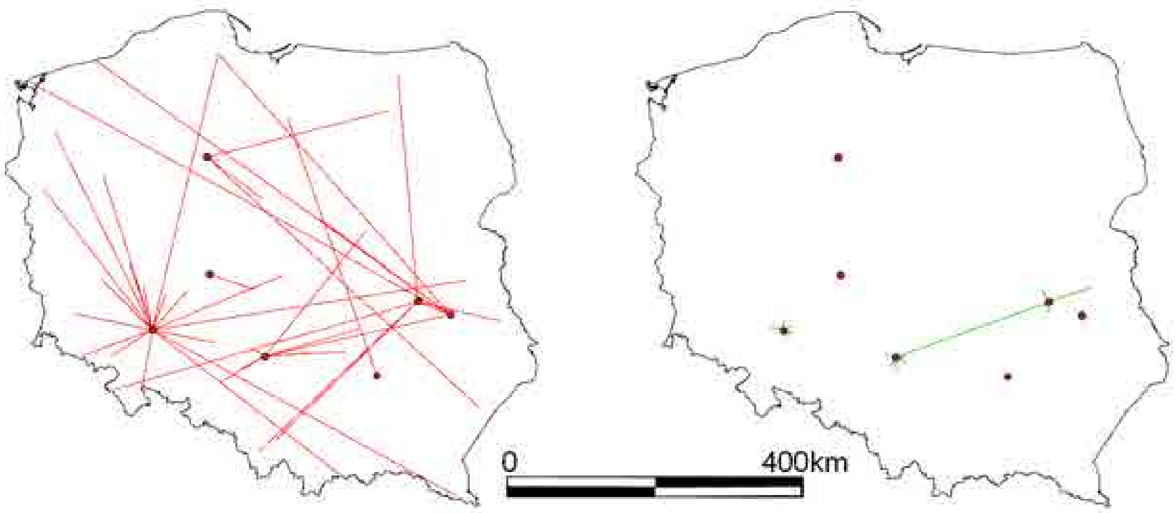

Figure S13. Maps of distances on which plants were transported depending on the sale type in *Quercus rubra.* Red lines indicate distances in the internet trade and green lines in a traditional trade. Red dots denote locations of garden shops.

8. *Reynoutria* sp.

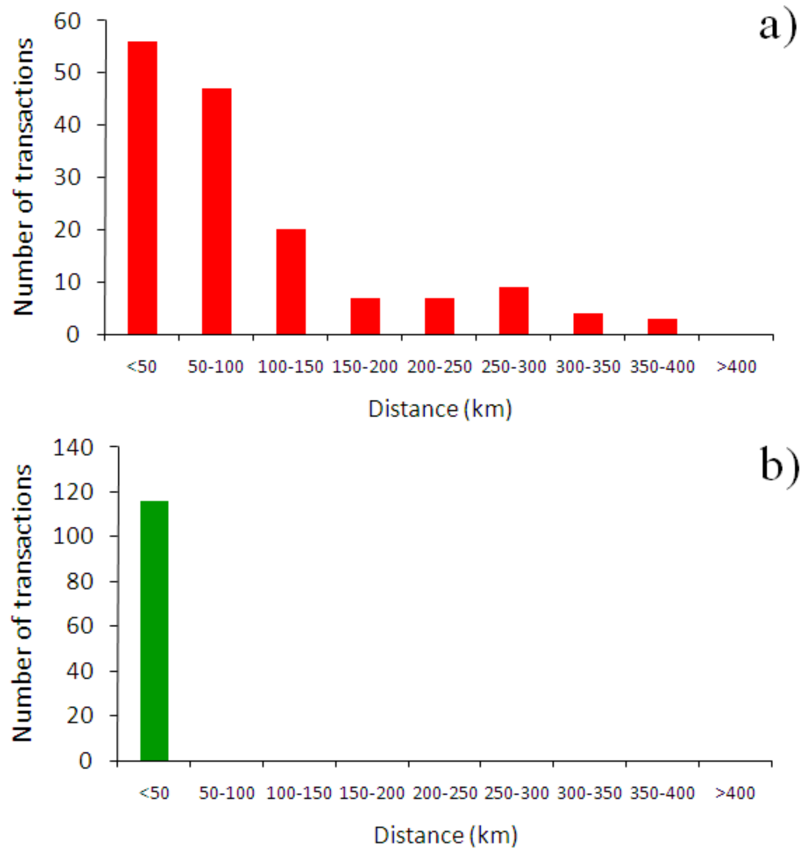

Figure S14. The distribution of the transportation distances of *Reynoutria* sp. in (a) the internet and (b) traditional sale in studied garden shops.

9. *Rhus typhina*

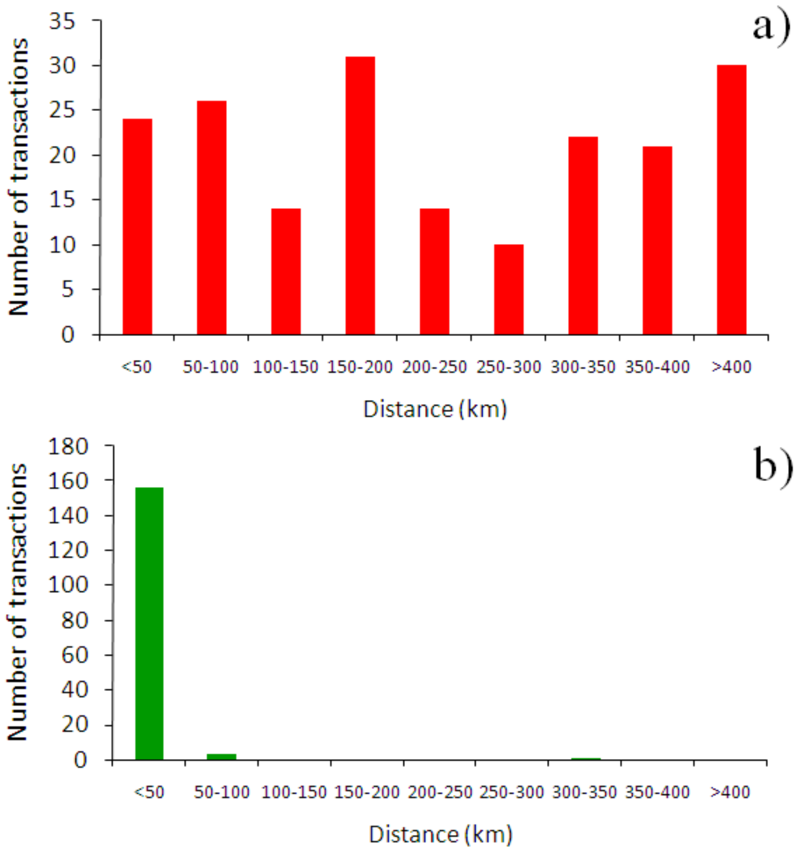

Figure S15. The distribution of the transportation distances of *Rhus typhina* in (a) the internet and (b) traditional sale in studied garden shops.

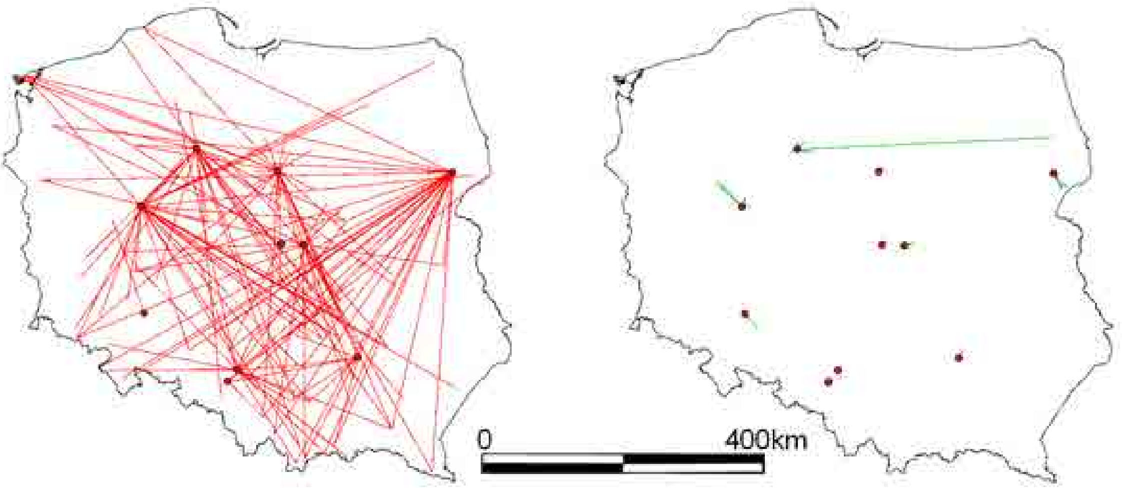

Figure S16. Maps of distances on which plants were transported depending on the sale type in *Rhus typhina.* Red lines indicate distances in the internet trade and green lines in a traditional trade. Red dots denote locations of garden shops.

10. *Robinia pseudoacacia*

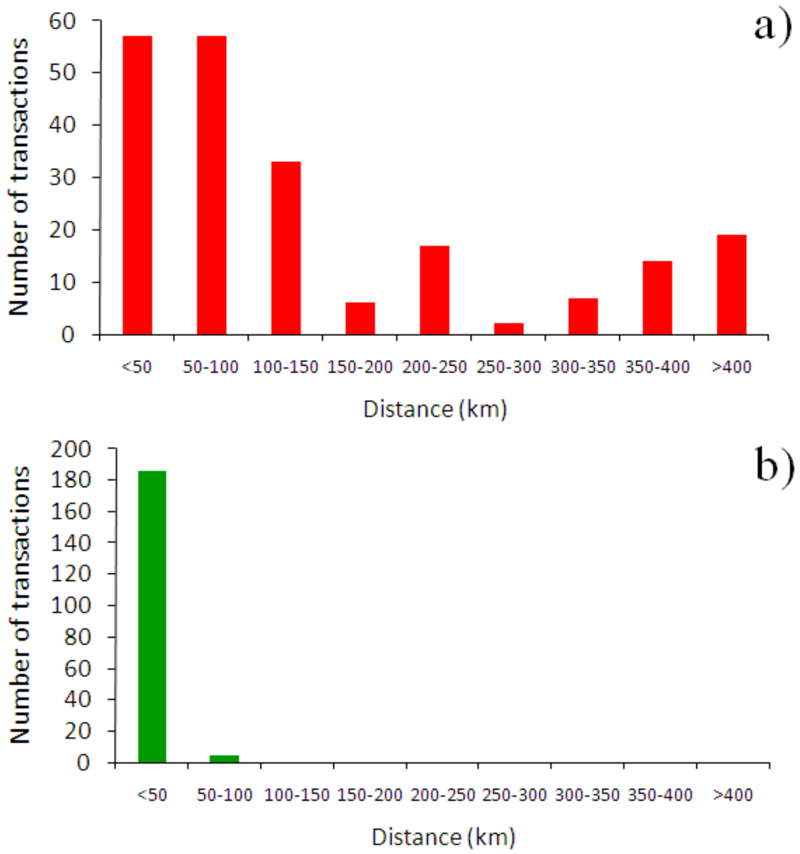

Figure S17. The distribution of the transportation distances of *Robinia pseudoacacia* in (a) the internet and (b) traditional sale in studied garden shops.

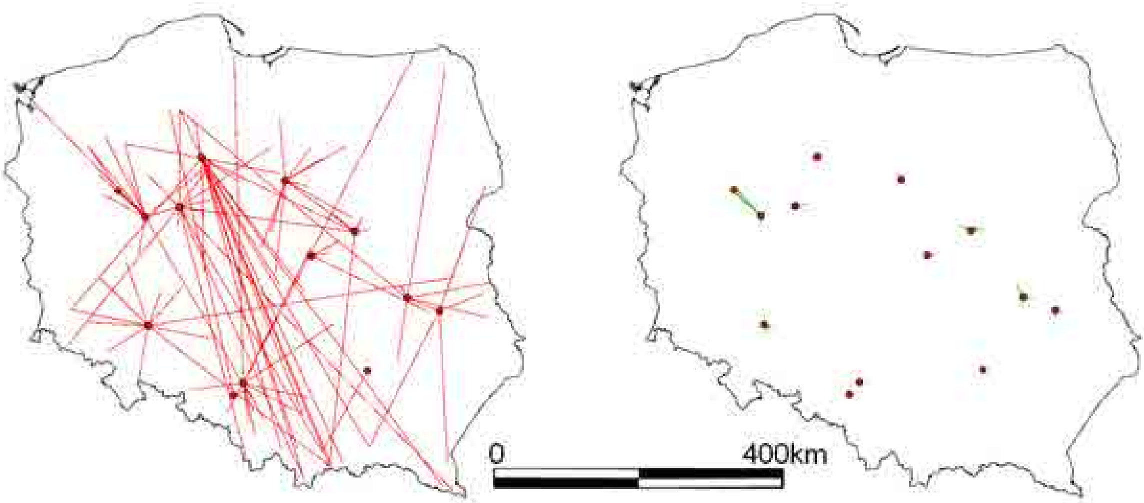

Figure S18. Maps of distances on which plants were transported depending on the sale type in *Robinia pseudoacacia.* Red lines indicate distances in the internet trade and green lines in a traditional trade. Red dots denote locations of garden shops.

11. *Rosa rugosa*

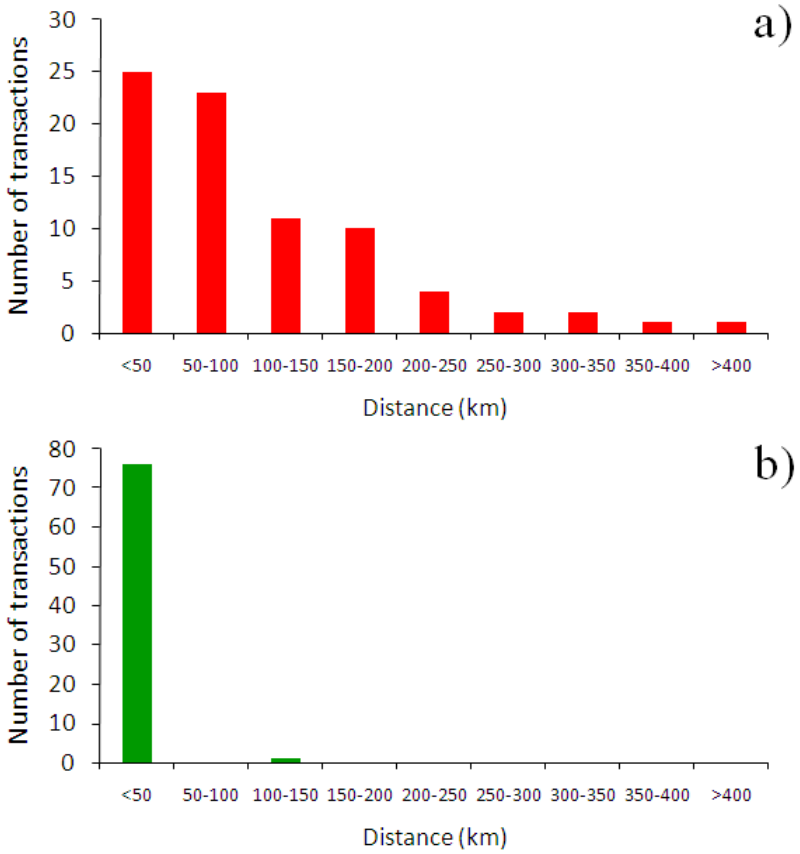

Figure S19. The distribution of the transportation distances of *Rosa rugosa* in (a) the internet and (b) traditional sale in studied garden shops.

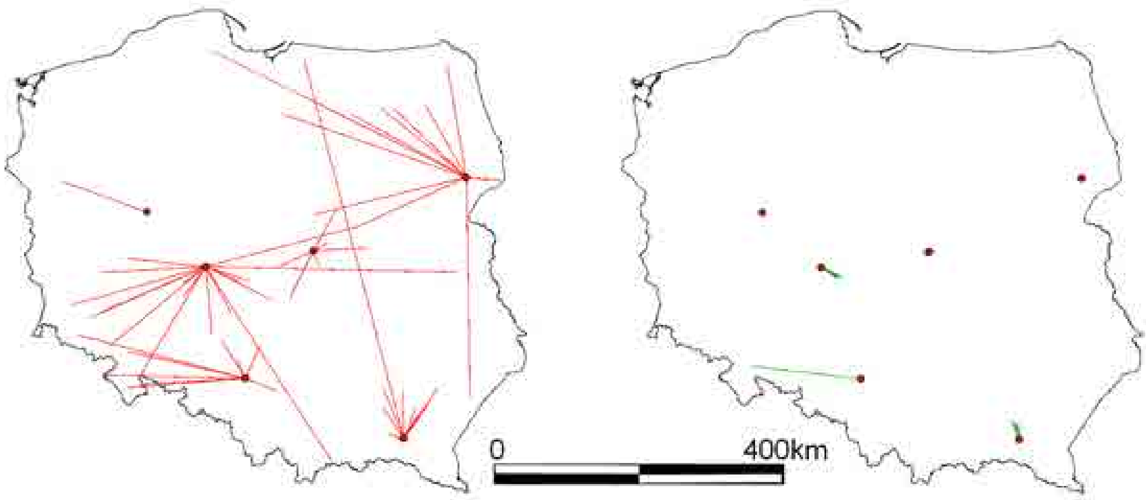

Figure S20. Maps of distances on which plants were transported depending on the sale type in *Rosa rugosa.* Red lines indicate distances in the internet trade and green lines in a traditional trade. Red dots denote locations of garden shops.

12. *Rudbeckia* sp.

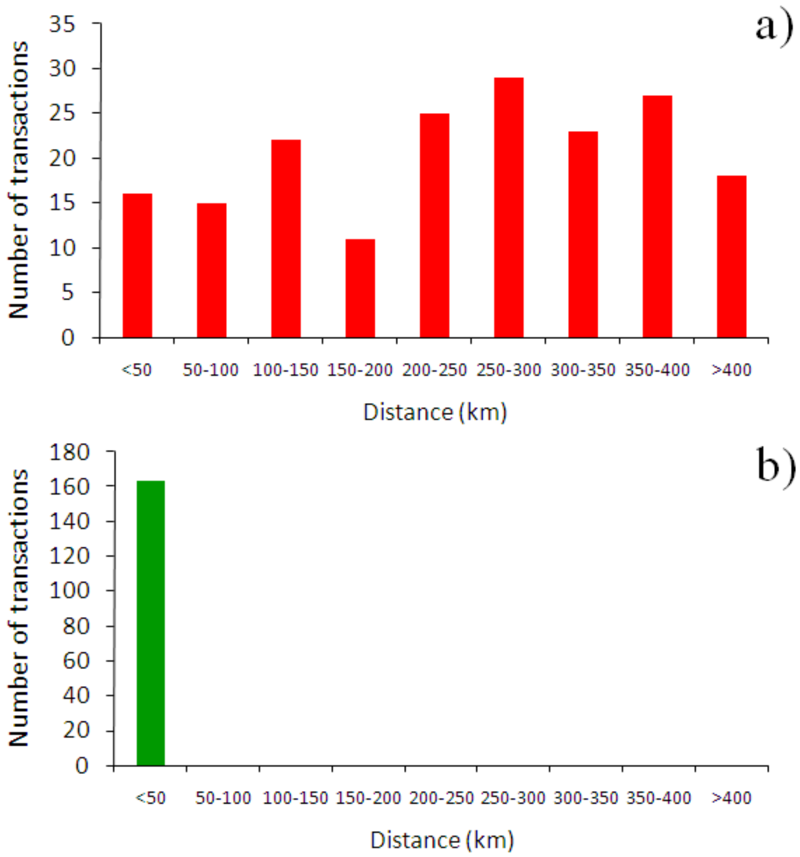

Figure S21. The distribution of the transportation distances of *Rudbeckia* sp. in (a) the internet and (b) traditional sale in studied garden shops.

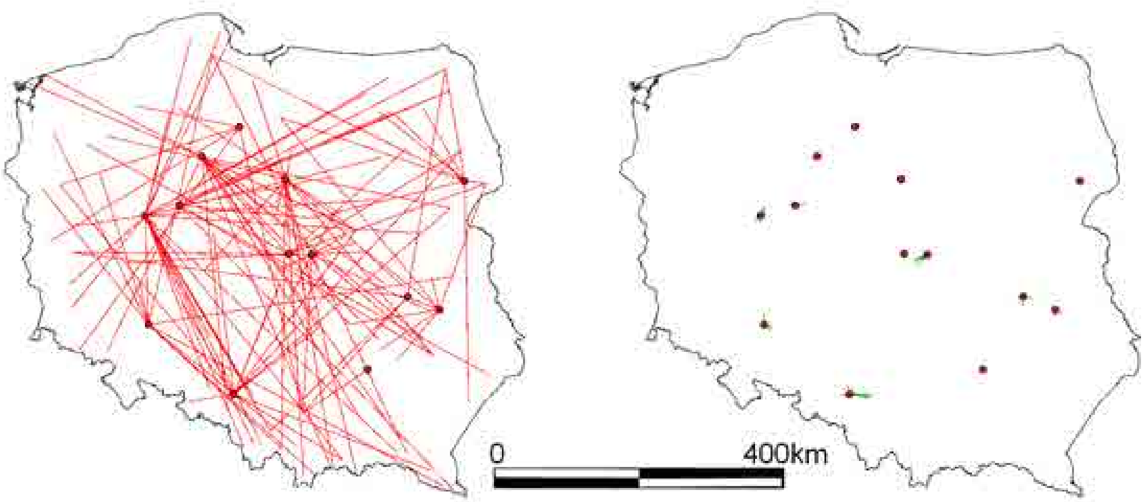

Figure S22. Maps of distances on which plants were transported depending on the sale type in *Rudbeckia* sp. Red lines indicate distances in the internet trade and green lines in a traditional trade. Red dots denote locations of garden shops.

13. *Solidago* sp.

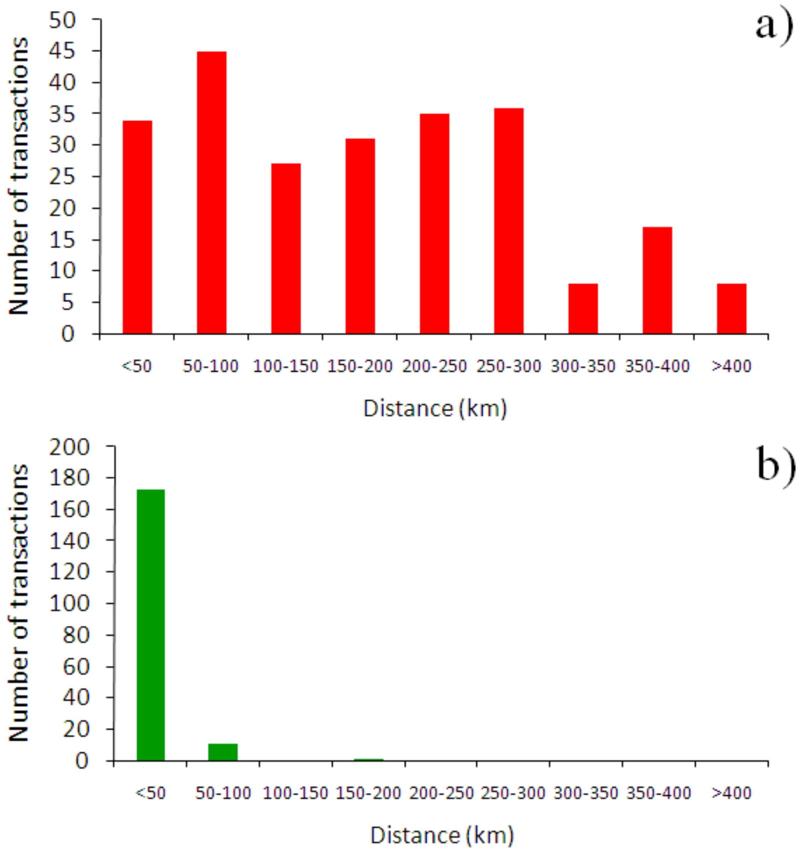

Figure S23. The distribution of the transportation distances of *Solidago* sp. in (a) the internet and (b) traditional sale in studied garden shops.

Detailed data on rate of ecommerce for 13 the most harmful invasive species in Europe sold during recent 6 years on the most popular polish auctioning internet portal Allegro

1. *Acer negundo*

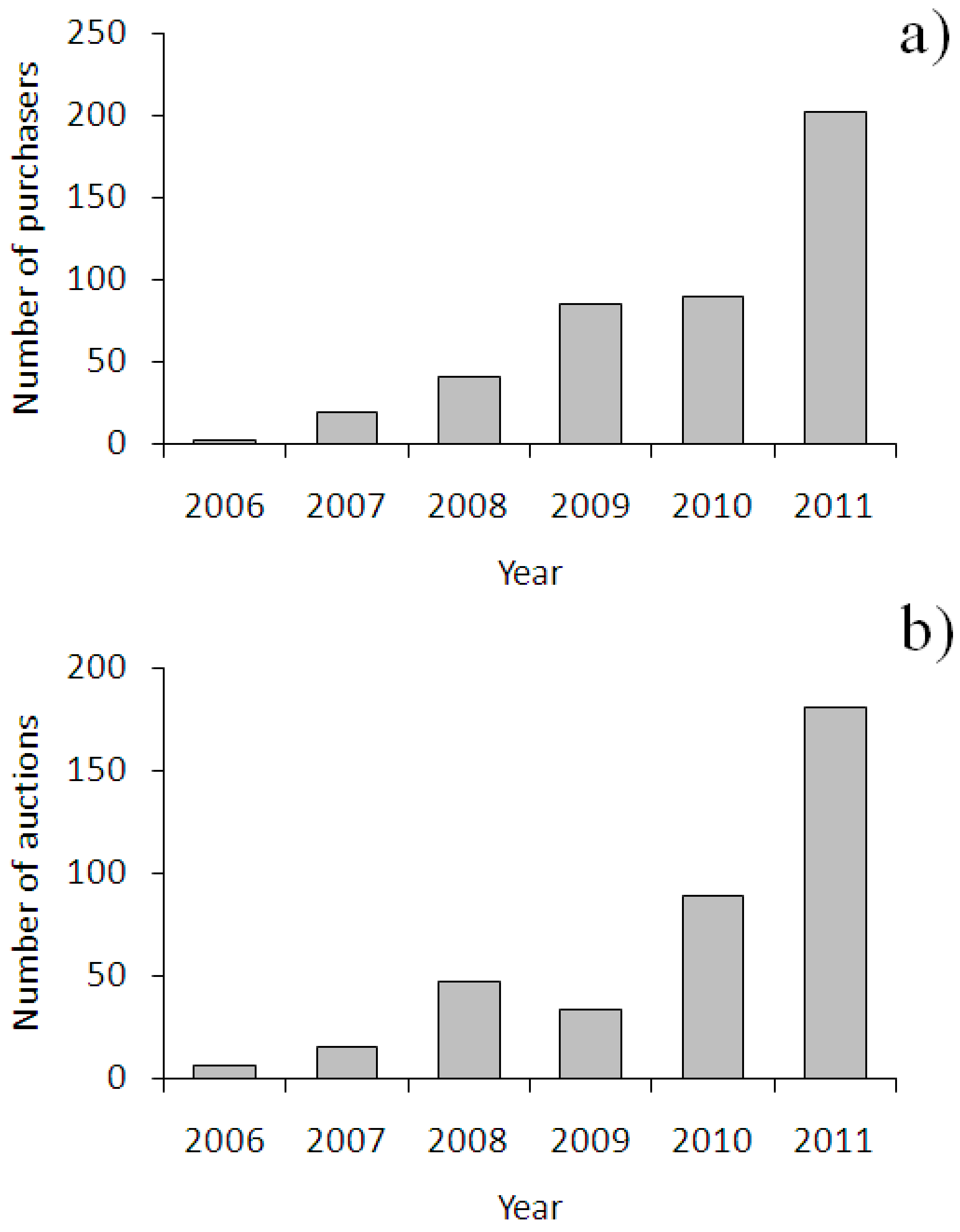

Figure S24. Number of purchasers (a) and number of auctions (b) of *Acer negundo* in different years in the largest polish internet auctioning portal.

2. *Buddleia davidii*

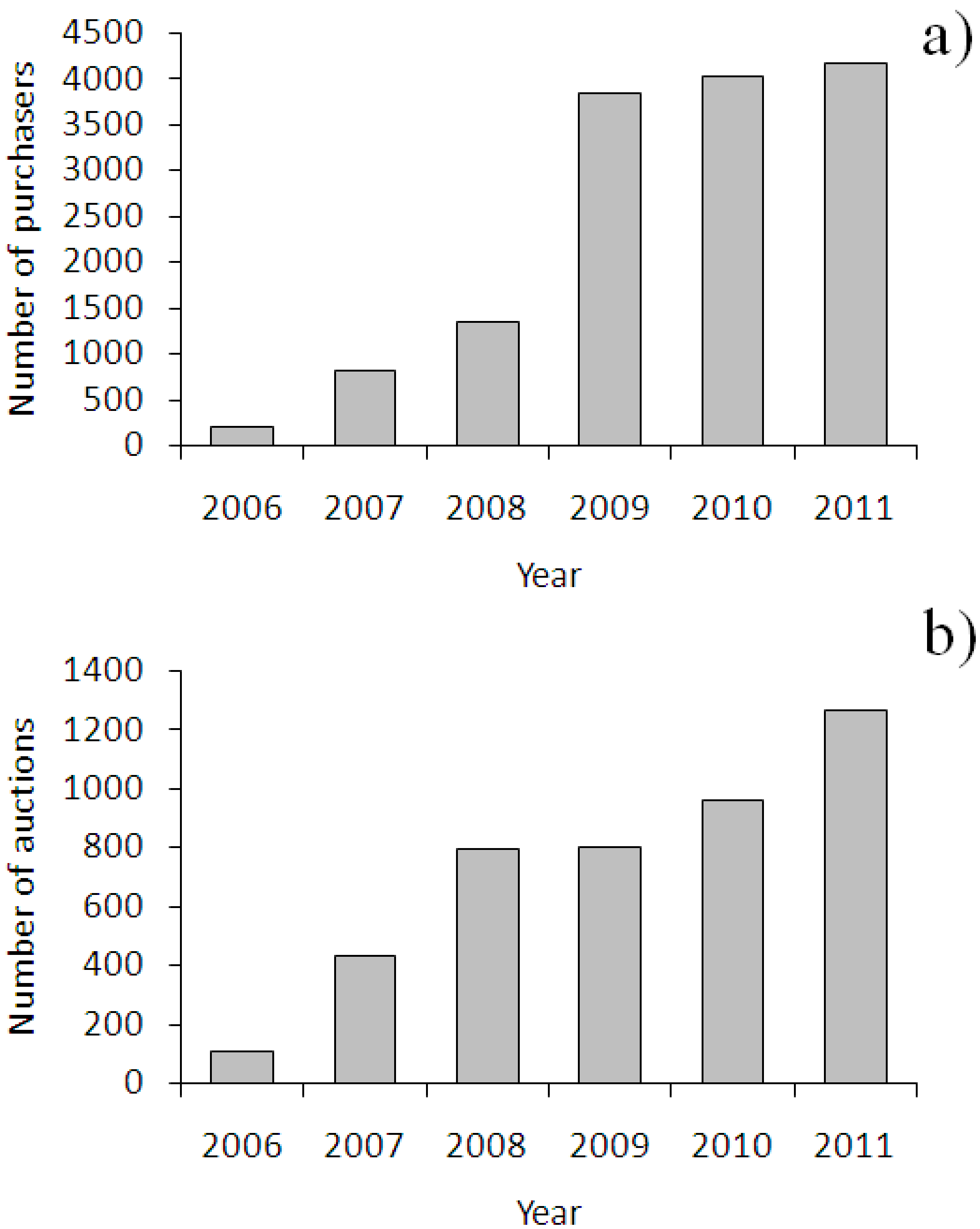

Figure S25. Number of purchasers (a) and number of auctions (b) of *Buddleia davidii* in different years in the largest polish internet auctioning portal.

3. *Echinocystis lobata*

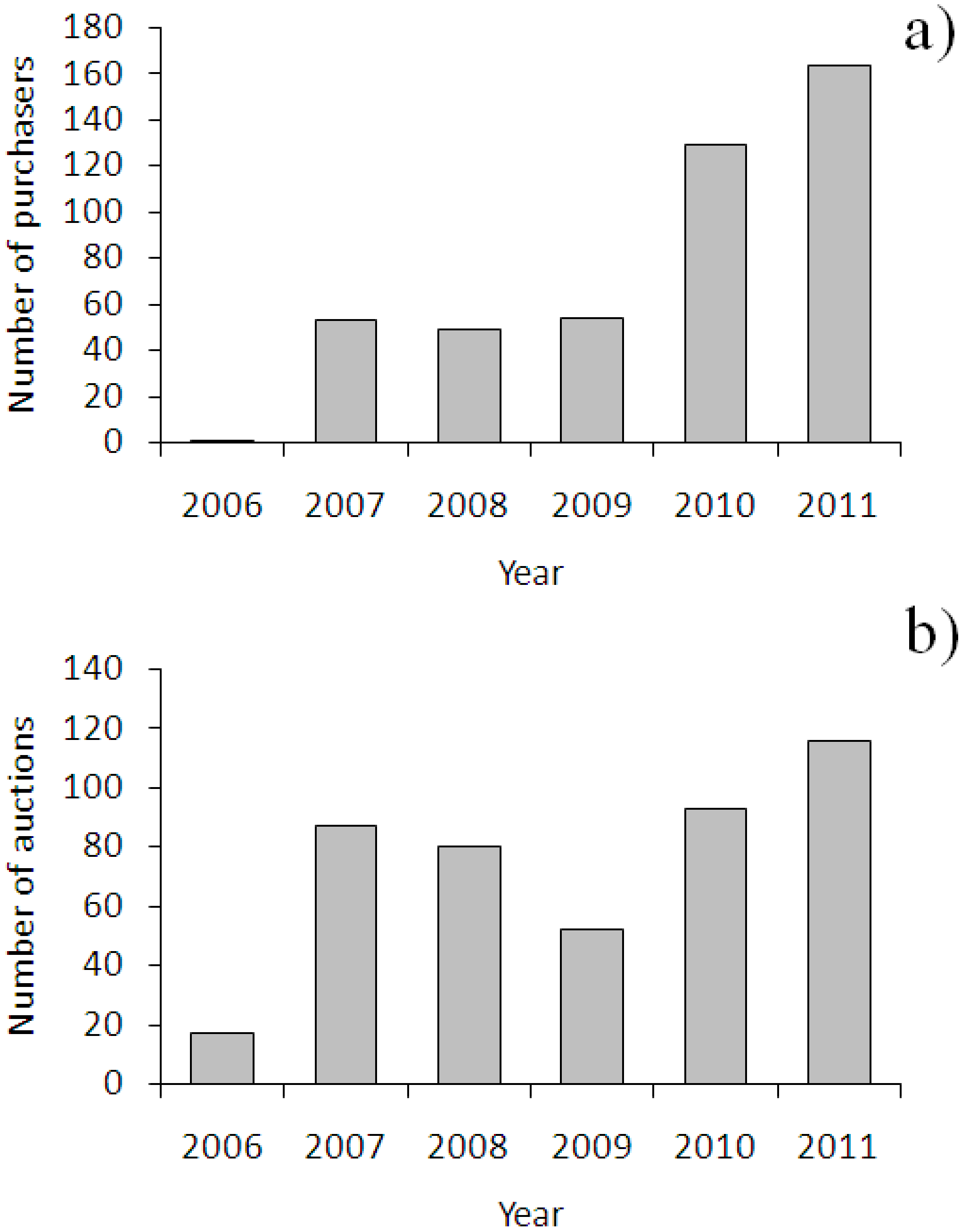

Figure S26. Number of purchasers (a) and number of auctions (b) of *Echinocystis lobata* in different years in the largest polish internet auctioning portal.

4. *Elodea canadensis*

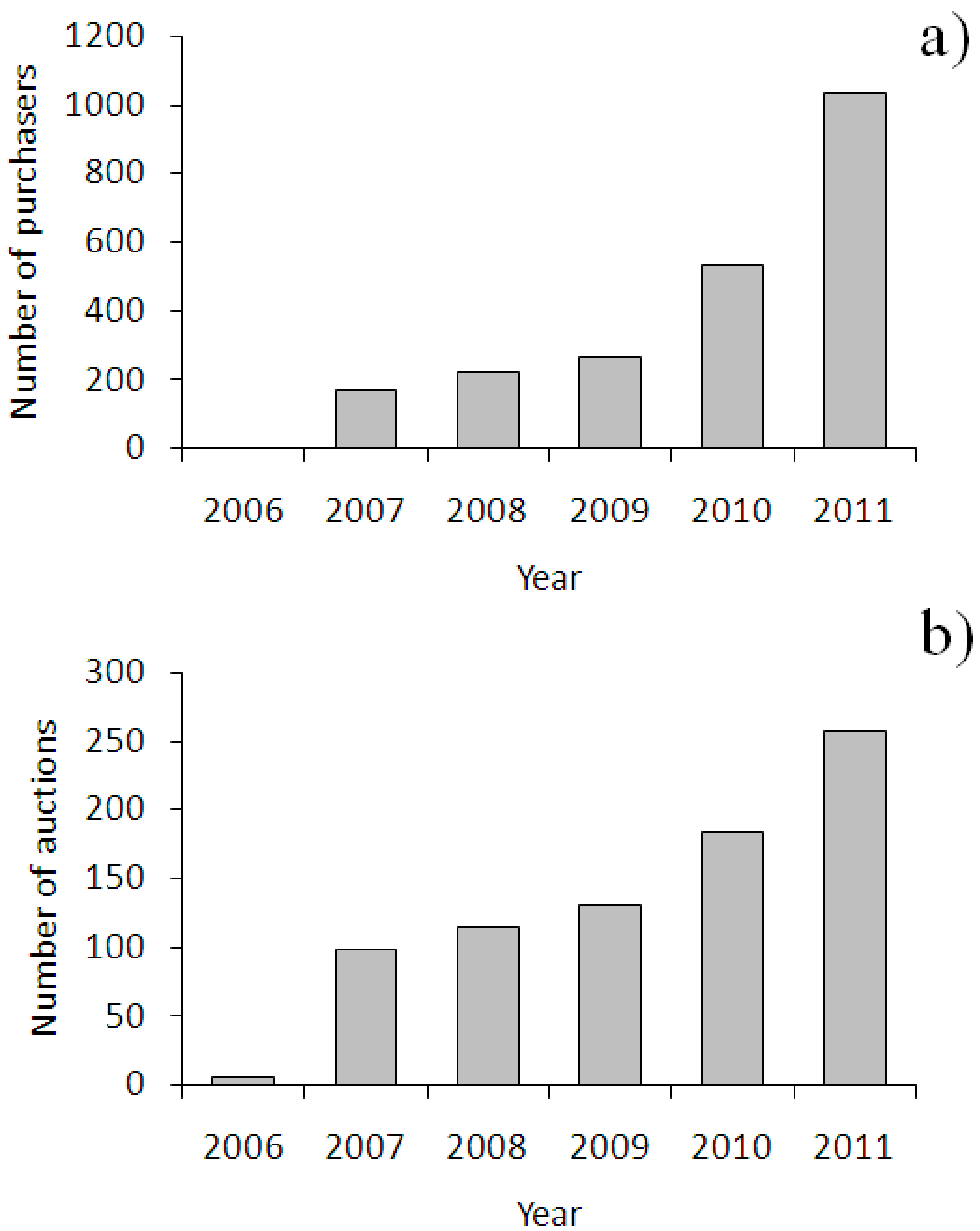

Figure S27. Number of purchasers (a) and number of auctions (b) of *Elodea canadensis* in different years in the largest polish internet auctioning portal.

5. *Impatiens glandulifera*

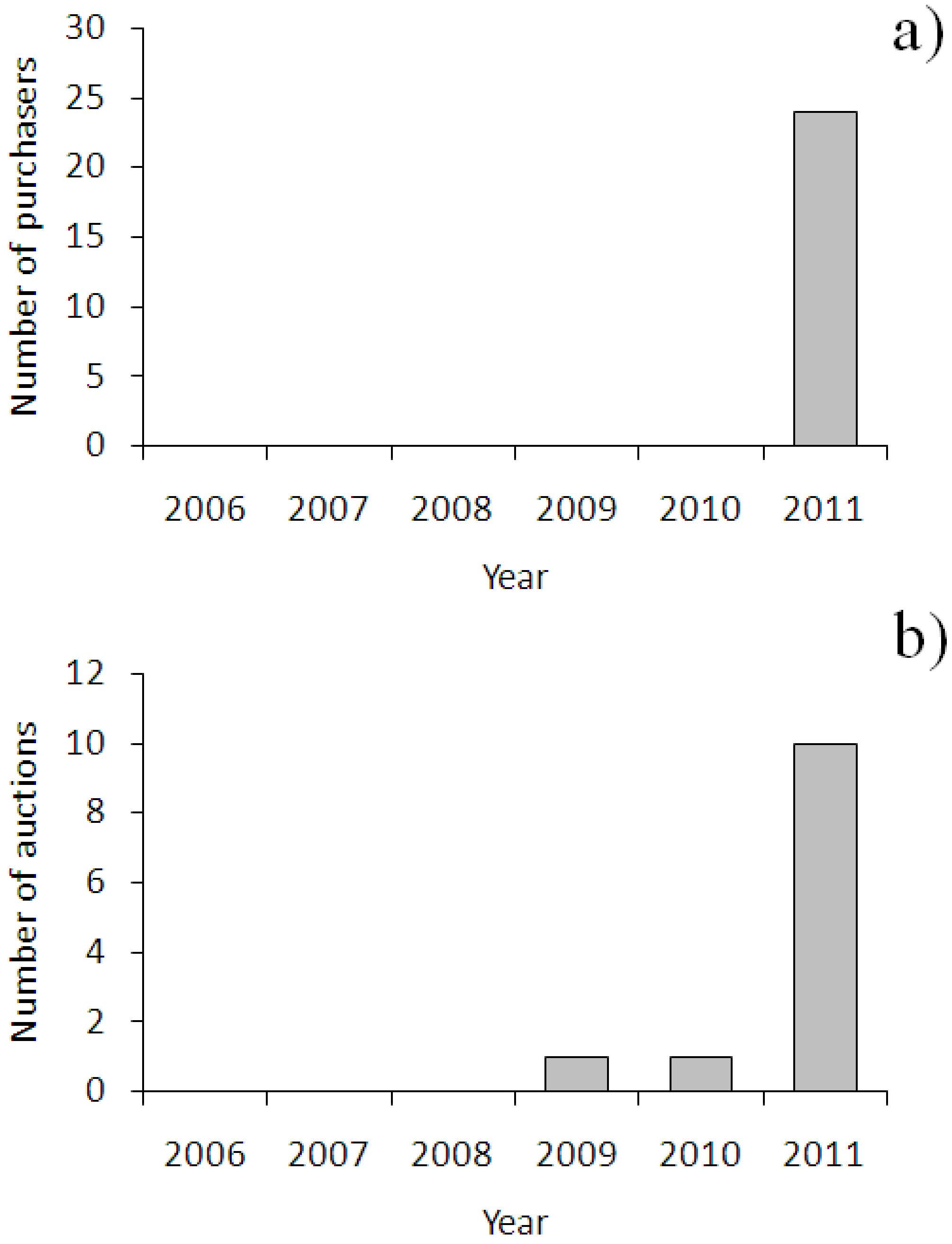

Figure S28. Number of purchasers (a) and number of auctions (b) of *Impatiens glandulifera* in different years in the largest polish internet auctioning portal.

6. *Prunus serotina*

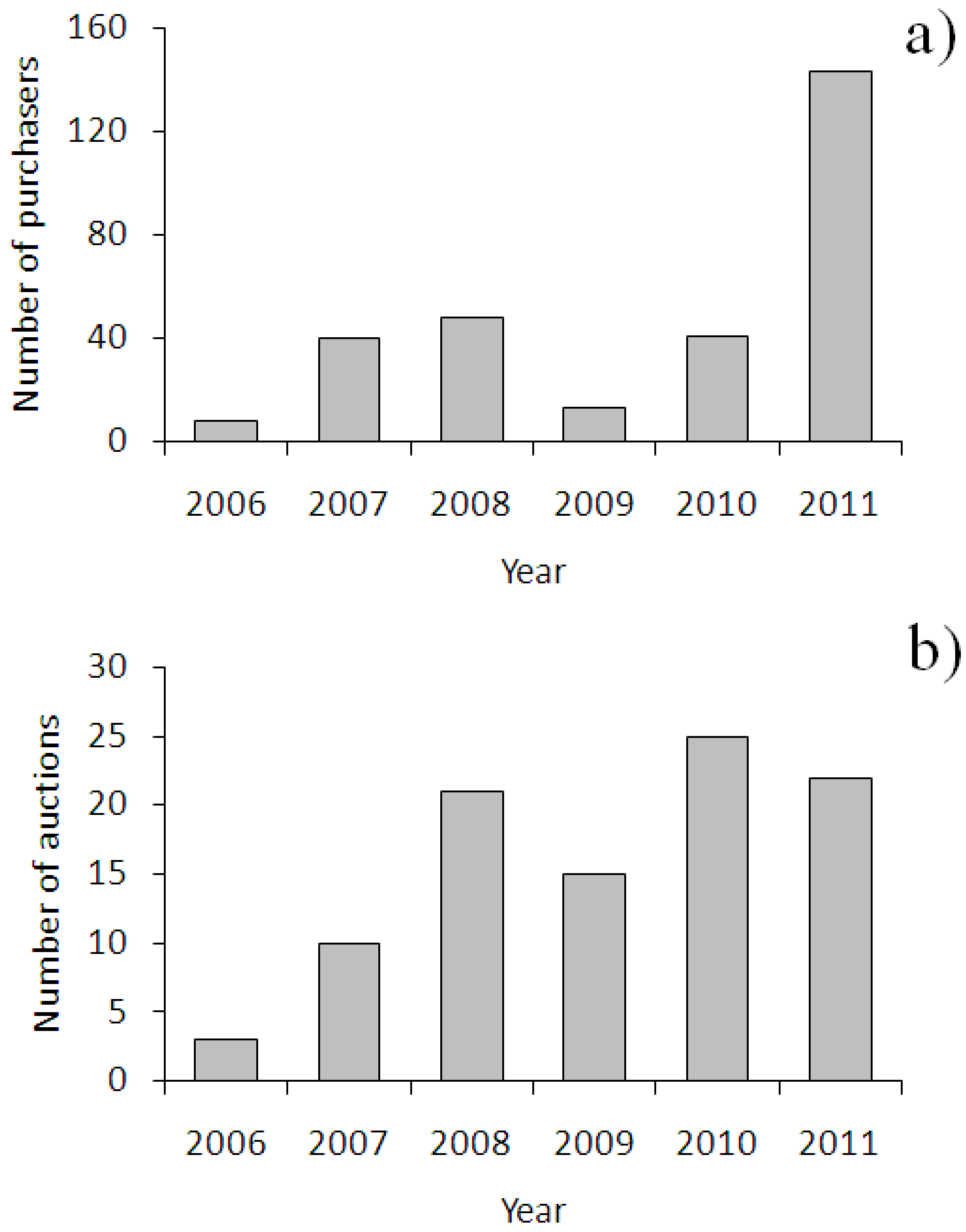

Figure S29. Number of purchasers (a) and number of auctions (b) of *Prunus serotina* in different years in the largest polish internet auctioning portal.

7. *Quercus rubra*

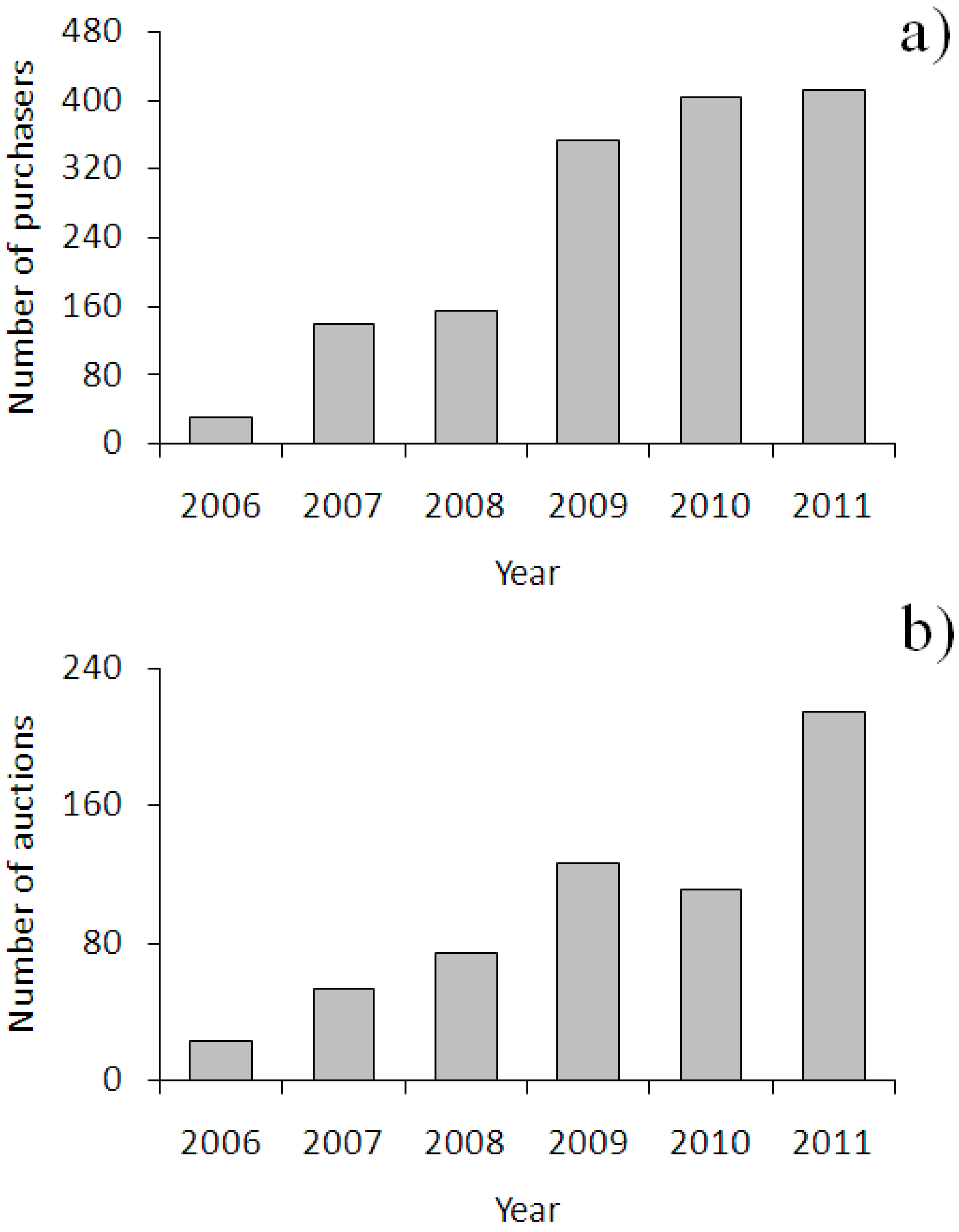

Figure S30. Number of purchasers (a) and number of auctions (b) of *Quercus rubra* in different years in the largest polish internet auctioning portal.

8. *Reynoutria sp.*

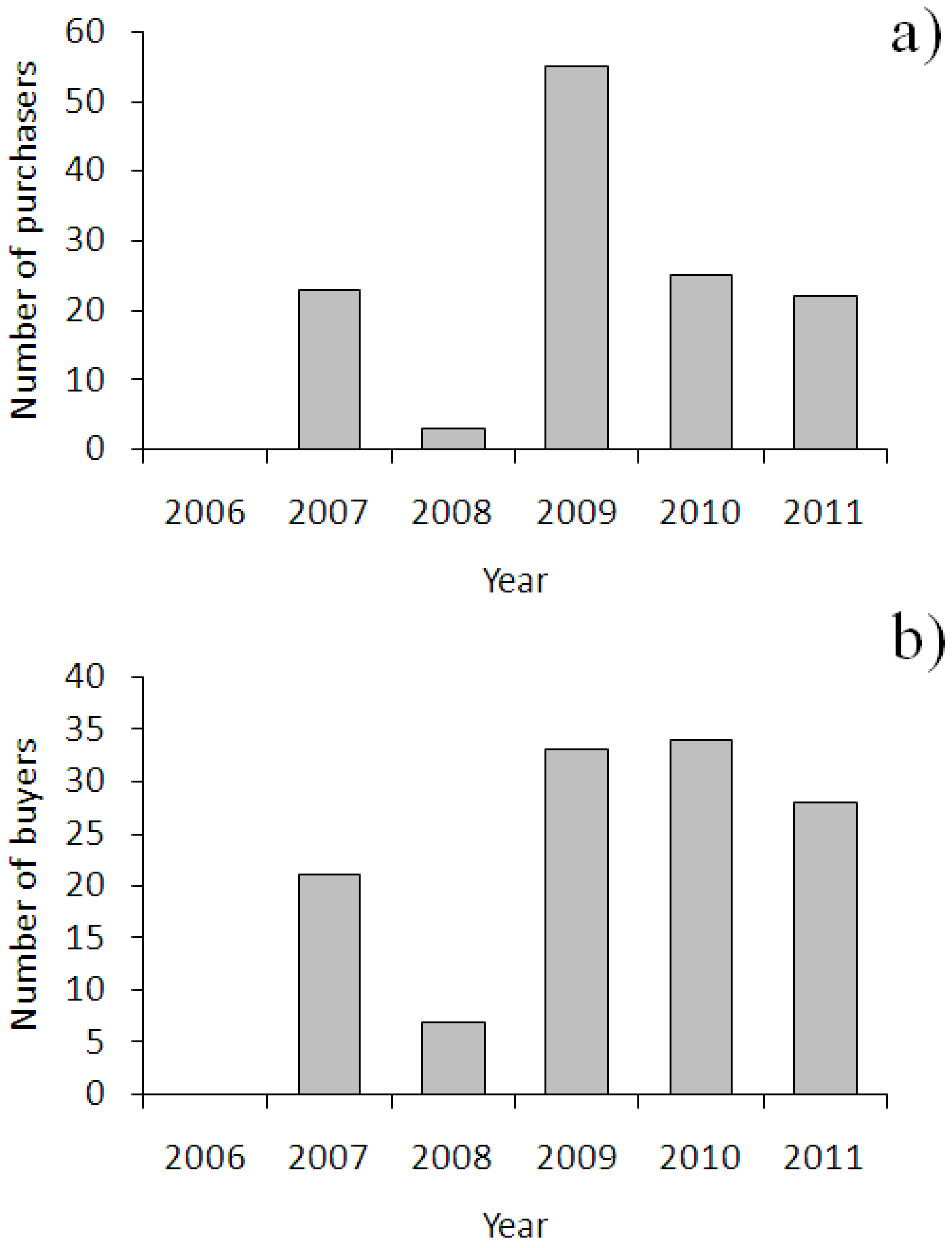

Figure S31. Number of purchasers (a) and number of auctions (b) of *Reynoutria* sp. in different years in the largest polish internet auctioning portal.

9. *Rhus typhina*

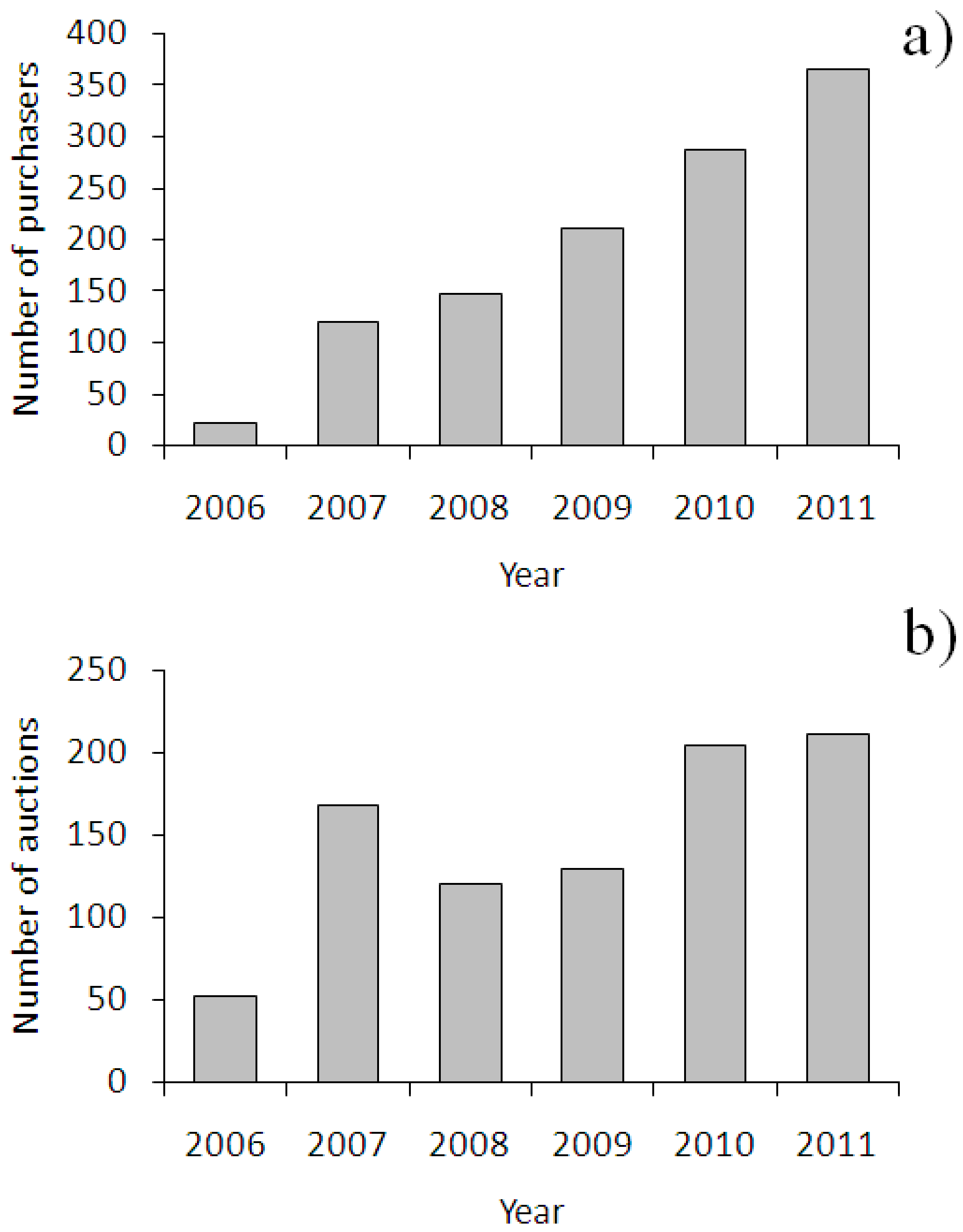

Figure S32. Number of purchasers (a) and number of auctions (b) of *Rhus typhina* in different years in the largest polish internet auctioning portal.

10. *Robinia pseudoacacia*

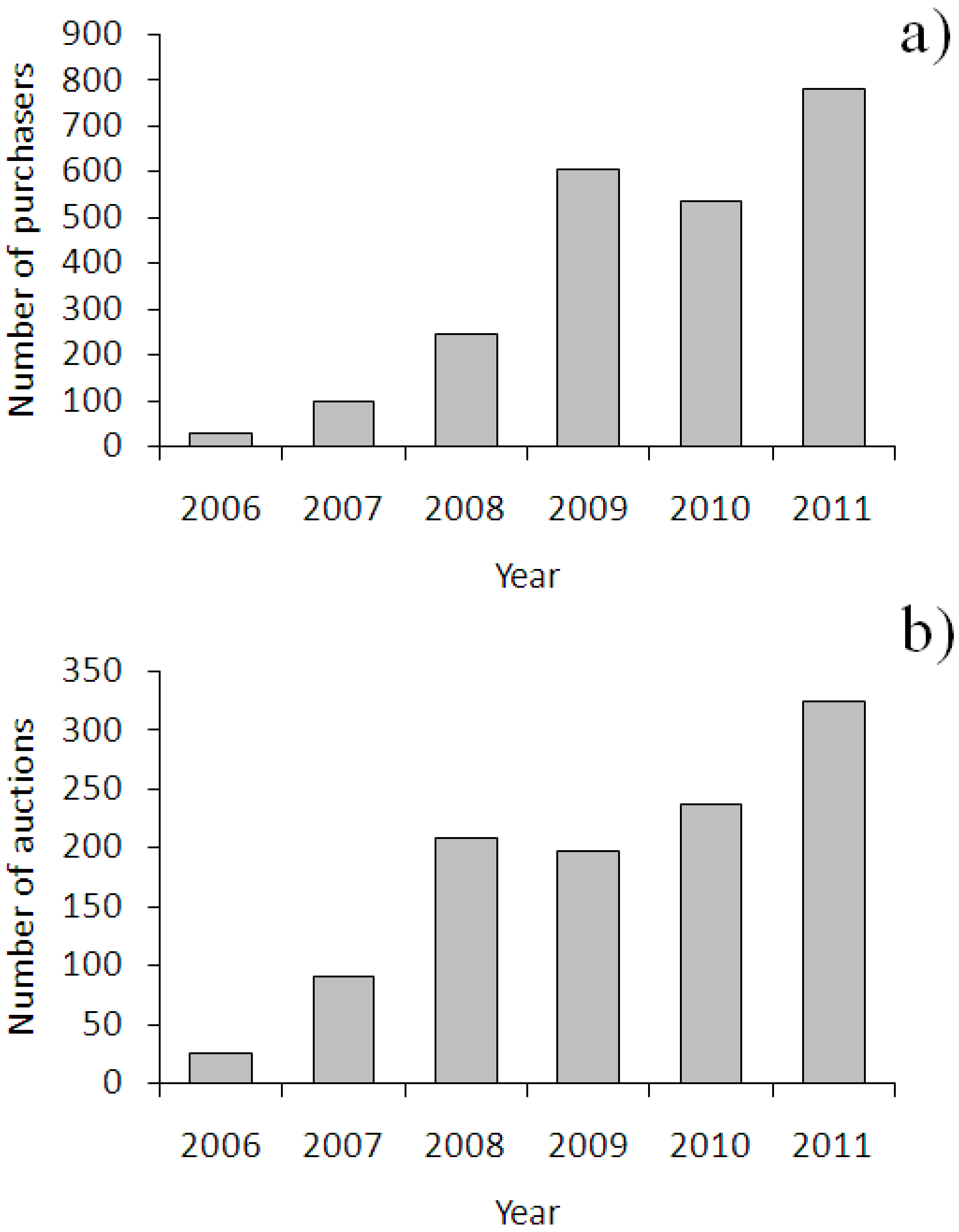

Figure S33. Number of purchasers (a) and number of auctions (b) of *Robinia pseudoacacia* in different years in the largest polish internet auctioning portal.

11. *Rosa rugosa*

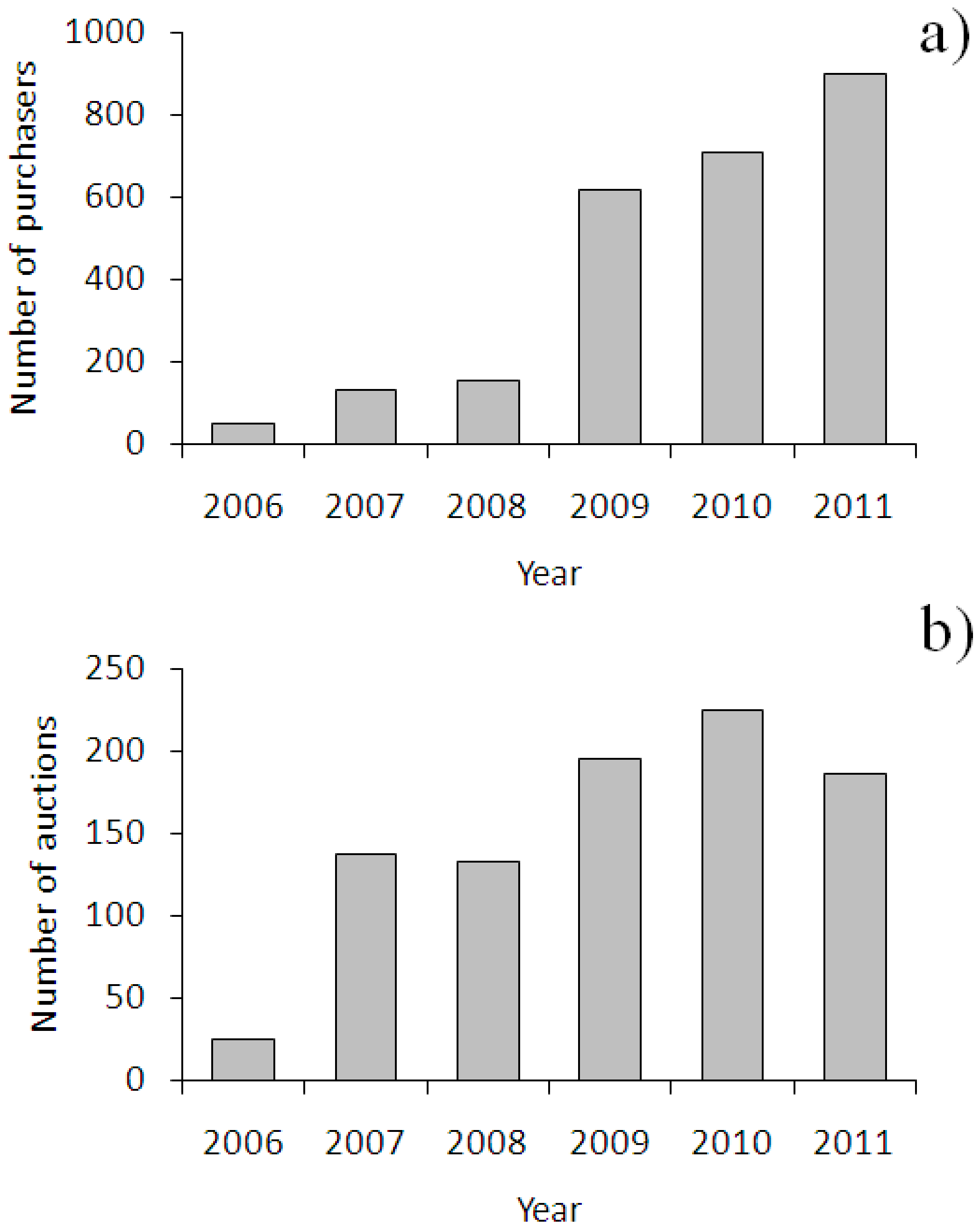

Figure S34. Number of purchasers (a) and number of auctions (b) of *Rosa rugosa* in different years in the largest polish internet auctioning portal.

12. *Rudbeckia* sp.

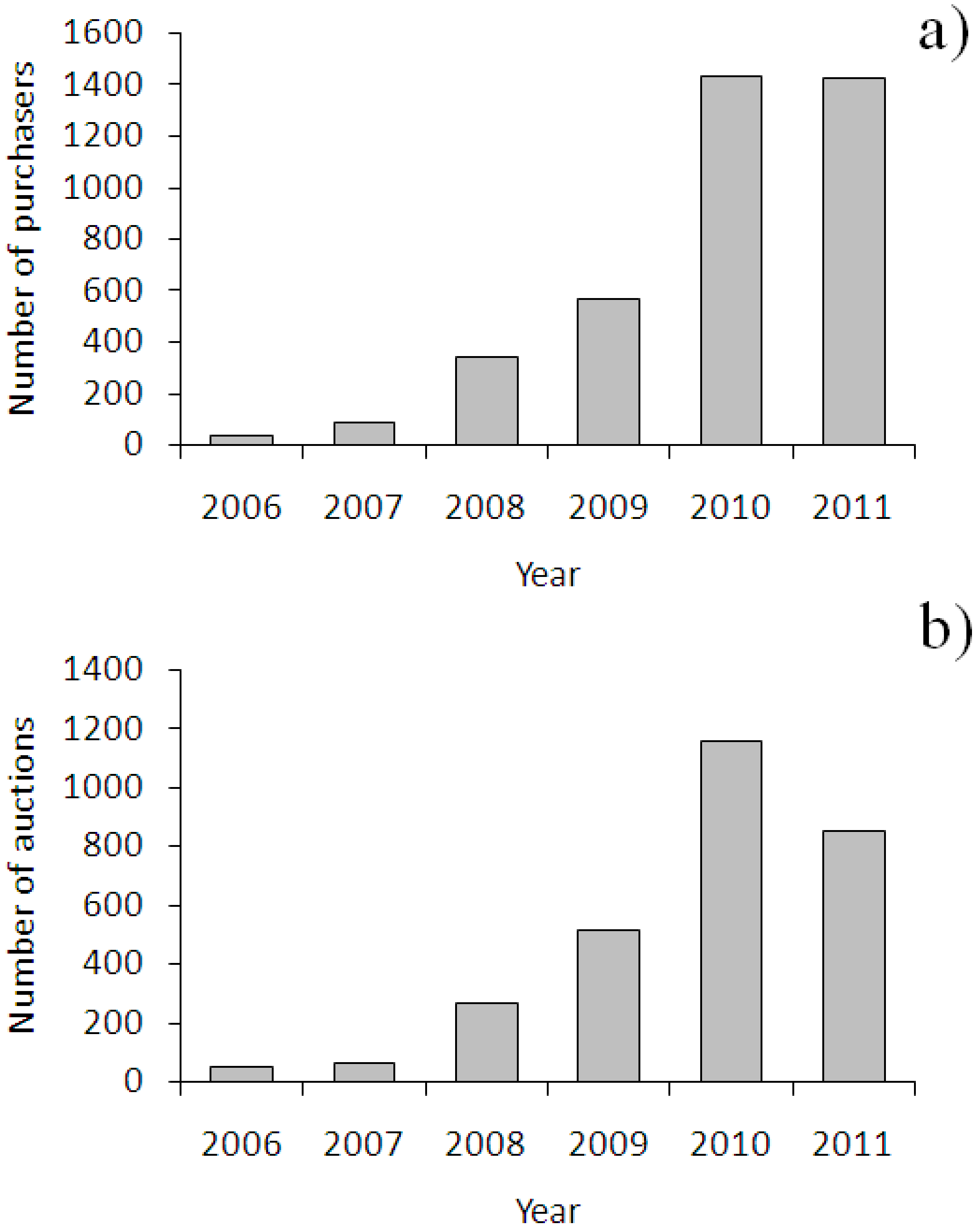

Figure S35. Number of purchasers (a) and number of auctions (b) of *Rudbeckia* sp. in different years in the largest polish internet auctioning portal.

13. *Solidago* sp.

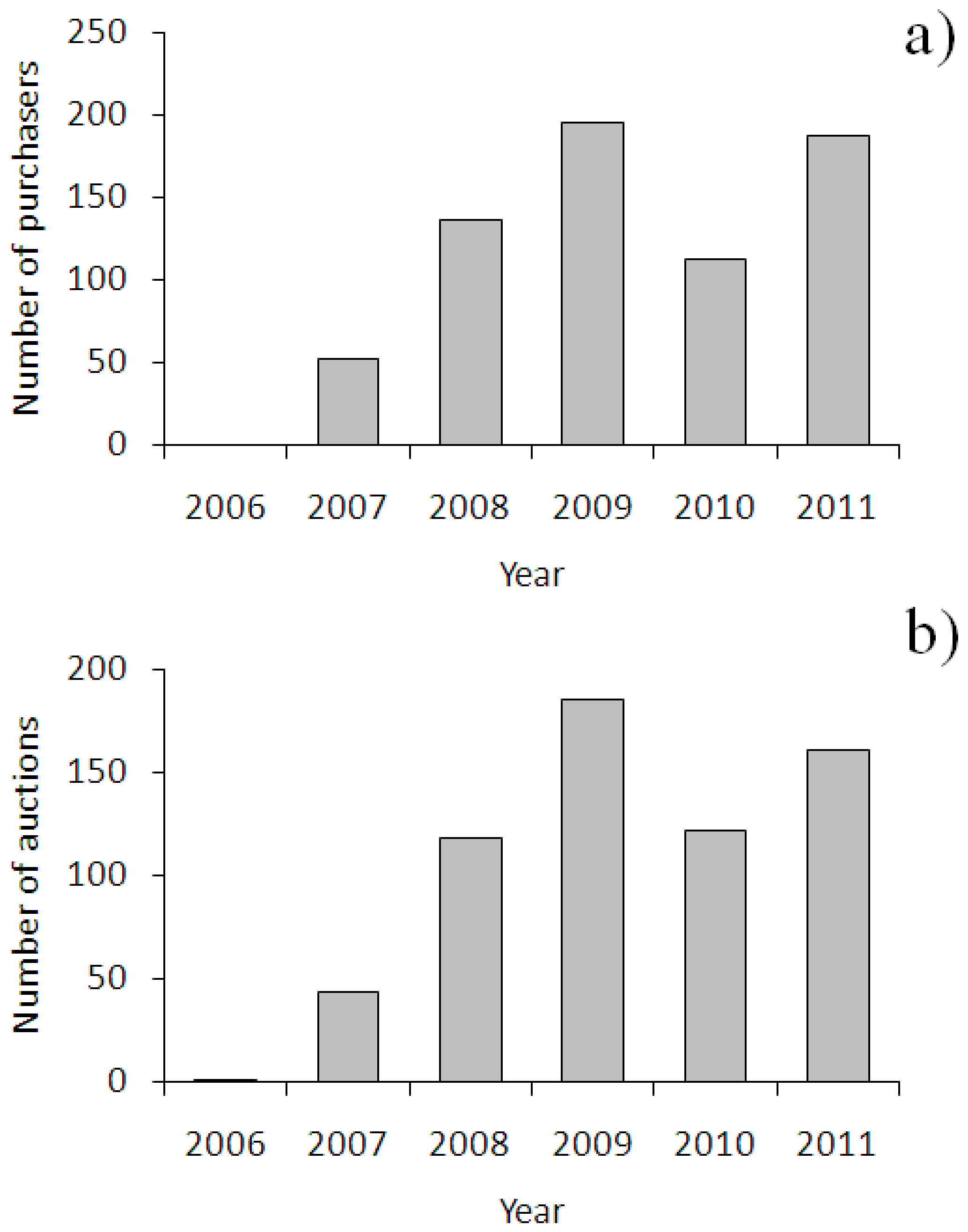

Figure S36. Number of purchasers (a) and number of auctions (b) of *Solidago* sp. in different years in the largest polish internet auctioning portal.